HERPETOLOGICAL CONSERVATION & BIOLOGY

June 2016 *Open Access Publishing* **Volume 11, Monograph 6**

Mona Rhinoceros Iguana (*Cyclura stejnegeri*), Guerreran Spiny-tailed Iguana (*Ctenosaura pectinata*), Campeche Spiny-tailed Iguana (*Ctenosaura alfredschmidti*), Jamaican Rock Iguana (*Cyclura collei*), Roatán Spiny-tailed Iguana (*Ctenosaura oedirhina*), Lesser Antillean Iguana (*Iguana delicatissima*), Veracruz Spiny-tailed Iguana (*Ctenosaura acanthura*), Exuma Rock Iguana (*Cyclura cychlura figginsi*), San Salvador Rock Iguana (*Cyclura rileyi rileyi*); Left to right, top to bottom.

Iguanas: Biology, Systematics, and Conservation

Monograph 6.

John B. Iverson, Tandora D. Grant, Charles R. Knapp, and Stesha A. Pasachnik (Editors)

ISSN: 1931-7603

Indexed by: Zoological Record, Scopus, Current Contents / Agriculture, Biology & Environmental Sciences, Journal Citation Reports, Science Citation Index Extended, EMBiology, Biology Browser, Wildlife Review Abstracts, Google Scholar, and is in the Directory of Open Access Journals.

IGUANAS: BIOLOGY, SYSTEMATICS, AND CONSERVATION

MONOGRAPH 6.

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Published in partnership with the IUCN SSC Iguana Specialist Group.

Cover photographs by (left to right, top to bottom) Thomas Wiewandt, Thomas Wiewandt, Catherine Stephen, Joseph Burgess, Ashley Goode, Charles Knapp, Jorge Morales Mávil, Charles Knapp, and John Binns. Cover photography design by John Binns.

Please cite this monograph in full as follows:
Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). 2016. Iguanas: Biology, Systematics, and Conservation. Herpetological Conservation and Biology 11(Monograph 6).

Please cite individual articles from within this monograph as follows:
Author name. 2016. Title of individual paper. Pp. XX–XX *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

DEDICATION

This monograph is dedicated to John Iverson and his selfless dedication to iguana research and his students. John's scientific outputs are impressive, but even more so is his desire to conduct quality investigations, collaborate with others, and mentor students and scientists alike. It is not a coincidence that John has authored, or advised the authors of, 10 manuscripts from this monograph on iguana biology, systematics, and conservation. John is the backbone of the IUCN SSC Iguana Specialist Group, a joy to work with in the field, and a true friend. We are grateful for all his past efforts and thankful that he continues to fuel the iguana conservation community.

Charles Knapp, Stesha Pasachnik, and Tandora Grant

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PEER REVIEWERS LIST

The guest editors for this monograph and the Editorial Staff of Herpetological Conservation & Biology, would like to acknowledge and thank the following peer reviewers for their expert opinions in compiling these manuscripts. Your efforts, dedication, and professionalism have ensured that Herpetological Conservation & Biology continues to be a success.

Daniel Ariano-Sanchez, Brian Bock, Kelly Bradley, Joseph Burgess, Gordon Burghardt, Fred Burton, Heidi Davis, Dale DeNardo, C. Kenneth Dodd, Jr., Arthur Echternacht, Wilfredo Falcon, Cielo Figuerola, Dick Franz, Susannah French, Miguel García, Glenn Gerber, Rachel Goodman, Kerry Hanskecht, William Hayes, Selina Heppell, Michael Hoffman, Sixto Inchaustegui, Scott Keogh, Fred Kraus, Julio Lemos-Espinal, Rodrigo Macio-Rios, Emilia Martins, Walter Meshaka, Chad Montgomery, Nestor Perez-Buitrago, Gad Perry, Robert Powell, Steve Reichling, Robert Graham Reynolds, Victor Hugo Reynoso, Kevin Shoemaker, Geoff Smith, Cynthia Steiner, Peter Tolson, Ann Ward, Bruce Weissgold, Kevin Willis, Byron Wilson, Alexander Wolf, Eugenia Zarza, J. Jaime Zuniga-Vega.

Herpetological Conservation and Biology 11(Monograph 6):1–3.
Submitted: 2 April 2015; Accepted: 12 November 2015, Published: 12 June 2016.

FOREWORD

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This compilation represents the third time that iguana researchers from around the world have collaborated to publish a diversity of papers on the behavior, ecology, evolution, and conservation of this unique taxonomic group. In 1982, Burghardt and Rand published *Iguanas of the World*, focused on systematics and biogeography, food and energetics, demography and life history strategies, adaptive behavior and communication, social organization, and conservation and management. The majority of papers featured *Iguana*, although every genus other than *Dipsosaurus* was represented by at least one contribution. At that time, 30 species were recognized, including a recently discovered species, *Brachylophus vitiensis*. The volume brought together a wealth of information on iguana biology and natural history, recognizing the importance of large body size and an herbivorous lifestyle in shaping observed life history traits. Potential threats to iguanas were identified and initial recommendations made for the protection of wild populations.

A second volume, *Iguanas: Biology and Conservation*, followed in 2004 (Alberts et al.). Much had changed in 22 years since the original publication, including a revised taxonomy that included 40 species. New molecular genetic technologies had emerged, allowing researchers to better understand genetic structuring within and between populations, and begin to apply this information to conservation decision-making. This volume focused on a deeper understanding of iguana diversity, behavior, ecology, and conservation, with a strong emphasis on *Cyclura* (12 of the 20 chapters), a genus that until then had received little attention. Notably, all seven conservation-themed chapters highlighted *Cyclura*, for which six of the nine recognized species had been classified as Endangered or Critically Endangered on the IUCN Red List of Threatened Species. A number of new approaches and techniques were tested and evaluated, including translocation, captive rearing, head-starting, and habitat restoration, significantly enhancing the toolbox available to iguana conservation practitioners.

The present volume complements and builds on the previous two, expanding our knowledge of iguana systematics, distribution and habitat, ecology, population biology, and conservation, while highlighting areas where further research is still needed. An updated taxonomy including 44 living species is presented, although genetic analyses in progress suggests this number may continue to grow (ITWG 2016). *Ctenosaura*, a species-rich genus only touched on in the first two volumes, is heavily emphasized in the current volume (Goode et al. 2016; Morales-Mávil et al. 2016a, b; Pasaschnik and Hudman 2016; Zarza et al. 2016). New information is presented on species distributions, habitat use, reproductive biology, and genetics that will be critical in guiding future conservation management decisions. Caribbean species are still featured prominently, with a continuing emphasis on applied research.

Technology is changing rapidly, a trend that will undoubtedly have a major impact on our knowledge of, and appreciation for, the world's iguanas. The advent of whole genome sequencing will change our understanding of species boundaries, as well as open new avenues for genetic management of populations. Sensor-enabled radio transmitters will give us insights into the physiology of free-ranging iguanas that were previously unattainable. Pioneering tools such as remote camera traps and unmanned aerial vehicles will significantly enhance our ability to monitor iguana populations in space and time. Collectively, these technological advances will not only provide a new level of biological understanding, but should also elucidate novel ways to help conserve dwindling wild populations.

Despite many advances in our knowledge of the phylogenetic relationships among iguana species (see ITWG 2016), a comprehensive phylogenetic analysis of the entire subfamily has yet to be published here or elsewhere (but see Fig. 1, adapted from Pyron et al. 2013). Addressing this gap must be a high priority for future researchers if we are to fully understand the adaptive significance of the morphology, physiology, behavior, and ecology reported for iguanas in these three dedicated volumes.

With each volume, the number of contributions from range country scientists has increased, reflecting a growing cadre of international researchers with an interest in iguana biology and conservation. Although the number of chapters is similar in each volume (23, 20, and 18, respectively), the number of contributors has more than doubled in the present volume, with 69

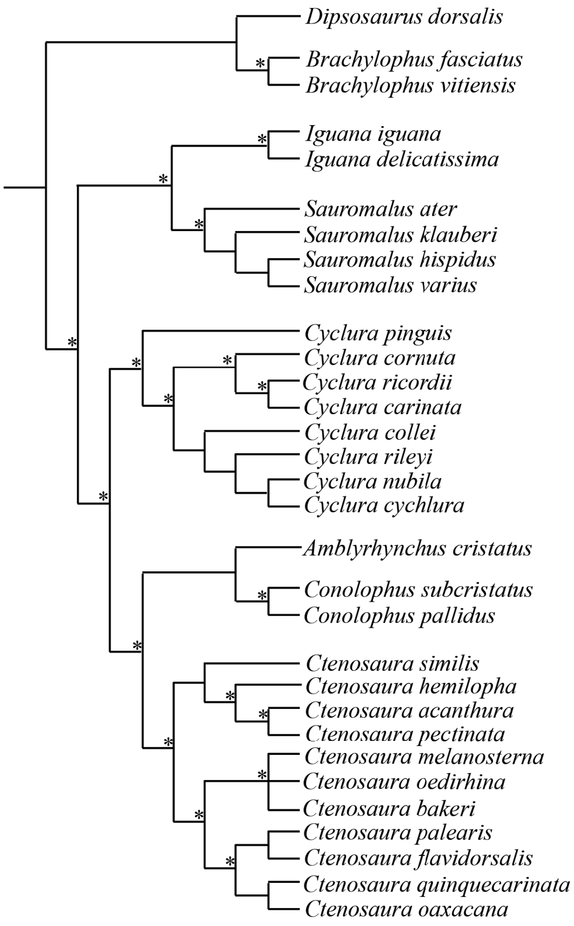

FIGURE 1. Cladogram for the subfamily Iguaninae adapted from Pyron et al. (2013). Structure reflects bootstrap values > 50, as in the original figure. Nodes with an asterisk reflect bootstrap values > 90. We acknowledge that 13 species (30% of species) are missing and that there are inconsistencies with previously published generic level work; however, this is the most complete tree for Iguaninae currently available.

authors represented, compared to 31 and 42 in the two previous volumes. Additionally, the percentage of contributions from scientists based outside the United States and Europe grew from 16% in the first two volumes to 42% in the current volume, with ten countries represented in total. Fifteen authors in the present volume also contributed to one or both of the previous two volumes, reflecting their long-term commitment to iguana research. Gordon Burghardt and John Iverson, who contributed to all three volumes, have dedicated much of their careers to furthering our understanding of iguana behavior and ecology. At the same time, they have trained a multitude of students – many of whom are authors in the current volume – who continue to expand our collective knowledge and bring new perspectives to a thriving field.

A major factor in bringing together this community has been the IUCN SSC Iguana Specialist Group (ISG), formed in 1997 and since expanded to 93 members in 25 countries, including representation from all regions in which iguanas occur naturally (http://www.iucn-isg.org). The group has worked with local government agencies and NGOs to draft 14 species recovery and conservation management plans that outline the most urgent research needs and conservation actions for individual taxa, many of which are reflected in the papers presented here. Not surprisingly, 29 (42%) of the 69 authors of this volume are ISG members. The commitment to assembling this volume was solidified during the group's 2013 annual meeting in Kingston, Jamaica. At that time, the group agreed to make this an online publication with the hope that it would be more immediately available and accessible to the rapidly increasing number of citizens worldwide with an interest in iguanas.

Major progress has been made in terms of stopgap measures to prevent the outright extinction of several iguana species, and a number of taxa seem to be tenuously on the road to recovery, including *Cyclura collei, C. lewisi, C. pinguis, C. cychlura inornata, C. cychlura figginsi*, and *C. rileyi cristata*. However, the large underlying threats that have led to their declines remain. It is especially troubling that over 90% of all threatened insular iguanas occur on at least one island with invasive vertebrates present (Tershy et al. 2016). Eradication of non-native species is becoming more feasible and economical over time, and several projects benefitting iguanas are under discussion. While the utility of head-starting as an emergency rescue measure has been proven, having dedicated habitat set aside for each iguana species is critical to their future survival. Nowhere has this been more evident than in the case of the Jamaican Iguana, which was saved from almost certain extinction by head-starting and invasive species control, but now faces the potential loss of its remaining wild habitat to development of a large-scale trans-shipment port (Wilson et al. 2016). Fortunately, as the papers in this volume attest, there is no shortage of passion and commitment within the iguana conservation community in seeking innovative ways to meet these challenges. The IUCN SSC Iguana Specialist Group is always open to new collaborators, and we enthusiastically welcome others who are interested in joining us. For more information, please visit http://www.iucn-isg.org.

LITERATURE CITED

Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). 2004. Iguanas: Biology and Conservation. University of California Press, Berkeley and Los Angeles, California, USA.

Burghardt, G.M., and A.S. Rand (Eds.). 1982. Iguanas of the World: Their Behavior, Ecology, and Conservation. Noyes Publications, Park Ridge, New Jersey, USA.

Goode, A.B.C., S.A. Pasachnik, and T.L. Maple. 2016. Habitat utilization of Roatán Spiny-tailed Iguanas (*Ctenosaura oedirhina*) and its implications for conservation. Pp. 79–89 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

ITWG (Iguana Taxonomy Working Group). 2016. A checklist of the iguanas of the world (Iguanidae; Iguaninae). Pp. 4–46 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Morales-Mávil, J.E., E.A. Bello-Sánchez, C.R. Corona-López. 2016a. Distribution and natural history of the Campeche Spiny-tailed Iguanas (*Ctenosaura alfredschmidti*). Pp. 168–176 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Morales-Mávil, J.E., E.A. Suárez-Domínguez, and C.R. Corona-López. 2016b. Biology and conservation of the Gulf Spiny-tailed Iguanas (*Ctenosaura acanthura*). Pp. 177–186 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Pasachnik, S.A., and S. Hudman. 2016. Conservation genetics of Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina.* Pp. 187–196 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Pyron, R.A., F.T. Burbrink, and J.J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13:93. doi:10.1186/1471-2148-13-93

Tershy, B., K.M. Newton, D.R. Spatz, K. Swinnerton, J.B. Iverson, R.N. Fisher, P. Harlow, N.D. Holmes, and D.A. Croll. 2016. The biogeography of threatened insular iguanas and opportunities for invasive vertebrate management. Pp. 222–236 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Wilson, B., T.D. Grant, R. van Veen, R. Hudson, D. Fleuchaus, O. Robinson, and K. Stephenson. 2016. The Jamaican Iguana (*Cyclura collei*): a report on 25 years of conservation effort. Pp. 237–254 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Zarza, E., V.H. Reynoso, and B.C. Emerson. 2016. Genetic tools for assisting sustainable management and conservation of the spiny-tailed iguana, *Ctenosaura pectinata.* Pp. 255–264 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

ALLISON C. ALBERTS serves San Diego Zoo Global as Chief Conservation and Research Officer. She is responsible for ongoing conservation science activities at the San Diego Zoo and Safari Park, including work at the Zoo's Institute for Conservation Research and field sites in 35 countries. She holds bachelor's and doctorate degrees in Biology from the University of California at Berkeley and San Diego, respectively, and is an adjunct professor at San Diego State University. As a reptile and amphibian specialist, she has participated in conservation programs for endangered iguanas in Costa Rica, Cuba, Turks and Caicos Islands, and Fiji, as well as working with komodo dragons, sea turtles, desert tortoises, and a variety of native California frogs, lizards, and snakes. Much of her research has focused on the development of innovative techniques for restoring critically endangered species to the wild. She is co-founder of the IUCN SSC Iguana Specialist Group and served as Co-chair of the ISG for over a decade. Currently, she is a member of the ISG steering committee and serves as President of the International Iguana Foundation. (Photographed by Jeffrey Lemm).

Herpetological Conservation and Biology 11(Monograph 6):4–46.
Submitted: 2 April 2015, Accepted: 12 November 2015, Published: 12 June 2016.

A CHECKLIST OF THE IGUANAS OF THE WORLD (IGUANIDAE; IGUANINAE)

IGUANA TAXONOMY WORKING GROUP (ITWG)
(ITWG members below are in alphabetical order and contributed to production of this checklist)

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***Abstract*.—This annotated checklist of the world's iguanas (Iguanidae; Iguaninae) represents an update by the Iguana Taxonomy Working Group (ITWG) of its 2011 list. We recognize 44 extant species (19 subspecies across six species) in eight genera. *Ctenosaura* (as currently recognized) is the most diverse, with 18 species, and *Amblyrhynchus* is the least diverse, with only one species, but seven subspecies. The list provides a comprehensive inventory of the taxonomy, common names, holotype(s), type locality, and distribution of all named taxa of iguanas. Extensive comments clarify contentious issues of nomenclature and/or distribution. Recently published papers suggest that additional diversity of iguanas remains to be described. Of the 44 included species, eight are listed as Critically Endangered (CR) on the IUCN Red List of Threatened Species, 11 as Endangered (EN), nine as Vulnerable (VU), two as Near Threatened (NT), three as Least Concern (LC), and one as Data Deficient (DD). Ten are not yet listed. Thus, over 82% of listed taxa are Threatened (28 of 34: CR, EN, or VU), placing this distinctive group among the most threatened vertebrate groups on the planet (surpassing turtles [50–58%], primates [ca. 49%], and amphibians [ca. 41%]).**

***Resumen*.—La siguiente lista anotada representa una actualización mundial para el grupo de iguanas (Iguanidae; Iguaninae) hecha por el Grupo de Trabajo Taxonómico de Iguanas. Reconocemos 44 especies existentes (19 subespecies en seis especies) correspondientes a ocho géneros. *Ctenosaura* es el grupo mas diverso, con 18 especies, y *Amblyrhynchus* es el grupo menos diverso, con solo una especie pero siete sub-especies. Esta lista representa un inventario taxonómico completo para el grupo de iguanas, con nombres comunes, holotipos, localidades, y distribución. Posee comentarios extensos que aclaran problemas de nomenclatura y/o distribución. Publicaciones recientes sugieren que aun existen especies de iguanas que necesitan ser descritas. De las 44 especies de iguanas, ocho están en peligro critico de extinción (CR) de acuerdo al criterio de la lista roja de especies amenazadas propuesta por la Unión Internacional para la Conservación de la Naturaleza, 11 están en peligro (EN), nueve están vulnerables (VU), dos casi amenazadas (NT), tres son consideradas de preocupación menor (LC), y uno es datos insuficientes (DD). Diez aun no están enlistadas. En resumen, mas del 82% del grupo de iguanas enlistadas están amenazadas (28 de 34: CR, EN, or VU), lo que pone este distintivo grupo dentro de los vertebrados mas amenazados del planeta (sobrepasando a las tortugas [50–58%], primates [ca. 49%], y anfibios [ca. 41%]).**

Key Words.—conservation status; nomenclature; Reptilia; taxonomy

INTRODUCTION

The true iguanas represent an assemblage of relatively large, mostly herbivorous lizards that has long been recognized as being monophyletic (Etheridge 1964). However, controversy exists (reviewed by Knapp and Gomez-Zlatar 2006) concerning whether the radiation should be ranked as a family (e.g., Hollingsworth 1998, 2004; Wiens and Hollingsworth 2000; Frost et al. 2001; Conrad 2008), or as a subfamily (e.g., Pough et al. 2004; Townsend et al. 2004; Smith 2009; Vitt and Caldwell 2009), or whether maintaining the associations between names and clades (monophyletic groups) is more important than reflecting taxonomic ranks (e.g., de Queiroz 1995; Schulte et al. 2003; see also de Queiroz and Gauthier 1990; Schwenk 1994). Considerable controversy also surrounds

Iguana Taxonomy Working Group. 2016. A checklist of the iguanas of the world (Iguanidae; Iguaninae). Pp. 4–46 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

the phylogenetic relationships among the eight genera in this family (e.g., see reviews in Hollingsworth 2004; Pyron et al. 2013).

This checklist was compiled by the Iguana Taxonomy Working Group (ITWG) of the IUCN SSC Iguana Specialist Group (ISG), and was based primarily on Etheridge (1982), Hollingsworth (2004), Etheridge and Frost (2001. Catalogues of the Pleurodont Iguanian Families. Available from http://www.amnh.org/our-research/vertebrate-zoology/herpetology/catalogues-of-the-pleurodont-iguanian-families [Accessed 25 November 2014]) and the ITWG (2011). The recognized species diversity in this clade has steadily increased over the past three decades, across those compilations. Etheridge (1982) recognized only 31 species, whereas Hollingsworth (2004) listed 40, and the ITWG (2011, herein) accepted 44.

We have not included full synonymies, as those are available from Hollingsworth (2004) and Etheridge and Frost (*op. cit.*). In compiling this checklist we have sought consensus on controversial issues, but have sometimes had to operate by majority rule. In this edition, we recommend a single Standard English Common Name for each taxon (following Crother 2012), but we have added other common names for many taxa. We recognize that although the IUCN prefers to recognize only a single common name for a taxon in each of their three official languages, in reality most taxa are known by multiple names. Distribution is restricted to established breeding populations and do not include waif occurrences. We have also added a final section to many species accounts that references other recent literature. These represent sources not mentioned in the taxon account itself, but which would provide the reader with additional information on distribution, taxonomy, systematics, and/or status of the taxon. Museum acronyms used in the text are explained in Appendix 1.

Because the lizards included in this clade are generally long-lived, have relatively large body sizes, and often have very narrow ranges (either insular or mainland), they are particularly vulnerable to habitat loss, overharvesting, and introduced predators and competitors. As a result, of the 44 included species (Appendix 2), eight are listed as Critically Endangered (CR) on the IUCN Red List of Threatened Species (IUCN. 2014. The IUCN Red List of Threatened Species. Available from http://www.iucnredlist.org [Accessed on 14 September 2014]), 11 as Endangered (EN), nine as Vulnerable (VU), two as Near Threatened (NT), three as Least Concern (LC), and one as Data Deficient (DD). Ten are not yet listed. Thus, over 82% of listed taxa are Threatened (28 of 34: CR, EN, or VU), placing this distinctive group among the most threatened vertebrate groups on the planet (Hoffman et al. 2010), surpassing even turtles (50–58%), primates (ca. 49%), and amphibians (ca. 41%). This subfamily also includes one species that has been extirpated in the last century (Powell 2000), *Cyclura onchiopsis*, and is included here (†) and classified on the Red List as Extinct (EX).

This clade is distributed across the New World tropics and subtropics including the West Indies and Galápagos Islands, and the Fiji and Tonga Islands (Etheridge 1982; de Queiroz 1987a; Hollingsworth 2004). Eight living genera and 44 living species are currently recognized; however, undescribed species are known to exist (e.g., see Malone and Davis 2004; Zarza et al. 2008; Gentile et al. 2009).

AMBLYRHYNCHUS BELL [MARINE IGUANAS]

Original name: *Amblyrhynchus* Bell 1825, Zoological Journal, London 2:206. Type species (by monotypy): *Amblyrhynchus cristatus* Bell 1825. Distribution: Galápagos Islands, Ecuador.

***Amblyrhynchus cristatus* Bell [Marine Iguanas].**— Other names: Iguanas Marinas (Galápagos); Amblyrhynque à crête, Iguane marin des Galapago, Iguane marin (Wrobel 2004). Original name: *Amblyrhynchus cristatus* Bell 1825, Zoological Journal, London 2:206. Holotype: OUM 6176 (Etheridge 1982; Olson 2014). Type locality: "Mexico." Corrected type locality: "Fernandina (Narborough)" (Eibl-Eibesfeldt 1956), although Olson (2014) suggested that the type more likely originated on Isabela (Albemarle), which has implications for the taxonomy of the subspecies (see Comment). Distribution: Galápagos Archipelago, Ecuador (Hollingsworth 2004). Comment: most authors have not recognized subspecies, although the subspecies recognized by Eibl-Eibesfeldt (1962) have not been formally rejected (see Rassmann et al. 1997a). Steinfartz et al. (2009), Lanterbecq et al. (2010), and MacLeod and Steinfartz (2016) demonstrated significant genetic structure among populations. Based on microsatellite data, the latter authors identified 10 island-specific genetic clusters: Fernandina (Narborough) and Isabela (Albemarle), Santiago (James), Pinta (Abingdon), Genovesa (Tower), Marchena (Bindloe), Santa Cruz (Indefatigable), Santa Fe (Barrington), Floreana (Charles) and Española (Hood), western San Cristobál (Chatham), and eastern San Cristobál. These groups ("management units") have only some correspondence with the previously described, morphology-based subspecies (see below), but the authors made no taxonomic recommendations. In addition to the sampled populations above, Marine Iguanas are also known to occur on the mid-sized islands of Baltra (South Seymour), Bartolomé (Bartholomew), Pinzón (Duncan), Plaza Norte, Plaza Sur, Rábida (Jervis), Seymour Norte, and many other smaller islands (Karl Campbell, pers. comm.). If Olson's (2014) correction of the type locality is confirmed by further analysis (e.g., genetic), *A. cristatus albemarlensis* would be a junior synonym of A. *cristatus cristatus* (the latter

FIGURE 1. Fernandina Marine Iguana, *Amblyrhynchus cristatus cristatus* (top left; photographed by Tandora Grant, Fernandina, Galápagos, Ecuador). Isabela Marine Iguana, *Amblyrhynchus cristatus albemarlensis* (top right; photographed by Jeffrey Lemm, Isabela, Galápagos, Ecuador). Santa Cruz Marine Iguana, *Amblyrhynchus cristatus hassi* (second row left; photographed by Jeffrey Lemm, Santa Cruz, Galápagos, Ecuador). San Cristóbal Marine Iguana, *Amblyrhynchus cristatus mertensi* (second row right; photographed by Tandora Grant, Santiago, Galápagos, Ecuador). Genovesa Marine Iguana, *Amblyrhynchus cristatus nanus* (third row left; photographed by Tandora Grant, Genovesa, Galápagos, Ecuador). Pinta Marine Iguana, *Amblyrhynchus cristatus sielmanni* (third row right; photographed by Sebastian Steinfartz, Pinta, Galápagos, Ecuador). Española Marine Iguana, *Amblyrhynchus cristatus venustissimus* (bottom right; photographed by Paquita Hoeck, Gardner by Floreana, Galápagos, Ecuador).

restricted to Isabela), and a new name would have to be proposed for the Fernandina population, assuming it is distinctive (but see MacLeod and Steinfartz 2016). In addition, Gray's 1830 name *ater* is synonymous with *A. cristatus*, and lacks a type or precise type locality, but might be available after further study. This species is known to hybridize with *Conolophus subcristatus* on Plaza Sur Island (Rassmann et al. 1997b). Additional literature: MacLeod et al. (2015); Wikelski (2005); Wikelski et al. (2005).

***Amblyrhynchus cristatus cristatus* Bell [Fernandina Marine Iguanas]**.—Original name: *Amblyrhynchus cristatus* Bell. See species account. Distribution: Fernandina (Narborough) Island, Galápagos Archipelago, Ecuador. Comment: see Comment for the species. Fig. 1, 2.

***Amblyrhynchus cristatus albemarlensis* Eibl-Eibesfeldt [Isabela Marine Iguanas]**.—Original name: *Amblyrhynchus cristatus albemarlensis* Eibl-Eibesfeldt 1962, Senckenbergiana Biologica 43(3):184. Holotype: Eibl-Eibesfeldt private coll. (Etheridge 1982) = SMF 64179. Type locality: "Insel Albemarle (Isabella)." Distribution: Isabela (Albemarle) Island, Galápagos Archipelago, Ecuador. Comment: see Comment for the species. Fig. 1, 2.

Amblyrhynchus cristatus hassi* Eibl-Eibesfeldt [Santa Cruz Marine Iguanas].—Original name: *Amblyrhynchus *cristatus hassi* Eibl-Eibesfeldt 1962, Senckenbergiana Biologica 43(3):181. Holotype: SMF 57407. Type locality: "Indefatigable Südküste, westliche Akademiebucht…, Galápagos-Inseln." Distribution: Santa Cruz (Indefatigable) Island, Galápagos Archipelago, Ecuador. Fig. 1, 2.

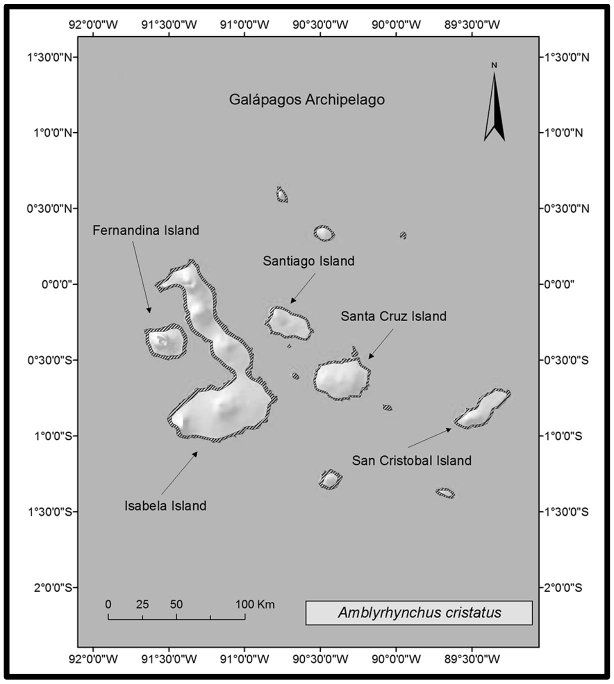


FIGURE 2. Range of Marine Iguanas, *Amblyrhynchus cristatus*. (All range distribution maps were generated by Jorge Morales-Mávil under the direction of the ITWG).

***Amblyrhynchus cristatus mertensi* Eibl-Eibesfeldt [San Cristóbal Marine Iguanas]**.—Original name: *Amblyrhynchus cristatus mertensi* Eibl-Eibesfeldt 1962, Senckenbergiana Biologica 43(3):185. Holotype: SMF 57430. Type locality: "etwa 3 km südwestlich der Wrack-Bucht der Insel Chatham (S. Cristobal)…, Galápagos-Inseln." Distribution: San Cristobal (Chatham) and Santiago (James), Islands, Galápagos, Archipelago, Ecuador. Fig. 1, 2.

***Amblyrhynchus cristatus nanus* Garman [Genovesa Marine Iguanas]**.—Original name: *Amblyrhynchus nanus* Garman 1892, Bulletin of the Essex Institute 24:8 (*Amblyrhynchus cristatus nanus* according to Eibl-Eibesfeldt 1962). Holotype: BMNH 99.5.4 = BMNH 1946.8.30.20 (Etheridge 1982). Type locality: "Tower Island" [Galápagos]. Distribution: Genovesa (Tower) Island, Galápagos Archipelago, Ecuador. Fig. 1, 2.

***Amblyrhynchus cristatus sielmanni* Eibl-Eibesfeldt [Pinta Marine Iguanas]**.—Original name: *Amblyrhynchus cristatus sielmanni* Eibl-Eibesfeldt 1962, Senckenbergiana Biologica 43(3):188. Holotype: SMF 57417. Type locality: "Westküste der Insel Abingdon." Distribution: Pinta (Abingdon) Island, Galápagos Archipelago, Ecuador. Fig. 1, 2.

***Amblyrhynchus cristatus venustissimus* Eibl-Eibesfeldt [Española Marine Iguanas]**.—Other name: Hood Island Marine Iguana (Wrobel 2004). Original name: *Amblyrhynchus cristatus venustissimus* Eibl-Eibesfeldt 1956, Senckenbergiana Biologica 37:90. Holotype: SMF 49851. Type locality: "Nordküste der Insel Hood (Española)." Distribution: Española (Hood) and Gardner Islands, Galápagos Archipelago, Ecuador. Fig. 1, 2.

BRACHYLOPHUS CUVIER [MELANESIAN IGUANAS]

Other names: Vokai (Fiji); Banded Iguanas, Fiji Iguanas, Fijian Crested Iguanas, Fijian Iguanas (Wrobel 2004). Original name: *Brachylophus* Cuvier 1829, *In* Guérin-Méneville, Iconographie du Règne Animal, Paris 1:9. Type species (by monotypy): *Iguana fasciata* Brongniart 1800. Distribution: Fiji Islands (reintroduced to Tonga Islands; introduced to Vanuatu). Comment: a phylogeny of populations of *Brachylophus* has been estimated by Keogh et al. (2008) based on sequences of two mitochondrial genes. However, additional taxa may exist (Fisher et al. 2009, 2012). Although the recent description of two new species clarifies the taxonomy of *Brachylophus*, the correct identification of the species occurring on many islands is not yet certain. This is complicated by introductions by humans (Kraus 2009). Additional literature: Burns et al. (2006).

Brachylophus bulabula **Fisher, Harlow, Edwards, and Keogh *In* Keogh, Edwards, Fisher, and Harlow [Central Fijian Banded Iguanas]**.—Other names: Fiji Iguanas, Fijian Banded Iguanas (IUCN. 2014. *op. cit.*). Original name: *Brachylophus bulabula* Fisher, Harlow, Edwards, and Keogh 2008, *In* Keogh, Edwards, Fisher, and Harlow, Philosophical Transactions of the Royal Society B 363(1508):3419. Holotype: CAS 172524. Type locality: "Navuloa Village, Ovalau Island, Republic of Fiji (17°42'05.95"S, 178°45'42.12"E)". Distribution: larger northwestern islands of the Viti group of Fijian islands, including at least Ovalau, Gau, Kadavu, and Viti Levu (Keogh et al. 2008). Comment: *B. bulabula* is the sister species of *B. vitiensis* (Keogh et al. 2008). Fig. 3.

Brachylophus fasciatus **(Brongniart) [Lau Banded Iguanas]**.—Other names: Tongan Banded Iguanas (IUCN. 2014. *op. cit.*); Banded Iguana, Brachylophe à bandes, Fiji Banded Iguana (Wrobel 2004). Original name: *Iguana fasciata* Brongniart 1800, Bulletin des Sciences, par la Société Philomathique, Paris 2:90. Holotype: apparently lost (Gibbons 1981). Type locality: none given; "Tonga", according to Keogh et al. (2008). Distribution: Lau Island group of Fiji, including at least Lakeba, Aiwa, Oneata, and Moce (Keogh et al. 2008); apparently extirpated from Tonga during prehistory (Pregill and Steadman 2004), but presumably re-introduced (Keogh et al. 2008). Introduced on Vanuatu (Kraus 2009). Comment: *B. fasciatus* is the sister species to the clade including *B. vitiensis* and *B. bulabula* (Keogh et al. 2008). Fig. 4.

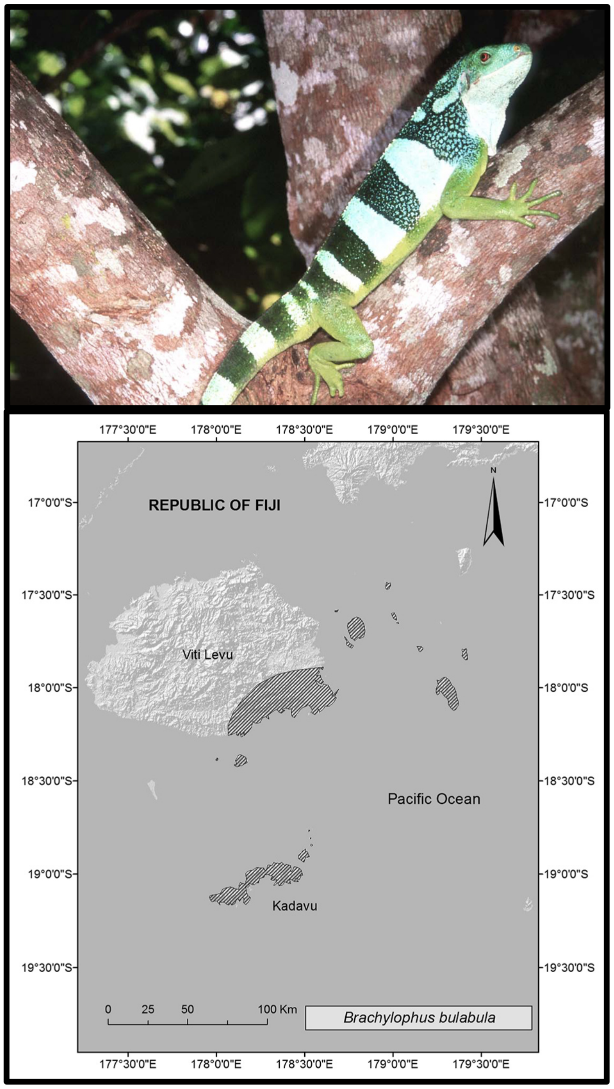


FIGURE 3. Central Fijian Banded Iguana, *Brachylophus bulabula* (Photographed by Peter Harlow, Ovalau, Fiji).

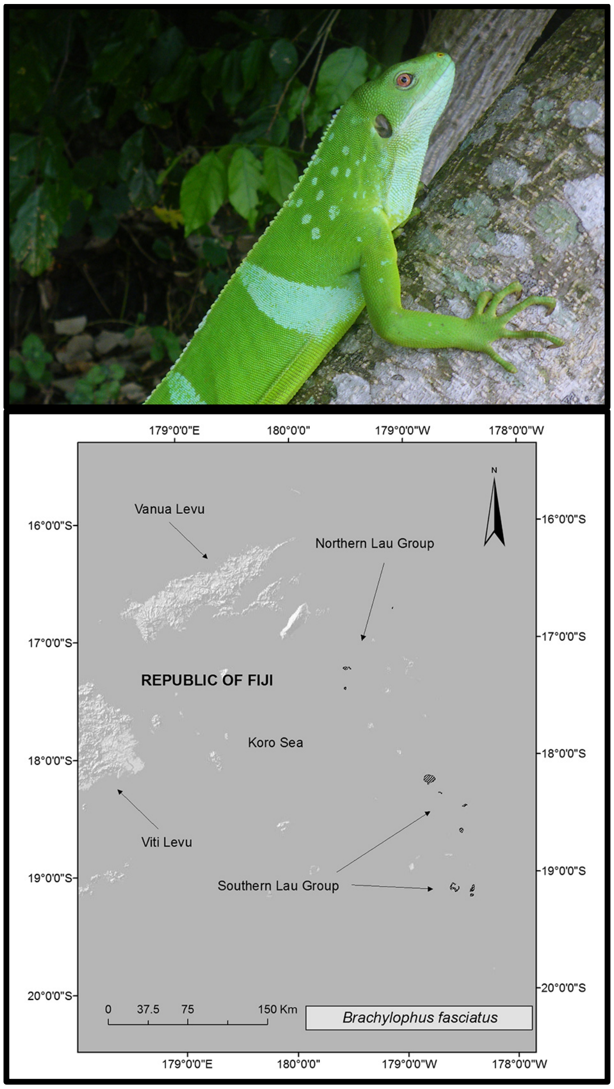


FIGURE 4. Lau Banded Iguana, *Brachylophus fasciatus*. (Photographed by Robert Fisher, Fiji).

***Brachylophus vitiensis* Gibbons [Fijian Crested Iguanas]**.—Other name: Fiji Crested Iguana (Wrobel 2004). Original name: *Brachylophus vitiensis* Gibbons 1981, Journal of Herpetology 15(3):257. Holotype: MCZ 157192. Type locality: "Yaduataba island (16°50'S; 178°20'E), Fiji." Distribution: Fiji Island group, found on the island of Yadua Taba and (presumably) the northern islands of the Yasawa group (Keogh et al. 2008). Comment: *B. vitiensis* is the sister species of *B. bulabula* (Keogh et al. 2008). Additional literature: Harlow et al. (2007). Fig. 5.

CONOLOPHUS FITZINGER [GALÁPAGOS LAND IGUANAS]

Other names: Iguanes terrestres, Land Iguanas (Wrobel 2004). Original name: *Hypsilophus* (*Conolophus*) Fitzinger 1843, Systema Reptilium, Wien 1:55. Type species (by original designation): *Amblyrinchus demarlii* Duméril and Bibron 1837 = *Amblyrhynchus subcristatus* Gray 1831 (according to Gray 1845). Distribution: Galápagos Islands (Gentile and Snell 2009). Comment: Tzika et al. (2008) and Gentile et al. (2009) have presented evidence that *Conolophus* includes five evolutionarily significant units, only three of which have been formally named. Additional literature: Márquez B. et al. (2010); Gentile et al. (2013); Ali and Aitchison (2014).

***Conolophus marthae* Gentile and Snell [Pink Land Iguanas]**.—Other names: Iguanas Rosadas (Galápagos); Pink Iguanas (IUCN. 2014. *op. cit.*). Original name: *Conolophus marthae* Gentile and Snell 2009, Zootaxa 2201:1. Holotype: a free-living adult male with a Passive Integrated Transponder #091–601–303. Type locality: "approximately four km north of the Equator on the top of Volcan Wolf, Isla Isabela Galápagos National Park,

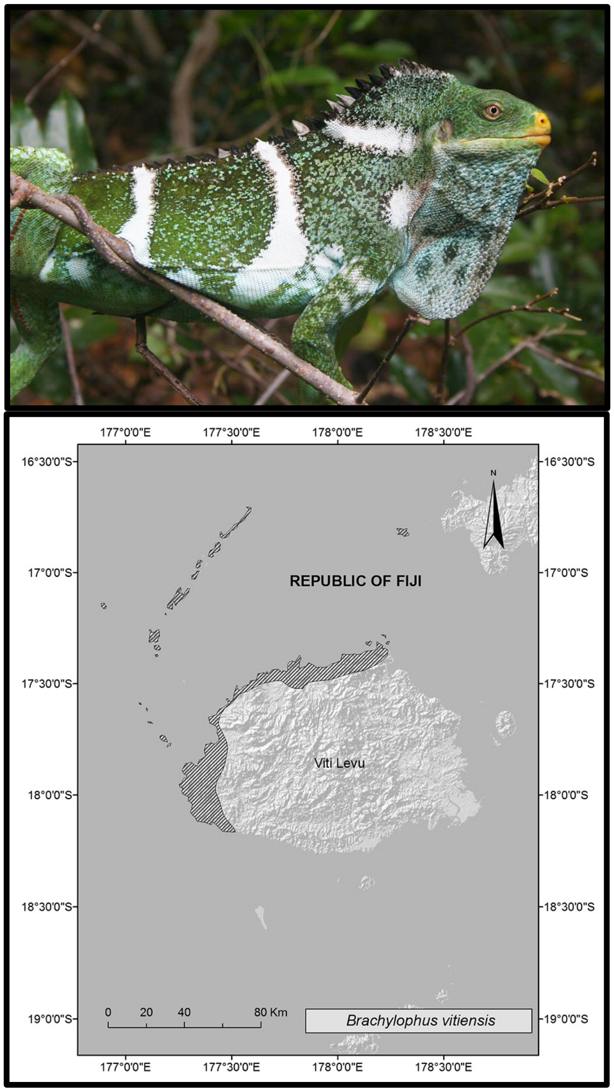


FIGURE 5. Fijian Crested Iguana, *Brachylophus vitiensis* (Photographed by Peter Harlow, Yadua Taba, Fiji).

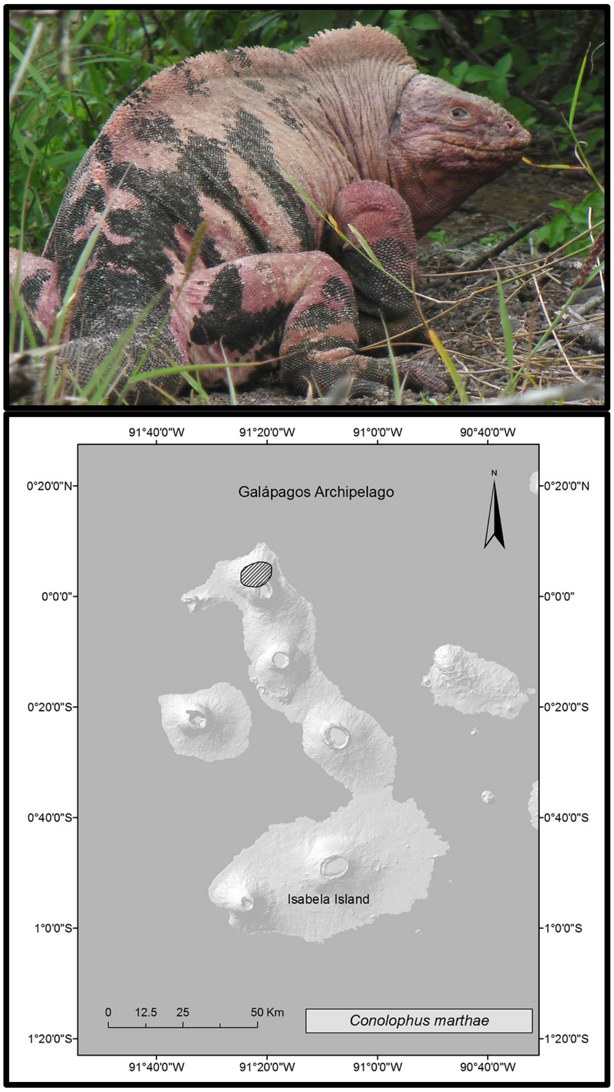


FIGURE 6. Pink Land Iguana, *Conolophus marthae* (Photographed by Gabriele Gentile, Isabela, Galápagos, Ecuador).

Ecuador (0.03792°N; 91.36324°W, datum WGS84…)." Distribution: Volcán Wolf, northern Isabela (Albemarle) Island, Galápagos Archipelago, Ecuador (Gentile and Snell 2009; Gentile et al. 2009). Comment: additional support for the recognition of this species appeared in Tzika et al. (2008) and Gentile et al. (2009). *C. marthae* is sister to the clade including the other two *Conolophus* species (Gentile et al. 2009). Additional literature: Donegan (2009); Nemesio (2009). Fig. 6.

Conolophus pallidus **Heller [Barrington Land Iguanas]**.—Other names: Iguanas Terrestres de Barrington, Santa Fe Land Iguana (IUCN. 2014. *op. cit.*); Barrington Island Iguana, Barrington Island Land Iguana (Wrobel 2004). Original name: *Conolophus pallidus* Heller 1903, Proceedings of the Washington Academy of Sciences 5:87. Holotype: CAS 4749. Type locality: "Barrington [= Santa Fe] Island, Galápagos Archipelago." Distribution: Santa Fe (Barrington) Island, Galápagos Archipelago, Ecuador (Gentile et al. 2009). Comment: this species appears to be sister to a clade composed of the western (Isabela and Fernandina) populations of *Conolophus subcristatus* (Gentile et al. 2009). Fig. 7.

Conolophus subcristatus **(Gray) [Galápagos Land Iguanas]**.—Other names: Iguanas Terrestres de Galápagos (IUCN. 2014. *op. cit.*); Land Iguana (Wrobel 2004). Original name: *Amb.[lyrhynchus] subcristatus* Gray 1831, The Zoological Miscellany, London 1831:6. Type: not located, although Olson (2014) inferred that it was collected on the voyage of the HMS *Blonde* expedition in March 1825. However, Olson was unable to confirm the current existence of the type. Type locality: "Galápagos?" Restricted type locality (Olson 2014): "Banks Bay, Albemarle (Isabela) Island, Galapagos". Distribution: Galápagos Archipelago, Ecuador, including the islands of Santa Cruz (Indefatigable), Isabela

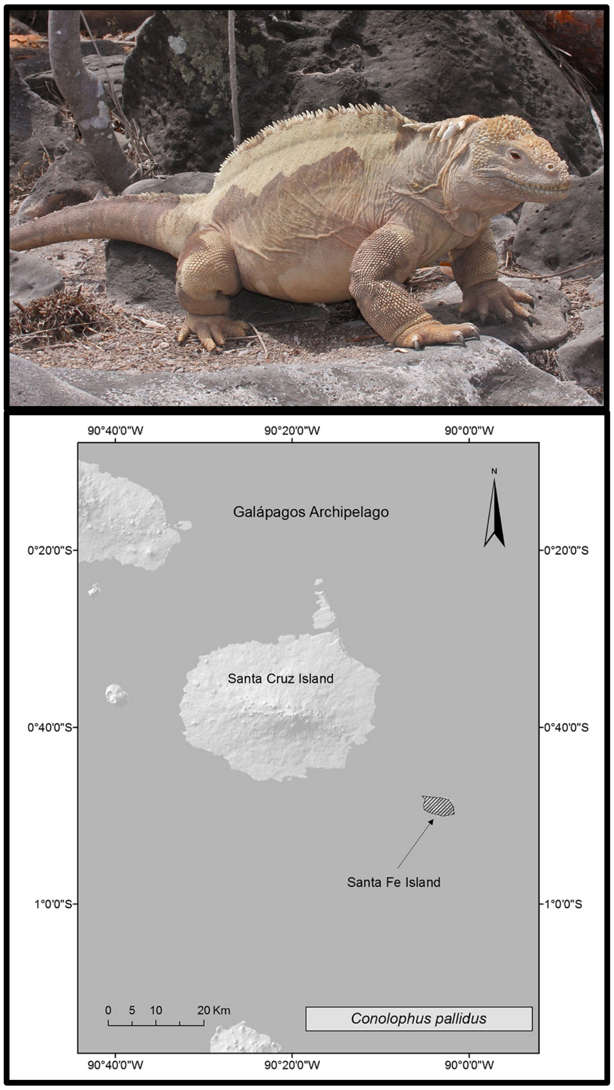


FIGURE 7. Barrington Land Iguana, *Conolophus pallidus* (Photographed by Joseph Burgess, Santa Fe, Galápagos, Ecuador).

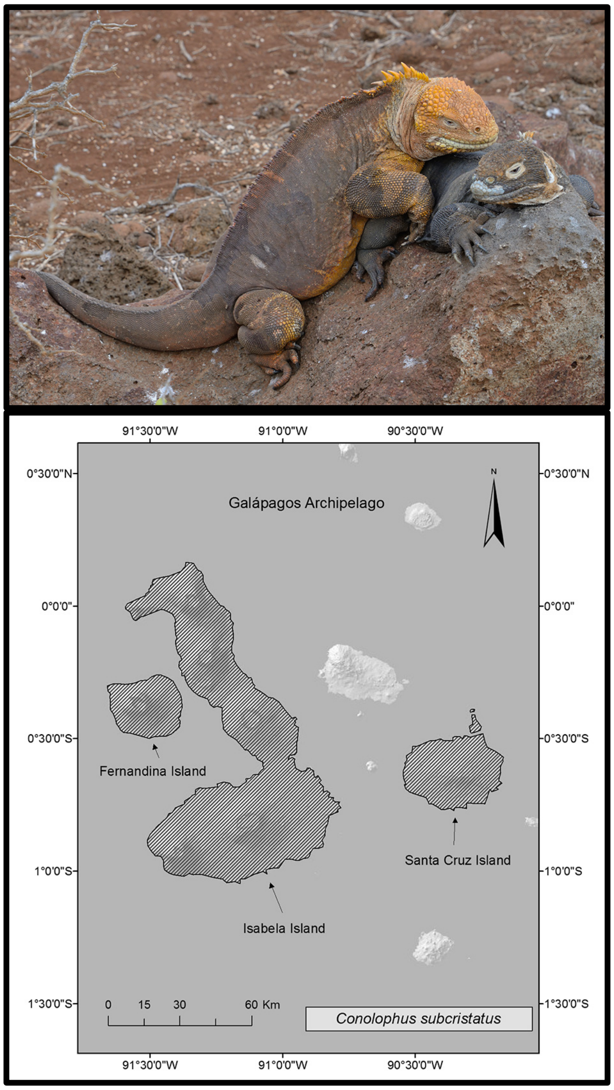


FIGURE 8. Galápagos Land Iguana, *Conolophus subcristatus* (Photographed by Jeffrey Lemm, Seymour Norte, Galápagos, Ecuador).

(Albemarle), Fernandina (Narborough), and Plaza Sur (Hollingsworth 2004; Gentile et al. 2009; Fabiani et al. 2011); extirpated from Santiago (James; Snell et al. 1984) and Rábida (Jervis; subfossil only, Steadman et al. 1991); introduced on Seymour Norte (North Seymour) in the 1930s (Phillips et al. 2005), Venecia in 1997 (Cayot et al. 1994), and Bartolomé (three individuals, non-breeding; Washington Tapia pers. comm.); and repatriated to Baltra (South Seymour; Cayot and Menoscal 1992; Phillips et al. 2005). Comment: Tzika et al. (2008) and Gentile et al. (2009) have reported genetic evidence suggesting that some populations of *C. subcristatus* may deserve recognition as species. The name *demarlii* Duméril and Bibron (1837, Erpétologie Génerale, Paris 4:197) is potentially available for a newly described form of *Conolophus*, although the type locality is unknown ("inconnue") and the holotype (originally in le Château-Musée de Boulogne-sur-Mer) has been lost (Céline Ramio and Roger Bour, pers. comm. to JBI 15 February 2010). Similarly, the name *pictus* Rothschild and Hartert (1899, Novitates Zoologicae 6:102; Syntypes BMNH 99.5.6.41–44; type locality "Narborough" [= Fernandina]), originally applied to a subspecies, is also available. This species is known to hybridize with *Amblyrhynchus cristatus* on Plaza Sur Island (Rassmann et al. 1997b). Fig. 8.

CTENOSAURA WIEGMANN [SPINY-TAILED IGUANAS]

Other names: Black Iguanas, Garrobos, or Jamos (locally); Greater Spinytail Iguanas (Wrobel 2004). Original name: *Ctenosaura* Wiegmann 1828, Isis von Oken, Leipzig 21:371. Type species (by subsequent designation by Fitzinger 1843): *Ctenosaura cycluroides* Wiegmann 1828 = *Lacerta acanthura* Shaw 1802 (according to Gray 1845). Distribution: México to Panamá. Comment: preliminary phylogenetic analyses including most species in *Ctenosaura* led Köhler et al. (2000) to erect subgenera for three included clades: *Ctenosaura* Wiegmann 1828 for *acanthura*, *hemilopha*, *similis*, and *pectinata*; *Enyaliosaurus* Gray 1845 for *alfredschmidti*, *clarki*, *defensor, flavidorsalis*, and *quinquecarinata*; and *Loganisaura* for *bakeri*, *melanosterna*, *oedirhina*, and *palearis*. This arrangement was only partially supported by Gutsche and Köhler (2008), based on partial sequences of a mitochondrial gene. De Queiroz (1987a, b) and unpublished work by Stephen et al. have found no evidence of a monophyletic group consisting of *acanthura*, *hemilopha*, *similis*, and *pectinata*. Unpublished molecular work by Stephen, Reynoso, Sabey, and Buckley also indicates that *alfredschmidti* and *defensor* are not closely related to other *Ctenosaura*, calling into question at least two of the three subgenera above, and possibly warranting the recognition of *alfredschmidti* and *defensor* as a separate clade from *Ctenosaura* (for which the name *Cachryx* Cope is available). A well-resolved phylogenetic hypothesis of all *Ctenosaura* is sorely needed.

***Ctenosaura acanthura* (Shaw) [Veracruz Spiny-tailed Iguanas]**.—Other names: Garrobos del Noreste (Liner and Casa-Andreu 2008); Chiguipiles, Iguanas Espinosas, Iguanas Negras, Tilcampos (México); Eastern Spinytail Iguana, Iguane noir du Mexique, Northeastern Spinytail Iguana (Wrobel 2004). Original name: *Lacerta Acanthura* Shaw 1802, General Zoology, London 3(1):216. Holotype: BMNH XXII.20.a (Bailey 1928) = BMNH RR 1946.8.30.19 (Etheridge 1982). Type locality: not given. Designated type localities: "California" (Boulenger 1885), in error (Smith and Taylor 1950); "Tampico, Tamaulipas, Mexico" (Bailey 1928), inappropriate restriction (de Queiroz 1995). Distribution: lowlands of eastern México, from Tamaulipas southward to the Isthmus of Tehuantepec in

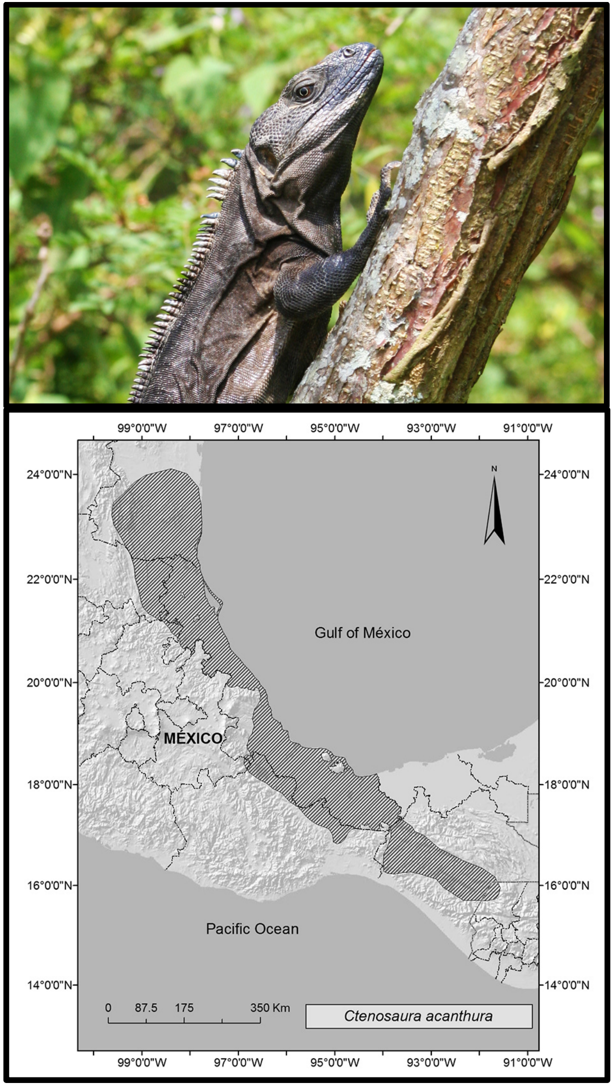


FIGURE 9. Veracruz Spiny-tailed Iguana, *Ctenosaura acanthura* (Photographed by Jorge Morales-Mávil, Los Tuxtlas, México).

southeastern Veracruz and eastern Oaxaca, México (Mendoza Quijano et al. 2002; Hollingsworth 2004; Zarza et al. 2008). Comment: Zarza et al. (2008) demonstrated that this taxon is nested within the diverse taxon currently called *C. pectinata*. Until the taxonomy of *C. pectinata* is clarified (see Comment on that species), we continue to recognize *acanthura* as a separate species from *pectinata*. See Comment for *C. pectinata* concerning the identity of spiny-tailed iguanas from the Central Depression in Chiapas and Guatemala. Additional literature: Morales-Mávil et al. (2016a). Fig. 9.

***Ctenosaura alfredschmidti* Köhler [Campeche Spiny-tailed Iguanas]**.—Other names: Garrobos de Campeche (Liner and Casas-Andreu 2008); Escorpiones (México); Campeche Spinytail Iguana (Wrobel 2004). Original name: *Ctenosaura alfredschmidti* Köhler 1995, Salamandra 31(1):5. Holotype: SMF 69019. Type locality: "70 km östl. von Escarcega auf der Straße nach Chetumal, Campeche, Mexico." Distribution: known only from near the type locality on the Yucatán Peninsula, in the Mexican state of Campeche. Comment: Radachowsky et al. (2003) reported this species from northeastern Guatemala, but Stephen et al. (unpubl. data) identified specimens from this population as *C. defensor*. Additional literature: Morales-Mávil et al. (2016b). Fig. 10.

***Ctenosaura bakeri* Stejneger [Útila Spiny-tailed Iguanas]**.—Other names: Swamper, Wishy-Willy (Honduras); Baker's Spinytail Iguana (IUCN. 2014. *op. cit.*); Utila Spinytail Iguana (Wrobel 2004). Original name: *Ctenosaura bakeri* Stejneger 1901, Proceedings of the United States National Museum 23:467. Holotype: USNM 26317. Type locality: "Utilla [sic] Island, Honduras." Distribution: Isla de Útila, Islas de la Bahía, Honduras (Pasachnik et al. 2009, 2010, 2011b). Comment: this species appears to be the sister taxon of

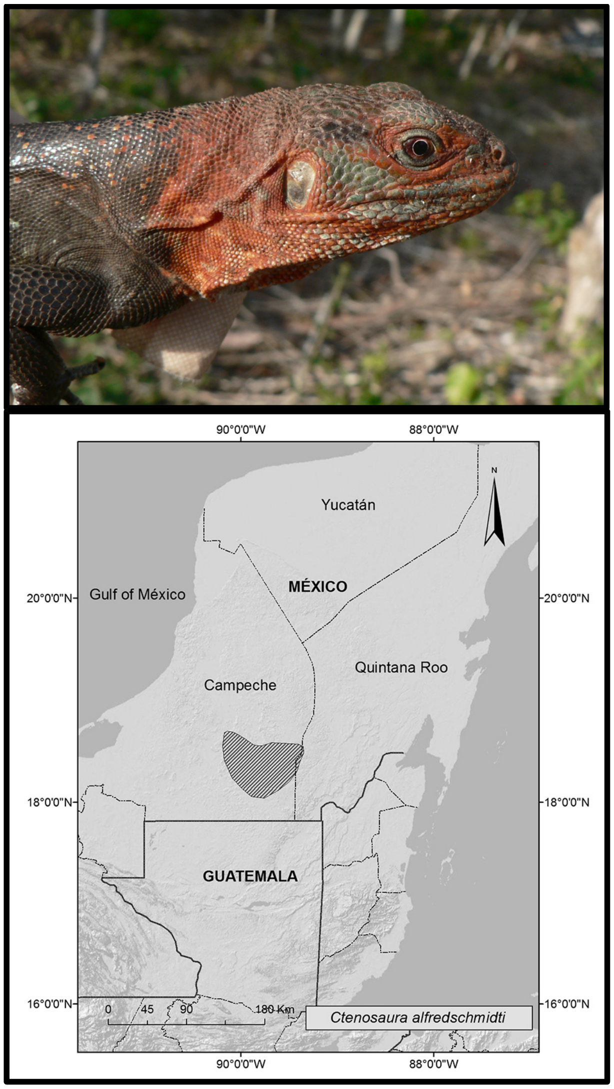


FIGURE 10. Campeche Spiny-tailed Iguana, *Ctenosaura alfredschmidti* (Photographed by Catherine Stephen, Campeche, México).

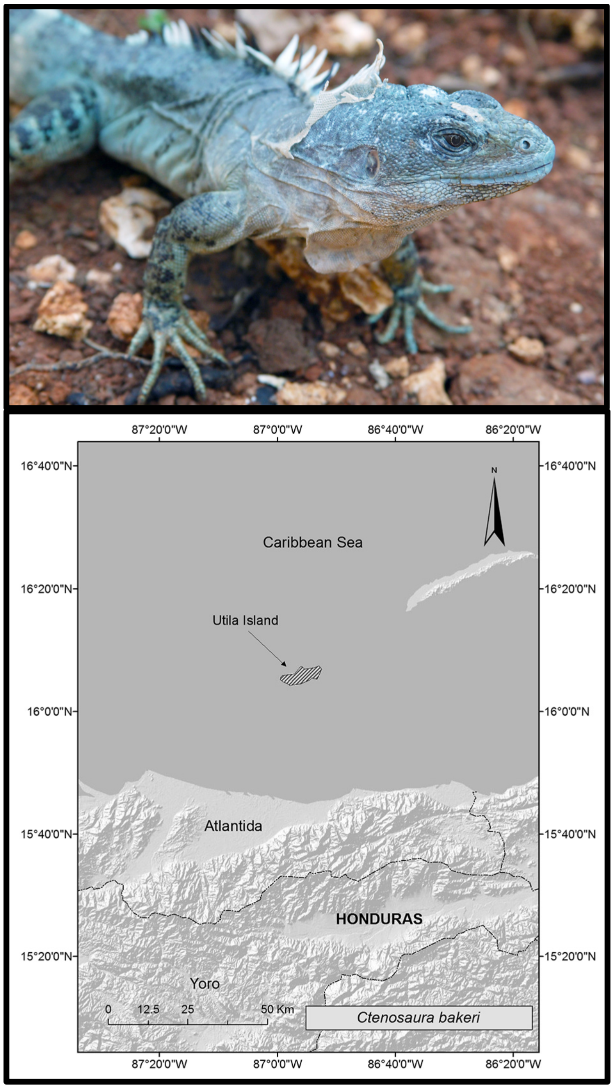


FIGURE 11. Útila Spiny-tailed Iguana, *Ctenosaura bakeri* (Photographed by John Binns).

C. oedirhina (Pasachnik et al. 2010), and is known to hybridize with *C. similis* (Pasachnik et al. 2009). Additional literature: Gutsche and Streich (2009); Schulte and Köhler (2010); Pasachnik et al. (2012b). Fig. 11.

Ctenosaura clarki **Bailey [Balsas Spiny-tailed Iguanas]**.—Other names: Nopiches (Duellman and Duellman 1959); Balsas Armed Lizards, Michoacán Dwarf Spiny-tailed Iguanas (IUCN. 2014. *op. cit.*); Mexican Club Tails, Nopilchis (Liner and Casas-Andreu 2008); Balsas Spinytail Iguana (Wrobel 2004). Original name: *Ctenosaura clarki* Bailey 1928, Proceedings of the United States National Museum 73(12):44. Holotype: MCZ 22454. Type locality: "Ovopeo, Michoacan, Mexico." Corrected type locality: "Oropeo…at an elevation of about 1,000 feet in the lower Tepalcatepec Valley about 8 miles south of La Huacana" (Duellman and Duellman 1959). Distribution: Southwestern México, in the Balsas-Tepalcatepec basin in the states of Michoacán (de Queiroz 1995), Jalisco (Larry Buckley, pers. comm.), and Guerrero (UNAM collection records from HerpNET), México. Fig. 12.

Ctenosaura conspicuosa **Dickerson [San Esteban Spiny-tailed Iguanas]**.—Other name: Garrobos de Isla San Esteban (Liner and Casas-Andreu 2008). Original name: *Ctenosaura conspicuosa* Dickerson 1919, Bulletin of the American Museum of Natural History 41(10):461. Holotype: AMNH 5027 = USNM 64440 (Bailey 1928; Cochran 1961; de Queiroz 1995). Type locality: "San Esteban Island, Gulf of California, Mexico." Distribution: Isla San Esteban and Isla Cholludo, Sonora, México (Grismer 1999a). Comment: previously regarded as a subspecies of *Ctenosaura hemilopha* (Smith 1972), *C. conspicuosa* was considered a separate species by Grismer (1999b), and this proposal was corroborated by mitochondrial DNA sequence data reported by Cryder (1999) and Davy et al. (2011).

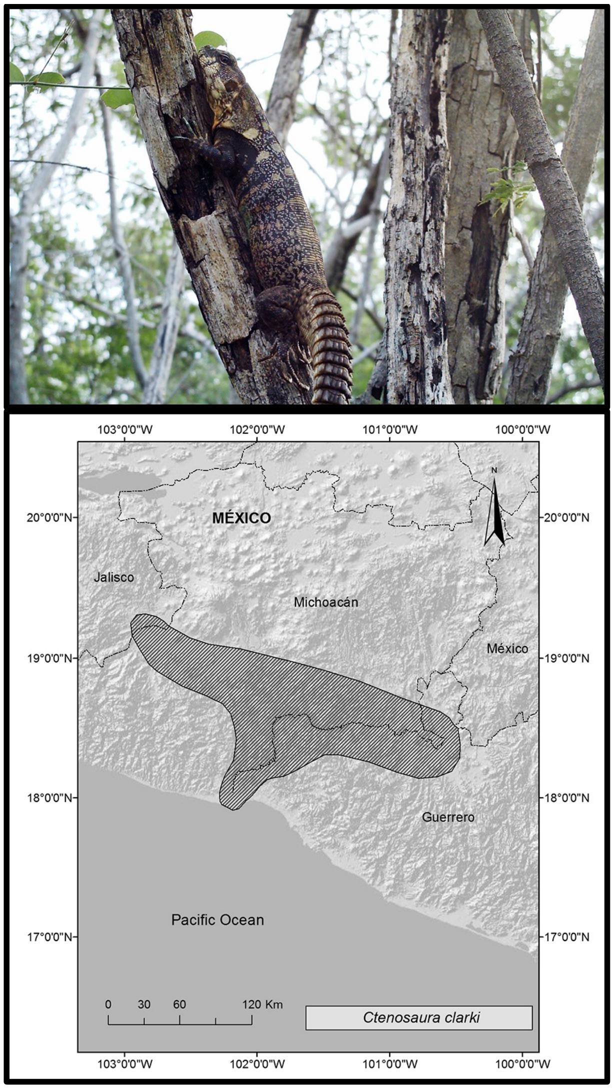


FIGURE 12. Balsas Spiny-tailed Iguana, *Ctenosaura clarki* (Photographed by Javier Alvarado-Diaz).

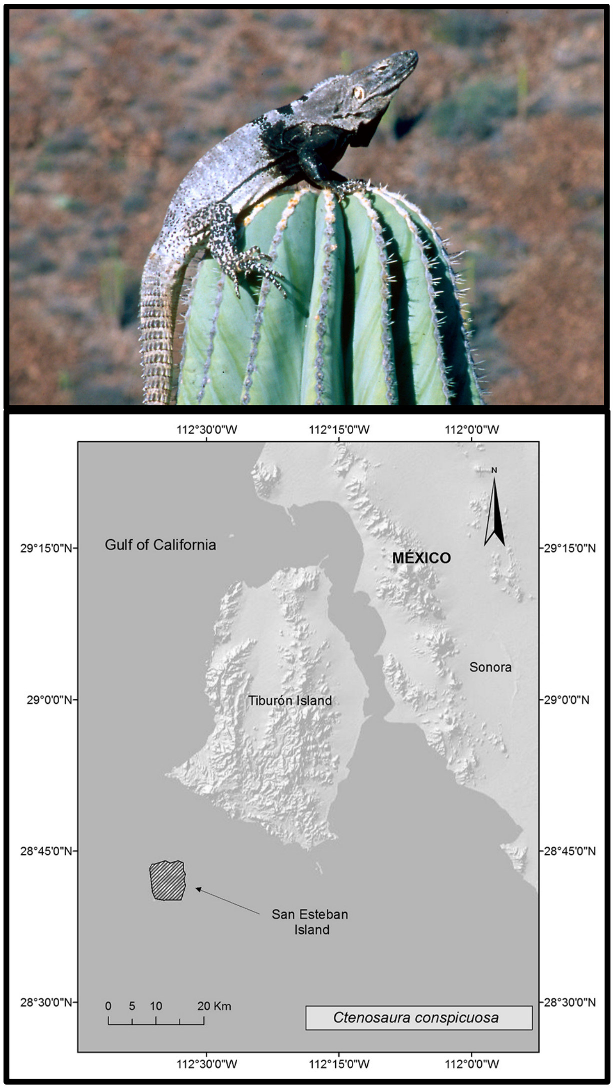


FIGURE 13. San Esteban Spiny-tailed Iguana, *Ctenosaura conspicuosa* (Photographed by Lee Grismer).

Grismer (1994, 2002) also argued that both the Isla San Esteban and Isla Cholludo populations represented descendants of individuals of *C. nolascensis* introduced by Seri native people; however, the divergence time estimates provided by Davy et al. (2011; see also Grismer 2002) indicate that *conspicuosa* diverged from *nolascensis* long before humans were present in the Americas. Mitochondrial haplotype data (Cryder 1999) and historical data (Nabhan 2002) indicate that the population of *conspicuosa* on Isla Cholludo was introduced there from Isla San Esteban by the Seri. Fig. 13.

Ctenosaura defensor **(Cope) [Yucatán Spiny-tailed Iguanas]**.—Other names: Chop (IUCN. 2014. *op. cit.*); Garrobos de Yucatán (Liner and Casas-Andreu 2008); Choop (Mayans); Yucatan Spinytail Iguana (Wrobel 2004). Original name: *Cachryx defensor* Cope 1866, Proceedings of the Academy of Natural Sciences of Philadelphia 18:124. Syntypes: USNM 12282 [3 specimens] (Bailey 1928; de Queiroz 1995). Type locality: not given; Yucatán, by implication (de Queiroz 1995). Restricted type locality: "Chichén Itzá, Yucatán, Mexico" (Bailey 1928), an inappropriate restriction (de Queiroz 1995). Distribution: Yucatán Peninsula in the Mexican states of Campeche and Yucatán (Hollingsworth 2004) and northeastern Guatemala (see Comment for *C. alfredschmidti*). Fig. 14.

Ctenosaura flavidorsalis **Köhler and Klemmer [Yellow-backed Spiny-tailed Iguanas]**.—Other names: Rumias (IUCN. 2014. *op. cit.*); Yellow-backed Spinytail Iguana (Wrobel 2004). Original name: *Ctenosaura flavidorsalis* Köhler and Klemmer 1994, Salamandra 30(3):197. Holotype: SMF 75845. Type locality: "1 km südl. La Paz (750 m ü. N.N.; 14°16', 87°40'; Dpto. La Paz, Honduras)." Distribution: Eastern Guatemala through northern El Salvador and southern Honduras (Köhler and Klemmer 1994; Hollingsworth 2004). Fig. 15.

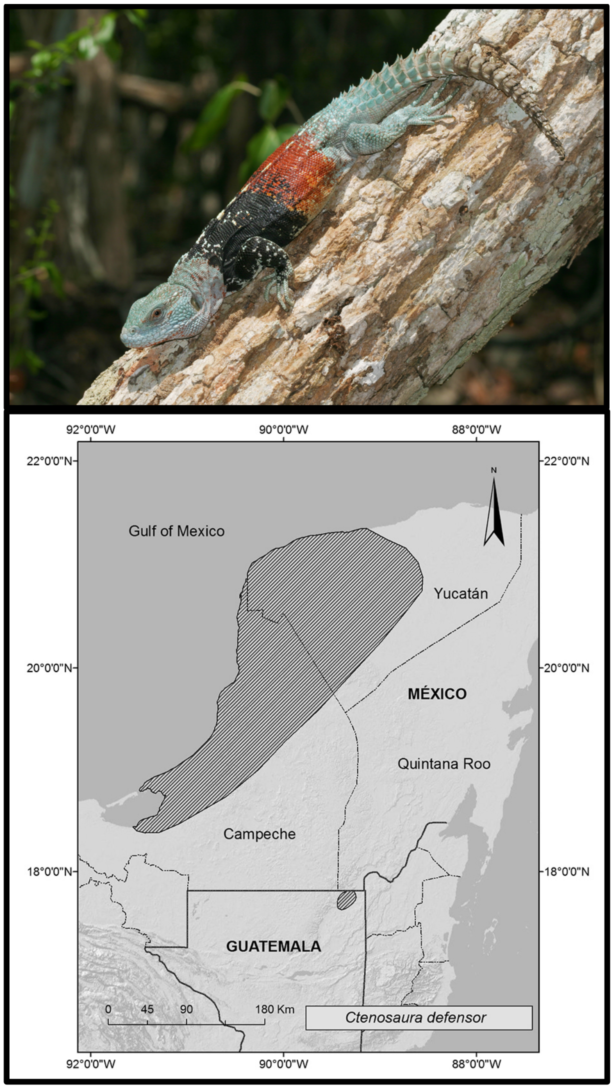


FIGURE 14. Yucatán Spiny-tailed Iguana, *Ctenosaura defensor* (Photographed by Joseph Burgess, Chencho, México).

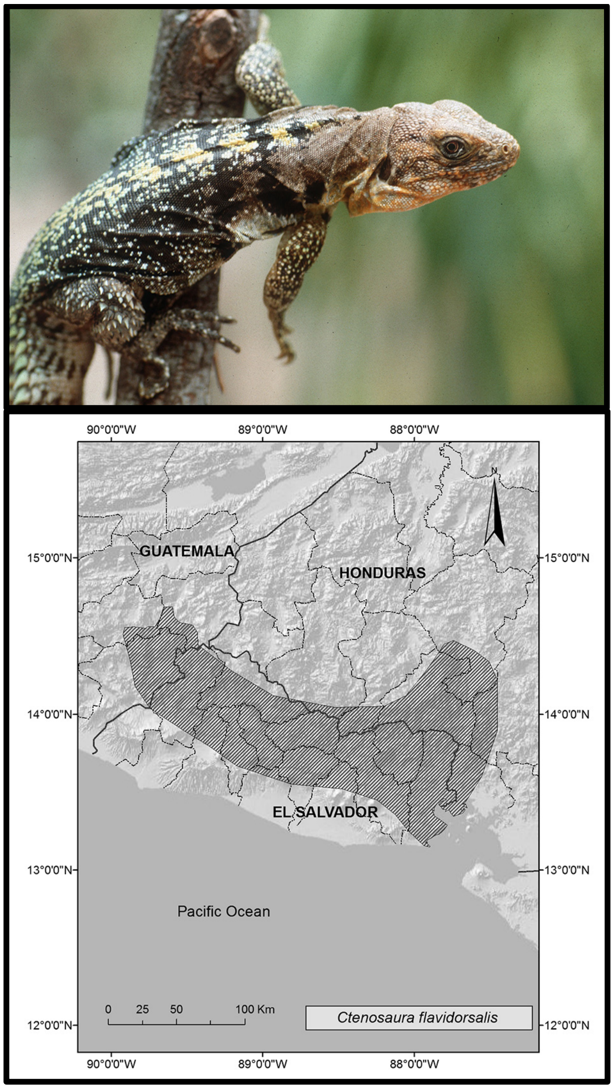


FIGURE 15. Yellow-backed Spiny-tailed Iguana, *Ctenosaura flavidorsalis* (Photographed by Gunther Köhler, La Paz, Honduras).

***Ctenosaura hemilopha* (Cope) [Baja California Spiny-tailed Iguanas]**.—Other names: Garrobos del Cabo (Liner and Casas-Andreu 2008); Garrobos, Iguanas del Desierto, Iguanas Negras (México); Cape Iguana, Cape Spinytail Iguana, Cape Spiny-tailed Iguana, Iguane à queue épineuse-et-crête courte, Iguane commun à queue épineuse, Northern False Iguana, Peninsular Spinytail Iguana (*C. hemilopha hemilopha*), Short-crested Spiny-tailed Iguana, Spiny-tailed Iguana (Wrobel 2004). Original name: *Cyclura* (*Ctenosaura*) *hemilopha* Cope 1863, Proceedings of the Academy of Natural Sciences of Philadelphia 15:105. Syntypes: USNM 5295 [4 specimens]; one recataloged as USNM 69489 (de Queiroz 1995). Type locality: "Cape St. Lucas"; "near Soria Ranch, Cape San Lucas, Baja California, Mexico" [USNM 5295] and "San Nicolás, between Cape San Lucas and La Paz, Baja California, Mexico" [USNM 69489] (Cochran 1961; de Queiroz 1995). Distribution: Baja California Sur, México, from the vicinity of Loreto southward through the Cape Region, and Isla Cerralvo (Hollingsworth 2004). Comment: three previously recognized subspecies (*conspicuosa*, *macrolopha*, and *nolascensis* following Smith 1972) were treated as separate species by Grismer (1999b). See Comments for those species. Other literature: Davy et al. (2011). Fig. 16.

***Ctenosaura macrolopha* Smith [Sonoran Spiny-tailed Iguanas]**.—Other name: Garrobos de Sonora (Liner and Casas-Andreu 2008). Original name: *Ctenosaura hemilopha macrolopha* Smith 1972, Great Basin Naturalist 32(2):104. Holotype: FMNH 108705. Type locality: "La Posa, San Carlos Bay, 10 mi NW Guaymas, Sonora." Distribution: Northwestern México, from the vicinity of Hermosillo, Sonora, southward through the northern third of Sinaloa, and extreme western Chihuahua (Hollingsworth 2004). Comment: previously regarded as a subspecies of *Ctenosaura hemilopha* (Smith 1972), *C. macrolopha* was considered

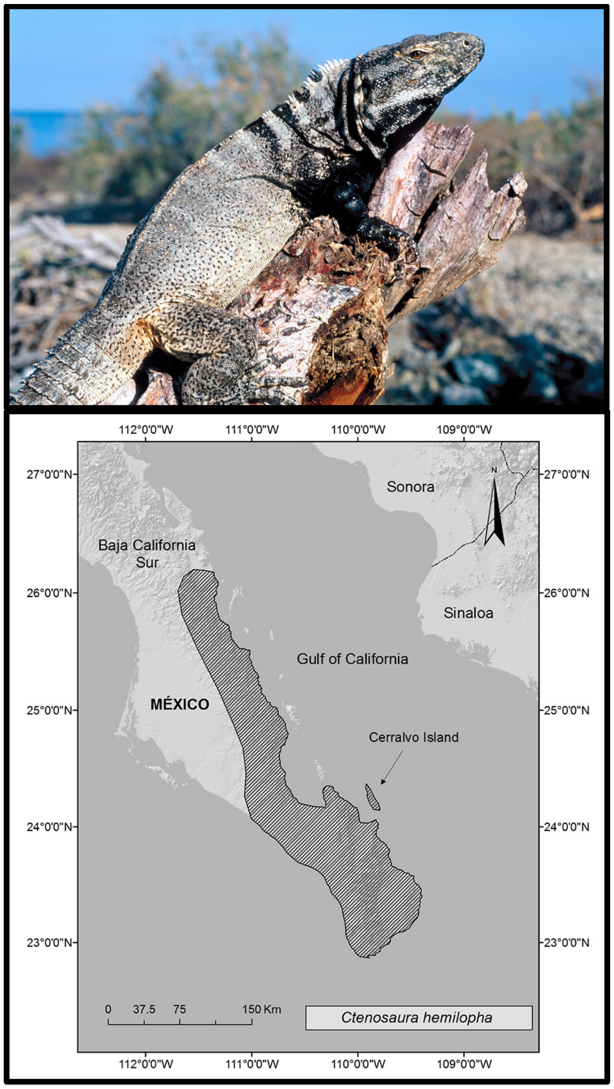


FIGURE 16. Baja California Spiny-tailed Iguana, *Ctenosaura hemilopha* (Photographed by Lee Grismer).

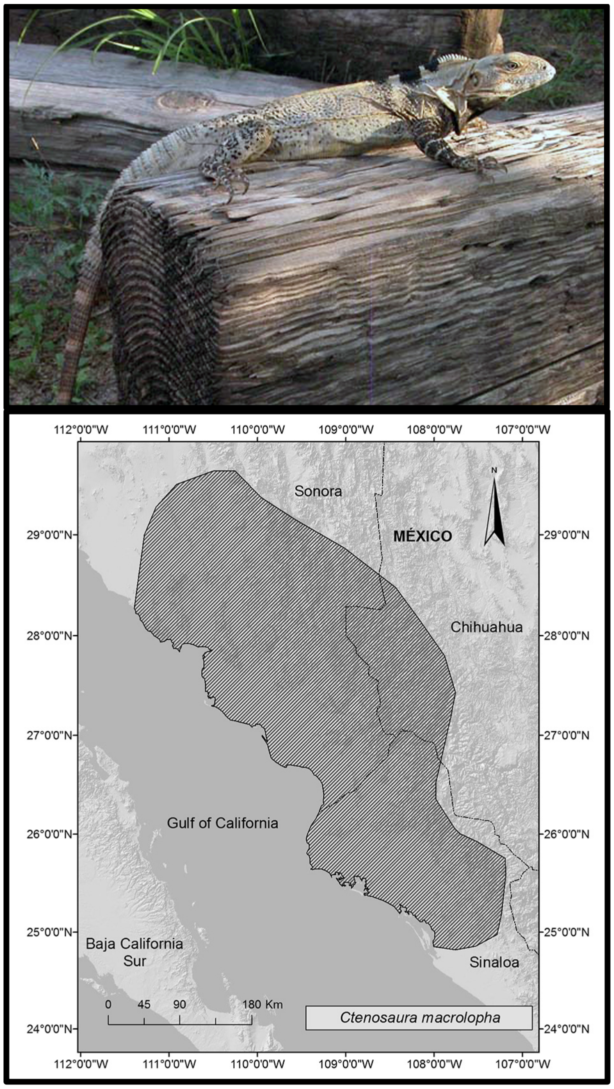


FIGURE 17. Sonoran Spiny-tailed Iguana, *Ctenosaura macrolopha* (Photographed by Victor Hugo Reynoso).

a separate species by Grismer (1999b), a proposal that was corroborated by mitochondrial DNA sequence data reported by Cryder (1999) and Davy et al. (2011). See Comment for *C. nolascensis* concerning introgression from that species to *C. macrolopha*. Fig. 17.

Ctenosaura melanosterna **Buckley and Axtell [Black-chested Spiny-tailed Iguanas]**.—Other names: Jamos (Honduras); Aguán Valley Iguanas, Cayos Cochinos Iguanas, Jamos Negros Río Aguán Iguanas (IUCN. 2014. *op. cit.*). Original name: *Ctenosaura melanosterna* Buckley and Axtell 1997, Copeia 1997(1):139. Holotype: KU 101441. Type locality: "2 km south of Coyoles Central, Departmento of Yoro, Honduras." Distribution: North-central Honduras in the Río Aguán Valley and Cayos Cochinos (Pasachnik et al. 2010, 2011a). Comment: this species was formerly considered part of *C. palearis,* but was recognized as a separate species by Buckley and Axtell (1997); the two species appear to be sister species (Pasachnik et al. 2010). Based on genetic differences between mainland and island populations, Pasachnik et al. (2011a) identified two evolutionarily significant units within *melanosterna*. Additional literature: Pasachnik et al. (2012c, 2014); Montgomery et al. (2014). Fig. 18.

Ctenosaura nolascensis **Smith [Nolasco Spiny-tailed Iguanas]**.—Other names: Iguanas Espinosas de Nolasco, San Pedro Nolasco Spiny-tailed Iguanas (IUCN. 2014. *op. cit.*); Garrobos de Isla San Pedro Nolasco (Liner and Casas-Andreu 2008). Original name: *Ctenosaura hemilopha nolascensis* Smith 1972, Great Basin Naturalist 32(2):107. Holotype: UCM 26391. Type locality: "Isla San Pedro Nolasco, Sonora." Distribution: Isla San Pedro Nolasco, Sonora, México (Grismer 1999a, b). Comment: previously regarded as a subspecies of *Ctenosaura hemilopha* (Smith 1972), *C. nolascensis* was considered a separate species by

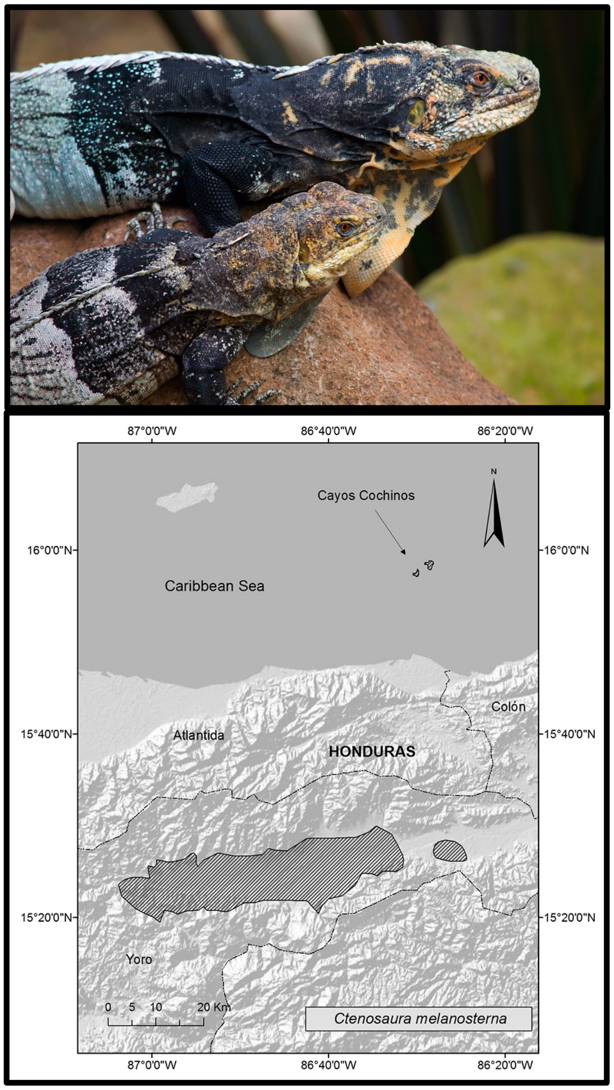


FIGURE 18. Black-chested Spiny-tailed Iguana, *Ctenosaura melanosterna* (Photographed by John Binns).

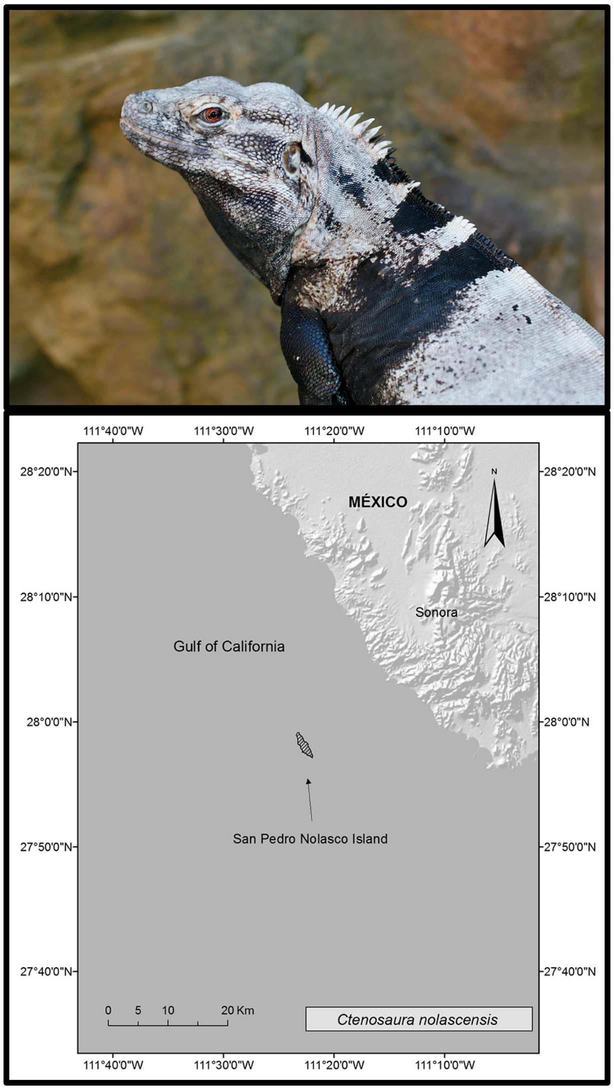


FIGURE 19. Nolasco Spiny-tailed Iguana, *Ctenosaura nolascensis* (Photographed by John Binns).

Grismer (1999b), a proposal that was corroborated by mitochondrial DNA sequence data reported by Cryder (1999) and Davy et al. (2011). Davy et al. (2011) recently demonstrated that *C. nolascensis* is a composite of at least two distantly related matrilines which likely represent two ancient independent colonizations not mediated by humans. They also found evidence suggesting that, prior to human occupation of the area, *C. nolascensis* dispersed back to the mainland and introgressed with *C. macrolopha*. Fig. 19.

Ctenosaura oaxacana **Köhler and Hasbún [Oaxaca Spiny-tailed Iguanas]**.—Other names: Guiou (IUCN. 2014. *op. cit.*); Garrobo de Oaxaca (Liner and Casas-Andreu 2008). Original name: *Ctenosaura oaxacana* Köhler and Hasbún 2001, Senckenbergiana Biologica 81(1/2):260. Holotype: SMF 43259. Type locality: "Tehuantepec, Estado de Oaxaca, México." Distribution: Pacific versant of the Isthmus of Tehuantepec, Estado de Oaxaca, México (Köhler and Hasbún 2001). Comment: this species was formerly considered part of *C. quinquecarinata*, but was recognized as a separate species by Köhler and Hasbún (2001); the two species appear to be sister species (Hasbún et al. 2005). Additional literature: Rioja et al. (2012). Fig. 20.

Ctenosaura oedirhina **de Queiroz [Roatán Spiny-tailed Iguanas]**.—Other names: Black Iguanas, Iguanas Negras, Wish-willys, (Honduras); De Queiroz's Spiny-tailed Iguanas, Garrobos (IUCN. 2014. *op. cit.*); De Queiroz's Spinytail Iguana, Roatan Spinytail Iguana (Wrobel 2004). Original name: *Ctenosaura oedirhina* de Queiroz 1987, Copeia 1987(4):892. Holotype: UF 28532. Type locality: "approx. 4.8 km (converted from 3 miles) west of Roatán on the path to Flowers Bay, Isla de Roatán, Departamento de las Islas de la Bahía, Honduras." Distribution: Islas de Roatán, Santa Elena, Barbareta, and various small islets surrounding Roatán, in the Islas de la

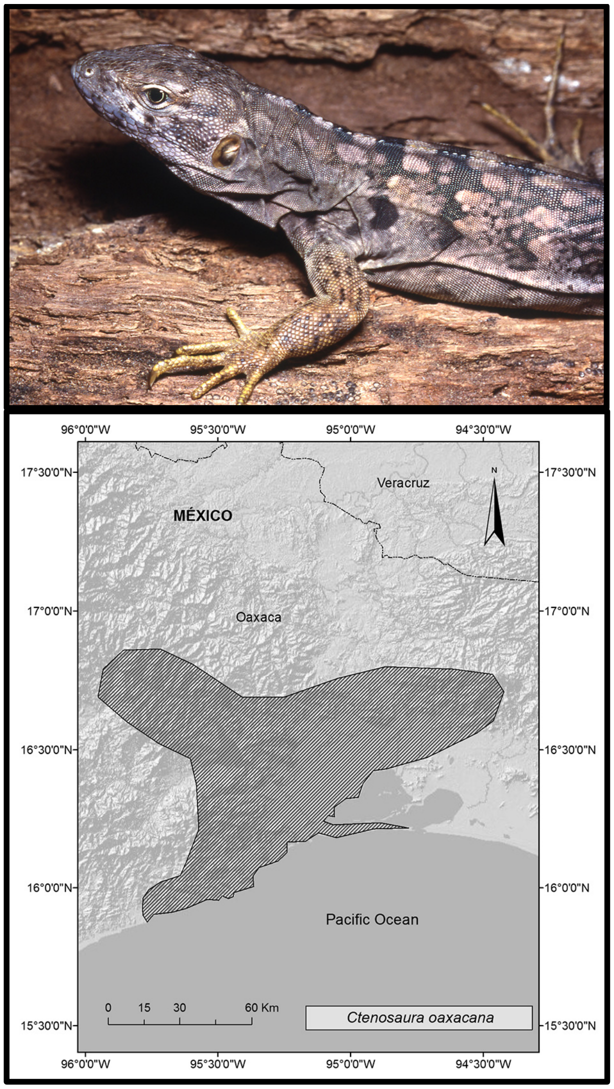


FIGURE 20. Oaxaca Spiny-tailed Iguana, *Ctenosaura oaxacana* (Photographed by John Iverson, México).

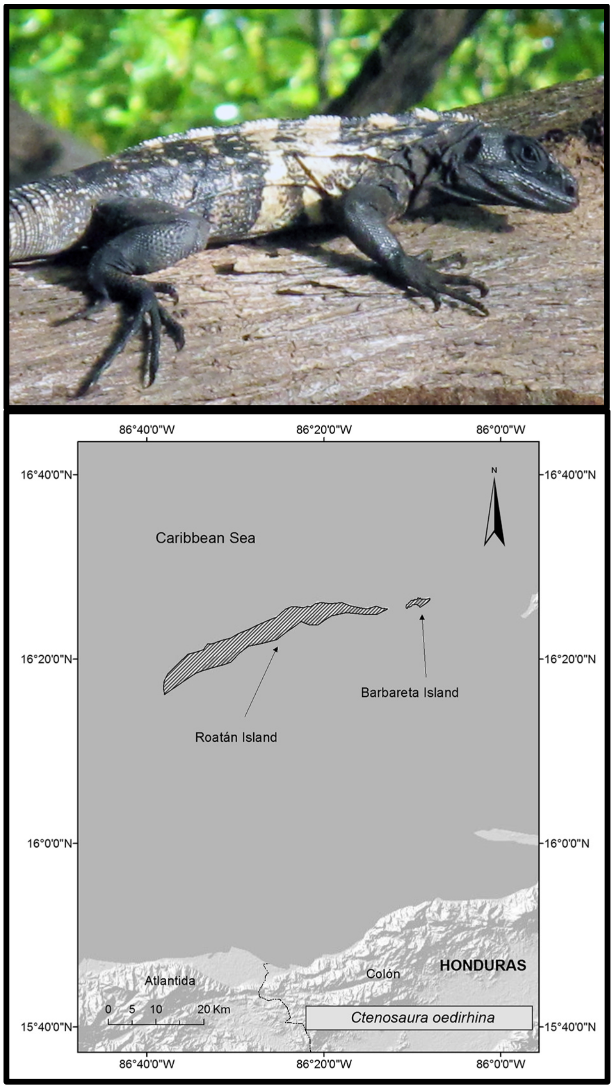


FIGURE 21. Roatán Spiny-tailed Iguana, *Ctenosaura oedirhina* (Photographed by Stesha Pasachnik).

Bahía, Honduras (Pasachnik 2013; Pasachnik et al. 2015). Comment: this species was considered part of *Ctenosaura bakeri* (Meyer and Wilson 1973; Wilson and Hahn 1973), but was recognized as a separate species by de Queiroz (1987b); the two species appear to be sister taxa (Pasachnik et al. 2010). Additional literature: Goode et al. (2016); Pasachnik and Hudman (2016). Fig. 21.

***Ctenosaura palearis* Stejneger [Motagua Spiny-tailed Iguanas]**.—Other names: Garrobos del Motagua, Guatemalan Black Iguanas, Guatemalan Spiny-tailed Iguanas, Iguanas de Órgano, Iguanas de Tuno (IUCN. 2014. *op. cit.*). Original name: *Ctenosaura palearis* Stejneger 1899, Proceedings of the United States National Museum 21:381. Holotype: USNM 22703. Type locality: "Gualan, Guatemala." Distribution: Southeastern Guatemala in the Río Motagua Valley (Ariano and Pasachnik et al. 2011). Comment: this species is the sister taxon of *C. melanosterna* (Pasachnik et al. 2010). Fig. 22.

***Ctenosaura pectinata* (Wiegmann) [Guerreran Spiny-tailed Iguanas]**.—Other names: Garrobos de Roca (Liner and Casas-Andreu 2008); Iguane à queue épineuse-et-crête courte, Mexican Spinytail Iguana, Spinytail Iguana, Spiny-tailed Iguana, Western Spiny-tailed Iguana (Wrobel 2004). Original name: *Cyclura pectinata* Wiegmann 1834, Herpetologica Mexicana, Berlin: 42. Syntypes: ZMB 574–575 (Taylor 1969; de Queiroz 1995). Type locality: "Mexico". Restricted type locality: "Colima, Colima, Mexico" (Bailey 1928), an inappropriate restriction (de Queiroz 1995). Distribution: Western México from north of Culiacán in Sinaloa southward at least to the Isthmus of Techuantepec in southeastern Oaxaca (see Comment), including Isla Isabela and Islas de las Tres Marías, Nayarit (Hollingsworth 2004; Zarza et al. 2008). Introduced to south Texas and south Florida, USA (Kraus 2009). Comment: Zarza et al. (2008) found that *C. pectinata* contains at least eight mutually exclusive

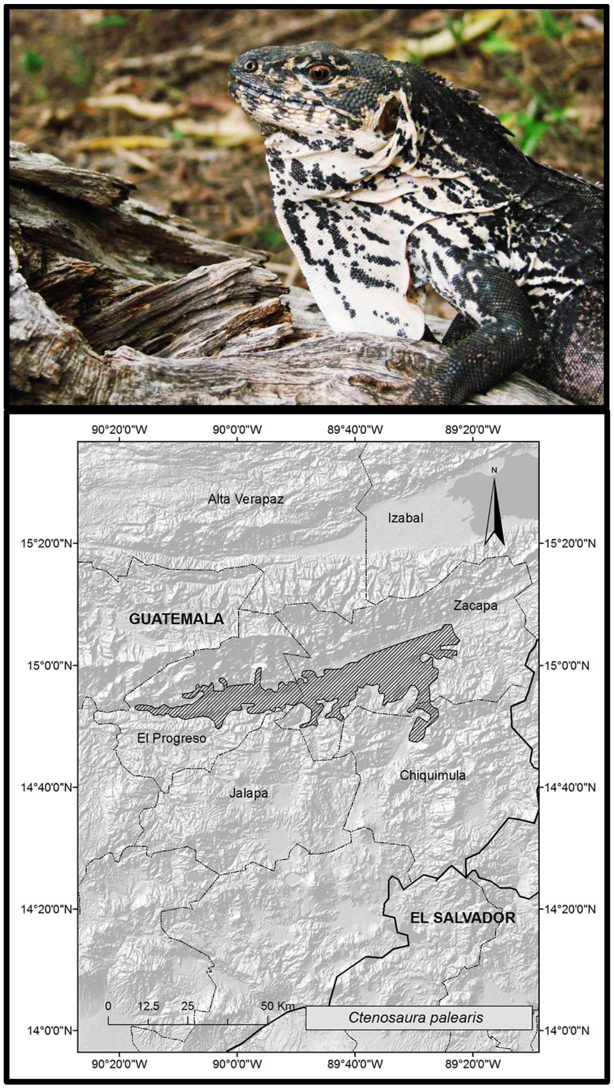


FIGURE 22. Motagua Spiny-tailed Iguana, *Ctenosaura palearis* (Photographed by Daniel Ariano).

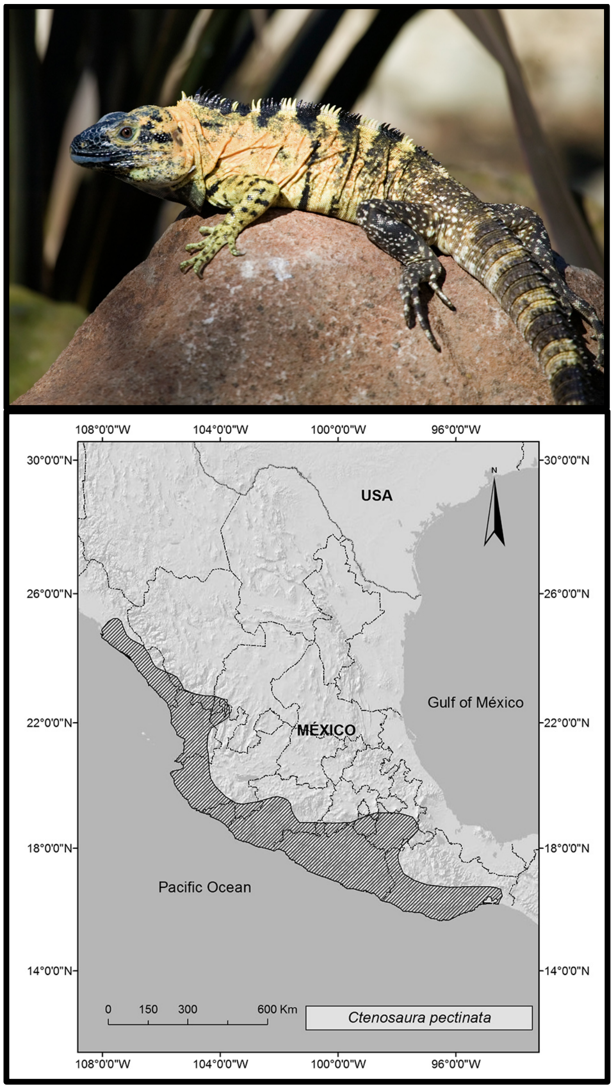


FIGURE 23. Guerreran Spiny-tailed Iguana, *Ctenosaura pectinata* (Photographed by John Binns).

mitochondrial DNA clades across its range (with *C. acanthura* closely related to members of the most southeastern clade). Zarza et al. (2011) presented evidence from 12 microsatellite loci sampled only across the central range in western México (where four of the eight mtDNA clades were found) that only two nuclear DNA clusters were present in the area and they were discordant with the mtDNA clades. More range-wide genetic and morphological sampling is needed to understand variation in this complex, and its taxonomic implications. Until specific taxonomic designations are made, we tentatively recognize two species: *C. acanthura* and *C. pectinata*. Spiny-tailed iguanas in the Central Depression of Chiapas and extreme western Guatemala have been referred to as both *C. pectinata* (Alvarez del Toro 1960, 1983; Johnson 1989, 1990) and *C. acanthura* (Köhler 2003; Acevedo 2006). The identity of these iguanas needs to be determined. Additional literature: Zarza et al. (2016). Fig. 23.

***Ctenosaura praeocularis* Hasbún and Köhler [Southern Honduran Spiny-tailed Iguanas]**.—Other name: Jamos (IUCN. 2014. *op. cit.*). Original name: *Ctenosaura praeocularis* Hasbún and Köhler 2009, Journal of Herpetology 43:197. Holotype: SMF 79520. Type locality: "Cerro Las Mesitas, 10 km east of Sabanagrande toward Nueva Armenia, Montegrande, Departamento Francisco Morazán, Honduras, 800 m, 13°46.43'N, 86°11.83'W." Distribution: Pacific versant of southeastern Honduras in the Departments of Francisco Morazán and Choluteca (Hasbún and Köhler 2009). Comment: this species appears to be most closely related to *C. flavidorsalis* (Hasbún et al. 2005). Fig. 24.

***Ctenosaura quinquecarinata* (Gray) [Five-keeled Spiny-tailed Iguanas]**.—Other names: Colas Chatas (IUCN. 2014. *op. cit.*); Nicaraguan Iguanas (Nicaragua); Central American Armed Lizard, Five-keeled Spinytail

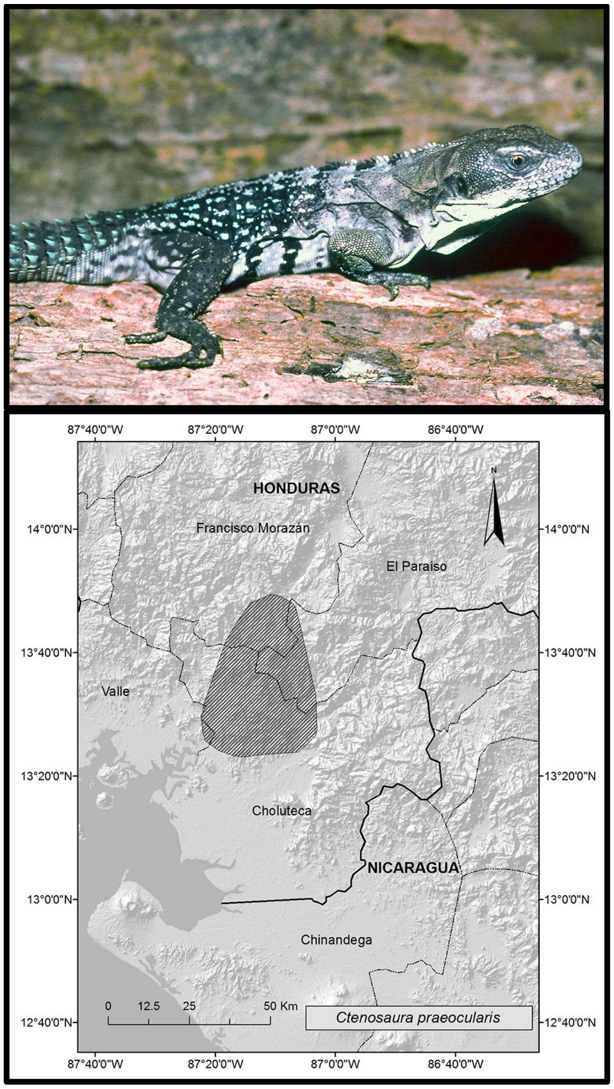


FIGURE 24. Southern Honduran Spiny-tailed Iguana, *Ctenosaura praeocularis* (Photographed by John Iverson).

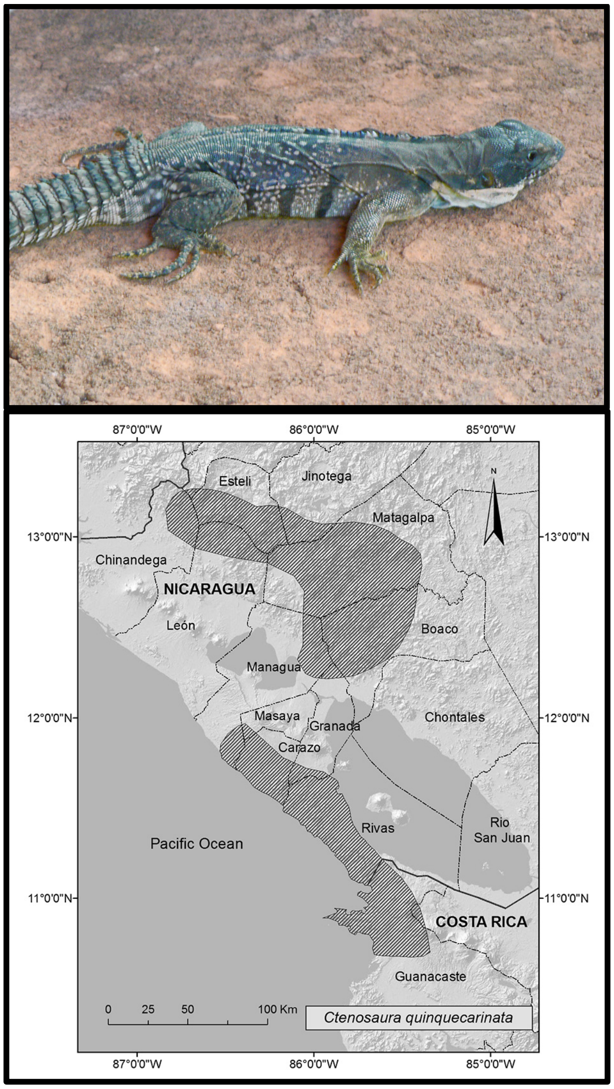


FIGURE 25. Five-keeled Spiny-tailed Iguana, *Ctenosaura quinquecarinata* (Photographed by Catherine Stephen, Leon, Nicaragua).

Iguana, Oaxacan Spinytail Iguana (Wrobel 2004). Original name: *Cyclura quinquecarinata* Gray 1842, Zoological Miscellany, London 1842:59. Holotype: BMNH 41.3.5.61 = BMNH RR 1946.8.30.48 (Etheridge 1982). Type locality: "Demerara?" [= Georgetown, Guyana], in error (de Queiroz 1995); "South America", in error (BMNH catalogue; de Queiroz 1995). Restricted type locality: "Tehuantepec, Oaxaca, Mexico" (Bailey 1928), an inappropriate restriction (de Queiroz 1995); restricted to "the southern portion of the distribution of *C. quinquecarinata* in Costa Rica and Nicaragua" (Hasbún and Köhler 2001). Distribution: Nicaragua to northwestern Costa Rica (Hasbún and Köhler 2001, 2009; Köhler and Hasbún 2001). Comment: this species appears to be sister to *C. oaxacana* (Hasbún et al. 2005). Fig. 25.

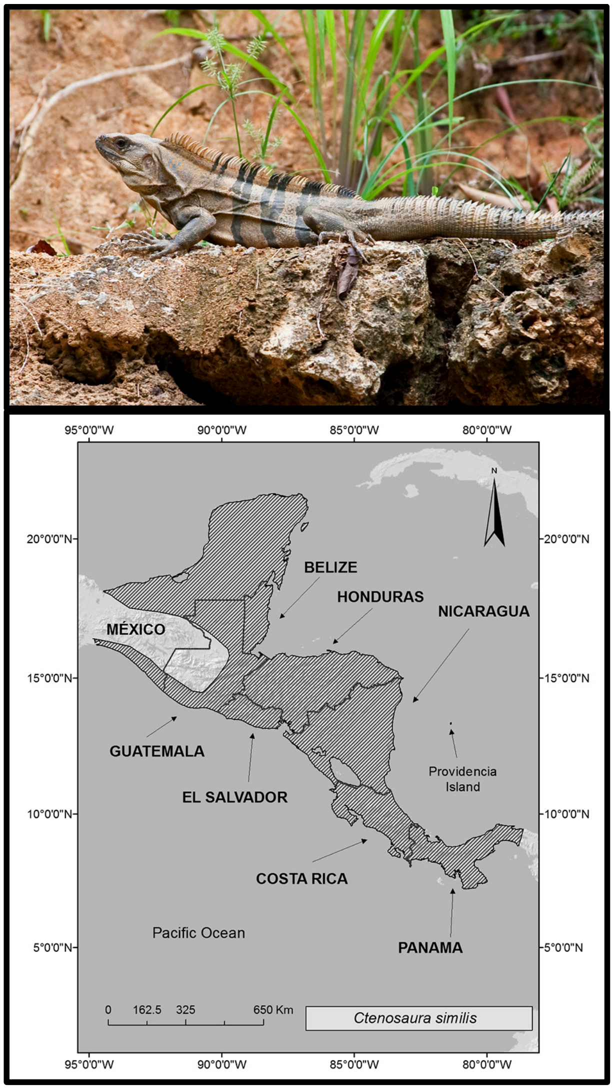


FIGURE 26. Common Spiny-tailed Iguana, *Ctenosaura similis* (Photographed by John Binns, Útila, Bay Islands, Honduras).

***Ctenosaura similis* (Gray) [Common Spiny-tailed Iguanas]**.—Other names: Iguanas de Roca, Sheros (Guatemala); Black Spiny-tailed Iguanas (IUCN. 2014. *op. cit.*); Garrobos Negros (Liner and Casas-Andreu 2008); Garrobos, Iguanas Negras (local names); Iguanas Rayadas (México); Black Iguana, Black Spinytail Iguana, Common Spinytail Iguana (Wrobel 2004). Original name: *Iguana (Ctenosaura) Similis* Gray 1830, *In* Griffith and Pidgeon, Cuvier's Animal Kingdom, London 9:38. Type: Mus. [of Mr.] Bell [number not given] (de Queiroz 1995), not located (Bailey 1928). Type locality: not given. Restricted type locality: "Tela, Honduras, Central America" (Bailey 1928), inappropriate restriction (de Queiroz 1995). Distribution: from the Isthmus de Tehuantepec southward through Central America on both versants to Panamá City and Colón, Panamá (de Queiroz 1995; Hollingsworth 2004). Introduced to south Florida, USA (Kraus 2009), and Maya Cay (off Roatán), Honduras (Stesha Pasachnik, pers. obs.), and the Berry Islands, The Bahamas (Knapp et al. 2011). Comment: preliminary phylogeographic studies (Pasachnik, Buckley, and Reynoso unpubl. data) have found considerable variation within this wide-ranging taxon; the name *Ctenosaura completa* Bocourt (type locality "Guatemala…. La Union [El Salvador]") is available if multiple species are recognized. Additional literature: Avery et al. (2014). Fig. 26.

***Ctenosaura similis similis* (Gray) [Common Spiny-tailed Iguanas]**.—Original name: *Iguana (Ctenosaura) Similis* (Gray 1830). See species account. Distribution: as for the species, excluding Isla de Providencia, Colombia.

***Ctenosaura similis multipunctata* Barbour and Shreve [Providence Spiny-tailed Iguanas]**.—Original name: *Ctenosaura similis multipunctata* Barbour and Shreve 1934, Occasional Papers of the Boston Society of Natural History 8:197. Holotype: MCZ 36830. Type locality: "Old Providence Island". Distribution: Isla de Providencia, Colombia (Barbour and Shreve 1934). Comment: given that the nominotypical subspecies occurs on nearby San Andrés Island (90 km distant), the validity of this subspecies should be re-evaluated.

CYCLURA HARLAN [ROCK IGUANAS]

Other names: Cyclures, Iguanes à cornes, Rhinoceros Iguanas (Wrobel 2004). Original name: *Cyclura* Harlan 1824, Journal of the Academy of Natural Sciences of Philadelphia 4:250. Type species (subsequent designation by Fitzinger 1843): *Cyclura carinata* Harlan 1824. Distribution: West Indies from The Bahamas through the Greater Antilles (Henderson and Powell 2009; Buckner et al. 2012). Comment: a well-resolved phylogenetic hypothesis was published by Malone et al. (2000).

Cyclura carinata **Harlan [Turks and Caicos Rock Iguanas]**.—Other names: Booby Cay Rock Iguanas (The Bahamas); Guanas (Turks and Caicos); Mayaguana Rock Iguana, Southern Bahamas Rock Iguana, Turks Island Iguana (Wrobel 2004). Original name: *Cyclura carinata* Harlan 1824, Journal of the Academy of Natural Sciences of Philadelphia 4:250. Type: not located (Etheridge 1982). Type locality: "Turk's Island." Distribution: Turks and Caicos Islands and Booby Cay off Mayaguana in The Bahamas (Henderson and Powell 2009; Buckner et al. 2012). Comment: Bryan et al. (2007) proposed sinking the previously recognized *Cyclura carinata bartschi* Cochran 1931 (from Booby Cay off Mayaguana in The Bahamas) based on the absence of diagnostic mtDNA haplotypes or morphological characters. Preliminary mitochondrial DNA data suggest that western populations in the Caicos Islands may be distinct from all other populations (Bryan et al. 2007; Mark Welsh, pers. comm.). This species is sister to *C. ricordii* (Malone et al. 2000). Additional literature: Reynolds (2011). Fig. 27.

Cyclura collei **Gray [Jamaican Rock Iguanas]**.—Other names: Jamaican Ground Iguanas (IUCN. 2014. *op. cit.*); Jamaican Iguanas (Jamaica); Jamaica Iguana (Wrobel 2004). Original name: *Cyclura Collei* Gray 1845, Catalogue of the Specimens of Lizards in the Collection of the British Museum, London: 190. Holotype: BMNH 1936.12.3.108. Type locality: "Jamaica." Distribution: Jamaica, currently restricted to the Hellshire Hills in the southeast (Henderson and Powell 2009). Comment: this species is sister to the clade comprising *C. cychlura*, *C. nubila*, *C. lewisi*, and *C. rileyi* (Malone et al. 2000). Additional literature: Wilson (2011); Wilson et al. (2016). Fig. 28.

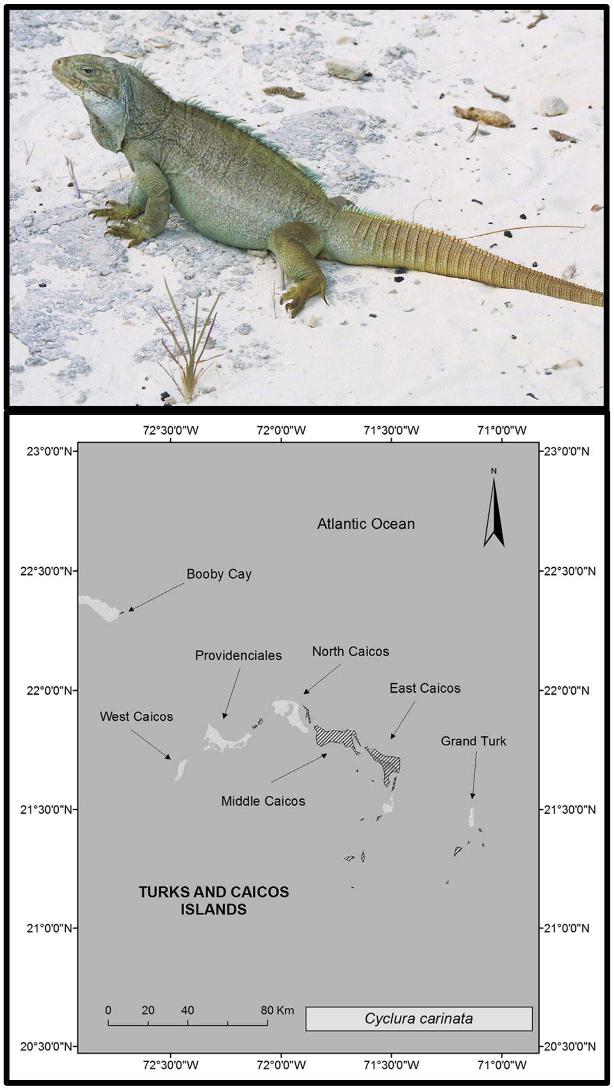


FIGURE 27. Turks and Caicos Rock Iguana, *Cyclura carinata* (Photographed by John Binns).

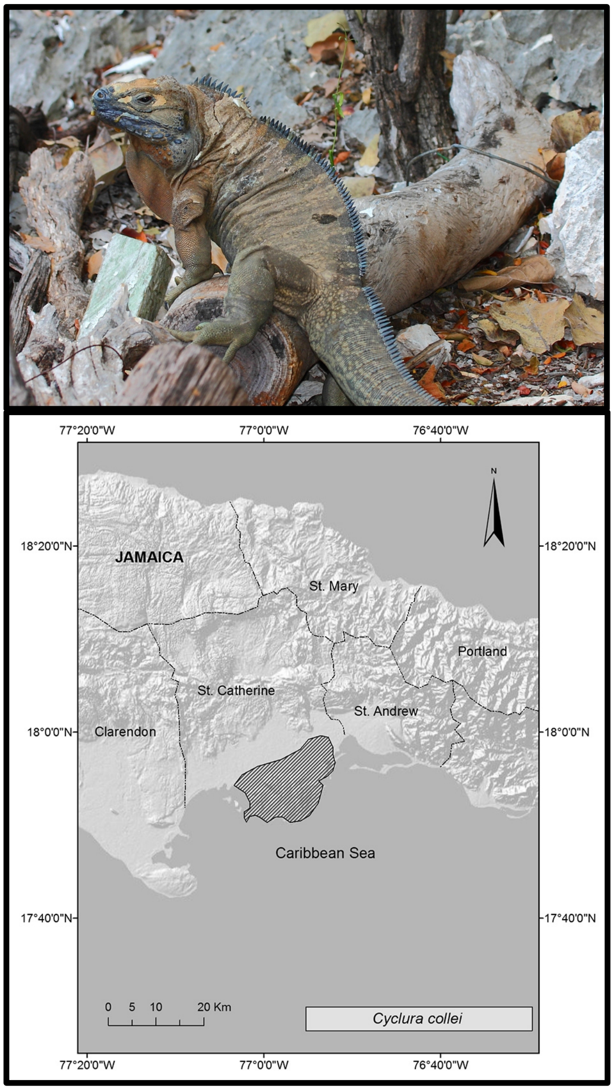


FIGURE 28. Jamaican Rock Iguana, *Cyclura collei* (Photographed by Joseph Burgess).

Cyclura cornuta **(Bonnaterre) [Hispaniolan Rhinoceros Iguanas]**.—Other names: Corned Iguana, Hispaniolan Rock Iguana, Iguane à cornes, Iguane cornu, Iguane rhinocéros, Rhinoceros Iguana, Rhinoceros Rock Iguana (Wrobel 2004). Original name: *Lacerta Cornuta* Bonnaterre 1789, Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature, Erpétologie, Paris: 40. Type: not located (Etheridge 1982). Type locality: "Sainte-Domingue…dans les mornes de l'hôpital, entre L'Artibonite and les Gonaives." Distribution: Hispaniola, including Isla Beata, Isla Saona, Île de la Gonâve, Île de la Petite Gonâve, Île Grande Cayemite, and Île de la Tortue (Henderson and Powell 2009). Comment: prior to 2000, most authors followed Schwartz and Carey (1977) and recognized *C. stejnegeri* from Mona Island and the extinct *C. onchiopsis* from Navassa Island as subspecies of *Cyclura cornuta*. That taxonomy has subsequently been followed by some authors (e.g., Malone et al. 2000; Pérez-Buitrago and Sabat 2007; Lemm and Alberts 2012, and references therein). However, Powell (1999), Glor et al. (2000), Powell and Glor (2000), Hollingsworth (2004), Henderson and Powell (2009), and Hedges (Hedges, S.B. 2015. Caribherp, Amphibians and Reptiles of Caribbean Islands. Available from http://www.caribherp.org [Accessed 15 September 2014]) have recommended recognizing all three taxa as species. We follow the latter taxonomy here, recognizing that Malone et al. (2000) found little difference (relative to other sister species comparisons) between the two living taxa based on mitochondrial DNA sequences. Fig. 29.

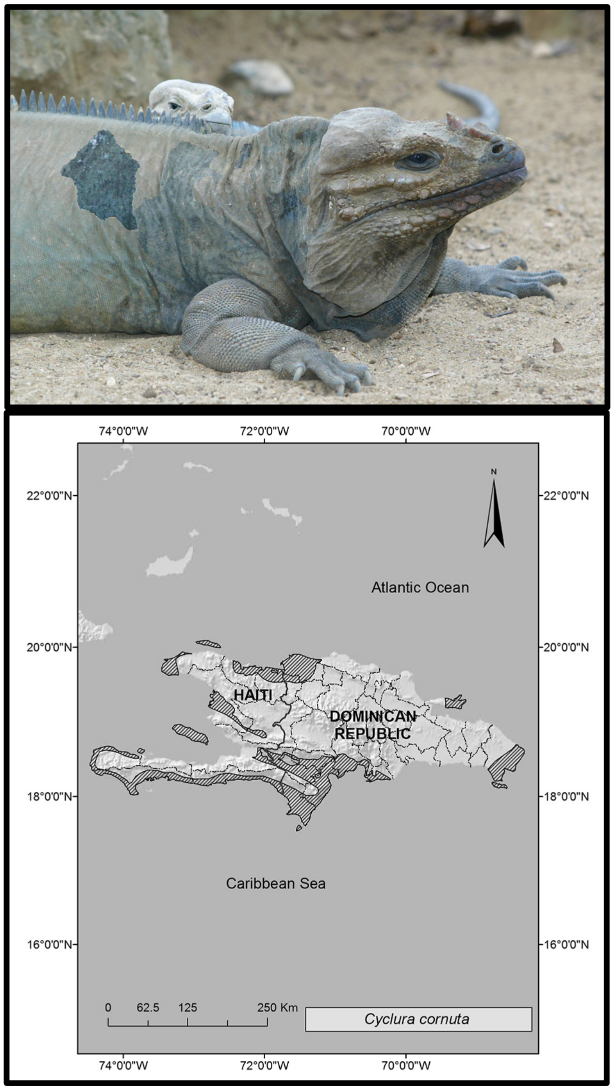


FIGURE 29. Hispaniolan Rhinoceros Iguana, *Cyclura cornuta* (Photographed by John Binns).

Cyclura cychlura **(Cuvier) [Northern Bahamian Rock Iguanas]**.—Other names: Allen Cays Rock Iguana, Exuma Island Ground Iguana, Northern Bahamas Rock Iguana (Wrobel 2004). Original name: *I.*[*guana*] *cychlura* Cuvier 1829, Le Règne Animal, Ed. 2, Paris 2:45. Holotype: MNHN 2367. Type locality: "Carolina." Corrected type locality: "Andros Island, Bahama Islands" (Schwartz and Thomas 1975). Distribution: Bahamas Archipelago, Great Bahama Bank on Andros Island (including North Andros, Mangrove Cay, and South Andros), and northern, central, and southern Exuma Islands (Henderson and Powell 2009). Fossils and archeological remains likely representing this species are known from New Providence (Pregill 1982) and Abaco (Steadman et al. 2014). Additional literature: Hines (2016).

Cyclura cychlura cychlura **(Cuvier) [Andros Rock Iguanas]**.—Original name: *I.*[*guana*] *cychlura* Cuvier. See species account. Distribution: Andros Island, The Bahamas (Henderson and Powell 2009). Fig. 30.

Cyclura cychlura figginsi **Barbour [Exuma Rock Iguanas]**.—Original name: *Cyclura figginsi* Barbour 1923, Proceedings of the New England Zoological Club 8:108. Holotype: MCZ 17745. Type locality: "Bitter Guana Cay, near Great Guana Cay, Exuma Group, Bahama Islands." Distribution: central and southern Exuma Islands, The Bahamas (Henderson and Powell 2009). Comment: genetic studies by Malone et al. (2000, 2003) found evidence for two phylogeographically distinct groups within *C. cychlura*: one corresponding to *C. cychlura cychlura* and the other to *C. cychlura figginsi* plus *C. cychlura inornata*, which were not clearly differentiated from one another. Further work is needed to clarify the status of the latter two taxa. Fig. 30.

Cyclura cychlura inornata **Barbour and Noble [Allen Cays Rock Iguanas]**.—Original name: *Cyclura inornata* Barbour and Noble 1916, Bulletin of the Museum of Comparative Zoology 60(4):151. Holotype: MCZ 11602. Type locality: "U Cay in Allan's Harbor, near Highborn Cay, Bahamas." Distribution: Allen Cays, Exuma Island group, The Bahamas (Henderson and Powell 2009); also introduced to several additional islands in the northern

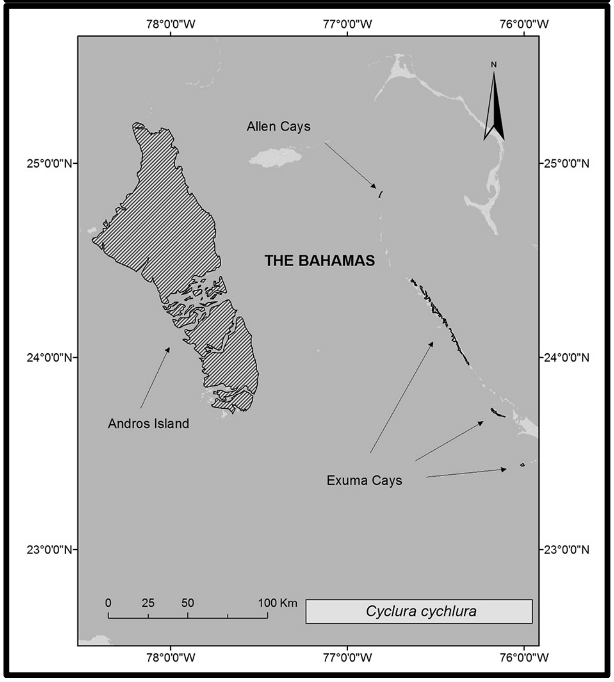


FIGURE 30. Andros Rock Iguana, *Cyclura cychlura cychlura* (top left; photographed by Joseph Burgess). Exuma Rock Iguana, *Cyclura cychlura figginsi* (top right; photographed by Charles Knapp). Allen Cays Rock Iguana, *Cyclura cychlura inornata* (middle; photographed by Charles Knapp).

Exumas, including Alligator Cay in the Exuma Cays Land and Sea Park (Knapp 2001). Comment: based on microsatellite data, Aplasca et al. (2016) identified significant differences between the two known natural populations of *C. cychlura inornata* on Leaf Cay and U Cay in the Allen Cays, but declined to make any taxonomic recommendations. Unfortunately, unauthorized movements of iguanas between these cays threaten their genetic integrity (Aplasca et al. 2016). Additional literature: Iverson et al. (2006); Smith and Iverson (2016). Fig. 30.

Cyclura lewisi **Grant [Grand Cayman Blue Rock Iguanas]**.—Other names: Blue Iguanas (Grand Cayman); Blue Rock Iguana, Grand Cayman Ground Iguana, Grand Cayman Iguana (Wrobel 2004). Original name: *Cyclura macleayi lewisi* Grant 1940, Bulletin of the Institute of Jamaica, Science Series 2:35. Holotype: BMNH 1939.2.3.68 = BMNH RR 1946.8.9.321 (Etheridge 1982). Type locality: "Battle Hill, east end of Grand Cayman." Distribution: Grand Cayman (Burton 2004; Henderson and Powell 2009; Echternacht et al. 2011). Comment: previously regarded as a subspecies of *Cyclura nubila* (Schwartz and Carey 1977), *C. lewisi* was considered a separate species by Burton (2004) based on morphological data as well as molecular data in Malone et al. (2000); however, additional study (including nuclear and mitochondrial genes) is sorely needed, and will require broad geographic sampling across Cuba (Starostová et al. 2010). Additional literature: Burton and Rivera-Milán (2014). Fig. 31.

Cyclura nubila **(Gray) [Clouded Rock Iguanas]**.—Other names: Iguanas (Cuba); Cayman Islands Ground Iguana, Cuban Ground Iguana, Cuban Iguana, Cuban Rock Iguana, Rock Iguana (Wrobel 2004). Original name: *Iguana (Cyclura) Nubila* Gray 1830, *In* Griffith and Pidgeon, Cuvier's Animal Kingdom, London 9:39. Holotype BMNH XXII. 8.a = 1946.8.29.88 (Etheridge 1982). Type locality: "South America?". Restricted type locality: "Cuba" (Schwartz and Thomas 1975). Distribution: Cuba, including many offshore islands; lesser Cayman Islands, including Cayman Brac and

Little Cayman (Henderson and Powell 2009; González Rossell et al. 2012). Introduced to Isla Magueyes off southwestern Puerto Rico (Kraus 2009). Comment: Starostová et al. (2010) have demonstrated that mitochondrial DNA haplotypes of Cuban *C. nubila* are diverse and paraphyletic relative to those from Cayman and Bahamian iguana populations currently recognized as different species (*lewisi* and *cychlura*).

Cyclura nubila nubila **(Gray) [Cuban Rock Iguanas]**.—Other names: Cuban Ground Iguanas, Cuban Iguanas (IUCN. 2014. *op. cit.*). Original name: *Iguana (Cyclura) Nubila* Gray. See species account. Distribution: Cuba (Henderson and Powell 2009; González Rossell et al. 2012). Introduced to Isla Magueyes off southwestern Puerto Rico (Kraus 2009). Additional literature: García and Gerber (2016); González et al. (2016). Fig. 32.

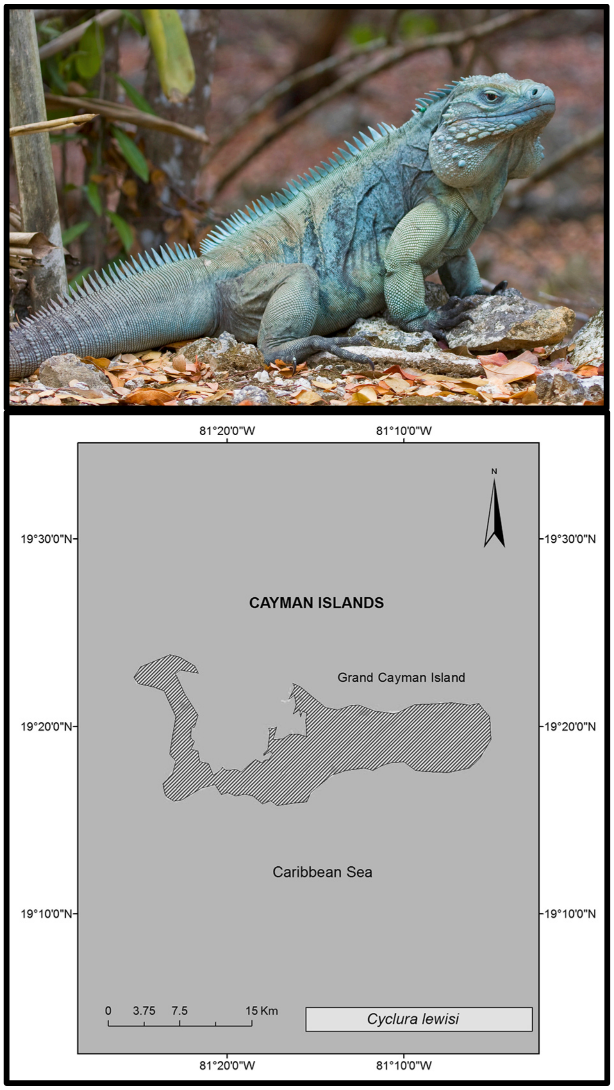


FIGURE 31. Grand Cayman Blue Rock Iguana, *Cyclura lewisi* (Photographed by John Binns).

Cyclura nubila caymanensis **Barbour and Noble [Sister Islands Rock Iguanas]**.—Other names: Sister Isles Rock Iguana (Cayman Islands); Cayman Islands Ground Iguanas, Lesser Caymans Rock Iguanas (IUCN.

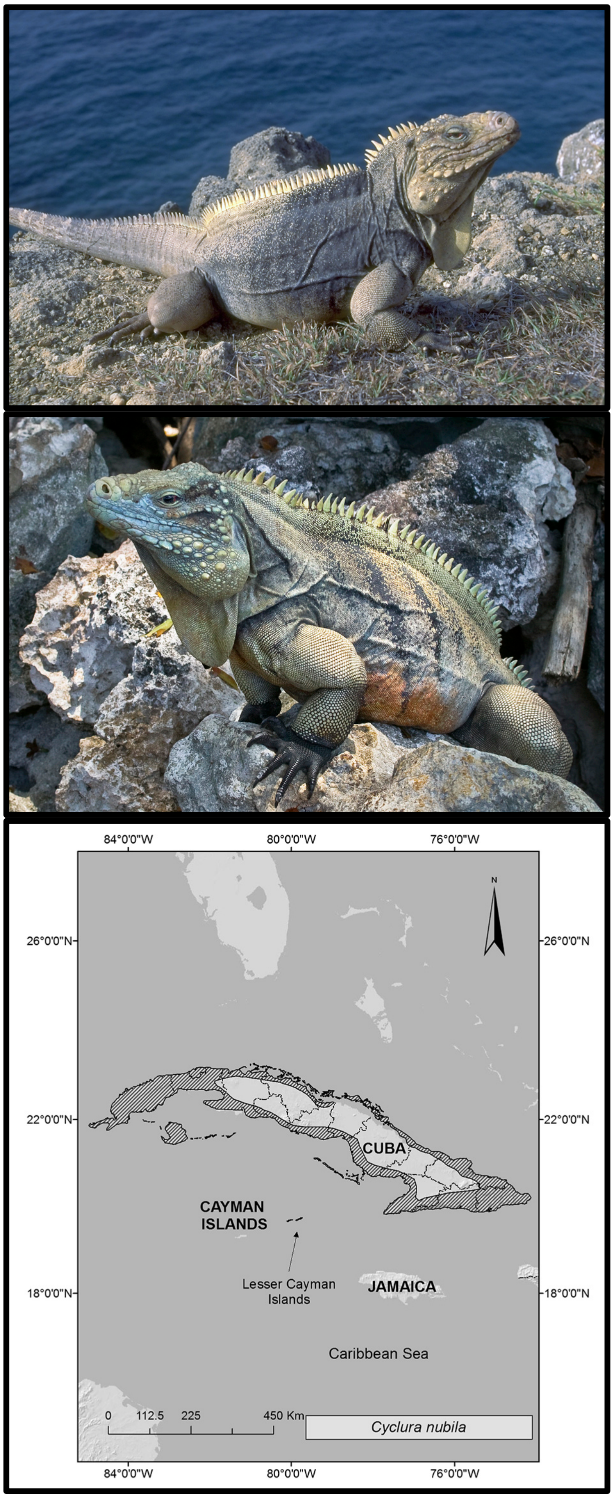


FIGURE 32. Cuban Rock Iguana, *Cyclura nubila nubila* (top; photographed by Allison Alberts, Guantánamo Bay, Cuba). Sister Islands Rock Iguana, *Cyclura nubila caymanensis* (middle; photographed by John Binns).

2014. *op. cit.*); Sister Isles Iguanas (Lemm and Alberts 2012). Original name: *Cyclura caymanensis* Barbour and Noble 1916, Bulletin of the Museum of Comparative Zoology 60(4):148. Holotype: MCZ 10534. Type locality: "Cayman Islands, probably Cayman Brac." Distribution: Cayman Brac and Little Cayman Islands (Henderson and Powell 2009). Comment: relative to the nominotypical subspecies, *caymanensis* is allopatric and diagnosable (Schwartz and Carey 1977); without explanation, Echternacht (2012) recognized it as a separate species from *C. nubila.* We retain it as a subspecies pending further study. Additional literature: Goetz (2008). Fig. 32.

***Cyclura onchiopsis*†** **Cope [Navassa Rhinoceros Iguanas]**.—Other names: Navassa Island Iguanas, Navassa Rock Iguanas (IUCN. 2014. *op. cit.*). Original name: *C.[yclura] onchiopsis* Cope 1885, American Naturalist 19:1006. Syntypes: USNM 9977, 12239, MCZ 4717. Type locality: "from an unknown locality." Restricted type locality: "Island of Navassa" (Cope 1886). Distribution: Navassa Island, off the southwest coast of Hispaniola (Powell 2000), but now extinct (Powell 1999; Henderson and Powell 2009). Comment: see Comment for *C. cornuta*. Sequencing of DNA from the type series of *C. onchiopsis* would be helpful for determining relationships within the *Cyclura cornuta* species group (including *C. onchiopsis* and *C. stejnegeri*). Fig. 33.

Cyclura pinguis **Barbour [Anegada Rock Iguanas]**.—Other names: Stout Iguana (García and Gerber 2016); Anegada Ground Iguanas (IUCN. 2014. *op. cit.*). Original name: *Cyclura pinguis* Barbour 1917, Proceedings of the Biological Society of Washington 30:100. Holotype: MCZ 12082. Type locality: "Anegada, British Virgin Islands." Distribution: Anegada Island (Henderson and Powell 2009); formerly occurred on Puerto Rico and Saint Thomas (Pregill 1981).

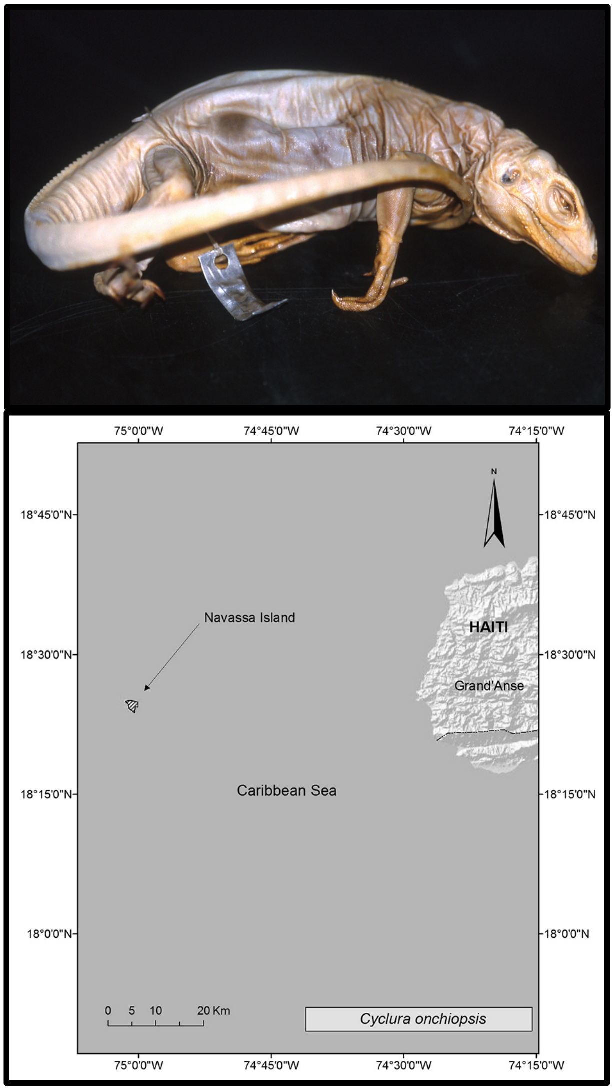


FIGURE 33. Navassa Rhinoceros Iguana, *Cyclura onchiopsis* (Photographed by Robert Powell).

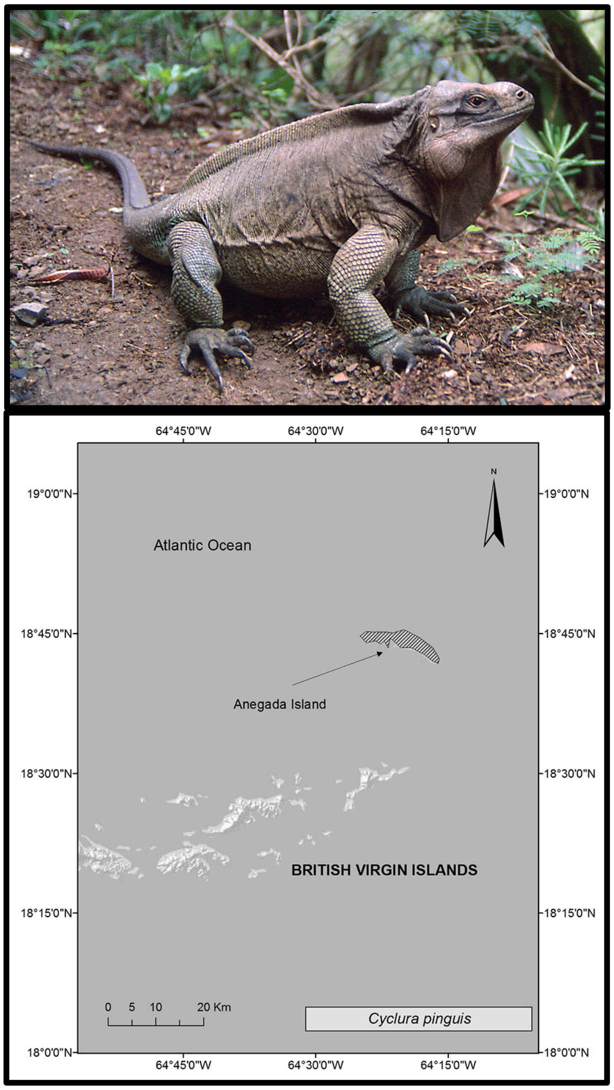


FIGURE 34. Anegada Rock Iguana, *Cyclura pinguis* (Photographed by Glenn Mitchell).

Introduced: Guana, Little Thatch, Moskito, Necker, and Norman Islands, British Virgin Islands (Anonymous 2004; Perry and Gerber 2006, 2011; Perry and Powell 2009). Comment: this species is sister to all other *Cyclura* (Malone et al. 2000). Additional literature: García and Gerber (2016). Fig. 34.

Cyclura ricordii **(Duméril and Bibron) [Ricord's Rock Iguanas]**.—Other names: Cyclures de Hispaniola, Cyclures de Ricord, Las Iguanas Ricordi, Ricord's Ground Iguanas (IUCN. 2014. *op. cit.*); Banded Rock Agama (Wrobel 2004). Original name: *Aloponotus Ricordii* Duméril and Bibron 1837, Erpétologie Génerale, Paris 4:190. Holotype: MNHN 8304. Type locality: "Sainte-Domingue." Distribution: Southwestern Dominican Republic (Valle de Neiba and the Peninsula de Barahona), and southeastern Haiti (Henderson and Powell 2009; Rupp and Accimé 2011). Comment: this species is sister to *C. carinata* (Malone et al. 2000). Fig. 35.

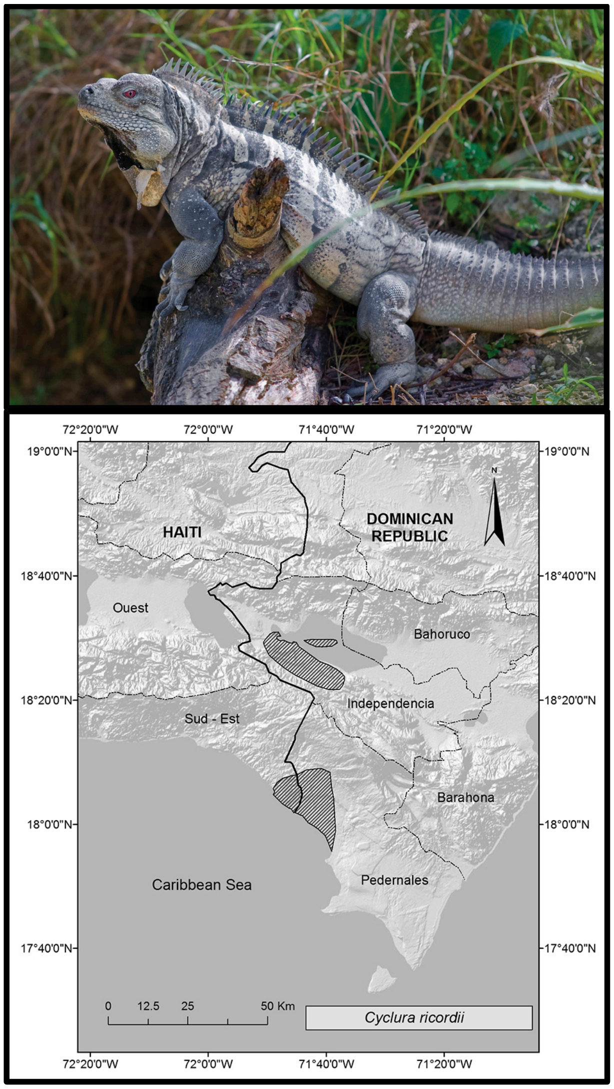


FIGURE 35. Ricord's Rock Iguana, *Cyclura ricordii* (Photographed by John Binns).

Cyclura rileyi **Stejneger [Central Bahamian Rock Iguanas]**.—Other names: Central Bahamas Rock Iguana, Watling Island Ground Iguana, White Cay Ground Iguana (Wrobel 2004). Original name: *Cyclura rileyi* Stejneger 1903, Proceedings of the Biological Society of Washington 16:130. Holotype: USNM 31969. Type locality: "Watlings Island, Bahamas." Distribution: Bahamas Archipelago, San Salvador and adjacent Cays, in the extreme southern Exumas on Sandy (= White) Cay, and in the Acklins Cays on Fish and North Cays (Henderson and Powell 2009). Comment: Malone et al. (2000) found no variation in one segment of mitochondrial DNA, which was polymorphic in other *Cyclura*, among the currently recognized subspecies of *C. rileyi*; further work is needed to test their validity. This species is sister to the clade comprising *C. cychlura*, *C. lewisi*, and *C. nubila* (Malone et al. 2000).

Cyclura rileyi rileyi **Stejneger [San Salvador Rock Iguanas]**.—Other name: Watling Island Iguanas (IUCN. 2014. *op. cit.*). Original name: *Cyclura rileyi* Stejneger. See species account. Distribution: San Salvador and nearby islands, The Bahamas (Henderson and Powell 2009; Buckner et al. 2012). Additional literature: Hayes et al. (2016a). Fig. 36.

Cyclura rileyi cristata **Schmidt [Sandy Cay Rock Iguanas]**.—Other name: White Cay Rock Iguanas (IUCN. 2014. *op. cit.*). Original name: *Cyclura cristata* Schmidt 1920, Proceedings of the Linnaean Society of New York 33:6. Holotype: AMNH 7238. Type locality: "White Cay [Exuma Islands], Bahama Islands". Distribution: known only from the type locality (Henderson and Powell 2009). Additional literature: Hayes et al. (2016b). Fig. 36.

Cyclura rileyi nuchalis **Barbour and Noble [Acklins Rock Iguanas]**.—Original name: *Cyclura nuchalis* Barbour and Noble 1916, Bulletin of the Museum of Comparative Zoology 60(4):156. Holotype: ANSP 11985. Type locality: "Fortune Island [= Long Cay off Crooked Island in the Acklins Islands], Bahamas." Distribution: Fish Cay and North Cay in the Acklins Islands, The Bahamas, but no longer found on Long Cay (Hayes et al. 2004); introduced to Bush Hill Cay in the Exuma Cays Land and Sea Park (Hayes et al. 2004; Buckner et al. 2012). Additional literature: Iverson et al. (2016). Fig. 36.

Cyclura stejnegeri **Barbour and Noble [Mona Rhinoceros Iguanas]**.—Other names: Mona Iguanas, Mona Island Iguanas (Puerto Rico); Mona Rock Iguana (Wrobel 2004). Original name: *Cyclura stejnegeri* Barbour and Noble 1916, Bulletin of the Museum of Comparative Zoology 60(4):163. Holotype: USNM 29367. Type locality: "Mona Island." Distribution: Isla Mona, situated

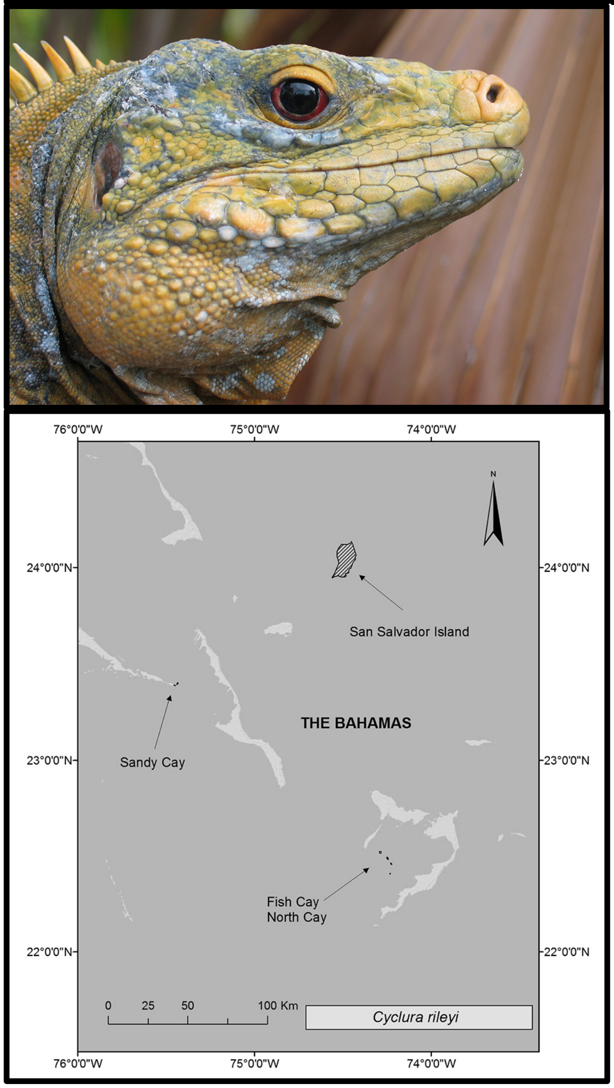


FIGURE 36. San Salvador Rock Iguana, *Cyclura rileyi rileyi* (top left; photographed by Charles Knapp). Sandy Cay Rock Iguana**,** *Cyclura rileyi cristata* (top right; photographed by Joseph Wasilewski). Acklins Rock Iguana, *Cyclura rileyi nuchalis* (middle; photographed by John Iverson, Bush Hill Cay, Exumas, The Bahamas).

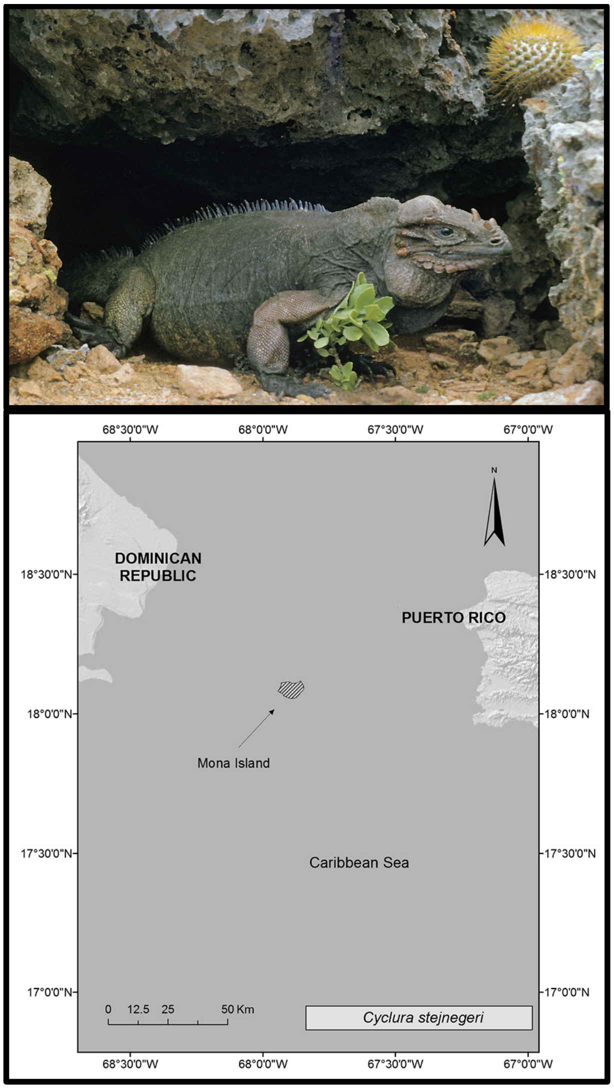


FIGURE 37. Mona Rhinoceros Iguana, *Cyclura stejnegeri* (Photographed by Thomas Wiewandt).

between Hispaniola and Puerto Rico (Henderson and Powell 2009). Comment: see Comment for *C. cornuta*. Additional literature: Perotto-Baldivieso et al. (2009); García and Gerber (2016); Pérez-Buitrago et al. (2016). Fig. 37.

DIPSOSAURUS HALLOWELL [DESERT IGUANAS]

Other names: Crested Lizards, Dipsosaures (Wrobel 2004). Original name: *Dipso-saurus* Hallowell 1854, Proceedings of the Academy of Natural Sciences of Philadelphia 7:92. Type species (by monotypy): *Crotaphytus dorsalis* Baird and Girard 1852. Distribution: Southwestern United States to northwestern México, including Baja California (Hollingsworth 2004). Comment: a detailed phylogeographic study of *Dipsosaurus* is needed.

Dipsosaurus catalinensis **Van Denburgh [Santa Catalina Desert Iguanas]**.—Other name: Cachorónes de Isla Santa Catalina (Liner and Casas-Andreu 2008). Original name: *Dipsosaurus catalinensis* Van Denburgh 1922, Occasional Papers of the California Academy of Sciences 10(1):83. Holotype: CAS 50505. Type locality: "Santa Catalina Island, Gulf of California, Mexico." Distribution: Isla Santa Catalina, Baja California Sur, México (Grismer 1999a, b). Comment: formerly considered a subspecies of *D. dorsalis* (Soulé and Sloan 1966) this taxon was recognized as a species by Grismer (1999b). Fig. 38.

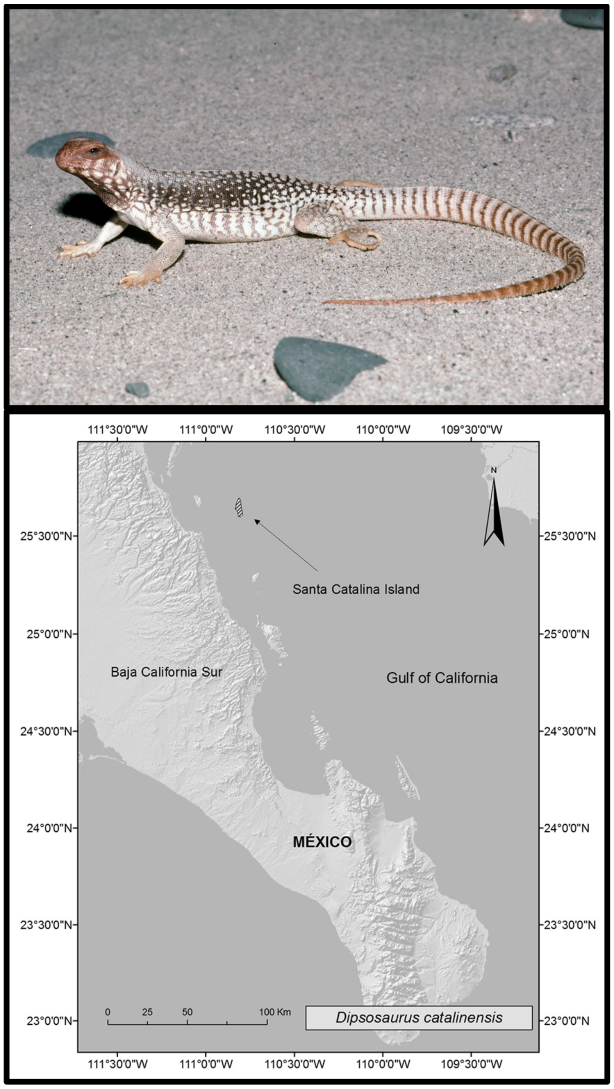


FIGURE 38. Santa Catalina Desert Iguana, *Dipsosaurus catalinensis* (Photographed by Lee Grismer).

Dipsosaurus dorsalis **(Baird and Girard) [Common Desert Iguanas]**.—Other names: Cachorónes Güero (Liner and Casas-Andreu 2008); Desert Iguana, Dipsosaure du desert, Iguane du désert, Keeled-back Iguana, Northern Crested Lizard, Pygmy Iguana (Wrobel 2004). Original name: *Crotaphytus dorsalis* Baird and Girard 1852, Proceedings of the Academy of Natural Sciences of Philadelphia 6:126. Holotype: USNM 2699 (Cochran 1961). Type locality: "Desert of Colorado, Cal.[ifornia]". Restricted type locality: "Winterhaven (= Fort Yuma), Imperial County", California (Smith and Taylor 1950), without justification (de Queiroz 1995). Distribution: Southwestern United States (in southern Nevada, southwestern Utah, southeastern California, and western Arizona), southward to northwestern México (in western Sonora and northwestern Sinaloa), the peninsula of Baja California, and islands of the Gulf of California (Hollingsworth 2004).

Dipsosaurus dorsalis dorsalis **(Baird and Girard) [Western Desert Iguanas]**.—Other names: Iguanas del Desierto (Liner and Casas-Andreu 2008); Desert Iguana, Northern Desert Iguana (Wrobel 2004). Original name: *Crotaphytus dorsalis* Baird and Girard. See species account. Distribution: Southwestern United States in southeastern California, southern Nevada, extreme southwestern Utah, and western Arizona; México in northwestern Sonora and Baja California east of the Sierra de Juárez and Sierra San Pedro Mártir south to the end of the peninsula, as well as the islands of Encantada Grande Ángel de la Guarda, San Marcos, Coronado, Carmen, Monserrate, San José, Espíritu Santo, and Cerralvo in the Gulf of California, and the islands of Magdalena and Santa Margarita in the Pacific Ocean (de Queiroz 1995). Comment: includes *D. carmenensis* VanDenburgh 1922 (according to Soulé and Sloan 1966) and *D. dorsalis lucasensis* (according to Grismer et al. 1994). Fig. 39.

Dipsosaurus dorsalis sonoriensis **Allen [Sonoran Desert Iguanas]**.—Other name: Iguana del Desierto Sonora (Liner and Casas-Andreu 2008). Original name: *Dipso-saurus dorsalis sonoriensis* Allen 1933, Occasional Papers of the Museum of Zoology, University of Michigan 259:4. Holotype: UMMZ 72121. Type locality: "Hermosillo, Sonora, Mexico." Distribution: Western Sonora from at least as far north as Puerto (30°11'N) southward to extreme northwestern Sinaloa (Bahía de Topolobampo), México (de Queiroz 1995). Fig. 39.

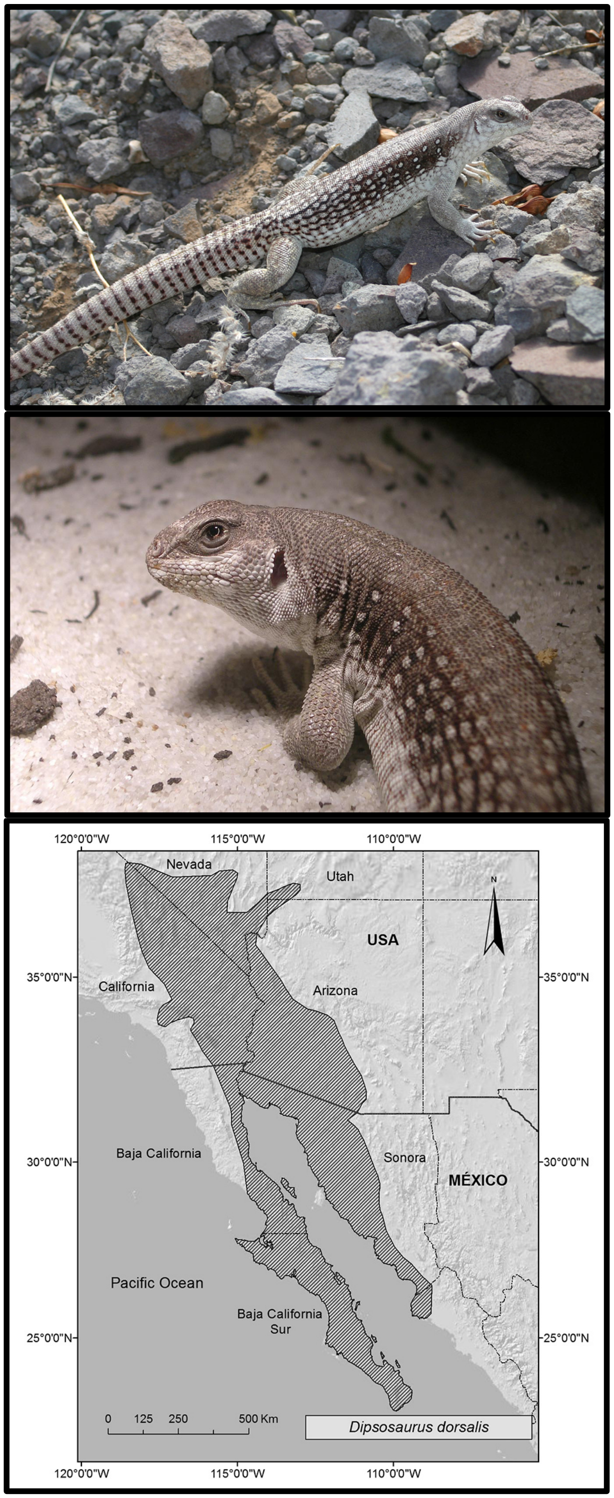


FIGURE 39. Western Desert Iguana, *Dipsosaurus dorsalis dorsalis* (top; Eastern Arizona, USA). Sonoran Desert Iguana, *Dipsosaurus dorsalis sonoriensis* (middle; both photographs by Joseph Burgess).

IGUANA LAURENTI [GREEN IGUANAS]

Other name: Common Iguanas (Wrobel 2014). Original name: *Iguana* Laurenti 1768, Specimen Medicum, Exhibens Synopsin Reptilium, Wein: 47. Type species (by tautonymy): *Lacerta iguana* Linnaeus 1758. Distribution: Northeastern México to Brazil and the Lesser Antilles (Lazell 1973; Henderson and Breuil 2012). Comment: a preliminary phylogenetic hypothesis of *Iguana* populations appeared in Malone and Davis (2004), and Stephen et al. (2013) presented evidence that *I. iguana* and *I. delicatissima* are reciprocally monophyletic.

Iguana delicatissima **Laurenti [Lesser Antillean Iguanas]**.—Other names: Lezas (Guadeloupe); Iguanes de Petites Antilles (IUCN. 2014. *op. cit.*); Iguanes Délicat (Lesser Antilles); Lizas (Martinique); Groene Leguaanes (Saba and Bonaire); Antillean Iguana, Iguane des Antilles, Iguane tuberculeux, Lesser Antillean Green Iguana, West Indian Iguana (Wrobel 2014). Original name: *Iguana delicatissima* Laurenti 1768, Specimen Medicum, Exhibens Synopsin Reptilium, Wein: 48. Holotype: assumed by Lazell (1973) and Etheridge (1982) to be in the Musei di Zoologia e Anatomia Comparata, Torino, but never located; however, Michel Breuil (pers. comm.) reported that Laurenti's material was actually in the collection of the Comte [Count] de Turn in Vienna and is now lost. Type locality: "Indiis." Restricted type locality: "island of Terre de Bas, Les Iles de Saintes, Département de la Guadaloupe, French West Indies" (Lazell 1973). Distribution: Lesser Antilles from: Anguilla; Saint-Martin/Sint Maarten (extirpated); Saint Barthélemy, including Île Fourchue and its satellites (Îlet au Vent and Petite Islette), Îlet Frégate [probably extirpated] and Îlet Chevreau (or Bonhomme) [probably extirpated]; St. Eustatius; Antigua (extirpated) and Barbuda (extirpated); St. Kitts (extirpated) and Nevis (extirpated); Guadeloupe (including Grande-Terre [likely extirpated via hybridization], Basse Terre, La Désirade, Îles de la Petite Terre, Les Îles des Saintes [likely extirpated via hybridization], and Marie-Galante [extirpated]); Dominica; and Martinique (including Îlet Chancel and Îlet à Ramiers [introduced]) (Pasachnik et al. 2006; Henderson and Powell 2009; Breuil et al. 2010; Powell and Henderson 2012). Comment: although Laurenti's (1768) diagnosis of *Iguana delicatissima* distinguishes that taxon from *I. iguana*, the plates in Seba associated with that description are of *Iguana iguana*, or in the case of Fig. 95.5, a hybrid between *I. iguana* and *I. delicatissima* (Pasachnik et al. 2006; Breuil 2013). See also Comment under *Iguana iguana*. This species is known to hybridize with *I. iguana* (Breuil 2013). Additional literature: Breuil (2011); Hodge et al. (2011); Lorvelec et al. (2011); Malhotra et al. (2011); Powell (2011); Knapp et al. (2016). Fig. 40.

***Iguana iguana* (Linnaeus) [Common Green Iguanas]**.— Other names: Iguanas Verdes, Iguanes Communes, Iguanes Vert (local names, throughout range); Garrobos (local name for males, various parts of range); Guachos (Costa Rica); Iguanas de Agua, Iguanas Doradas, Shilianas (Guatemala); Iguanas de Ribera (Liner and Casas-Andreu 2008); Gallinas de Palo (Panamá); Gwo Zandolois, Kwéyòl, Lézas (Saint Lucia); Common Iguana, Green Iguana, Green Mexican Iguana, Iguane vrai (Wrobel 2014). Original name: *Lacerta iguana* Linnaeus 1758, Systemya Naturae, Ed. 10, Stockholm 1:206. Syntypes: NHRM [one specimen, no number given]; ZMUU [one specimen, no number given] (Lönnberg 1896; Andersson 1900; Hoogmoed 1973; de Queiroz 1995). Type locality: "Indiis." Restricted type locality: "island of Terre de Haut, Les Iles des Saintes, Département de la Guadeloupe, French West Indies" (Lazell 1973), inappropriate restriction (de Queiroz 1995); "confluence of the Cottica River and Perica Creek, Surinam" (Hoogmoed 1973); however, Duellman (2012) argued that the type locality was most likely the "vicinity of Paramaribo, Surinam". Distribution: Northern México, from Sinaloa and Veracruz, southward through Central America and into northeastern South America to the Tropic of Capricorn in Paraguay and southeastern Brazil. The species also occurs on numerous islands, including Cozumel, Útila, Roatán, Guanaja, the Corn Islands, Providencia, San Andres, Aruba, Trinidad, Tobago, and others in the Lesser Antilles (Henderson and Powell 2009). It has been introduced to Anguilla, Antigua, Barbuda, British Virgin Islands, Canary Islands, Cayman Islands, Dominican Republic, Fiji, Guadeloupe, Japan, Marie Galante, Martinique, Puerto Rico, Saint-Martin/Sint Maarten, The Bahamas, U.S. Virgin Islands, and the USA (Florida, Hawaii) (Kraus 2009; Henderson and Powell 2009; Lindsay and Mussington 2009; Harlow and Thomas 2010; Hailey et al. 2011; Thomas et al. 2011; Arce-Nazario and Carlo 2012; Falcón et al. 2012, 2013; Pasachnik et al.

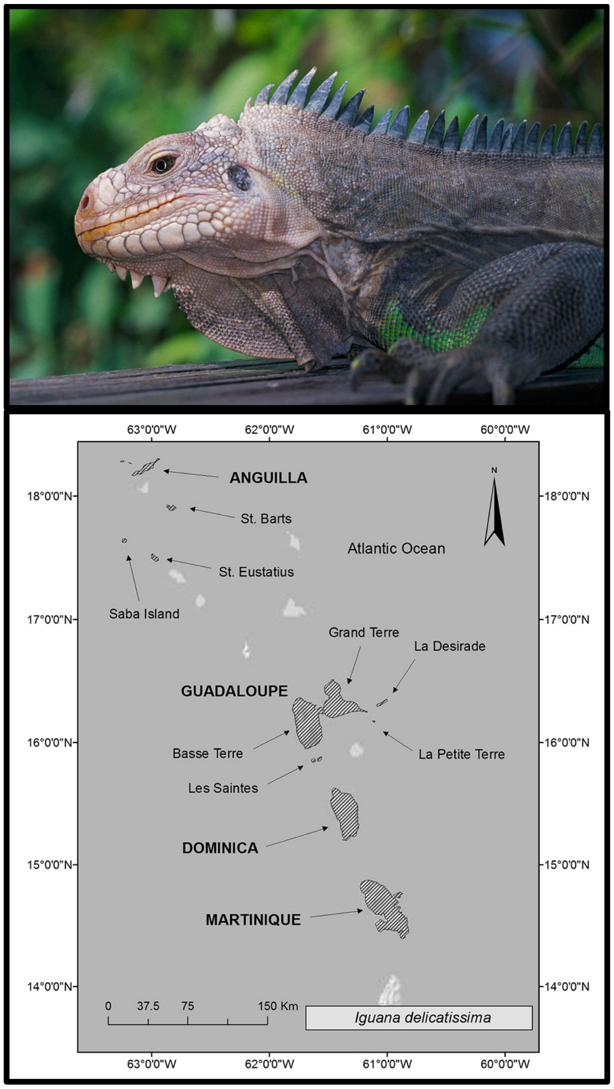


FIGURE 40. Lesser Antillean Iguana, *Iguana delicatissima* (Photographed by Robert Powell, St. Eustatius).

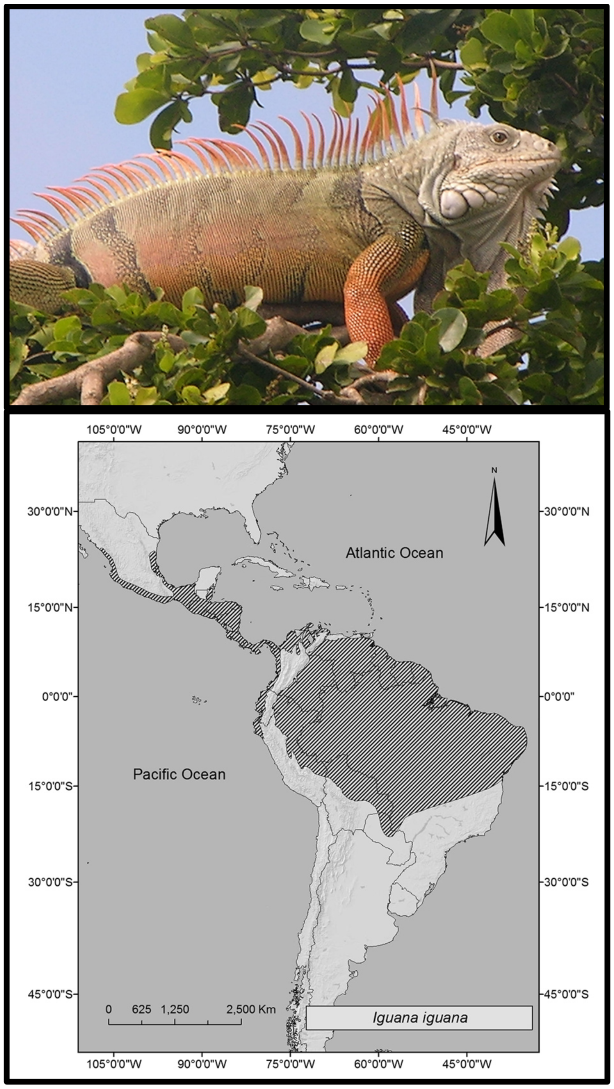


FIGURE 41. Common Green Iguana, *Iguana iguana* (Photographed by Steve Conners).

2012a; Powell and Henderson 2012). Comment: although Lazell (1973) synonymized the formerly recognized subspecies *I. iguana iguana* (South America) and *I. iguana rhinolopha* (Central America), Breuil (2013) argued for their recognition. Based on mitochondrial and nuclear DNA data, Stephen et al. (2013) recognized two well-supported genetic groups as evolutionarily significant units: Central America (México to Panamá) and South America (including Curaçao and the Lesser Antilles), but they declined to propose any taxonomic changes pending further sampling across Panamá and South America. Should the two groups be recognized as separate species, the name *I. iguana* would apply to the South American populations, and Wiegmann's (1834) name *rhinolophus(a)* (presumably from México: Etheridge 1982; de Queiroz 1995) is available for the Central American and Mexican populations. Finally, based on morphological comparisons, Breuil (2013) demonstrated significant differences among populations on St. Lucia, Saba, and mainland South America, but did not propose any taxonomic changes. Additional literature: López-Torres et al. (2011); Bock et al. (2016). Fig. 41.

SAUROMALUS DUMÉRIL [CHUCKWALLAS]

Original name: *Sauromalus* Duméril 1856, Archives du Museum d'Histoire Naturelle, Paris 8:535. Type species (by monotypy): *Sauromalus ater* Duméril 1856. Distribution: Southwestern United States and northwestern México. Comment: although several phylogenetic hypotheses for Chuckwalla populations have been published (Petren and Case 1997, 2002; Hollingsworth 1998), there are significant differences among them.

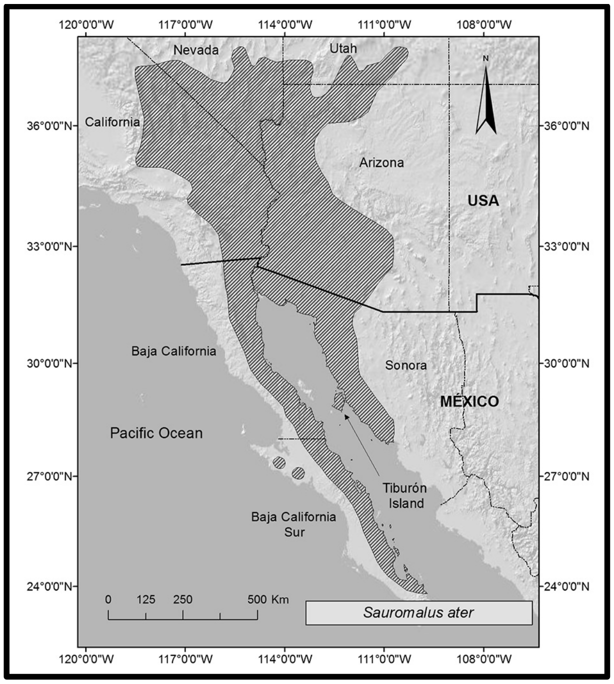


FIGURE 42. Common Chuckwalla, *Sauromalus ater* (Photographed by Bradford Hollingsworth; top: Joshua Tree National Park, California, USA; second row: Baja California Sur, México; third row: Mountain Spring, Imperial County, California, USA; bottom: Sonora, México).

Sauromalus ater **Duméril [Common Chuckwallas]**.— Other names: Northern Chuckwallas (IUCN. 2014. *op. cit.*); Cachorónes de Roca (Liner and Casas-Andreu 2008); Peninsula Chuckwalla (*S. australis*), Glen Canyon Chuckwalla (*S. obesus multiforminatus*), Great Basin Chuckwalla and Western Chuckwalla (*S. obesus obesus*), Arizona Chuckwalla (*S. obesus tumidus*) (Wrobel 2004). Original name: *Sauromalus ater* Duméril 1856, Archives du Museum d'Histoire Naturelle, Paris 8:536. Holotype: MNHN 813. Type locality: not given. Restricted type locality: "one of the following islands in the Gulf of California: Espíritu Santo, Isla Partida, San Marcos, San Diego, Santa Cruz, or San Francisco" (Shaw 1945); further restricted to "Espíritu Santo Island" (Smith and Taylor 1950), without justification (de Queiroz 1995), and "southern coastal Sonora" (Hollingsworth 1998; but see Montanucci 2000); further restricted to "the vicinity of Guaymas Bay" (Montanucci 2008). Distribution: Southwestern United States (in southern Nevada, southwestern Utah, southeastern California, and western Arizona), southward to northwestern México (in western Sonora), the peninsula of Baja California, and the following islands in the Gulf of California: Alcatraz (possibly introduced), Ballena, El Coyote, Espíritu Santo, Gallo, Partida Sur, San Cosme, San Diego, San Francisco, San Jose, San Marcos, Santa Cruz, Tiburon, and Willard (Hollingsworth 1998) and Isla Párajos across from Guaymas Bay (Ventura-Trejo et al. 2008). Comment: Hollingsworth (1998) synonymized the names *Sauromalus ater* and *S. obesus*, and applied the name *ater* to the species. Although the International Commission on Zoological Nomenclature (ICZN) was petitioned to suppress the name *ater* in favor of *obesus* (Montanucci et al. 2001), that petition was rejected by the ICZN (2004). Petren and Case (2002) suggested the possibility that *Sauromalus ater* (as currently recognized) is composed of multiple species. Fig. 42.

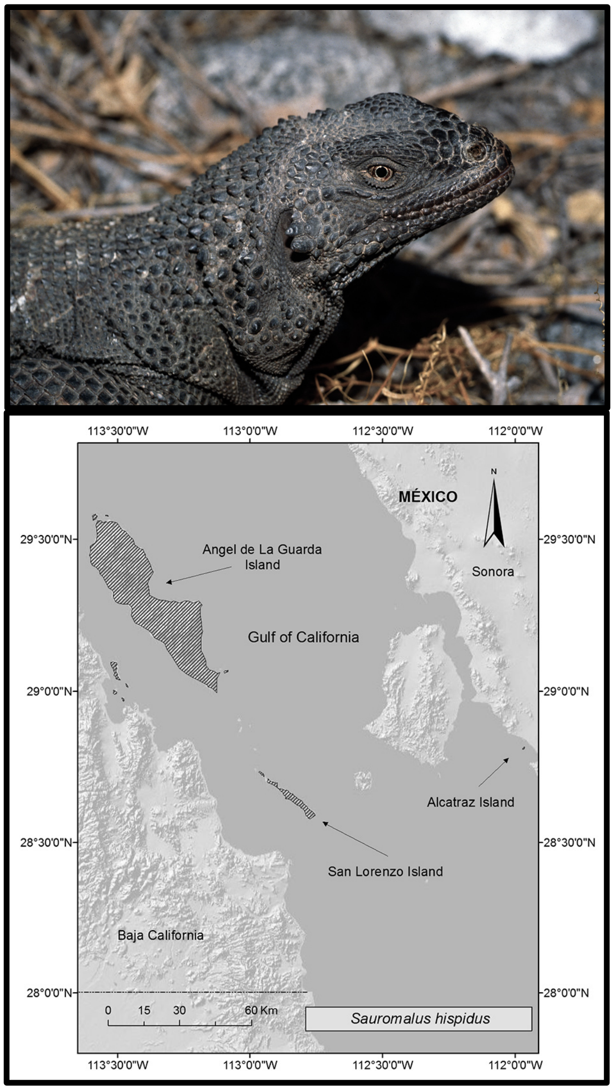


FIGURE 43. Spiny Chuckwalla, *Sauromalus hispidus* (Photographed by Bradford Hollingsworth; Isla San Lorenzo Sur, Baja California, México).

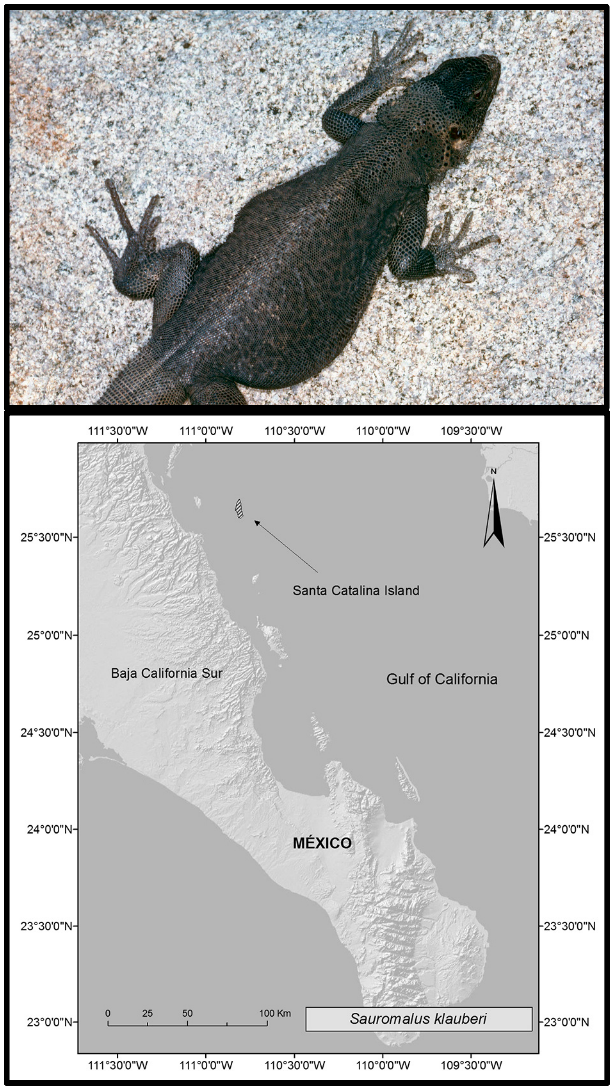


FIGURE 44. Catalina Chuckwalla, *Sauromalus klauberi* (Photographed by Bradford Hollingsworth).

Sauromalus hispidus **Stejneger [Spiny Chuckwallas]**.—Other names: Black Chuckwallas (IUCN. 2014. *op. cit.*); Iguanas Espinosas de Pared (Liner and Casas-Andreu 2008). Original name: *Sauromalus hispidus* Stejneger 1891, Proceedings of the United States National Museum 14(864):409. Holotype: USNM 8563. Type locality: "Angel de la Guardia [Guarda] Island, Gulf of California." Distribution: the islands of Angel de La Guarda, Granito, Mejía, Pond, San Lorenzo Norte, San Lorenzo Sur, numerous islands in Bahía de Los Ángeles, and Alcatraz Island (possibly introduced), Gulf of California, México (Hollingsworth 1998). A single specimen has been reported from Isla Rasa (Velarde et al. 2008). Fig. 43.

Sauromalus klauberi **Shaw [Catalina Chuckwallas]**.—Other names: Iguanas de Pared Manchada (sic: Liner and Casas-Andreu 2008; Iguanas Manchadas de Pared); Klauber's Chuckwalla, Spotted Chuckwalla (Wrobel 2004). Original name: *Sauromalus klauberi* Shaw 1941, Transactions of the San Diego Society of Natural History 9(28):285. Holotype: SDNHM 6859. Type locality: "Santa Catalina Island, Gulf of California, Mexico." Distribution: Isla Santa Catalina, Baja California Sur, México (Hollingsworth 1998). Fig. 44.

Sauromalus slevini **Van Denburgh [Slevin's Chuckwallas]**.—Other names: Iguanas de Pared de Monserrat (Liner and Casas-Andreu 2008); Monserrat Chuckwalla (Wrobel 2004). Original name: *Sauromalus slevini* Van Denburgh 1922, Occasional Papers of the California Academy of Sciences 10(1):97. Holotype: CAS 50503. Type locality: "South end of Monserrate Island, Gulf of California, Mexico." Distribution: Islas Carmen, Danzante, Los Coronados, and Monserrate, Baja California Sur, México (Hollingsworth 1998; Murphy and Aguirre-Léon 2002; Montanucci 2004). Fig. 45.

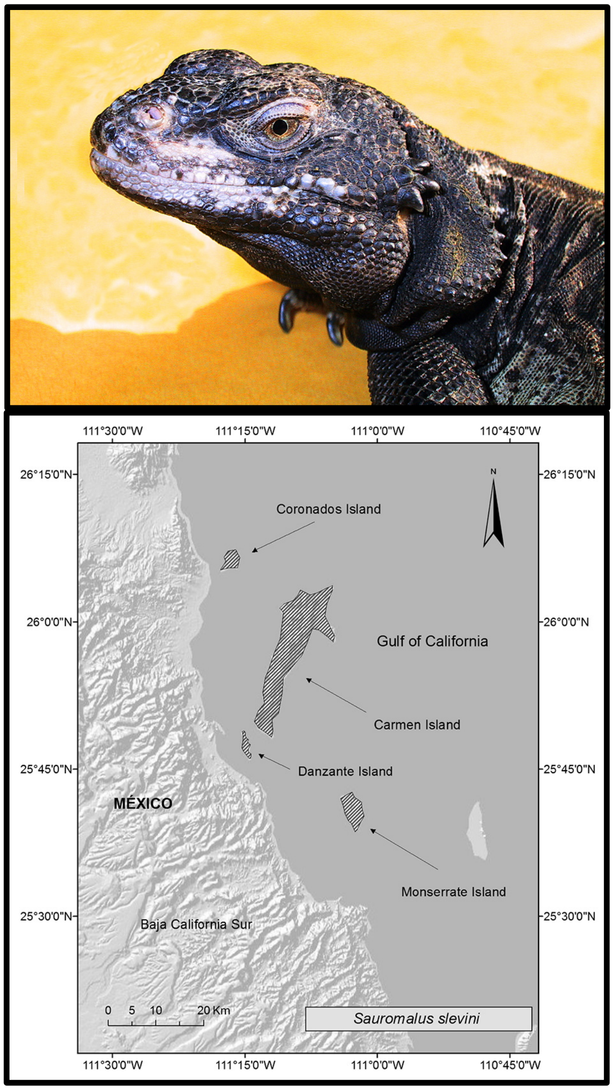


FIGURE 45. Slevin's Chuckwalla, *Sauromalus slevini* (Photographed by Joseph Burgess).

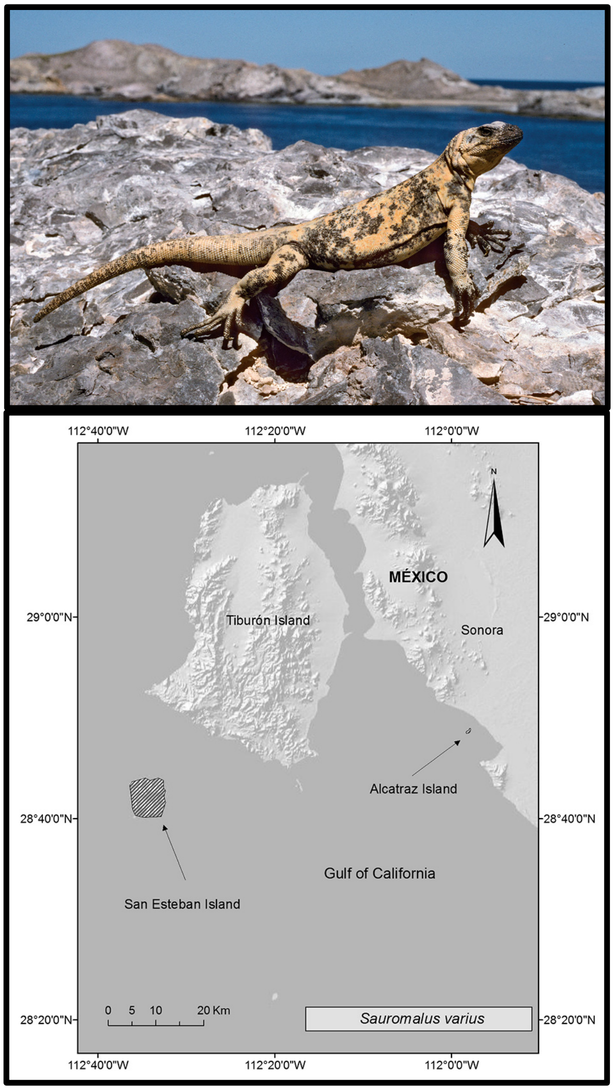


FIGURE 46. Piebald Chuckwalla, *Sauromalus varius* (Photographed by Bradford Hollingsworth).

***Sauromalus varius* Dickerson [Piebald Chuckwallas]**.—Other name: Iguanas de Pared de Piebald (sic: Liner and Casas-Andreu 2008; Iguanas Picazas de Pared); San Esteban Island Chuckwalla (Wrobel 2004). Original name: *Sauromalus varius* Dickerson 1919, Bulletin of the American Museum of Natural History 41(10):464. Holotype: AMNH 5633 (= USNM 64441, Cochran 1961). Type locality: "San Esteban Island, Gulf of California, Mexico." Distribution: Isla San Esteban and Isla Alcatraz (possibly introduced), Sonora, and Isla Roca Lobos, Baja California, México (Hollingsworth 1998). Fig. 46.

Acknowledgments.—Comments by S. Blair Hedges were greatly appreciated. Peter Harlow and Bill Hayes provided obscure literature. Roger Bour assisted with efforts to locate early type specimens. Glenn Gerber and Jose Ignacio Pareja provided valuable editorial assistance. John Binns provided valuable help in collating and formatting the photographs. Jorge Morales-Mávil created the distibution maps, and Robert Powell and Javier Torres provided additional proofing. Karl Campbell provided an update on Galápagos Iguana distribution. The IUCN SSC Iguana Specialist Group provided valuable feedback concerning appropriate common names.

LITERATURE CITED

Acevedo, M. 2006. Anfibios y reptiles de Guatemala: una breve síntesis con bibliografía. Pp. 487–524 *In* Biodiversidad de Guatemala. Cano, E. (Ed.). Universidad de Valle de Guatemala, Guatemala.

Ali, J.R., and J.C. Aitchison. 2014. Exploring the combined role of eustasy and oceanic island thermal subsidence in shaping biodiversity on the Galápagos. Journal of Biogeography 41:1227–1241.

Allen, M.J. 1933. Report on a collection of amphibians and reptiles from Sonora, México, with the description of a new lizard. Occasional Papers of the Museum of Zoology, University of Michigan 259:1–15.

Alvarez del Toro, M. 1960. Los Reptiles de Chiapas. Instituto Zoológico de Estado, Tuxtla Gutiérrez, Chiapas, México.

Alvarez del Toro, M. 1983. Los Reptiles de Chiapas. 3ra ed. Instituto Zoológico de Estado, Tuxtla Gutiérrez, Chiapas, México.

Andersson, L.G. 1900. Catalogue of Linneaus' Reptilia in the Royal Museum in Stockholm. Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar, Stockholm 26:1–29.

Anonymous. 2004. Iguana newsbriefs: Stout Iguana conservation. Iguana (Journal of the International Iguana Society) 11:129.

Aplasca, A.C., J.B. Iverson, G. Colosimo, E. Welch, and E.R. Hekkala. 2016. Genetic diversity and structure of the endangered Allen Cays Rock Iguana, *Cyclura cychlura inornata*. PeerJ 4:e1793. doi.org/10.7717/peerj.1793

Arce-Nazario, J.A., and T.A. Carlo. 2012. *Iguana iguana* invasion in Puerto Rico: facing the evidence. Biological Invasions 14:1981–1984.

Ariano-Sánchez, D., and S.A. Pasachnik. 2011. *Ctenosaura palearis*. The IUCN Red List of Threatened Species. Version 2014.4. Available from http://www.iucnredlist.org/details/44192/0 [Accessed on 14 September 2014].

Avery, M.L., E.A. Tillman, C. Spurfeld, R.M. Engeman, K.P. Maciejewski, J.D. Brown, and E.A. Fetzer. 2014. Invasive Black Spiny-tailed Iguanas (Ctenosaura similis) on Gasparilla Island, Florida, USA. Integrative Zoology 9:590–597.

Bailey, J.W. 1928. A revision of the lizards of the genus *Ctenosaura*. Proceedings of the United States National Museum 73:1–55.

Baird, S.F., and C.F. Girard. 1852. Characteristics of some new reptiles in the Museum of the Smithsonian Institution. Part II. Proceedings of the Academy of Natural Sciences of Philadelphia 6:125–129.

Barbour, T. 1917. Notes on the herpetology of the Virgin Islands. Proceedings of the Biological Society of Washington 30:97–104.

Barbour, T. 1923. Another new Bahamian iguana. Proceedings of the New England Zoological Club 8:107–109.

Barbour, T., and G.K. Noble. 1916. A revision of the lizards of the genus *Cyclura*. Bulletin of the Museum of Comparative Zoology 60:140–164.

Barbour, T., and B. Shreve. 1934. A new race of Rock Iguana. Occasional Papers of the Boston Society of Natural History 8:197–198.

Bell, T. 1825. On a new genus of Iguanidae. Zoological Journal, London 2:204–208.

Bock, B.C., V.P. Páez, A.S. Rand, and G.M. Burghardt. 2016. Life table and stochastic matrix projection analysis for a population of Green Iguanas (*Iguana iguana*): implications for conservation and control. Pp. 47–60 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Bonnaterre, P.J. 1789. Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature, Erpétologie. Panckouke, Paris, France.

Boulenger, G.A. 1885. Catalogue of the Lizards in the British Museum (Natural History). London: Printed by Order of the Trustees, 2nd Edition 2:1–497.

Breuil, M. 2011. The terrestrial herpetofauna of Martinique: past, present, future. Pp. 311–338 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Breuil, M. 2013. Caractérisation morphologique de l'Iguane Commun *Iguana iguana* (Linnaeus, 1758), de l'Iguane des Petites Antilles *Iguana delicatissima* Laurenti, 1768 et de leurs hybrides. Bulletin de la Société Herpétologique de France 147:309–346.

Breuil, M., M. Day, and C. Knapp. 2010. *Iguana delicatissima*. The IUCN Red List of Threatened Species. Version 2014.3. Available from http://www.iucnredlist.org/details/10800/0 [Accessed on 14 September 2014].

Brongniart, A.T. 1800. Essai d'une classification naturelle des reptiles. II Partie. Bulletin des Sciences, par la Société Philomathique, Paris 2:89–91.

Bryan, J.J., G.P. Gerber, M.E. Welch, and C.L. Stephen. 2007. Re-evaluating the taxonomic status of the Booby Cay Iguana, *Cyclura carinata bartschi*. Copeia 2007:734–739.

Buckley, L.J., and R.W. Axtell. 1997. Evidence for the specific status of the Honduran lizards formerly referred to *Ctenosaura palearis* (Reptilia: Squamata: Iguanidae). Copeia 1997:138–150.

Buckner, S., R. Franz, and R.G. Reynolds. 2012. Bahama Islands and Turks and Caicos Islands. Pp. 93–110 *In* Island Lists of West Indian Amphibians and Reptiles. Powell, R., and R.W. Henderson (Eds.). Bulletin of the Florida Museum of Natural History 51:85–166.

Burns, E.L., B.H. Costello, and B.A. Houlden. 2006. Three evolutionarily significant units for conservation in the iguanid genera *Brachylophus*. Pacific Conservation Biology 12:64–77.

Burton, F.J. 2004. Revision to species of *Cyclura nubila lewisi*, the Grand Cayman Blue Iguana. Caribbean Journal of Science 40:198–203.

Burton, F.J., and F.F. Rivera-Milán. 2014. Monitoring a population of translocated Grand Cayman Blue Iguanas: assessing the accuracy and precision of distance sampling and repeated counts. Animal Conservation 17:40–47.

Cayot, L.J., and R. Menoscal. 1992. Land Iguanas return to Baltra. Noticias de Galápagos 51:11–13.

Cayot, L.J., H.L. Snell, W. Llerena, and H.M. Snell. 1994. Conservation biology of Galápagos reptiles: twenty-five years of successful research and management. Pp. 297–305 *In* Captive Management and Conservation of Amphibians and Reptiles. Murphy, J.B., K. Adler, and J.T. Collins (Eds.). Society for the Study of Amphibians and Reptiles, Ithaca, New York.

Cochran, D.M. 1931. New Bahaman reptiles. Journal of the Washington Academy of Sciences 21:39–41.

Cochran, D.M. 1961. Type specimens of the reptiles and amphibians in the U.S. National Museum. United States National Museum Bulletin 220:1–291.

Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. Bulletin of the American Museum of Natural History 310:1–182.

Cope, E.D. 1863. Descriptions of new American Squamata. Proceedings of the Academy of Natural Sciences of Philadelphia 15:100–106.

Cope, E.D. 1866. Fourth contribution to the herpetology of tropical America. Proceedings of the Academy of Natural Sciences of Philadelphia 18:123–132.

Cope, E.D. 1885. The large iguanas of the Greater Antilles. American Naturalist 19:1006–1007.

Cope, E.D. 1886. On the species of Iguanidae. Proceedings of the American Philosophical Society 23:261–271.

Crother, B. (Ed.). 2012. Scientific and standard English names of amphibians and reptiles of North America north of México with comments regarding confidence in our understanding. 7th Edition. Society for the Study of Amphibians and Reptiles, Herpetological Circular 39:1–68.

Cryder, M.R. 1999. Molecular systematics and evolution of the *Ctenosaura hemilopha* complex (Squamata: Iguanidae). M.Sc. Thesis, Loma Linda University, Loma Linda, California, USA. 57 p.

Cuvier, G.L.C.F.D. 1829. Le Règne Animal Distribué d'Après son Organisation, pour Servir de Base à l'Histoire Naturelle des Animaux et d'Introduction à l'Anatomie Comparée. Nouvelle Edition, Revue et Augmentée par P.A. Latreille. Volume 2. Deterville, Paris, France.

Davy, C.M., F.R. Méndez de la Cruz, A. Lathrop, and R.W. Murphy. 2011. Seri Indian traditional knowledge and molecular biology agree: no express train for island-hopping Spiny-tailed Iguanas in the Sea of Cortés. Journal of Biogeography 38:272–284.

de Queiroz, K. 1987a. Phylogenetic systematics of iguanine lizards: a comparative osteological study. University of California Publications in Zoology 118:1–203.

de Queiroz, K. 1987b. A new Spiny-tailed Iguana from Honduras, with comments on relationships within *Ctenosaura* (Squamata: Iguania). Copeia 1987:892–902.

de Queiroz, K. 1995. Checklist and key to the extant species of Mexican iguanas (Reptilia: Iguaninae). Publicaciones Especiales del Museu de Zoología (UNAM) 9:1–48.

de Queiroz, K., and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. Systematic Zoology 39:307–322.

Dickerson, M.C. 1919. Diagnoses of twenty-three new species and a new genus of lizards from lower California. Bulletin of the American Museum of Natural History 41:461–477.

Donegan, T.M. 2009. Type specimens, samples of live individuals, and the Galápagos Pink Land Iguana. Zootaxa 2201:12–20.

Duellman, W.E. 2012. Linnaean names in South American herpetology. Bibliotheca Herpetologica 9:87–97.

Duellman, W.E., and A.S. Duellman. 1959. Variation, distribution, and ecology of the iguanid lizard *Enyaliosaurus clarki* of Michoacan, México. Occasional Papers of the Museum of Zoology, University of Michigan 598:1–10.

Duméril, A.H.A. 1856. Description des reptiles nouveaux ou imparfaitement connus de la collection du Muséum d'Histoire Naturelle et remarques sur la classification et les caractères des reptiles. Archives du Museum d'Histoire Naturelle, Paris 8:437–588.

Duméril, A.M.C., and G. Bibron. 1837. Erpétologie Génerale ou Historie Naturelle Complete des Reptiles. Volume 4. Histoire de Quarante-six Genres et de Cent Quarante-six Espèces de la Famille des Iguaniens, de l'Ordre des Sauriens. Libraire Encyclopedique de Roret, Paris, France.

Echternacht, A.C. 2012. Cayman Islands. Pp. 111–112 In Island lists of West Indian Amphibians and Reptiles. Powell, R., and R.W. Henderson (Eds.). Bulletin of the Florida Museum of Natural History 51:85–166.

Echternacht, A.C., F.J. Burton, and J.M. Blumenthal. 2011. The amphibians and reptiles of the Cayman Islands: conservation issues in the face of invasions. Pp. 129–147 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Eibl-Eibesfeldt, I. 1956. Eine neue Rasse der Merrechse, *Amblyrhynchus cristatus venustissimus*, nebst einigen Bemerkungun über *Amblyrhynchus cristatus cristatus*. Senckenbergiana Biologica 37:87–100.

Eibl-Eibesfeldt, I. 1962. Neue Unterarten der Meerechse, *Amblyrhynchus cristatus*, nebst weiteren Angaben zur Biologie der Art. Senckenbergiana Biologica 43:177–199.

Etheridge, R.E. 1964. The skeletal morphology and systematic relationships of sceloporine lizards. Copeia 1964:610–631.

Etheridge, R.E. 1982. Checklist of the iguanine and Malagasy iguanid lizards. Pp. 7–37 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Fabiani, A., E. Trucchi, S. Rosa, C. Marquez, H.L. Snell, W. Tapia Aguilera, and G. Gentile. 2011. Conservation of Galápagos Land Iguanas: genetic monitoring and predictions of a long-term program on the island of Santa Cruz. Animal Conservation 14:419–429.

Falcón, W., J.D. Ackerman, and C.C. Daehler. 2012. March of the Green Iguana: non-native distribution and predicted geographic range of *Iguana iguana* in the Greater Carribean Region. IRCF Reptiles and Amphibians: Conservation and Natural History 19:150–160.

Falcón, W., J.D. Ackerman, W. Recart, and C.C. Daehler. 2013. Biology and impacts of Pacific Island invasive species. 10. *Iguana iguana*, the Green Iguana (Squamata: Iguanidae). Pacific Science 67:157–186.

Fisher, R., P. Harlow, H. Davis, L. Chemnick, O. Ryder, and S. Keogh. 2009. Another new *Brachylophus* iguana from Fiji? New genetic evidence and further use of morphology to discriminate among the described living species. Abstract. Joint annual meetings of ASIH, HL, and SSAR. Portland, Oregon. Available from http://library.iucn-isg.org/biblio_display_info.php?id=3017&q=

Fisher, R., P. Harlow, J. Niukula, P. Biciloa, T. Osborne, N. Thomas, L. Chemnick, H. Davis, and O. Ryder. 2012. Further assessment of Fijian Iguana (*Brachylophus* sp.) populations in the Fijian Islands and development of a microsatellite library. Report to International Iguana Foundation.

Fitzinger, L.J.F.J. 1843. Systema Reptilium. Fasciculus Prima. Braumüller et Seidel, Wien, Austria.

Frost, D.R., R.E. Etheridge, D. Janies, and T. Titus. 2001. Total evidence, sequence alignment, the evolution of polychrotid lizards, and a reclassification of the Iguania (Squamata: Iguania). American Museum Novitates 3343:1–38.

García, M.A., and G.P. Gerber. 2016. Conservation and management of *Cyclura* iguanas in Puerto Rico. Pp. 61–67 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Garman, S. 1892. The reptiles of the Galápagos Islands. Bulletin of the Essex Institute 24:73–87.

Gentile, G., and H. Snell. 2009. *Conolophus marthae* sp. nov. (Squamata, Iguanidae), a new species of Land Iguana from the Galápagos archipelago. Zootaxa 2201:1–10.

Gentile, G., M. Ciambotta, and W. Tapia. 2013. Illegal wildlife trade in Galápagos: molecular tools help the taxonomic identification of confiscated iguanas and guide their repatriation. Conservation Genetics Resources 5:867–872.

Gentile, G., A. Fabiani, C. Marquez, H.L. Snell, H.M. Snell, W. Tapia, and V. Sbordoni. 2009. An overlooked pink species of land iguana in the Galápagos. Proceedings of the National Academy of Science 106:507–511.

Gibbons, J.R.H. 1981. The biogeography of *Brachylophus* including the description of a new species, *B. vitiensis* from Fiji. Journal of Herpetology 15:255–273.

Glor, R.E., R. Powell, and J.S. Parmerlee, Jr. 2000. *Cyclura cornuta*. Catalogue of American Amphibians and Reptiles 709:1–6.

Goetz, M. 2008. The Cayman Sister Isles Iguana project: identifying the conservation needs of *Cyclura nubila caymanensis*. Iguana: Conservation, Natural History, and Husbandry of Reptiles 15:13–19.

González, A., V. Berovides, D. Cobián, L. Espinosa, J. Milián, G. Abad, E. Palacio, M. Alonso-Tabet, M. López, and Y. Alonoso. 2016. Monitoring the density of the Cuban Rock Iguana (*Cyclura nubila nubila*) from protected areas in southern Cuba. Pp. 68–78 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

González Rossell, A., V. Berovides Álvarez, M. Alonso Tabet, and D. Cobián Rojas. 2012. *Cyclura nubila* Gray, 1831. Pp. 99–102 *In* Libro Rojo de los Vertebrados de Cuba. González Alonso, H., L. Rodríguez Schettino, A. Rodríguez, C.A. Mancina, and I. Ramos García (Eds.). Instituto de Ecología y Sistemática, Havana, Cuba.

Goode, A.B.C., S.A. Pasachnik, and T. Maple. 2016. Habitat utilization of Roatán Spiny-tailed Iguanas (*Ctenosaura oedirhina*) and its implications for conservation. Pp. 79–89 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Grant, C. 1940. The herpetology of the Cayman Islands, with an appendix on the Cayman Islands and marine turtles by C. Bernard Lewis. Bulletin of the Institute of Jamaica. Science Series 2:1–65.

Gray, J.E. 1830. A synopsis of the species of the Class Reptilia. Pp. 1–110 *In* The Animal Kingdom Arranged in Conformity with its Organization, by the Baron Cuvier, with Additional Descriptions of all the Species Hitherto Named, and of Many not before Noticed, by Edward Griffith. Volume 9. Supplement. The Class Reptilia Arranged by the Baron Cuvier with Specific Descriptions by Edward Griffith, F.L.S., A.S., & c. and Edward Pigeon, Esq. Griffith, E. (Ed.). Whittaker, Treacher, and Compny, London, England.

Gray, J.E. 1831. Description of a new species of *Amblyrhynchus* of Mr. Bell, in the British Museum. Zoological Miscellany 1831:6.

Gray, J.E. 1842. Description of some new species of reptiles, chiefly from the British Museum collection. Zoological Miscellany, London 1842:57–59.

Gray, J.E. 1845. Catalogue of the Specimens of Lizards in the Collection of the British Museum. Printed by Order of the Trustees, Edward Newman, London, England.

Grismer, L.L. 1994. Geographic origins for the reptiles on islands in the Gulf of California, México. Herpetological Natural History 2:17–40.

Grismer, L.L. 1999a. Checklist of amphibians and reptiles on islands in the Gulf of California, México. Bulletin of the Southern California Academy of Sciences 98:45–56.

Grismer, L.L. 1999b. An evolutionary classification of reptiles on islands in the Gulf of California, México. Herpetologica 55:446–469.

Grismer, L.L. 2002. Spiny-tailed Iguanas, insular evolution, and Seri Indians: how long does it take to make a new species and does it matter who makes it? Iguana Times (Journal of the International Iguana Society) 9:3–8.

Grismer, L.L., J.A. McGuire, and B.D. Hollingsworth. 1994. A report on the herpetofauna of Vizcaíno Peninsula, Baja California, México, with a discussion of its biogeographic and taxonomic implications. Bulletin of the Southern California Academy of Sciences 93:45–80.

Guérin-Méneville, F.E. 1829–1838. Iconographie du Règne Animal de G. Cuvier ou Représentation d'Après Nature de l'une des Espèces les plus Remarquables et Souvent non Encore Figurées, et Chaque Genre d'Animaux, avec un Texte Descriptif mis au Courant de la Science. Tome I. Reptiles. J.B. Baillière, Libraire de l'Académie Royale Médecine, Paris, France.

Gutsche, A., and F. Köhler. 2008. Phylogeography and hybridizaton in *Ctenosaura* species (Sauria, Iguanidae) from Caribbean Honduras: insights from mitochondrial and nuclear DNA. Zoosystematics and Evolution 84:245–253.

Gutsche, U., and W.J. Streich. 2009. Demography and endangerment of the Útila Island Spiny-tailed Iguana, *Ctenosaura bakeri*. Journal of Herpetology 43:105–113.

Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). 2011. Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Brill Academic Publishers, Leiden, The Netherlands.

Hallowell, E. 1854. Descriptions of new reptiles from California. Proceedings of the Academy of Natural Sciences of Philadelphia 7:91–97.

Harlan, R. 1824. Description of two species of Linnean *Lacerta*, not before described, and construction of the new genus *Cyclura*. Journal of the Academy of Natural Sciences of Philadelphia 4:242–251.

Harlow, P.S., and N. Thomas. 2010. American Iguana Eradication Project: Herpetologists' Final Report. Unpublished report to the Department of Environment, Fiji, and NatureFiji-MareqetiViti. 16 p.

Harlow, P.S., M. Fisher, M. Tuiwawa, P.N. Biciloa, J.M. Mersai, S. Naidu, A. Naikatini, B. Thaman, J. Niukula, and E. Strand. 2007. The decline of the endemic Fijian Crested Iguana *Brachylophus vitiensis* in the Yasawa and Mamanuca archipelagos, western Fiji. Oryx 41:44–50.

Hasbún, C.R., and G. Köhler. 2001. On the identity of the holotype of *Ctenosaura quinquecarinata* (Gray 1842) (Reptilia, Squamata, Iguanidae). Senckenbergiana Biologica 81:247–255.

Hasbún, C.R., and G. Köhler. 2009. New species of *Ctenosaura* (Squamata, Iguanidae) from southeastern Honduras. Journal of Herpetology 43:1972–204.

Hasbún, C.R., A. Gómez, G. Köhler, and D.H. Lunt. 2005. Mitochondrial DNA phylogeography of the Mesoamerican spiny-tailed lizards (*Ctenosaura quinquecarinata* complex): historical biogeography, species status, and conservation. Molecular Ecology 14:3095–3107.

Hayes, W.K., R.L. Carter, S. Cyril, Jr., and B. Thornton. 2004. Conservation of an endangered Bahamian Rock Iguana, I. Population assessments, habitat restoration, and behavioral ecology. Pp. 232–257 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Hayes, W.K., S. Cyril, Jr., T. Crutchfield, J.A. Wasilewski, T.A. Rothfus, and R.L. Carter. 2016b. Conservation of the endangered San Salvador Rock Iguanas (*Cyclura rileyi rileyi*): population estimation, invasive species control, translocation, and headstarting. Pp. 90–105 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Hayes, W.K., R.A. Escobar III, S.K. Fry, E.M. Fortune, J.A. Wasilewski, D.M. Tuttle, K.S. West, J.B. Iverson, S.D. Buckner, and R.L. Carter. 2016a. Conservation of the endangered Sandy Cay Rock Iguanas (*Cyclura rileyi cristata*): invasive species control, population response, pirates, poaching, and translocation. Pp. 106–120 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Heller, E. 1903. Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899. XIV. Reptiles. Proceedings of the Washington Academy of Sciences 5:39–98.

Henderson, R.W., and M. Breuil. 2012. Lesser Antilles. Pp. 148–159 *In* Island Lists of West Indian Amphibians and Reptiles. Powell, R., and R.W. Henderson (Eds.). Bulletin of the Florida Museum of Natural History 51:85–166.

Henderson, R.W., and R. Powell. 2009. Natural History of West Indian Reptiles and Amphibians. University Press Florida, Gainesville, Florida, USA.

Hines, K.N. 2016. Food habits of Northern Bahamian Rock Iguanas (*Cyclura cychlura*) in the Exuma Islands, with a dietary review of Rock Iguanas (genus *Cyclura*). Pp. 121–138 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Hodge, K.V.D., R. Powell, and E.J. Censky. 2011. Conserving the herpetofauna of Anguilla. Pp. 3–15 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Hoffmann, M., C. Hilton-Taylor, A. Angulo, M. Böhm, T.M. Brooks, S.H.M. Butchart, K.E. Carpenter, J. Chanson, B. Collen, N.A. Cox, et al. 2010. The impact of conservation on the status of the world's vertebrates. Science 330:1503–1509.

Hollingsworth, B.D. 1998. The systematics of Chuckwallas (*Sauromalus*) with a phylogenetic analysis of other iguanid lizards. Herpetological Monographs 12:39–191.

Hollingsworth, B.D. 2004. The evolution of iguanas: an overview of relationships and a checklist of species. Pp. 19–44 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Hoogmoed, M.S. 1973. Notes on the Herpetofauna of Surinam. IV. The Lizards and Amphisbaenians of Surinam. W. Junk, The Hague, The Netherlands.

ICZN. 2004. Opinion 2072 (Case 3143). Bulletin of Zoological Nomenclature 61:74–75.

Iguana Taxonomy Working Group (ITWG). 2011. Iguanas of the World Taxonomic Checklist. Version 2011.1. IUCN SSC Iguana Specialist Group. Available from http://www.iucn-isg.org/species/iguana-taxonomy

Iverson, J.B., S.J. Converse, G.R. Smith, and J.M. Valiulis. 2006. Long-term trends in the demography of the Allen Cays Rock Iguana (*Cyclura cychlura inornata*): human disturbance and density-dependent effects. Biological Conservation 132:300–310.

Iverson, J.B., G.R. Smith, S.A. Pasachnik, K.N. Hines, and L. Pieper. 2016. Growth, coloration, and demography of an introduced population of the Acklins Rock Iguana (*Cyclura rileyi nuchalis*) in the Exuma Islands, The Bahamas. Pp. 139–153 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Johnson, J.D. 1989. A biogeographic analysis of the herpetofauna of northwestern nuclear Central America. Milwaukee Public Museum Contributions in Biology and Geology 76:1–66.

Johnson, J.D. 1990. Biogeographic aspects of the herpetofauna of the Central Depression of Chiapas, México, with comments on surrounding areas. Southwestern Naturalist 35:268–278.

Keogh, J.S., D.L. Edwards, R.N. Fisher, and P.S. Harlow. 2008. Molecular and morphological analysis of the critically endangered Fijian Iguana reveals cryptic diversity and a complex biogeographic history. Philosophical Transactions of the Royal Society B 363(1508):3413–3426.

Knapp, C.R. 2001. Status of a translocated *Cyclura* iguana colony in The Bahamas. Journal of Herpetology 35:239–245.

Knapp, C.R., and P. Gomez-Zlatar. 2006. Iguanidae or Iguaninae? A taxonomic summary and literature-use analysis. Herpetological Review 37:29–34.

Knapp, C.R., J.B. Iverson, S.D. Buckner, and S.V. Cant. 2011. Conservation of amphibians and reptiles in The Bahamas. Pp. 53–88 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Knapp, C.R., L. Prince, and A. James. 2016. Movements and Nesting of the Lesser Antillean Iguana (*Iguana delicatissima*) from Dominica, West Indies: Implications for Conservation. Pp. 154–167 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Köhler, G. 1995. Eine neue Art der Gattung *Ctenosaura* (Sauria: Iguanidae) aus dem südlichen Campeche, México. Salamandra 31:1–14.

Köhler, G. 2003. Reptiles of Central America. Herpeton, Offenbach, Germany.

Köhler, G., and C.R. Hasbún. 2001. A new species of Spiny-tailed Iguana from México formerly referred to *Ctenosaura quinquecarinata* (Gray 1842). Senckenbergiana Biologica 81:257–267.

Köhler, G., and K. Klemmer. 1994. Eine neue Schwarzleguanart der Gattung *Ctenosaura* aus La Paz, Honduras. Salamandra 30:197–208.

Köhler, G., W. Schroth, and B. Streit. 2000. Systematics of the *Ctenosaura* group of lizards (Reptilia: Sauria: Iguanidae). Amphibia-Reptilia 21:177–191.

Kraus, F. 2009. Alien Reptiles and Amphibians: a Scientific Compendium and Analysis. Invading Nature – Springer Series in Invasion Ecology 4:1–563.

Lanterbecq, D., S. Glaberman, K.N. Vitousek, S. Steinfartz, E. Benavides, M. Wikelski, and A. Caccone. 2010. Genetic differentiation between Marine Iguanas from different breeding sites on the island of Santa Fé (Galápagos Archipelago). Journal of Heredity 101:663–675.

Laurenti, J.N. 1768. Specimen Medicum, Exhibens Synopsin Reptilium Emendatam cum Experimentis Circa Venena et Antidota Reptilium Austriacorum. J.T. de Trattern, Wein, Austria.

Lazell, J.D., Jr. 1973. The lizard genus *Iguana* in the Lesser Antilles. Bulletin of the Museum of Comparative Zoology 145:1–28.

Lemm, J.M., and A.C. Alberts. 2012. *Cyclura*: Natural History, Husbandry, and Conservation of West Indian Rock Iguanas. Academic Press, San Diego, California, USA.

Lindsay, K., and J. Mussington. 2009. *Iguana iguana* in Antigua and Barbuda, West Indies. Applied Herpetology 6:189–190.

Liner, E.A., and G. Casas-Andreu. 2008. Nombres estándar en Español en Inglés y nombres científicos de los anfibios y reptiles de México. Standard Spanish, English, and scientific names of the amphibians and reptiles of México. 2nd Edition. SSAR Herpetological Circular 38:1–162.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. 10th Edition. Volume 1. Holmiae, Stockholm, Sweden.

Lönnberg, E. 1896. Linnean type-specimens of birds, reptiles, batrachians, and fishes in the Zoological Museum of the Royal University of Uppsala. Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar, Stockholm, Sweden 22:1–45.

López-Torres, A.L., H.J. Claudio-Hernández, C.A. Rodríguez-Gómez, A.V. Longo, and R.L. Joglar. 2011. Green Iguanas (*Iguana iguana*) in Puerto Rico: is it time for management? Biological Invasions 14:35–45.

Lorvelec, O., M. Pascal, C. Pavis, and P. Feldmann. 2011. Amphibians and reptiles of the French West Indies: inventory, threats, and conservation. Pp. 205–237 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

MacLeod, A., A. Rodríguez, M. Vences, P. Orozco-terWengel, C. García, F. Trillmich, G. Gentile, A. Caccone, G. Quezada, and S. Steinfartz. 2015. Hybridization masks speciation in the evolutionary history of the Galápagos Marine Iguana. Proceedings of the Royal Society B: Biological Sciences 282:20150425. doi:10.1098/rspb.2015.0425

MacLeod, A., and S. Steinfartz. 2016. The conservation status of the Galápagos Marine Iguanas, *Amblyrhynchus cristatus*: a molecular perspective. Amphibia-Reptilia 37:91–109.

Malhotra, A., R.S. Thorpe, E. Hypolite, and A. James. 2011. A report on the status of the herpetofauana of the Commmonwealth of Dominica, West Indies. Pp. 149–166 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Malone, C.L., and S.K. Davis. 2004. Genetic contributions to Caribbean iguana conservation. Pp. 45–57 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Malone, C.L., C.R. Knapp, J.F. Taylor, and S.K. Davis. 2003. Genetic consequences of Pleistocene fragmentation: isolation, drift, and loss of diversity in Rock Iguanas (*Cyclura*). Conservation Genetics 4:1–15.

Malone, C.L., T. Wheeler, J.F. Taylor, and S.K. Davis. 2000. Phylogeography of the Caribbean Rock Iguana (*Cyclura*): implications for conservation and insights on the biogeographic history of the West Indies. Molecular Phylogenetics and Evolution 17:269–279.

Márquez B., C.M., E.A. Muñoz H., G. Gentile, W.H. Tapia A., F.J. Zabala, S.A. Naranjo L., and A.J. Llerena. 2010. Estado populacional de las iguanas terrestres (*Conolophus subcristatus*, *C. pallidus* y *C. marthae*: Squamata, Iguanidae), Islas Galápagos. Boletin Técnico 9, Serie Zoológica 6:19–37.

Mendoza Quijano, F., S. de M.A. Mejenes López, M. Hernández Aquino, and G. Köhler. 2002. *Ctenosaura acanthura* (Shaw, 1802). An addition to the known fauna of the Mexican state of Hidalgo. Herpetozoa 15:91–92.

Meyer, J.R., and L.D. Wilson. 1973. A distributional checklist of the turtles, crocodilians, and lizards of Honduras. Contributions in Science, Natural History Museum of Los Angeles County 244:1–39.

Montanucci, R.R. 2000. Comments on the restriction of the type locality and nomenclature of the Chuckwalla, *Sauromalus ater* Duméril 1856. Herpetological Review 31:138–142.

Montanucci, R.R. 2004. A note on the identity of Chuckwallas inhabiting Isla Danzante, Baja California Sur. Herpetological Review 35:223–224.

Montanucci, R.R. 2008. Historical evidence for the type locality of *Sauromalus ater* Duméril, 1856. Herpetological Review 39:326–328.

Montanucci, R.R., H.M. Smith, K. Adler, D.L. Auth, R.W. Axtell, T.J. Case, D. Chiszar, J.T. Collins, R. Conant, R. Murphy, et al. 2001. *Euphryne obesus* Baird, 1858 (Reptilia, Squamata): proposed precedence of the specific name over that of *Sauromalus ater* Duméril, 1856. Bulletin of Zoological Nomenclature 58:37–40.

Montgomery, C.E., S.A. Pasachnik, L.E. Ruyle, J.A. Frazier, and S.E.W. Green. 2014. Natural history of the Black-chested Spiny-tailed Iguanas, *Ctenosaura melanosterna* (Iguanidae), on Cayos Cochino Menor, Honduras. The Southwestern Naturalist 59:280–285.

Morales-Mávil, J.E., E.A. Bello-Sánchez, and C.R. Corona-López. 2016b. Distribution and natural history of the Campeche Spiny-tailed Iguanas (*Ctenosaura alfredschmidti*). Pp. 168–176 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Morales-Mávil, J.E., E.A. Suárez-Domínguez, and C.R. Corona-López. 2016a. Biology and conservation of the Gulf Spiny-tailed Iguanas (*Ctenosaura acanthura*). Pp. 177–186 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Murphy, R.W., and G. Aguirre-Léon. 2002. Distributional checklist of nonavian reptiles and amphibians on the islands in the Sea of Cortés. Pp. 580–594 *In* A New Island Biogeography of the Sea of Cortes. Case, T.J., M.L. Cody, and E. Ezcurra (Eds.). Oxford University Press, Oxford, United Kingdom.

Nabhan, G.P. 2002. Cultural dispersal of plants and reptiles. Pp. 407–416 *In* A New Island Biogeography of the Sea of Cortes. Case, T.J., M.L. Cody, and E. Ezcurra (Eds.). Oxford University Press, Oxford, United Kingdom.

Nemesio, A. 2009. On the live holotype of the Galápagos Pink Land Iguana, *Conolophus marthae* Gentile & Snell, 2009 (Squamata: Iguanidae): is it an acceptable exception? Zootaxa 2201:21–25.

Olson, S. 2014. The early scientific history of Galápagos iguanas. Archives of Natural History 41:141–153.

Pasachnik, S.A. 2013. Growth, reproduction, and diet of Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina*, with notes on the status of the species. Herpetological Conservation and Biology 8:191–198.

Pasachnik, S.A., and S. Hudman. 2016. Conservation genetics of Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina*. Pp. 187–196 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Pasachnik, S., D. Ariano-Sánchez, J. Burgess, C.E. Montgomery, and G. Köhler. 2015. *Ctenosaura oedirhina*. The IUCN Red List of Threatened Species. Version 2015.2. Available from http://www.iucnredlist.org/details/44191/0 [Accessed on 1 July 2015].

Pasachnik, S.A., M. Breuil, and R. Powell. 2006. *Iguana delicatissima*. Catalogue of American Amphibians and Reptiles 811:1–14.

Pasachnik, S.A., R. Carreras de Leon, V.H. Reynoso, Y.M. León, and S.J. Incháustegui. 2012a. Green Iguanas (*Iguana iguana*) in the Dominican Republic. IRCF Reptiles and Amphibians: Conservation and Natural History 19:132–134.

Pasachnik, S.A., J.A. Danoff-Burg, E.E. Antúnez, and J.P. Corneil. 2014. Local knowledge and use of the Valle de Aguán Spiny-tailed Iguana, *Ctenosaura melanosterna* in Honduras. Herpetological Conservation and Biology 9:436-447.

Pasachnik, S.A., A.C. Echternacht, and B.M. Fitzpatrick. 2010. Gene trees, species, and species trees in the *Ctenosaura palearis* clade. Conservation Genetics 11:1767–1781.

Pasachnik, S.A., A.C. Echternacht, and B.M. Fitzpatrick. 2011a. Population genetics of the Honduran Spiny-tailed Iguana *Ctenosaura melanosterna*: implication for conservation and management. Endangered Species Research 14:113–126.

Pasachnik, S.A., B.M. Fitzpatrick, T.J. Near, and A.C. Echternacht. 2009. Gene flow between an endangered endemic iguana, and its wide spread relative, on the island of Útila, Honduras: when is hybridization a threat? Conservation Genetics 10:1247–1254.

Pasachnik, S.A., A. Martinez, and M.S. Perez. 2011b. *Ctenosaura bakeri*. The IUCN Red List of Threatened Species. Version 2014.3. Available from http://www.iucnredlist.org/details/44181/0 [Accessed on 14 September 2014].

Pasachnik, .A., C.E. Montgomery, A. Martinez, N. Belal, S. Clayson, and S. Faulkner. 2012b. Body size, demography, and body condition in Útila Spiny-tailed Iguanas, *Ctenosaura bakeri*. Herpetological Conservation and Biology 7:391–398.

Pasachnik, S.A., C.E. Montgomery, L.E. Ruyle, J.P. Corneil, and E.E. Antúnez. 2012c. Morphological and demographic analyses of *Ctenosaura melanosterna* across its range: implications for population level management. Herpetological Conservation and Biology 7:399–406.

Pérez-Buitrago, N., and A. Sabat. 2007. Natal dispersal, home range, and habitat use of hatchlings of the Mona Island Iguana (*Cyclura cornuta stejnegeri*). Applied Herpetology 4:365–376.

Pérez-Buitrago, N., A.M. Sabat, and W.O. McMillan. 2016. Nesting migrations and reproductive biology of the Mona Rhinoceros Iguana, *Cyclura stejnegeri*. Pp. 197–213 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Perotto-Baldivieso, H.L, E. Melendez-Ackerman, M.A. Garcia, P. Leimgruber, S.M. Cooper, A. Martinez, P. Calle, O.M. Ramos Gonzales, M. Quinones, C.A. Christen, and G. Pons. 2009. Spatial distribution, connectivity, and the influence of scale: habitat availability for the endangered Mona Island Rock Iguana. Biodiversity and Conservation 18:905–917.

Perry, G., and G.P. Gerber. 2006. Conservation of amphibians and reptiles in the British Virgin Islands: status and patterns. Applied Herpetology 3:237–256.

Perry, G., and G.P. Gerber. 2011. Conservation of amphibians and reptiles of the British Virgin Islands: status and patterns. Pp. 105–128 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Perry, G., and R. Powell. 2009. The herpetofauna of Guana Island: an annotated checklist and travelogue. IRCF Reptiles and Amphibians: Conservation and Natural History 16:42–47.

Petren, K., and T.J. Case. 1997. A phylogenetic analysis of body size evolution and biogeography in Chuckwallas (*Sauromalus*) and other iguanines. Evolution 51:206–219.

Petren, K., and T.J. Case. 2002. Updated mtDNA phylogeny for *Sauromalus* and implications for the evolution of gigantism. Pp. 574–579 *In* A New Island Biogeography of the Sea of Cortes. Case, T.J., M.L. Cody, and E. Ezcurra (Eds.). Oxford University Press, Oxford, United Kingdom.

Phillips, R.B., B.D. Cooke, K. Campbell, V. Carrion, C.M. Marquez B., and H.L. Snell. 2005. Eradicating feral cats to protect Galápagos Land Iguanas: methods and strategies. Pacific Conservation Biology 11:257–267.

Pough, F.H., R.M. Andrews, J.E. Cadle, M.C. Crump, A.H. Savitsky, and K.D. Wells. 2004. Herpetology. Pearson Prentice Hall, Upper Saddle River, New Jersey, USA.

Powell, R. 1999. Herpetology of Navassa Island, West Indies. Caribbean Journal of Science 35:1–13.

Powell, R. 2000. *Cyclura onchiopsis*. Catalogue of American Amphibians and Reptiles 710:1–3.

Powell, R. 2011. Conservation of the herpetofauna on the Dutch Windward Islands: St. Eustatius, Saba, and St. Maarten. Pp. 189–204 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Powell, R., and R.E. Glor. 2000. *Cyclura stejnegeri*. Catalogue of American Amphibians and Reptiles 711:1–4.

Powell, R., and R.W. Henderson (Eds.). 2012. Island lists of West Indian amphibians and reptiles. Bulletin of the Florida Museum of Natural History 51:85–166.

Pregill, G.K. 1981. An appraisal of the vicariance hypothesis of Caribbean biogeography and its application to West Indian terrestrial vertebrates. Systematic Zoology 30:147–155.

Pregill, G.K. 1982. Fossil amphibians and reptiles from New Providence Island, Bahamas. Smithsonian Contributions in Paleobiology 48:8–21.

Pregill, G.K., and D.W. Steadman. 2004. South Pacific iguanas: human impacts and a new species. Journal of Herpetology 38:15–21.

Pyron, R.A., F.T. Burbrink, and J.J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 1,461 species of lizards and snakes. BMC Evolutionary Biology 13:93.

Radachowsky, J., R.G. Anleu, and G. Köhler. 2003. First record of *Ctenosaura alfredschmidti* Köhler, 1995 in Guatemala. Salamandra 39:11–13.

Rassmann, K., D. Tautz, F. Trillmich, and C. Glidon. 1997a. The microevolution of the Galápagos Marine Iguana *Amblyrhynchus cristatus* assessed by nuclear and mitchondrial genetic analyses. Molecular Ecology 6:437–452.

Rassmann, K., F. Trillmich, and D. Tautz. 1997b. Hybridization between the Galápagos Land and Marine Iguana (*Conolophus subcristatus* and *Amblyrhynchus cristatus*) on Plaza Sur. Journal of Zoology 242:729–739.

Reynolds, R.G. 2011. Status, conservation, and introduction of amphibians and reptiles in the Turks and Caicos Islands, British West Indies. Pp. 377–406 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Rioja, T., A. Carillo-Reyes, E. Espinoza-Medinilla, and S. López-Mendoza. 2012. Basic ecology of the Oaxacan Spiny-tailed Iguana *Ctenosaura oaxacana* (Squamata: Iguanidae), in Oaxaca, México. Revista de Biología Tropical 60:1613–1619.

Rothschild, W., and E. Hartert. 1899. A review of the ornithology of the Galápagos Islands with notes on the Webster-Harris expedition. Novitates Zoologicae 6:85-205.

Rupp, E., and M. Accimé. 2011. Discovery of Ricord's Iguana (*Cyclura ricordii*) in Haiti. IRCF Reptiles and Amphibians: Conservation and Natural History 18:148–153.

Sabaj Pérez, M.H. (Ed.). 2010. Standard Symbolic Codes for Institutional Resource Collections in Herpetology and Ichthyology: an Online Reference. Version 2.0. American Society of Ichthyologists and Herpetologists, Washington D.C. Available from http://www.asih.org/

Schmidt, K.P. 1920. A new *Cyclura* from White Cay. Proceedings of the Linnaean Society of New York 33:6–7.

Schulte, J.A., J.P. Valladares, and A. Larson. 2003. Phylogenetic relationships within Iguanidae inferred using molecular and morphological data and a phylogenetic taxonomy of iguanian lizards. Herpetologica 59:399–419.

Schulte, U., and G. Köhler. 2010. Microhabitat selection in the Spiny-tailed Iguana *Ctenosaura bakeri* on Útila Island, Honduras. Salamandra 46:141–146.

Schwartz, A., and M. Carey. 1977. Systematics and evolution in the West Indian iguanid genus *Cyclura*. Studies on the Fauna of Curaçao and other Caribbean Islands 173:15–97.

Schwartz, A., and R. Thomas. 1975. A check-list of West Indian Amphibians and Reptiles. Special Publications of the Carnegie Museum of Natural History 1:1–216.

Schwenk, K. 1994. Systematics and subjectivity: the phylogeny and classification of iguanian lizards. Herpetological Review 25:53–57.

Shaw, C.E. 1941. A new Chuckwalla from Santa Catalina Island, Gulf of California, México. Transactions of the San Diego Society of Natural History 9:285–288.

Shaw, C.E. 1945. The Chuckwallas, genus *Sauromalus*. Transactions of the San Diego Society of Natural History 10:269–306.

Shaw, G. 1802. General Zoology or Systematic Natural History. Volume III, Part 1. Amphibia. Thomas Davidson, London, England.

Smith, G.R., and J.B. Iverson. 2016. Effects of tourism on body size, growth, condition, and demography in the Allen Cays Iguana, *Cyclura cychlura inornata*, on Leaf Cay, The Bahamas. Pp. 214–221 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Smith, H.M. 1972. The Sonoran subspecies of the lizard *Ctenosaura hemilopha*. Great Basin Naturalist 32:104–111.

Smith, H.M., and E.H. Taylor. 1950. An annotated checklist and key to the reptiles of México exclusive of the snakes. United States National Museum Bulletin 199:1–253.

Smith, K.T. 2009. Eocene lizards of the clade *Geiseltaliellus* from Messel and Geiseltal, Germany, and the early radiation of Iguanidae (Reptilia, Squamata). Bulletin of the Peabody Museum of Natural History 50:219–306.

Snell, H.L., H.M. Snell, and C.R. Tracy. 1984. Variation among populations of Galápagos Land Iguanas (*Conolophus*): contrasts of phylogeny and ecology. Biological Journal of the Linnean Society 21:185–207.

Soulé, M., and A.J. Sloan. 1966. Biogeography and distribution of the reptiles and amphibians on islands in the Gulf of California, México. Transactions of the San Diego Society of Natural History 14:137–156.

Starostová, Z., I. Réhak, and D. Frynta. 2010. New haplotypes of *Cyclura nubila* from Cuba changed the phylogenetic tree of Rock Iguanas: a challenge for conservation strategies. Amphibia-Reptilia 31:134–143.

Steadman, D.W., N.A. Albury, P. Maillis, J.I. Mead, J. Slapcinsky, K.L. Krysko, and H.M. Singleton. 2014. Late-Holocene faunal and landscape change in The Bahamas. The Holocene 24:220–230.

Steadman, D.W., T.W. Stafford, Jr., D.J. Donahue, and A.J.T. Jull. 1991. Chronology of Holocene vertebrate extinction in the Galápagos Islands. Quaternary Research 36:126–133.

Steinfartz, S., S. Glaberman, D. Lanterbecq, M.A. Russello, S. Rosa, T.C. Hanley, C. Marquez, H.L. Snell, H.M. Snell, G. Gentile, et al. 2009. Progressive colonization and restricted gene flow shape island-dependent population structure of the Galápagos Marine Iguanas (*Amblyrhynchus cristatus*). BMC Evolutionary Biology 9:297.

Stejneger, L. 1891. Description of a new North American lizard of the genus *Sauromalus*. Proceedings of the United States National Museum 14:409–411.

Stejneger, L. 1899. Description of a new species of Spiny-tailed Iguana from Guatemala. Proceedings of the United States National Museum 21:381–383.

Stejneger, L. 1901. On a new species of Spiny-tailed Iguana from Utilla [sic] Island, Honduras. Proceedings of the United States National Museum 23:467–468.

Stejneger, L. 1903. A new species of large iguana from the Bahama Islands. Proceedings of the Biological Society of Washington 16:129–132.

Stephen, C.L., V.H. Reynoso, W.S. Collett, C.R. Hasbun, and J.W. Breinholt. 2013. Geographical structure and cryptic lineages within Common Green Iguanas, *Iguana iguana*. Journal of Biogeography 40:50–62.

Taylor, E.H. 1969. Wiegmann and the herpetology of México. Pp. iii–vi *In* Herpetologica Mexicana. Society for the Study of Amphibians and Reptiles. Facsimile Reprint in Herpetology, Athens, Ohio.

Thomas, N., K. Macedru, W. Mataitoga, J. Surumi, S. Qeteqete, J. Niukula, A. Naikatini, A. Heffernan, R. Fisher, and P. Harlow. 2011. *Iguana iguana* – a feral population in Fiji. Oryx 45:321–323.

Townsend, T.M., A. Larson, E. Louis, and J.R. Macey. 2004. Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. Systematic Biology 53:735–757.

Tzika, A.C., S.F.P. Rosa, A. Fabiani, H.L. Snell, H.M. Snell, C. Marquez, W. Tapia, K. Rassmann, G. Gentile, and M.C. Milinkovitch. 2008. Population genetics of the Galápagos Land Iguana (genus *Conolophus*) remnant populations. Molecular Ecology 17:4943–4952.

Van Denburgh, J. 1922. Reptiles of western North America. Volume 1. Lizards. Occasional Papers of the California Academy of Sciences 10:1–611.

Velarde, E., B.D. Hollingsworth, and J.P. Rebman. 2008. Geographic distribution. *Sauromalus hispidus* (Spiny Chuckwalla). Herpetological Review 39:368.

Ventura-Trejo, J., J.H. Valdez-Villavicencio, and B.D. Hollingsworth. 2008. *Sauromalus ater* (Common Chuckwalla). Herpetological Review 39:239–240.

Vitt, L.J., and J.P. Caldwell. 2009. Herpetology. Academic Press, San Diego, California, USA.

Wiegmann, A.F.A. 1828. Beyträge zur Amphibienkunde. Isis von Oken, Leipzig 21:364–383.

Wiegmann, A.F.A. 1834. Herpetologica Mexicana seu descriptio amphibiorum Novae Hispaniae quae itineribus comitis de Sack, Ferdinandi Deppe et Chr. Guil. Schiede in Museum Zoologicum Berolinense pervenerunt. Pars prima, Saurorum species amplectens, adiecto Systematis Saurorum Prodom, additisque multis in hunc amphibiorum ordinem observationibus. Lüderitz, Berlin, Germany.

Wiens, J.J., and B.D. Hollingsworth. 2000. War of the iguanas: conflicting molecular and morphological phylogenies and long-branch attraction in iguanid lizards. Systematic Biology 49:143–159.

Wikelski, M. 2005. Evolution of body size in Galápagos Marine Iguanas. Proceedings of the Royal Society B, Biological Sciences 272:1985–1993.

Wikelski, M., S.S. Steiger, B. Gall, and K.N. Nelson. 2005. Sex, drugs, and mating role: testosterone-induced phenotype-switching in Galápagos Marine Iguanas. Behavioral Ecology 16:260–268.

Wilson, B.S. 2011. Conservation of Jamaican amphibians and reptiles. Pp. 273–310 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Wilson, B.S., T.D. Grant, R. van Veen, R. Hudson, D. Fleuchaus, O. Robinson, and K. Stephenson. 2016. The Jamaican Iguana (*Cyclura collei*): a report on 25 years of conservation effort. Pp. 237–254 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Wilson, L.D., and D.E. Hahn. 1973. The herpetofauna of the Islas de la Bahía, Honduras. Bulletin of the Florida State Museum, Biological Sciences 17:93–150.

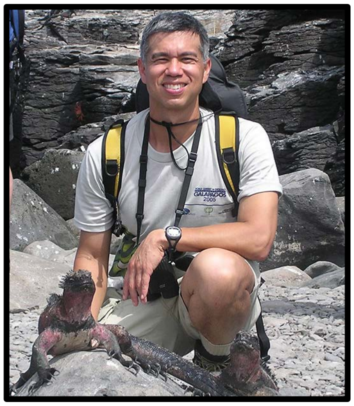
Wrobel, M. (Ed.). 2004. Elsevier's Dictionary of Reptiles: In Latin, English, German, French and Italian. Elsevier, Amsterdam, The Netherlands.

Zarza, E., V.H. Reynoso, and B.C. Emerson. 2008. Diversification in the northern neotropics: mitochondrial and nuclear DNA phylogeography of the iguana *Ctenosaura pectinata* and related species. Molecular Ecology 17:3259–3275.

Zarza, E., V.H. Reynoso, and B.C. Emerson. 2011. Discordant patterns of geographic variation between mitochondrial and microsatellite markers in the Mexican Black Iguana (*Ctenosaura pectinata*) in a contact zone. Journal of Biogeography 38:1394–1405.

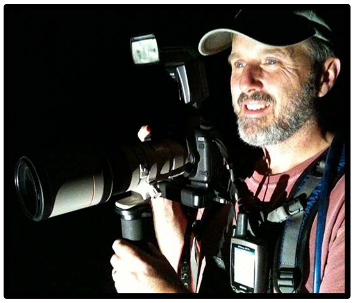
Zarza, E., V.H. Reynoso, and B.C. Emerson. 2016. Genetic tools for assisting sustainable management and conservation of the spiny-tailed iguana, *Ctenosaura pectinata*. Pp. 255–264 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Larry J. Buckley earned his Ph.D. in Zoology from Southern Illinois University (SIU) at Carbondale, his master's in Biology from SIU at Edwardsville, and his bachelor's in Biology at the University of Missouri, St. Louis. He held a postdoctoral fellowship at the National Museum of Natural History, Smithsonian Institution in the Herpetology Division of the Department of Vertebrate Zoology. He is now in life sciences at the Rochester Insitute of Technology where he serves as Department Head. His research focus is on phylogenetics and vertebrate systematics especially reptiles and amphibians, with an emphasis on systematics and population genetics of iguanid lizards. He also enjoys development of courses in evolutionary biology, population genetics, biogeography, and comparative anatomy. (Photographed by Susan Tontaraski).



Kevin de Queiroz is a Research Zoologist and Curator of the collection of amphibians and reptiles at the National of Natural History, Smithsonian Institution. He did research for his M.Sc. on the phylogenetic systematics of iguan Diego State University and for his Ph.D. on the evolution of North American Sand Lizards at the University of Cali Berkeley. Afterwards, he continued his herpetological research as a Tilton Postdoctoral Fellow at the California Ac Sciences. His primary research interests are in the systematics and evolutionary biology of reptiles and the theory a practice of systematic biology. Kevin is a member of the IUCN SSC Anoline Lizard Specialist Group and Iguana S Group, and he has held various elected and appointed offices in the American Society of Ichthyologists and Herpet the Herpetologists' League, the Society for the Study of Amphibians and Reptiles, the Society of Systematic Biolog the International Society for Phylogenetic Nomenclature. (Photographed by Molly R. Morris).

Tandora D. Grant received a bachelor's degree in Biochemistry and Molecular Biology from the University of C Santa Cruz. Currently a Research Coordinator at the San Diego Zoo Institute for Conservation Research, her work focused primarily on conservation recovery strategies for Caribbean iguanas, San Clemente Loggerhead Shrike, an Diego Coast Horned Lizard. Tandora serves as Program Officer for the IUCN SSC Iguana Specialist Group (ISG), Red List Authority evaluating the conservation status for all iguana species. She is the Species Coordinator and Po Management Advisor for the AZA Species Survival Plans for Jamaican and Grand Cayman Blue Iguanas. Having studbooks for these species, she assesses genetic and demographic statistics to determine optimum captive breeding release candidates. She is incorporating molecular data in this analysis to further define the fitness of reintroduced populations and guide management actions. Most recently, she developed websites for the ISG, International Iguan Foundation, and the Save Goat Islands website providing information opposing development in Jamaican Iguana ha (Photographed by Jeffrey Lemm).



Bradford D. Hollingsworth is currently the Curator of Herpetology at the San Diego Natural History Museum (SDNHM) and an Adjunct Professor at San Diego State University (SDSU). He received his Bachelor and Masters of Science at SDSU and his doctorate at Loma Linda University, both located in southern California. He has been interested in the diversity of amphibian and reptiles for his entire life and his research focuses on the systematics and biogeography in California, the Baja California peninsula, and islands in the Pacific Ocean and Gulf of California. His most recent project is the Amphibian and Reptile Atlas of Peninsular California (herpatlas.sdnhm.org), which aims to document the distributions of species from this region. (Photographed by Maggie Reinbold).

John B. Iverson holds a Ph.D. in Biology from the University of Florida and is Biology Research Professor at Earlham College in Richmond, Indiana. Because of his interests in the natural history, ecology, and evolution of iguanas and turtles, he is currently on the steering committees (and founding member) of the IUCN SSC Iguana Specialist Group, and the Tortoise and Freshwater Turtle Specialist Group. He has been involved with the Turtle Survival Alliance since its inception in 2001 (currently a board member), and serves on the board of the Turtle Conservation Fund. He has been active in several herp societies, serving as editor and president of the Herpetologists' League. He has maintained long-term field research sites since 1980 for Rock Iguanas in the Exumas in The Bahamas, and since 1981 for turtles at the Crescent Lake National Wildlife Refuge in western Nebraska. His hobby is restoring a 76-acre woodlot/cornfield (now in a conservation easement) to a mature hardwood forest. (Photographed by Rick Flamm).

Stesha A. Pasachnik began her research career with iguanas as an undergraduate at Earlham College, in Richmond, Indiana. She received her Ph.D. from the University of Tennessee, Knoxville, in 2010. Her dissertation research focused on the conservation genetics of the *Ctenosaura palearis* complex in Honduras and Guatemala. After completing her Ph.D. she worked as Conservation Director for the Roatán Branch of the Bay Islands Foundation in Honduras, where she began a long-term research project on *C. oedirhina*. She is now a Postdoctoral Research Associate at the San Diego Zoo Institute for Conservation Research in San Diego, California, where she studies the *Cyclura* of Hispaniola. In general her research goals are to bring genetics, ecology, and education together to approach issues of conservation in a holistic way. She currently sits on the editorial advisory board of Biodiversity and Ecosystems Loss and is Co-chair of the IUCN SSC Iguana Specialist Group. (Photographed by Stesha Pasachnik).

Catherine L. Stephen received her Ph.D. in Genetics from Texas A & M University where she focused primarily on the evolutionary history of Caribbean Rock Iguanas and population genetics of Northern Bahamian Rock Iguanas. As a Postdoctoral Fellow at Purdue University, her attention turned for a short time to using population genetic data to guide management decisions in American Pronghorn Antelope. Currently an Associate Professor at Utah Valley University, Catherine teaches a variety of courses, always trying to foster in her students a deep appreciation and understanding of the beauty and complexity of the natural world. Her research with her collaborators and undergraduate students continues to focus on the use of genetic tools to address conservation concerns and explore evolution in iguanids. Throughout her career she has been an active member with the IUCN SSC Iguana Specialist Group and currently serves on the Steering Committee. (Photographed by Codi Lance).

Appendix 1. Museum acronyms referencing specimens of Iguanidae (following Sabaj Pérez 2010).

AMNH	American Museum of Natural History, Central Park West at 79th Street, New York City, New York 10024, USA.
ANSP	Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103, USA.
BMNH	British Museum (Natural History), Department of Zoology, Cromwell Road, London SW7 5BD, United Kingdom.
CAS	California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, USA.
FMNH	Field Museum of Natural History, Roosevelt Road and Lake Shore Drive, Chicago, Illinois 60605, USA.
KU	University of Kansas, Museum of Natural History, Lawrence, Kansas 66045, USA.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A
MNHN	Museum National d'Histoire Naturelle, 43 Rue Cuvier, 75231 Paris, France.
NHRM	Naturhistoriske Riksmuseum, Frescativagen 40, Stockholm 114 18, Sweden.
OUM	Oxford University Museum, Parks Road, Oxford, Oxfordshire, United Kingdom.
SDNHM	San Diego Natural History Museum, 1788 El Prado, San Diego, California 92101, USA.
SMF	Natur-Museum und Forschung-Institut Senckenberg, Senckenberg Anlage 25, 6000 Frankfurt-am-Main 1, Germany.
UCM	University of Colorado Museum of Natural History, Broadway between 15th and 16th Streets, Boulder, Colorado 80309, USA.
UF	Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA.
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109, USA.
USNM	U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA.
ZMB	Museum für Naturkunde, Universitat Humboldt, Invalidenstrasse 43, 104 Berlin, Germany.
ZMUU	Zoologiska Museet, Uppsala Universitet, PO Box 561, S–751 22 Uppsala, Sweden.

APPENDIX 2. Abbreviated checklist of the iguanas, with IUCN Red List status, IUCN estimates of population size (UN, unknown), IUCN population trend (DE, decreasing; IN, increasing; ST, stable; UN, unknown; or NL, not listed), and year when last assessed by the IUCN. Status categories are: Extinct (EX), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD), and not listed (NL).

Taxon	IUCN Status	Pop. Estm.	Pop. Trend	Year Assessed
Amblyrhynchus cristatus [Marine Iguanas]	VU	UN	UN	2004
Amblyrhynchus cristatus cristatus [Fernandina Marine Iguanas]	VU	80,000–150,000	ST	2004
Amblyrhynchus cristatus albemarlensis [Isabela Marine Iguanas]	VU	20,500–40,000	UN	2004
Amblyrhynchus cristatus hassi [Santa Cruz Marine Iguanas]	VU	6,000–10,000	ST	2004
Amblyrhynchus cristatus mertensi [San Cristóbal Marine Iguanas]	EN	UN	UN	2004
Amblyrhynchus cristatus nanus [Genovesa Marine Iguanas]	EN	1,500	DE	2004
Amblyrhynchus cristatus sielmanni [Pinta Marine Iguanas]	VU	2,500–6,000	UN	2004
Amblyrhynchus cristatus venustissimus [Española Marine Iguanas]	VU	10,000–21,000	ST	2004
Brachylophus bulabula [Central Fijian Banded Iguanas]	EN	6,000 +	DE	2012
Brachylophus fasciatus [Lau Banded Iguanas]	EN	UN	DE	2012
Brachylophus vitiensis [Fijian Crested Iguanas]	CR	UN	DE	2012
Conolophus marthae [Pink Land Iguanas]	CR	192	UN	2012
Conolophus pallidus [Barrington Land Iguanas]	VU	UN	NL	1996
Conolophus subcristatus [Galápagos Land Iguanas]	VU	UN	NL	1996
Ctenosaura acanthura [Veracruz Spiny-tailed Iguanas]	NL			
Ctenosaura alfredschmidti [Campeche Spiny-tailed Iguanas]	NT	UN	UN	2004
Ctenosaura bakeri [Útila Spiny-tailed Iguanas]	CR	< 5,000	DE	2013
Ctenosaura clarki [Balsas Spiny-tailed Iguanas]	VU	< 2,500	UN	2004
Ctenosaura conspicuosa [San Esteban Spiny-tailed Iguanas]	NL			
Ctenosaura defensor [Yucatán Spiny-tailed Iguanas]	VU	< 2,500	UN	2004
Ctenosaura flavidorsalis [Yellow-backed Spiny-tailed Iguanas]	EN	< 2,500	DE	2004
Ctenosaura hemilopha [Baja California Spiny-tailed Iguanas]	NL			
Ctenosaura macrolopha [Sonoran Spiny-tailed Iguanas]	NL			
Ctenosaura melanosterna [Black-chested Spiny-tailed Iguanas]	EN	< 5,000	DE	2012
Ctenosaura nolascensis [Nolasco Spiny-tailed Iguanas]	VU	< 2,500	ST	2012
Ctenosaura oaxacana [Oaxaca Spiny-tailed Iguanas]	CR	< 2,500	DE	2004
Ctenosaura oedirhina [Roatán Spiny-tailed Iguanas]	EN	< 2,500	DE	2010
Ctenosaura palearis [Motagua Spiny-tailed Iguanas]	EN	< 2,000	DE	2013
Ctenosaura pectinata [Guerreran Spiny-tailed Iguanas]	NL			
Ctenosaura praeocularis [Southern Honduran Spiny-tailed Iguanas]	DD	UN	UN	2013
Ctenosaura quinquecarinata [Five-keeled Spiny-tailed Iguanas]	EN	< 2,500	DE	2004
Ctenosaura similis [Common Spiny-tailed Iguanas]	LC	UN	ST	2010
Ctenosaura similis similis [Common Spiny-tailed Iguanas]	NL			
Ctenosaura similis multipunctata [Providence Spiny-tailed Iguanas]	NL			
Cyclura carinata [Turks and Caicos Rock Iguanas]	CR	~ 30,000	DE	2004
Cyclura collei [Jamaican Rock Iguanas]	CR	UN	UN	2010
Cyclura cornuta [Hispaniolan Rhinoceros Iguanas]	VU	10,000–17,000	DE	1996
Cyclura cychlura [Northern Bahamian Rock Iguanas]	VU	< 5,000	DE	2004
Cyclura cychlura cychlura [Andros Rock Iguanas]	EN	2,000–5,000	DE	2004
Cyclura cychlura figginsi [Exuma Rock Iguanas]	CR	< 1,300	DE	2004
Cyclura cychlura inornata [Allen Cays Rock Iguanas]	EN	< 500	ST	2004
Cyclura lewisi [Grand Cayman Blue Rock Iguanas]	EN	443	IN	2012
Cyclura nubila [Clouded Rock Iguanas]	VU	UN	NL	2012
Cyclura nubila nubila [Cuban Rock Iguanas]	VU	40,000–60,000	DE	1996
Cyclura nubila caymanensis [Sister Islands Rock Iguanas]	CR	1,200–1,500	DE	2012
Cyclura onchiopsis [Navassa Rhinoceros Iguanas]	EX			
Cyclura pinguis [Anegada Rock Iguanas]	CR	< 200	NL	1996
Cyclura ricordii [Ricord's Rock Iguanas]	CR	2,000–4,000	DE	1996
Cyclura rileyi [Central Bahamian Rock Iguanas]	EN	UN	NL	1996
Cyclura rileyi rileyi [San Salvador Rock Iguanas]	CR	< 1,000	DE	2000
Cyclura rileyi cristata [Sandy Cay Rock Iguanas]	CR	150–200	UN	1996
Cyclura rileyi nuchalis [Acklins Rock Iguanas]	EN	> 13,000	UN	2000
Cyclura stejnegeri [Mona Rhinoceros Iguanas]	EN	1,500–2,000	DE	2000
Dipsosaurus catalinensis [Santa Catalina Desert Iguanas]	NL			
Dipsosaurus dorsalis [Common Desert Iguanas]	LC	> 100,000	ST	2007
Dipsosaurus dorsalis dorsalis [Western Desert Iguanas]	NL			
Dipsosaurus dorsalis sonoriensis [Sonoran Desert Iguanas]	NL			
Iguana delicatissima [Lesser Antillean Iguanas]	EN	< 20,000	DE	2010
Iguana iguana [Common Green Iguanas]	NL			
Sauromalus ater [Common Chuckwallas]	LC	> 100,000	ST	2007
Sauromalus hispidus [Spiny Chuckwallas]	NT	< 10,000	UN	2010
Sauromalus klauberi [Catalina Chuckwallas]	NL			
Sauromalus slevini [Slevin's Chuckwallas]	NL			
Sauromalus varius [Piebald Chuckwallas]	NL			

Herpetological Conservation and Biology 11(Monograph 6):47–60.
Submitted: 14 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

LIFE TABLE AND STOCHASTIC MATRIX PROJECTION ANALYSIS FOR A POPULATION OF GREEN IGUANAS (*IGUANA IGUANA*): IMPLICATIONS FOR CONSERVATION AND CONTROL

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***Abstract.*—The Green Iguana (*Iguana iguana*) may be the most studied of all Neotropical squamate species. Given that many populations are over-exploited, and other introduced populations represent problems for native species, it is surprising that so few of the publications on the species have had a demographic focus. Here we resurrect data that formed the basis of previous publications on a population of Green Iguanas in Panamá that included female growth rates, nest site fidelity, and nesting migrations and hatchling growth rates and dispersal. We reanalyze these data from a demographic perspective, using a maximum likelihood modeling approach, to obtain estimates of survival for nesting females and hatchlings. These results, combined with available information on age at first reproduction, fecundities, and hatching success rates, permit us to construct a life table for this population that is concordant with information on its demographic tendencies (a 13.6% annual decline in number of nesting females). We then produce a stochastic projection matrix and conduct sensitivity and elasticity analyses to identify those vital rates that most influence the population growth rate. Both analyses suggest that survival rates during the first two to three years of life most strongly influence demographic tendencies. These results are interpreted both from the perspective of proposing management measures to help over-exploited iguana populations recover, and also to help control or eliminate introduced populations. We suggest that modifying hatchling and juvenile survival and growth rates would be a viable strategy for either augmenting or reducing Green Iguana population sizes.**

***Resumen.*—La Iguana Verde (*Iguana iguana*) bien puede ser la especie más estudiada de todos los escamados neotropicales. Sin embargo, es sorprendente el reducido número de investigaciones que han tenido un enfoque demográfico, teniendo en cuenta que muchas de sus poblaciones son sobrecosechadas, y algunas poblaciones introducidas son consideradas problemáticas para las especies nativas. En este trabajo, resucitamos datos utilizados en publicaciones previas sobre las tasas de crecimiento ontogénico, fidelidad a los sitios de anidación y migraciones durante la estación reproductiva de las hembras reproductivas, así como información sobre la dispersión de neonatos de una población de iguana verde en Panamá. Reanalizamos estos datos desde un punto de vista demográfico, empleando modelos de máxima-verosimilitud, para obtener estimaciones de las tasas de sobrevivencia de hembras anidantes y los neonatos. Con estos resultados, y en combinación con la información disponible sobre la edad de reclutamiento, tasas de fecundidad y de eclosión de nidos, construimos una tabla de vida para las hembras, concordante con la tendencia demográfica de esta población (declive anual del 13,6% en el número de hembras anidantes). Adicionalmente, elaboramos una matriz de proyección poblacional estocástica, con la cual realizamos análisis de sensibilidad y elasticidad para identificar las tasas vitales que más afectan la tasa finita de crecimiento poblacional. Ambos análisis sugieren que las tasas de sobrevivencia anual de las primeras clases de edad (hembras de dos y tres años), son las transiciones que influyen más en las tendencias demográficas. Estos resultados son interpretados tanto desde la formulación de medidas de manejo para recuperar poblaciones en declive, como para controlar o eliminar poblaciones introducidas. Argumentamos que la modificación de las tasas de sobrevivencia de neonatos y juveniles y sus tasas de crecimiento ontogénico, son estrategias viables ya sea para aumentar o reducir los tamaños poblaciones de la Iguana Verde.**

Key Words.—demography; Iguanidae; management; nesting aggregation; Panamá; sensitivity and elasticity analyses

INTRODUCTION

Thanks to its wide distribution and economic importance, the Green Iguana (*Iguana iguana*) is the best-studied species in the family Iguanidae, and perhaps even the best known of all Neotropical squamate species (Bock 2014). Many Green Iguana populations are over-exploited (Fitch and Henderson 1977; Fitch et al. 1982; Stephen et al. 2011), but at the same time introduced populations outside of the natural range of distribution of the species are considered ecologically harmful to native fauna and flora (Smith et al. 2006, 2007; Meshaka et al.

Bock, Brian C., Vivian P. Páez, A. Stanley Rand, and Gordon M. Burghardt. 2016. Life table and stochastic matrix projection analysis for a population of Green Iguanas (*Iguana iguana*): implications for conservation and control. Pp. 47–60 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

2007; Garcia-Quijano et al. 2011; López-Torres et al. 2011; Pasachnik et al. 2012; Falcón et al. 2013). Yet there have been relatively few demographic studies conducted on this species.

Like most other species in the family Iguanidae, Green Iguanas exhibit a restricted annual nesting season (Wiewandt 1982), with mature females nesting only once each year. Evidence also suggests females nest every year after attaining sexual maturity (Bock et al. 1985; Rand and Bock 1992). Capture-mark-recapture studies of juveniles have documented declines in recapture rates during the first year of life (Henderson 1974; Harris 1982; van Devender 1982; Burghardt and Rand 1985), but without attempting to estimate what proportion of the decline was due to mortality, emigration, or changes in detectabilities with ontogenetic changes in habitat preferences. Finally, juvenile and adult Green Iguana densities have been estimated using different methods, including direct censuses (Dugan 1982; Rodda 1992) or analyses of capture-mark-recapture and transect data (Henderson 1974; Muñoz et al. 2003; Smith et al. 2007; López-Torres et al. 2011). But to date, a rigorous estimation of population age- or stage-specific demographic parameters has not been attempted, despite the need for such analyses to permit development of optimal management strategies for population recovery or control.

Here we resurrect data from studies initiated by ASR in the 1960s on a population of *Iguana iguana* in Panamá that investigated growth rates, nest site fidelity, and nesting migrations of females, as well as hatchling growth rates and dispersal (Burghardt 2004). We reanalyze these data from a demographic perspective, using a maximum likelihood modeling approach, to obtain estimates of annual survival rates of nesting females and weekly survival rates of hatchlings. These results, combined with available information on age at first reproduction, female fecundities, and nest hatching success rates, permit us to construct a life table for this population and produce stochastic projection matrices to conduct sensitivity and elasticity analyses. Our results may have implications both for management of recovering natural Green Iguana populations and control or elimination of exotic populations.

MATERIALS AND METHODS

Study site.—The study site was the Barro Colorado Nature Monument under stewardship of the Smithsonian Tropical Research Institute in Panamá, and specifically the portion of the iguana population associated with the Slothia communal nesting aggregation. Slothia is a small islet located approximately 20 m off the Barro Colorado Island (BCI) shoreline where ASR (1968) discovered a small artificial clearing where an estimated 150–200 female iguanas nested each February and March. Gravid female iguanas were shown to migrate each year from BCI to Slothia (Bock et al. 1985, 1989) to nest communally, competing amongst each other for nest burrows (Rand and Rand 1976, 1978). The iguanas nesting on Slothia and inhabiting adjacent areas of BCI were intensively studied by ASR, GMB, and students during more than two decades, yielding over 30 publications on different aspects of the ecology and behavior of the species (Burghardt 2004).

Nesting female survival.—Studies of nesting female iguanas on Slothia were observational until 1980, when approximately 70% (65) of the gravid iguanas that visited the nesting clearing were captured by noosing them from a blind. They were measured, individually marked by systematically cutting crest scales, and released immediately. When all but 15 of these females were seen after their release as they continued to attempt to nest in the clearing, it was decided that the manipulation was not adversely affecting their behavior, so during the next four nesting seasons (1981–1984), an attempt was made to capture and mark all female iguanas that appeared at the aggregation each year. These data were analyzed to document nesting site fidelity (Bock 1984; Bock et al. 1985), adult female growth rates (Rand and Bock 1992), and annual survival rates (Rand and Bock 1992). However, annual survival was not rigorously estimated; rather, it was argued that the average annual return rate of 40% provided a minimum estimate of annual survival, given the evidence obtained from the simultaneous study of other nesting sites in the area indicating that female iguanas rarely changed nesting sites between years (Bock 1984; Bock et al. 1985).

Here we re-analyze these capture-mark-recapture data using a maximum-likelihood modeling approach using the software package MARK (White and Burnham 1999). We used the Cormack-Jolly-Seber model (Lebreton et al. 1992) to decompose the observed return rates of marked individuals into estimates of the two components of this parameter: apparent survival probability (Φ) and detection probability (p; symbols follow Lebreton et al. 1992). We constructed an *a priori* candidate model set where Φ and p were either constant or variable over years. We also included models where Φ and p were constrained to exhibit increasing or decreasing trends over years. Finally, we used the initial snout-vent length (SVL) recorded for each nesting female as an individual covariate, to permit inspection of models where Φ was a function of female body size.

MARK uses information-theoretic methods to fit different candidate models to the data and uses probability theory to estimate the likelihood of each model (Anderson et al. 2000). It also permits the use of a multi-model approach, in which Akaike information indices (AIC) are used to compute weighted overall estimates of Φ and p (Burnham and Anderson 1998). This model-averaging approach allows the simultaneous evaluation of various models, giving models with larger AIC weights greater influence on the overall model-averaged estimates of Φ and p.

Age at first reproduction.—During the 1982 and 1983 nesting seasons, the ultimate and penultimate phalanges of one digit were removed from a forefoot of each female iguana captured on Slothia, and also from females captured from other nearby nesting sites. Bones in these phalanges were prepared and examined to quantify the number of lines of arrested growth and marks of skeletal growth in the bone cross-sections, as a means of estimating the ages of these individuals (Zug and Rand 1987). Comparison of these skeletochronology estimates with the known encounter histories of the Slothia iguanas allowed corroboration of the estimates, and also provided data on the ages of those iguanas that were nesting on Slothia for the first time. Surprisingly, there was considerable variation in the estimated ages of first-nesting females in this sample (3–8 y of age). However, Zug and Rand (1987), like Rand and Bock (1992), assumed that because someone was present in the blind on Slothia during daylight hours during the entire nesting season each year, along with the evidence of limited inter-change among nesting sites by female iguanas from year to year, that the detectability at the Slothia nesting site was close to 1.0 (100% detection). Here, we use the mean of the detection probabilities estimated for 1982 and 1983 in the previous analysis (= 0.55) to adjust the distribution of ages at first nesting reported by Zug and Rand (1987). These adjustments recognize the possibility that almost half of the female iguanas assumed to be nesting for the first time by Zug and Rand (1987) may have actually nested undetected in a preceding year, and thus provide a more robust estimate of the ages at first reproduction of females in this population.

Fecundity.—Rand (1984) collected data on SVL and clutch size in 30 adult female iguanas obtained during the nesting season from different sites in central Panamá (but not BCI) and documented a significant positive relationship between these two variables. We used the regression equation from this study and the SVL of each female iguana captured on Slothia from 1980 to 1984 (first-capture measurements) to estimate mean clutch size and the range of clutch sizes oviposited on Slothia during the five years of this study.

Nest hatching success rate.—Two studies have used different methods to estimate nest hatching success rates at the Slothia nesting site. Rand and Dugan (1980) excavated the site immediately after hatchling emergence had ended and compared the number of slit-opened egg shells (successfully incubated eggs) vs. number of eggs containing dead embryos or signs of having been opened by invertebrates (eggs that failed to hatch). They recognized that their estimate (21.5% egg mortality) was an under-estimate, because it failed to consider eggs that were oviposited and subsequently dug out by later nesting females using the same burrow system. Such eggs excavated onto the surface of the clearing were usually consumed by waiting vultures (Rand 1968; Sexton 1975).

Bock and Rand (1989) used the SVL measurements of nesting female iguanas during the 1981–1984 nesting seasons, along with the previously documented positive relationship between female SVL and clutch size (Rand 1984), to estimate the number of eggs laid on Slothia during these four years. They also quantified the number of eggs observed destroyed by being dug out onto the surface of the clearing. Finally, they fenced the nesting area before hatching began to attempt to capture all hatchling iguanas to emerge each year. Thus, they could calculate the percentage of all eggs oviposited each year that hatched, and also obtain an estimate of the percentage of laid eggs that were destroyed by other excavating females. Here, we used the mean percent of laid eggs that were destroyed from this study to adjust the earlier Rand and Dugan (1980) hatching success rate estimate, to yield five comparable estimates of the annual nest hatching success rate on Slothia.

Hatchling survivorship.—Several studies have captured and marked hatchling iguanas on Slothia and adjacent areas of BCI and attempted to recapture them to study their social group dynamics, growth rates (Burghardt and Rand 1985), and dispersal away from the nesting site (Drummond and Burghardt 1982; Bock 1984). Prior to 1983, all hatchlings were individually marked with toe clips, but in 1983 Bock (1984) individually marked hatchling iguanas by attaching different patterns of colored beads to plastic monofilaments pierced through the mid-dorsal flap of skin on their neck. Iguanas also were marked by painting 1 cm diameter spots on each side of the body with a paint that was dull during daylight hours, but reflected brilliantly when illuminated by artificial light at night (Rodda et al. 1988). A fence around the nesting area facilitated the capture of almost all hatchlings to emerge on Slothia that year (279 individuals captured, marked, and released).

On 44 nights during the seven weeks following the beginning of hatchling emergence on Slothia in 1983, 5 km of adjacent forested shoreline on BCI was searched from a boat at night with a spotlight in attempts to relocate the hatchlings as they dispersed to suitable juvenile habitat (low vegetation in open or riparian areas). This search distance was chosen based on data from the previous year of censusing that showed the maximum dispersal distance of hatchlings from Slothia in either direction along the shoreline of BCI was 1.6 km (Bock 1984). On each night of censusing in 1983, vegetation in the nearby laboratory clearing on BCI also was searched on foot with a headlamp, to insure all available hatchling habitat was censused each night. The reflective paint facilitated detection of the marked hatchlings, and the bead marking technique had the advantage of permitting their identification without capturing and handling them (as is required with toe-clipped individuals), and often without even awakening them. This resulted in much higher recapture rates in 1983 as compared to comparable efforts in 1982 to monitor toe-clipped iguanas, where individuals were found to move higher in the vegetation to sleep on nights following their first recapture (Rodda et al. 1988).

During the 1983 censuses, unmarked hatchling iguanas that had emerged from other nesting areas also were found along the BCI shoreline and in the laboratory clearing. Ninety of these individuals also were captured, marked with beads and paint, and released so that their movements could be documented during subsequent nights of surveying. Here, we use these recapture data for the 1983 hatchlings marked on Slothia and BCI to compare the survival and detectability estimates of these pre- and largely post-dispersal individuals, using MARK. The *a priori* candidate model set contrasted models where Φ and p either were constant or variable over time (the seven sampling weeks) and were either identical or different for the Slothia and BCI individuals. Evidence of over-dispersion of the data under the fully parameterized model (site and time differences in Φ and p) was addressed by adjusting $\hat{c}$ to 2.4 for subsequent analyses. Again, parameter estimates were obtained by model averaging.

Life table approximation.—Green Iguanas reproduce annually (Rand and Greene 1982; Bock et al. 1985; Rand and Bock 1992), so we constructed an age-based life table, with the exception of dividing the first year of life into three separate stages (egg incubation, hatchling dispersal period, and post-dispersal period). There are estimates available for most of the elements of this life table, but we lack estimates for several key transitions. For example, the weekly post-dispersal survivorship rate estimated for the 1983 BCI hatchlings was clearly unsustainable (because almost no hatchlings would attain 1 y of age with that level of weekly mortality). Numerous studies have mentioned the massive mortality hatchling iguanas suffer immediately following emergence (Henderson 1974; Harris 1982; van Devender 1982; Burghardt and Rand 1985; Knapp and Abarca 2009), both because hatchlings are especially vulnerable to predators while they are dispersing (Greene et al. 1978) and because predators congregate in hatchling habitat at this time of year (Drummond and Burghardt 1982). But once hatchlings have settled, their survival probability presumably increases over time, both because predators disperse once hatchling densities are depleted, and because hatchlings are vulnerable to a smaller suite of predators as they grow (Greene et al. 1978). Unfortunately, the mortality they suffer during their first year following dispersal makes the rigorous estimate of post-dispersal survival using capture-mark-recapture methods impossible, due to the sparse recaptures.

The other two parameters for the Green Iguana life table that we cannot estimate from available data are sub-adult (1–2 y of age) and non-reproductive adult (age > 2 y) annual survival rates. As iguanas grow, they move higher into the vegetation (Hirth 1963; Henderson 1974), making it even more difficult to study their survival rates using capture-mark-recapture methods. Also, the Zug and Rand (1987) data indicated that female iguanas begin to nest at different ages, and while we were able to estimate annual survival rates for reproductive adult females, non-reproductive females of the same age likely enjoy higher survival because they do not suffer the energetic costs and risks associated with producing clutches (Rand 1984), migrating to and from the nesting site (Bock et al. 1989), and constructing a nest (Rand and Rand 1976, 1978; Dugan et al. 1981). Thus, to produce a complete life table, we made the assumptions that non-reproductive adult female annual survival was higher than the reproductive female annual survival rate we estimated, and also that it was higher than sub-adult survival, which in turn was higher than survival rates for post-dispersal hatchling iguanas. Finally, we selected transition probabilities for the proportion of non-reproductive females to become reproductive in the next age class so as to generate a distribution of ages for first-nesting females similar to the distribution of adjusted estimates obtained from Zug and Rand (1987).

One approach to completing the life table would be to assume this protected Green Iguana population was at its carrying capacity and not changing in density, and then ask the question of what values for the three un-estimated parameters would produce a life table that yields a stable population size (λ = 1)? However, while there was no evidence that iguana densities on BCI were changing during the study period, the number of female iguanas using the Slothia nesting site was declining. In the 1960s, an estimated 150–200 females nested there annually (Rand 1968), but when it was perceived that fewer iguanas were nesting there each year, a monitoring program was initiated in 1972, consisting of enlisting a resident of BCI each year to observe the nesting clearing on Slothia through a telescope from the front porch of the BCI dormitory building each day around midday. Each year from 21 January to 17 March (spanning the entire nesting season) the number of nesting females visible in the clearing was recorded on most days, producing a remarkable but unpublished dataset spanning a 26 y period (1972–1997).

Here, we calculated the daily mean number of female iguanas observed in the clearing on Slothia for each year of monitoring and used linear regression on the natural log transformed values to estimate the intrinsic rate of increase of the population (r), and calculated λ as e^r. We then completed the life table by determining the values for the three un-estimated parameters that would produce a population of nesting females on Slothia that was declining at the same rate ($\lambda < 1$), in the following manner.

First, we constrained the life table so that non-reproductive adult female annual survival was greater than 0.58 (the mean reproductive female annual survival rate, see Results below). To reflect how survival increases as iguanas grow, we set sub-adult (1–2 y of age) annual survival to 0.50 of the non-reproductive adult female rate, and post-dispersal hatchling survival for the months until they completed their first year of life at 0.50 of the sub-adult rate. We then assigned potential values for non-reproductive female survival (and hence also for sub-adult and post-dispersal hatchling survival) in an interpolative fashion until values were obtained that yielded approximately the correct value of λ.

We then converted this life table into a 9 X 9 Leslie matrix by collapsing the first three stage classes (eggs, pre-dispersal hatchlings, and post-dispersal hatchlings) into a 0–1 y age class, and also combined the non-reproductive and reproductive adult female classes for the 2–3 to 7–8 y age classes. This annual demographic matrix yielded a mathematical representation of the life-cycle, where all transitions among, and reproductive contributions of, each age class may be observed in yearly time steps, with each column corresponding to one year in the life of a female iguana. The first row of the matrix represents effective fecundity values of different aged females (F_x) and diagonal elements represent between-age class progressions (G). F_x is the average number of female hatchlings produced during a year by an average female from the corresponding adult size category. We calculated these age-specific effective fecundities employing the equations of Caswell (2001) for a birth-pulse population with post-breeding censuses, as: $F_x = (G_{x-1})$ (probability of reproducing at age x) (m_x); where F_x is the effective fecundity for age class x, G is the progression (survival until progression to a larger age class is achieved), and m_x representing the number of female eggs a female lays in a year for age class x.

Finally, we incorporated stochasticity into the projection to reflect effects of environmental variability by allowing population vital rates to vary each year. The way we estimated the mean fecundity rate and established the range of possible values around this mean, as well as the mean annual survival rates and ranges of permissible values around those means for all age classes, are described in the Results section. In the stochastic projection, we randomly sampled from a triangular distribution around these means for these vital rates, where the range of possible random numbers were distributed between the minimum and maximum estimated rates. This permitted the calculation of confidence intervals for model results on the stable age distribution (SAD), λ_S (the stochastic finite rate of population growth), reproductive values (RV), and sensibilities and elasticities, using the Monte Carlo feature of PopTools add-in for Microsoft® Excel software (G.M. Hood. 2010. PopTools v3.2.5. Available from http://www.poptools.org [Accessed 13 January 2015]) with 40 iterations. λ_S is the long-term projected rate of change for a population governed by this Leslie matrix with environmental stochasticity. RVs represent the relative contribution of individuals within an age class to current and future reproduction (Fisher 1930) and are derived from the combination of estimates of age-specific survival and current and future potential fecundity (Wallace et al. 2008). Sensitivity analyses measure the absolute change in λ if an absolute value of a particular vital rate in the matrix is modified while holding all other values constant, while elasticity analyses are the proportional sensitivities of λ to proportional changes in vital rates within the matrix (Caswell 2001).

RESULTS

Nesting female survival.—The AIC rankings of the models in the candidate model set are presented in Table 1. There was no support for models that examined the possibility that apparent survival was related to the body sizes of the nesting iguanas. The best-supported model was the one that included a trend over years for both survival rates and detection probabilities, with the former increasing and the later decreasing over time. Model-averaged estimates for these annual parameters are presented in Table 2. The mean annual survival rate

TABLE 1. AIC rankings for the nine candidate models examined with the nesting female Green Iguana (*Iguana iguana*) capture-mark-recapture data from the Slothia nesting site on Barro Colorado Island, Panamá. Φ represents apparent annual survival rate and p represents detection probability. A period in the model specification denotes constancy over time, Time represents variation over time, and Trend represents a unidirectional change over time. Models with SVL examined how body size influenced Φ.

Model	AIC_c	Delta AIC_c	AIC_c weight	Number of parameters
Φ(Trend)p(Trend)	354.0	0.0	0.57	4
Φ(.)p(.)	356.1	2.1	0.18	2
Φ(Time)p(Trend)	358.0	4.0	0.07	6
Φ(Trend)p(Time)	358.0	4.0	0.07	6
Φ(Time)p(.)	358.6	4.6	0.05	5
Φ(./SVL)p(.)	359.0	5.0	0.04	2
Φ(Time)p(Time)	360.0	6.0	0.03	7
Φ(.)p(Time)	360.2	6.2	0.02	2
Φ(./SVL-SVL2)p(.)	361.0	7.0	0.02	5

TABLE 2. Model-averaged estimates of apparent annual survival rates (Φ) and detection probability (p) of nesting female Green Iguanas (*Iguana iguana*) at the Slothia nesting site on Barro Colorado Island, Panamá. Models that included the individual covariate (SVL) were not included in the weighted averages.

	Weighted average	Standard error	Lower 95% confidence interval	Upper 95% confidence interval
1980–1981 Φ	0.434	0.063	0.278	0.610
1981–1982 Φ	0.592	0.070	0.426	0.739
1982–1983 Φ	0.700	0.104	0.338	0.908
1981 p	0.738	0.075	0.446	0.913
1982 p	0.624	0.073	0.454	0.768
1983 p	0.476	0.082	0.252	0.710
1984 p	0.359	0.083	0.096	0.747

TABLE 3. Estimates of the ages of Green Iguanas (*Iguana iguana*) nesting for the first time at the Slothia nesting site on Barro Colorado Island, Panamá, based upon an adjustment of the data presented by Zug and Rand (1987) using the mean of the detection probabilities (p) estimated for 1982 and 1983.

Age at first nesting	Number of individuals reported by Zug and Rand (1987)	Adjusted number of individuals	Percentage of the total
2	-	0.45	1.3%
3	1	4.60	13.3%
4	9	9.45	27.0%
5	10	9.10	26.0%
6	8	7.10	20.3%
7	6	3.75	10.7%
8	1	0.55	0.6%

of reproductive adult females (1980–1983) was 0.575, with a range of 0.434–0.700. We assume that survival varies from year to year in a comparable way for both reproductive and non-reproductive adult females, so applied this same range around the mean annual survival rate estimate for the combined non-reproductive and reproductive adult female age classes in the stochastic matrix projection analysis.

Age at first reproduction.—Even after accounting for the possibility that some of the iguanas assumed by Zug and Rand (1987) to be nesting on Slothia for the first time had actually nested undetected the previous year, there was a surprisingly wide range in the adjusted estimated ages at first nesting (Table 3). Female iguanas apparently first nest from 2–8 y of age, with the modal age being 4–5 y old. The maximum age for a reproductive female in this sample was 9 y old (Zug and Rand 1987).

Fecundity.—Estimated clutch sizes of female iguanas captured on Slothia from 1980 to 1984 averaged 44.2 ± (SD) 6.8 eggs/clutch (range, 25.5–59.7 eggs/clutch; all five years, *n* = 165). Because clutch size and age are not correlated in Green Iguanas (Zug and Rand 1987) and sex is determined by heterogametic sex chromosomes (Rovatsos et al. 2014), in the life table we set the fecundities of all reproductive females to 22.1 "female eggs"/y (44.2/2) and used the range of 12.8–29.9 for the stochastic matrix analysis.

Nest hatching success rate.—In 1981, which was the wettest year in over 85 years of data for this area of Panamá, a single clutch of 25 atypically small neonates emerged one month later than the normal onset of hatchling emergence on Slothia. Since an estimated 1,780 eggs were oviposited that year, the estimated hatching success rate was only 1.4%. Hatching success rates in 1982, 1983, and 1984 were 27.0%, 34.0%, and 46.2%, respectively. Given that approximately 22% of the eggs laid on Slothia from 1981 to 1984 were dug out onto the surface by other nesting iguanas, the adjusted hatching success rate from the Rand and Dugan (1980) study was 64.1%, for a mean hatching success rate over these five years of 34.5%, and a mean hatching success rate over the four "typical" years (1981 excluded) of 42.8 ± 16.2% (range, 27.0–64.1%).

Hatchling survival.—Nineteen percent of the 279 hatchling iguanas captured, marked, and released on Slothia in 1983 were recaptured on BCI in one or more subsequent weeks, and 56% of the 90 hatchlings first captured on BCI also were recaptured in subsequent weeks. The AIC rankings of the 10 models in the candidate model set are presented in Table 4. It is important to bear in mind that these are weekly survival estimates, with the most supported model showing a lower apparent survival estimate for the pre-dispersal Slothia individuals, although the apparent survival of the largely post-dispersal individuals first captured on BCI also was low (Table 5). Also, the model indicated that detectability of the pre-dispersal Slothia individuals was lower than that of the individuals first marked on BCI (Table 5).

TABLE 4. AIC rankings for the ten candidate models examined with the hatchling Green Iguana (*Iguana iguana*) capture-mark-recapture data from 1983. Φ represents apparent weekly survival rate and p represents detection probability. Site refers to a difference between pre-dispersal hatchlings marked on Slothia vs. largely post-dispersal hatchlings marked on Barro Colorado Island, Panamá. A period in the model specification denotes constancy over time, and Time represents variation over time.

Model	AIC_c	Delta AIC_c	AIC_c weight	Number of parameters
Φ(Site.)p(Site.)	348.6	0.0	0.485	4
Φ(Site.)p(.)	349.7	1.1	0.287	3
Φ(.)p(Site.)	350.2	1.6	0.224	3
Φ(SiteTime)p(.)	359.1	10.5	0.001	13
Φ(.)p(.)	361.5	12.9	0.001	2
Φ(Time)p(SiteTime)	363.5	14.9	< 0.001	17
Φ(SiteTime)p(Time)	366.2	17.6	< 0.001	17
Φ(Time)p(Time)	367.0	18.4	< 0.001	11
Φ(SiteTime)p(SiteTime)	369.2	20.6	< 0.001	22
Φ(.)p(SiteTime)	370.2	21.6	< 0.001	7

TABLE 5. Model-averaged estimates of apparent weekly survival rates (Φ) and detection probabilities (p) of hatchling Green Iguanas (*Iguana iguana*) marked at the Slothia nesting site (pre-dispersal) or marked on Barro Colorado Island (BCI; largely post-dispersal).

	Weighted average	Standard error	Lower 95% confidence interval	Upper 95% confidence interval
Slothia hatchling Φ	0.471	0.060	0.316	0.631
BCI hatchling Φ	0.650	0.067	0.470	0.796
Slothia hatchling p	0.393	0.081	0.204	0.621
BCI hatchling p	0.604	0.091	0.372	0.799

Life table approximation.—Nesting iguana monitoring data were collected for Slothia on an average of 41.2 d during the 57-d observation period each year, over the 25 y for which data were available (monitoring data from the 1982 nesting season were lost). Regression of Ln (mean number of iguanas seen per day) against the year of the study (-1900) revealed a significant negative relationship ($F = 33.7$, df = 22, $P < 0.001$; Fig. 1), with a slope (r) of -0.146, which yielded an estimate of $\lambda = e^r = 0.864$.

As explained above, our estimates for the life table analysis for the range in fecundities was approximately ± 8.6 female eggs/clutch around the mean of 22.1 female eggs/clutch, and the range of adult reproductive survival rates was approximately ± 0.133 around a mean annual survival rate of 0.575 for the 8–9 y old age class where all individuals reproduced. We also set this same range around higher annual survival rates in earlier age classes composed of both reproductive and non-reproductive adult females. But we lacked means to estimate the annual extent of variation around our estimates for the composite 0–1 y age class and our derived 1–2 y age class. We therefore arbitrarily set the ranges around the mean survival rates for these age classes to ± 0.013 and ± 0.133, respectively (Table 6).

We found that a post-dispersal hatchling survivorship of 0.194, a sub-adult iguana survivorship of 0.387, and a non-reproductive female survivorship of 0.774 yielded a life table that exhibited a 13.6% annual decline ($\lambda = 0.864$). The different components of this female iguana life table are diagrammed in Fig. 2A. Upon pooling the first three stages of the life cycle into a 0–1 y age class and combining non-reproductive and reproductive females in the same age classes (diagrammed in Fig. 2B) and projecting the matrix until it attained an SAD with a $\lambda = 0.864$, the corresponding 9 X 9 Leslie matrix was generated (Fig. 3). After 40 iterations, the projected stochastic finite rate of increase from the Monte Carlo simulation was $\lambda_S = 0.806$ (SD = 0.176).

The sensitivity and elasticity values of each transition produced by this projection differed in similar ways. In the sensitivity analysis, the progression from the 0–1 y age class to the 1–2 y age class produced the greatest absolute change in λ, followed by the 1–2 y old to 2–3

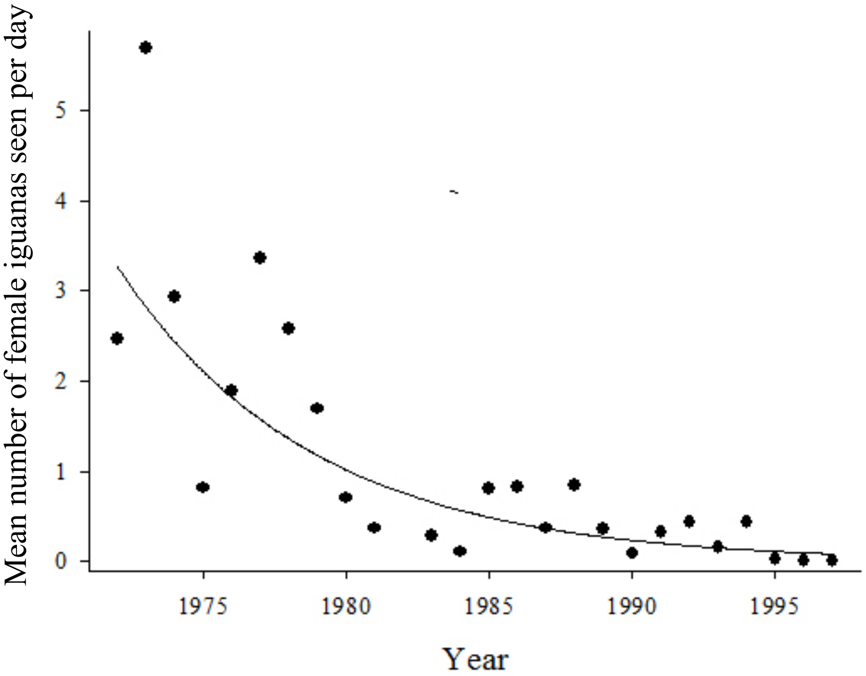

FIGURE 1. Decline in the mean daily number of nesting Green Iguanas (*Iguana iguana*) seen in the clearing on the Slothia nesting site on Barro Colorado Island, Panamá from 1972–1997, when nesting activity on Slothia had ended. Mean number of iguanas seen daily = 12.22 + -0.13 X (y-1900).

TABLE 6. Demographic parameters for female Green Iguanas (*Iguana iguana*) from the Slothia nesting aggregation in Panamá. F_x is the effective fecundity for age class x, G is the progression (survival until progression to the next age class is achieved), and m_x representing the number of female eggs a female lays in a year for age class x. Ranges for G_x used in the stochastic projection are in parentheses.

Age class	n_x	Probability of reproduction	m_x	G_x	F_x	SAD	RV
0–1	1,000	0	0	0.039 (0.026–0.040)	0	0.849	1.00
1–2	38.924	0	0	0.387 (0.254–0.520)	0	0.044	20.02
2–3	15.064	0.010	22.1	0.973 (0.820–1.000)	0.008	0.019	34.02
3–4	14.663	0.085	22.1	0.757 (0.544–0.810)	0.154	0.022	27.94
4–5	11.109	0.252	22.1	0.725 (0.523–0.789)	1.062	0.019	30.96
5–6	8.055	0.441	22.1	0.688 (0.499–0.765)	3.116	0.016	29.91
6–7	5.546	0.717	22.1	0.634 (0.466–0.732)	7.825	0.012	31.77
7–8	3.521	0.931	22.1	0.593 (0.441–0.707)	12.160	0.009	27.53
8–9	2.089	1.000	22.1	0	13.11	0.006	16.54

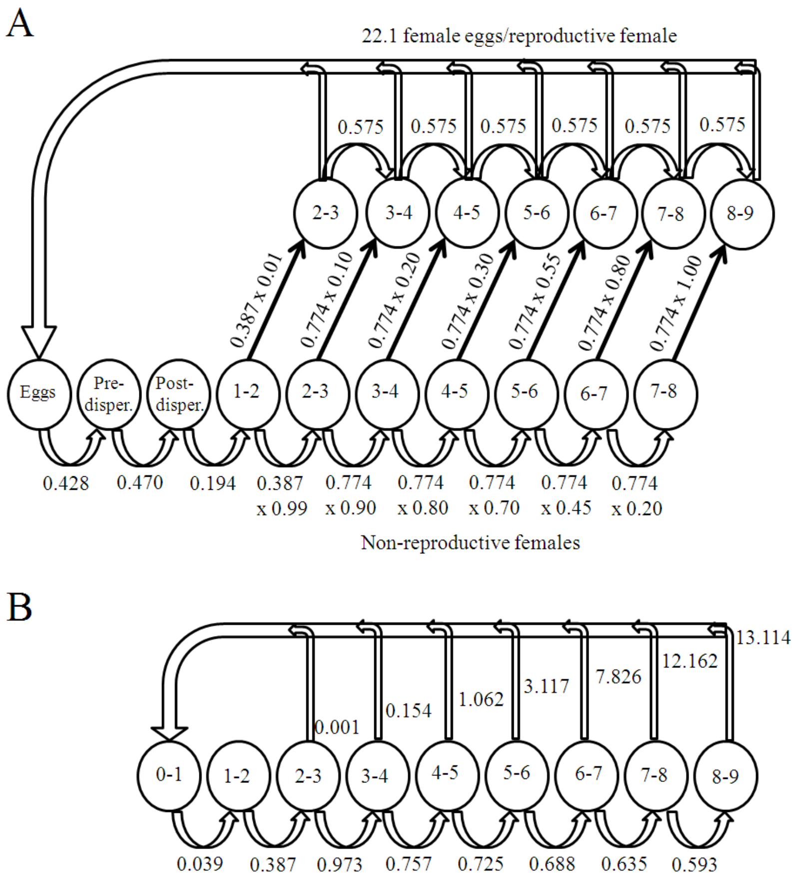

FIGURE 2. (A) Diagram of the female Green Iguana (*Iguana iguana*) life cycle based on data from the Slothia nesting site on Barro Colorado Island, Panamá, showing transition probabilities and reproductive contributions of the different age classes. (B) Diagram of the annual life cycle after pooling the initial three stages into the 0–1 y age class and combining reproductive and non-reproductive female categories. This diagram summarizes the values obtained from the projection analysis that attained a stable age distribution with $\lambda = 0.864$. Circles are age classes, curved arrows connecting circles are transition rates among age classes, diagonal arrows are transition rates from non-reproductive to reproductive status, and vertical arrows are age-specific fecundities.

year old survival probability (Fig. 4A). Similarly, in the elasticity analysis the highest values were for survival (progression rates) of young, primarily pre-reproductive females (from 1–4 y old), followed by progression rates of older females (from 5–7 y old). The relative importance of fecundity for population growth rate was much lower (summed elasticity values = 0.13). When the elasticity values of progression from young females are combined (1–4 y old classes), they represent 0.52 of the overall demographic effects on population growth. The projected trajectory of this *I. iguana* population based upon these vital parameter estimates predicted the local extinction of the population in 20 y.

DISCUSSION

The two previous studies that yielded demographic parameters useful for our analysis in this study were both surprising. First, Zug and Rand (1987) provided evidence that the age at first nesting in female Green Iguanas varies considerably. Most demographic studies of reptile species establish the minimum size or age at first reproduction from a sample of individuals (using histology or capture-mark-recapture data) and then assume most individuals in the population begin reproducing at or near this point. This assumption usually is reasonable, given the expectation that natural selection should rapidly eliminate any variation around the optimal timing of reproductive maturation, given the important fitness consequences of this trait. The evidence that female Green Iguanas may first nest at anywhere from 2–8 y of age (Zug and Rand 1987) is therefore remarkable, and it implies that the source of this large variance must have an environmental basis (rather than reflecting genetic differences; e.g., Andrews 1989).

$$A = \begin{pmatrix} 0.000 & 0.000 & 0.008 & 0.154 & 1.062 & 3.116 & 7.825 & 12.16 & 13.11 \\ 0.039 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.387 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.973 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.757 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.725 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.688 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.634 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.593 & 0.000 \end{pmatrix}$$

FIGURE 3. 9 × 9 Leslie matrix of the female Green Iguana (*Iguana iguana*) life cycle based on data from the Slothia nesting site on Barro Colorado Island, Panamá.

A

$$S = \begin{pmatrix} 0.000 & 0.000 & 0.003 & 0.004 & 0.004 & 0.004 & 0.003 & 0.002 & 0.002 \\ 2.698 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.224 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.106 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.132 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.127 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.154 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.089 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.044 & 0.000 \end{pmatrix}$$

B

$$E = \begin{pmatrix} 0.000 & 0.000 & 0.000 & 0.000 & 0.006 & 0.018 & 0.031 & 0.041 & 0.034 \\ 0.131 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.131 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.131 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.131 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.124 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.106 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.075 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.034 & 0.000 \end{pmatrix}$$

FIGURE 4. (A) S matrix = results of the sensitivity analysis. (B) E matrix = results of the elasticity analysis. Both were based on the stochastic projections of the 9 X 9 Leslie matrix of the female Green Iguana (*Iguana iguana*) life cycle based on data from the Slothia nesting site on Barro Colorado Island, Panamá.

Growth rate data on maturing female iguanas are lacking, but Burghardt and Rand (1985) showed that growth rates in hatchling iguanas were highly variable, but averaged 0.31 mm SVL/d over the first few months of life (which translates into a rate of 133 mm SVL/y). In contrast, female Green Iguanas grow very little each year after they begin to nest (mean = 6.8 mm SVL/y; Rand and Bock 1992). If an averaged sized (72 mm SVL) hatchling iguana were able to maintain a mean initial growth rate of 0.31 mm SVL/d for a period of two years, it would be able to attain the minimum size at first reproduction (295 mm SVL) in less than two years, as do female iguanas maintained on supplemented diets in captivity (Werner 1991). However, growth rates in maturing juvenile iguanas surely decline over time. Presumably, in the wild, the few female iguanas that are able to reproduce at 2–3 y of age are those that had significantly above-average initial growth rates, and that they were able to remain above-average during their ontogeny as their growth rates slowed. So while the available growth rate data for pre-reproductive iguanas are limited, they are consistent with the conclusion of Zug and Rand (1987) that most female iguanas nest for the first time at four years of age or older.

The other surprising result from a previous study used in this analysis was the evidence from Rand and Bock (1992) that reproductive female iguana annual survival rates were so low. An annual survival rate of only 0.58 means that most reproductive females only nest once or twice in their lives. Combined with the evidence for the relatively late maturation in many female iguanas, it also implies a substantial number of female iguanas that attain two years of age never nest at all. However, the Cormack-Jolly-Seber model employed in the analyses of the Slothia female iguana capture-mark-recapture data actually estimates "apparent survival", because it is not able to distinguish between disappearances due to mortality vs. emigration.

In an effort to document rates of cross-over among nesting sites, 177 nesting female iguanas were trapped at alternate nesting sites around Slothia in 1981–1984 (Bock 1984; Bock et al. 1985). The pattern that emerged was that once a female iguana began using a nesting site, she tended to return to that site in all subsequent years until her presumed death, or until the study ended.

Nesting site fidelity was not absolute, however. On 13 occasions, a female iguana marked on Slothia failed to return in the following year, but nested on Slothia again in a subsequent year. These iguanas would impact the Cormack-Jolly-Seber analyses by decreasing estimates of detectabilities, and although relatively few iguanas skipped years on Slothia, the trend in decreasing detectabilities over the course of the study indicates that with each subsequent year of capturing effort on Slothia, the tendencies of the females to skip years increased. Female iguanas that skipped nesting seasons on Slothia did not grow more than females that nested on Slothia the year they were absent, so we assume they nested elsewhere undetected. However, only one instance of genuine cross-over between Slothia and another established nesting site was documented (a female marked on Slothia was recaptured at another site located approximately 1 km distance from Slothia in one nesting season, but returned to nest again on Slothia the following year). These results support the conclusion that most of the disappearance of reproductive females from the Slothia nesting site was actually due to mortality rather than emigration.

There also was additional evidence suggesting that mortality rates in the reproductive females captured on Slothia were high. Two individuals were observed being killed during the study by a nest-guarding female American Crocodile (*Crocodylus acutus*) that also nested in the clearing on Slothia each year (Dugan et al. 1981; Bock and Rand 1989). Also, 37% of the female iguanas on Slothia had regenerating tails on first capture, and 27% of the recaptured females lost portions of their complete or already regenerating tails in the interval between being first marked and recaptured. Finally, the fact that the oldest nesting iguana in the Zug and Rand (1987) skeletochronology study was only 9 y old, when longevity in Green Iguanas in captivity is approximately 20 y (Castanet 1994; Slavens and Slavens 1999), argues that mortality rates in adult females in the wild are high.

Thus, we were obliged to construct a life table for the Slothia Green Iguana nesting aggregation that included variable ages at first nesting and relatively high reproductive female annual mortality rates. The model also included other estimates of demographic parameters available in previous publications on this population and we also made certain assumptions concerning how survival rates must increase as female iguanas grow early in life, to produce a biologically plausible life table consistent with the independent monitoring data indicating this population was in decline.

The demise of the Slothia nesting aggregation might be considered surprising, since early publications on this site stressed its advantage of lacking terrestrial nest predators common on BCI (Rand and Robinson 1969; Drummond 1983). But costs associated with nesting in aggregation that also were documented on Slothia included the need for females to compete with each other for partially-completed nest burrows (Rand and Rand 1976, 1978), the risk of having nests disturbed by subsequent excavating females (Sexton 1975; Rand and Dugan 1980), and the risk of predation from the nest-defending American Crocodile (Dugan et al. 1981; Bock and Rand 1989).

The 30-year decline in numbers of nesting female iguanas on Slothia was not due to the manipulation of capturing females there, because the trend began well before and continued after this five-year period of intensive study. The decline also was not due to successional habitat changes altering the suitability of the site for nesting, because ASR periodically cut back vegetation that encroached into the artificial clearing where iguanas nested. Capture-mark-recapture data on nesting female iguanas (Bock 1984) also indicated that the decline was not due to adult females abandoning the site in preference for other areas, despite the fact that alternative nesting areas were available. During the five years of intensive capturing study on Slothia, well-established alternate sites were available 2 km distance from Slothia, and in 1981 a construction project on BCI near Slothia created a new open area suitable for nesting. In 1993, an even larger perturbation in the same location produced a permanent open clearing as the new laboratory, dining, and residence facilities on BCI were constructed. Finally, several atypical nesting sites on BCI or on small islands adjacent to BCI have been discovered where iguanas nest in the forest in sites where tree falls or other disturbances have produced gaps in the canopy (Bock et al. 1998). We suspect that the decline in numbers of nesting females on Slothia was due to reduced recruitment of newly matured females to this site as they opted to nest in these alternative areas. Thus, our estimates of "apparent survival" of pre-reproductive females in our model may be under-estimates of true survival rates because they combine true mortality with this emigration of iguanas that hatched on Slothia, but that selected alternative nesting sites when they matured.

Our life table for *Iguana iguana* differs considerably from the few others available for other species in the Family Iguanidae (Chuckwalla, *Sauromalus ater*, Abts 1987; Turks and Caicos Rock Iguana, *Cyclura carinata*, Iverson 1979; Allen Cays Rock Iguana, *Cyclura cychlura inornata*, Iverson 2007), with Green Iguanas exhibiting lower juvenile and adult survival rates, shorter times to maturity (with respect to *Cyclura*), shorter life spans, and larger clutch sizes. Wiewandt (1982) argued that climate and predator pressures were the primary determinants in the evolution of life history differences in the Iguanidae, and while our results generally support these ideas, it is clear there is a need for more life table studies on additional iguana species in order to more rigorously test hypotheses on life history evolution in this family.

There is also a need for more intra-specific studies, because life history characteristics of a population may vary greatly depending upon whether it is stable, declining locally due to over-exploitation, or expanding in areas outside its natural range of distribution. While we recognize the limitations inherent in generalizing from one population to another, we still believe that, lacking more information from other populations, the female Green Iguana life table and projection matrix we constructed may have relevance for other iguana populations.

The BCI iguana population on which this study was based was protected from poaching, but most natural iguana populations experience harvests that specifically target nesting females (Fitch and Henderson 1977; Fitch et al. 1982; Stephen et al. 2011). The sensitivity analysis we conducted indicated that the most effective means to increase λ in our population would have been to raise survival rates during the first two years of life, while the elasticity analyses highlighted the importance of survival during the first four years of life. While it might seem complicated to implement predator control programs or other intensive management strategies such as headstarting to increase juvenile survival rates, thanks to their unique biology, this might not be necessary for Green Iguanas. Body size is correlated with age in young Green Iguanas, but they grow at variable rates (Burghardt and Rand 1985; Werner 1991) and their growth trajectories seem to asymptote at very different SVLs, so that in nesting females, age is no longer correlated with body size (Zug and Rand 1987). But faster growing hatchling and juvenile iguanas suffer lower predation rates (Greene et al. 1978), meaning that by increasing their growth rates, their survival also would increase. For example, Werner (1991) divided 12 pairs of captive-reared sibling female Green Iguanas into control (natural diet) and experimental (enhanced diet) groups for the first seven months of life, and produced a 32% difference in body mass between groups. Only one of the 12 control females reproduced at two years of age, while half of the experimental group nested at this age. Obviously, enhancing juvenile growth rates in over-exploited Green Iguana populations holds great promise for altering their demographics so they may better withstand harvests. Planting optimal diet items in juvenile habitat is one possible strategy, and inoculating hatchlings with microbial gut faunas that have been shown to spur growth is another (Troyer 1984a, b).

Our life table and projection matrix also might be applicable to exotic Green Iguana populations in need of control, for example where an exotic population has reached its carrying capacity and females are emigrating in search of less crowded nesting sites, thereby expanding the range of the introduction. As before, it could be by altering juvenile survival rates that the demographics of such a population might best be managed. And again, one need not contemplate intensive juvenile eradication projects. There are other means to lower hatchling and juvenile growth rates, and thereby their survival rates and perhaps also increase their ages at first reproduction, that also are based upon their herbivory and associated gut microbial faunas. Wikelski et al. (2002) documented a 60% decline in Marine Iguana (*Amblyrhynchus cristatus*) densities following a minor oil spill that lightly covered the algae that these iguanas consume. The iguanas did not die immediately, but apparently starved to death with full stomachs after losing their microbial gut faunas, and hence their ability to digest their food. Such a light application on the vegetation of some environmentally innocuous agent capable of deactivating juvenile Green Iguana gut faunas might help control or even eliminate introduced populations.

Acknowledgments.—This study was supported by NSF grants BNS 78-14196 and BNS 82-17569 to GMB, Smithsonian Scholarly Studies grants to ASR, and the Adopt your Logo project of Ecopetrol and the Instituto von Humboldt to BCB and VPP, and Smithsonian Exxon Fellowships that supported many of the field assistants. Thanks to our field assistants Barbara Allen Savitsky, Carlos Avila, Eric Castillo, Leo Fleishman, José Hin, Roberto Ibañez, Mathew Kramer, Maria Elena Leon, Lauri McHarque, Luis Paz, Vania de Silva Nunes, Frank Solis, and Katherine Troyer.

LITERATURE CITED

Abts, M.L. 1987. Environment and variation in life history traits of the Chuckwalla, *Sauromalus obesus*. Ecological Monographs 57:215–232.

Andrews, R.M. 1989. Intra-population variation in age of sexual maturity of the tropical lizard *Anolis limifrons* in Panama. Copeia 1989:751–753.

Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912–923.

Bock, B.C. 1984. Movement patterns relative to nesting site locations in a population of Green Iguanas (*Iguana iguana*) in Panama. Ph.D. Dissertation, University of Tennessee, Knoxville, Tennessee, USA. 139 p.

Bock, B.C. 2014. *Iguana iguana* Linnaeus 1758. Common Green Iguana. IUCN SSC Iguana Specialist Group. Available from http://www.iucn-isg.org/species/iguana-species [Accessed 13 January 2015].

Bock, B.C., and A.S. Rand. 1989. Factors influencing nesting synchrony and hatching success at a Green Iguana nesting aggregation in Panama. Copeia 1989:978–986.

Bock, B.C., V.P. Páez, and A.S. Rand. 1998. Temperaturas del suelo atípicas en áreas comunales de anidación de la Iguana Verde (*Iguana iguana*) en Colombia y Panamá. Crónica Forestal y del Medio Ambiente 13:55–70.

Bock, B.C., A.S. Rand, and G.M. Burghardt. 1985. Seasonal migration and nesting site fidelity in the Green Iguana. Pp. 435–443 *In* Migration: Mechanisms and Adaptive Significance. Rankin, M.A. (Ed.). University of Texas Marine Science Institute, Port Aransas, Texas, USA.

Bock, B.C., A.S. Rand, and G.M. Burghardt. 1989. Nesting season movements of female Green Iguanas (*Iguana iguana*) in Panama. Copeia 1989:214–216.

Burghardt, G.M. 2004. Iguana research: looking back and looking ahead. Pp. 1–6 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Burghardt, G.M., and A.S. Rand. 1985. Group size and growth rate in hatchling Green Iguanas (*Iguana iguana*). Behavioral Ecology and Sociobiology 18:101–104.

Burnham, K.P., and D.R. Anderson. 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, New York, USA.

Castanet, J. 1994. Age estimation and longevity in reptiles. Gerontology 40:174–192.

Caswell, H. 2001. Matrix Population Models. Construction, Analysis, and Interpretation. 2nd Edition. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, USA.

Drummond, H. 1983. Adaptiveness of island nest-sites of Green Iguanas and Slider Turtles. Copeia 1983:529–530.

Drummond, H., and G.M. Burghardt. 1982. Orientation in dispersing hatchling Green Iguanas, *Iguana iguana*. Pp. 271–291 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Dugan, B.A. 1982. The mating behavior of the Green Iguana, *Iguana iguana*. Pp. 320–341 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Dugan, B.A., A.S. Rand, G.M. Burghardt, and B.C. Bock. 1981. Interactions between nesting crocodiles and iguanas. Journal of Herpetology 15:409–414.

Falcón, W., J.D. Ackerman, W. Recart, and C.C. Daehler. 2013. Biology and impacts of Pacific island invasive species. 10. *Iguana iguana*, the Green Iguana (Squamata: Iguanidae). Pacific Science 67:157–186.

Fisher, R.A. 1930. The Genetical Theory of Natural Selection. Oxford at the Claredon Press, Cambridge, United Kingdom.

Fitch, H.S., and R.W. Henderson. 1977. Age and sex differences, reproduction, and conservation of *Iguana iguana*. Milwaukee Public Museum Contributions to Biology and Geology 13:1–21.

Fitch, H.S., R.W. Henderson, and D.M. Hillis. 1982. Exploitation of iguanas in Central America. Pp. 397–416 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

García-Quijano, C.G., T.A. Carlo, and J.A. Arce-Nazario. 2011. Human ecology of a species introduction: interactions between humans and introduced Green Iguanas in a Puerto Rican urban estuary. Human Organization 70:164–178.

Greene, H.W., G.M. Burghardt, B.A. Dugan, and A.S. Rand. 1978. Predation and the defensive behavior of Green Iguanas (Reptilia, Lacertilia, Iguanidae). Journal of Herpetology 12:169–176.

Harris, D.M. 1982. The phenology, growth, and survival of the Green Iguana, *Iguana iguana*, in northern Colombia. Pp. 150–161 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Henderson, R.W. 1974. Aspects of the ecology of the juvenile Common Iguana (*Iguana iguana*). Herpetologica 30:327–332.

Hirth, H.F. 1963. Some aspects of the natural history of *Iguana iguana* on a tropical strand. Ecology 44:613–615.

Iverson, J.B. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bulletin of the Florida State Museum, Biological Sciences 24:175–358.

Iverson, J.B. 2007. Juvenile survival in the Allen Cays Rock Iguana (*Cyclura cychlura inornata*). Copeia 2007:740–744.

Knapp, C.R., and J.G. Abarca. 2009. Effects of radio transmitter burdening on locomotor ability and survival of iguana hatchlings. Herpetologica 65:363–372.

Lebreton, J.D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

López-Torres, A.L., H.J. Claudio-Hernández, C.A. Rodríguez-Gómez, A.V. Longo, and R.L. Joglar. 2011. Green Iguanas (*Iguana iguana*) in Puerto Rico: is it time for management? Biological Invasions 14:35–45.

Meshaka, W.E., Jr., H.T. Smith, E. Golden, J.A. Moore, S. Fitchett, E.M. Cowan, R.M. Engeman, S.R. Sekscienski, and H.L. Cress. 2007. Green Iguanas (*Iguana iguana*): the unintended consequence of sound wildlife management practices in a south Florida park. Herpetological Conservation and Biology 2:149–156.

Muñoz, E.M., A.M. Ortega, B.C. Bock, and V.P. Páez. 2003. Demografía y ecología de anidación de la Iguana Verde, *Iguana iguana* (Squamata: Iguanidae), en dos poblaciones explotadas en la Depresión Momposina, Colombia. Revista de Biología Tropical 51:229–240.

Pasachnik, S.A., R. Carreras de Léon, V.H. Reynoso, E. Rupp, Y.M. Léon, and S.J. Incháustegui. 2012. Green Iguana (*Iguana iguana*) in the Dominican Republic. IRCF Reptiles and Amphibians Conservation and Natural History 19:1–3.

Rand, A.S. 1968. A nesting aggregation of iguanas. Copeia 1968:552–561.

Rand, A.S. 1984. Clutch size in *Iguana iguana* in central Panama. Pp. 115–122 *In* Vertebrate Ecology and Systematics. Segal, R.A., L.E. Hunt, J.L. Knight, L. Malaret, and N.L. Zuschlag (Eds.). University of Kansas Museum of Natural History, Lawrence, Kansas, USA.

Rand, A.S., and B.C. Bock. 1992. Size variation, growth, and survivorship in nesting Green Iguanas (*Iguana iguana*) in Panama. Amphibia-Reptilia 13:147–156.

Rand, A.S., and B.A. Dugan. 1980. Iguana egg mortality within the nest. Copeia 1980:531–534.

Rand, A.S., and H.W. Greene. 1982. Latitude and climate in the phenology of reproduction in the Green Iguana. Pp. 142–149 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Rand, A.S., and W.M. Rand. 1978. Display and dispute settlement in nesting iguanas. Pp. 245–251 *In* Behavior and Neurology of Lizards: An Interdisciplinary Colloquium. Greenberg, N., and P.D. MacLean (Eds.). National Institute of Mental Health, Rockville, Maryland, USA.

Rand, A.S., and M.H. Robinson. 1969. Predation on iguana nests. Herpetologica 25:172–174.

Rand, W.M., and A.S. Rand. 1976. Agonistic behavior in nesting iguanas: a stochastic analysis of dispute settlement dominated by the minimization of energy costs. Zeitschrift für Tierpsychologie 40:279–299.

Rodda, G.H. 1992. The mating behavior of *Iguana iguana*. Smithsonian Contributions to Zoology 534:1–40.

Rodda, G.H., B.C. Bock, G.M. Burghardt, and A.S. Rand. 1988. Techniques for identifying individual lizards at a distance reveal influences of handling. Copeia 1988:905–913.

Rovatsos, M., M. Pokorná, M. Almanová, and L. Kratochvíl. 2014. Cretaceous park of sex determination: sex chromosomes are conserved across iguanas. Biology Letters 10:20131093. doi:10.1098/rsbl.2013.1093

Sexton, O.J. 1975. Black Vultures feeding on iguana eggs in Panamá. American Midland Naturalist 93:463–468.

Slavens, F.L., and K. Slavens. 1999. Reptiles and Amphibians in Captivity: Breeding, Longevity, and Inventory. Woodland Park Zoological Gardens, Seattle, Washington, USA.

Smith, H.T., E. Golden, and W.E. Meshaka, Jr. 2007. Population density estimates for a Green Iguana (*Iguana iguana*) colony in a Florida state park. Journal of the Kansas Herpetological Society 21:19–20.

Smith, H.T., W.E. Meshaka, Jr., R.M. Engeman, S.M. Crossett, M.E. Foley, and G. Bush. 2006. Raccoon predation as a potential limiting factor in the success of the Green Iguana in southern Florida. Journal of the Kansas Herpetological Society 20:7–8.

Stephen, C., S. Pasachnik, A. Reuter, P. Mosig, L. Ruyle, and L. Fitzgerald. 2011. Survey of Status, Trade, and Exploitation of Central American Iguanas. Report, Department of Interior, United States Fish and Wildlife Service, Washington, D.C., USA.

Troyer, K. 1984a. Diet selection and digestion in *Iguana iguana*: the importance of age and nutrient requirements. Oecologia 61:201–207.

Troyer, K. 1984b. Behavioral acquisition of the hindgut fermentation system by hatchling *Iguana iguana*. Behavioral Ecology and Sociobiology 14:189–193.

van Devender, R.W. 1982. Growth and ecology of Spiny-tailed and Green Iguanas in Costa Rica, with comments on the evolution of herbivory and large body size. Pp. 162–183 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Wallace, B.P., S.S. Heppell, L.L. Lewison, S. Kelez, and L.B. Crowder. 2008. Impacts of fisheries bycatch on Loggerhead Turtles worldwide inferred from reproductive value analyses. Journal of Applied Ecology 45:1076–1085.

Werner, D.I. 1991. The rational use of Green Iguanas. Pp. 181–201 *In* Neotropical Wildlife Use and Conservation. Robinson, J.G., and K.H. Redford (Eds.). University of Chicago Press, Chicago, Illinois, USA.

White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–138.

Wiewandt, T.A. 1982. Evolution of nesting patterns in iguanine lizards. Pp. 119–141 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Wikelski, M., V. Wong, B. Chevalier, N. Rattenborg, and H.L. Snell. 2002. Galápagos islands: Marine Iguanas die from trace oil pollution. Nature 417:607–608.

Zug, G.R., and A.S. Rand. 1987. Estimation of age in nesting female *Iguana iguana*: testing skeleto-chronology in a tropical lizard. Amphibia-Reptilia 8:237–250.

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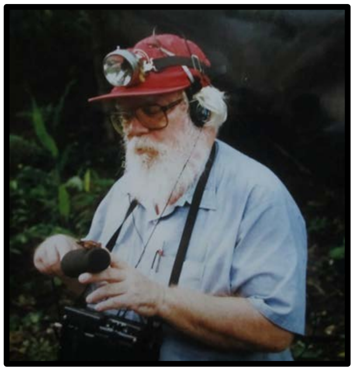

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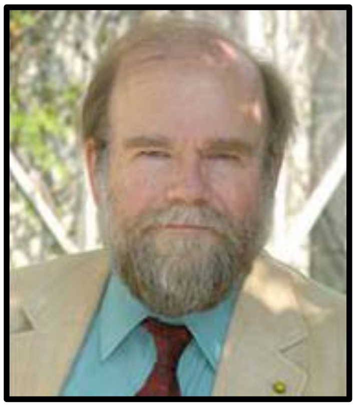

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Herpetological Conservation and Biology 11(Monograph 6):61–67.
Submitted: 10 October 2014; Accepted: 12 November 2015; Published: 12 June 2016.

CONSERVATION AND MANAGEMENT OF *CYCLURA* IGUANAS IN PUERTO RICO

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Abstract.—**Three species of iguanas in the genus *Cyclura* are or were once found in the Puerto Rican Archipelago including the native Mona Island Iguana (*C. stejnegeri*), the extirpated Anegada or Stout Iguana (*C. pinguis*), and the introduced Cuban Iguana (*C. nubila nubila*). These species are included in conservation and management plans within the Commonwealth of Puerto Rico aimed at recovery, reintroduction, and removal, respectively. To date, recovery efforts for Mona Island Iguanas include a fence to protect coastal nesting sites from feral pigs, a headstart program to improve population age structure and bolster recruitment, and feral cat control to improve juvenile survival. As a result of these actions, the population structure of *C. stejnegeri* has improved and all age classes are represented. However, full recovery of *C. stejnegeri* will require removal of feral mammals from Mona Island. As a first step toward reintroducing *C. pinguis* to Puerto Rico, numerous offshore islands were evaluated to determine their potential as reintroduction sites. Several suitable islands have been identified but most will require some restoration prior to reintroduction of *C. pinguis*. Exotic Cuban Iguanas on Magueyes Island have been identified as a species that should be removed. As such, they provide a unique opportunity to serve as surrogates for testing potentially risky conservation initiatives needed for some endangered *Cyclura* populations, such as the use of rodenticides on islands with native iguanas. The implementation of these conservation and management actions for all three *Cyclura* species will rely on funding, and for *C. pinguis* on the ability to acquire individuals for reintroduction.**

Resumen.—**Tres especies de *Cyclura* se encuentran o se han encontrado en el Archipiélago de Puerto Rico: la iguana nativa de Isla de Mona (*C. stejnegeri*), la extirpada iguana de Anegada o Robusta (*C. pinguis*), y la iguana introducida Cubana (*C. nubila nubila*). Estas especies forman parte de planes de conservación y manejo por parte del Estado Libre Asociado de Puerto Rico dirigidos a su recuperación, reintroducción, y remoción, respectivamente. Al presente, los esfuerzos de recuperación para la iguana de Mona incluyen una verja para proteger los sitios de reproducción costeros contra los cerdos asilvestrados, un programa de crianza asistida para mejorar las estructura de edades en la población y aumentar el reclutamiento, y un programa de control de gatos asilvestrados para mejorar la supervivencia de los juveniles. Como resultado de estas acciones la estructura poblacional de *C. stejnegeri* ha mejorado y hay representación de todos los estadíos. Sin embargo, la recuperación completa of *C. stejnegeri* requerirá de la remoción de los mamíferos asilvestrados de la Isla de Mona. Como un primer paso hacia la reintroducción de *C. pinguis* a Puerto Rico evaluamos numerosas islas separadas de la costa para determinar su potencial como sitio de reintroducción. Varias islas han sido identificadas como adecuadas, pero la mayoría requerirán de alguna restauración antes de reintroducir *C. pinguis*. Las iguanas cubanas exóticas de Magueyes han sido identificadas como una especie que debe ser removida del lugar. Por lo tanto, ellas proveen una oportunidad única para servir como especies de reemplazo para experimentar iniciativas de conservación potencialmente riesgosas pero necesarias para otras *Cyclura* consideradas en peligro, como la aplicación de rodenticidas en islas con iguana nativas. La implementación de estas acciones de conservación y manejo recaerá en la identificación del financiamiento requerido y, en el caso de *C. pinguis*, en la disponibilidad de individuos fundadores.**

Key Words.—headstart; invasive mammals; Mona; *nubila*; *pinguis*; reintroduction; *stejnegeri*

OVERVIEW

Iguanas in the genus *Cyclura* are among the largest terrestrial vertebrates and dominant herbivores native to the West Indies (Wiewandt 1977; Iverson 1979). They disperse seeds (Iverson 1985) and promote seedling germination (Hartley et al. 2000). Most species or subspecies are restricted to a single island or bank and face similar threats – competition and predation from alien invasive mammals, and habitat modification (Alberts 2000). Centrally located in the West Indies is Puerto Rico, an island nation classified as a Commonwealth under the political jurisdiction of the United States of America.

As an array of several islands and cays, Puerto Rico harbors a high percentage of endemic species, particularly reptiles and amphibians (Rivero 1978; García et al. 2005; Joglar et al. 2007). U.S. state (New

García, Miguel A., and Glenn P. Gerber. 2016. Conservation and management of *Cyclura* iguanas in Puerto Rico. Pp. 61–67 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Wildlife Act of Puerto Rico #241, Department of Natural and Environment Resources 1999) and federal laws (Endangered Species Act 1973, Title 16 United States Code, Sections 1531–1544) and regulations protect all of these species. *Cyclura* iguanas are a peculiar case because Puerto Rico harbors one endemic species, the Mona Island Iguana (*C. stejnegeri*) and one exotic species, the Cuban Iguana (*C. nubila nubila*). Moreover, another species, the Anegada or (hereafter) Stout Iguana (*C. pinguis*), was apparently once native to Puerto Rico (Pregill 1981). Today, the only extant populations of this species are in the British Virgin Islands (BVI; Perry and Gerber 2011), which are part of the Puerto Rican Bank and were contiguous with Puerto Rico during the last glacial maximum when sea levels were much lower (Pregill 1981). However, late Pleistocene fossils of *C. pinguis* from limestone cave deposits in northern Puerto Rico (Miller 1918; Pregill 1981), and remains from Native American middens on the island of St. Thomas in the U.S. Virgin Islands (Barbour 1919; Pregill 1981) suggest a much wider historical distribution. Exactly when or why the species became restricted to Anegada is unknown and is subject to considerable debate (Perry and Gerber 2011). We use Stout Iguana instead of Anegada Iguana since this latter common name does not represent adequately the biogeographical distribution of the species and limits its funding attractiveness from the Puerto Rican side. The species of *Cyclura* currently or previously found within the Puerto Rican Archipelago have been part of different conservation and management initiatives in Puerto Rico. Here, we describe efforts aimed at recovery of the Mona Island Iguana, reintroduction of the Stout Iguana, and removal of the Cuban Iguana.

MONA ISLAND IGUANA (*CYCLURA STEJNEGERI*)

Mona Island (5,301 ha) is a nature reserve, administered by the Puerto Rico Department of Natural and Environmental Resources (DNER). It is located approximately midway between the islands of Puerto Rico and Hispaniola but it is not part of the Puerto Rican or Hispaniolan Bank. The reserve is managed for mixed use (e.g., nature tourism, fishing, hiking, bird watching, and hunting) and there is a biological station for wardens and visiting scientists. While it lacks a permanent human settlement, it has experienced severe habitat modification in the past for guano mining, forestry, and agricultural purposes (Wiewandt 1977; García 2004). Rats, cats, pigs, and goats are established on the island, and coupled with habitat alteration, present major threats to the survival of Mona Island Iguanas. Hunting is allowed and encouraged, however, as a control measure for pigs and goats.

Cyclura stejnegeri is closely related to the Hispaniolan Rhinoceros Iguana (*C. cornuta*) and was previously considered a subspecies of *C. cornuta* (Powell and Henderson 1999). Mona Island Iguanas are classified as Endangered by the Regulation to Govern the Endangered and Threatened Species in the Commonwealth of Puerto Rico (Department of Natural and Environmental Resources 2004), the IUCN Red List of Threatened Species (García et al. 2000), and considered Threatened by the U.S. Fish and Wildlife Service (USFWS). These classifications have permitted the allocation of state and federal funds for the recovery of this species since 1998. The first significant field research on the Mona Island Iguana occurred from 1972–1975 when Thomas Wiewandt studied this species for his doctoral dissertation (Wiewandt 1977). Among several findings, Wiewandt (1977) concluded that Mona Island Iguana numbers (2,000 individuals) and densities (0.33 iguanas/ha) were “abnormally low” for a *Cyclura* species. This laid the foundation for a recovery program that started approximately ten years later with several conservation initiatives undertaken or led by DNER.

The first conservation action aimed to increase the survival of Mona Island Iguanas was the installation of a fence on the coastal plain to protect nesting areas from egg predation by feral pigs in 1984. This structure lasted (although in poor condition) until 2005 when it was replaced by a fence of much higher quality and with a mesh size that excluded pigs yet allowed iguanas to pass through and nest in historic areas.

Despite the exclusion of pigs from coastal nesting grounds, investigators noted that Mona Island Iguanas exhibited a population structure composed mostly of adult and aging individuals (Wiewandt and García 2000). This was considered to be the result of years of predation on hatchlings by feral cats, and was later confirmed when research documented a 13% survival rate for hatchling iguanas during their first five months (Pérez-Buitrago 2000). To address predation of hatchlings by cats and bolster recruitment rates of the Mona Island Iguana population, a headstart (HST) program was established in 2000 by DNER. Hatchling iguanas emerging from nests were collected each year and transferred to a captive facility on-island for rearing to a less vulnerable size.

The Mona Island HST program has been very successful (García et al. 2007). Over the last 14 years, 316 headstarted individuals have been released back into the wild. Iguanas of 22.5 cm snout-vent length, a size deemed large enough to survive in the wild with cats, were produced within two years. Documented survival of released HST iguanas was at least 40.3% (García et al. 2007), but this is a conservative calculation as it is based on recapture rates. The density of mid-sized iguanas increased by 71% within the study site and HST iguanas 4–5 years of age were observed breeding (Pérez-Buitrago et al. 2008). Thus, the short-term goals of improving the population structure and bolstering recruitment of Mona Island Iguanas were achieved with the HST program.

Despite the success of the HST program, it only serves as a stopgap measure. Since the primary threats to Mona Island Iguanas are invasive mammalian species, the focus is now on the eradication of feral pigs, cats, and rats. To accomplish this conservation objective, a collaborative relationship has been established with Island Conservation (IC), a non-governmental organization (NGO) devoted to island restoration through the removal of alien invasive species. The first step toward this goal was the completion of a feasibility study to eradicate feral pigs, cats, and rats from Mona Island. Cats have been eradicated from six islands larger than Mona and pigs from 11 larger islands. However, rats have not yet been eradicated from any tropical island as large as Mona (Island Conservation, University of California Santa Cruz Coastal Conservation Action Laboratory, IUCN SSC Invasive Species Specialist Group, University of Auckland, and Landcare Research New Zealand. 2014. Database of Island Invasive Species Eradications. Available from http://diise.islandconservation.org [Accessed 19 September 2014]). In addition to ecological and logistical challenges, a major hurdle will be securing the estimated 8.2 million US dollars required for eradicating pigs, cats, and rats (Island Conservation 2013). Feral goats are not part of the proposed eradications because they pose less of a threat to Mona Island Iguanas and are actively hunted, restricting the goat population so that minimal impact is noted on island vegetation (Joglar et al. 2007).

STOUT IGUANA (*CYCLURA PINGUIS*)

The only natural, extant population of *C. pinguis* is on Anegada Island (3,900 ha; Schomburgk 1832; Barbour 1917), located on the northeastern edge of the Puerto Rican Bank in the British Virgin Islands. Habitat degradation and alien invasive mammals have threatened the Anegada population of *C. pingui*s for centuries, (Carey 1975; Mitchell 1999; Island Resource Foundation 2013). To bolster low recruitment due to heavy predation of juveniles by feral cats, a HST program was established in 1997 (Gerber 2004). This program has been very successful (Bradley and Gerber 2006; Perry and Gerber 2011) and the wild adult population has doubled in size as a result. However, similar to *C. stejnegeri*, headstarting is a stopgap measure and not considered a permanent solution. Habitat protection and feral mammal removal are needed to safeguard the long-term survival of the Anegada population (Island Conservation 2006; Gerber and Pagni 2012). As a hedge against extinction on Anegada, *C. pinguis* has been introduced successfully to several private islands in the BVI. Unfortunately, all of the introduced populations stem from just eight founders moved from Anegada to Guana Island in the mid-1980s (Goodyear and Lazell 1994), raising concerns regarding inbreeding and genetic diversity (Perry and Gerber 2011).

A comprehensive management strategy for *C. pinguis* is needed and should include habitat protection and invasive mammal eradications on Anegada, genetic management of introduced populations in the BVI, and establishment of the species on the most suitable, protected islands elsewhere in the Puerto Rican Bank. The island of Puerto Rico is not appropriate for *C. pinguis* due to urban development, alien invasive species, and potential poaching. However, there are several small islands and cays near Puerto Rico where *C. pinguis* could be established to help secure the species' long-term survival.

We assessed seven islands and cays with the goal of determining their suitability to support *C. pinguis* populations (Table 1). The evaluated sites were: Caja de Muertos, Cayo Icacos, Cayo Ratones, Cayo Diablo, Cayo Lobos, Culebrita, and Luis Peña. The first four belong to the national system of natural reserves administered by the Puerto Rico DNER, but Cayo Lobos is privately owned. Culebrita and Luis Peña are wildlife refuges under the administration of the Municipality of Culebra Island and the USFWS.

Caja de Muertos and Cayo Icacos stand out as the best choices for introducing *C. pinguis*. Caja de Muertos is a relatively large (202 ha) limestone island, located off the

TABLE 1. Puerto Rican islands surveyed for their suitability to support *Cyclura pinguis*. Size and vegetation parameters were assessed rapidly during island visits. Size was determined in relative terms (large: > 200 ha; medium: 50–200 ha; small: < 50 ha) and vegetation was related to the overall condition (excellent = typical tropical dry forest vegetation similar in condition to the undisturbed sites on Anegada Island; good = disturbed tropical dry forest vegetation).

Island	Size	Vegetation	Substrate	Cats	Rats	Other	Common Green Iguanas	Designation	Facilities
Caja de Muertos	Large	Excellent	Limestone	No	Yes	No	Yes	DNER	Yes
Icacos	Medium	Excellent	Limestone	Yes	Yes	No	Yes	DNER	No
Ratones	Small	Good	Limestone	No	No	No	Yes	DNER	No
Lobos	Small	Good	Limestone	No?	Yes	No	Yes	Private	No
Diablo	Small	Good	Limestone	No	No	No	No	DNER	No
Luis Peña	Medium	Good	Volcanic	No?	Yes	Goat	Yes	USFWS	No
Culebrita	Medium	Good	Volcanic	No?	Yes	Deer	Yes	USFWS	No

south-central coast of Puerto Rico, with dense tropical dry forest. It has abundant food resources and is the only island surveyed with facilities (dock and field station) and the presence of a resident biologist and DNER rangers. The only serious drawback to this island is the presence of non-native rats and Common Green Iguanas (*Iguana iguana*; refuge manager, pers. comm.), which must be removed prior to introducing *C. pinguis*. Cayo Icacos is a somewhat smaller (66 ha) uninhabited, limestone island located off the northeast coast of Puerto Rico. The vegetation structure is open tropical dry forest that is nearly identical to that on Anegada. Like Caja de Muertos, Icacos is inhabited by rats, Common Green Iguanas, and feral cats. At the very least, the Green Iguanas and cats would have to be removed prior to introducing *C. pinguis*. Nonetheless, in our opinion, Cayo Icacos has the best habitat for *C. pinguis* of all the islands we surveyed. Moreover, it is part of the Cordillera Cays Nature Reserve that includes three other small, suitable islands (Cayo Ratones, Cayo Lobos, and Cayo Diablo), which could be managed along with Cayo Icacos as a metapopulation for *C. pinguis*.

Caja de Muertos and Cayo Icacos beaches are both visited regularly by day-trippers. These tourists stay mainly on the beachfront, thus they are not expected to impact iguana habitat. We are aware of detrimental effects caused by the inappropriate habit of feeding iguanas from other islands in the region (Knapp et al. 2013). DNER intends to manage this practice with a comprehensive educational campaign that showcases this wildlife restoration initiative (i.e., *C. pinguis* introduction) and explains appropriate behavior towards the animals and the need for eradicating invasive species as a prerequisite.

Biosecurity protocols for both reserves, as in any eradication project, will have to be developed and implemented (Tershy et al. this volume). The partnership between IC and DNER will maximize the probability for success, as IC will provide needed expertise and DNER will carry out the implementation and the enforcement of the prescribed actions. Integrating the two private islands (i.e., Cayo Lobos and Palominos) within the Cordillera Cays Natural Reserve in the eradication program is critical, particularly for rats and Common Green Iguanas. Therefore, a proactive approach and invitation to the owners must be included in a management plan. Notwithstanding the usual challenges of implementing biosecurity measures, Caja de Muertos represents a relatively easier situation since it is more isolated and harbors a permanent staff (i.e., manager and rangers). We propose giving priority status to removing exotic mammalian vertebrates from Caja de Muertos and the islands of the Cordillera Cays Nature Reserve so that *C. pinguis* can be introduced to the Puerto Rican Archipelago. This international initiative will require the full cooperation and involvement of the US Commonwealth of Puerto Rico DNER, the USFWS, and the United Kingdom Dependent Territory of the BVI National Parks Trust and BVI Conservation and Fisheries Department.

CUBAN IGUANA (*CYCLURA NUBILA NUBILA*)

***Cuban Iguana (*Cyclura nubila nubila*)*.**—In the late 1960s a small but unknown number of Cuban Iguanas (*C. nubila nubila*) escaped from a zoo in Puerto Rico, and were then introduced and became established on Magueyes Island (7.2 ha) located off the southwest coast of Puerto Rico (Rivero 1978). The Cuban Iguana is listed as Threatened by the USFWS but the Puerto Rican population is excluded from this designation (Office of the Federal Register 1983). Unfortunately, this duality has the potential to create confusion for law enforcement, as it is easy to mistakenly assume that federal laws protect the introduced Puerto Rican population. In the 1980s this isolated population was estimated at 167 iguanas and was experiencing predation from feral and pet cats (Christian et al. 1986). In the early 2000s population densities increased to 55–70 iguanas/ha after the implementation of a rat and cat control program on the island (Allan Lewis, pers. comm.; Ricardo López-Ortiz, pers. comm.). In 2005, 422 iguanas were counted individually on the island, which is equivalent to a density of almost 60 animals/ha (López-Ortiz unpubl. data). This population density is abnormally high when compared to the 5.3 ± 1.4 iguanas/ha reported for the natural populations found in the Guantánamo Naval Base in Cuba (Alberts et al. 2001).

The high density of Cuban Iguanas on Magueyes Island forced interactions with the personnel and students associated with the University of Puerto Rico's Department of Marine Science (DMS), which is located on the island. Iguanas were sometimes fed and subsequently began harassing people in search of food. Despite staff and visitor complaints about iguana attacks, most of the residents and visitors believe iguanas represent a cultural emblem of Magueyes Island. As the problems associated with human-iguana interactions intensified, the DMS administration requested intervention by the DNER, whose jurisdiction includes iguanas and departmental policies to support controlling exotic and invasive species. Furthermore, should iguanas disperse from the island and establish on the mainland, it could have profound impacts on the environment and tourism. As a consequence, the DNER granted a permit to a private collector to export 100 Cuban Iguanas from Magueyes in 2008. These animals were shipped to and arrived safely in Miami, but their current status or ultimate destination is unknown.

Managing the introduced population on Magueyes is complicated because local laws and regulations support its eradication, but the population also presents unique opportunities for scientific research. Studies of Cuban Iguanas have been limited relative to other species (but see González et al. and references therein this volume). Alien invasive mammals are a major threat to *Cyclura* iguanas throughout their range, and eradication of alien invasive mammals from Caribbean islands has been amply recommended for the protection of iguanas and other native wildlife (see Tershy et al. this volume). However, several efficient techniques used to capture or kill cats and rats could potentially harm iguanas. For example, iguanas can enter box traps, get caught in leg-hold traps, or eat bait impregnated with rodenticide. Therefore, thoughtful evaluations of these techniques and how to adapt them for use in habitats with native iguanas are compulsory and timely. For this, the Cuban Iguana population on Magueyes represents a unique opportunity to serve as a surrogate for testing mitigation strategies for eradicating alien invasive mammals on other islands with iguanas.

CONCLUSIONS AND RECOMMENDATIONS

Implementation of the recommended actions suggested here depends principally on obtaining the necessary financial support. Invasive species eradications are expensive but necessary for further recovery of *C. stejnegeri* on Mona Island and reintroduction of *C. pinguis* to the Puerto Rican Archipelago. Therefore, we must strengthen fundraising capabilities, which require new approaches involving local, national, and international collaborations between NGOs and governments. In the specific case of *C. pinguis*, an agreeable position from the government of the BVI to allow the movement of animals outside its national borders is needed.

Acknowledgments.—We thank Peter Tolson (Toledo Zoo), Alberto Álvarez, and Cielo Figuerola for their contributions to the Mona Island Iguana Recovery Project. Likewise, for their contributions to the Anegada Iguana Recovery Project, we thank Kelly Bradley, Rick Hudson, and Mike Fouraker (all Fort Worth Zoo), Jeff Lemm and Allison Alberts (both San Diego Zoo), and the staff of the British Virgin Islands National Parks Trust. Special thanks are extended to José L. Herrera and Kirsty Swinnerton from Island Conservation. Funding for work conducted in Puerto Rico was provided principally from the US Fish and Wildlife Service Section 6 Projects.

LITERATURE CITED

Alberts, A. (Ed.). 2000. West Indian Iguanas: Status Survey and Conservation Action Plan. IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Alberts, A.C., T.D. Grant, G.P. Gerber, K.E. Comer, P.J. Tolson, J.M. Lemm, and D. Boyer. 2001. Critical Reptile Species Management on the U.S. Naval Base, Guantánamo Bay, Cuba. Report to United States Navy for Project No. 62470-00-M-5219. 84 p.

Barbour, T. 1917. Notes on the herpetology of the Virgin Islands. Proceedings of the Biological Society of Washington 30:97–104.

Barbour, T. 1919. A new rock iguana from Porto Rico. Proceedings of the Biological Society of Washington 32:145–148.

Bradley, K.A., and G.P. Gerber. 2006. Release of headstarted iguanas in Anegada, British Virgin Islands. Re-introduction News 25:14–16.

Carey, W.M. 1975. The rock iguana, *Cyclura pinguis*, on Anegada, British Virgin Islands, with notes on *Cyclura ricordi* and *Cyclura cornuta* on Hispaniola. Bulletin of the Florida State Museum, Biological Sciences 19:189–233.

Christian, K. 1986. Aspects of the life history of Cuban Iguanas on Isla Magueyes, Puerto Rico. Caribbean Journal of Science 22:159–164.

Department of Natural and Environmental Resources. 1999. New Wildlife Act of Puerto Rico #241. Department of State, San Juan, Puerto Rico. 26 p. Available from http://www.oslpr.org/v2/LeyesPopUpEn.aspx?yr=1999

Department of Natural and Environmental Resources. 2004. Regulation #6766 to Govern the Endangered and Threatened Species in the Commonwealth of Puerto Rico. San Juan, Puerto Rico. 60 p. Available from http://www.drna.pr.gov/

García, M.A. 2004. The effect of exotic tree plantations on the biodiversity of leaflitter arthropods in tropical islands. Ph.D. Dissertation, University of Michigan, Ann Arbor, Michigan, USA. 216 p.

García M.A., J.A. Cruz-Burgos, E. Ventosa-Febles, and R. López-Ortiz. 2005. Puerto Rico Comprehensive Wildlife Conservation Strategy. Department of Natural and Environmental Resources, San Juan, Puerto Rico. 164 p. Available from http://www.drna.pr.gov/

García, M.A., N. Pérez-Buitrago, A.O. Álvarez, and P.J. Tolson. 2007. Survival, dispersal and reproduction of headstarted Mona Island Iguanas, *Cyclura cornuta stejnegeri*. Applied Herpetology 4:357–363.

García, M., N. Pérez, and T. Wiewandt. 2000. *Cyclura stejnegeri*. The IUCN Red List of Threatened Species. Version 2014.2. Available from http://www.iucnredlist.org/details/29605/0 [Accessed 30 September 2014].

Gerber, G.P. 2004. An update of the ecology and conservation of *Cyclura pinguis* on Anegada. Iguana (Journal of the International Iguana Society) 11:23–26.

Gerber, G.P., and L. Pagni (Eds.). 2012. Anegada Iguana, *Cyclura pinguis* Species Recovery Plan, 2006–2010. IUCN SSC Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom. 29 p.

González, A., V. Berovides, D. Cobián, L. Espinosa, J. Milián, G. Abad, E. Palacio, M. Alonso-Tabet, M. López, and Y. Alonso. 2016. Monitoring the density of the Cuban Rock Iguana (*Cyclura nubila nubila*) from protected areas in southern Cuba. Pp. 68–78 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Goodyear, N.C., and J. Lazell. 1994. Status of a relocated population of endangered *Iguana pinguis* on Guana Island, British Virgin Islands. Restoration Ecology 2:43–50.

Hartley, L.M., R.E. Glor, A.L. Sproston, R. Powell, and J.S. Parmerlee. 2000. Germination rates of seeds consumed by two species of rock iguanas (*Cyclura* spp.) in the Dominican Republic. Caribbean Journal of Science 36:149–151.

Island Conservation. 2006. Restoration of the Anegada Rock Iguana population on Anegada Island, British Virgin Islands. Island Conservation, Santa Cruz, California, USA. Available on request from Island Conservation.

Island Conservation. 2013. The restoration of Mona Island Reserve: feasibility assessment for the removal of invasive pigs, cats, and rodents. Island Conservation, Santa Cruz, California, USA. 38 p. Report available on request from Island Conservation.

Island Resources Foundation. 2013. An environmental profile of the island of Anegada, British Virgin Islands. Island Resource Foundation, Tortola, British Virgin Islands and Washington, D.C., USA. Available from http://www.irf.org

Iverson, J. 1979. Behavior and ecology of the rock iguana, *Cyclura carinata*. Bulletin of the Florida State Museum, Biological Sciences 24:175–358.

Iverson, J.B. 1985. Lizards as seed dispersers? Journal of Herpetology19:292–293.

Joglar, R.L., A.O. Álvarez, T.M. Aide, D. Barber, P.A. Burrowes, M.A. García, A. León-Cardona, A.V. Longo, N. Pérez-Buitrago, A. Puente, N. Rios-López, and P.J. Tolson. 2007. Conserving the Puerto Rican herpetofauna. Applied Herpetology 4:327–345.

Knapp, C.R., K.N. Hines, T.T. Zachariah, C. Perez-Heydrich, J.B. Iverson, S.D. Buckner, S.C. Halach, C.R. Lattin, and L.M. Romero. 2013. Physiological effects of tourism and associated food provisioning in an endangered iguana. Conservation Physiology 1:cot032. doi:10.1093/conphys/cot032

Miller, G.S., Jr. 1918. Mammals and reptiles collected by Theodoor de Booy in the Virgin Islands. Proceedings of the United States National Museum 54:507–511.

Mitchell, N.C. 1999. Effect of introduced ungulates on density, dietary preferences, home range, and physical condition of the iguana (*Cyclura pinguis*) on Anegada. Herpetologica 55:7–17.

Office of the Federal Register. 1983. Endangered and threatened wildlife and plants; listing of 17 species of foreign reptiles as endangered or threatened species. Federal Register 48:28460–28464.

Pérez-Buitrago, N. 2000. Survival and dispersal of rock iguana hatchlings (*Cyclura cornuta stejnegeri*) on Mona Island, Puerto Rico. M.Sc. Thesis, University of Puerto Rico, Rio Piedras, Puerto Rico. 232 p.

Pérez-Buitrago, N., M.A. García, A. Sabat, J. Delgado, A. Álvarez, O. McMillan, and S.M. Funk. 2008. Do headstart programs work? Survival and body condition in headstarted Mona Island Iguanas *Cyclura cornuta stejnegeri*. Endangered Species Research 6:55–65.

Perry, G., and G.P. Gerber. 2011. Conservation of amphibians and reptiles in the British Virgin Islands: status and patterns. Pp. 105–127 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Powell, R., and R.W. Henderson. 1999. Addenda to the checklist of West Indian amphibians and reptiles. Herpetological Review 30:137–139.

Pregill, G. 1981. Late Pleistocene herpetofaunas from Puerto Rico. University of Kansas Museum of Natural History Miscellaneous Publication 71:1–72.

Rivero, J.A. 1978. Los Anfibios y Reptiles de Puerto Rico. Imprenta de la Universidad de Puerto Rico, Río Piedras, Puerto Rico.

Schomburgk, R.H. 1832. Remarks on Anegada. Journal of the Royal Geographic Society of London 2:152–170.

Tershy, B., K.M. Newton, D.R. Spatz, K. Swinnerton, J.B. Iverson, R.N. Fisher, P. Harlow, N.D. Holmes, and D.A. Croll. 2016. The biogeography of threatened insular iguanas and opportunities for invasive vertebrate management. Pp. 222–236 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Wiewandt, T.A. 1977. Ecology, behavior, and management of the Mona Island Ground Iguana, *Cyclura stejnegeri*. Ph.D. Dissertation, Cornell University, Ithaca, New York, USA. 338 p.

Wiewandt, T.A., and M. García. 2000. Mona Island Iguana (*Cyclura cornuta stejnegeri*). Pp. 27–31 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

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Herpetological Conservation and Biology 11(Monograph 6):68–78.
Submitted: 8 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

MONITORING THE DENSITY OF THE CUBAN ROCK IGUANA (*CYCLURA NUBILA NUBILA*) FROM PROTECTED AREAS IN SOUTHERN CUBA

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Abstract.—**The Cuban Rock Iguana (*Cyclura nubila nubila*) inhabits coastal regions of Cuba and satellite cays surrounding the island. The species is considered Vulnerable according to International Union for Conservation of Nature (IUCN) Red List of Threatened Species criteria and the Libro Rojo de los Vertebrados de Cuba. The main threats to the species include the alteration and degradation of coastal habitat and, to a lesser extent, poaching. Though some populations have been studied in the past, information concerning biology, ecology, and the status of many populations remain unknown. For three years we monitored 12 iguana populations from six study sites (two populations each site), located within protected areas from three mainland and three offshore sites from southern Cuba. This study represents the longest continuous monitoring program for *C. nubila nubila* in Cuban protected areas, as well as the first study ever conducted at four of our sites. We recorded spatial and temporal trends in iguana density, sex ratio, and age structure. Our results suggest higher inter-annual density variation from sites located on the Cuban mainland than from offshore cays. Across all sites, sex ratios varied between the reproductive and post-reproductive seasons, while the number of non-adults identified in the surveys fluctuated by approximately 30%. Iguana monitoring programs located in protected areas are necessary to quantify population impacts from acute (e.g., fire, hurricane) or prolonged (e.g., human impacts) events in order to test the efficacy of protected areas in maintaining iguana populations. Management implications derived from our data are discussed.**

Resumen.—**La Iguana Cubana (*Cyclura nubila nubila*) habita en las costas y en numerosos cayos que rodean a la isla de Cuba. La especie está considerada como Vulnerable de acuerdo con los criterios de la Lista Roja de Especies Amenazadas de la Unión Internacional para la Conservación de la Naturaleza (UICN) y el Libro Rojo de los Vertebrados de Cuba. La principal amenaza para esta especie ha sido la alteración y degradación de los hábitats costeros y, en menor medida, la caza furtiva. Aunque la especie ha sido objeto de estudio en el pasado, aún se desconocen importantes aspectos de su biología, su ecología y el estado de muchas de sus poblaciones. Durante tres años se monitorearon 12 poblaciones de iguana en seis sitios de estudio (dos poblaciones por sitio) localizadas en tres áreas protegidas de la isla principal y tres en cayos del sur de Cuba. Este estudio representa el programa de monitoreo continuo más extenso para *C. nubila nubila* en áreas protegidas cubanas, así como el primer estudio realizado en cuatro de estos sitios. Se obtuvieron tendencias espaciales y temporales de la densidad de iguanas, así como valores del cociente sexual y estructura de edades. Los resultados sugieren una mayor variación interanual de la densidad en sitios localizados en la isla de Cuba respecto a los localizados en los cayos. En todos los sitios, el cociente sexual varió entre las etapas reproductiva y post-reproductiva, mientras que el número de no adultos identificados fluctuó en aproximadamente 30%. Los programas de monitoreo de iguanas en áreas protegidas resultan necesarios para cuantificar impactos de eventos extremos (incendios, huracanes) o prolongados (impactos humanos) para probar la eficacia de las áreas protegidas en el mantenimiento de las poblaciones de iguanas. Se discuten algunas implicaciones para el manejo derivadas de los resultados.**

Key Words.—Caribbean; conservation; demography; Iguanidae; management; populations

INTRODUCTION

The Cuban Rock Iguana (*Cyclura nubila nubila*) is an endemic subspecies that was once common on the island of Cuba. It has, however, experienced recent population declines due to urbanization and indiscriminate hunting (Buide et al. 1974; Garrido and Jaume 1984; Berovides 1995). Nevertheless, the species is still relatively abundant in certain coastal sites on the mainland and associated offshore cays (Schwartz and Carey 1977), and is currently listed as Vulnerable by the International Union for Conservation of Nature (IUCN;

González, Amnerys, Vicente Berovides, Dorka Cobián, Leonardo Espinosa, Julio Milián, Gretel Abad, Ernesto Palacio, Manuel Alonso-Tabet, Manuel López, and Yairen Alonso. 2016. Monitoring the density of the Cuban Rock Iguana (*Cyclura nubila nubila*) from protected areas in southern Cuba. Pp. 68–78 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Alberts and Perera 1996) and the Libro Rojo de los Vertebrados de Cuba (González et al. 2012). The species has a patchy distribution along nearly 2,573 km^2 of mainland coastline as well as from numerous offshore cays. These habitats are generally characterized by coastal xerophytc vegetation (Schwartz and Carey 1977; Schwartz and Henderson 1991; Rodríguez 2003). The only inland, remnant populations are found in the Pinar del Río Province from Sierra de Galeras and Sierra Derrumbada in Viñales.

Our general lack of life history and population-trend information for the iguana across its entire range hinders developing broad conservation strategies (Berovides 1980). Indeed, current population assessments for the Cuban Iguana are limited (but see González et al. 2001, 2004, 2007; Cobián et al. 2008; Collazo et al. 2010). These assessments are critical, especially given that coastal areas are particularly sensitive to acute human perturbations and the effects of global climate change (e.g., loss of wetlands and mangrove forests, saltwater penetration in the freshwater lens; IPCC 2007). Contemporary and future impacts will further reduce the effective area of distribution and quality of habitat for the Cuban Iguana. Moreover, limited ranges and reduced populations of iguanas could further impact coastal habitat and restrict restoration efforts because the iguana is a potentially important seed disperser for native plant species (Iverson 1985; Alberts 2000a; Grant and Alberts 2001).

Monitoring populations of species constitutes an essential component of wildlife management and conservation science (Witmer 2005; Marsh and Trenham 2008). Effective monitoring programs can provide basic information on species distributions, identify species that are at-risk due to small or declining populations, provide insight on how management actions affect populations, and evaluate population responses to landscape alteration and climate change (Lyons et al. 2008; Lindenmayer and Likens 2009). Monitoring programs for species of conservation concern therefore represent a major tool for setting and evaluating conservation action priorities.

Although the designation of protected areas has undoubtedly improved the conservation status of endangered species worldwide (Chape et al. 2005), monitoring populations within such areas is critical to ensure that they are serving their conservation objectives. The objectives of this study were to record densities, sex ratios, and demography (% non-adults) of the Cuban Iguana across six protected areas on the southern mainland coast and offshore cays of Cuba. Results will help confirm the efficacy of protected areas in maintaining iguana populations on Cuba, allow managers to better understand density and demographic differences between mainland and insular iguana populations, and inform site-specific management strategies.

MATERIALS AND METHODS

Study areas.—This study was conducted from 2011 to 2013 in six protected areas along the southern coast of Cuba (Fig. 1): Guanahacabibes National Park (GH), Delta del Cauto Fauna Refuge (DC), Desembarco del Granma National Park (DG), Cayos de San Felipe National Park (CSF), Cayos de Ana María Fauna Refuge (CAM) and Jardines de la Reina National Park (CJR). The first three areas are located on the mainland, while

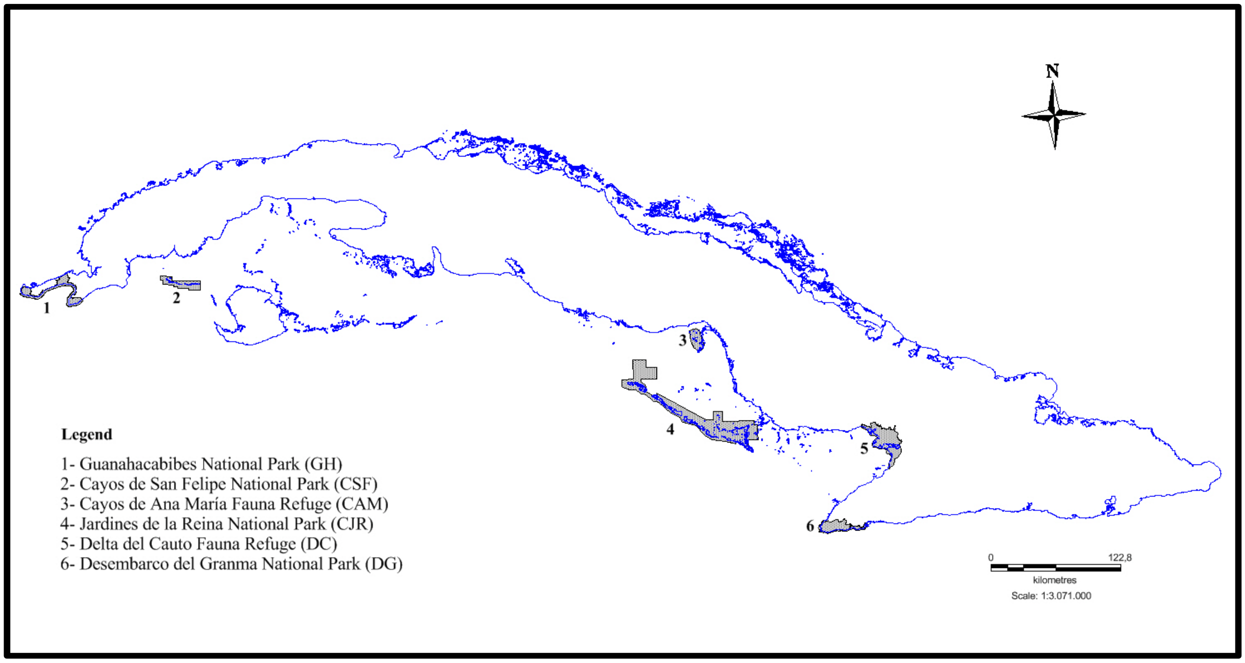


FIGURE 1. Geographic location of the six study sites for *Cyclura nubila nubila* in Cuba.

the other three are located on offshore cays. We defined each protected area as a study site. National parks in Cuba are generally extensive natural areas with scarce or no human population that aim to protect the representative landscapes, ecosystems, communities, and species in their natural habitats of national, regional, or international importance. Fauna refuges aim to protect and maintain populations of species, zoological communities, and habitats of autochthonous fauna that have regional, national, or local significance. Fauna refuges are generally less extensive areas than national parks, and are not always completely natural territories.

Study sites differed in size, geomorphology, and vegetation type (Table 1). Five vegetation formations, as described by Capote and Berazaín (1984), were represented at the study sites: (1) mangrove forests (MF) comprising of four characteristic species that can reach up to 15 m high including *Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*, and *Conocarpus erectus*; (2) sandy coastal vegetation (SC) with herbaceous plants such as *Sesuvium maritimum*, *Suriana maritima*, *Uniola paniculata*, and *Tournefortia gnaphalodes*, and tree species such as *Coccoloba uvifera* and *Coccothrinax littoralis*; (3) rocky coastal vegetation (RC) on limestone substrates, with ≥ 50 cm high shrubs such as *Oplonia tetrastichia* and *Flaveria linearis*; (4) coastal and subcoastal xeromorphic shrub (CX) communities with esclerofic shrubs, palms, and lianas such as *Croton micradenus*, *Calliandra colleticides*, *Neea shaferi*, and *Phyllostylon brasiliense*, and cactus species such as *Dendrocereus nudiflorus* and *Consolea macracantha*; and (5) microphyllous evergreen forest (MEF) with deciduous species up to 15 m high, spinous shrubs, lianas, and epiphytes such as *Bursera glauca*, *Drypetes mucronata*, *Amyris balsamifera*, and *Diospyros grisebachii.*

Although the level of anthropogenic disturbance in protected areas is generally low compared to non-protected areas, disturbance may occur in these areas. For example, in mainland national parks such as GH and DG, public activities for nature leisure and entertainment are allowed, such as birdwatching. The offshore protected areas (CSF, CAM, and CJR) are located within areas with active fishing boats and permanent fishing.

TABLE 1. General characteristics of study sites and survey design for monitoring Cuban Iguanas inhabiting protected areas of Cuba. Total and terrestrial area of sites, and surveyed area per site are indicated. Vegetation types include: MF (mangrove forests); SC (sandy coastal vegetation); RC (rocky coastal vegetation); CX (coastal and subcoastal xeromorphic shrub); and MEF (microphyllous evergreen forest).

Study site	Area (ha): Total Terrestrial Surveyed	Geo-morphologic structure	Vegetation types	Transect size (m): Length, min–max; Width	# of transects	# of walks (monthly mean and range)	# of maximum density estimates	Years and months surveyed		
								2011	2012	2013
Guanacahabibes National Park (GH)	39,830 23,880 842	Limestone	SC CX MEF RC	700–1,800 10	19	684 (28, 27–30)	26	Apr, Jun, Jul, Aug	Apr, May, Jun, Jul, Oct	Apr, Jun, Jul, Aug
Delta del Cauto Fauna Refuge (DC)	66,370 53,830 5,724	Delta River System	SC MF	400–1,500 10	9	224 (37, 12–68)	134	All 12 months	All 12 months	All 12 months
Desembarco del Granma National Park (DG)	32,576 26,180 443	Limestone	SC CX MEF RC	50–2,500 5	6	85 (44, 31–56)	41	-	Mar, May, Jul, Aug, Sep	Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov
Cayos San Felipe National Park (CSF)	26,250 2,041 234	Beaches and Sand Dunes	SC CX MF	800 10	4	112 (13, 6–16)	22	Jun, Sep, Dec	Mar, Jun, Sep, Dec	Mar, Jun, Sep, Dec
Cayos Ana María Fauna Refuge (CAM)	19,100 980 190	Beaches and Sand Dunes	SC MF	50–200 10	46	158 (53, 32–90)	28	Apr, May, Jun	Jul, Aug, Sep	Mar, Jun, Sep
Cayos Jardines de la Reina National Park (CJR)	217,036 16,079 4,670	Beaches, Limestone, and Sand Dunes	SC CX MF	500–1,000 10	20	112 (37, 25–60)	24	Apr, Jun, Sep	Mar, Jun, Oct, Nov	May, Nov

There is also a strong fishing presence at DC, an area located on the mainland but in the Cauto River Delta. In general, however, the greatest anthropogenic disturbance in protected areas occurs on the mainland because they are easier to access than offshore cays.

At sites with large geographic areas, iguanas were monitored in two populations per study site, separated by distances of 1 to 25 km. At our DG site, however, we conducted surveys in six areas because of habitat patchiness. Our offshore sites represent multiple smaller cays. For example, our CSF site includes two cays (88.2 and 146.0 ha), our CAM survey locations include nine cays (3.0 to 86.0 ha), while our CJR site included seven cays (9.0 to 861.0 ha). The total area surveyed per site varied from 190.2 ha in CAM to 5,724.1 ha in DC (Table 1).

Transect and survey methodology.—Transects were walked through homogeneous habitats, following Iverson (1979), Perera (1985), Hayes and Carter (1996), and Berovides et al. (2005) methodologies. Table 1 summarizes the characteristics of transects and surveys per study site. Transect number and size differed according to the geographic structure, total area, accessibility, and vegetation type at sites. Number of transects varied from 9 to 46 per site, for a total of 104 throughout all sites. Transect size varied from 50 to 1,800 m in length, and from 5 to 10 m in width (Table 1). Transects were fixed at all sites except for CAM and CJR, which were random due to small area size and patchy habitat, respectively. In all cases transects were separated at least 20 m from each other. A total of 21 observers (three per site) with similar experience working with Cuban Iguanas participated in the surveys. When under study, sites were visited from one to three times per month (mean = 1.4 ± (SD) 1.1 monthly walks). A total of 1,375 transects was walked during the study.

Sex and age structure (adult, non-adult) were recorded from two offshore sites (CSF and CJR), and two inland sites (GH and DC). Adult males and females were differentiated based on sexual dimorphism and secondary sexual traits described by Schwartz and Carey (1977) such as relative head size, length of dorsal crest scales, and gular fold (more conspicuous in males than in females). Individuals were identified as adults and non-adults based on body size and the presence of a dorsal chevron pattern in non-adults.

Surveys were conducted in different months of the year to include the reproductive and non-reproductive seasons. Based on information from other *Cyclura* species (Alberts 2000b) and our own experience with the Cuban Iguana, we performed pre-nesting surveys from March to May (courtship and copulation), reproductive surveys from June to August (oviposition and hatching), and post-reproductive surveys from September to February (absence of reproductive activity). We constrained our transect walks to times of maximum iguana activity (0930 to 1430; Perera 1985) and sunny days with little to no wind.

Data analyses.—To focus on the reproductively active population, we used only adult iguana sightings in our density analyses. Whenever possible, populations were visited in as many months as logistically feasible. Maximum number of adults observed per transect was recorded monthly, and data from each population were combined per site. To reduce the chance of artificially inflating or deflating population estimates based on seasonal fluctuations, total density per site was computed as the average of all monthly density estimations expressed as iguanas/ha, considering:

$$\mathrm{d} = \frac{\sum_{\mathrm{i}=1}^{\mathrm{n}} \mathrm{D}}{\mathrm{n}}$$

where d = mean of all density estimations per transects expressed as iguanas/ha; D = density estimation per individual transect expressed as iguanas/ha; and n = number of ha.

We analyzed density by year, season, and site; however, one study site (DG) was not sampled in 2011. Additionally, sex ratio and age structure were not obtained in only one of the populations at the DC site due to reduced visibility of individual characteristics in that habitat. We used non-parametric statistics because our dependent variable (density) was not normal after transformation. To evaluate spatial (among sites) and temporal (among the different years of study) density differences, we used Mann-Whitney and Kruskal-Wallis tests (Siegel and Castellan 2001). Finally, we used chi-squared tests to analyze sex ratio (% of females) and age structure (% of non-adults) per year, season, and site. We used the Bonferroni correction to reduce the familywise error rate for multiple comparisons. Therefore, the significance level was set at $\alpha = 0.003$ throughout the paper.

RESULTS

Density patterns.—Density of iguanas per year and site are shown in Table 2. We recorded the highest densities at the CSF (32.6 iguanas/ha) and CAM (26.9 iguanas/ha) sites, and the lowest density at GH (1.9 iguanas/ha). Mean density with all years combined differed statistically among sites ($H = 135.37$, df = 5, $P < 0.0001$; $n = 274$) and between combined mainland and combined offshore areas ($U = 2395.00$, $P < 0.0001$; $n = 274$).

We noted two sites with statistically significant differences in densities among the three years. In 2013, density decreased at the CSF site ($H = 15.59$, df = 2, $P = 0.0004$; $n = 22$), while density increased at the DC site ($H = 25.43$, df = 2, $P < 0.0001$; $n = 134$). Among

TABLE 2. Density (adults/ha) of *Cyclura nubila nubila* from six protected areas in Cuba. Mean and coefficient of variation (CV) are reported per year and for the entire study. *n* is the number of maximum density estimates.

Study Site	Year	Density	CV	*n*	Total Density	Total CV	Total *n*
Guanahacabibes (GH)	2011	1.9	44.4	8	1.9	42.2	26
	2012	1.8	43.9	10			
	2013	1.9	44.4	8			
Delta del Cauto (DC)	2011	5.3	95.2	51	8.3	98.8	134
	2012	6.7	100	53			
	2013	12.7	67.4	30			
Desembarco del Granma (DG)	2011	-	-	0	9.2	60.2	41
	2012	9.2	92.3	9			
	2013	9.2	60.3	32			
Cayos San Felipe (CSF)	2011	34.7	7.9	6	32.6	17.4	22
	2012	37.5	5.9	8			
	2013	26.2	12.0	8			
Cayos Ana María (CAM)	2011	26.7	19.9	7	26.9	17.0	28
	2012	31.5	6.0	6			
	2013	25.1	15.2	15			
Cayos Jardines de la Reina (CJR)	2011	4.9	57.5	8	7.2	88.9	24
	2012	6.0	57.7	6			
	2013	9.8	90.6	10			

the offshore sites, variability in densities (as recorded using the coefficient of variation) was higher in the CJR site relative to the CSF and CAM sites (Table 2).

Density did not differ by season ($H = 6.19$, df = 2, $P = 0.069$; $n = 274$), although monthly densities showed a variable pattern. Density of iguanas per month at two representative mainland and offshore study sites are shown in Fig. 2. Mainland areas showed density peaks that varied annually (at GH), or were consistent over time (June at the DC site; Fig. 2). Density estimates for iguanas inhabiting offshore protected areas (CSF and CAM) showed no monthly peaks (Fig. 2). Using our density estimates for each study site and all years, we estimate the population's size to be: 1,490.3 ± 123.0 iguanas at GH; 7,634.9 ± 719.4 iguanas at CSF; 5,116.4 ± 221.1 iguanas at CAM; 8,437.8 ± 1,212.2 iguanas at CJR; 8,818.8 ± 990.9 iguanas at DC; and 8,852.0 ± 1,022.2 iguanas at DG.

Sex ratio (% females) and age structure (% non-adults) patterns.—We recorded sex ratio and age structure at four sites (GH, CSF, CJR, and DC) over the entire three-year study (Fig. 3). Percent females averaged 52.9 ± 5.7% (range, 38.9–84.0%). Across all years and seasons, sex ratios were equivalent between males and females (minimum $\chi^2 = 0.19$, df = 2, all $P > 0.003$; Table 3). Age structure (% non-adults) averaged 30.8 ± 11.0% (range, 13.3–89.9%) for the

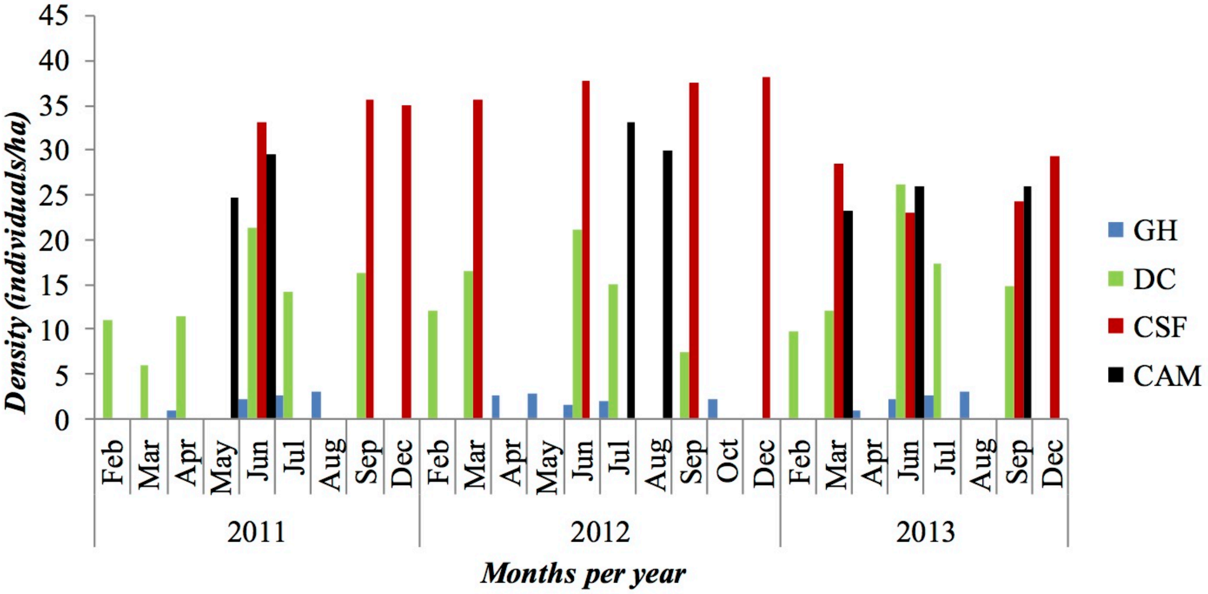


FIGURE 2. Seasonal changes in density (individuals/ha) of *Cyclura nubila nubila* in four sites in Cuba: Guanahacabibes (GH), Delta del Cauto (DC), Cayos de San Felipe (CSF), and Cayos de Ana María (CAM).

TABLE 3. Mean sex ratio (% females) and age structure (% non-adults) of Cuban Iguanas reported by season identified in this study. Standard deviation (SD) and coefficient of variation (CV) are reported. *n* is the number of maximum density estimates.

Season	Sex ratio (% females)				Age structure (% non-adults)			
	Mean	SD	CV	*n*	Mean	SD	CV	*n*
Pre-nesting	53.8	17.2	31.9	11	31.1	12.8	41.2	11
Reproductive	64.6	15.7	24.4	22	29.1	11.6	39.8	13
Post-reproductive	65.3	8.6	13.1	6	44.3	20.7	46.8	13

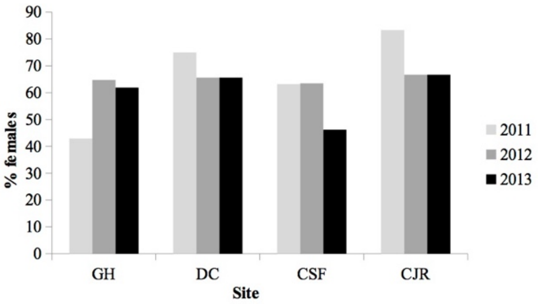


FIGURE 3. Sex ratio (% females) for *Cyclura nubila nubila* across three years at four study sites in Cuba: Guanahacabibes (GH), Delta del Cauto (DC), Cayos de San Felipe (CSF), and Cayos Jardines de la Reina (CJR).

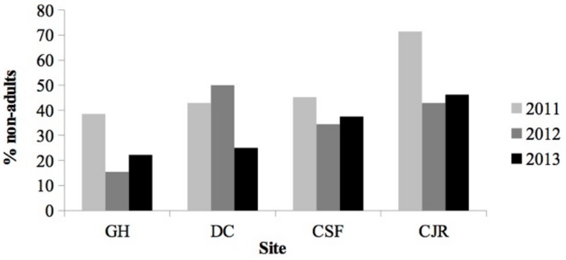


FIGURE 4. Age structure (% non-adults) for *Cyclura nubila nubila* across three years at four study sites of in Cuba: Guanahacabibes (GH), Delta del Cauto (DC), Cayos de San Felipe (CSF), and Cayos Jardines de la Reina (CJR).

three years at the four study sites (Fig. 4). Across all years and seasons, there was a general trend towards a decrease from 2011 to 2013 (Fig. 4) and an increase in the post-reproductive season (Table 3) of non-adult iguanas detected, although not statistically significant (all P > 0.003).

DISCUSSION

Density patterns.—This study represents the longest, continuous monitoring effort for the Cuban Rock Iguana inhabiting Cuba. The work is significant, especially because four of the six study sites (CAM, CJR, DC, and DG) had never been surveyed prior to this study. Results suggest that iguana densities vary depending on geography and location (mainland or offshore). The offshore sites, including Cayos de San Felipe National Park (CSF) and the Cayos de Ana María Fauna Refuge (CAM), supported the highest densities of iguanas (32.6 and 26.9 iguanas/ha, respectively). Relatively high densities for rock iguanas inhabiting smaller cays (higher than 26.9 iguanas/ha) have also been documented in The Bahamas. For example, the Allen Cays Rock Iguana (*Cyclura cychlura inornata*) can reach densities of 150.0 iguanas/ha (Iverson et al. 2006), while the Acklins Rock Iguana (*Cyclura rileyi nuchalis*) can reach densities of 92.7 iguanas/ha (Iverson et al. this volume). The higher densities reported at two of our offshore sites may be influenced by constrained geographic area and subsequent higher detection probabilities, lack of predators, and relatively less human disturbance. Interestingly, iguana densities were low (7.2 iguanas/ha) in the offshore Jardines de la Reina National Park (CJR). This density estimate is equivalent to our mainland populations, and may be influenced by the larger area of cays, higher prevalence of patchy vegetation structure, higher tourism and poaching pressure during the 1990s (G.R. Abad, pers. comm.), and habitat alteration due to recent natural events (hurricanes).

Our mainland sites, Guanahacabibes National Park (GH), Delta del Cauto (DC), and Desembarco del Granma National Park (DG), supported the lowest densities (1.9, 8.3, and 9.2 iguanas/ha, respectively). In general, mainland sites (i.e., larger islands) with rock iguanas typically support lower densities. For example, densities of *C. cychlura cychlura* from Andros Island (6,000 km^2) reach 2.5 adults/ha and up to 150 adults/ha for *C. cychlura inornata* inhabiting the Exuma Cays (4 ha; Knapp et al. 2006). The lower reported densities from mainland sites may be the result of increased predation pressure from a higher diversity and density of predators (e.g., snakes and birds). Indeed, snakes have been reported to be the most significant predators of iguana hatchlings from other islands (Knapp et al. 2010) and may be absent from some offshore cays. Lower overall density estimates, as well as higher seasonal and annual variability in densities, at the three mainland sites could also be driven by unconstrained space and a resultant increase in seasonal mobility, as well as lower detection rates.

Anthropogenic pressure may also influence iguana density and variability at mainland sites on Cuba. The mainland protected areas in our study are subject to measured levels of human visitation and feeding because of public access and the use of recreation facilities. Elsewhere on Cuba, negative effects of anthropogenic activities have been documented for *C. nubila,* including more intense social interactions and aggressive behavior among individuals (Alberts et al. 2001, Lacy and Martins 2003). Anthropogenic threats from roads are multifaceted and often relate to a species' specific ecological and life-history traits, behaviors, and movement patterns (Forman et al. 2003). Iguanas, in particular, are susceptible to road mortality (see Knapp et al. this volume), and a relatively recent constructed road at our mainland GH site may be responsible for the low iguana density and lack of observed monthly density peaks (Fig. 2). Subsequent to a road being built through the GH site in 2004, iguana density decreased from 8.9 iguanas/ha to 4.3 iguanas/ha in 2006 (Cobián et al. 2008). Iguana densities were consistently lower at this study site (1.9 iguanas/ha) over three years (Table 2). Our long-term density estimates in the Cayos de San Felipe National Park (CSF) suggest a decrease in 2013, which coincides with a fire that same year. Alternatively, our estimates at the Delta del Cauto Fauna Refuge (DC) site suggest an increase, which may be attributed to effectiveness of protective measures such as an increase in the number of rangers, with the consequent decrease in illegal hunters and fishermen in the area. Although longer time scales are necessary for confident inferences, our collective monitoring efforts suggest that long-term surveys have potential to detect both acute and persistent perturbations, as well as assess the efficacy of protection efforts.

Previous research on *C. nubila nubila* throughout Cuba from 2001 to 2006 also explored spatial and temporal trends in population densities from several populations (González et al. 2007; Table 4). The authors surveyed 16 populations inhabiting a group of cays in northern Cuba (Sabana-Camagüey Archipelago), a population in Guanahacabibes National Park, three populations on cays in the south of Cuba (Los Canarreos Archipelago), six populations in the Jardines de la Reina Archipelago, three populations in the eastern part of mainland Cuba, and one population in southern Sancti Spiritus Province. The study revealed a similar density pattern for mainland and offshore populations (González et al. 2007; Table 4). Future research should evaluate body size among mainland and offshore iguana populations to determine if proximate environmental effects (e.g., plant species diversity, rainfall, etc.) influence body size, growth rates, fecundity, and age to maturity as seen in other rock iguanas such as *Cyclura cychlura* inhabiting large and small islands (Knapp et al. 2006). A better understanding of site-specific ecology for the species would be useful for effective management and conservation across its range.

Sex ratio (% females) and age structure (% non-adults) patterns.—Unexpectedly, sex ratios did not differ significantly among seasons throughout the study. We suspected that our sex-specific detection probabilities might differ between seasons because of potentially variable movement patterns between the sexes. Knapp and Owens (2005) reported that home ranges expanded and movement increased for males during the pre-reproductive and reproductive seasons as males searched for mating opportunities. Home ranges and movements, however, decreased for females during the same seasons as they oviposited and guarded their nest sites. It is possible that we were not 100% accurate with determining the sex of observed individuals, or females and males may have unique movement and nest guarding behavior relative to their populations, and other species. The possible increase in non-adult iguanas observed in the post-reproductive season most likely is attributed to a pulse of hatchlings from the previous nesting season. Over time, these individuals can be removed from the population through natural (Knapp et al. 2010), or un-natural predation from invasive mammalian species (Wiewandt and García 2000, Pérez-Buitrago 2007, Pérez-Buitrago et al. 2008).

Implications for management.—As the potential for anthropogenic impacts increases within Cuban protected areas, long-term monitoring is crucial to rapidly detect perturbations and apply effective mitigation strategies targeted for specific populations. Rapid detection is especially critical at insular sites, which are constrained in area yet support highly dense populations. Impacts may take longer to manifest in mainland protected areas but these areas are more likely subject to persistent pressures over time. Long-term density data derived from monitoring allow managers to quantify impacts of acute perturbations such as fire (e.g., Cay Sijú in 2013) or the potential introduction of non-native mammals (e.g., feral cats). Long-term monitoring data also can quantify impacts that take longer to reveal such as human encroachment on sensitive areas, periodic

TABLE 4. Minimum and maximum values of density (adults/ha) obtained in this and a previous study of *Cyclura nubila nubila* throughout Cuba.

Geographic area	Minimum density	Maximum density	Source
Cays on northern shore	5.6	35.0	González et al. (2007)
Cays on southern shore	6.5	37.5	González et al. (2007)
Cays on southern shore	7.2	32.6	this study
Island of Cuba	2.6	24.2	González et al. (2007)
Island of Cuba	1.8	9.2	this study

poaching, or iguana behavior changes associated with human interactions.

The National System of Protected Areas of Cuba has technical, capable, and professional personnel mandated with managing and protecting the flora and fauna within the System. There is substantial opportunity to conduct simultaneous monitoring with standardized protocols throughout the country. The challenge is to retain consistent funding and equipment for long-term, simultaneous monitoring efforts. This study should justify the benefits of such a program.

Acknowledgments.—We thank the administrations for their logistic support. We thank the national park rangers, technicians, and specialists working in the protected areas who participated in this study. Our work would not have been possible without the participation of the National Enterprise for Flora and Fauna Protection, the Center for Environmental Research and Services (ECOVIDA), and the Center for Coastal Ecosystem Research (CIEC) of Cuba. Particular appreciation for their participation and support go to our colleagues José Luis Linares who works at Guanahacabibes National Park and José M. Corona who works at Delta del Cauto Fauna Refuge. We thank Josabel Belliure for her help in reviewing the manuscript and to Andrés González Ramos for the English translation of the manuscript. This work was developed within the framework of a project for developing a regional approach to marine and coastal protected area management in the archipelagos to the south of Cuba. This effort is supported financially by the United Nations Development Programme (UNDP) and Global Environment Facility (GEF), and implemented by the National Center for Protected Areas.

LITERATURE CITED

Alberts, A. 2000a. Taxon report: Cuban Iguana (*Cyclura nubila nubila*). IUCN West Indian Iguana Specialist Group Newsletter 3(1):6–7.

Alberts, A. (Ed.). 2000b. West Indian Iguanas: Status Survey and Conservation Action Plan. IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Alberts, A., and A. Perera. 1996. *Cyclura nubila* ssp. *nubila*. The IUCN Red List of Threatened Species. Version 2013.1. Available from http://www.iucnredlist.org/details/6045/0 [Accessed 16 July 2013].

Alberts, A., T.D. Grant, G.P. Gerber, K.E. Comer, P.T. Tolson, J.M. Lemm, and D. Boyer. 2001. Critical reptile species management on the U.S. Naval Base, Guantanamo Bay, Cuba. Report to the United States Navy for Project No. 62470-00-M-5219. Center for Reproduction of Endangered Species, Zoological Society of San Diego, San Diego, California, USA. 45 p.

Berovides, V. 1980. Notas sobre la ecología de la iguana (*Cyclura nubila*) en Cayo del Rosario. Ciencias Biológicas 5:112–115.

Berovides, V. 1995. Situación actual en Cuba de las especies de vertebrados en peligro de extinción. Revista Biología 9:3–13.

Berovides, V., J.A. Ramos, and L.G. Díaz. 2005. Densidad y selección de hábitat de *Cyclura nubila nubila* (Sauria: Iguanidae) en el Refugio de Fauna Cayos de San Felipe, Pinar del Río, Cuba. Revista Biología 19:33–39.

Buide, M., J.F. Milera, F.G. Montaña, O. Garrido, H. de los Santos, G. Silva, and L. Varona. 1974. Las especies amenazadas de vertebrados cubanos. Academia de Ciencias de Cuba, La Habana, Cuba. 32 p.

Capote, R., and R. Berazaín. 1984. Clasificación de las formaciones vegetales de Cuba. Revista del Jardín Botánico Nacional 5(2):27–75.

Chape S, J. Harrison, M. Spalding, and I. Lysenko. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philosophical Transactions of the Royal Society B 360:443–455.

Cobián, D., A. González, and V. Berovides. 2008. Densidad de la Iguana Cubana (*Cyclura nubila nubila*) en la zona de los farallones del Parque Nacional Guanahacabibes, Pinar del Río, Cuba. Mesoamericana 12(1):6–14.

Collazo J.L., M. Morales, and V. Berovides. 2010. Morfometría, abundancia y refugios de la Iguana Cubana (*Cyclura nubila nubila*) en el Refugio de Fauna Las Picúas, Villa Clara. Cubazoo 21:11–14.

Forman, R.T.T., D. Sperling, J.A. Bissonette, A.P. Clevenger, C.D. Cutshall, V.H. Dale, L. Fahrig, R. France, C.R. Goldman, K. Heanue, J.A. Jones, F.J. Swanson, T. Turrentine, and T.C. Winter. 2003. Road Ecology. Science and Solutions. Island Press, Washington, D.C., USA.

Garrido, O.H., and M. Jaume. 1984. Catálogo descriptivo de los anfibios y reptiles de Cuba. Doñana, Acta Vertebrata 11(2):1–128.

González, A., V. Berovides, M. Alonso, and D. Cobián. 2012. *Cyclura nubila nubila*. Pp. 99–102 *In* Libro Rojo de los Vertebrados de Cuba. González, H., L. Rodríguez, A. Rodríguez, C. Mancina, and I. Ramos (Eds.). Editorial Academia, La Habana, Cuba.

González, A., V. Berovides, and M.A. Castañeira. 2001. Aspectos de morfometría, abundancia y alimentación de la Iguana Cubana (*Cyclura nubila nubila*) en el Archipiélago de los Canarreos, Cuba. Revista Biología 15(2):98–104.

González, A., V. Berovides, and M.A. Castañeira. 2004. Variación intrapoblacional de la densidad y las características de los refugios de la Iguana Cubana (*Cyclura nubila nubila*) en Cayo del Rosario, Archipiélago de los Canarreos, Cuba. Revista Biología 18(1):50–56.

González, A., V. Berovides, and D. Cobián. 2007. Densidades de la iguana (*Cyclura nubila nubila*) en algunas áreas protegidas de Cuba. Cubazoo 16:39–42.

Grant, T.D., and A. Alberts. 2001. Recovery of a locally depleted population of Cuban Iguanas (*Cyclura nubila*) following habitat disturbance at the U.S. Naval Base, Guantanamo Bay, Cuba. Iguana Specialist Group Newsletter 4(2):4–5.

Hayes, W., and R. Carter. 1996. Population monitoring. Pp. 79–85 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group. IUCN, Gland, Switzerland and Cambridge, United Kingdom.

IPCC. 2007. Summary for policymakers. Pp. 1–18 *In* Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Solomon, S., D. Qin, M. Manning, Z. Enhen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller (Eds.). Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA.

Iverson, J.B. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bulletin of the Florida State Museum, Biological Sciences 24:175–358.

Iverson, J.B. 1985. Lizards as seed dispersers? Journal of Herpetology 19:292–293.

Iverson, J.B., S.J. Converse, G.R. Smith, and J.M Valiulis. 2006. Long-term trends in the demography of the Allen Cays Rock Iguana (*Cyclura cychlura inornata*): human disturbance and density-dependent effects. Biological Conservation 132:300–310.

Iverson, J.B., G.R. Smith, S.A. Pasachnik, K.N. Hines, and L. Pieper. 2016. Growth, coloration, and demography of an introduced population of the Acklins Rock Iguana (*Cyclura rileyi nuchalis*) in the Exuma Islands, The Bahamas. Pp. 139–153 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Knapp, C.R., and A.K. Owens. 2005. Home range and habitat associations of a Bahamian iguana: implications for conservation. Animal Conservation 8:269–278.

Knapp, C.R., S. Alvarez-Clare, and C. Perez-Heydrich. 2010. The influence of landscape heterogeneity and dispersal on survival of neonate insular iguanas. Copeia 2010:62–70.

Knapp, C.R., J.B. Iverson, and A.K. Owens. 2006. Geographic variation in nesting behavior and reproductive biology of an insular iguana (*Cyclura cychlura*). Canadian Journal of Zoology 84:1566–1575.

Knapp, C.R., L. Prince, and A. James. 2016. Movements and nesting of the Lesser Antillean Iguana (*Iguana delicatissima*) from Dominica, West Indies: implications for conservation. Pp. 154–167 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Lacy, K.E., and E.P. Martins. 2003. The effect of anthropogenic habitat usage on the social behaviour of a vulnerable species, *Cyclura nubila*. Animal Conservation 6:3–9.

Lindenmayer, D.B., and G.E. Likens. 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. Trends in Ecology and Evolution 24:482–486.

Lyons, J.E., M.C. Runge, H.P. Laskowski, and W.L. Kendall. 2008. Monitoring in the context of structured decision-making and adaptive management. Journal of Wildlife Management 72:1683–1692.

Marsh, D.M., and P.C. Trenham. 2008. Current trends in plant and animal population monitoring. Conservation Biology 22:647–655.

Perera, A. 1985. Datos sobre abundancia y actividad de *Cyclura nubila* (Sauria: Iguanidae) en los alrededores de Cayo Largo del Sur, Cuba. Poeyana 288:1–17.

Pérez-Buitrago, N.F. 2007. Spatial and reproductive biology of the Mona Island Iguana: implications for conservation. Ph.D. Dissertation, Universidad de Puerto Rico, Rio Piedras Campus. 145 p.

Pérez-Buitrago, N.F., M.A. García, A. Sabat, J. Delgado, A. Álvarez, O. McMillan, and S.M. Funk. 2008. Do headstart programs work? Survival and body condition in headstarted Mona Island Iguanas *Cyclura cornuta stejnegeri*. Endangered Species Research 6:55–65.

Rodríguez, L. (Ed.). 2003. Anfibios y Reptiles de Cuba. UPC Print, Vaasa, Finlandia.

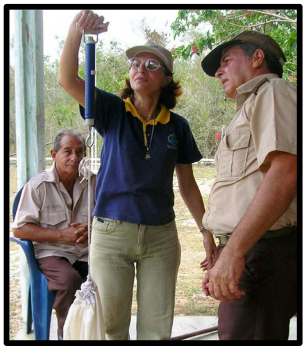
Schwartz, A., and M. Carey. 1977. Systematics and evolution in the West Indian iguanid genus *Cyclura*. Studies on the Fauna of Curaçao and other Caribbean Islands 53:16–97.

Schwartz, A., and R.W. Henderson. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. University of Florida Press, Gainesville, Florida, USA.

Siegel, S., and N.I. Castellan. 2001. Estadística no paramétrica. Editorial Trillas, México.

Wiewandt T.A., and M. García. 2000. Mona Island Iguana: *Cyclura cornuta stejnegeri*. Pp. 27–31 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Witmer, G.W. 2005. Wildlife population monitoring: some practical considerations. Wildlife Research 32:259–263.



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Herpetological Conservation and Biology 11(Monograph 6):79–89.
Submitted: 12 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

HABITAT UTILIZATION OF ROATÁN SPINY-TAILED IGUANAS (*CTENOSAURA OEDIRHINA*) AND ITS IMPLICATIONS FOR CONSERVATION

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Abstract.—**Resources available for *in situ* species conservation are limited. In order to make the most of what is available, habitats must be prioritized for protection. Biodiversity hotspots are one form of prioritization, e.g., identifying areas with many endemic species that are threatened by habitat loss. Within these larger areas, the habitats that make up the range of endemic species can also be prioritized in order to use limited conservation resources most effectively. With data gathered from use/availability surveys, resource selection functions can identify habitats and environmental variables associated with the presence of a species. Herein, we used these techniques to better understand the distribution of the Roatán Spiny-tailed Iguanas (*Ctenosaura oedirhina*), a narrow-range endemic on the island of Roatán, Honduras. Though certain environmental variables did influence the distribution of this species, our results indicate that protection from harvesting is the most important factor in determining their distribution across the island. In order to protect this species and insure its persistence in the wild, regulation and enforcement of harvesting practices must be applied, coupled with proper community education and outreach.**

Resumen.—**Los recursos disponibles para la conservación de especies *in situ* son limitados. Con el fin de obtener el máximo provecho de los recursos disponibles se deben priorizar los hábitats para su protección. Los centros de biodiversidad son una forma de priorización, donde se identifican áreas con una gran cantidad especies endémicas que están amenazadas por la pérdida de hábitat. Dentro de estas áreas de gran tamaño, los hábitats que contienen la mayor gama de especies endémicas pueden ser priorizadas con el fin de utilizar los recursos limitados en una manera más eficiente. Con los datos obtenidos de los sondeos de uso/disponibilidad, se pueden utilizar funciones de selección de recursos para identificar los hábitats y las variables ambientales asociados con la presencia de una especie. Aquí, hemos utilizado estas técnicas con el fin de entender mejor la distribución de las iguanas de cola espinosa de Roatán (*Ctenosaura oedirhina*), una especie endémica de rango limitado a la isla de Roatán, Honduras. Aunque ciertas variables ambientales an influido en la distribución de esta especie, nuestros resultados indican que la intensidad de caza es el factor más importante que determina su distribución en toda la isla. La regulación y la implementación de políticas adecuadas para control de la cacería deben ser aplicadas, junto con una educación comunitaria adecuada, con el fin de proteger a esta especie y asegurar su sobrevivencia en su estado silvestre.**

Key Words.—biodiversity hotspot; endemic species; habitat prioritization; habitat usage; hunting pressure; resource selection functions

INTRODUCTION

Prioritization of habitat protection is an important aspect of *in situ* species conservation. This is especially true when dealing with limited resources, as is often the case in conservation (Murdoch et al. 2007; Bottrill et al. 2008). Biodiversity hotspots are areas of high diversity that may be undergoing severe habitat degradation. These hotspots harbor high numbers of endemic species within small areas, such that the conservation of these areas protects a large proportion of global biodiversity (Myers et al. 2000). This same concept can be applied to smaller scale situations, such as the range of a single threatened species. Not all habitats are equal in their value to a species and some taxa may use habitat disproportionately to its availability. Species can actively select for a certain attribute, such as vegetation type or distance to water, or modify their niche preference based on dietary needs, thermoregulation, competition, and/or predation (Manly et al. 1992). In turn, conservationists can prioritize habitats for protection by identifying the environmental variables a species selects (Boyce and MacDonald 1999).

Use/availability surveys are used to determine what habitat a species uses and is able to access. These data can then be used to describe the habitat, or habitat variables, a species utilizes within a landscape (i.e., Resource Selection Functions (RSFs); Boyce and

Goode, Ashley B.C., Stesha A. Pasachnik, and Terry L. Maple. 2016. Habitat utilization of Roatán Spiny-tailed Iguanas (*Ctenosaura oedirhina*) and its implications for conservation. Pp. 79–89 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

MacDonald 1999). Many studies use RSFs to focus resources for conservation initiatives. For example, using these methods Smith et al. (2004) found that current pastoral management techniques of the European Hare (*Lepus europeaus*) were not in fact helping to increase the hare population because the hares were selecting for different habitats than previously assumed. Changing management practices to increase heterogeneous pastoral habitat is thus more efficient for the farmers and also benefits the hares and the biodiversity of the region (Smith et al. 2004). RSFs can also be used to map currently and historically used habitat, which sometimes results in locating useful study sites and identifying possible reintroduction locations. Cleve et al. (2011) showed that the environmental variables used to predict habitat likely to contain the threatened Sierra Nevada Red Fox (*Vulpes vulpes necator*) successfully predicted an area that housed a new, previously unknown population. Naves et al. (2003) used resource modeling via logistic regression to outline the possible historic range of the Brown Bear (*Ursus arctos*) in Europe. These data could one day be used to repatriate individuals into previously inhabited areas.

RSFs and use/availability studies can also be used to develop maps of habitats that are worth delineating for official protection or for use in land management decisions. Chetkiewicz and Boyce (2009) used RSFs to identify habitat corridors for Grizzly Bears (*Ursus arctos*) and Mountain Lion (*Puma concolor*). These RSF data can then be used in future land management and planning (Chetkiewicz and Boyce 2009). Likewise, Smith et al. (2014), employing use/availability and habitat selection models, found that Greater Sage-grouse (*Centrocercus urophasianus*) selected against anthropogenically disturbed habitats and suggested that land managers prioritize distinct subunits of sage-grouse habitat when planning new development. When debating land planning and management, this type of information could be the difference between a species persisting in an area or being extirpated.

In this study, we employed use/availability surveys to develop RSFs which identify critical habitat for an endangered, narrow-range endemic iguana. Roatán Spiny-tailed Iguanas (*Ctenosaura oedirhina*) are found only on the 146 km^2 island of Roatán, ~ 50 km off the northern coast of Honduras (Fig. 1). Habitat destruction and fragmentation, the introduction of exotic species, and over-harvesting for consumption threaten this species (Pasachnik et al. 2015). Described in 1987 (de Queiroz), the Honduran government acknowledged this species as in need of protection in 1994 (Wilson and McCranie 2004), the IUCN listed them as Endangered on the Red List of Threatened Species in 2004, and they were included in Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) in 2010 (Pasachnik and Ariano 2010). Since its description, only larger-scale genetic and taxonomic studies have been conducted on this species (Kohler et al. 2000; Pasachnik et al. 2010) until recently (Pasachnik 2013; Pasachnik and Hudman this volume).

While it is officially illegal to hunt *C. oedirhina*, there is little to no enforcement on the island, and individual iguanas are regularly taken for food. In addition, there are legally protected areas and habitats (e.g., national parks), but the protection of these areas is not enforced. The growing tourism industry on the island heightens cause for concern. In less than 20 years, the urban area on the island increased from 1.8 km^2 in 1985 to 17.1 km^2 in 2001 (Aiello 2007) and over one million tourists visit the island a year (Doiron and Weissenberger 2014). Not only does this result in habitat destruction, but also an influx in people from the mainland arriving in hopes of finding jobs. This in turn increases hunting pressure on the local wildlife, particularly iguanas, as many recent immigrants are not able to find work and it is a custom on the mainland to consume iguanas (Fitch et al. 1982; Pasachnik et al. 2014). With no recognized protection for this iguana or other threatened species, protection through local grassroots efforts, such as localized hunting prohibition, is all that exists. This grassroots movement, which consists of private landowners, resorts, and tourist parks, has limited resources so the effort put forth must be used to the greatest effect.

Habitat utilization is an important ecological aspect that has direct implications for conservation. RSFs estimate the habitat usage and preference for specific resources for a given species. It is important not only to protect where the animals spend most of their time (i.e., their typical home range) but also the habitat(s) that they may use for just a small yet vital portion of the year (e.g., nest sites). It is also important to realize that both sexes have core areas of use within their home ranges and that these may change in size or location due to breeding or other seasonal factors. Thus, the protection of many habitat types may be necessary to support a given species. The objective of this study was to survey the habitat and environmental variables across the island of Roatán in order to determine those characteristics that define the preferred habitat of *Ctenosaura oedirhina*. Since so little land is actually protected for this species, it is imperative that the most utilized habitats be incorporated.

METHODS AND MATERIALS

We collected data over a two-year period, during spring (April–May, 2012 and 2013), fall (August, 2012 and 2013), and winter (November–December 2012) on Roatán, Islas de la Bahia, Honduras (Fig. 1). We focused on two main seasons, the rainy season (September–January) and the dry season (February–August). Breeding and nesting occur in March–June and hatching in early August, after a 70–100 day incubation period (Pasachnik 2013).

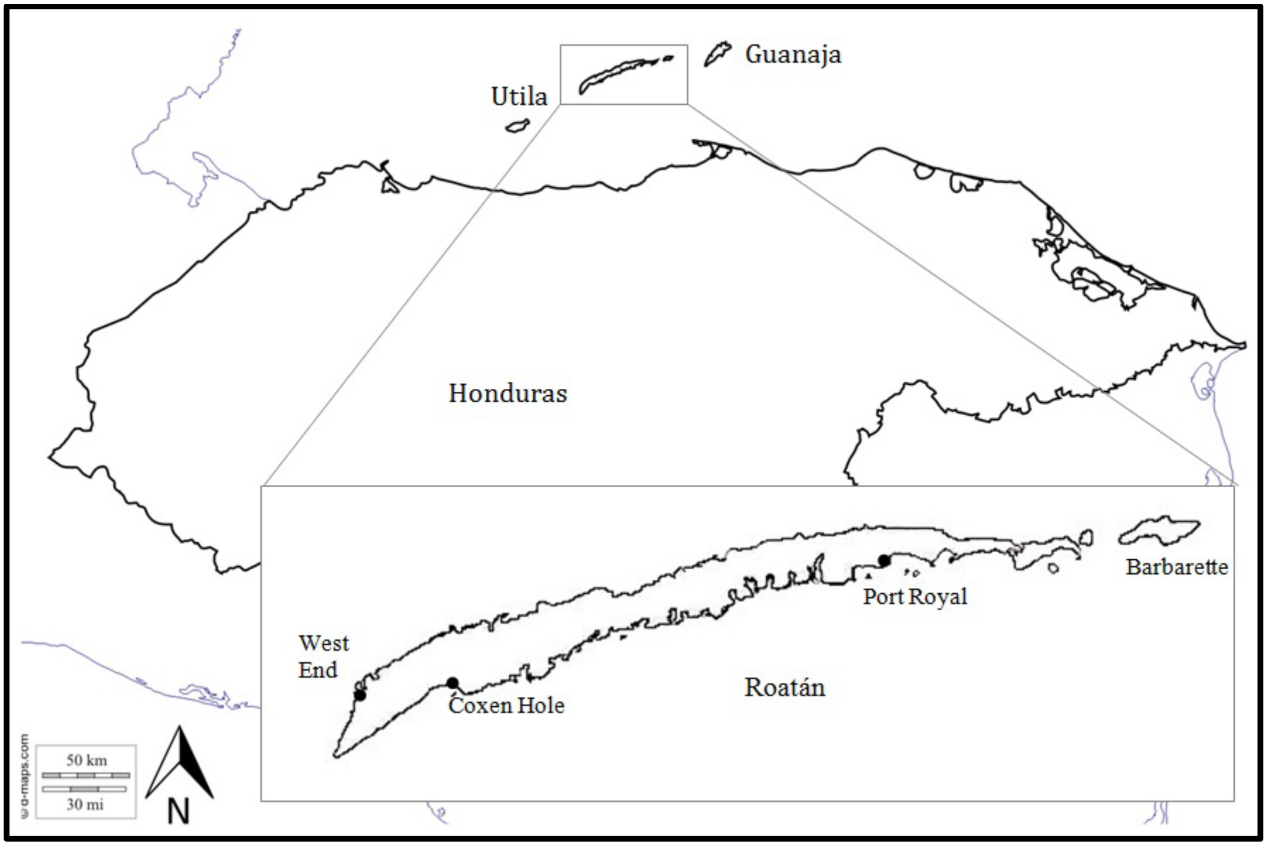

FIGURE 1. Map of Honduras and the Bay Islands, highlighting the study island, Roatán. D-maps.com. 2014. Map of Honduras (boundaries). Available from http://d-maps.com/pays.php?num_pay=146&lang=en [Accessed 25 August 2014].

***Study location*.**—Roatán is covered primarily in seasonally dry tropical forest. The coastline is either white sand, rocky, or mangrove forest. Smaller islands and cays surround the main island of Roatán, some of which harbor iguanas. Barbareta is the largest (~ 5 km^2) of these and is located off the east end of Roatán. It is privately owned, and we could not obtain permission to survey it during our timeframe. Therefore, it has been excluded from our analyses. Because of the endangered status of this species, specific information about research sites is available only upon justifiable request.

***Data collection*.**—We used Google Earth to map and calculate the area of available habitats on the island down to 100 m^2 sections. The latest available satellite photos (2013–2014) were used with data from Scripps Institute of Oceanography, National Oceanic and Atmospheric Association, U.S. Navy, National Geospatial-Intelligence Agency, and General Bathymetric Chart of the Oceans (Map data: Google, TerraMetrics). We ground-truthed all areas where the habitat classification was questionable. Since reliable satellite imagery is unavailable for the island for long-term habitat change analysis, we used ground cover data from Aiello (2007) and Programa REDD/CCAD-GIZ (2014) to make relative comparisons. As the Programa REDD/CCAD-GIZ (2014) work was not available during the design of this study, our habitat definitions vary slightly and thus direct comparisons are difficult (see below for additional details).

We conducted use/availability surveys along line transects located at nine study sites. To sample all of the available habitat types we non-randomly distributed transect locations across the island. Each transect was ~ 100 m long (range 90–110 m), and each location had at least three transects, for a total of 50 transects. We included both natural and altered landscapes, ranging from undisturbed to heavily disturbed, in our habitat surveys. We conducted surveys on multiple days between 0800 and 1500 during May (2013, 11 days), June (2013, two days), August (2012, 11 days; 2013, four days), November (2012, 11 days) and December (2012, one day). Due to logistics, trips were of varying lengths. Each site was surveyed during each season: spring (May–June), summer (August), and winter (November–December). While not all sites were surveyed an equal number of times, all were surveyed at least twice during each season. During each survey, at least one of us walked each transect and noted every iguana sighted on or along it, with its distance along and perpendicular

FIGURE 2. Representative examples of habitat types on Roatán. (A) Shore; (B) "Cleaned" forest; (C) "Uncleaned" forest; (D) Mangroves; (E) Stripped land (strip); (F) Agricultural land; (G) Anthropogenic land (anthro); and (H) Rock cliff (cliff). See Appendix for more details. Photographs by Ashley Goode.

distance from the transect to the nearest meter. We considered these the "used" points, and noted a suite of environmental variables for each point (e.g., habitat type, substrate type, distance to water, and disturbance level; see Fig. 2 and Appendix for details). We used a random number generator to select points along the transect, which we surveyed for the same variables. We considered these the "available" points. We also used the location of "used" points along each transect to determine the density of iguanas at each location.

Data analysis.—To determine if any changes occurred over time in either used or available habitat, we used χ^2 tests of the percentage of each habitat at each location using the chisq.test function in the R software package ($\alpha = 0.05$ throughout) (R Development Core Team, Vienna, Austria). To make the Google Earth data comparable to the data from Aiello (2007), we used only the areas of anthropogenic, forest ("cleaned" and "uncleaned" forest combined, see Appendix for definitions), and sandy shore habitats in our analysis. Unfortunately, the Programa REDD/CCAD-GIZ (2014) data was not available during the setup of this study and thus direct comparisons were not possible due to variations in habitat type descriptions (see below for more detail). We compared data between and among study sites using contingency tables (chisq.test function in the R software package). We compared data between the study sites and the island as a whole in the same way. We replicated simulated *P* values 100,000 times because of the prevalence of zeros and small numbers in the data set. To establish the usage of each habitat type, we performed a logistic regression on the "used" and "available" points (logreg function in SAS® software) to determine resource selection functions (SAS Institute Inc., Cary, North Carolina, USA). We then used Akaike Information Criterion (AIC) to determine the preferred model, i.e., the model that best balanced goodness of fit and complexity (Anderson et al. 1998). After testing the global model, following models were pared down by grouping variables by similar *P* values (i.e., *P* values were binned and then variables that fell within those bins were grouped together). We used the program Distance to determine the density of iguanas at each study site (Thomas et al. 2010). The program calculated the density of iguanas along each transect based on "used" points from the use/availability transects (i.e., the distance along the transect and perpendicular distance from the transect of each iguana).

RESULTS

From the areas calculated using Google Earth, mainly seasonally dry tropical forests (~ 77%), coastal mangrove stands (~ 7%), and urbanized areas (~ 14%) cover the island. The remainder is mostly agricultural (< 1%, either pasture land for cattle and horses, or stands of bananas) or stripped land (< 1%, mostly cleared for new development, but some for mining operations) (Table 1). Satellite images cannot distinguish "cleaned" versus "uncleaned" forest, so we grouped them together. We compared these data to Aiello's (2007) study, which reported data from 1985 and 2001, and to data from 2014, compiled by the Honduran government (Programa

TABLE 1. Total available habitat for *Ctenosaura oedirhina* on the island of Roatán, Honduras.

Habitat	Area (km^2)	Percent of Total
Forest	99.08	77.65
Urban	18.29	14.33
Mangrove	8.90	6.98
Sandy Shore	0.48	0.38
Agriculture	0.46	0.36
Rocky Shore	0.21	0.16
Stripped	0.17	0.14

TABLE 2. Change in percentage of habitat area over time on Roatán, Honduras. The 2013 data are from Google Earth, the 1985 and 2001 data are from Aiello (2007), the 2014 data are from the Honduran government (Programa REDD/CCAD-GIZ 2014). It should be noted that the government map used differing definitions for some habitat types and thus direct comparison is not always appropriate (see methods for additional clarification).

Habitat	1985	2001	2013	2014
Urban	0.95%	13.87%	14.50%	6.84%
Forest	95.77%	85.47%	85.12%	85.17%
Sand	3.28%	0.66%	0.38%	7.99%

REDD/CCAD-GIZ 2014). We determined that large reductions in forest and sandy habitats occurred, while urban area increased dramatically (Table 2) between Aiello's (2007) study and ours. However when we attempted to compare our data to the 2014 data (Programa REDD/CCAD-GIZ 2014), it was apparent that different definitions of each habitat type were used. While the percent of forest cover seemed to be comparable across years/studies, there were discrepancies in urban areas and sandy habitats. Like Aiello (2007) we classified villages as "urban" even if they were not "urbanized" with paved roads, as much of the island is not paved but still contains high population density centers. The 2014 (Programa REDD/CCAD-GIZ) data, however, had a narrower classification, only delineating densely populated, paved areas as urban. Likewise our study defined sandy habitat as sand substrate with little to no vegetation occurring predominately along the shoreline, whereas the 2014 (Programa REDD/CCAD-GIZ) data used only the presence of a sand substrate and lack of dense vegetation to define this type of habitat. This possibly led to areas that our study delineated as "stripped" habitat to be identified as "sandy" habitat on the 2014 map. Some degree of discrepancy may also be due to the Honduran government (Programa REDD/CCAD-GIZ 2014) having access to more detailed aerial/satellite images that are not available to public.

From our surveys we concluded that used and available habitats at the study sites did not vary significantly from those available on the island as a whole (100,000 replicates; $P = 1$ for all combinations); however, the habitat did vary significantly among the study sites (100,000 replicates; $P < 0.0001$). Some sites are predominantly anthropogenic habitat while others are exclusively "uncleaned" forest with little to no direct anthropogenic impact. Iguanas were found in all habitat types, but not at all of the surveyed sites. Only six of our nine study sites contained iguanas. While other native fauna (such as Roatán Island Agouti (*Dasyprocta ruatanica*)) was noted within the grassroots protected study sites, neither iguanas nor other native terrestrial vertebrates were seen during surveys at nationally protected locations.

The global model for the resource selection function used all seasonal data from 2012–2013 and contained all 25 variables (nine habitats, nine substrates, four distances to water, and three disturbance levels; Table 3; see Appendix for details on variables). The global model had the best AIC value. However, when using relatively large datasets, AIC tends to select models with too many variables (e.g., the global models) (Hastie et al. 2001). In our case we believe that the global model, while deemed "best" by AIC, is not ecologically significant so the next best model was used for all further analysis. The second-most supported model, based on the AIC value, included the habitat variables anthropogenic, stripped, "uncleaned" forest, and shore, as well as vegetation and substrate variables most optimal for thermoregulation (rock, concrete, and gravel). Coefficient estimates showed that shore, "uncleaned" forest, stripped, and undisturbed habitats were "avoided", while anthropogenic, vegetation, rock, gravel, and concrete substrates were "preferred" (Table 4).

TABLE 3. Resource selection models describing the preferred habitat used by *Ctenosaura oedirhina* across Roatán, Honduras, and are in order of AIC score. See Appendix for variable details.

Model	df	χ^2	AIC	ΔAIC
Global – all variables	25	533.7	3518.2	0
Shore, Unclean, Strip, Anthro, Rock, Veg, Undist, Conc, Gravel	9	524.1	3698.2	180.0
Shore, Unclean, Strip, Anthro, Rock, Veg, Undist	7	485.9	3743.9	45.7
Shore, Unclean, Strip, Anthro, Rock, Veg, Conc, Gravel, Clean, Cliff, Dirt	11	600.1	3768.8	24.9
Shore, Unclean, Strip, Anthro, Rock, Veg	6	540.7	3844.5	75.7
Rocky cliff, Rock, Sand, Shore, <50m water	5	395.0	4112.1	267.7
Anthropogenic, Heavy dist	2	187.7	4284.8	172.6
Cleaned, Low dist	2	7.4	4477.4	192.6
Null – intercept only	0	–	4480.7	3.3

Locations containing the highest densities of iguanas had significant differences in used versus available habitat between the seasons (mainly between spring and fall, less so in winter) (Table 5). Iguanas exist in the highest densities within grassroots protected areas (Table 6). These protected areas make up only ~ 0.6 km^2 of the island (less than 0.01% of the total area of the island). We found iguanas almost non-existent in areas unprotected by the grassroots movement, (densities of 0–5 iguanas per km^2).

DISCUSSION

With limited resources, conservationists need to understand the specific distribution of a species, be it based on suitable habitat or human disturbance, so that limited resources can have the greatest impact (Caughly and Gunn 1996). Animals often select habitats and habitat characteristics based on food abundance, thermoregulation, predation, and competition. In these cases, conservation of the species can start with protecting

TABLE 4. Resource Selection Function coefficient estimates. Positive coefficients indicate a "preference" for those habitat variables on Roatán, Honduras by *Ctenosaura oedirhina*, while negative coefficients indicate "avoidance".

Variable	Estimate
Shore	-0.227
Uncleaned Forest	-0.638
Stripped	-2.297
Anthropogenic	0.552
Rock Substrate	1.963
Vegetation Substrate	2.131
Undisturbed	-2.224
Concrete Substrate	0.808
Gravel Substrate	0.805

TABLE 5. Differences in used and available habitat by location and season, for *Ctenosaura oedirhina* across Roatán, Honduras. A significant *P* value indicates a preference for a specific habitat during that season, i.e., the iguanas were selecting for a habitat more so than the availability of that habitat would indicate. Only six of the nine locations contained iguanas, so only those results are listed here.

Location/ Season	χ^2	*P* value	Predominant Used Habitat Type	Predominant Available Habitat Type
1/Spring	256.9	0.003	Anthropogenic	Anthropogenic
1/Fall	308.8	0.005	Anthropogenic/"Cleaned" forest	"Cleaned" forest
1/Winter	250.0	0.001	Anthropogenic/"Cleaned" forest	"Cleaned" forest
2/Spring	154.1	0.042	Anthropogenic	"Uncleaned" forest/Anthropogenic
2/Fall	265.9	0.002	"Cleaned" forest	"Cleaned" forest/"Uncleaned" forest
2/Winter	84.4	0.060	Anthropogenic	"Cleaned" forest/"Uncleaned" forest
3/Spring	229.7	0.005	Anthropogenic	Anthropogenic
3/Fall	296.3	0.001	"Cleaned" forest	"Cleaned" forest
3/Winter	129.6	0.075	Mangroves	"Cleaned" forest/Anthropogenic
4/Spring	105.3	0.007	Anthropogenic	Anthropogenic
4/Fall	137.1	0.001	Anthropogenic	"Cleaned" forest/Anthropogenic
5/Spring	225.0	0.036	Rock cliff	Mangroves/"Uncleaned" forest
5/Fall	312.1	0.026	Rock cliff	Mangroves/"Uncleaned" forest
5/Winter	379.4	0.112	Rock cliff	Mangroves/"Cleaned" forest
6/Spring	25.0	0.050	"Cleaned" forest	"Cleaned" forest
6/Fall	18.6	0.251	"Cleaned" forest	"Cleaned" forest

TABLE 6. *Ctenosaura oedirhina* densities at each study location across Roatán, Honduras. Densities were calculated using the program Distance (Thomas et al. 2010) and extrapolated to km^2. The densities shown are not the actual population size at any location, as none of the study locations were more than 0.2 km^2.

Location	Grassroots Protection Status	Sightings	Calculated Density (iguanas/km^2)	Site Area (km^2)
1	Protected	275	7,504	0.115
2	Protected	72	2,513	0.293
3	Protected	150	2,688	0.100
4	Protected	19	2,439	0.004
5	Protected	179	5,288	0.096
6	Not Protected	2	1	0.670
7	Not Protected	1	1	0.130
8	Not Protected	0	0	0.100
9	Not Protected	0	0	5.320

specific habitats discerned by RSF or other similar means (Boyce and McDonald 1999). Our RSF model suggests that *C. oedirhina* selects habitats at least in part based on thermoregulation, selecting more often for rock, concrete, and gravel (i.e., substrates that heat up quickly in the sun and hold that heat for much of the day). *Ctenosaura oedirhina* also selects for altered habitats; however, many acres of altered habitat on the island contain almost no iguanas, suggesting that another factor is likely accounting for the observed distribution.

The RSF model chosen to describe the distribution of *C. oedirhina* contained a mix of both undisturbed (undisturbed habitat, "uncleaned" forest) and heavily disturbed habitats (stripped habitat, anthropogenic habitat, concrete, and gravel substrate), and indicated an avoidance of "uncleaned" forest, stripped, and undisturbed habitat (Table 4). "Uncleaned" forest, stripped land, and undisturbed habitat have one very important thing in common: they are usually areas that are accessible to hunters. "Uncleaned", undisturbed areas, such as Port Royal National Park, offer little protection for wildlife against poachers as the area is not fenced or guarded. These locations look pristine, but appear to lack most of the native fauna that should accompany such habitats, based on our observations. Stripped land is available near many of the urban areas on the island, and is an effect of the developing tourist industry. Construction crews working in these locations have been observed by authors SAP and ABCG to hunt iguanas. In one instance, a home construction crew eliminated all of the iguanas within a previously densely populated area in a matter of months. The shore habitat is also "avoided" based on the model parameters (Table 4), but from our camera trap data, we know that iguanas use the shore early in the morning for very short amounts of time (3–5 minutes) to warm up, and then do not return there for the rest of the day. The shore typically does not offer refuge from the sun or hunters, and the sand also remains hot all day.

It is interesting that the selected model, discussed above, demonstrates that iguanas prefer anthropogenic habitat, considering the usual perils there, such as increased hunting pressure or domestic dogs and cats. However, on Roatán, iguanas are also afforded protection from hunting in many of the anthropogenic areas. Based on our model, we should find iguanas over a much wider area considering that the variables in the model account for over 15% of the island's area. However, less than 30 years after the description of this species (de Queiroz 1987) we find iguanas in stable densities on less than 1% of the island.

Hunting pressure has been shown to alter the distribution of a species (e.g., Madsen 1998; Grignolio et al. 2011; Imong 2013). Humans have likely hunted *C. oedirhina* for subsistence since they colonized the island approximately four thousand years ago (Fitch et al. 1982). The increase in human population and the onset of tourism on the island, however, has put an accelerated strain on the iguana population. Both local residents and curious tourists consume the iguanas, and recently the threat of poaching for the illegal pet trade has become more serious (Pasachnik and Ariano 2010). With over one million people visiting the island each year (Doiron and Weissenberger 2014), the iguana population simply will not be able to withstand the pressure from these growing threats. Although forests (seasonally dry tropical forest and mangroves) cover most of the island, the increase in urban area is substantial and observable even over the two years of this study. Much of the island is still pristine forest, but hunting pressure has caused these areas to be nearly devoid of vertebrate life. High densities of iguanas occur only in sites where grassroots efforts prohibit hunting, even though the sites themselves are generally small, from 0.008 km^2 (approximately two acres) to 0.25 km^2, and are quite disturbed. The iguanas are almost non-existent outside of these areas, even in comparable or more pristine habitat.

It should be noted, however, that iguana density reflects habitat usage, but not necessarily individual health. Pasachnik (2013) showed that body condition index (BCI) is highest in the sites with the greatest anthropogenic influence, but an unhealthy diet of scavenged fatty human food could account for this (see Smith and Iverson this volume). Additional research is needed in order to better understand this facet, as well as whether or not stress is induced by daily interactions with humans (e.g., Knapp et al. 2013). This will then elucidate the health of these dense populations, and in turn the overall stability of this species.

Hunting pressure is an important factor determining habitat usage for many species (Imong et al. 2013; Stoner et al. 2013). While some aspects of the habitat (e.g., shore, rock, gravel) of *C. oedirhina* are selected for more than others, the decisive factor in determining whether or not iguanas occupy a site is the degree of protection it affords. This has important implications for conservation efforts. The management and grassroots protection of specific sites is currently very unstable. If the ownership or management of any one of the sites changes, one of these businesses closes, or a private resident moves, it could easily result in the local extirpation of this species. Instead of attempting to protect specific habitats, our results suggest that enforcing protection of the iguanas themselves should be most effective. To achieve this, however, a strong outreach and education campaign involving all stakeholders will be necessary. Many people living on the island are unaware or choose to ignore the endangered status of this species, and the fact that it is distinct from the sympatric Green Iguana (*Iguana iguana*) and other species of ctenosaurs that inhabit the mainland and neighboring islands.

We note that the consumption of iguana meat is of some cultural importance to the people of Roatán, and does provide an important protein source for some people. We thus suggest management approaches that ensure the persistence of this and other endemic species on the island alongside the preservation of cultural traditions and dietary demands. The development of a national conservation plan for this species with the cooperation and input of all stakeholders, including island residents and business owners, local authorities, non-governmental organizations (NGOs), governmental agencies, and scientists is the first step in increasing awareness and ensuring long-term commitments from all parties. Such a plan must consist of actions that guarantee the enforcement of the existing laws occurs, while modifying these laws to consider the needs of the local community. Enacting and enforcing a hunting season in a restricted area is one option. Another option is to work toward refocusing hunting efforts on similar but non-threatened species. Green Iguanas are native to the island but not Endangered. They are already being consumed to some degree, so farming them or purchasing them from mainland farms may be feasible. These actions should not be taken lightly and a strong education component must be incorporated. Accompanying these efforts, managers might also consider a captive breeding program for *Ctenosaura oedirhina*, with the necessary habitat protection enforced by the government, including local law enforcement agencies. Our results clearly show the generalist nature of this species, thus a reintroduction program is very feasible as long as habitat protection can be assured and hunting can be regulated or prevented.

Acknowledgments.—We would like to thank Mikel Belcaries, Henry Montalvan, and Joseph Anderson for field assistance, and Dale Gawlik and Erik Noonburg for their assistance with the statistical analysis. This project would not have been possible without the generosity of the International Iguana Foundation, Mohamed bin Zayed Species Conservation Fund, Phoenix Zoo, Riverbanks Zoo and Gardens, San Diego Zoo Institute for Conservation Research (providing salary for SAP), and our in-country support Andrea Martinez and the Kanahua Utila Research and Conservation Facility. This study was approved by the Florida Atlantic University International Animal Care and Use Committee (Protocol A12-06) and the Honduran Government (Honduran Conservation Permit DVS-ICF-054-2010). Our work was also supported by the National Science Foundation under NSF Grant No. DGE: 0638662. Our conclusions or recommendations do not necessarily reflect the views of the NSF.

LITERATURE CITED

Aiello, D.P. 2007. Coast to coral: evaluating terrestrial development's relationship to coral ecosystem condition in Roatán, Honduras. Ph.D. Dissertation, Ohio University, Columbus, Ohio, USA. 120p.

Anderson, D.R., K.P. Burnham, and G.C. White. 1998. Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture-recapture studies. Journal of Applied Statistics 25:263–282.

Bottrill, M.C., L.N. Joseph, J. Carwardine, M. Bode, C. Cook, E.T. Game, H. Grantham, S. Kark, S. Linke, E. McDonald-Madden, et al. 2008. Is conservation triage just smart decision making? Trends in Ecology and Evolution 23:649–654.

Boyce, M.S., and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.

Caughly, G., and A. Gunn. 1996. Conservation Biology in Theory and Practice. Blackwell Science, Cambridge, Massachusetts, USA.

Chetkiewicz, C.L.B., and M.S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46:1036–1047.

Cleve, C., J.D. Perrine, B. Holzman, and E. Hines. 2011. Addressing biased occurrence data in predicting potential Sierra Nevada Red Fox habitat for survey prioritization. Endangered Species Research 14:179–191.

De Queiroz, K. 1987. A new spiny-tailed iguana from Honduras, with comments on relationships within *Ctenosaura* (Squamata: Iguania). Copeia 1987:892–902.

Doiron, S., and S. Weissenberger. 2014. Sustainable dive tourism: social and environmental impacts — The case of Roatán, Honduras. Tourism Management Perspectives 10:19–26.

Fitch, H.S., R.W. Henderson, and D.M. Hillis. 1982. Exploitation of iguanas in Central America. Pp. 397–417 *In* Iguanas of the World: Their Behavior, Ecology and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Grignolio, S., E. Merli, P. Bongi, S. Ciuti, and M. Apollonio. 2011. Effects of hunting with hounds on a non-target species living on the edge of a protected area. Biological Conservation 144:641–649.

Hastie, T., T. Tibshirani, and J. Friedman. 2001. The Elements of Statistical Learning: Data Mining, Inference, and Prediction. Springer, New York, New York, USA.

Imong, I., M.M. Robbins, R. Mundry, R. Bergl, and H.S. Kuhl. 2013. Distinguishing ecological constraints from human activity in species range fragmentation: the case of Cross River gorillas. Animal Conservation 17:323–331.

Knapp, C.R., K.N. Hines, T.T. Zachariah, C. Perez-Heydrich, J.B. Iverson, S.D. Buckner, S.C. Halach, C.R. Lattin, and L.M. Romero. 2013. Physiological effects of tourism and associated food provisioning in an endangered iguana. Conservation Physiology 1:cot032. doi:10.1093/conphys/cot032

Köhler, G., W. Schroth, and B. Streit. 2000. Systematics of the *Ctenosaura* group of lizards (Reptilia: Sauria: Iguanidae). Amphibia Reptilia 21:177–192.

Madsen, J. 1998. Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. Journal of Applied Ecology 35:398–417.

Manly, B.F., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 1992. Resource Selection by Animals. Kluwer Academic Publishers, Norwell, Massachusetts, USA.

Murdoch, W., S. Polasky, K.A. Wilson, H.P. Possingham, P. Kareiva, and R. Shaw. 2007. Maximizing return on investment in conservation. Biological Conservation 139:375–388.

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Naves, J., T. Wiegand, E. Revilla, and M. Delibes. 2003. Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. Conservation Biology 17:1276–1289.

Pasachnik, S.A. 2013. Growth, reproduction, and diet of Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina*, with notes on the status of the species. Herpetological Conservation and Biology 8:191–198.

Pasachnik, S.A., and D. Ariano. 2010. CITES Appendix II listing of the *Ctenosaura palearis* clade. IRCF Reptiles and Amphibians Conservation and Natural History 17:136–139.

Pasachnik, S., D. Ariano-Sánchez, J. Burgess, C.E. Montgomery, and G. Köhler. 2015. *Ctenosaura oedirhina*. The IUCN Red List of Threatened Species. Version 2015.2. Available from http://www.iucnredlist.org/details/44191/0 [Accessed on 25 June 2015].

Pasachnik, S.A., J.A. Danoff-Burg, E.E. Antúnez, and J.P. Corneil. 2014. Local knowledge and use of the Valle de Aguán Spiny-tailed Iguana, *Ctenosaura melanosterna*, in Honduras. Herpetological Conservation and Biology 9:436–447.

Pasachnik, S.A., A.C. Echternacht, and B.M. Fitzpatrick. 2010. Gene trees, species, and species trees in the *Ctenosaura palearis* clade. Conservation Genetics 11:1767–1781.

Pennington, R.T., and J.A. Ratter (Eds.). 2010. Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation. CRC Press, London, England.

Programa REDD/CCAD-GIZ. 2014. Carbono Forestal en los Países de Centroamérica y República Dominicana. Plataforma Regional de Datos Forestales Geoespaciales (GEO-Forest+): Herramienta +Carbono. Fuente original de los datos: Programa REDD-CCAD/GIZ.

Smith, G.R., and J.B. Iverson. 2016. Effects of tourism on body size, growth, condition, and demography in the Allen Cays Iguana, *Cyclura cychlura inornata*, on Leaf Cay, The Bahamas. Pp. 214–221 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Smith, K.T., C.P. Kirol, J.L. Beck, and F.C. Blomquist. 2014. Prioritizing winter habitat quality for Greater Sage-grouse in a landscape influenced by energy development. Ecosphere 5:art15. doi:10.1890/ES13-00238.1

Smith, R.K., N.V. Jennings, A. Robinson, and S. Harris. 2004. Conservation of European Hares Lepus europaeus in Britain: is increasing habitat heterogeneity in farmland the answer? Journal of Applied Ecology 41:1092–1102.

Stoner, D.C., M.L. Wolfe, W.R. Rieth, K.D. Bunnell, S.L. Durham, and L.L. Stoner. 2013. De facto refugia, ecological traps and the biogeography of anthropogenic cougar mortality in Utah. Diversity and Distributions 19:1114–1124.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, J.R.B. Bishop, T.A. Marques, and K.P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Wilson, L.D., and J.R. McCranie. 2004. The conservation status of the herpetofauna of Honduras. Amphibian and Reptile Conservation 3:6–33.

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APPENDIX. Environmental variables used in the Resource Selection Functions (RSFs) to describe the habitat accessible to *Ctenosaura oedirhina* across Roatán, Honduras.

Habitat type.—The general habitat types found across Roatán include: shore, "cleaned" forest, "uncleaned" forest, mangroves, stripped land (strip), agricultural land, anthropogenic land (anthro), water, and rock cliff (cliff) (Fig. 2).

Shore	Consists of sandy beach habitat along a salt body of water. Shore is naturally narrow (< 5 m) on the island, but humans have altered it in some areas to be wider for tourism. Shore has a sand substrate, but often there is washed-up vegetation from the ocean and occasionally live vegetation (*Ipomoea* spp.) growing low on the ground.
Forest	Consists primarily of seasonally dry tropical forest (Pennington and Ratter 2010). Canopies of Gumbo-limbo (*Bursera simaruba*), Dogwood (*Piscidia piscipula*), Hog Plum (*Spondias mombin*), and Bullhorn Acacia (*Vachellia cornigera*) are commonly found, some reaching heights of 10–20 m. The understory includes Palmettos (*Sabal* spp.), Wild Grape (*Vitis* spp.), and perennial grasses when an understory is still present. "Cleaned" forests are areas cleaned of their understory, often around houses and businesses. "Uncleaned" forests have an intact understory that is often very dense.
Mangrove	Consists of mainly Red Mangroves, but sometimes also contains White and Black Mangroves. This habitat often has standing salt or brackish water for most of the year; usually shallow (< 0.5 m).
Stripped land	Consists of land stripped of all vegetation down to a sand, dirt, or gravel substrate. This is usually done in preparation for development or mining operations.
Agricultural land	Consists of land primarily being used to graze livestock (cattle or horses) or grow crops (mainly bananas).
Anthropogenic	Land consisting of landscaped areas, usually around residences or in parks, and urban areas.
Water	Habitat consisting of any open water, fresh or salt.
Rock cliff	Habitat consisting of cliffs 5–15 m high along a marine body of water. Cliffs have sheer faces or are boulder strewn, with some boulders measuring 1–2 m across.

Substrate type.—The substrates within the habitat type consist of rock, dirt, sand, mulch, grass, other vegetation (veg), gravel, water, and concrete (conc).

Distance from water (salt or fresh).—Distance from water is measured in four levels – 0 (in water), < 50 m, 50–100 m, > 100 m.

Anthropogenic effects.—Anthropogenic effects were divided into three levels: undisturbed (undist), lightly disturbed (light dist), and heavily disturbed (heavy dist).

Undisturbed	Areas consisting of undeveloped land with no human residents or livestock. There were no streets, buildings, or other infrastructure except for hand-cut walking trails.
Lightly disturbed	Areas that have some development or infrastructure, but not significant amounts, and there is no landscaping. These areas had natural vegetation and low human or livestock populations.
Heavily disturbed	Areas that have been significantly altered by humans. This consists of urbanized districts: streets, buildings, or large-scale landscaping, and high human or livestock populations were found in these areas.

Seasonality.—Data were also divided by season: (1) spring (April–May); (2) summer (August); and winter (November–December).

Herpetological Conservation and Biology 11(Monograph 6):90–105.
Submitted: 30 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

CONSERVATION OF THE ENDANGERED SAN SALVADOR ROCK IGUANAS (*CYCLURA RILEYI RILEYI*): POPULATION ESTIMATION, INVASIVE SPECIES CONTROL, TRANSLOCATION, AND HEADSTARTING

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***Abstract.*—This study describes our efforts to identify and ameliorate threats to San Salvador Rock Iguanas (*Cyclura rileyi rileyi*). Repeated surveys during 1994–2013 of the six small cays occupied suggest a fairly stable population of 429–646 individuals, but with impaired carrying capacity due to habitat deterioration from storm damage and invasive species. Cactus Moth (*Cactoblastis cactorum*) larvae dramatically reduced the biomass of *Opuntia stricta* cacti on several cays inhabited by iguanas. Black Rat (*Rattus rattus*) presence was positively associated with cay size, and a greater proportion of inland-lake cays were occupied compared to offshore cays. We eradicated rats in 2000 and Australian Pines (*Casuarina equisetifolia*) in 2005 on Low Cay, but detected no subsequent increase in iguanas. Of two translocation efforts, the illegal transfer of iguanas to the San Salvador Club Med Resort in 2000 failed for unknown reasons, and the sanctioned establishment of iguanas on Cut Cay in 2005 experienced reproduction failure, possibly because of rat predation. Iguanas at Club Med (altered environment) but not those on Cut Cay (natural vegetation) increased dramatically in body size compared to their source population, suggesting that nutrition of these herbivores affects body size more than low population density and reduced social interactions. We established an iguana headstarting facility at the Gerace Research Centre to augment the wild population (by release of captive-raised iguanas), enhance conservation education, and promote formal habitat protection within a proposed national park. Collectively, these findings provide useful details for monitoring and managing this taxon in the future.**

Key Words.—Bahamas; *Cactoblastis cactorum; Casuarina equisetifolia*; conservation education; eradication; population surveys; *Rattus rattus*

INTRODUCTION

Among the West Indian Rock Iguanas, the Central Bahamian Rock Iguanas, *Cyclura rileyi*, remain one of the most threatened species, with two of the three recognized subspecies deemed Critically Endangered (*C. rileyi cristata*, *C. rileyi rileyi*) and the third (*C. rileyi nuchalis*) as Endangered by the IUCN Red List of Threatened Species (IUCN. 2014. The IUCN Red List of Threatened Species. Available from http://www.iucnredlist.org [Accessed 30 September 2014]). Although each subspecies formerly occupied large islands, today these mostly herbivorous lizards are confined to small, remote, uninhabited cays of three island groups (Hayes et al. 2004). At present, Sandy Cay or White Cay Rock Iguanas (*C. rileyi cristata*) are restricted to Sandy (White) Cay in the southern Exumas, where an estimated 1000+ individuals persist (Hayes et al. 2004, this volume). Acklins Rock Iguanas (*Cyclura rileyi nuchalis*) exist naturally on just two cays in the Acklins Bight of the Crooked/Acklins Island group, but a third population has been introduced to a cay in the central Exumas (Iverson et al. this volume). Although as many as 10,000 individuals of this taxon may remain, the current distribution represents a tiny fraction (0.2%) of its former range (Hayes et al. 2004). San Salvador Rock Iguanas (*Cyclura rileyi rileyi*) are largely confined to four tiny offshore cays and two islets within the hypersaline lakes of San Salvador Island, though a small and possibly non-sustaining population persists on the main island itself, where non-native predators and vehicles threaten persistence (Hayes et al. 2004 and further described here). With fewer than 600 individuals remaining, this taxon similarly occupies a mere fraction (0.2%) of its former range. Morphometric analyses suggest that these three taxa warrant status as distinct

Hayes, William K., Samuel Cyril Jr., Tom Crutchfield, Joseph A. Wasilewski, Thomas A. Rothfus, and Ronald L. Carter. 2016. Conservation of the endangered San Salvador Rock Iguanas (*Cyclura rileyi rileyi*): population estimation, invasive species control, translocation, and headstarting. Pp. 90–105 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

subspecies and independent management units (Carter and Hayes 2004; Hayes and Carter 2005), but Malone et al. (2000) found no mtDNA sequence differences among the three forms. Nevertheless, some authorities consider the three taxa to be distinct species (Powell and Henderson 2011).

Lamentably, San Salvador Rock Iguanas continue to decline. In recent decades, a number of populations have become extirpated (Barn Cay in the 1970s; High Cay in the 1980s; Gaulin Cay in 1999). The identified threats include illicit smuggling, invasive species, disease, and catastrophic storms that have damaged both soil and vegetation (e.g., Hurricanes Erin in 1995, Bertha and Lili in 1996, Floyd in 1999, Frances in 2004, Irene in 2011, and Sandy in 2012).

This report summarizes our work on San Salvador Rock Iguanas from 1994 through 2014, and provides an update of the early activities summarized only briefly by Carter and Hayes (2004) and Hayes et al. (2004). It encompasses three major efforts. First, to better understand potential threats and assess management efforts, we repeatedly surveyed the population size and age structure of each iguana population using both mark-resighting and transect surveys. Repeated surveys on one cay with marked iguanas provided useful information on the factors related to detection of iguanas during surveys, including the sex and age class of iguanas, and the time of day that surveys were conducted. Second, we undertook several mitigation measures intended to benefit the lizards, including invasive species control and population translocation. In doing so, we evaluated the success of these efforts and considered hypotheses regarding the factors associated with presence of Black Rats (*Rattus rattus*) and the relative influence of nutrition versus population density on iguana body size. Third, we initiated a headstarting program implemented in part to boost the wild population of iguanas by raising hatchlings in captivity and eventually releasing them at a size less vulnerable to predators and other risks (Alberts et al. 2004; Alberts 2007; Escobar et al. 2010). We conclude by discussing some of the opportunities and obstacles associated with the conservation of this threatened Bahamian endemic.

MATERIALS AND METHODS

Study site.—The island of San Salvador occupies its own bank on the eastern side of the Bahamas archipelago. Although a relatively small island (163 km^2) composed of limestone with karst features, it nevertheless supports diverse habitats, including coastal rock, sand strand and Sea Oats (*Uniola paniculata*), coastal coppice, blacklands coppice, and mangrove communities (Smith 1993). Numerous small islets occur within the extensive system of mostly hypersaline lakes in the island's interior, and eleven small cays occur offshore. Iguana populations occur primarily on six of the cays (Fig. 1). Some of these cays also host substantial seabird colonies and several species compete with the iguanas for burrows (Hayes 2003; Hayes et al. 2004; Trimm and Hayes 2005). Five additional native reptile species co-occur with the iguanas, including one small snake, the San Salvador Threadsnake (*Epictia columbi*, Hayes et al. 2004; Hillbrand et al. 2011).

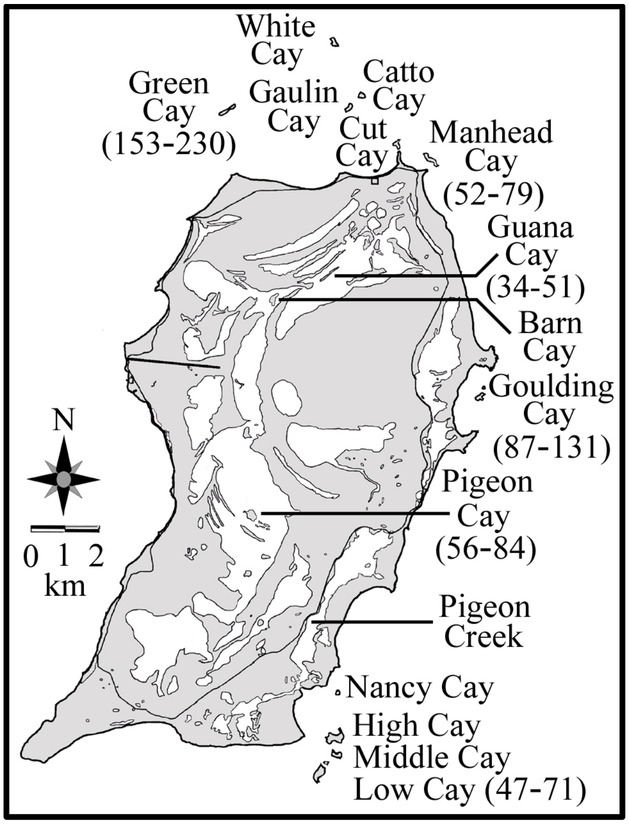

FIGURE 1. San Salvador Island, The Bahamas, with its offshore and inland lake cays. Estimated population size of San Salvador Rock Iguanas (*Cyclura rileyi rileyi*) is indicated for those cays that currently host natural populations. Populations have become extirpated on Barn, Gaulin, and High Cays. A very small population occurs on the main island. A translocated population (14 adults) was established on Cut Cay in 2005, but has been non-viable, presumably due to presence of Black Rats (*Rattus rattus*).

Iguana body size and sex.—We captured iguanas by noose or by hand to measure a number of morphological variables, including mass (nearest gram weighed by Pesola spring scale) and snout-vent length (SVL, to nearest millimeter). We determined the sex of iguanas by probing of cloacal pouches. We marked the lizards individually using colored glass beads sutured to the nuchal crest (Hayes et al. 2000). During summer 1999 on Green Cay, we also painted an alphanumeric code on both sides of the animal using white enamel paint for short-term identification (Cyril 2001). Methods and analyses of morphological data appear elsewhere (Carter and Hayes 2004; Hayes et al. 2004, 2012); these summarize sexual differences, variation in body size and scalation among the populations, effects of habitat change on body condition, the relationship between body size and reproductive parameters, and ecological factors associated with toe and tail injuries. Here, we compare body size between translocated iguanas and other individuals from the source cay.

Iguana population surveys.—We conducted two sets of iguana surveys. The first set consisted of entire-cay visual-encounter surveys (Hayes et al. 1995; Hayes and Carter 2000) of each of the six iguana populations on the offshore and inland-lake cays using a standardized route and method. Individual populations were surveyed from three to 14 times during the period 1994 to 2013, with dates (month and year) provided in Table 1. Two to three researchers (always including WKH) spread out and walked slowly through all accessible habitat on each cay, and gently prodded the vegetation with bamboo fishing rods or sticks to flush iguanas. The route walked varied from cay to cay, depending on cay size and habitat structure, but followed the habitat structure rather than lines or strips, and was standardized for each cay. We recorded all iguanas detected by sight or by sound (as they scampered noisily into the vegetation) and the size of all iguanas seen sufficiently well. We paid careful attention not to double-count iguanas, which was made easier by the small size of the cays, the relatively small number of iguanas, limited vegetation structure to impede observation of iguana movements, and communication among observers. On Green Cay, where double-counting was expected to be most problematic due to high population density, most of the adult iguanas were marked, and the unmarked individuals including smaller numbers of juveniles and subadults, were spatially dispersed and easy to keep track of. We visually categorized iguanas into four size classes based on approximate snout-vent length: juveniles (< 12 cm), subadults (12–19 cm), small adults (20–27 cm), and large adults (> 28 cm). These size classes were fairly easy to distinguish except at the boundary of adjacent categories, where some error was inevitable. The observers came to a collective agreement on categorizing size before and during the survey; most iguanas were observed by more than one researcher during the surveys. With the exception of Low Cay, which has mostly large adults, we eventually discontinued distinguishing between the two adult size classes. We conducted surveys between mid-morning and mid-afternoon (1000–1500) during dry weather. Surveys were generally completed within 1 h.

To verify and better interpret our survey results, we conducted a second set of intensive surveys of a single iguana population. One of us (SC) independently (without helpers) conducted 37 surveys of iguanas on Green Cay, where numerous marked individuals were present, from 23 June to 22 July 1999. Using an approach similar to the first set, these surveys encompassed 80% of the cay while avoiding a dense seabird colony that had settled on the eastern end that year. Surveys were done during the morning (0800–1030), midday (1300–1430), and evening (1700–1930) hours, and required 30–75 minutes to complete. Usually two or three surveys were conducted per day, typically separated by 6 h or more, but always by a minimum of 3 h to maintain independence between successive surveys. The sequence of approach for surveying three demarcated regions of the cay was randomized to help reduce iguana detection of the oncoming investigator. During each survey, all iguanas seen were identified as marked or unmarked, and the size class was recorded when possible. To evaluate how iguana activity levels and detectability varied with gender and time of day, we examined the proportion of marked iguanas resighted during each survey using a 2 x 3 (sex x time of day) repeated-measures analysis of variance (ANOVA, Green and Salkind 2005) via SPSS (SPSS v13.0 for Windows, Statistical Package for the Social Sciences, Inc., Chicago, Illinois, USA, 2004), with alpha = 0.05. We treated sex as a within-subjects factor because both sexes were surveyed at the same time (i.e., to avoid pseudo-replication, surveys were used as the appropriate unit of replication for degrees-of-freedom), and time of day as a between-subjects factor. We followed this with Least Significant Difference multiple comparisons. Proportions were arcsine-transformed prior to analysis, and parametric assumptions were met. We computed effect sizes as partial eta-squared (η^2), interpreted as approximate percent of variance explained by an effect or interaction, with values of ~ 0.01, ~ 0.06 and ≥ 0.14 loosely regarded as small, moderate, and large effects, respectively (Cohen 1988). For each survey, a population estimate was also derived based on the Lincoln-Petersen equation (Hayes et al. 1995; Hayes and Carter 2000). The number of marked iguanas increased from 62 to 76 between the first and last surveys, and the number used in the equation was adjusted each day that new iguanas were captured and marked. A one-way ANOVA (with assumptions met) was used to compare Lincoln-Petersen population estimates for the three times of day. To compare the proportions of individuals of each age class that were observed during surveys, we used a 3 x 3 (age class x time of day) ANOVA that treated age class (juveniles, subadults, adults) as a within-subjects factor (because all three age classes were surveyed at the same time) and time of day as a between-subjects factor. Proportions were rank-transformed prior to analysis (with assumptions met) to avoid problems associated with proportions summing to 1.0. Finally, we computed coefficients of variation (CV = SD x 100/mean) to compare the precision of iguana counts for each age class, the count of all iguanas, and for the Lincoln-Petersen estimates.

Previous mark-resighting surveys of *C. rileyi* subspecies on six cays (including four of those studied here; Hayes et al. 2004), and repeated surveys of *C. rileyi nuchalis* (Thornton 2000) and *C. rileyi rileyi* (see results of this study) within single populations, indicated detectability in the range of 0.25 to 0.5, with a mean of 0.33 for 37 surveys on Green Cay (reported here). Thus, for each survey in the first set, which encompassed all of the inhabited cays, we divided the total number of iguanas detected by 0.33 and by 0.5 to derive a range for each population estimate. All population estimates of each population (excluding autumn surveys with a large pulse of neonate iguanas) were then averaged to yield a final estimate, which was similarly expressed as a range.

***Invasive species*.**—We continually monitored each cay harboring iguanas to identify any invasive species present. Numerous non-native species exist on the main island, including many plant species, Red Imported Fire Ants (*Solenopsis invicta*), and feral companion animals (*Canis familiaris*, *Felis catus*) and farm animals (*Bos taurus*, *Sus* sp.; Smith 1993; Deyrup 1994; Smith 2010; William Hayes pers. obs.). However, we focused on the three invasive species that have become established on the offshore and inland lake cays: Australian Pines (*Casuarina equisetifolia*), Cactus Moths (*Cactoblastis cactorum*), and Black Rats (*Rattus rattus*).

TABLE 1. Population estimates for San Salvador Rock Iguanas (*Cyclura rileyi rileyi*), expressed as a range, and age class percentages (within parentheses) of juveniles, subadults, small adults, and large adults, respectively. Population estimates based on standardized visual encounter survey densities divided by detectability of 0.33 and 0.5 (Thornton 2000; Hayes et al. 2004; Table 2 of this study) to provide a range. Brackets indicate that the percentages of small and large adults were combined for some surveys. Mean estimate = mean of all surveys excluding those conducted in October and November.

Date	Goulding Cay	Green Cay	Guana Cay	Low Cay	Manhead Cay	Pigeon Cay
May, July 1994	60–90	158–237	16–24	50–75	56–84	
June 1998	116–174 (5.26.61.7)	130–195 (6.16.60.18)	30–45 (20.27.33.20)	42–63 (0.0.7.93)	32–48 (14.43.43.0)	70–105 (3.6.77.14)
June 1999			56–84 (4.11.61.25)			38–57 (0.11.84.5)
October 1999		142–213 (1.11.[87])		96–144 (46.6.4.44)	56–84 (31.23.46.0)	
May 2000				36–54 (0.6.0.94)		
November 2000		192–288 (1.7.[92])		106–159 (26.7.5.63)	36–54 (29.18.53.0)	
June 2001				54–81 (0.0.14.86)		58–87 (0.19.[81)]
May 2002				64–96 (0.5.10.86)		
October 2002		160–240 (12.8.[81])		50–75 (0.11.22.67)		
June 2003	86–129 (0.43.[57])			42–63 (0.14.7.79)		
July 2004		200–300 (6.7.[87])		46–69 (0.7.21.71)	70–105 (29.35.35.0)	
February 2005				54–81 (5.0.10.86)		
June 2005		122–183 (3.7.[90])				
June 2006		172–258 (7.7.[86])		54–81 (0.5.14.82)		
June 2007				52–78 (0.20.5.75)		
May 2012		136–204 (3.18.[78])				
June 2013				28–42 (0.0.0.100)		
Mean Estimate	87–131 (*n* = 3)	153–230 (*n* = 6)	34–51 (*n* = 3)	47–71 (*n* = 11)	52–79 (*n* = 3)	56–84 (*n* = 3)
Trend	Stable	Stable	Unclear	Declining?	Unclear	Unclear

We removed all Australian Pines from Low Cay by hand or by machete, without applying chemicals, and monitored their potential reestablishment on subsequent visits to the cay. To measure Prickly Pear Cacti (*Opuntia stricta*) loss due to grazing by Cactus Moth larvae, we recorded the number of cactus pads (cladodes) and maximum height of individual plants (to nearest centimeter) on three representative 2 m^2 plots on the western portion of Green Cay in August 1994, May 1995, November 1995, June 1998, and June 1999. Browsing by the moth larvae will generally kill smaller *Opuntia* plants and destroy the terminal segments of larger plants, thereby reducing their overall size (Jezorek 2011; Jezorek et al. 2012). Each plot appeared to have numerous plants, but we could not distinguish individuals reliably due to vegetative multiplication (Reyes-Agüero et al. 2006). Considering the small sample size, we limited statistical analysis to computation of effect size as Kendall's *W*, with 0.1, 0.3, and 0.5 corresponding loosely to small, medium, and large effects (Green and Salkind 2005). Compared to statistical significance, effect size is independent of sample size, biologically more meaningful, and can be more readily compared among different studies (Nakagawa and Cuthill 2007).

We used collapsible Sherman aluminum live rodent traps (7.5 x 9 x 23 cm; H.P. Sherman, Tallahassee, Florida, USA) baited with several peanuts to assess the presence of rats on all offshore cays and at one location on the main island. Trapping was conducted during various months of the year, but mostly in June and October. Our goal was to identify their presence rather than population density; *R. rattus* can breed seasonally or year-round, and population size and trap success can fluctuate independent of season (Ewer 1971; Tamarin and Malecha 1972; Clark 1980). Traps were set in the evening after darkness and retrieved early in the morning, as the rats are primarily nocturnal. Any rats captured during the 310 trap nights were euthanized by cervical dislocation. We employed stepwise binary logistic regression (Mertler and Vannatta 2004) using SPSS software and $\alpha = 0.05$ to test which factors influenced the confirmed presence of rats among the 12 cays. The predictors included cay size, water body type (inland lake versus ocean, a categorical predictor), and distance from the main island. We used a stepwise model because of the small sample size (12 cays).

We attempted rat eradication on Low Cay in summer 1999 by using brodifacoum rodenticide, but the effort failed when abundant Hermit Crabs (*Clibanarius tricolor*) blocked access to the bait stations. The rodenticide and application over a 20 m grid system are partially described in Day et al. (1998) and Hayes et al. (2004), but we provide more details on the bait stations here. To reduce the risk of incidental poisoning of iguanas and birds, we secured the bait blocks via wire within rectangular plastic bait stations (roughly 20 × 7.5 × 7.5 cm; Fig. 2A). We repeated the procedure in summer 2000 with a modified bait delivery system, in which the same bait stations were elevated 15–20 cm above the ground on a single PVC stake to limit entry of Hermit Crabs into the stations (Fig. 2B, 2C). Each station had holes drilled through it to insert the stake, and was held in place on the stake by a plastic zip tie secured around the stake and beneath the station.

Translocation.—Two iguana translocations were undertaken. The first, conducted illegally by employees of Club Med in 2000 or earlier, involved the removal of six or more adult iguanas (sex ratio unknown) from Green Cay to the resort grounds on the main island. We gleaned details about the iguanas from interviews of staff at the resort and by observing and capturing iguanas there in October 2002. The second translocation, conducted with permission of the landowner and a permit from the Bahamas Ministry of Agriculture, involved the transfer of 14 adult iguanas (6 ♂♂, 8 ♀♀) from Green Cay to Cut Cay in February 2005. These animals were transported individually, out of direct sunlight, within cloth pillowcases (51 x 91 cm). Prior to the second translocation, we set rat traps on Cut Cay and on the adjacent main island (North Point) to determine whether rats were present. We compared the body sizes of adult iguanas captured at Club Med (October 2002) and those observed at Cut Cay (June 2012) to the large sample captured at Green Cay, the source population (1993–1999). We hypothesized that translocated iguanas on Club Med and Cut Cay would attain a larger body size (length and mass) than those of Green Cay (the source of origin) due to a richer food source and potential supplemental feeding (at Club Med), less food competition (both locations), and/or fewer social inter-actions that would otherwise constrain time devoted to feeding (both populations; see Carter and Hayes 2004; Hayes et al. this volume; Iverson et al. this volume). We used an independent samples *t*-test (Green and Salkind 2005) to compare the body sizes of adult (≥ 20 cm) male iguanas from Club Med and Green Cay, and a one-sample *t*-test (Green and Salkind 2005) to compare the body size of the one adult female iguana from Club Med to adult females from Green Cay. We had no iguana recaptures from Cut Cay, but their body size relative to Green Cay iguanas could readily be inferred by observation in the field.

RESULTS

Iguana population estimates.—For the repeated surveys on Green Cay in 1999, we conducted separate analyses of marked iguanas and counts of all iguanas. The 2 x 3 (sex x time of day) ANOVA revealed that the mean proportion of marked adult iguanas detected during a given survey was similar for the two sexes ($F_{1,34} = 0.23$, $P = 0.63$, partial $\eta^2 < 0.01$) but varied

FIGURE 2. Bait station (plastic drain pipe roughly 25 × 7.5 × 7.5 cm) for delivering brodifacoum (Weatherblock XT® Rodenticide) to eradicate non-native Black Rats (*Rattus rattus*) on Low Cay, San Salvador, The Bahamas. (A) Three bait blocks secured by wire within the bait station. (B) Failed station placement on ground in 1999, when abundant Hermit Crabs (*Clibanarius tricolor*) swarmed the stations and blocked rat access to the bait. (C) Successful station placement 15–20 cm above ground on a single PVC stake in 2000, which precluded Hermit Crab entry but allowed access by rats. (Photographed by William K. Hayes).

TABLE 2. Percentages (mean ± 1 SE) of marked adult San Salvador Rock Iguanas resighted during 37 surveys on Green Cay between 23 June and 22 July 1999, and corresponding Lincoln-Petersen (L-P) estimates of adult population size. Surveys were undertaken during morning (0800–1030), midday (1300–1430), and evening (1700–1930) hours.

Time of day	*n*	Males (%)		Females (%)		All iguanas (%)		L-P estimate	
		Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Morning	16	30.6 ± 1.6	22–47	30.7 ± 2.7	11–47	31.2 ± 1.8	19–47	133.6 ± 4.1	114–168
Midday	5	20.0 ± 5.4	6–38	24.1 ± 3.0	16–34	22.8 ± 3.2	17–31	128.9 ± 14.6	105–181
Evening	16	38.7 ± 1.8	25–50	37.3 ± 2.3	21–49	38.6 ± 1.8	24–47	132.9 ± 3.8	112–165

significantly with time of day ($F_{2,34}$ = 11.01, $P < 0.001$, partial $\eta^2 = 0.39$). Proportions (= detectability) for both sexes combined averaged 0.31 in the morning (*n* = 16 surveys), 0.23 at midday (*n* = 5), and 0.39 in the evening (*n* = 16; Table 2, reported as percentages). Post-hoc comparisons indicated that proportions for each time of day differed from each of the other times. No interaction existed between sex and time of day ($F_{2,34} = 0.49$, $P = 0.62$, partial $\eta^2 = 0.03$), indicating that relative levels of activity and detectability of males and females were similar during the three time periods. Mean overall detectability for the 37 surveys was 0.33. The one-way ANOVA for Lincoln-Petersen estimates, in contrast, showed no effect for time of day ($F_{2,34} = 0.13$, $P = 0.88$, partial $\eta^2 < 0.01$). Thus, the mean population estimate from surveys was similar for the three times of day (129–134), though individual survey estimates ranged from 105–181, with an overall mean of 133 (Table 2). Assuming that 133 iguanas was the actual adult population size within the study area, the maximum Lincoln-Petersen estimate error for an individual survey was 18.0% (24 iguanas) below and 36.1% (48 iguanas) above this number.

The 3 x 3 (age class x time of day) ANOVA for proportions of each age class detected during surveys revealed significant differences among the age classes ($F_{2,68}$ = 213.71, $P < 0.001$, partial $\eta^2 = 0.86$), with representation greatest for adults (71.3%), less for subadults (25.3%), and least for juveniles (3.4%; Table 3). However, no differences existed for time of day ($F_{2,34}$ = 0.58, $P = 0.57$, partial $\eta^2 = 0.03$), and there was no interaction between age class and time of day ($F_{4,68}$ = 0.11, $P = 0.98$, partial $\eta^2 < 0.01$). Thus, relative levels of activity and detectability were highly similar among all age classes regardless of time of day. We do not know the actual detectability of juveniles and subadults due to insufficient marked individuals, but assuming it is similar to adults, the 71.3% representation for 133 adult iguanas suggests a conservative estimate of 187 iguanas within the study area during June–July 2009.

TABLE 3. Percentages (mean ± 1 SE) of San Salvador Rock Iguanas of three age classes sighted during 37 surveys on Green Cay between 23 June and 22 July 1999. Surveys were undertaken during morning (0800–1030), midday (1300–1430), and evening (1700–1930) hours.

		Juveniles (%)		Subadults (%)		Adults (%)	
Time of day	*n*	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Morning	16	3.1 ± 0.8	0–11	25.8 ± 1.6	16–42	71.1 ± 1.6	58–79
Midday	5	3.9 ± 1.7	0–9	24.2 ± 3.9	14–33	71.9 ± 4.4	62–84
Evening	16	3.6 ± 0.5	0–8	25.1 ± 1.2	16–33	71.3 ± 1.1	65–82

With means of 1.6, 11.6, and 32.7 juvenile, subadult, and adult iguanas detected per survey, respectively, corresponding CV values were 82.7, 34.9, and 26.1. Thus, although representation of age classes was consistent among surveys, the precision for number of animals detected was comparatively low for juveniles in particular. With 48.1 total iguanas detected per survey (including those of undetermined size class), the CV for total iguana counts was 26.1. With a mean Lincoln-Petersen estimate of 133 adult iguanas, the CV for iguana mark-resighting estimates was 13.7, approximately half that of the counts for adults, indicating greater precision. Given the inherent variation in population estimates, these results encouraged us to report the population-wide surveys (below) as a range based on detectability of 0.33–0.5 (see Discussion for further justification).

Surveys of all iguana populations indicated that population size and age structure varied substantially among the cays (Table 1). However, several trends were evident. First, the largest estimates occurred during autumn surveys, when a large pulse of hatchlings typically increased the population. For the one exception, most of the nests were apparently destroyed on Green Cay in September 1999, when Hurricane Floyd swept over much of the low-lying island (hatchlings comprised 1% compared to 46% and 31% on Low and Manhead Cays, respectively, in late October 1999). This hurricane also extirpated the small Gaulin Cay population (Hayes et al. 2004). Low hatchling numbers on Green Cay occurred again in November 2000, but hatchling success was improved in early October 2002 (apparently before nest emergence on Low Cay). Second, some populations consistently experienced more recruitment of juveniles into the population than others. The Low Cay population, for example, was comprised almost exclusively of adults throughout the study (usually > 90% during the summer months), whereas Manhead Cay had much greater representation of juveniles and subadults (57–64% during the summer months). Third, we saw no detectable increase in recruitment and population growth on Low Cay following eradication of rats in 2000. Finally, those populations sampled most often have appeared to be stable, except that the last survey of Low Cay suggested a possible recent decline. The sum of estimates from all islands (Table 1) provided a total population estimate of 429–646 across our 20-year study.

Because iguanas are encountered only rarely on the main island, the sparse and possibly non-viable population there could not be surveyed. In the 1980s, John Winter (pers. comm.) observed two adults on the eastern side of the island, one on the western shore of Six Pack Pond, and the other on the northeastern shore of Granny Lake. For the past two decades, we and others have occasionally seen up to two adults at the Fortune Hill Ruins, also on the east side of the island. Shortly after Hurricane Floyd in 1999, Eberth Jones (pers. comm.) reported an adult on the northeastern end of the island near North Point. Finally, between 2005 and 2011, we observed three different adults that appeared briefly at the Gerace Research Centre on the northern end of the island. One of the latter was killed by a vehicle on the main highway (Vince Voegeli, pers. comm.).

Invasive species and their control.—Although Australian Pine occurs abundantly on the main island, we found it present on only one offshore cay (Low Cay) and on none of the sampled inland lake cays. In July 2004, we pulled up and cut down ca. 10 saplings on the northeastern portion of Low Cay. Three of these trees were nearly 3 m high. No regrowth occurred through 2013.

We confirmed Cactus Moths in 1994 on Green Cay (Hayes et al. 1995). At that time, substantial Prickly Pear Cacti remained, though some loss might have occurred. During the period 1994–1999, the cactus patches declined precipitously in biomass, with an 86.6 ± (SE) 6.3% loss

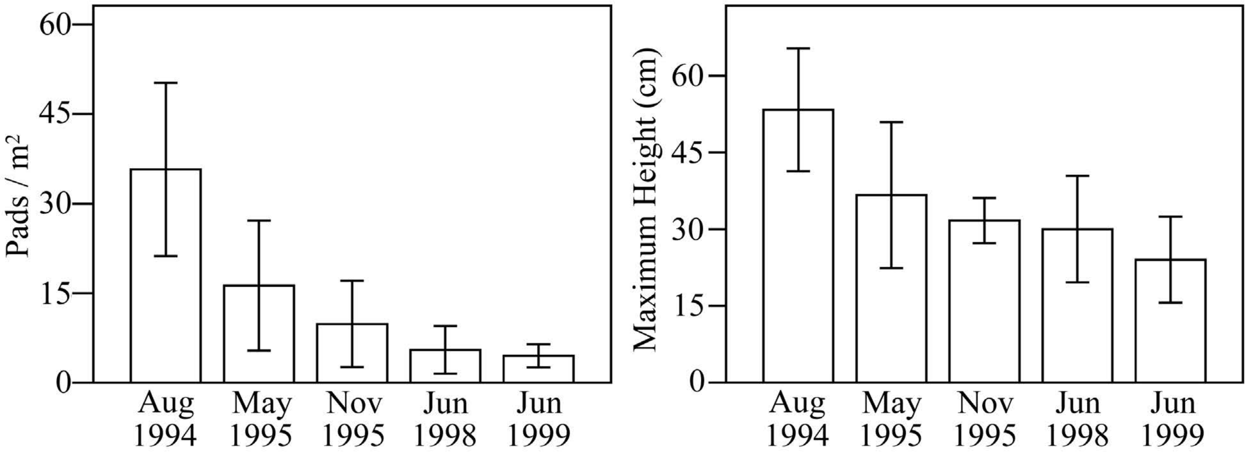

FIGURE 3. Mean (± 1 SE) number of Prickly Pear Cacti (*Opuntia stricta*) pads (cladodes) and maximum height recorded in three 2-m^2 plots on the west end of Green Cay, San Salvador, The Bahamas, from 1994–1999. The biomass decline resulted from intense herbivory by non-native larvae of Cactus Moths (*Cactoblastis cactorum*), and continued beyond June 1999 (data not obtained).

TABLE 4. Presence of Black Rats (*Rattus rattus*) on offshore cays, inland lake cays, and North Point of San Salvador Island, The Bahamas (see Fig. 1). Distance provided between each cay and the main island of San Salvador, which serves as a reservoir for invasion. Sherman rodent live trap results from 1999–2001. S = sighting; C = carcass; T = trap capture.

Location	Area (ha)	Distance to island (m)	Water body	Trap nights	Trap captures	Rats confirmed
Catto	1.9	2,050	Ocean	16	0	
Cut	3.0	30	Ocean	40	0	S (2012)
Gaulin	1.6	2,000	Ocean	11	0	
Goulding	2.9	590	Ocean	15	0	
Green	5.1	1,950	Ocean	11	0	
Guana	1.6	180	Lake	4	0	S (before 1994)
High	13.4	580	Ocean	42	0	C (1995)
Low	10.8	1,010	Ocean	14	2	S (1994–2000), T (1999–2000)
Manhead	3.3	280	Ocean	66	0	
Middle	2.7	960	Ocean	15	0	
Nancy	1.0	350	Ocean	10	0	
North Point	—	—	—	22	3	T (2001)
Pigeon Cay	7.8	900	Lake	44	0	S (1995)

(range, 74.7–96.4%) in the number of pads and 49.1% loss ± (SE) 20.0% (range, 16.7–85.0%) in maximum plant height (n = 3 plots, Kendall's W = 0.73 and 0.59, respectively; both values represent a large effect size; Fig. 3). Further loss occurred in subsequent years (not quantified), resulting in persistent patches of stunted cacti mostly < 30 cm in height. Large cactus patches experienced dramatic reductions during this time also on Manhead and Gaulin Cays, and on two other cays devoid of iguanas (Catto and Middle Cays). Widespread cactus patches were lost on High Cay and Low Cay prior to this period, where extensive areas of small cactus plants remained as of 2013. We have not attempted to control this moth.

Our trapping efforts for rats yielded positive results at two locations (Low Cay and North Point on the main island adjacent to Cut Cay), and negative results at all other locations (Table 4). We observed up to three rats on Low Cay during daylight hours (Hayes et al. 1995) on virtually every trip to the island through 2000. Rats also were reported on Guana Cay in the inland lake (Don Gerace, pers. comm.); a carcass was found on High Cay in 1995 (John Iverson, pers. comm.; Auffenberg, cited in Hayes et al. 1995, thought rats might have caused extirpation of these iguanas); and we observed a rat on Pigeon Cay in 1995 (Table 4). Stepwise binomial logistic regression yielded a significant model (χ^2 = 10.04, df = 2, P = 0.007, Nagelkerke R^2 = 0.76) for confirmed rat presence (last column of Table 4), which predicted the presence of rats on a given cay with 91.7% success (7/7 cays with rats absent; 4/5 cays with rats present). However, neither of the two predictors in the final model attained independent significance (cay size: P = 0.17; water body type: P = 0.999), due in part to limited statistical power. The odds ratio for cay size (1.85, 95% CI = 0.76–4.51) exceeded 1.0, which suggested that large cays were more likely to have a confirmed rat presence than small cays. Rats were documented on both of the inland lake cays, but only on three of the 10 offshore cays. Distance from the main island was excluded from the final stepwise model.

Our attempt to eradicate the rats on Low Cay in 1999 failed, but we believe we succeeded with the modified bait system in 2000, as described in Hayes et al. (2004). Subsequent trapping effort in 2000 (37 trap-nights) and absence of rat sightings during daylight in the years since suggest the continued absence of rats on Low Cay through 2013.

Prior to translocating iguanas to Cut Cay, we failed to catch rats there despite relatively intense trapping (40 trap nights). This assumed absence of rats contrasted sharply with trap success on North Point on the adjacent portion of the main island (three captures in 22 trap nights; Table 4). However, we sighted a rat on Cut Cay during an iguana survey in May 2012.

Body size and translocation.—In November 2000, we observed fresh iguana tracks on the Club Med grounds during an overnight visit, and were told by employees that they had colored glass beads affixed to their nuchal crests (Hayes et al. 2000, 2004). In October 2002, we observed five adult iguanas and one subadult, confirming that breeding took place, as reported to us by the staff. The resort reportedly removed all stray cats and dogs, and poisoned the rats; we encountered one rat that was obviously incapacitated and dying. We captured three unmarked iguanas (two males, one female), which we recognized beforehand as being exceptionally massive, and the data confirmed that they were, indeed, substantially larger than any iguana measured previously on Green Cay (n = 92; Fig. 4). The two males from Club Med (34.8 and 36.0 cm SVL) were significantly larger than the 39 adult males from Green Cay captured between 1993 and 1999 (t_{39} = 5.28, two-tailed P < 0.001), and the single female from Club Med (29.5 cm SVL) was significantly larger than the 36 adult females from Green Cay (t_{35} = 16.50, two-tailed P < 0.001). Although some supplemental feeding occurred (Janet Storr, pers. comm.), the iguanas we found were skittish, wary of our approach, and mostly ignored the food items we tossed to them to facilitate capture. We

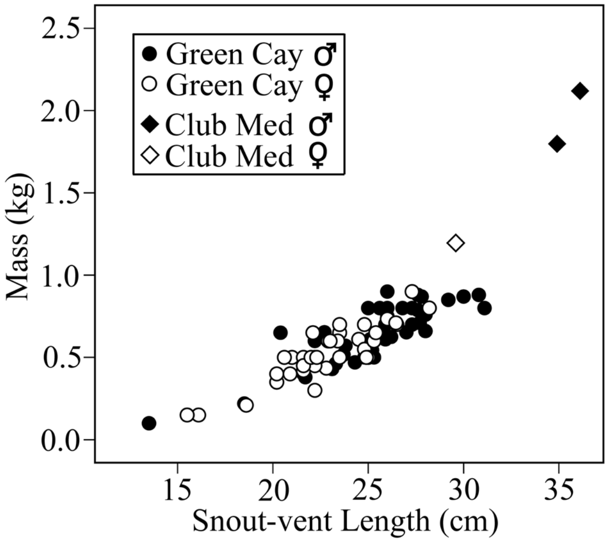

FIGURE 4. Body sizes of male and female San Salvador Rock Iguanas, illustrating the substantially larger size of specimens translocated to the San Salvador Club Med Resort (*n* = 1 ♀, 2 ♂♂), presumably in 2000 or earlier and measured in October 2002, compared to those of their source population on Green Cay (*n* = 92).

obtained permission to return to Club Med again in June 2007, when we managed to locate (but not capture) only two large adult iguanas despite extensive searching. We were told that a few others were still present, but that no more breeding was occurring. The population subsequently dwindled to the point that none remained as of 2012, according to Club Med staff who declined to give us permission to enter the property. At least two iguanas escaped over the fence and were killed by vehicles on the main highway (Janet Storr, pers. comm.).

We translocated adult iguanas (6 ♂♂, 8 ♀♀) from Green Cay to Cut Cay in February 2005. No hatchlings or subadults were observed during visits by us in June 2006, June 2007, January 2012, May 2012, and June 2013. During the May 2012 survey, we sighted 12 of the 14 translocated adult iguanas. The four iguanas for which we had unobstructed views (others were in the shrubs) appeared to be similar in size to those on Green Cay.

DISCUSSION

Our standardized population surveys have provided us with useful data to evaluate conservation threats and management actions for San Salvador Rock Iguanas. Unfortunately, population estimation remains imprecise, as estimates can be affected by numerous environmental and methodological factors. One key concern is the proportion of iguanas detected, which can substantially affect estimates via visual encounter surveys and distance transects (Hayes and Carter 2000; Lovich et al. 2012; Burton and Rivera-Milán 2014). Our data suggest that detectability is similar for males and females, but that time of day can have an influence, with iguanas generally becoming less active at midday, resulting in reduced detections during surveys. Similar patterns of bimodal activity, with higher levels during morning and evening, have been reported for *Cyclura carinata* (Iverson 1979), *Cyclura rileyi nuchalis* (Thornton 2000), *Cyclura cychlura* (Wilcox et al. 1973), and *Cyclura nubila caymanensis* (Carey 1966), however, *Cyclura lewisi* concentrated activity in the midday during the fall and spread out activity over the entire day during the summer (Goodman 2007). Although time-intensive and costly, our data suggest that mark-resighting estimates offer greater precision (coefficient of variation = 13.7) than count data (25.5), and can overcome problems that result from variation in detectability. By comparison, Burton and Rivera-Milán (2014) reported coefficients of 10 to 15 for distance sampling and repeated counts of *C. lewisi* on Grand Cayman. However, the accuracy of mark-resighting becomes limited if there is bias among representation of different age groups, such that separate estimates may be required of each size class. Our data further indicate that juvenile iguanas are more difficult to detect and to survey reliably than other age groups, as evidenced by the relatively high CV values from our surveys (82.7 versus 34.8 for subadults and 26.1 for adults). Collectively, these difficulties prompted us to report population estimates derived from counts as a range of values. Although mean detectability of iguanas on Green Cay was 0.33, we suspect this value was low because of the frequent nature of surveys (up to three per day) and ongoing capture efforts, which probably caused the previously captured iguanas to become more wary. Additional mark-resighting surveys of six *C. rileyi* ssp. populations, which allowed for more time after marking, provided detectability values of up to 0.55 (Hayes et al. 2004). Similar repeated surveys of marked *C. rileyi nuchalis* in the Acklins Bight averaged 0.47 in the morning, 0.24 at midday, and 0.44 during the evening (Thornton 2000). We suggest that detectability of 0.33–0.50 is reasonable for our taxon and location. For comparison, Burton and Rivera-Milán (2014) reported a mean detectability of 0.57 for male and female *C. lewisi* combined. Differences in detectability among studies and populations could result not only from survey methods, but also from population or species differences in activity and habitat use.

Despite the limitations of our surveys, we now have meaningful baseline data, some of which has allowed us to identify trends of potential relevance. We have documented: (1) the negative impact of Hurricane Floyd in 1999 on iguana reproduction on Green Cay and the extirpation of an entire population on Gaulin Cay; (2) obvious differences in age class representation and recruitment among the populations, which presumably relate to food availability, rat presence, and/or disease (Hayes et al. 2004); (3) the absence of a demographic or population response to rat eradication on Low Cay; and

(4) general stability among the populations sampled most frequently, with the possible exception of an apparent recent decline on Low Cay. Some populations have not been surveyed in more than a decade, which needs to be addressed. Although we lack quantitative data, the vegetation on Green Cay, which hosts the largest iguana population, is steadily deteriorating, presumably due to soil loss from catastrophic storms and this merits continued monitoring and further study.

Iguana populations on San Salvador appear to be impacted to some extent by invasive species, particularly the Cactus Moths and Black Rats. Although Australian Pines have the potential to become established and destroy habitat on a number of cays that host iguanas (Hayes et al. this volume), seedlings are easily detected and can be readily managed, as we demonstrated on Low Cay. Unfortunately, large stands exist on the main island (Rodgers 2005; Rodgers and Gamble 2008), which unless controlled will remain a source of more colonizing seedlings in the future.

Our survey of Prickly Pear Cacti stands on Green Cay illustrates the rapid devastation of formerly extensive cactus stands by the larvae of the Cactus Moths. When *Opuntia* cacti are available, the iguanas associate with and feed preferentially on it (Cyril 2001). We suspect that cactus loss has reduced the carrying capacity of iguanas on a number of cays, including Green Cay. Our previous analysis of morphological measures suggested that iguanas prior to (or during) the cactus decline on Green Cay (1993–1995) had comparatively more body mass than after the cactus decline (1998–1999), and this was reinforced by the absence of a similar trend in two populations unaffected by cactus loss (Goulding Cay and Pigeon Cay; Hayes et al. 2004). However, Hurricanes Erin in 1995 and Lili in 1996 may have impacted Green Cay's vegetation to a greater extent than the other cays, offering an alternative explanation. Iguana body condition has been linked to habitat quality in iguanas elsewhere (Pasachnik et al. 2012a, b; Pasachnik 2013). Our iguana population surveys on Green Cay do not suggest an ongoing population decline, but iguanas there have become accustomed to frequent human visitation (and occasional feeding), and detectability may have increased in the past decade (e.g., Hines 2011; Knapp et al. 2013; Smith and Iverson this volume), resulting in greater population estimates. We have not made an effort to control the moth, though new developments suggest feasibility through pheromonal attraction, release of sterile individuals, and fungal, bacterial, parasitoid, or nematode biological control agents (Zimmerman et al. 2004; Hight et al. 2005; Heath et al. 2006).

Accumulating evidence suggests that rats can also impact the iguanas. Populations coexisting with rats, for example, tend to have reduced population density (Hayes et al. 2004) and a greater frequency of tail injuries and tail furcations resulting from rodent bites (Carter and Hayes 2004; Hayes et al. 2012). Unfortunately, our trapping data underscore the difficulty of documenting the presence of rats. When a presumably dense rat population exists, capture rates are fairly high, as occurred on Low Cay and on North Point (14.3% and 13.6% per trap-night, respectively; Table 2), on the main island of San Salvador (16.2–20.5%, Hall and Dougherty 2003), and on Sandy Cay in the Exumas (9.3%, Hayes et al. this volume). Although rats have been documented on High Cay and Pigeon Cay, the populations there appear to be either unstable or of low density, as suggested by an absence of captures despite fairly intensive trapping effort (Table 4). Temporary rat infestations of small islands may be frequent, especially for those having limited water and unfavorable vegetation (Palmer and Pons 2001). The logistic regression results hinted that larger cays and those within the inland lake were more likely to have rat presence confirmed. Distance from the main island appears to have less predictive power, which may result, in part, from the relative strength of water currents that separate the land masses (the northern cays are amidst stronger currents than the southern cays). A similar analysis of rat presence on 14 islets in Spain's Cabrera Archipelago Maritime-Terrestrial National Park determined that plant composition rather than geographic variables (island area, height, storm exposure) best explained the presence of rats (Palmer and Pons 2001).

We expected a vigorous demographic and population response following rat eradication on Low Cay, but this has not happened. Undetected rat recolonization remains a possible explanation. Although the iguana population is not particularly dense on Low Cay, perhaps it has been at carrying capacity, possibly reduced following the massive loss of cactus stands on the cay (a large area of very small cactus plants remains), rendering substantial recruitment unlikely. Nesting habitat abounds, and large numbers of hatchlings have been observed in the autumn, so reproductive capacity is unlikely to be the limiting factor. High levels of territoriality, particularly by adult males, may contribute to the low population density (Pérez-Buitrago et al. 2010), presumably by excluding young animals from suitable habitat, and therefore subjecting them to greater mortality.

The two translocation failures add to our understanding of what it takes to successfully establish a new population. The Club Med Resort provided a lush environment for the herbivorous iguanas, and for a time they appeared to be breeding and successfully established. We do not know what went wrong. We have no information on the exact number or sex ratio of iguanas originally translocated to the property, though we observed six individuals on one visit, captured individuals of both sexes, and observed one young animal. Despite the suitable habitat, some threats still remained, including auto collision, dog attack, secondary poisoning from consuming poisoned rodents (compare Luther et al. 2012), and disease. More surprising, however, was the complete failure of the Cut Cay translocation in 2005. We expected substantial population growth in the eight subsequent years, similar to that seen for other translocated populations of *Cyclura* (reviewed by Knapp and Hudson 2004; Iverson et al. 2006, this volume). Only one explanation stands out, as the habitat is exceptional, the iguanas on the cay are clearly thriving, and suitable nesting habitat abounds. Despite our initial confidence that rats were absent from the Cay, we sighted one in daylight in 2012. We therefore suspect that rat predation on nests and hatchlings was responsible for the failure. Although iguanas in some areas coexist with rats, we suspect that small iguana populations are much more vulnerable due to the higher ratio of rats to their prey (Hayes et al. 2012). One possibility to help this iguana population to become viable would be to increase iguana density on Cut Cay to the point where nests and eggs would saturate the predatory capacity of rats. Another option, of course, would be to eradicate the rats.

Comparison of body size of translocated iguanas to the source population allowed us to test the hypothesis that translocated iguanas on Club Med and Cut Cay would attain a larger body size (length and mass) due to a richer food source (at Club Med), less food competition (both locations), and/or fewer social interactions that would otherwise constrain time devoted to feeding (both populations), as discussed elsewhere (Carter and Hayes 2004; Hayes et al. this volume; Iverson et al. this volume). The contrast between the translocated populations was unambiguous: iguanas at Club Med became massive compared to those on Green Cay (Fig. 4), whereas those translocated to Cut Cay showed no obvious increase in body size. This finding suggests that nutrition may exert a more profound influence on adult body size of *C. rileyi rileyi* than does population density. Iguanas of both translocated populations were at low density, but those at Club Med had access to the rich, exotic foliage maintained by the grounds crew, and may have benefitted from supplemental feeding by humans, whereas those on Cut Cay persisted on natural vegetation similar to that of the source cay. Other explanations may also exist; for example, the Club Med location is on the leeward side of the main island, and may offer thermoregulatory advantages for digestive efficiency (Tracy et al. 2005).

Figure 5. Exhibition and education enclosure of the San Salvador Iguana Conservation Centre, a headstarting facility partially completed and opened at the Gerace Research Centre in 2012. (Photographed by William K. Hayes).

At present, no acceptable options for translocation exist to augment the natural population of *C. rileyi rileyi*. Several cays currently uninhabited by iguanas are too small to support a sizeable population (e.g., Catto, Gaulin, Middle, Nancy), and others of questionable quality in the inland lake have ownership issues and, very likely, rats. High Cay would clearly be the best translocation site due to its large size and superb habitat, but the owners have firmly declined permission for such an undertaking. Translocating iguanas to the main island might work, but only to remote areas, preferably with limited human access, devoid of feral dogs, cats, and hogs. Two locations may be feasible: the peninsula east of Pigeon Creek, and the western shore of Green's Bay, where Goulding Cay is located (Fig. 1). Natural features limit access to those locations, and fencing could be used strategically to secure a predator-free area and to contain the iguanas. Some adult iguanas do live on the main island, but they are widely dispersed and rarely encountered, suggesting a minimally viable population subject to non-native predators and vehicle collisions. Dozens, if not hundreds, of neonates currently die each year on the inhabited cays because the populations are at carrying capacity and support only limited recruitment of young into the adult population. These hatchlings could be translocated to the main island, but they are much less likely to survive than headstarted or adult iguanas (e.g., Pérez-Buitrago and Sabat 2007; Knapp et al. 2010; see also Iverson 2007), yet we are reluctant to remove a large number of adults from the cays. Given these considerations, we have sought to implement a headstarting program for many years.

We opened a small headstarting facility, the San Salvador Iguana Conservation Centre, in May 2012. This facility initially included a large (9 x 6 m), block-walled exhibition and education enclosure designed to house up to 3 adult ♂♂ and 5 adult ♀♀ iguanas that were transferred from Green Cay (Fig. 5). We planned on constructing a number of smaller enclosures later. Due to lack of soil stability and moisture retention associated with root growth (extensive root penetration of the soil can take many months), we were uncertain whether nesting would be successful in the large enclosure the first year, but one young iguana emerged in October 2012. With several setbacks we were unable to house additional iguanas in smaller pens through 2014. Gravid females dug burrows and deposited eggs in the exhibition and education enclosure in 2013 and 2014, but no hatchlings appeared those years.

The future of this facility remains unclear. The original concept sought to achieve three purposes: (1) to enhance awareness of the iguanas and promote environmental education for island inhabitants and guests of the Gerace Research Centre; (2) to stimulate renewed efforts to protect critical habitats supporting diverse marine and terrestrial wildlife, including a number of threatened and endangered species; and (3) to boost the wild iguana population through release of headstarted individuals.

At this point, we appear to be succeeding with the first two goals. Those who visit the facility express considerable appreciation for seeing the animals. Although we plan to keep the facility small, its expansion with additional smaller cages and animals, a rock pathway with natural vegetation, and additional information signage will enhance the visitor experience. We anticipate that visits to the facility will ease some of the ecotourism pressure on Green Cay. Ecotourism, and supplemental feeding in particular, may have detrimental effects on rock iguanas (Hines 2011; Knapp et al. 2013; Smith and Iverson this volume). Perhaps most important, the Bahamas National Trust has now revived its decade-old proposal to create a new national park that would protect the most critical iguana, seabird, and marine populations on San Salvador, tentatively including Green, Goulding, Manhead, and Pigeon Cays. The island residents appear to support this plan, and a prior education program that focused on the iguanas (Carter et al. 2005) has helped to pave the way. However, to make progress with the third goal, that of augmenting the wild iguana population, we need to finish construction of the smaller pens and stock them with hatchling iguanas taken from the cays. Some of these headstarted iguanas could then be released to create new populations on remote parts of the main island, as described above, released on Cut Cay to supplement the low-density population there, or taken to a cay that might eventually become available for translocation. Others can be retained to form the core of a small breeding group. A wild population could conceivably be managed in anthropogenic habitat, such as Club Med or the Gerace Research Centre, with proper predator control and roadway signs to urge caution. Headstarting has benefited recovery efforts for many endangered iguanas, including the Anegada Iguana (Cyclura pinguis, Bradley and Gerber 2005), Cuban Iguana (Cyclura nubila nubila, Alberts et al. 2004), Grand Cayman Blue Iguana (Cyclura lewisi, Knapp and Hudson 2004), Jamaican Iguana (Cyclura collei, Wilson et al. 2004), Mona Island Iguana (Cyclura stejnegeri, Garcia et al. 2007; Pérez-Buitrago et al. 2008), and Galápagos Land Iguana (Conolophus subcristatus, Cayot et al. 1994). This iguana could benefit as well.

In summary, San Salvador Rock Iguanas face an uncertain future. Our population surveys over the course of two decades give us a tool and a history that will be integral to further conservation and management efforts on behalf of this taxon. Unfortunately, the small and isolated iguana populations have been plagued by catastrophic storms and invasive species, such that there is no tangible hope of population expansion without serious intervention. We see opportunity to benefit the 600 or fewer remaining iguanas through more aggressive efforts at invasive species control, translocation with limited options, and a headstarting program that can not only augment the wild population, but also enhance iguana awareness, conservation education, and the pursuit of formal habitat protection. Management would also benefit from detailed genetic studies at the population and subspecies levels. Inbreeding depression may have contributed, for example, to the extirpation of populations in recent decades (e.g., Barn Cay, High Cay), and some of the extant populations may be prone as well.

Acknowledgments.—We thank the many students and colleagues without whose support this work could not have been accomplished; there have been too many to list here. Research was approved by the Institutional Animal Care and Use Committees (IACUC) of Southern College (no protocol number supplied) and of Loma Linda University (protocols 77011, 82033, 83013, 84053, 85011, 89008, and 8100013). Research was also conducted under permits issued by the Bahamas Ministry of the Environment. Financial support was provided by the Bahamas Ministry of Agriculture, Chicago Zoological Society, Denver Zoological Society, Disney Foundation, Gerace Research Centre, Insular Species Conservation Society, International Iguana Foundation, International Reptile Conservation Foundation, Loma Linda University, Seacology, and out-of-pocket funds.

LITERATURE CITED

Alberts, A.C. 2007. Behavioral considerations of headstarting as a conservation strategy for endangered Caribbean Rock Iguanas. Applied Animal Behaviour Science 102:380–391.

Alberts, A.C., J.M. Lemm, T.D. Grant, and L.A. Jackintell. 2004. Testing the utility of headstarting as a conservation strategy for West Indian Iguanas. Pp. 210–219 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds). University of California Press, Berkeley and Los Angeles, California, USA.

Bradley, K.A., and G.P. Gerber. 2005. Conservation of the Anegada Iguana (*Cyclura pinguis*). Iguana: Conservation, Natural History, and Husbandry of Reptiles 12:78-85.

Burton, F.J., and F.F. Rivera-Milán. 2014. Monitoring a population of translocated Grand Cayman Blue Iguanas: assessing the accuracy and precision of distance sampling and repeated counts. Animal Conservation 17:40–47.

Carey, W.M. 1966. Observations of the ground iguana *Cyclura macleayi caymanensis* on Cayman Brac, British West Indies. Herpetologica 22:265–268.

Carter, R.L., and W.K. Hayes. 2004. Conservation of an endangered Bahamian iguana. II. Morphological variation and conservation recommendations. Pp. 258–273 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Carter, R.L., W.K. Hayes, V. Voegeli, and S. Voegeli. 2005. Celebrating Biodiversity 2002 – Conservation education: a responsibility of higher education. Pp. 12–17 *In* Proceedings of the 10th Symposium on the Natural History of the Bahamas. Buckner, S., and T. McGrath (Eds.). Gerace Research Centre, San Salvador Island, The Bahamas.

Cayot, L.J., H.L. Snell, W. Llerena, and H.M. Snell. 1994. Conservation biology of Galápagos reptiles: twenty-five years of successful research and management. Pp. 297–305 *In* Captive Management and Conservation of Amphibians and Reptiles. Murphy, J.B., K. Adler, and J.T. Collins (Eds.). Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA.

Clark, D.B. 1980. Population ecology of *Rattus rattus* across a desert-montane forest gradient in the Galápagos Islands. Ecology 61:1422–1433.

Cohen, J. 1988. Statistical Power Analysis for the Behavioral Sciences, 2nd edition. Erlbaum, Hillsdale, New Jersey, USA.

Cyril, S., Jr. 2001. Behavioral ecology of the endangered San Salvador Rock Iguana (*Cyclura rileyi rileyi*) in The Bahamas. M.Sc. Thesis, Loma Linda University, Loma Linda, California, USA. 59 p.

Day, M., W. Hayes, K. Varnham, T. Ross, E. Carey, T. Ferguson, J. Monestine, S. Smith, C. Armstrong, and A. Buckle, et al. 1998. Rat eradication to protect the White Cay Iguana. Aliens 8:22–24.

Deyrup, M. 1994. Biogeographical survey of the ants of the island of San Salvador, Bahamas. Pp. 21–28 *In* Proceedings of the 5th Symposium on the Natural History of The Bahamas. Kass, L.B. (Ed.). Bahamian Field Station, San Salvador Island, The Bahamas.

Escobar, R.A., III, E. Besier, and W.K. Hayes. 2010. Evaluating headstarting as a management tool: post-release success of Green Iguanas (*Iguana iguana*) in Costa Rica. International Journal of Biodiversity and Conservation 2:204–214.

Ewer, R.F. 1971. The biology and behaviour of a free-living population of Black Rats (*Rattus rattus*). Animal Behaviour Monographs 4:125–174.

García, M.A., N. Pérez-Buitrago, A.O. Alvarez, and P.J. Tolson. 2007. Survival, dispersal and reproduction of headstarted Mona Island Iguanas, *Cyclura cornuta stejnegeri*. Applied Herpetology 4:357–363.

Goodman, R.M. 2007. Activity patterns and foraging behavior of the endangered Grand Cayman Blue Iguana, *Cyclura lewisi*. Caribbean Journal of Science 43:73–86.

Green, S.B., and N.J. Salkind. 2005. Using SPSS for Windows and Macintosh: Analyzing and Understanding Data. 4th edition. Pearson Prentice Hall, Upper Saddle River, New Jersey, USA.

Hall, J.S., and P.L. Dougherty. 2003. Further studies of the Black Rat on San Salvador Island, Bahamas. Pp. 87–90 *In* Proceedings of the 9th Symposium on the Natural History of The Bahamas. Smith, D.L., and S. Smith (Eds.). Gerace Research Centre, San Salvador, The Bahamas.

Hayes, W.K. 2003. Can San Salvador's iguanas and seabirds be saved? Bahamas Journal of Science 11:2–8.

Hayes, W., and R. Carter. 2000. Population monitoring. Pp. 79–85 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Hayes, W.K., and R.L. Carter. 2005. Biology and conservation of *Cyclura rileyi,* an endangered Bahamian rock iguana. Pp. 69–82 *In* Proceedings of the 10th Symposium on the Natural History of the Bahamas. Buckner, S.D., and T.A. McGrath (Eds.). Gerace Research Centre, San Salvador, The Bahamas.

Hayes, W.K., R.L. Carter, S. Cyril, Jr., and B. Thornton. 2004. Conservation of an endangered Bahamian Rock Iguana, I. Population assessments, habitat restoration, and behavioral ecology. Pp. 232–257 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Hayes, W., R. Carter, and N. Goodyear. 2000. Marking techniques. Pp. 77–79 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Hayes, W.K., R.A. Escobar III, S.K. Fry, E.M. Fortune, J.A. Wasilewski, D.M. Tuttle, K.S. West, J.B. Iverson, S.D. Buckner, and R.L. Carter. 2016. Conservation of the endangered Sandy Cay Rock Iguanas (*Cyclura rileyi cristata*): invasive species control, population response, pirates, poaching, and translocation. Pp. 106–120 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Hayes, W.K., D.M. Hayes, D. Brouhard, B. Goodge, and R.L. Carter. 1995. Population status and conservation of the endangered San Salvador Rock Iguana, *Cyclura r. rileyi*. Journal of the International Iguana Society 4:21–30.

Hayes, W.K., J.B. Iverson, C.R. Knapp, and R.L. Carter. 2012. Do invasive rodents impact endangered insular iguana populations? Biodiversity and Conservation 21:1893–1899.

Heath, R.R., P.E. Teal, N.D. Epsky, B.D. Dueben, S.D. Hight, S. Bloem, J.E. Carpenter, T.J. Weissling, P.E. Kendra, J. Cibrian-Tovar, et al. 2006. Pheromone-based attractant for males of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). Environmental Entomology 35:1469–1476.

Hillbrand, P.A., A.T. Sloan, and W.K. Hayes. 2011. The terrestrial reptiles of San Salvador Island, Bahamas. IRCF Reptiles and Amphibians: Conservation and Natural History 18:29–40.

Hight, S.D., J.E. Carpenter, S. Bloem, and K.A. Bloem. 2005. Developing a sterile insect release program for *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae): effective overflooding ratios and release-recapture field studies. Environmental Entomology 34:850–856.

Hines, K.N. 2011. Effects of ecotourism on endangered Northern Bahamian Rock Iguanas (*Cyclura cychlura*). Herpetological Conservation and Biology 6:250–259.

Iverson, J.B. 1979. Behavior and ecology of the rock iguana, *Cyclura carinata*. Bulletin of the Florida State Museum, Biological Sciences 24:175–358.

Iverson, J.B. 2007. Juvenile survival in the Allen Cays Rock Iguana (*Cyclura cychlura inornata*). Copeia 2007:740–744.

Iverson, J.B., S.J. Converse, G.R. Smith, and J.M. Valiulis. 2006. Long-term trends in the demography of the Allen Cays Rock Iguana (*Cyclura cychlura inornata*): human disturbance and density-dependent effects. Biological Conservation 132:300–310.

Iverson, J.B., G.R. Smith, S.A. Pasachnik, K.N. Hines, and L. Pieper. 2016. Growth, coloration, and demography of an introduced population of the Acklins Rock Iguana (*Cyclura rileyi nuchalis*) in the Exuma Islands, The Bahamas. Pp. 139–153 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Jezorek, H. 2011. The invasive Cactus Moth, *Cactoblastis cactorum*: host plant testing, species interactions, and effects on local *Opuntia* populations. Ph.D. Dissertation, University of South Florida, Tampa, Florida, USA. 154 p.

Jezorek, H., A.J. Baker, and P. Stiling. 2012. Effects of *Cactoblastis cactorum* on the survival and growth of North American *Opuntia*. Biological Invasions 14:2355–2367.

Knapp, C.R., and R.D. Hudson. 2004. Translocation strategies as a conservation tool for West Indian Iguanas: evaluations and recommendations. Pp. 199–209 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds). University of California Press, Berkeley and Los Angeles, California, USA.

Knapp, C.R., S. Alvarez-Clare, and C. Perez-Heydrich. 2010. The influence of landscape heterogeneity and dispersal on survival of neonate insular iguanas. Copeia 2010:62–70.

Knapp, C.R., K.N. Hines, T.T. Zachariah, C. Perez-Heydrich, J.B. Iverson, S.D. Buckner, S.C. Halach, C.R. Lattin, and L.M. Romero. 2013. Physiological effects of tourism and associated food provisioning in an endangered iguana. Conservation Physiology 1:cot032. doi:10.1093/conphys/cot032

Lovich, R.E., W.K. Hayes, H. Mushinsky, and G.H. Rodda. 2012. Transect surveys, including line distance. Pp. 227–234 *In* Reptile Biodiversity: Standard Methods for Inventory and Monitoring. McDiarmid, R.W., M.S. Foster, C. Guyer, J.W. Gibbons, and N. Chernoff (Eds.). University of California Press, Berkeley, California, USA.

Luther, B., C.R. Knapp, D.U. Greene, S.D. Buckner, and J.B. Iverson. 2012. *Cyclura cychlura figginsi* (Exuma Island Rock Iguana). Rodent kill. Herpetological Review 43:483.

Malone, C.L., T. Wheeler, J.F. Taylor, and S.K. Davis. 2000. Phylogeography of the Caribbean rock iguana (*Cyclura*): implications for conservation and insights on the biogeographic history of the West Indies. Molecular Phylogenetics and Evolution 17:269–279.

Mertler, C.A., and R.A. Vannatta. 2004. Advanced and Multivariate Statistical Methods: Practical Application and Interpretation, 3rd edition. Pyrczak Publishing, Los Angeles, California, USA.

Nakagawa, S., and I.C. Cuthill. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biological Reviews of the Cambridge Philosophical Society 82:591–605.

Palmer, M., and G.X. Pons. 2001. Predicting rat presence on small islands. Ecography 24:121–126.

Pasachnik, S.A. 2013. Growth, reproduction, and diet of Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina*, with notes on the status of the species. Herpetological Conservation and Biology 8:191–198.

Pasachnik, S.A., C.E. Montgomery, A. Martinez, N. Belal, S. Clayson, and S. Faulkner. 2012a. Body size, demography, and body condition in Utila Spiny-tailed Iguanas, *Ctenosaura bakeri*. Herpetological Conservation and Biology 7:391–398.

Pasachnik, S.A., C.E. Montgomery, L.E. Ruyle, J.P. Corneil, and E.E. Antunez. 2012b. Morphological and demographic analyses of the Black-chested Spiny-tailed Iguana, *Ctenosaura melanosterna*, across their range: implications for population level management. Herpetological Conservation and Biology 7:399–406.

Pérez-Buitrago, N., and A. Sabat. 2007. Natal dispersal, home range and habitat use of hatchlings of the Mona Island Iguana (*Cyclura cornuta stejnegeri*). Applied Herpetology 4:365–376.

Pérez-Buitrago, N., M.A. García, A. Sabat, J. Delgado, A. Álvarez, O. McMillan, and S.M. Funk. 2008. Do headstart programs work? Survival and body condition in headstarted Mona Island Iguanas *Cyclura cornuta stejnegeri*. Endangered Species Research 6:55–65.

Pérez-Buitrago, N., A.M. Sabat, and W.O. McMillan. 2010. Spatial ecology of the endangered Mona Island Iguana *Cyclura cornuta stejnegeri*: does territorial behavior regulate density? Herpetological Monographs 24:86–110.

Powell, R., and R.W. Henderson. 2011. Introduction. Bulletin of the Florida Museum of Natural History 51:86–90.

Reyes-Agüero, J.A., J.R. Aguirre R., and A. Valiente-Banuet. 2006. Reproductive biology of *Opuntia*: a review. Journal of Arid Environments 64:549–585.

Rodgers, J.C. 2005. The distribution of *Casuarinas* on San Salvador Island, The Bahamas. Southeastern Geographer 45:222–238.

Rodgers, J.C., III, and D.W. Gamble. 2008. The impact of Hurricane Frances (2004) on the invasive Australian Pine (*Casuarina equisetifolia* L.) on San Salvador Island, The Bahamas. Journal of the Torrey Botanical Society 135:367–376.

Smith, G.R., and J.B. Iverson. 2016. Effects of tourism on body size, growth condition, and demography in the Allen Cays Iguana, *Cyclura cychlura inornata*, on Leaf Cay, The Bahamas. Pp. 214–221 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Smith, R.L. 2010. Invasive alien plant species of The Bahamas and biodiversity management. M.Sc. Thesis, Miami University, Oxford, Ohio, USA. 122 p.

Smith, R.R. 1993. Field Guide to the Vegetation of San Salvador Island, The Bahamas. 2nd Edition. Bahamian Field Station, San Salvador, The Bahamas.

Tamarin, R.H., and S.R. Malecha. 1972. Reproductive parameters in *Rattus rattus* and *Rattus exulans* of Hawaii, 1968 to 1970. Journal of Mammalogy 53:513–528.

Thornton, B.J. 2000. Nesting ecology of the endangered Acklins Bight Rock Iguana, *Cyclura rileyi nuchalis*, in The Bahamas. M.Sc. Thesis, Andrews University, Berrien Springs, Michigan, USA. 85 p.

Tracy, C.R., K.M. Flack, L.C. Zimmerman, R.E. Espinoza, and C.R. Tracy. 2005. Herbivory imposes constraints on voluntary hypothermia in lizards. Copeia 2005:12–19.

Trimm, N.A., Jr., and W.K. Hayes. 2005. Distribution of nesting Audubon's Shearwaters (*Puffinus lherminieri*) on San Salvador Island, Bahamas. Pp. 137–145 *In* Proceedings of the 10th Symposium on the Natural History of the Bahamas. Buckner, S.D., and T.A. McGrath (Eds.). Gerace Research Centre, San Salvador Island, The Bahamas.

Wilcox, K., J.Y. Carter, and L.V. Wilcox. 1973. Range extension of *Cyclura figginsi* Barbour in The Bahamas. Caribbean Journal of Science 13:211–213.

Wilson, B.S., A.C. Alberts, K.S. Graham, R.D. Hudson, R.K. Bjorkland, D.S. Lewis, N.P. Lung, R. Nelson, N. Thompson, J.L. Kunna, et al. 2004. Survival and reproduction of repatriated Jamaican Iguanas. Pp. 220–231 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Zimmermann, H., S. Bloem, and H. Klein. 2004. Biology, history, threat, surveillance and control of the Cactus Moth, *Cactoblastis cactorum*. Pp. 1–40 *In* Proceedings: Joint FAO/IAEA Programme of Nuclear Techniques in Food and Agriculture. International Atomic Energy Agency, Vienna, Austria.

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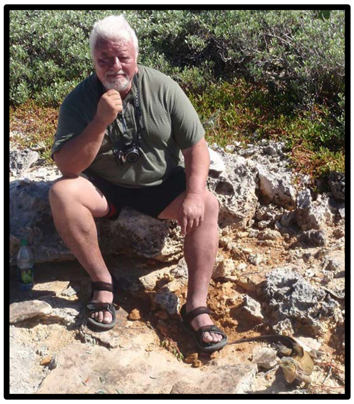
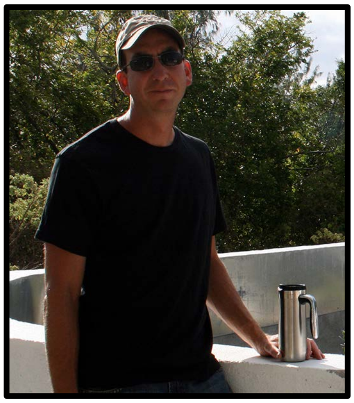


Tom Crutchfield is currently retired and lives on a reptile farm in Homestead, Florida, where he breeds a large variety of unusual reptiles. He attended Florida Southwestern State College in Ft. Myers, Florida, and has been an entrepreneurial professional herpetologist his entire career. He has studied Rock Iguanas both *in situ* and under captive conditions, and has extensive knowledge of the husbandry and reproductive biology of *Cyclura*, having successfully bred four species under his care. Additionally, he has served on the IUCN SSC Crocodile Specialist Group, and has written a number of articles on Rock Iguanas. He continues to pursue an avid interest in reptile conservation, which he promotes at every opportunity. (Photographed by Joseph A. Wasilewski).

Joseph A. Wasilewski grew up in the city of Chicago, but after landing in the U.S. Army in 1973, where he worked with sentry dogs, he became employed at the Miami Serpentarium and began a long career of hands-on work with reptiles in southern Florida. He graduated in 1981 from Florida International University, Miami, with a B.S. in Biology. Joe is President of Natural Selections of South Florida, an environmental consulting firm, and is the Director of Biodiversity at Jadora International, LLC. He serves as a member of the IUCN SSC Crocodile Specialist Group and the IUCN SSC Iguana Specialist Group. He has made numerous appearances on television news programs, including NBC's Today Show, the Tonight Show (with both Johnny Carson and Jay Leno), ABC Evening News, and CBS Nightly News. He also regularly consults with natural history productions, national and international news outlets, and television and motion picture productions, including CSI Miami and Pirates of the Caribbean. (Photographed by Steve Connors).



Thomas A. Rothfus earned his Ph.D. in Geology in 2005 from the University of Chicago in Illinois. His background is in geology and invertebrate paleontology. His dissertation research and scholarly publications focus on the burial processes (taphonomy) of mollusks, primarily brachiopods and other bivalves, and on the problems inherent in data collection in taphonomy. His approach to understanding these processes involves investigation of contemporary community ecology and life history traits. In 2007, Tom became the Executive Director of the Gerace Research Centre on San Salvador Island, The Bahamas, where he remains to this day. His responsibilities include coordinating and hosting the visits of numerous academic groups and researchers who visit the field station. (Photographed by William K. Hayes).

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Herpetological Conservation and Biology 11(Monograph 6):106–120.
Submitted: 15 October 2014; Accepted: 12 November 2015; Published: 12 June 2016.

CONSERVATION OF THE ENDANGERED SANDY CAY ROCK IGUANAS (*CYCLURA RILEYI CRISTATA*): INVASIVE SPECIES CONTROL, POPULATION RESPONSE, PIRATES, POACHING, AND TRANSLOCATION

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Abstract**.—We describe the ongoing population recovery of the critically endangered Sandy (or White) Cay Rock Iguanas (*****Cyclura rileyi cristata*****), which occur on just one 14.9 hectare island in the southern Exuma Cays, The Bahamas. These large lizards were brought to the brink of extinction in 1997 by a single feral Raccoon (*****Procyon lotor*****), which preyed heavily on adult iguanas. By the time the Raccoon and a dense population of Black Rats (*****Rattus rattus*****) were eradicated (1997–1998), surveys suggested that only 112–168 iguanas remained. Subsequent periodic surveys confirmed population growth through 2008, with more than 2,000 iguanas likely present. Tests of four hypotheses indicated: (1) exponential population growth subsequent to invasive mammal removal; (2) even distribution of iguanas across the cay despite an elevation and habitat gradient; (3) no increase in iguana body size as a consequence of low population density; and (4) reduced frequencies of tail injury following alien mammal eradication. In 2005, we initiated removal of invasive Australian Pines (*****Casuarina equisetifolia*****). During portions of 2005–2006, scenes from the Disney movie series *****Pirates of the Caribbean***** were filmed on the cay. Although this major cinema production posed tangible risks to the iguanas and their only home, no deleterious consequences were apparent, so we offer the environmental management plan as a model for managing impacts to endangered species in sensitive environments. We also detail the illegal poaching of 13 iguanas in 2014, which ultimately resulted in establishing a new iguana population on a nearby cay via translocation.**

Key Words.—Bahamas; body size; *Casuarina equisetifolia*; cinema production; population surveys; *Procyon lotor*; *Rattus rattus*; tail injury

INTRODUCTION

Islands have suffered disproportionate biodiversity losses. Their floras and faunas are especially susceptible to invasive species because they generally lack co-evolved traits that help them cope with novel predators and superior competitors (Whittaker and Fernández-Palacios 2007). Insular iguana populations are particularly vulnerable to invasive species. Non-native herbivorous (Mitchell 1999) and predatory mammals (e.g., cats, dogs, mongooses, and hogs; Iverson 1978, 1979; Henderson 1992; Haneke 1995; Tolson 2000), for example, have devastated a number of iguana populations. Invasive rats (*Rattus* spp.) and mice (*Mus* spp.) are pernicious predators that also negatively affect insular faunas (Towns et al. 2006; Wanless et al. 2007; Jones et al. 2008; Towns 2011), yet their full negative impact on insular iguana populations remains unclear (Mitchell et al. 2002; Hayes et al. 2004, 2012; Wilson et al. this volume). Predator eradication (Rodríguez et al. 2006; Harper et al. 2011; Samaniego-Herrera et al. 2011) and iguana translocation (Knapp and Hudson 2004; Perry and Gerber 2006; Iverson et al. this volume) programs are sometimes necessary to rescue insular lizard populations.

Among the West Indian Rock Iguanas, *Cyclura rileyi* remains one of the most threatened species, with two of its three recognized subspecies deemed Critically Endangered and the third Endangered according to The IUCN Red List of Threatened Species (Carter and Hayes

Hayes, William K., Ricardo A. Escobar III, Shawn K. Fry, Edgar M. Fortune, Joseph A. Wasilewski, Donald M. Tuttle, Kathryn S. West, John B. Iverson, Sandra D. Buckner, and Ronald L. Carter. 2016. Conservation of the endangered Sandy Cay Rock Iguanas (*Cyclura rileyi cristata*): invasive species control, population response, pirates, poaching, and translocation. Pp. 106–120 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

1996; Carter et al. 2000a, b). Although they formerly occupied large islands, today these mostly herbivorous lizards are confined to small, remote, uninhabited cays of three island groups (Hayes et al. 2004). At present, *C. rileyi cristata* is restricted to Sandy (White) Cay in the southern Exumas, where an estimated 1,500 individuals persist (Hayes et al. 2004, this paper). *Cyclura rileyi nuchalis* survives naturally on just two cays in the Acklins Bight of the Crooked/Acklins Island group, but a third population has been introduced to a cay in the central Exumas (Iverson et al. this volume). Although as many as 10,000 individuals may remain, the current habitat of this taxon represents a tiny fraction (0.2%) of its former range (Hayes et al. 2004). Finally, *Cyclura rileyi rileyi* is largely confined to four tiny offshore cays and two islets within the hypersaline lakes of San Salvador Island, though a small and probably non-sustaining population persists on the main island itself. With fewer than 600 individuals remaining (Hayes et al. this volume), this subspecies similarly occupies a mere fraction (0.2%) of its former range. Morphometric analyses suggest that these three taxa warrant status as distinct subspecies and independent management units (Carter and Hayes 2004; Hayes and Carter 2005). Although Malone et al. (2000) found no mtDNA sequence differences among the three forms, the ITWG (this volume) recognizes the three taxa to be distinct subspecies, and some authors even consider them species (Powell and Henderson 2011).

Sandy Cay Rock Iguanas (*C. rileyi cristata*) boast an unusual history for living on such a small (14.9 ha) remote island. One of us (JBI) spent two half-days on Sandy Cay in mid-March 1980, finding a dense but skittish iguana population with abundant juveniles and no evidence of invasive vertebrates, though exotic Australian Pines (*Casuarina equisetifolia*) were present on the southeastern part of the cay. Upon return to the cay in 1996 with others (WKH, RLC, SDB), we discovered invasive mammals that had brought the iguanas to the verge of extinction, prompting us to initiate a long-term study (Carter and Hayes 2004; Hayes et al. 2004). We undertook eradication campaigns of mammalian predators and Australian Pine, and monitored subsequent recovery of the iguana population. During our study, scenes from the Disney movie series *Pirates of the Caribbean* (Walt Disney Pictures in association with Jerry Bruckheimer Films) were filmed (2005 and 2006). In addition, iguanas were repeatedly poached illegally from the cay on several occasions, including a highly publicized event in 2014.

This study summarizes our work on behalf of and selected events that impacted the Sandy Cay Rock Iguanas from 1996 through 2014. We provide complete details and a much-needed update of the early activities summarized only briefly by Carter and Hayes (2004) and Hayes et al. (2004). We describe here the invasive species that we documented on the cay, our attempts to control them, and the iguana population's response to these efforts. We tested four hypotheses: (1) the trajectory of iguana population recovery after invasive mammal eradication has been exponential, and has not yet reached carrying capacity; (2) iguanas are evenly distributed across the cay despite an elevation and habitat gradient, and a change from low to high iguana population density; (3) an increase in iguana body size results as a consequence of low population density; and (4) tail injury frequencies decline after removal of the alien mammalian predators. We also characterize efforts to manage and mitigate effects of the cinema production of *Pirates of the Caribbean*, and we detail the events and fate surrounding the recent iguana smuggling event that ultimately led to establishing a new assurance population.

MATERIALS AND METHODS

Study site.—Sandy Cay is situated at the southern end of the Exuma Cays, an extended chain of islands in the central portion of the Great Bahamas Bank. Most of the 14.9 ha cay (Fig. 1) is composed of soft limestone rock with interspersed patches of sand. The rock forms wavelike ridges up to 5 m high, which are most pronounced along the northern shore. Tidal flats extend from the eastern and southern portions of the island to large, vegetated sand dunes (2–5 m elevation) and smaller protrusions of limestone rock. Vegetation density on Sandy Cay (excluding the dunes) declines along a west-east gradient corresponding to an elevation decline from ca. 8 m to sea level. *Coccothrinax argentata*, which dominates the higher-elevation western portion, is

FIGURE 1. Sandy Cay, Exuma Cays, The Bahamas, the only native home of the Sandy Cay Rock Iguana (*Cyclura rileyi cristata*). Note the elevation and vegetation gradient from west to east (ca. 8 m elevation, dominated by dense *Coccothrinax argentata* palm forest, to sea level with transition to primarily *Coccoloba uvifera* and *Strumpfia maritima*), and extensive stands of invasive Australian Pine (*Casuarina equisetifolia*, the dark green vegetation) along the southern shoreline and on the offshore dunes to the south (across an intertidal flat). A small rock islet to the southwest is omitted. Image from Google Earth 2005.

replaced primarily by *Coccoloba uvifera* and *Strumpfia maritima* eastward. *Scaevola plumieri* covers much of the offshore dunes. At least two seabirds, one bird of prey (Osprey, *Pandion haliaetus*), and five other terrestrial bird species nest on the cay.

Invasive species and their control.—We identified on Sandy Cay a single invasive plant species, Australian Pine (*C. equisetifolia*), and three invasive mammal species: Black Rat (*Rattus rattus*), House Mouse (*Mus musculus*), and a single Raccoon (*Procyon lotor*; Hayes et al. 2004). We initially exterminated the invasive mammals and then began removing the Australian Pines, which had become established on portions of the cay and offshore dunes where it was overtaking the native vegetation. We attempted to kill the Raccoon in July 1996 by an overdose of phenobarbital anesthetic (supplied by Bahamian authorities, dose unknown to us) inserted into dead fish as bait. In April and May 1998, a team from Fauna and Flora International attempted eradication of rodents (mice and rats) using the rodenticide brodifacoum (Weatherblock XT® Rodenticide; donated by Zeneca Agrochemicals Products, United Kingdom), a second generation anticoagulant that was delivered in solid bait blocks over a 20-m grid system on Sandy Cay and the offshore dunes, as described by Day et al. (1998; see photos of bait traps in Hayes et al. this volume). We looked for signs of rat presence during each subsequent trip (May 1997, October 1999, November 2000, October 2002, February 2005, October 2006, June 2007, July 2008, May–June 2009, May 2011, and May–June 2012), and collected quantitative data on rodent presence before and after the eradication effort via collapsible Sherman aluminum live rodent traps (7.5 x 9 x 23 cm; H.P. Sherman, Tallahassee, Florida, USA) baited with peanuts or peanut butter. We set the traps in darkness and retrieved them early in the morning. We euthanized captured rodents by cervical dislocation, measured mass to nearest gram (by Pesola scale) and total length (snout to tail tip) to nearest millimeter (handheld ruler; see Fry 2001 for additional measures), and dissected their stomachs to assess presence of iguana material.

In February 2005, we initiated a long-term program to eradicate the Australian Pine, which occurred on large portions of Sandy Cay and its offshore dunes. To destroy these trees, we severed the trunks by chain saw and/or handsaws, and applied one of several formulations of trichlopyr herbicide (e.g., Garlon 4®, Dow Agrosciences, Indianapolis, Indiana, USA) to the exposed stump (Fig. 2). We then gathered the downed timber and burned it.

Iguana body size, sex, injuries, and marking.—We captured iguanas during five visits to the cay (June 1996, May–July 1997, October 2006, June 2007, and July 2008) to measure a number of morphological variables, including mass to nearest gram (by Pesola spring scale) and snout-vent length (SVL) to nearest millimeter (handheld ruler), as well as injuries to the tail. For tail injuries, we distinguished between tail breaks and tail furcations (regenerated tail divided into branches resulting in multiple tail forks; Hayes

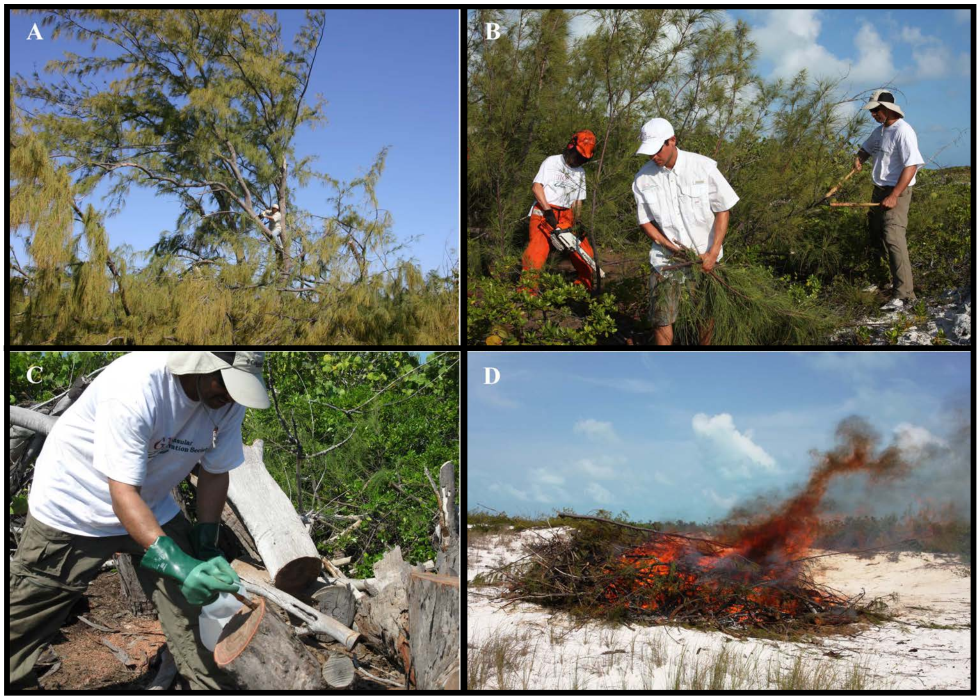

FIGURE 2. Removal methods for the invasive Australian Pine (*Casuarina equisetifolia*), from Sandy Cay, Exuma Cays, The Bahamas. Methods included: (A) cutting of trunks (note investigator with chainsaw on trunk) and (B) saplings; (C) painting the trunk or stem with a systemic triclopyr-based herbicide; and (D) gathering and burning the timber. (Photographed by Joseph A. Wasilewski (A) and Ricardo A. Escobar (B–D)).

et al. 2012). We determined sex of iguanas by probing of cloacal pouches; however, several different individuals did this procedure during 2006–2008, and we considered those data on sex unreliable for analysis. We marked the lizards individually using colored glass beads sutured to the nuchal crest (Hayes et al. 2000). We also injected passive integrated transponder (PIT) tags (from two manufacturers: Trovan Ltd., Weymouth, United Kingdom; AVID Identification Systems, Norco, California, USA) subdermally in the posterior hip region of most individuals. In 1997 and 2006, we painted an alphanumeric code on both sides of the animal using white enamel paint for short-term identification during behavioral studies. In 1997, we secured radio transmitters by silicone cement to the posterior hips of 10 subadult and adult iguanas for behavioral study (see Fry 2001 for details). Body size, sex ratio, mensural, meristic (scale counts), and injury data from captured animals have been analyzed elsewhere (Carter and Hayes 2004; Hayes et al. 2004, 2012). Here, we summarize long-term changes in body size and tail injury frequency based on additional data from captures in 2006–2008. We procured iguanas by noose, by hand, and in a few instances via glue trap followed by use of mineral oil to release them (Bauer and Sadlier 1992). However, we excluded glue-trap captures from sex-ratio computation because they were female-biased (Fry 2001). We retained captured iguanas temporarily (usually less than 2 h, but sometimes overnight) within generic cloth pillowcases (51 x 91 cm), always in shade, and then released them near or at their site of capture.

Iguana population surveys.—We conducted repeated classical strip surveys (Hayes et al. 1995; Hayes and Carter 2000; Lovich et al. 2012) between 1997 and 2008 using a standardized approach. These surveys comprised 4–10 north-south linear transects spaced relatively evenly (60–100 m apart) across the full extent of the island. Initially (1997–2002), two to three researchers (always including WKH) walked slowly in zig-zag fashion (with greater effort toward the center line) along a 36 m width belt. Subsequent surveys were undertaken by single individuals (WKH 2005, 2007; RAE 2006, 2008) walking similarly along a 20 m width belt. During each survey, we gently prodded the vegetation with bamboo fishing rods or sticks. We recorded all iguanas detected (by sight or by sound as they scampered into the vegetation), and the size of all iguanas seen sufficiently well. We visually categorized iguanas into three size classes based on approximate SVL: juveniles (< 12 cm), subadults (12–19 cm), and adults (> 20 cm). We conducted surveys between mid-morning (0900) and mid-afternoon (1600) during dry weather. Surveys were generally completed within 4–6 hr, but sometimes over a 2–3-day period.

Previous mark-resighting surveys of *C. rileyi* subspecies on six cays (Hayes et al. 2004) and repeated surveys of *C. rileyi nuchalis* (Thornton 2000) and *C. rileyi rileyi* (Cyril 2001) within single populations indicated detectability in the range of 0.25 to 0.5 (proportion of all known iguanas sighted), with an average of 0.33 for 37 surveys on Green Cay of San Salvador (Cyril 2001). Thus, for each survey, we divided the total number of iguanas detected by the proportion of island surveyed ([sum of transect lengths x transect width] / 14.9 ha), and then multiplied this quotient by two and by three to derive a range for each population estimate. We suspect that detectability increased during the study, with iguanas noticeably skittish early on (1997–2000) after several years or more of predation by invasive mammals, and less skittish in subsequent years, perhaps due in part to increasing human visitation (including likely supplemental feeding at the eastern and western ends of the cay where boats typically land). Regardless, we did not adjust our estimates. We also examined iguana density among the transects to assess whether iguanas were evenly dispersed across the west-east habitat gradient (excluding offshore dunes).

Iguana mortality.—We estimated iguana mortality during 1996–1997 using several approaches. First, we compared capture rates of iguanas (numbers of iguanas captured and processed per person per day) in 1996 (three people over 2 days) and in 1997 (three people over first 2 days). Second, we compared the proportion of iguanas marked in June 1996 that were resighted in 1997 to the proportion of animals marked between 2–15 May 1997 that were resighted after 15 May of that year.

We identified the primary causes of mortality by several means. We recorded the number of adult iguana carcasses found each year between 1996, 1997, 1998, and 1999 (we never found carcasses of young iguanas), and standardized these counts for the first 12 person-days on the island during each year's expedition to the island. In 1997, we also examined Raccoon feces for iguana remains, scrutinized iguana carcasses for causes of death, and investigated radio transmitters recovered from dead radio-tracked iguanas (or from those that shed the transmitter) for bite marks.

Finally, we assessed potential predation on hatchling iguanas in June 1997 using 10 rubber lizard models that were similar in size to hatchling iguanas (SVL 6–7 cm). Six of these models were placed under the cover of vegetation, and four were placed in open areas to test for attacks by rodents and birds (a sizeable Laughing Gull (*Leucophaeus atricilla*) colony breeds on the main island during spring and summer). Models were left in place for two weeks and checked morning and evening each day. We recorded attempted predation or "attacks" as any form of physical damage, such as chew marks, or disappearance of the model.

Iguana social interactions.—Due to the scarcity of iguanas in 1997, we rarely observed social interactions (two or more iguanas seen within 2 m of each other or heard in conflict). To quantify this for future comparison at higher population density, we recorded the total number of social interactions observed per the sum of hours devoted to capture effort (walking throughout the island), ethological observations (standing near a single iguana), and radio-telemetry tracking (walking throughout the island in search of transmittered iguanas).

Supplemental feeding.—We noted occasional incidents of supplemental feeding by tourists visiting the cay, and inferred the extent of it based on obvious tameness of iguanas.

Impacts and mitigation of cinema production.—Portions of Episodes Two and Three of the *Pirates of the Caribbean* film series were produced on Sandy Cay during the periods 27 May–11 June 2005, 11–18 November 2005, and 7–15 January 2006. The Bahamas government permits were issued for film production subject to a 35-page environmental management plan prepared by Islands by Design Ltd. in association with Bethell Environmental Ltd. This document outlined parameters for filming, including vessel approach (avoiding seagrass areas) and locations for anchoring, sewage disposal (bathrooms placed aboard vessels and emptied/cleaned on Great Exuma), fueling and refueling, spills and accidents (none occurred), environmental monitoring (a biologist present during all filming activities, including scouting visits), vegetation trimming (very limited), and temporary palm relocation (not done for filming). Required mitigation included continued removal of Australian Pine, removal of all trash on the island (some left by visitors), and replacement of an informational sign about the iguanas. At times, substantial equipment and up to 250 people were on the island. A list of rules and procedures was signed by all and was posted on the cay. Much of the island was off-limits; food was forbidden on the cay, equipment was cleaned to avoid transfer of microbes, plant seeds, fire ants, and rodents, and interaction with iguanas was prohibited.

Poaching and translocation.—In February 2014, United Kingdom Border Force officers at London Heathrow Airport confiscated 13 adult *C. rileyi* iguanas (one deceased) of unknown provenance and subspecies from the luggage of two Romanian wildlife traffickers (Isaacs 2014). Working together, Bahamian and UK conservation authorities developed a plan to repatriate these iguanas to The Bahamas, and ultimately to establish a new population via *de facto* translocation.

Analyses.—We tested four sets of hypotheses using SPSS v13.0 for Windows (v.2004, SPSS Inc., Chicago, Illinois, USA), with alpha set at 0.05. First, we used curve-fitting regression to describe the trajectory of iguana population growth between 1997 and 2008. We regressed population size for adults (multiplied by 2.5, assuming 0.4 detectability) against number of years subsequent to 1997 (set at year zero), and tested for exponential, linear, and logistic population growth. Second, we tested evenness of iguana distribution across the cay at low (1997) and high (2008) population density by computing the correlation coefficient (*r*) between iguana density and transect number (west to east), with the latter corresponding inversely to relative vegetation density (high on western end, low on eastern end; Fig. 1). Third, we examined changes in iguana body size between the periods of low (1996–1997) and high (2006–2008) population density using a chi-square (χ^2) test to compare the proportion of subadult and adult iguanas captured each period that were ≥ 25 cm SVL. We assumed that iguanas growing larger during the period of low density would retain their large size as the population density increased. We removed juveniles from this analysis due to mild capture bias among the different years. Fourth, we tested whether tail-break and tail-furcation frequencies declined between the periods of invasive mammal presence (1996–1997) and mammal absence (2006–2008) using a chi-square test for each measure. For the chi-square tests, we computed phi (φ) as a measure of effect size, with values of 0.1, 0.3, and 0.5 deemed small, medium, and large, respectively (Cohen 1988). We report mean ± 1 SE values.

RESULTS

Invasive species and eradication success.—We never observed the single Raccoon despite extensive efforts to locate it during both day and night hours. We observed its footprints daily, however, across the cay and on the offshore dunes. The footprints established that this animal was largely, if not entirely, active at night. We successfully euthanized it in July 1997; the carcass was found by a visitor to the cay shortly afterward.

Rats were locally abundant prior to eradication. We first encountered rats during nighttime at our campsite on the eastern end of the island in 1996, when multiple individuals attempted to forage on our food supplies. In 110 trap nights at this location between 3–17 May 1997, we captured 10 rats (9.3% trap success, excluding available traps that captured mice) and three mice (3.0% success, excluding available traps that captured rats). In 67 additional trap nights at this location through 31 May 1997, we captured just one more rat (1.5% success). In 315 trap nights at dispersed locations on the cay from 24 May to 14 July 1997, we captured only three more rats (1.0% success). Seven (54%) of 13 captured rats were male, with means for all 13 specimens = 38.0 ± (SE) 0.4 cm total length (range, 35.9–40.6 cm) and 129 ± (SE) 5 g (range, 105–175 g). Two mice averaged 21.8 ± 1.1 cm total length and 22 ± 0 g. We also observed rat footprints on the offshore dunes.

During rodent eradication in April–May 1998, only two rat carcasses were found, but the highest level of rodenticide consumption occurred in the silver thatch palm forest at the western portion of the cay (Day et al. 1998). Subsequent to rodent eradication, we captured no rodents in 23 trap nights in October 1999 (15 at east point) and 24 trap nights (six at east point) in October 2002. We searched for but observed no rodent footprints on the offshore dunes.

We found Australian Pine distributed largely along the southern shoreline and on the offshore sand dunes (Fig. 1). In portions of these areas the trees formed a dense forest, were spreading rapidly, and crowding out native vegetation. One large tree was in the rocks on the northwestern shoreline. In February 2005, WKH and JAW cut down and applied herbicide to nearly all of the largest trees on the main island and a few on the offshore dunes, but we left the downed timber. In 2005, Disney continued the work by gathering and burning much of the downed timber and cutting down additional trees. Members of the Global Insular Conservation Society (GICS) furthered the work in May–June 2009, May 2011, and May–June 2012, by which time 95–97% of the pines were removed. Unfortunately, sprouts can reappear from the extensive root system if systemic herbicide application is not immediate or sufficient. The GICS strategy (Fig. 2) involved a two-person crew, with one individual cutting the tree down and the other immediately brushing the herbicide onto the stump. When extensive "forests" of small trees sprouted from intact root systems, a team member worked while kneeling on the ground, cutting the thin stems with loppers, and immediately applying herbicide. The crew remained near the burning timber to monitor the flames and ensure that no iguanas approached them (none attempted to do so).

Iguana population estimates, demography, and body size.—Our surveys revealed an initially slow but exponential population increase ($Y = 55.6e^{0.251x}$, where x = time in years, $P < 0.001$, $r^2 = 0.882$) subsequent to removal of the Raccoon (1997) and rodents (1998), growing from an estimated 112–168 individuals in 1997 to 2,208–3,312 by 2008 (Table 1). These latter numbers represent a mean annual population growth rate (λ) of 31.1%. Sex ratio based on noose and hand captures was strongly male-biased early in this period (95.2% of 62 captures in 1996–1997). The ratio certainly shifted closer to equality by 2006–2008, but we judged the sex data too unreliable from 2006–2008 to provide a ratio. The proportion of juvenile iguanas sighted was generally highest during the autumn surveys following emergence of hatchlings (18.6–36.8%, October–November), dwindled during the winter (24.7%, February 2005), and bottomed by mid-summer (6.7–9.7%, June 2007, July 2008). During the period of rapid population growth in 2002–2007, the proportion of subadults (31.6–48.0%) was generally similar to that of adults (31.6–45.3%), but was notably less in 2008 (33.1% and 57.2%, respectively). There was no correlation between iguana density and transect number (corresponding to vegetation density) in either 1997 ($r = -0.067$, $P = 0.85$, $n = 10$ transects) or 2008 ($r = 0.048$, $P = 0.91$, $n = 8$ transects).

We detected no upward shift in body size. The proportion of subadult and adult iguanas > 25 cm SVL during the period 1996–1997 (13.0% of 69 captures) was similar to that of the period 2006–2008 (20.5% of 117 captures; $\chi^2 = 1.66$, df = 1, $P = 0.20$, $\varphi = 0.09$).

Iguana injuries.—Tail-break frequency among iguanas declined significantly between 1996–1997 (42.7% of 75 captures) and 2006–2008 (28.9% of 121 captures; $\chi^2 = 3.89$, df = 1, $P = 0.049$), though the effect size was fairly small ($\varphi = 0.14$). Tail-furcation frequency similarly declined between 1996–1997 (5.3%) and 2006–2008 (0%; $\chi^2 = 6.59$, df = 1, $P = 0.010$, $\varphi = 0.18$).

Iguana mortality.—We obtained two estimates for mortality between June 1996 and May 1997. First, in 1996, 5.33 iguanas were caught and marked per person

TABLE 1. Results of standardized classical strip surveys for *Cyclura rileyi cristata* on Sandy Cay, Exuma Cays, The Bahamas. Invasive mammalian predators were removed in 1997 (a single Raccoon, *Procyon lotor*) and 1998 (Black Rat, *Rattus rattus*; House Mouse, *Mus musculus*). Population estimates = iguana density applied to entire island (14.9 ha) multiplied by two and by three (detectability of 0.33–0.5) to derive a range. Iguanas seen well enough to determine body size (i.e., "known size") were assigned to one of three age classes (juvenile, subadult, adult). Area surveyed was the sum of transect areas divided by total area of main island (excluding offshore dunes).

Survey period	Juveniles (%)	Subadults (%)	Adults (%)	Known size (#)	Total iguanas (#)	Area surveyed (%)	Population estimate (N)
May 1997	17.2	17.2	65.5	29	34	61	112–168
Oct 1999	31.3	15.6	53.1	32	36	48	150–225
Nov 2000	26.5	32.4	41.2	34	37	48	154–231
Oct 2002	36.8	31.6	31.6	76	82	48	342–513
Feb 2005	24.7	37.0	38.4	73	77	20	770–1155
Oct 2006	18.6	47.1	34.3	102	116	24	966–1449
Jun 2007	6.7	48.0	45.3	75	80	14	1142–1713
Jul 2008	9.7	33.1	57.2	278	298	27	2208–3312

per day (number of observers multiplied by days of capture effort), whereas only 1.67 iguanas were caught and marked per person-day of effort in 1997. This suggests a 68.7% reduction in the iguana population between 1996 and 1997. Second, only seven (30.4%) of 23 iguanas marked in 1996 were resighted between 1 May and 15 July 1997, whereas 46.0% of 51 iguanas assumed to be alive in 1997 (those resighted from 1996 and marked in 1997) were seen a second time. If the seven iguanas marked in 1996 and resighted in 1997 represented 46% of the marked iguanas that were alive and sightable in 1997, then approximately 15 of the 23 marked in 1996 remained alive in 1997, and eight of the original 23 were presumably dead, yielding a mortality estimate of 34.8% between 1996 and 1997. These two estimates of mortality, although indirect, suggest an annual rate of mortality in the preceding year of 35–69%. With an estimated iguana population of 112–168 in 1997 (Table 1), extrapolation using the extreme values of 35% and 69% mortality suggests a population of 162–480 iguanas in 1996, with 57–331 iguanas presumably killed between June 1996 and the period May–July 1997.

In the first 12 person-days of June 1996, May 1997, and April 1998, we encountered five, six, and zero iguana carcasses, respectively. In the four person-days of 1999, we found no additional carcasses. Thus, iguana mortality subsided immediately after Raccoon eradication in mid-July 1997. Of 14 total iguana carcasses found in 1997, two were opened near the head, with the skin peeled backward past the abdomen and the anterior portion of the body consumed (other carcasses were badly deteriorated). One sample of Raccoon feces had iguana remains in it. Three recovered radio transmitters during the brief study in May–July 1997 were badly chewed, with bits of iguana jaw and skin associated with one of these transmitters, suggesting predation on at least one of the 10 radio-tracked iguanas. No identifiable iguana remains were found in rodent stomachs (*n* = 13 rats, 3 mice).

Five of six rubber lizard models placed under vegetation cover in June 1977 were bitten, with a mean of 1.5 attacks per model during the two-week period (note bite marks matching rat incisors in Fig. 3). One of these bitten models eventually disappeared. One of four models in the open disappeared, but no bite marks were seen, with a mean of 0.5 attacks per model. All attacks on models occurred at night. We never witnessed birds attacking the models.

Iguana social interactions.—In March 1980, iguana social interactions were very common, including head-bobbing, chasing, and stereotypical fighting. However, in May-July 1997, we observed only 17 social interactions spaced out across 43 days, which included 187 h of capture effort, 26 h of ethological observation, 37 h of radio-telemetry tracking, and 342 iguana sightings. Thus, social interactions during this period of low population density were observed at a rate of approximately one occurrence every 14.7 h in the field, and only 5.0% of iguana observations. We did not record social interactions during subsequent visits, but they became common again as the population size increased.

Supplemental feeding.—Tourist visitation to Sandy Cay has increased over the past decade, according to local Bahamians. Iguanas appear to be regularly fed where boats land at the eastern and western ends of the cay, as evidenced by obvious iguana tameness at these sites but not elsewhere on the cay. No obvious tameness was evidenced in 1980 or during 1996–2002.

Impacts and mitigation of cinema production.—Overall, the filming of *Pirates of the Caribbean* had very little if any negative impact on the environment that we could quantify. The cast and the crew were cooperative, respectful, and curious about the iguanas. Some inquisitive iguanas had to be encouraged to move away from equipment (Fig. 4). No iguanas were disturbed otherwise. The appointed biologist (JAW) signed a document each day ensuring compliance with the management plan. No new invasive species have been found by us subsequent to the end of film production in January 2006.

Poaching and translocation.—Of the thirteen adult *C. rileyi* iguanas of unknown provenance and subspecies confiscated in February 2014 at the London Heathrow Airport, one was already deceased. The surviving 12 iguanas were repatriated to The Bahamas in July 2014, where they were housed in individual pens at the Iguana Conservation Center at the Gerace Research Centre on San Salvador Island for nine weeks. Three died within 24 h of arrival. Provenance became certain when three specimens were found to possess PIT tags installed by us on Sandy Cay in 2011. The remaining nine specimens of *C. rileyi cristata* were transferred in September 2014 to an uninhabited cay in the southern Exumas to establish a new population.

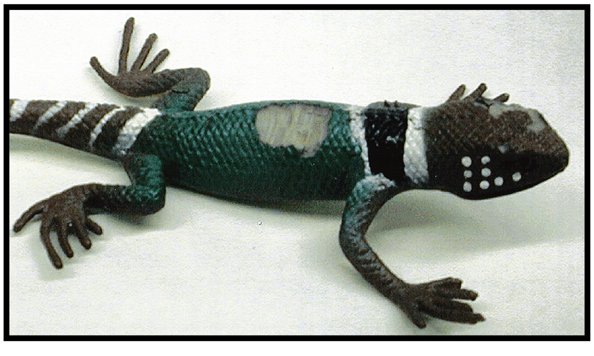

FIGURE 3. Bite marks, presumably from Black Rat (*Rattus rattus*), on a rubber lizard similar in size (6–7 cm snout-vent length) to a hatchling Sandy Cay Rock Iguana (*Cyclura rileyi cristata*), placed on Sandy Cay, Exuma Cays, The Bahamas. (Photographed by William K. Hayes).

Discussion

Much of our work on Sandy Cay has centered on the control of invasive species. Invasive mammals have no doubt exerted the largest effect on the iguana population. Of the three species we documented (Black Rat, House Mouse, Raccoon), the single Raccoon clearly had the greatest impact on iguanas. We conclude this based on two lines of evidence. First, we found numerous iguana carcasses on the island prior to exterminating the Raccoon in July 1997, and the rate of carcass discovery immediately declined even though rats remained for another year. Second, we found indirect evidence for Raccoon predation on the iguanas, including iguana remains in a Raccoon fecal sample, partially-skinned and consumed adult iguanas beyond the capability of mice and rats (though Osprey predation cannot be ruled out), and iguana body parts near a chewed radio transmitter, suggesting predation on one of the 10 radio-tracked iguanas. As pernicious mesopredators, Raccoons have been documented elsewhere to prey heavily on iguanas and plunder their nests, most notably in an urban maritime park in Florida where invasive Common Green Iguana (*Iguana iguana*) populations experienced explosive population growth similar to that which we have documented on Sandy Cay after removal of Raccoons (Platt et al. 2000; Meshaka et al. 2007, 2009). The Raccoon presumably arrived by one of three means: by jumping from a ship at sea, by deliberate release on Sandy Cay, or by swimming on its own from nearby Hog Cay where a pair of Raccoons was present prior to our study (Roy Albury, pers. comm.).

We have every reason to believe that the rodent eradication was successful. Similar eradications have been implemented to benefit iguanas elsewhere (Rodríguez et al. 2006; Harper et al. 2011; Samaniego-Herrera et al. 2011). We found no evidence of harm to iguanas or other species (Day et al. 1998), but no post-eradication monitoring took place until our next visit to the cay 16 months later. A similar project documented the death of six Galápagos Land Iguanas (*Conolophus subcristatus*) more than two months after brodifacoum application, apparently resulting from consumption of poisoned rats (Harper et al. 2011). Delayed mortality from brodifacoum was observed in Telfair's Skinks (*Leiolopisma telfairii*) on Round Island, Mauritius, as well (Merton 1987), though other rodenticide applications have not adversely affected lizards (reviewed by Harper et al. 2011).

Accumulating evidence suggests that rats can impact iguanas severely. Populations coexisting with rats, for example, tend to have reduced population densities (Hayes et al. 2004) and a greater frequency of tail injuries resulting from rodent bites (Carter and Hayes 2004; Hayes et al. 2012). As predicted, the frequency of tail breaks and tail furcations on Sandy Cay declined significantly during the decade following extirpation of the Raccoon and rats. The relatively high frequency of tail breaks and tail furcations on Sandy Cay during 1996–1997 could have resulted from predation attempts by either the Raccoon or the rats, but iguana tail-break frequency was no higher on Sandy Cay than on 10 other Bahamian islands infested with rats only, suggesting rats as the primary cause (Hayes et al. 2012). One case of iguana translocation to establish a new

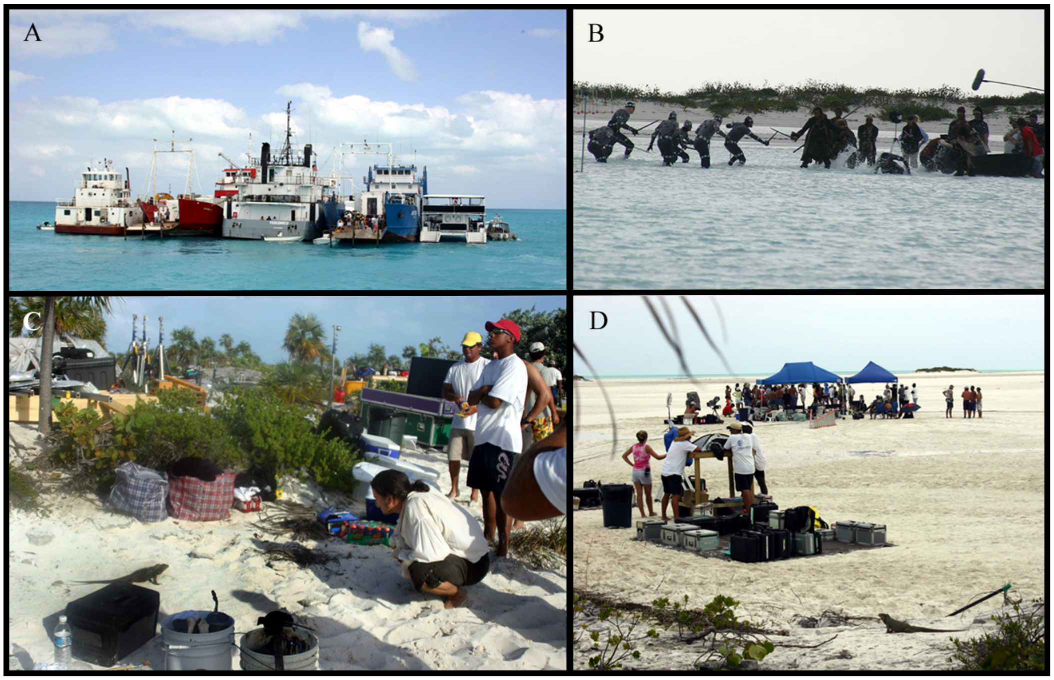

Figure 4. Images from the cinema production of portions of Episodes Two and Three of the Disney film series *Pirates of the Caribbean*, filmed on Sandy Cay, southern Exuma Cays, The Bahamas. (A) Support barges required to reduce impact on the cay; (B) cinematic fight scene; and (C and D) Sandy Cay Rock Iguanas (*Cyclura rileyi cristata*) approaching near equipment and people on their own volition. (Photographed by Joseph Wasilewski).

population of *C. rileyi rileyi* on an offshore cay of San Salvador Island failed, most likely due to the presence of rats (Hayes et al. this volume). Although we are skeptical that rats can prey successfully upon adult iguanas, they chewed on rubber models similar in size to hatchling iguanas during the nighttime hours (Fig. 3), suggesting a proclivity to attack sleeping iguanas (see further comments on iguana sleep behavior in Hayes et al. 2004). The reduced frequency of tail injuries in 2006–2008 supports our conclusion from limited post-eradication trapping and lack of encounters while camping that rats have remained absent from Sandy Cay at least through 2012. Rodent body size can vary among populations (e.g., Yosida et al. 1971; Patton et al. 1975; Michaux et al. 2002), and invasive mice have been known to attain exceptional body size when coexisting with and preying upon insular seabird populations (Berry et al. 1979; Wanless et al. 2007). We provided body size measures of rats and mice for future investigators who wish to examine variation within the Bahamas archipelago.

We did not quantify the area occupied by Australian Pine on the main cay or on the offshore dunes, but it was rapidly expanding and could have eventually formed dense stands across virtually all of the iguana habitat, crowding out the natural vegetation that the iguanas depend upon for food. We also did not attempt to measure the iguana population response to its removal. Nevertheless, invasive Australian Pine can alter numerous ecosystem-level processes, including erosion, shoreline stability, nitrogen fixation, stand structure, recruitment of native plants, and resource competition (Gordon 1998). Although we observed native plants flourishing at the perimeter of the pines, they do not grow beneath them, and leaf litter accumulation precludes iguana nesting (Wiewandt 1977). On Mona Island, *C. stejnegeri* avoids extensive areas of Australian Pine due to the lack of native vegetation required as food (Haneke 1995; Pérez-Buitrago and Sabat 2000; Pérez-Buitrago et al. 2008). On Sandy Cay, the trees provided perches for large raptors (Merlin, *Falco columbarius*, and Peregrine Falcon, *F. peregrinus*) that occur commonly during migration (WKH, pers. obs.) and potentially prey upon the iguanas. We found pine removal to be incomplete given the propensity of sprouts to emerge at a later time. Nevertheless, we have expanded the available habitat for iguanas and plan on continued removal of Australian Pine during the years to come. Herbicide application has become the accepted approach for removal of Australian Pine, as fire and mechanical removal are less effective and biological control agents remain under development (Klukas 1969; Morton 1980; Wheeler et al. 2011; Dechoum and Ziller 2013). Girdling, which involves removal of a ring of bark and cambium around the entire circumference of the trunk of the tree, warrants further investigation (Dechoum and Ziller 2013; Carol Landry, pers. comm.). Some of the local Bahamians expressed disaffection toward our efforts to remove the shade-producing trees, which mirrored sentiments associated with removal of Australian Pine in South Florida, USA (Klukas 1969). A local environmental education program (e.g., Carter et al. 2005) could address this.

The Sandy Cay Rock Iguana narrowly escaped extinction. At the rate of predation we estimated (81–368 iguanas between 1996 and 1997), the remaining population of 112–168 individuals would likely have disappeared within a few months or years. Population recovery subsequent to invasive mammal removal has proceeded at an exponential rate (ca. 31.1% per year), with no evidence through 2008 of reaching carrying capacity. If we assume a population estimate of 2,760 in 2008 (mean of low and high estimates, Table 1), and a mean body mass of 0.371 kg (Carter and Hayes 2004), standing crop biomass would have been 68.7 kg/ha in 2008, well under the maximum estimated standing crop biomass of 100 kg/ha for *Cyclura* proposed by Iverson et al. (2006). Thus, further population growth seems plausible. Considering the extreme male-biased sex ratio in 1997 (95% male), we have been surprised by the rapid population growth. Unfortunately, we were unable to confirm whether the sex ratio has shifted toward equality.

The current iguana population almost certainly exceeds 2,000 individuals (Table 1). However, population estimation remains imprecise, as estimates can be affected by numerous environmental and methodological factors. We suspect, for example, that iguanas have become less skittish in the years subsequent to heavy predation, resulting in higher levels of detectability and potential overestimation of population size. If detectability was higher in 2008, at 0.7 for example, then the estimate for the 2008 survey would be 1,577 individuals, which still represents a substantial population increase in only a decade. Similar high rates of population increase (ca. 16–32% per year) have been reported in other small iguana populations (reviewed by Iverson et al. 2006; also Iverson et al. this volume).

Intraspecific variation in body size occurs widely among rock iguanas and other iguana genera. Several translocated rock iguana populations are characterized by much larger body size than the source populations (Knapp 2001; Carter and Hayes 2004; Iverson et al. 2004), and this could result from differences in food availability and quality, competition and social interactions associated with reduced population density, or habitat-specific thermodynamics (Carter and Hayes 2004; Hayes et al. this volume; Iverson et al. this volume). On Sandy Cay, we hypothesized that iguana body size would increase as a result of reduced population density during and following the years of invasive mammal predation. However, our analyses indicated the absence of any shift in body size following predator eradication. This finding supports the conclusion that diet may have a far greater influence on maximal body size of an iguana population than the aforementioned effects associated with low population density, as can be seen from two translocated populations of *C. rileyi rileyi* on San Salvador Island, The Bahamas (Hayes et al. this volume). Iguanas translocated to a resort on the main island with lavish vegetation and supplemental feeding attained exceptional sizes within a few years, whereas those translocated to an offshore cay with native vegetation showed no obvious increase in body size.

Although a distinct gradient exists in vegetation structure and density on Sandy Cay (Fig. 1), the iguanas appeared to be evenly dispersed across the habitat (excluding the offshore sand dunes). This was evident during periods of both low (1997) and high (2008) iguana density, and suggests the absence of social clumping or redistribution relative to population density. The spacing of iguanas presumably results from their social structure and territoriality. Our survey in May 1997 was presumably during the mating season (Hayes et al. 2004), when we might have expected clumping to occur during the period of low iguana density. Social interactions were remarkably scarce during that season compared to what we see under higher densities (WKH pers. obs.). Nevertheless, some iguanas do wander, as evidenced by a handful of individuals beginning in 2005 that traversed the intertidal flats (> 100 m distance) during low tide, left their tracks on the offshore dunes, and possibly set up new home ranges there. Iguanas occupied the dunes in 1980 (JBI pers. obs.), but we never saw their tracks on these dunes between 1996 and 2005.

Supplemental feeding of iguanas by tourists appears to be taking place, and can have detrimental consequences (Hines 2011; Knapp et al. 2013; Smith and Iverson this volume), including placing the iguanas at greater risk of poaching. At present, the feeding on Sandy Cay appears to be limited to the two landing beaches on the island. Several informational signs have been posted on the cay, and we recommend that the next installation include a request that iguanas are not to be fed. The sign should also describe the need for Australian Pine removal. Local boat operators often provide transportation to guests visiting the cay, thus, a local environmental education program could address this issue as well.

Commercial interests, such as cinema production, sometimes collide with the need to protect sensitive habitats and threatened species. Filming of the *Pirates of the Caribbean* episodes posed manageable risks to the fate of the Sandy Cay Rock Iguana and their only home. In this particular case, the production team adhered faithfully to the environmental management plan, resulting in no detectable short- or long-term detriment to either the habitat or the more sensitive species on Sandy Cay, including the iguana and nesting birds. This case, therefore, serves as a useful model for managing such a large-scale project on a small and vulnerable landscape.

Unfortunately, endangered rock iguanas remain a much-sought-after entity in both the legal and illegal market for herpetoculture. Iguanas were smuggled from Sandy Cay previously (Hayes et al. 2004), and the event in 2014 underscores the ongoing attractiveness and vulnerability of these iguanas to poachers. In spite of this unfortunate incident, accompanied by considerable fanfare and media publicity, the two governments involved (The Bahamas and United Kingdom) worked together to repatriate the iguanas to their native country. Given the risks associated with potential transfer of pathogens to the parent population, these iguanas were ultimately placed on an uninhabited, government-owned (Crown land) cay in the southern Exumas as an assurance colony for the taxon. Bahamian officials plan to transfer additional animals to this newly established population to ensure its long-term viability.

In summary, Sandy Cay Rock Iguanas have returned from the brink of extinction. Although they faced and continue to be susceptible to a number of threats (particularly from invasive species), we have reason to believe that we can secure the future for this iguana species.

Acknowledgments.—We thank the many students and colleagues without whose support this work could not have been accomplished; there have been too many to list here. Research was approved by the Institutional Animal Care and Use Committees (IACUCs) of Southern College, Collegedale, Tennessee (no protocol number assigned), and of Loma Linda University (protocols 77011, 82033, 83013, 84053, 85011, 89008, and 8100013). Research was also conducted under annual permits issued by The Bahamas Ministry of the Environment (96-004, 97-85, 98-64, 99-13, 05-44, 06-56, 07-13, 08-29, and unnumbered permits in other years). Financial support was provided by The Bahamas Ministry of Agriculture, Chicago Zoological Society, Denver Zoological Society, Disney Wildlife Conservation Fund, Gerace Research Centre, Insular Species Conservation Society, International Iguana Foundation, International Reptile Conservation Foundation, Loma Linda University, Seacology, and out-of-pocket funds.

LITERATURE CITED

Bauer, A.M., and R.A. Sadlier. 1992. The use of mouse glue traps to capture lizards. Herpetological Review 23:112–113.

Berry, R.J., W.N. Bonner, and J. Peters. 1979. Natural selection in mice from South Georgia (South Atlantic Ocean). Journal of Zoology (London) 189:385–398.

Carter, R.L., and W.K. Hayes. 1996. *Cyclura rileyi* ssp. *cristata*. The IUCN Red List of Threatened Species. Version 2014.3. Available from http://www.iucnredlist.org/details/6046/0 [Accessed on 14 September 2014].

Carter, R.L., and W.K. Hayes. 2004. Conservation of an endangered Bahamian iguana. II. Morphological variation and conservation recommendations. Pp. 258–273 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds). University of California Press, Berkeley and Los Angeles, California, USA.

Carter, R.L., W.K. Hayes, V. Voegeli, and S. Voegeli. 2005. Celebrating Biodiversity – 2002. Conservation education: a responsibility of higher education. Pp. 12–17 *In* Proceedings of the 10th Symposium on the Natural History of The Bahamas. Buckner, S., and T. McGrath (Eds.). Gerace Research Centre, San Salvador Island, The Bahamas.

Carter, R.L., W.K. Hayes, and West Indian Iguana Specialist Group. 2000a. *Cyclura rileyi* ssp. *nuchalis*. The IUCN Red List of Threatened Species. Version 2014.3. Available from http://www.iucnredlist.org/details/6047/0 [Accessed on 14 September 2014].

Carter, R.L., W.K. Hayes, and West Indian Iguana Specialist Group. 2000b. *Cyclura rileyi* ssp. *rileyi*. The IUCN Red List of Threatened Species. Version 2014.3. Available from http://www.iucnredlist.org/details/6048/0 [Accessed on 14 September 2014].

Cohen, J. 1988. Statistical Power Analysis for the Behavioral Sciences, 2nd Edition. Erlbaum, Hillsdale, New Jersey, USA.

Cyril, S., Jr. 2001. Behavioral ecology of the endangered San Salvador Rock Iguana (*Cyclura rileyi rileyi*) in The Bahamas. M.Sc. Thesis, Loma Linda University, Loma Linda, California, USA. 59 p.

Day, M., W. Hayes, K. Varnham, T. Ross, E. Carey, T. Ferguson, J. Monestine, S. Smith, C. Armstrong, and A. Buckle, et al. 1998. Rat eradication to protect the White Cay Iguana. Aliens 8:22–24.

Dechoum, M. de S., and S.R. Ziller. 2013. Métodos para controle de plantas exóticas invasoras. Biotemas 26:69–77.

Fry, S.K. 2001. Ecology of the endangered Sandy Cay Rock Iguana, *Cyclura rileyi cristata*, in The Bahamas. M.Sc. Thesis, Loma Linda University, Loma Linda, California, USA. 50 p.

Gordon, D.R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Applications 8:975–989.

Haneke, B. 1995. A study of Mona Rock Iguana (*Cyclura cornuta stejnegeri*) nesting sites on Mona Island, Puerto Rico. Iguana Times (Journal of the International Iguana Society) 4:61–71.

Harper, G.A., J. Zabala, and V. Carrion. 2011. Monitoring of a population of Galápagos Land Iguanas (*Conolophus subcristatus*) during a rat eradication using brodifacoum. Pp. 309–312 *In* Island Invasives: Eradication and Management. Veitch, C.R., M.N. Clout, and D.R. Towns (Eds.). IUCN, Gland, Switzerland.

Hayes, W., and R. Carter. 2000. Population monitoring. Pp. 79–85 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Hayes, W.K., and R.L. Carter. 2005. Biology and conservation of *Cyclura rileyi,* an endangered Bahamian rock iguana. Pp. 69–82 *In* Proceedings of the 10th Symposium on the Natural History of the Bahamas. Buckner, S.D., and T.A. McGrath (Eds.). Gerace Research Centre, San Salvador, The Bahamas.

Hayes, W.K., R.L. Carter, S. Cyril, Jr., and B. Thornton. 2004. Conservation of an endangered Bahamian Rock Iguana, I. Population assessments, habitat restoration, and behavioral ecology. Pp. 232–257 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds). University of California Press, Berkeley and Los Angeles, California, USA.

Hayes, W., R. Carter, and N. Goodyear. 2000. Marking techniques. Pp. 77–79 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. A. Alberts (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Hayes, W.K., S. Cyril, Jr., T. Crutchfield, J.A. Wasilewski, T. Rothfus, and R.L. Carter. 2016. Conservation of the endangered San Salvador Rock Iguanas (*Cyclura rileyi rileyi*): invasive species control, translocation, and headstarting. Pp. 90–105 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Hayes, W.K., D.M. Hayes, D. Brouhard, B. Goodge, and R.L. Carter. 1995. Population status and conservation of the endangered San Salvador Rock Iguana, *Cyclura r. rileyi*. Iguana Times (Journal of the International Iguana Society) 4:21–30.

Hayes, W.K., J.B. Iverson, C.R. Knapp, and R.L. Carter. 2012. Do invasive rodents impact endangered insular iguana populations? Biodiversity and Conservation 21:1893–1899.

Henderson, R.W. 1992. Consequences of predator introductions and habitat destruction on amphibians and reptiles in the post-Columbus West Indies. Caribbean Journal of Science 28:1–10.

Hines, K.N. 2011. Effects of ecotourism on endangered Northern Bahamian Rock Iguanas (*Cyclura cychlura*). Herpetological Conservation and Biology 6:250–259.

Iguana Taxonomy Working Group (ITWG). 2016. A checklist of the iguanas of the world (Iguanidae; Iguaninae). Pp. 4–46 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Isaacs, M. 2014. Report on the smuggling of Bahamian rock iguanas. Sixty-fifth Meeting of the Standing Committee of the Convention on International Trade in Endangered Species of Wild Fauna and Flora, Geneva, Switzerland. SC65 Inf. 4:1–6.

Iverson, J.B. 1978. The impact of feral cats and dogs on populations of the West Indian rock iguana *Cyclura carinata*. Biological Conservation 14:63–73.

Iverson, J.B. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bulletin of the Florida State Museum 24:175–358.

Iverson, J.B., S.J. Converse, G.R. Smith, and J.M. Valiulis. 2006. Long-term trends in the demography of the Allen Cays Rock Iguana (*Cyclura cychlura inornata*): human disturbance and density-dependent effects. Biological Conservation 132:300–310.

Iverson, J.B., G.R. Smith, S.A. Pasachnik, K.N. Hines, and L. Pieper. 2016. Growth, coloration, and demography of an introduced population of the Acklins Rock Iguana (*Cyclura rileyi nuchalis*) in the Exuma Islands, The Bahamas. Pp. 139–153 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Iverson, J.B., G.R. Smith, and L. Pieper. 2004. Factors affecting long-term growth of the Allen Cays Rock Iguana in The Bahamas. Pp. 176–192 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds). University of California Press, Berkeley and Los Angeles, California, USA.

Jones, H.P., B.R. Tershy, E.S. Zavaleta, D.A. Croll, B.S. Keitt, M.E. Finkelstein, and G.R. Howald. 2008. Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology 22:16–26.

Klukas, R.W. 1969. Exotic terrestrial plants in South Florida with emphasis on Australian Pine (*Casuarina equisetifolia*). Report No. 33030. Everglades National Park, Homestead, Florida.

Knapp, C.R. 2001. Status of a translocated *Cyclura* iguana colony in The Bahamas. Journal of Herpetology 35:239–248.

Knapp, C.R., and R.D. Hudson. 2004. Translocation strategies as a conservation tool for West Indian Iguanas: evaluations and recommendations. Pp. 199–209 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds). University of California Press, Berkeley and Los Angeles, California, USA.

Knapp, C.R., K.N. Hines, T.T. Zachariah, C. Perez-Heydrich, J.B. Iverson, S.D. Buckner, S.C. Halach, C.R. Lattin, and L.M. Romero. 2013. Physiological effects of tourism and associated food provisioning in an endangered iguana. Conservation Physiology 1:cot032. doi:10.1093/conphys/cot032

Lovich, R.E., W.K. Hayes, H. Mushinsky, and G.H. Rodda. 2012. Transect surveys, including line distance. Pp. 227–234 *In* Reptile Biodiversity: Standard Methods for Inventory and Monitoring. McDiarmid, R.W., M.S. Foster, C. Guyer, J.W. Gibbons, and N. Chernoff (Eds.). University of California Press, Berkeley, California, USA.

Malone, C.L., T. Wheeler, J.F. Taylor, and S.K. Davis. 2000. Phylogeography of the Caribbean rock iguana (*Cyclura*): implications for conservation and insights on the biogeographic history of the West Indies. Molecular Phylogenetics and Evolution 17:269–279.

Merton, D.V. 1987. Eradication of rabbits from Round Island, Mauritius: a conservation success story. The Dodo 24:19–24.

Meshaka, W.E., Jr., H.T. Smith, H.L. Cress, S.R. Sekscienski, W.R. Mapp, E.M. Cowan, and J.A. Moore. 2009. Raccoon (*Proycon lotor*) removal and the rapid colonization of the Green Iguana (*Iguana iguana*) on a public land in South Florida: a conservation opportunity for the Caribbean. Caribbean Journal of Science 45:15–19.

Meshaka, W.E., Jr., H.T. Smith, E. Golden, J.A. Moore, S. Fitchett, E.M. Cowan, R.M. Engeman, S.R. Sekscienski, and H.L. Cress. 2007. Green Iguanas (*Iguana iguana*): the unintended consequence of sound wildlife management practices in a south Florida park. Herpetological Conservation and Biology 2:149–156.

Michaux, J.R., D. Bellocq, J. Goüy, M. Sarà, and S. Morand. 2002. Body size increase in insular rodent populations: a role for predators? Global Ecology and Biogeography 11:427–436.

Mitchell, N.C. 1999. Effect of introduced ungulates on density, dietary preferences, home range, and physical condition of the iguana *Cyclura pinguis* on Anegada. Herpetologica 55:7–17.

Mitchell, N., R. Haeffner, V. Veer, M. Fulford-Gardner, W. Clerveaux, C.R. Veitch, and G. Mitchell. 2002. Cat eradication and the restoration of endangered iguanas (*Cyclura carinata*) on Long Cay, Caicos Bank, Turks and Caicos Islands, British West Indies. Pp. 206–212 *In* Turning the Tide: The Eradication of Invasive Species. Veitch, C.R., and M.N. Clout (Eds.). IUCN World Conservation Union, Gland, Switzerland.

Morton, J.F. 1980. The Australian Pine or Beefwood (*Casuarina equisetifolia* L.), an invasive "weed" tree in Florida. Proceedings of the Florida State Horticultural Society 93:87–95.

Patton, J.L., S.Y. Yang, and P. Myers. 1975. Genetic and morphologic divergence among introduced rat populations (*Rattus rattus*) of the Galápagos archipelago, Ecuador. Systematic Biology 24:296–310.

Pérez-Buitrago, N., and A. Sabat. 2000. Population status of the Rock Ground Iguana (*Cyclura cornuta stejnegeri*) in Mona Island, Puerto Rico. Acta Cientifica 14:67–76.

Pérez-Buitrago, N., M.A. García, A. Sabat, J. Delgado, A. Álvarez, O. McMillan, and S.M. Funk. 2008. Do headstart programs work? Survival and body condition in headstarted Mona Island Iguanas *Cyclura cornuta stejnegeri*. Endangered Species Research 6:55–65.

Perry, G., and G.P. Gerber. 2006. Conservation of amphibians and reptiles in the British Virgin Islands: status and patterns. Applied Herpetology 3:237–256.

Platt, S.G., T.R. Rainwater, B.W. Miller, and C.M. Miller. 2000. Notes on the mammals of Turneffe Atoll, Belize. Caribbean Journal of Science 36:166–168.

Powell, R., and R.W. Henderson. 2011. Introduction. Island Lists of West Indian Amphibians and Reptiles. Bulletin of the Florida Museum of Natural History 51:86–90.

Rodríguez, C., R. Torres, and H. Drummond. 2006. Eradicating introduced mammals from a forested tropical island. Biological Conservation 130:98–105.

Samaniego-Herrera, A., A. Aguirre-Muñoz, M. Rodríguez-Malagón, R. González-Gómez, F. Torres-García, F. Méndez-Sánchez, M. Félix-Lizárraga, and M. Latofski-Robles. 2011. Rodent eradications on Mexican islands: advances and challenges. Pp. 350–355 *In* Island Invasives: Eradication and Management. Veitch, C.R., M.N. Clout, and D.R. Towns (Eds.). IUCN, Gland, Switzerland. Available from https://portals.iucn.org/library/efiles/documents/ssc-op-042.pdf

Smith, G.R., and J.B. Iverson. 2016. Effects of tourism on body size, growth, condition, and demography in the Allen Cays Iguana, *Cyclura cychlura inornata*, on Leaf Cay, The Bahamas. Pp. 214–221 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Thornton, B.J. 2000. Nesting ecology of the endangered Acklins Bight Rock Iguana, *Cyclura rileyi nuchalis*, in The Bahamas. M.Sc. Thesis, Andrews University, Berrien Springs, Michigan, USA. 85 p.

Tolson, P.J. 2000. Control of introduced species. Pp. 86–89 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A.C. (Ed). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Towns, D.R. 2011. Invasive mammal eradications: the value of an ecosystem view. Animal Conservation 14:466–467.

Towns, D.R., I.A.E. Atkinson, and C.H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8:863–891.

Wanless, R.M., A. Angel, R.J. Cuthbert, G.M. Hilton, and P.G. Ryan. 2007. Can predation by invasive mice drive seabird extinctions? Biological Letters 3:241–244.

Wheeler, G.S., G.S. Taylor, J.F. Gaskin, and M.F. Purcell. 2011. Ecology and management of Sheoak (*Casuarina* spp.), an invader of coastal Florida, USA. Journal of Coastal Research 27:485–492.

Whittaker, R.J., and J.M. Fernández-Palacios. 2007. Island Biogeography: Ecology, Evolution, and Conservation. Oxford University Press, Oxford, United Kingdom.

Wiewandt, T.A. 1977. Ecology, behavior, and management of the Mona Island Ground Iguana, *Cyclura stejnegeri*. Ph.D. Dissertation, Cornell University, Ithaca, New York, USA. 338 p.

Wilson, B., T.D. Grant, R. van Veen, R. Hudson, D. Fleuchaus, O. Robinson, and K. Stephenson. This volume. The Jamaican Iguana (*Cyclura collei*): a report on 25 years of conservation effort. Pp. 237–254 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Yosida, T.H., K. Tsuchiya, and K. Moriwaki. 1971. Karyotypic differences of Black Rats, *Rattus rattus*, collected in various localities of East and Southeast Asia and Oceania. Chromosoma 33:252–267.

William K. Hayes serves as a Professor of Biology and the Director of the Center for Biodiversity and Conservation Studies at Loma Linda University, Loma Linda, California. He earned his B.S. and M.Sc. degrees in Biology at Walla Walla University, Walla Walla, Washington, where he first began studying the behavior of rattlesnakes. He then explored venom expenditure by rattlesnakes for his Ph.D. in 1991 at University of Wyoming. He and his graduate students study a range of venomous animals, including rattlesnakes, spiders, scorpions, and centipedes. They also study the behavioral ecology and conservation of endangered reptiles and birds, with emphases in the California and Caribbean Islands biodiversity hotspots. In addition to his publications in scientific journals, he has co-edited the *Iguanas: Biology and Conservation* volume and *The Biology of Rattlesnakes*. (Photographed by Pat Hayes).

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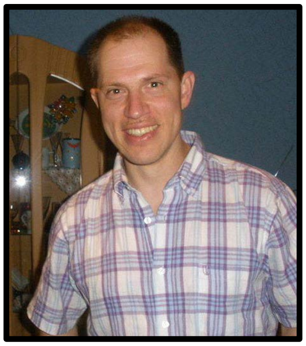

Shawn K. Fry grew up in the Pacific Northwest, where he developed an engaging interest in herpetology. He earned his B.S. in Biology in 1996 at Walla Walla University, Walla Walla, Washington. He then studied the Sandy Cay Rock Iguana for his M.Sc. thesis at Loma Linda University, Loma Linda, California, completing his degree in 2001. After working as a field technician on several herpetology projects at Idaho State University, he joined the United States Army in 2004, and was stationed in Fort Campbell, Kentucky, and in Baumholder, Germany. While in the Army, he obtained licensure as a Medical Laboratory Technician and as a Medical Technologist. After his recent promotion to First Lieutenant, he returned to the U.S. and is currently the officer in charge of the Core Laboratory of Martin Army Community Hospital, Fort Benning, Georgia. (Photographed by Amelia Rauch-Fry).

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Kathryn S. West practices veterinary medicine at the Linwood Animal Clinic in Milwaukie, Oregon. She earned her undergraduate and master's degrees at Oregon State University before attending veterinary school at the University of Florida. Returning to the Pacific Northwest after graduation, she has worked in both the Portland, Oregon, and Seattle, Washington, areas. She has a special interest in non-traditional (exotic) pets, including rabbits, ferrets, pocket pets, and reptiles. She spends some of her free time doing volunteer work at local zoos and assisting conservation groups working in The Bahamas, Costa Rica, and Africa. She has also served as a board member of the Seattle-based Insular Species Conservation Society. (Photographed by Roy Toft).

John B. Iverson holds a Ph.D. in Biology from the University of Florida and is Biology Research Professor at Earlham College in Richmond, Indiana. Because of his interests in the natural history, ecology, and evolution of iguanas and turtles, he is currently on the steering committees (and founding member) of the IUCN SSC Iguana Specialist Group, and the Tortoise and Freshwater Turtle Specialist Group. He has been involved with the Turtle Survival Alliance since its inception in 2001 (currently a board member), and serves on the board of the Turtle Conservation Fund. He has been active in several herp societies, serving as Editor and President of the Herpetologists' League. He has maintained long-term field research sites since 1980 for Rock Iguanas in the Exumas in The Bahamas, and since 1981 for turtles at the Crescent Lake National Wildlife Refuge in western Nebraska. His hobby is restoring a 76-acre woodlot/cornfield (now in a conservation easement) to a mature hardwood forest. (Photographed by Deanna McCartney).

Sandra D. Buckner is a past president of the Bahamas National Trust and was for 12 years the chair of its Wildlife Committee. She moved to The Bahamas with her family from the United Kingdom in 1977, and soon became interested in the history of herpetology in The Bahamas, the distribution of reptiles and amphibians throughout the Bahamian archipelago, and the ecology of the islands. In particular, she studies and concentrates on the conservation of the endangered species of the Bahamian Rock Iguanas (*Cyclura* species). Over the past 25 years, she has studied alongside researchers in a number of disciplines in the natural sciences and has co-authored 30 papers concerned with the natural history of The Bahamas. She was a founding Co-chair of the IUCN SSC West Indian Iguana Specialist Group, now known as the Iguana Specialist Group. (Photographed by Scott Johnson).

Ronald L. Carter serves as the Provost of Loma Linda University, Loma Linda, California. He earned his Ph.D. in 1977 at Loma Linda University, and received post-graduate training in molecular systematics from Claremont Colleges, Claremont, California. He eventually returned in 1989 to Loma Linda University to teach in the Department of Earth and Biological Sciences, where he later became the chair. During this time, much of his research was focused on West Indian Rock Iguanas and Galápagos Marine Iguanas. In 2005, he became the founding dean of the newly established School of Science and Technology; in 2006, he was selected to be the Vice Chancellor for Academic Affairs, and in 2008 he was appointed to the position of Provost. Deeply committed to his research roots in conservation genetics, Dr. Carter has contributed numerous articles to refereed volumes and journals. (Photographed by William K. Hayes).

Herpetological Conservation and Biology 11(Monograph 6):121–138.
Submitted: 15 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

FOOD HABITS OF NORTHERN BAHAMIAN ROCK IGUANAS (*CYCLURA CYCHLURA*) IN THE EXUMA ISLANDS, WITH A DIETARY REVIEW OF ROCK IGUANAS (GENUS *CYCLURA*)

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Abstract.—**This study examined the natural diet of Northern Bahamian Rock Iguanas (*Cyclura cychlura*) in the Exuma Islands. The diet of *Cyclura cychlura* in the Exumas, based on fecal samples (scat), encompassed 74 food items, mainly plants but also animal matter, algae, soil, and rocks. This diet can be characterized overall as diverse. However, within this otherwise broad diet, only nine plant species occurred in more than 5% of the samples, indicating that the iguanas concentrate feeding on a relatively narrow core diet. These nine core foods were widely represented in the samples across years, seasons, and islands. A greater variety of plants were consumed in the dry season than in the wet season. There were significant differences in parts of plants eaten in dry season versus wet season for six of the nine core plants. Animal matter occurred in nearly 7% of samples. Supported by observations of active hunting, this result suggests that consumption of animal matter may be more important than previously appreciated. A synthesis of published information on food habits suggests that these results apply generally to all extant *Cyclura* species, although differing in composition of core and overall diets.**

Key Words.—Bahamas; Caribbean; carnivory; diet; herbivory; predation; West Indian Rock Iguanas

INTRODUCTION

Northern Bahamian Rock Iguanas (*Cyclura cychlura*) are one of 10 extant species of rock iguanas distributed on islands in the West Indies. Listed as Vulnerable by the IUCN Red List of Threatened Species, Northern Bahamian Rock Iguanas occur only on the islands of the Exumas and Andros, both in The Bahamas (Knapp et al. 2004). Two subspecies are described from the Exumas, *Cyclura cychlura inornata* and *Cyclura cychlura figginsi*. In the Exumas, *Cyclura cychlura* is confined to a limited number of small islands. As a group, rock iguanas are among the most endangered lizards in the world owing to diminished and degraded habitat, introduced species, hunting and poaching, and perhaps tourism (Alberts 2000; Hines 2011; Lemm and Alberts 2012). Historically they were the largest terrestrial vertebrate on their islands, have been considered to be almost entirely herbivorous, and likely function in seed dispersal of some of the plants they consume (Iverson 1982, 1985).

As is the case for most other *Cyclura* species, the natural diet of *Cyclura cychlura* in the Exumas remains poorly known, despite conservation concerns arising from potentially negative effects of their being fed by tourists (James et al. 2006; Hines 2011; Knapp et al. 2013). Viewing and feeding these iguanas have become significant tourist activities in The Bahamas and several companies provide visitation opportunities on a few of the islands. I previously compared food eaten at places where these iguanas were being artificially provisioned versus food eaten in unaffected areas on the same island, finding differences in both diet and behavior (Hines 2011). Physiological effects from food provisioning, such as elevated glucose and uric acid levels, have also been suggested (James et al. 2006; Knapp et al. 2013). However, a comprehensive understanding of the natural food habits of these iguanas is lacking and is desirable both to characterize habitat needs of this vulnerable species and to fully assess alterations in the diet and potential effects of tourist activities. The primary goal of this paper is to characterize the overall natural diet of *Cyclura cychlura* in the Exumas.

In addition, I provide a synthesis of documented diets for several *Cyclura* species for which information exists, including the *Cyclura cychlura* data reported in this study. Food habits of rock iguanas have been studied to varying degrees over the past several decades. *Cyclura carinata* from the Turks and Caicos is the most comprehensively examined (Iverson 1979; Auffenberg 1982), others far less so. Although some summarization of existing diet information has been done (e.g., Iverson 1979; Lemm and Alberts 2012), similarities and differences in their diets have not been comprehensively compared.

METHODS

Study site.—I studied the food habits of *Cyclura cychlura* in the Exuma Island chain of The Bahamas on 15 islands within the natural range of the species. All islands in the study share the same geology, plant

Hines, Kirsten N. 2016. Food habits of Northern Bahamian Rock Iguanas (*Cyclura cychlura*) in the Exuma Islands, with a dietary review of Rock Iguanas (genus *Cyclura*). Pp. 121–138 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

species richness and diversity (Knapp et al. 2013), and climate (see Iverson et al. 2004 for detailed description of two of the study islands). Situated in the Great Bahama Bank along the Exuma Sound, these islands are characterized by an exposed limestone shoreline, punctuated by sand beaches on some islands. Coastal shoreline vegetation transitions into mixed hardwood forest (locally called coppice) within the islands' interior, where sand and rock are interspersed. The islands studied are each only a few hectares in size and are uninhabited by human residents. Roughly one-third of the 15 islands studied are visited regularly by tourists, some of whom feed the iguanas, but feeding activities are limited to landing beaches (Hines 2011). The climate is seasonal; the cooler dry season occurring November–April and the warmer wet season May–October (Sealey 2006).

Diet of* Cyclura cychlura *in the Exumas.—The overall diet of *Cyclura cychlura* in the Exumas was studied through examination of fecal (scat) samples. This non-intrusive method was used because the vulnerable status of the species precluded sacrificing individuals for stomach content analysis, and in my prior testing, stomach flushing of both *Cyclura cychlura* and Green Iguanas (*Iguana iguana*) proved ineffective. Although fecal (scat) analysis presents limitations due to differential digestion, particularly under-representing soft food items such as fungi and soft-bodied insects, scat analysis has been found in *Cyclura* to be nearly as reliable as stomach analysis for determining food species eaten and their frequency of occurrence (Iverson 1979; Auffenberg 1982).

To assess the overall diet and to capture the full array of natural dietary components, samples were collected over multiple islands, years and months to the extent allowed by logistical difficulties posed by the remote location. For all analyses samples were pooled across years and islands. Geographic sampling bias is unexpected given the uniformity of geology and vegetative composition of the different islands (see Study site above), and sampling years and seasons were within normal ranges for temperature, rainfall, and storms (Sealey 2006). Scat samples were collected during six years, between 2006 through 2013, from 15 islands across the entire range of *Cyclura cychlura* in the Exumas (Appendix 1). Samples analyzed were collected from ten islands in March, April, and July of 2006; five islands in June and July of 2007; six islands in March and May of 2008; six islands in July of 2009; seven islands in March, April, and May of 2010; and eight islands in January 2013. Samples were collected from natural areas of each island, avoiding landing beaches visited by tourists. All samples were uniformly dried and dissected into their distinct components. Each food item was categorized, such as fruit, leaf, flower, feather, etc., and identified to species if possible. The overall diet was evaluated using frequency of occurrence and dry mass. To assess frequency of occurrence, presence and/or absence of dietary components was recorded for 405 samples. Dry mass composition of the overall diet was determined from a subset of 113 samples drawn from 12 islands and five years of the study (Appendix 1). Mass of dietary components was measured using a S213 Veritas Precision Balance (Hogentogler & Co., Columbia, Maryland, USA).

To assess dietary differences between wet season and dry season, frequency of occurrence of plant species and other dietary components was compared ($n = 405$) using a pairwise chi-square test. Differences in the wet season versus dry season use of plant parts (leaves, fruit, flowers) were further evaluated for plants occurring in greater than 5% of scat samples (where a natural break in the data existed both for frequency of occurrence and dry mass measures; see Tables 1 and 2), using pairwise chi-square tests with a Holms-Bonferroni correction. Scientific and English names of plants identified in this study followed Correll and Correll (1996).

***Review of diet in* Cyclura**.—To compare and contrast diet among the *Cyclura* species, available information in the literature was synthesized, including results reported in the present study for *Cyclura cychlura*. Sources ranged from extensive dietary studies (e.g., Iverson 1979; Auffenberg 1982) to natural history notes in species accounts (e.g., Schwartz and Henderson 1991; Vogel 2000) and popular narratives (e.g., Burton 2010), for a total of 29 referenced sources. Where identifiable, foods were excluded that were associated with people, such as tourist feeding and non-native plants. Data were tallied by iguana species (combining any data for subspecies, including the three subspecies of *Cyclura cychlura*), by plant species (combining records of various plant parts), and by animal higher taxon (combining lower level taxonomic identifications). Because of the divergence of methods, sampling effort, and reporting used by different authors, the data were simply evaluated for presence/absence. Species names are those used in the original literature. Iguana scientific and common names are based on the Checklist of the Iguanas of the World (ITWG this volume).

RESULTS

Diet of* Cyclura cychlura *in the Exumas.—Pooling all data across islands and sampling visits, 74 different items were recorded in scat samples from *Cyclura cychlura* in the Exumas (Appendix 2). Samples contained between 1–12 unique food items each, with a mean of 2.76 items per sample. Of the 74 food items, 54 were identifiable plant species. Seven plant species had a frequency of occurrence of greater than 5% – *Casasia* *clusiifolia*, *Conocarpus erectus*, *Rhachicallis americana*, *Manilkara bahamamensis*, *Guaiacum sanctum*, *Suriana maritima*, and *Jacquinia keyensis*. Each of these plants was observed in the diet on at least 60% of the islands and in at least five of the six years of the study (Appendix 2). Nearly 6% of the samples contained plant material that was too fragmented for accurate identification. Animal prey occurred in 6.95% of the samples, with iguana skin (2.17%), bird remains (1.45%), and *Cerion incanum* snails (1.45%) being most pervasive. One bird remains was identifiable as *Columbina passerina*, and six other animal species were identifiable. Other items included soil, seaweed, charcoal, and rocks. Of these, only soil appeared regularly (3.86% of total samples and in more than half of the islands and years).

Relative contribution of food items to the diet, based on percentage of total dry mass (n = 113), revealed that seven plant species accounted for 5% or more of the total mass (Appendix 3). *Conocarpus erectus* made the greatest contribution (17%). *Casasia clusiifolia* (15%) was the only other item to account for more than 10% of the total mass. Unidentified plant parts constituted just over 5% of the total mass. Undigested animal prey remains accounted for 1.4% of total mass and soil for 2.8%.

Combining the findings of the two analyses, only nine plants had a frequency of occurrence and/or dry mass dietary contribution of greater than 5%. This core diet was further analyzed for seasonality in the consumption of these plants and their parts (Appendix 4). Consumption of seven plant parts from six of these core plants varied significantly between seasons. *Casasia clusiifolia* fruit and leaves were eaten more in the dry season, as were *Coccothrinax argentata* fruit, and *Jacquinia keyensis* and *Guaiacum sanctum* leaves. *Manilkara bahamensis* flowers and *Conocarpus erectus* fruit were eaten more in the wet season. Overall, the diversity of dietary components and the diversity of plants eaten were greater in the dry season than in the wet season (Overall: 67 species, n = 180 in dry season vs 41 species, n = 225 in wet season, χ^2 = 13.609, df = 1, P = 0.0002; Plants: n = 54 in dry season vs n = 29 in wet season, χ^2 = 14.293, df = 1, P = 0.0002).

***Review of diet in* Cyclura.**—Based on pooled natural diet data reported for all *Cyclura* species (Tables 4 and 5), 351 food items have been recorded, including those reported in the present study for *Cyclura cychlura*. Of those, 270 items were identified to plant species, with another 15 plant items having been identified to broader categories (e.g., genus, family, or grouping such as "cactus" or "grass"). Of the consumed plant species, 31% were recorded for two or more of the *Cyclura* species. *Coccoloba uvifera* was consumed by six iguana species and five plants (*Capparis flexuosa*, *Conocarpus erectus*, *Erithalis fruticosa, Ernodea littoralis,* and *Opuntia stricta*) were consumed by five *Cyclura* species. Including the present paper and other published data, the most food items documented were 109 for *Cyclura cychlura*, 84 of which are plant material. The number of food items documented for other well studied species include: 101 for *Cyclura lewisi*, 87 of which are plants; 92 for *Cyclura carinata*, 70 of which are plants; and 82 for *Cyclura stejnegeri*, 69 of which are plants.

All *Cyclura* (other than *Cyclura ricordii* from the Dominican Republic, the known diet of which is currently limited to reports of two species of plants) have been documented as eating some type of animal matter (Tables 4 and 5). Based on pooled diet data, 59 categories of animal matter have been identified as being consumed by *Cyclura,* including mammals, reptiles, birds, fish, and invertebrates (Appendix 6). Crabs (including land, marine, and hermit crabs) were the most widely reported animal food, documented for seven of the *Cyclura* species, followed by *Cyclura* skin, which was reported for six of the iguanas. The greatest diversity of animal matter was documented for *Cyclura cychlura* (21 types), *Cyclura carinata* (18 types), *Cyclura nubila* (13 types), and *Cyclura stejnegeri* (13 types).

Half of the *Cyclura* species were also documented to consume items that were neither plant nor animal (seven categories; Appendix 5), including algae, feces, fungus, and substrate (soil, sand, or rocks as separate categories). Feces was the most widespread of these items with four species reported to have consumed some type of feces, including that of iguanas, birds, mammals, and from unidentified sources.

DISCUSSION

This study shows that the native diet of *Cyclura cychlura* in the Exumas consists of a combination of a relatively few core plants supplemented by a wider range of foods consumed infrequently. Those plants that occur in greater than 5% of the samples (based on either frequency of occurrence or proportion of total dry mass) may be considered to compose a core diet. These nine core foods were widely represented in the diet across the islands, years, and seasons. *Casasia clusiifolia* and *Conocarpus erectus* were observed in over 30% of the samples and in proportions greater than 10% of the total dry mass, representing the most consumed foods. Habitat conservation measures for these iguanas should take the availability of these nine plant species into consideration.

The present scat analysis showed that *Cyclura cychlura* in the Exumas consumed 74 food items. Of these, 61% of the items occurred in fewer than 1% of the samples. This result indicates that *Cyclura cychlura* overall has a very broad diet. The idea that rock iguanas are generalist foragers has been suggested previously, such as by Auffenberg (1982) for *Cyclura carinata*. The synthesis of the diets of all *Cyclura*, showing that 351 food items have been recorded for the group collectively, reinforces that rock iguanas in general have a very diverse diet.

Although the consumption of favored foods has occasionally been noted in the literature, the importance of a few plants as forming a core diet appears not to have been sufficiently appreciated. For *Cyclura carinata* in the Turks and Caicos, two species of plants provided leaves and five species of plants provided fruits at greater than 10% of the total volume (Auffenberg 1982). For *Cyclura stejnegeri* in Mona Island, three plant species (*Capparis flexuosa*, *Centrosema virginiana*, and *Galactia dubia*) comprised greater than a third of the leaves in samples, and were eaten in all areas throughout the year (Wiewandt 1977). For *Cyclura pinguis* in Anegada, *Croton discolor* and *Byrsonima lucida* each accounted for nearly a quarter of the diet with *Coccoloba uvifera* representing another 16% (Mitchell 1999).

Cyclura cychlura consumed a greater diversity of food components in the dry season, and for six core plants, *Cyclura cychlura* differentially consumed flowers, fruit, or leaves in the two different seasons (Appendix 4). These findings were based on analyses of seasonally pooled data across years and islands, suggesting that these differences occurred despite any potential inter-annual climatic differences. Assessments of plant availability and nutritional content of the plants and parts being consumed might clarify reasons for these apparent seasonal shifts.

Seasonal differences in diet have also been noted for other species of *Cyclura*. *Cyclura carinata* has limited fruits and flowers in its winter diet corresponding to limited seasonal availability of those items (Iverson 1979) and have been shown to shift their consumption of different species throughout the fruiting season (Auffenberg 1982). When fruits and flowers are available, *Cyclura carinata* have been documented to feed habitually at the same location until the source is exhausted (Iverson 1979). Seasonal fruits and flowers have been shown to attract *Cyclura nubila* (Gerber 2000; Perera 2000). Seasonal feeding patterns have also been documented for *Cyclura lewisi* of Grand Cayman, including higher consumption of leaves in the dry season when seasonal fruits are less available (Burton 2000, 2010). Wiewandt (1977) noted that *Cyclura stejnegeri* primarily ate leaves and flowers in the spring and early summer before small fruits were available, but that these fruits became the most prevalent items eaten once present. Hayes et al. (2004) noted a positive correlation between iguana density and plant diversity, hypothesizing that iguanas might choose to live in areas with maximal food options and that this choice may be particularly important in winter when cooler temperatures reduce digestive efficiency at a time when potential food is less abundant.

Despite their proclivity and adaptations for herbivory (Iverson 1982), the food habits of *Cyclura cychlura* in the Exumas clearly include animal matter, with nearly 7% of the samples in the present study containing some animal remnant. Based on dry mass, the dietary contribution of animal matter was 1.3%. Animal food in adult *Cyclura carinata* diets was 6.1% by frequency of occurrence and 2.8% by volume (Auffenberg 1982). The proportionally lower dietary contributions based on mass and volume speak to one of the weaknesses of relying on scat samples in that animal protein is more thoroughly digested, and therefore likely under-represented in the samples. Nonetheless, the inter-specific comparison (Appendix 5) showed that all but one rock iguana species (*Cyclura ricordii*, the diet of which has been insufficiently recorded) have been documented eating some type of animal matter. These results suggest that animal material is not an insignificant part of *Cyclura* diet.

The consumption of animal matter has often been considered to be accidental. Wiewandt (1977) qualified his observations of snails, weevils, and feathers in the scat of *Cyclura stejnegeri* as being consumed unknowingly or because they were inadvertently collected with the samples. Wiewandt (1977) also discounted an observation by his field assistant of *Cyclura stejnegeri* eating a dead Common Ground Dove (*Columbina passerina*), a species that was also discovered in *Cyclura cychlura* scat samples in the present study. Auffenberg (1982) concluded that some insects, such as a beetle common on one of the main food plants of *Cyclura carinata*, were likely eaten inadvertently. But, he also suggested that termites were likely hunted.

The array of animal matter consumed by various species of *Cyclura* (Appendix 6) seems extensive for presumably solely herbivorous animals. As early as the 1970s, Carey (1975) noted that juveniles of six different *Cyclura* species preferentially consumed insects over vegetation, and adults of three species readily accepted dog food, mice, and rats to eat. Corroborating the latter observation, my own experience with a captive *Cyclura cornuta* is that meat is not only readily accepted but often preferred over vegetation. In recent years, observations of *Cyclura* species eating animal matter in the wild have increased. There are many records of scavenged carrion from fish, birds, mammals, reptiles, and invertebrates (Appendix 6), including photographic evidence of White-winged Dove (*Zenaida asiatica*) consumption by *Cyclura lewisi* (Burton 2010). Additionally, *Cyclura* have been observed eating live birds (Hines et al. 2002; Lemm and Alberts 2012), live mammals (Luther et al. 2012), conspecific juveniles (Iverson 1979; Hayes et al. 2004; Lemm and Alberts 2012), and invertebrates (Cyril 2001; Goodman 2007; Burton 2010). Published photographs illustrate the capture of a Black Rat (*Rattus rattus*) by *Cyclura cychlura* (Luther et al. 2012) and a conspecific juvenile by *Cyclura carinata* (Lemm and Alberts 2012). These data and observations suggest that hunting may play a larger role than usually acknowledged.

A literature survey of over 450 lizard species also suggests that omnivory is more widespread than traditionally acknowledged (Cooper and Vitt 2002). While plant consumption long has been considered atypical and rare among lizards, over half of the species were documented as eating at least some plant matter (Greene 1982; Cooper and Vitt 2002). Conversely, primarily herbivorous lizards are known to readily consume animal products in captivity (Carey 1975; Cooper and Vitt 2002; pers. obs.). True herbivores among lizards, estimated at only 2% (Pough 1973), 3% (Iverson 1982), or 4.3% (Cooper and Vitt 2002) of the total lizard species, are characterized by having physiological adaptations to herbivory. The genus *Cyclura* is a classic example of such primarily herbivorous lizards based on their adaptations to eating plants, particularly (and distinctively) leaves. They have specialized dentition (Hotton 1955; Montacnucci 1968; Throckmorton 1976), enlarged colons with specialized valves (Iverson 1980, 1982) and an intestinal flora to assist with cellulose digestion (Iverson 1982; McBee and McBee 1982). Nonetheless, these iguanas do eat animal material. Findings in this study suggest that more attention to the role of animals in the diet of rock iguanas is warranted, as might additional attention to the consumption of plants by predominantly carnivorous lizards.

The broad foraging of *Cyclura* extends beyond plants and animals. In the case of *Cyclura cychlura* in the Exumas, soil, seaweed, charcoal, and rock were also consumed. It is unclear how important these might be in the diet, although some might provide energy or minerals. From my observations, iguanas actively forage with tongue-flicking while exploring the ground and plants for potential food, likely using chemosensory cues as many other lizard species do (Cooper and Vitt 2002). *Cyclura cychlura* bite at and consume some, but not all of the objects they encounter. It seems that such items as seaweed, rocks, and charcoal may be consumed purposefully. Such sampling of initially unfamiliar foods certainly preceded adoption of the unnatural foods being presented by tourists on beaches, which include fruits, vegetables, and prepared human food. Sampling behavior may also lead them to eat potentially hazardous items such as marine sponges (Iverson et al. 2011). Other material, such as soil and sand, could be picked up as it adheres to target foods, which certainly is the case on tourist beaches where the consumption of sand attached to, or near, food thrown on the beach sand may have adverse consequences (Hines 2011; see also Knapp et al. 2013). In the present study, soil occurred in 3.9% of the samples and so was not insignificant. As is the case for animal materials, the role, if any, of substrate and charcoal in the diet of *Cyclura* deserves objective attention, both as a dietary supplement and for the potential negative effect of sand consumption occurring on feeding beaches.

Feces have been recorded in the diet of four species of *Cyclura*. Coenen (1995) reported iguanas on Guana Cay in the southern Exumas feeding on bird feces, particularly those of White-crowned Pigeons (*Patagioenas leucocephala*). *Cyclura lewisi* was observed eating Central American Agouti (*Dasyprocta punctuata*) feces in the wild (Goodman 2007). *Cyclura carinata* in the Turks and Caicos and *Cyclura nubila* from Cuba have been noted eating conspecific feces (Jeff Lemm, pers. comm.). This may be a method of obtaining necessary gut microfauna (Iverson 1979, 1982), but it seems unlikely that this is essential as only two *Cyclura* species have so far been reported to eat iguana feces. I found no evidence of coprophagy for *Cyclura cychlura* in the Exumas.

The present study showed *Cyclura cychlura* in the Exumas depend on relatively few plant species for the core of their natural diet. Additionally they consume smaller amounts of a wide variety of food and non-food items. The diet varies somewhat seasonally, from wet season to dry season. Although predominantly herbivorous, animal matter is not unimportant in their diet, and may well be the result of active hunting more than is generally appreciated. Dependence on a few species of plants makes these plants critical components of suitable habitat, and potential targets for habitat enhancement if ever required. These overall conclusions appear to be generally the case for other species of *Cyclura* so far studied in depth. Our understanding of the natural diet of *Cyclura* would benefit from increased diet documentation, especially for under-studied species such as *Cyclura ricordii.* The purpose of this study was to characterize the importance of certain plants in the diet, not to address the question of how the lizards select among those plants available. Future studies of selectivity might show if differences in availability affect plant species consumption. Finally, as previously mentioned, the consumption of animal matter and substrate deserve further examination.

*Acknowledgments.—*Research permits were provided by The Bahamas Environment, Science and Technology (BEST) Commission and The Bahamas Department of Agriculture with assistance from The Bahamas National Trust. Samples were exported under Department of Agriculture Permits AGR/NAT/9 and AGR/NAT/1 in January and July 2013, respectively. I would like to thank the following for their various forms of support: Keith Bradley, Sandra Buckner, Eric Carey, Bruce Dunham, Ethan Fried, George Gann, Cynthia Guerra, Louis Harts, John Iverson, Jill Jollay, Chuck Knapp, Andrew Kriz, James Kushlan, Darcy Lesh, Predensa Moore, Mary Rose, John Sheldon, John Thompson, Sheila Young, and numerous volunteers in the field.

LITERATURE CITED

Alberts, A. (Ed.). 2000. West Indian Iguanas: Status Survey and Conservation Action Plan. IUCN SSC West Indian Iguana Specialist Group. IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Auffenberg, W. 1982. Feeding strategy of the Caicos Ground Iguana, *Cyclura carinata*. Pp. 84–116 *In* Iguanas of the World: Their Behavior, Ecology and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Beovides-Casas, K., and C.A. Mancina. 2006. Natural history and morphometry of the Cuban Iguana (*Cyclura nubila* Gray, 1831) in Cayo Sijú, Cuba. Animal Biodiversity and Conservation 29:1–8.

Burton, F. 2000. Grand Cayman Iguana (*Cyclura nubila lewisi*). Pp. 45–47 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Burton, F. 2010. The Little Blue Book: A Short History of the Grand Cayman Blue Iguana. International Reptile Conservation Foundation, San Jose, California, USA.

Burton, F. 2011. Population restoration for a critically endangered reptile – the Grand Cayman Blue Iguana (*Cyclura lewisi*). Reptiles Australasia 1:35–44.

Carey, W.M. 1975. The rock iguana, *Cyclura pinguis*, on Anegada, British Virgin Islands, with notes on *Cyclura ricordi* and *Cyclura cornuta* on Hispaniola. Bulletin of the Florida State Museum 19:189–234.

Coenen, C. 1995. Observations on the Bahamian Rock Iguana of the Exumas. Bahamas Journal of Science 2:8–14.

Cooper, W.E., Jr., and L.J. Vitt. 2002. Distribution, extent, and evolution of plant consumption by lizards. Journal of Zoology, London 257:487–517.

Correll, D.S., and H.B. Correll. 1996. Flora of the Bahama Archipelago. A.R.G. Gantner Verlag K.-G., Vaduz, Germany (reprint).

Cyril, S., Jr. 2001. Behavioral ecology of the endangered San Salvador Rock Iguana (*Cyclura rileyi rileyi*) in The Bahamas. M.Sc. Thesis, Loma Linda University, Loma Linda, California, USA. 59 p.

Gerber, G.P. 2000. Lesser Caymans Iguana (*Cyclura nubila caymanensis*). Pp. 41–43 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Gerber, G.P., T.D. Grant, and A.C. Alberts. 2002. *Cyclura nubila nubila* (Cuban Iguana). Carrion feeding. Herpetological Review 33:133–134.

González Rossell, A., V.B. Alvarez, and M.A.C. Colomé. 2001. Aspectos de morfometría, abundancia y alimentación de la Iguana Cubana (*Cyclura nubila nubila*) Archipiélago de los Canarreos, Cuba. Revista Biología 15:98–104.

Goodman, R.M. 2007. Activity patterns and foraging behavior of the endangered Grand Cayman Blue Iguana, *Cyclura lewisi*. Caribbean Journal of Science 43:73–86.

Greene, H.W. 1982. Dietary and phenotypic diversity in lizards: why are some organisms specialized. Pp. 107–128 *In* Environmental Adaptations and Evolution. Mossakowski, D., and G. Roth (Eds.). Gustav Fischer, New York, New York, USA.

Hartley, L.M., R.E. Glor, A.L. Sproston, R. Powell, and J.S. Parmer-Lee. 2000. Germination rates of seeds consumed by two species of rock iguanas (*Cyclura* spp.) in the Dominican Republic. Caribbean Journal of Science 36:149–151.

Hayes, W.K., R.L. Carter, S. Cyril, Jr., and B. Thornton. 2004. Conservation of an endangered Bahamian Rock Iguana, I. Population assessments, habitat restoration, and behavioral ecology. Pp. 232–257 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Hines, K.N. 2011. Effects of ecotourism on endangered Northern Bahamian Rock Iguanas (*Cyclura cychlura*). Herpetological Conservation and Biology 6:250–259.

Hines, K.N., J.B. Iverson, and J.M. Valiulis. 2002. *Cyclura cychlura inornata* (Allen Cays Rock Iguana): bird predation. Herpetological Review 33:306.

Hotton, N., III. 1955. A survey of adaptive relationships of dentition and diet in the North American Iguanidae. American Midland Naturalist 53:88–114.

Iguana Taxonomy Working Group (ITWG). This volume. Checklist of the iguanas of the world. Pp. 4–46. *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Iverson, J.B. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bulletin of the Florida State Museum 24:175–358.

Iverson, J.B. 1980. Colic modifications in iguanine lizards. Journal of Morphology 163:79–93.

Iverson, J.B. 1982. Adaptations to herbivory in Iguanine lizards. Pp. 60–76 *In* Iguanas of the World: Their Behavior, Ecology and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Iverson, J.B. 1985. Lizards as seed dispersers? Journal of Herpetology 19:292–293.

Iverson, J.B., K.N. Hines, and J.M. Valiulis. 2004. The nesting ecology of the Allen Cays Rock Iguana, *Cyclura cychlura inornata*, in The Bahamas. Herpetological Monographs 18:1–36.

Iverson, J.B., C.R. Knapp, K.N. Hines, S.A. Pasachnik, and L. Pieper. 2011. *Cyclura cychlura inornata* (Allen Cays Rock Iguana): mortality. Herpetological Review 42:274.

James, S.B., J. Iverson, V. Greco, and B.L. Raphael. 2006. Health assessment of Allen Cays Rock Iguana, *Cyclura cychlura inornata*. Journal of Herpetological Medicine and Surgery 16:93–100.

Knapp, C.R. 1995. A flora and fauna survey of Guana Cay, with an emphasis on its rock iguana. Bahamas Journal of Science 2:2–7.

Knapp, C.R. 2005. Ecology and conservation of the Andros Iguana (*Cyclura cychlura cychlura*). Ph.D. Dissertation, University of Florida, Gainesville, Florida, USA. 140 p.

Knapp, C.R., J.B. Iverson, and S. Buckner. 2004. *Cyclura cychlura*. The IUCN Red List of Threatened Species. Version 2014.2. Available from http://www.iucnredlist.org/details/6035/0 [Accessed on 30 August 2014].

Knapp, C.R., K.N. Hines, T.T. Zachariah, C. Perez-Heydrich, J.B. Iverson, S.D. Buckner, S.C. Halach, C.R. Lattin, and L.M. Romero. 2013. Physiological effects of tourism and associated food provisioning in an endangered iguana. Conservation Physiology 1:cot032. doi:10.1093/conphys/cot032

Lemm, J.M., and A.C. Alberts. 2012. *Cyclura*: Natural History, Husbandry, and Conservation of West Indian Rock Iguanas. Academic Press, San Diego, California, USA.

Lemm, J.M., N. Lung, and A.M. Ward. 2010. Husbandry Manual for West Indian Iguanas. International Iguana Foundation, Ft. Worth, Texas, USA. Available from http://www.iucn-isg.org/publications/general-publications

Luther, B., C.R. Knapp, D. Greene, S.D. Buckner, and J.B. Iverson. 2012. *Cyclura cychlura figginsi* (Exuma Island Iguana): rodent kill. Herpetological Review 43:483.

McBee, R.H., and V.H. McBee. 1982. The hindgut fermentation in the Green Iguana, *Iguana iguana*. Pp. 77–82 *In* Iguanas of the World: Their Behavior, Ecology and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Mitchell, N.C. 1999. Effect of introduced ungulates on density, dietary preferences, home range, and physical condition of the iguana (*Cyclura pinguis*) on Anegada. Herpetologica 55:7–17.

Mitchell, N. 2000. Anegada Island Iguana (*Cyclura pinguis*). Pp. 47-49 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Montanucci, R.R. 1968. Comparative dentition in four iguanid lizards. Herpetologica 24:305–315.

Perera, A. 1985. Datos sobre la dieta de *Cyclura nubila* (Sauria: Iguanidae) en los alrededores de Cayo Largo del Sur, Cuba. Poeyana 291:1–12.

Perera, A. 2000. Cuban Iguana (*Cyclura nubila nubila*). Pp. 36–37 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Pough, F.H. 1973. Lizard energetics and diet. Ecology 54:837–844.

Schwartz, A., and R.W. Henderson. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. University of Florida Press, Gainesville, Florida, USA.

Sealey, N.E. 2006. Bahamian Landscapes. 3rd Edition. Macmillan Publishers, Oxford, United Kingdom.

Throckmorton, G.S. 1976. Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and *Uromastyx aegyptius* (Agamidae). Journal of Morphology 148:363–390.

Vogel, P. 2000. Jamaican Iguana (*Cyclura collei*). Pp. 19–22 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Wiewandt, T.A. 1977. Ecology, behavior, and management of the Mona Island Ground Iguana, *Cyclura stejnegeri*. Ph.D. Dissertation, Cornell University, Ithaca, New York, USA. 353 p.

Wiewandt, T., and M. García. 2000. Mona Island Iguana (*Cyclura cornuta stejnegeri*). Pp. 27–31 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts. A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

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Appendix 1. Number of *Cyclura cychlura* scat samples from the Exuma Islands of The Bahamas analyzed for frequency of occurrence and biomass (in parentheses).

Island[1]	**2006**[2]	**2007**[3]	**2008**[2]	**2009**[3]	**2010**[2]	**2013**[4]
Alln	1	1				
Allg		29				
Bgc						11 (11)
Frrc	18 (2)	15	7 (5)	18 (5)	20 (4)	2 (2)
Glnc					8	4 (4)
Gunc	1					
Hhc						2 (2)
Lcal	10	3	10	9 (2)	19	5 (5)
Lnpc	6		1 (1)			8 (8)
Nwc		4				3 (3)
Nddc	7 (6)		1 (1)	19 (12)	21 (1)	1 (1)
Nadc	6 (1)			15 (8)	17 (1)	
Pasc	11 (3)					
Swal	3 (3)		9 (1)	14	16 (1)	
Wbc	16 (4)		14 (10)	10 (5)	10 (1)	
Totals	**79 (19)**	**52**	**42 (18)**	**85 (32)**	**111 (8)**	**36 (36)**

[1] Islands names are coded for conservation purposes. [2] Samples from both dry and wet seasons. Values represent total number of samples across seasons. [3] Samples from wet season. [4] Samples from dry season.

Appendix 2. Frequency of occurrence, listed in descending order, of items found within 405 scat samples of *Cyclura cychlura* from the Exuma Islands of The Bahamas, across 15 sampled islands and in six sampling years (2006 to 2013).

Food Item	**Scientific Name**	**Frequency of Occurrence (%)**	**Island Occurrence (%)**	**Year Occurrence (%)**
Plants				
Seven-year Apple	*Casasia clusiifolia*	39.28	100.00	100.00
Buttonwood	*Conocarpus erectus*	31.33	80.00	100.00
Sandfly-bush	*Rhachicallis americana*	28.43	73.33	100.00
Wild Dilly	*Manilkara bahamensis*	27.47	60.00	100.00
Lignum Vitae	*Guaiacum sanctum*	11.08	60.00	83.33
Bay Cedar	*Suriana maritima*	10.36	73.33	100.00
Joe-wood	*Jacquinia keyensis*	7.23	73.33	100.00
Coast Sophora	*Sophora tomentosa*	4.10	40.00	66.67
Pigeon-plum	*Coccoloba diversifolia*	3.61	40.00	66.67
Darling Plum	*Reynosia septentrionalis*	3.37	53.33	83.33
Silver Thatch	*Coccothrinax argentata*	3.37	53.33	50.00
Ram's-horn	*Pithecellobium keyense*	3.37	53.33	100.00
Wild Saffron	*Bumelia americana*	2.89	46.67	83.33
Common Ernodea	*Ernodea littoralis*	2.65	33.33	66.67
	Strumpfia maritima	2.65	33.33	83.33
Wild Tamarind	*Lysiloma latisiliquum*	2.41	20.00	50.00
Black Torch	*Erithalis fruticosa*	2.17	33.33	50.00
Turtle-grass	*Thalassia testudinum*	1.93	26.67	83.33
Buffalo-top	*Thrinax morrisii*	1.93	33.33	33.33
Common Prickly Pear	*Opuntia stricta*	1.69	20.00	50.00
Sea Ox-eye	*Borrichia arborescens*	1.45	13.33	50.00
Narrow-leaved Blolly	*Guapira discolor*	1.45	33.33	83.33
Sea Oats	*Uniola paniculata*	0.96	13.33	33.33
Crabwood	*Ateramnus lucidus*	0.96	13.33	33.33
	Sesuvium portulacastrum	0.96	20.00	33.33
Slender Paspalum	*Paspalum caespitosum*	0.72	6.67	16.67
Sea Grape	*Coccoloba uvifera*	0.72	13.33	33.33
	Catesbaea parviflora	0.72	20.00	33.33
Seashore Rush-grass	*Sporobolus virginicus*	0.72	13.33	33.33

APPENDIX 2. CONTINUED

Food Item	Scientific Name	Frequency of Occurrence (%)	Island Occurrence (%)	Year Occurrence (%)
White Stopper	*Eugenia axillaris*	0.72	20.00	50.00
	Ziziphus taylori	0.72	20.00	33.33
Caper-tree	*Capparis flexuosa*	0.72	6.67	16.67
Strong-back	*Bourreria ovata*	0.72	20.00	16.67
Bushy Salmea	*Salmea petrobiodes*	0.48	13.33	33.33
Bastard Torch	*Nectandra coriacea*	0.48	13.33	33.33
Bahama Stopper	*Psidium longipes*	0.48	13.33	16.67
Smooth Passion-flower	*Passiflora cupraea*	0.48	6.67	16.67
Whitewood	*Drypetes divserifolia*	0.24	6.67	16.67
Bay Lavender	*Mallotonia gnaphalodes*	0.24	6.67	16.67
Buccaneer Palm	*Pseudophoenix sargentii*	0.24	6.67	16.67
Coast Spurge	*Euphorbia mesemrianthemifolia*	0.24	6.67	16.67
Coco Plum	*Chrysobalanus icaco*	0.24	6.67	16.67
Morning Glory	*Ipomea indica*	0.24	6.67	16.67
Spanish Stopper	*Eugenia foetida*	0.24	6.67	16.67
	Paspalum sp.	0.24	6.67	16.67
	Jacquemontia havanensis	0.24	6.67	16.67
Locust-berry	*Byrsonima lucida*	0.24	6.67	16.67
Sword-bush	*Phyllanthus epiphyllanthus*	0.24	6.67	16.67
Goosegrass	*Eleusine indica*	0.24	6.67	16.67
Sampire	*Caraxeron vermicularis*	0.24	6.67	16.67
Wild Coffee	*Psychotria nervosa*	0.24	6.67	16.67
Canker-berry	*Solanum bahamense*	0.24	6.67	16.67
Cinnecord	*Acacia choriophylla*	0.24	6.67	16.67
Granny-bush	*Croton linearis*	0.24	6.67	16.67
Unidentified Plant Fragments		5.54	66.67	50.00
Bark		1.45	20.00	66.67
Twig		1.45	33.33	66.67
Animals				
Iguana Skin	*Cyclura cychlura*	2.17	40.00	66.67
Bird Feathers & Wing		1.45	20.00	50.00
Gray Peanut Snail	*Cerion incanum*	1.45	33.33	66.67
Beetle	Coleoptera	0.72	13.33	33.33
True Bug	Hemiptera	0.72	20.00	50.00
Ghost Crab	*Oxypode quadrata*	0.48	13.33	33.33
Hermit Crab	*Coenobita clypeatus*	0.48	13.33	16.67
Fly maggots	Brachycera	0.48	13.33	33.33
House Fly	*Musca domestica*	0.24	6.67	16.67
Tick	*Amblyomma torrei*	0.24	6.67	16.67
Worm	Oligochaeta	0.24	6.67	16.67
Snail		0.24	6.67	16.67
Other				
Organic Soil		3.86	53.33	66.67
Sargassum Weed	*Sargassum* sp.	0.48	13.33	33.33
Balloon Seaweed	*Colpomenia* sp.	0.24	6.67	16.67
Charcoal		0.24	6.67	16.67
Rock		0.24	6.67	16.67

Appendix 3. Food items from *Cyclura cychlura* scat samples (n = 113) from the Exumas, listed in descending order (except for unidentified plant matter) of percentage contribution to dry mass. See Appendix 2 for corresponding common names.

Food Item	**Percent of Total Mass (%)**	**Food Item**	**Percent of Total Mass (%)**
Plants		**Animals**	
Conocarpus erectus	17.07	Bird	0.55
Casasia clusiifolia	14.79	*Cyclura cychlura* Skin	0.48
Manilkara bahamensis	8.46	Crab	0.31
Coccothrinax argentata	7.78	Snail	<0.01
Rhachicallis americana	6.97		
Erithalis fruticosa	5.99	**Other**	
Jacquinia keyensis	5.03	Organic Soil	2.77
Guaiacum sanctum	2.77	Rock	<0.01
Capparis flexuosa	2.66		
Suriana maritima	2.29		
Thrinax morrisii	2.25		
Coccoloba diversifolia	1.92		
Sophora tomentosa	1.81		
Passiflora cupraea	1.35		
Strumpfia maritima	1.15		
Ziziphus taylori	0.94		
Ateramnus lucidus	0.90		
Psidium longipes	0.90		
Nectandra coriacea	0.89		
Pithecellobium keyense	0.89		
Coccoloba uvifera	0.83		
Reynosia septentrionalis	0.56		
Bourreria ovata	0.47		
Sesuvium portulacastrum	0.46		
Uniola paniculata	0.30		
Opuntia stricta	0.28		
Bumelia americana	0.17		
Jacquemontia havanensis	0.16		
Guapira discolor	0.12		
Chrysobalanus icaco	0.08		
Ernodea littoralis	0.07		
Lysiloma latisiliquum	0.07		
Drypetes divserifolia	0.06		
Phyllanthus epiphyllanthus	0.05		
Byrsonima lucida	0.05		
Paspalum caespitosum	0.03		
Thalassia testudinum	0.03		
Borrichia arborescens	0.02		
Euphorbia mesemrianthemifolia	0.02		
Eugenia axillaris	0.02		
Psychotria nervosa	0.01		
Catesbaea parviflora	0.01		
Paspalum sp.	0.01		
Solanum bahamense	<0.01		
Sporobolus virginicus	<0.01		
Acacia choriophylla	<0.01		
Caraxeron vermicularis	<0.01		
Croton linearis	<0.01		
Eleusine indica	<0.01		
Unidentified Plant Fragments	5.12		
Bark	0.05		
Twig	0.02		

APPENDIX 4. Seasonal differences in plant parts for nine primary food species consumed in dry season versus wet season by *Cyclura cychlura* in the Exuma Islands of The Bahamas. NS = not significant.

Plant	Food Item	Dry Season (n = 174) Frequency of Occurrence (%)	Wet Season (n = 201) Frequency of Occurrence (%)	χ^2 -value	Corrected P-value
Casasia clusiifolia	flowers	0.00	1.00	1.730	NS
	fruit	50.00	22.89	19.333	0.0021
	leaves	24.14	2.99	32.602	0.002
Suriana maritima	flowers	0.57	1.49	0.730	NS
	fruit	2.87	2.99	0.004	NS
	leaves	9.77	7.96	0.347	NS
Erithalis fruticosa	flowers	0.57	0	1.155	NS
	leaves	3.45	1.49	1.486	NS
Conocarpus erectus	flowers	0.00	2.99	5.194	NS
	fruit	5.17	17.41	11.909	0.0102
	leaves	23.56	30.35	1.579	NS
Jacquinia keyensis	fruit	6.90	6.47	0.026	NS
	leaves	5.17	0	10.397	0.0195
Guaiacum sanctum	leaves	23.56	2.99	10.397	0.0019
Rhachicallis americana	flowers	0	4.48	7.791	NS
	leaves	27.01	32.34	0.886	NS
Coccothrinax argentata	fiber	1.15	0	35.283	NS
	fruit	8.05	0	16.172	0.0018
Manilkara bahamensis	flowers	1.15	23.38	35.283	0.016
	fruit	15.52	19.40	0.800	NS
	leaves	3.45	10.45	6.346	NS

APPENDIX 5. Comparison of the natural diets of the ten extant species of the genus *Cyclura*, showing dietary components as recorded in the literature. Number annotation indicate sources; plant names are those used by the authors.

Food Items	***carinata*** 5, 9, 10	***collei*** 5, 10, 16, 28	***cornuta*** 10, 12, 26	***cychlura*** 4, 9, 21, 22, 23, 24, 25, 30	***lewisi*** 3, 5, 19, 27, 28, 29	***nubila*** 2, 8, 10, 11, 14, 15, 18	***pinguis*** 1, 5, 10, 15, 20	***ricordii*** 10, 12	***rileyi*** 5, 7, 13	***stejnegeri*** 6, 10, 17, 28
Plants										
Acacia acuifera	X									
Acacia anegadensis							X			
Acacia choriophylla				X						
Acalypha alcopercuroidea					X					
Alysicarpus vaginalis					X					
Ambrosia hispida	X					X				
Amyris elemifera	X									X
Andropogon glomeratus	X									
Andropogon bicornis						X				
Angadenia sagraei				X						
Amaranthus sp.					X					
Annona glabra				X						
Antirhea acutata										X
Antirhea myrtifolia	X			X						
Argusia gnaphalodes				X						
Argythamnia argentata	X									
Argythamnia candicans										X
Argythamnia seriacea	X									
Asystasia gangetica					X					
Auerodendron northropianum				X						
Avicennia germinans				X		X				
Ayenia pusilla										X

APPENDIX 5. CONTINUED

Food Items	***carinata*** *5, 9, 10*	***collei*** *5, 10, 16, 28*	***cornuta*** *10, 12, 26*	***cychlura*** *4, 9, 21, 22, 23, 24, 25, 30*	***lewisi*** *3, 5, 19, 27, 28, 29*	***nubila*** *2, 8, 10, 11, 14, 15, 18*	***pinguis*** *1, 5, 10, 15, 20*	***ricordii*** *10, 12*	***rileyi*** *5, 7, 13*	***stejnegeri*** *6, 10, 17, 28*
Batis maritima						X	X			
Bauhinia divaricata		X				X				
Bidens alba					X					
Blechum brownei					X					
Blutaparon vermiculare				X	X					
Boerhaavia diffusa										X
Boerhaavia erecta					X					X
Borrichia arborescens				X					X	
Bourreria ovata	X			X						
Bourreria succulenta							X			X
Bucida buceras	X									
Bumelia americana	X			X						
Bumelia salicifolia				X						
Bunchosia media		X								
Bursera simaruba				X						
Byrsonima cuneata	X									
Byrsonima lucida				X			X			
Caesalpinea divergens										X
Callisia repens										X
Calyptranthes paliens	X									
Canavalia maritima						X				
Canavalia rosea						X				
Canella winterana					X					
Capparis cynophallophora						X				X
Capparis ferruginea		X			X					
Capparis flexuosa				X	X	X	X			X
Capraria biflora					X					X
Casasia clusiifolia	X			X						
Cassia biflora	X									
Cassia lineata	X									
Cassine xylocarpa							X			
Cassytha filiformis				X						
Catesbaea foliosa	X									
Catesbaea parviflora				X						
Cattleyopsis lindenii				X						
Centrosema virginiana										X
Chamaecrista nictitans					X					
Chamaecyce opthalmica					X					
Chamaescyce buxifolia	X									
Chamaescyce camagueyensis						X				
Chamaescyce hirta					X					
Chamaescyce hypericifolia					X					
Chamaescyce mesembrianthemifolia					X					
Chamaescyce prostrata					X					X
Chamaescyce veginulata	X									
Chiococca alba					X					
Chiococca parvifolia				X						
Chionanthus caymanensis					X					
Chloris petraea	X									
Chrysobalanus icaco				X		X				
Cissus caustica										X
Cissus trifoliata					X					

APPENDIX 5. CONTINUED

Food Items	***carinata*** *5, 9, 10*	***collei*** *5, 10, 16, 28*	***cornuta*** *10, 12, 26*	***cychlura*** *4, 9, 21, 22, 23, 24, 25, 30*	***lewisi*** *3, 5, 19, 27, 28, 29*	***nubila*** *2, 8, 10, 11, 14, 15, 18*	***pinguis*** *1, 5, 10, 15, 20*	***ricordii*** *10, 12*	***rileyi*** *5, 7, 13*	***stejnegeri*** *6, 10, 17, 28*
Citharexylum fruticosum						X				
Clitoria ternatea					X					
Coccoloba sp.							X			
Coccoloba diversifolia				X						X
Coccoloba krugii	X						X			
Coccoloba microstachya										X
Coccoloba uvifera	X			X		X	X		X	X
Coccothrinax argentata				X						
Coccothrinax inaguensis	X									
Coccothrinax proctorii					X					
Commelina virginica										X
Comocladia veluntina		X								
Conocarpus erectus	X			X		X	X		X	
Corchorus aestuans					X					
Corchorus hirsutus					X					X
Corchorus siliquosus					X					
Cordia bahamensis	X									
Cordia caymanensis					X	X				
Cordia rupicola							X			
Cordia sebestena					X	X				
Crossopetalum rhacoma	X						X			X
Croton betulinus										X
Croton discolor							X			X
Croton humilis										X
Croton linearis	X			X						
Cuscuta americana	X									
Cynanchium lineare										X
Cynanchium monensis										X
Cynanchum eggersii	X									
Cyperus fuligineus	X									
Cyperus gigantus						X				
Dalechampia scandens				X						
Desmodium mollis										X
Desmodium incanum					X					
Digitaria filiformis	X									
Dodonaea viscosa							X			
Drypetes diversifolia				X						
Echites umbellata				X						
Elaeodendron xylocarpum							X			
Eleusine indica				X						
Eragrostis salzmani						X				
Erithalis fruticosa	X			X		X	X			X
Ernodea littoralis	X			X	X	X	X			
Ernodia millspaughii	X									
Erythroxylon areolatum					X					X
Erythroxylum rotundifolium					X					
Eugenia axillaris				X	X		X			
Eugenia foetida	X			X						
Eupatorium corymbosum										X
Eupatorium odoratum					X					
Euphorbia blodgettii				X						
Euphorbia mesembrianthemifoliea	X			X						
Euphorbia petiolaris										X

Appendix 5. Continued

Food Items	***carinata*** *5, 9, 10*	***collei*** *5, 10, 16, 28*	***cornuta*** *10, 12, 26*	***cychlura*** *4, 9, 21, 22, 23, 24, 25, 30*	***lewisi*** *3, 5, 19, 27, 28, 29*	***nubila*** *2, 8, 10, 11, 14, 15, 18*	***pinguis*** *1, 5, 10, 15, 20*	***ricordii*** *10, 12*	***rileyi*** *5, 7, 13*	***stejnegeri*** *6, 10, 17, 28*
Evolvulus sp.	X									
Evolvulus squamosus	X									
Exostema caribacum				X						
Ficus aurea					X					
Ficus citrifolia										X
Ficus crassinvervia										X
Fimbristilis spatacea						X				
Galactia dubia										X
Gayoides crispum										X
Guaiacum sanctum	X			X						
Guapira discolor	X			X	X	X				
Guapira obtusata	X									
Guettarda krugii	X									
Gundlachia corymbosa	X									
Gramineae				X						
Gunlachia corymbosa				X						
Gyminda latifolia										X
Gymnanthes lucida				X						
Hamelia cuprea					X					
Harrisia portoricensis										X
Hibiscus esculentus					X					
Hibiscus tilaceus		X								
Hippomane mancinella			X		X	X				X
Hylocereus triangularis		X								
Hypelate trifoliata	X				X					X
Ipomea indica				X	X					
Ipomoea pes-caprae	X				X	X				
Ipomoea trilobata					X					X
Ipomoea violacea					X	X				
Indigophora suffruticosa										X
Jacquemontia pentantha										X
Jacquemontia havanensis				X						
Jacquinia arborea							X			X
Jacquinia keyensis	X			X						
Jatropha multifida										X
Krugiodendron ferreum										X
Laguncularia racemosa						X				
Lantana bahamensis					X					
Lantana involucrata		X			X	X	X			X
Lantana reticulata							X			
Lasiacis divaricata		X			X					
Leucaena leucocephala				X						
Lysiloma latisiliquum				X						
Manilkara bahamensis	X			X						
Manilkara zapota				X						
Maytenus buxifolia	X									
Melocactus intortus	X						X			
Metopium brownii		X								
Metopium toxiferum	X			X		X				X
Momordica charantia					X					
Morinda citrifolia					X					
Morinda royoc		X			X					
Myrcianthes fragrans				X	X	X				
Nectandra coriacea				X						

APPENDIX 5. CONTINUED

Food Items	***carinata*** *5, 9, 10*	***collei*** *5, 10, 16, 28*	***cornuta*** *10, 12, 26*	***cychlura*** *4, 9, 21, 22, 23, 24, 25, 30*	***lewisi*** *3, 5, 19, 27, 28, 29*	***nubila*** *2, 8, 10, 11, 14, 15, 18*	***pinguis*** *1, 5, 10, 15, 20*	***ricordii*** *10, 12*	***rileyi*** *5, 7, 13*	***stejnegeri*** *6, 10, 17, 28*
Opuntia sp.			X		X	X	X			
Opuntia spinosissima		X								
Opuntia stricta	X			X		X			X	X
Panicum maximum										X
Paspalum sp.				X						
Paspalum caespitosum				X						X
Paspalum glabrum										X
Paspalum laxum	X									
Passiflora bahamensis				X						
Passiflora cupraea				X	X					
Passiflora pectinata	X									
Petiveria sp.		X								
Phyla nodiflora					X					
Phyllanthus amarus					X					
Phyllanthus epiphyllanthus	X			X						
Picrodendron baccatum					X	X				
Pisonia albida										X
Pisonia rotundata							X			
Pisonia subcordata							X			
Pithecellobium guadelupense	X					X				
Pithecellobium keyense	X			X						
Pithecellobium unguis-cati	X						X			
Plumeria obtusa	X									X
Portulaca oleracea					X		X			
Portulaca sp.										X
Pseudophoenix sargentii				X						
Psidium longipes	X			X						
Priva lappulacea					X					
Psychotria ligustrifolia				X						
Psychotria nervosa				X	X					
Rauwolfia tetraphylla										X
Randia aculeata	X			X	X					
Reynosia septentrionalis	X			X			X			
Reynosia uncinata							X			X
Rhachicallis americana	X			X		X			X	
Rhizophora mangle	X			X		X			X	
Rhynchosia minima					X					
Rivina humilis					X		X			X
Ruellia tuberosa					X					
Salmea petrobiodes				X						
Sarcomphalus taylori										X
Sarcostemma clausum					X					
Savia bahamensis				X						
Scaevola plumerieri	X									
Scaevola seriacea					X					
Schaefferia frutescens										X
Scleria lithosperma					X					
Selenicerus grandiflorus						X				
Sesuvium portulacastrum				X	X	X			X	
Sida acuminata										X
Sida glabra										X
Sida glutinosa					X					

APPENDIX 5. CONTINUED

Food Items	***carinata*** *5, 9, 10*	***collei*** *5, 10, 16, 28*	***cornuta*** *10, 12, 26*	***cychlura*** *4, 9, 21, 22, 23, 24, 25, 30*	***lewisi*** *3, 5, 19, 27, 28, 29*	***nubila*** *2, 8, 10, 11, 14, 15, 18*	***pinguis*** *1, 5, 10, 15, 20*	***ricordii*** *10, 12*	***rileyi*** *5, 7, 13*	***stejnegeri*** *6, 10, 17, 28*
Sida stipularis					X					
Smilax auriculata				X						
Solanum bahamense				X						
Solanum persicifolium							X			
Solanum racemosum							X			
Sophora tomentosa				X						
Sorghum halepense						X				
Spermacoce assurgens					X					
Spermacoce confusa					X					
Spigelia anthelmia					X					
Spilanthes urens					X					
Sporobolus dominguensis						X				
Sporobolus virginicus				X		X	X			
Stachytarpheta jamaicensis					X					X
Strumpfia maritima	X			X		X	X			
Stigmaphyllon periplocifolium										X
Stylosanthes hamata				X	X	X	X			X
Suriana maritima				X		X				
Swietenia mahagoni				X						
Tabebuia bahamensis	X			X						
Tabebuia heterophylla					X	X	X			X
Tabebuia riparia		X								
Tecoma stans					X					
Tephrosia cinerea										X
Teramnus labialis					X					
Tetramirca canalicula							X			
Thalasia testudinum				X		X				
Thrinax microcarpa	X									
Thrinax morrisii				X						
Thrinax parviflora						X				
Thrinax radiata						X				
Thyralis sp.	X									
Tillandsia utriculata							X			
Torrubia discolor										X
Tournefortia microphylla										X
Tournefortia volubilis	X									
Tribulus cistoides										X
Tridax procumbens					X					
Turnerna ulmifolia					X					
Uniola paniculata				X						
Vernonia divaricata					X					
Vigna luteola					X					
Waltheria indica					X					
Zanthoxylum flavum	X									
Ziziphus rignonii			X				X	X		
Ziziphus taylori	X			X						
Unidentified Cactus			X				X	X		
Unidentified Grass					X		X			
Unidentified Flowers					X					
Unidentified Fruits, Nuts					X					
Unidentified Leaves, Stems				X	X					
Unidentified Twigs, Bark				X						

Appendix 5. Continued

Food Items	***carinata*** *5, 9, 10*	***collei*** *5, 10, 16, 28*	***cornuta*** *10, 12, 26*	***cychlura*** *4, 9, 21, 22, 23, 24, 25, 30*	***lewisi*** *3, 5, 19, 27, 28, 29*	***nubila*** *2, 8, 10, 11, 14, 15, 18*	***pinguis*** *1, 5, 10, 15, 20*	***ricordii*** *10, 12*	***rileyi*** *5, 7, 13*	***stejnegeri*** *6, 10, 17, 28*
Animals										
Annelida				X						
Arthropoda	X		X	X	X	X	X		X	X
Aves	X			X	X	X			X	X
Mammalia				X		X				
Mollusca	X	X		X	X	X				X
Pisces	X									
Porifera				X						
Reptilia	X			X	X	X	X		X	X
Unspecified Invertebrates							X			
Other										
Algae				X						
Feces	X			X	X	X				
Fungus	X				X					
Rock				X	X				X	
Sand	X								X	
Soil	X			X	X				X	
Unidentified					X					

(1) Mitchell 1999; (2) Beovides-Casas and Mancina 2006; (3) Goodman 2007; (4) Knapp 2005; (5) Lemm et al. 2010; (6) Wiewandt 1977; (7) Cyril 2001; (8) Gerber et al. 2002; (9) Auffenberg 1982; (10) Iverson 1979; (11) González Rossell et al. 2001; (12) Hartley at al. 2000; (13) Hayes et al. 2004; (14) Perera 1985; (15) Lemm and Alberts 2012; (16) Vogel 2000; (17) Wiewandt and Garcia 2000; (18) Gerber 2000; (19) Burton 2000; (20) Mitchell 2000; (21) Coenen 1995; (22) Knapp 1995; (23) Hines et al. 2002; (24) Iverson et al. 2011; (25) Luther et al. 2012; (26) Schwartz and Henderson 1991; (27) Burton 2010; (28) Carey 1975; (29) Burton 2011; (30) This study.

Appendix 6. Detailed comparison of animal material in the natural diets of the 10 extant species of the genus *Cyclura*, except *Cyclura ricordii* that has no records of animal consumption. Items are checked for the most specific category possible. See Appendix 5 for associated citations.

Food Items	***carinata***	***collei***	***cornuta***	***cychlura***	***lewisi***	***nubila***	***pinguis***	***rileyi***	***stejnegeri***
ANNELIDA									
Oligochaeta (earthworm)				X					
ARTHROPODA									
Arachnida									
Amblyomma torrei (tick)				X					
Solpugidae	X								
Chilopoda (centipede)							X		
Insecta									
Ascia monuste (Great So. White Butterfly)									X
Blattodea (cockroach)							X		
Blattodea (termite)	X			X					
Coleoptera (beetle)	X			X		X	X		
Curculionidae (weevil)	X								X
Diptera (maggot)				X					
Diptera (fly larvae)	X								
Insecta (unspecified insects)				X			X	X	X
Lepidoptera (bee)							X		
Lepidoptera (caterpillar)							X		X
Lepidoptera (honeybee)	X								
Musca domestica (House Fly)				X					

APPENDIX 6. Detailed comparison of animal material in the natural diets of the 10 extant species of the genus *Cyclura*, except *Cyclura ricordii* that has no records of animal consumption. Items are checked for the most specific category possible. See Appendix 5 for associated citations.

Food Items	***carinata***	***collei***	***cornuta***	***cychlura***	***lewisi***	***nubila***	***pinguis***	***rileyi***	***stejnegeri***
Nasutitermes costatus (termite)	X								
Odonata	X								
Ollanta sp. (cicada)	X				X				
Orthoptera (grasshopper)								X	
Pseudosphinx sp.									X
Pseudosphinx tetrio (Tetrio Sphinx Moth)			X		X				X
Scarabaeidae									X
Strategus sarpedon						X			
Malacostraca									
Cardisoma guanahumi (Blue Land Crab)	X					X		X	
Clibanarius sp. (hermit crab)	X							X	
Coenobita clypeatus (Caribbean Hermit Crab)				X					
Decapoda (unspecified crab)	X		X	X	X	X	X		X
Gecarcinus lateralis (Red Land Crab)									X
Gecarcinus ruricola (Black Land Crab)					X				
Ocypode quadrata (Atlantic Ghost Crab)				X					
CHORDATA									
Aves									
Bird Carrion	X			X				X	
Bird Live				X		X			
Columbidae (dove)					X	X			
Columbina passerina (Common Ground Dove)				X					
Feathers	X			X					X
Porphyrula martinica (Purple Gallinule)								X	
Puffinus lherminieri (Audubon's Shearwater)				X					
Sterna anaethetus (Bridled Tern)								X	
Tiaris canora (Cuban Grassquit)						X			
Zenaida asiatica (White-winged Dove)					X	X			
Zenaida macroura (Mourning Dove)						X			
Mammalia									
Capromys pilorides (Hutia)						X			
Rattus rattus (Black Rat)				X					
Pisces									
Fish Carrion	X								
Reptilia									
Alsophis cantherigerus Skin (Cuban Racer)						X			
Cyclura Juvenile (conspecific)	X							X	
Cyclura Skin (conspecific)	X			X	X	X	X		X
MOLLUSCA									
Cerion incanum (Gray Peanut Snail)				X					
Drymaeus elongatus (tree snail)									X
Gastropoda (slug)	X								
Gastropoda (snail)		X		X					
Melampus coffeus (Coffee Bean Snail)						X			
Veronicella sp. (slug)					X				
PORIFERA									
Marine Sponge				X					

Herpetological Conservation and Biology 11(Monograph 6):139–153.
Submitted: 10 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

GROWTH, COLORATION, AND DEMOGRAPHY OF AN INTRODUCED POPULATION OF THE ACKLINS ROCK IGUANA (*CYCLURA RILEYI NUCHALIS*) IN THE EXUMA ISLANDS, THE BAHAMAS

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***Abstract*.—In 1973, five Acklins Rock Iguanas (*Cyclura rileyi nuchalis*) from Fish Cay in the Acklins Islands, The Bahamas, were translocated to Bush Hill Cay in the northern Exuma Islands. That population has flourished, despite the presence of invasive rats, and numbered > 300 individuals by the mid-1990s. We conducted a mark-recapture study of this population from May 2002 through May 2013 to quantify growth, demography, and plasticity in coloration. The iguanas from Bush Hill Cay were shown to reach larger sizes than the source population. Males were larger than females, and mature sizes were reached in approximately four years. Although the sex ratio was balanced in the mid-1990s, it was heavily female-biased throughout our study. Juveniles were rare, presumably due to predation by rats and possibly cannibalism. The estimated population size declined by > 60% over the course of our study. The causes could not be precisely identified, but predation by and competition with rats, and possibly poaching, were likely responsible. We strongly recommend the eradication of rats to prevent further loss of iguanas. Iguanas from Bush Hill Cay are polymorphic in color, with adults exhibiting two major color transition patterns: a yellow body color with minimal mottling (10–15% of individuals), and a brown or orange background with gray or blue-gray mottling that variably fades in some individuals. Even though there is evidence that this was a successful translocation, recent declines in the estimated population size suggest that the future of this population is uncertain and will require continued monitoring.**

Key Words.—color polymorphism; conservation; density; introduction; rats; sex ratio; translocation

INTRODUCTION

The translocation of individuals of threatened or endangered species to new areas or to previously occupied areas has been a controversial conservation strategy (e.g., McCoy and Berry 2008; Seddon 2010; Perez et al. 2012). Some reviews suggest that translocations and reintroductions of amphibians and reptiles are generally not successful (e.g., Dodd and Seigel 1991); however, others suggest that this is not always the case or that generalizations across taxa are not useful (e.g., Burke 1991). Indeed, a more recent review of amphibian and reptile translocations has found an increase in success rates for such translocations in more recent years (Germano and Bishop 2009).

Despite the many differences of opinion and given the increasing anthropogenic impacts on the natural world, translocations of organisms will, by necessity, become a much more frequent conservation management strategy. The International Union for Conservation of Nature (IUCN) first developed rudimentary international guidelines in 1998, and then in 2013 published their formal guidelines for reintroductions and translocations (IUCN 2013). Setting aside these controversies, it remains that many translocations (both authorized and unauthorized) have been done, and hence assessing the success and value of these actions is of great conservation importance, falling on the shoulders of field biologists.

Multiple translocations or reintroductions have been conducted with populations of Rock Iguanas (genus *Cyclura*) as they often have narrow and threatened ranges (e.g., Knapp and Hudson 2004). In some cases, the reintroduction of headstarted juveniles has been attempted, with good evidence of success (e.g., *C. collei*: Wilson et al. 2004, Wilson 2011; *C. lewisi*: Echternacht et al. 2011; *C. nubila*: Alberts et al. 1998, 2004; *C. pinguis*: Gerber 2004, Bradley and Gerber 2005, Perry and Gerber 2011; see also reviews in Alberts and Phillips 2004, Alberts 2007). In addition, translocations of "colonies" of Rock Iguanas to previously unoccupied areas or islands have occurred, either as part of a

Iverson, John B., Geoffrey R. Smith, Stesha A. Pasachnik, Kirsten N. Hines, and Lynne Pieper. 2016. Growth, coloration, and demography of an introduced population of the Acklins Rock Iguana (*Cyclura rileyi nuchalis*) in the Exuma Islands, The Bahamas. Pp. 139–153 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

conservation program or as an independent act of private citizens or unknown persons (Table 1). In many of these cases, it appears that successful, self-maintaining populations of *Cyclura* have been created (Table 1), as Rock Iguanas appear to have life history traits that facilitate successful translocation (Knapp and Hudson 2004), such as density-dependent individual (Knapp 2001) and population growth (Iverson et al. 2006).

However, in several cases, little about the ecology and natural history of these translocated populations is known, particularly as they relate to the natural source population. Understanding these details is vital to the persistence of the population, if not the species as a whole. For the best studied translocated iguana population to date, Knapp has examined the demography and spatial ecology of the translocated population of *Cyclura cychlura inornata* on Alligator Cay, The Bahamas (Knapp 2000, 2001; Knapp and Malone 2003). In addition, Goodman et al. (2005a, b) have examined habitat use and spatial ecology in captive-bred *C. lewisi* released in a botanical park on Grand Cayman as part of a reintroduction program (see also Burton and Rivera-Milán 2014).

Here we examine the growth, color patterns, and demography of an introduced population of the endangered Acklins Rock Iguana, *Cyclura rileyi nuchalis* in The Bahamas. Hayes et al. (2004a) reported that five individual *Cyclura rileyi nuchalis* were introduced to Bush Hill Cay within the Exuma Cays Land and Sea Park from Fish Cay in the Acklins Islands (~ 350 km SE of Bush Hill Cay) in 1973 (see also Hayes and Montanucci 2000). Very little is known about the ecology and natural history of this species and subspecies in its native range (but see Hayes and Montanucci 2000; Carter and Hayes 2004; Hayes et al. 2004a). Nevertheless, the population on Bush Hill Cay has flourished and now inhabits nearly every square meter of the island. Unfortunately, the island also supports a large population of rats (Hayes et al. 2004a, 2012). While this introduction was not part of an authorized conservation or management project, we believe it can serve as an informative translocation "experiment," shedding light on similar situations.

MATERIALS AND METHODS

Study species and site.—*Cyclura rileyi nuchalis* is listed as Endangered on the IUCN Red List of Threatened Species (Carter et al. 2000), is strictly

TABLE 1. Known translocations of Rock Iguanas (*Cyclura*), arranged by approximate declining latitude of source population.

Taxon	Location	Founders/Source	Status	References
C. cychlura inornata	Alligator Cay, The Bahamas	8 juveniles from Leaf Cay (1988, 1990)	75–90 (1999)	Knapp 2000, 2001; Knapp and Malone 2003
	Flat Rock Reef Cay, The Bahamas	< 10 from U and Leaf Cays (1996)	> 200 (2013)	Iverson, unpublished; Aplasca 2013
	Guana Cay, Little San Salvador, The Bahamas	11 from Leaf Cay (2005)	Reproducing	Hines, unpublished
C. cychlura figginsi	Pasture Cay, central Exumas, The Bahamas	16 from Leaf Cay S. Exumas (2002, 2006)	> 20 (2014)	Knapp and Hudson 2004; Knapp, pers. comm.
C. rileyi nuchalis	Bush Hill Cay, The Bahamas	5 from Fish Cay (1973)	> 200 (2013)	Hayes et al. 2004a; this study
C. rileyi rileyi	Low Cay, San Salvador, The Bahamas	14 from Green Cay (2005)	12 (2012); no reproduction	Hayes et al. this volume
C. carinata	Six Hills, French, Bay, and Middle Cays, TCI	18–82 from Big & Little Ambergris Cays, TCI (2002–2003)	"extremely successful"	Gerber 2007; Reynolds 2011
	Long Cay, Caicos, TCI	800 from Big Ambergris Cay, TCI (2000)	"established"	Mitchell et al. 2002; Reynolds 2011
C. nubila nubila	Isla Magueyes, Puerto Rico	"a few" from Cuba (mid-1960s)	167 (mid-1980s)	Christian 1986; Knapp and Hudson 2004
C. lewisi	Northeastern Grand Cayman (GC)*	405 captive headstarted, Grand Cayman (2004–2012)	> 40	Goodman et al. 2005a, b; Echternacht et al. 2011; Burton and Rivera-Milán 2014
C. pinguis	Guana Island, BVI	8 from Anegada (1984–1986)	100 (2002); > 300 (2004)	Goodyear and Lazell1994; Anonymous 2004; Perry and Gerber 2011
	Necker Island, BVI	4 from Guana Island, BVI (1995)	"successful"	Lazell 1995, 2002; Perry and Gerber 2011
	Norman Island, BVI	12 from Guana Island (2000s)	unknown	Perry and Gerber 2011

*Reintroduction

protected by The Bahamas under the "Wild Animals Protection Act" of 1968 and the "Wildlife Conservation and Trade Act" of 2004, and is listed on Appendix I (the most restrictive category) of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). *Cyclura rileyi nuchalis* is native to Long Cay (the type locality), Fish Cay, and North Cay in the Acklins Islands, The Bahamas, although it has been extirpated (by unknown causes) from Long Cay (Hayes et al. 2004a). In January of 1973, G.C. Clough released 11 Bahaman Hutias (*Geocapromys ingrahami*) from East Plana Cay in the southeastern Bahamas to Little Wax Cay in the Exuma Islands (immediately adjacent to Bush Hill Cay). It was apparently on the same trip that Clough also collected five iguanas from Fish Cay. According to Oris Russell (pers. comm. to Richard Franz), in 1973 Clough brought the iguanas to him on New Providence and Russell released them on Bush Hill Cay. The descendants of those five individuals constitute the population that we have studied for the past 12 years. Bush Hill Cay (BHC; 3.3 ha) lies within the Exuma Cays Land and Sea Park near the northern limit. Its precise location is withheld for conservation purposes. The lowland portion of the island is dominated by a palm forest (*Coccothrinax argentata*) on a primarily sand substrate. The upland (to 13.4 m elevation) is primarily rocky coppice vegetation. Field work was performed on BHC on sunny to partly cloudy days during periods when iguanas were active (e.g., 0900 to 1800) on 21–22 May 2002 (4 hours; 15 persons), 20–21 May 2003 (9 hours; 14 persons), 17–18 May 2004 (8 hrs; 13 persons), 17–18 May 2005 (11 hours; 16 persons), 26–27 June 2007 (15 hrs; 12 persons), 17–18 May 2008 (14 hrs; 16 persons), 23–24 May 2009 (15 hrs; 15 persons), 17–18 May 2010 (15 hrs; 15 persons), 22–23 May 2011 (12 hrs; 17 persons), and 22–23 May 2013 (11 hrs; 18 persons). Iguanas were captured by hand, dipnet, noose, or live trap.

***Protocol*.**—Processing methods followed those of Iverson et al. (2004a). Snout-vent length (SVL in mm), tail length (TL in mm), tail condition (with lengths in mm of any regenerated segments), and body mass (BM in grams) were measured on each capture. Body and limb injuries were also recorded.

Missing digits and regenerated tails (some forked; see Hayes et al. 2012) were common for iguanas on BHC. We incorporated the information on the extent of missing digits (e.g., toe completely missing) into our marking system based on toe clips (no PIT tags used), such that only one or two toes (and only one per limb) were typically clipped by us (Langkilde and Shine 2006; Perry et al. 2011). When used in combination with notes about body size, scars, regenerated tails, sex, and color, accurate identification of individuals was possible, even when additional digits disappeared between captures (presumably through intraspecific aggression and/or mauling by rats).

FIGURE 1. Ventral view of pelvic region of male (top) versus female (bottom) *Cyclura rileyi nuchalis* on Bush Hill Cay illustrating secondary sexual differences in femoral pore and proximal tail morphology (larger pores and obvious hemipenial bulges evident in males). (Photographed by John B. Iverson).

Lizards were sexed initially by cloacal probing (Dellinger and Hegel 1990) until we were confident that differences in the external morphology of the cloacal region accurately reflected the animal's sex (Fig. 1). However, we were not confident in our sexing of juveniles and smaller subadults by either probing or external morphology, and thus those individuals were excluded from relevant analyses.

Iguanas from Bush Hill Cay exhibit striking variation in body and head coloration (Figs. 2–6). Hence, brief notes on body color were also recorded for each individual at each capture. For consistency, particularly given subtle changes in color depending on lizard body temperature (warmer: colors brighter), all color determinations were made by author JBI. Body color in subadults and adults was scored on two qualitative dimensions: presence of gray to blue-gray mottling (generally noted as obviously mottled versus little or no mottling), and general body color (see below). Juveniles bear a distinctly different pattern from adults, being basically gray with dorsal and dorsolateral longitudinal stripes (Fig. 2, top), and were simply color-scored as "juvenile". Many, but not all lizards were photographed during each capture event.

Von Bertalanffy growth models were calculated from our recapture data using SVL only at first and last capture (Fabens 1965), but excluding recapture intervals of only one year or less. Curves were anchored by the mean size of five first-year iguanas (9.56 cm) estimated to be 0.83 years of age when captured in May.

We submitted our capture/recapture matrix (only for subadult or adult iguanas ≥ 20 cm SVL; size at maturity according to Hayes et al. 2004a) to Program MARK (Available from http://warnercnr.colostate.edu/~gwhite/mark/mark.htm) to obtain annualized survival estimates and capture probabilities (White and Burnham 1999), separately for males and females. All other statistics (two-tailed t-tests, least-squares regression analysis, ANOVA) were calculated with Statview™ software (formerly Abacus Concepts, Berkeley, California, USA).

FIGURE 2. Body size transition in color pattern from juveniles (ca. 16 cm SVL, top two photographs) to subadults (ca. 20 cm SVL, bottom two photographs) for *Cyclura rileyi nuchalis* on Bush Hill Cay; all images from different individuals. Note the retention of juvenile striping anteriorly in the third individual, but loss in the fourth. (Photographed by John B. Iverson and students).

RESULTS

Over our 11-year study period we captured 337 individual iguanas (122 males, 203 females, 12 unsexed juveniles) a total of 862 times (i.e., 525 recaptures; Table 2). The mean number of recaptures was 2.61 for males (range, 1–8 recaptures; $n = 80$) and 2.39 for females (range, 1–7 recaptures; $n = 133$). Mean recapture interval from first to last capture was 4.8 y (range, 1–11 y) for males and 5.5 for females (range, 1–11 y). The sex ratio (203 females, 122 males) was significantly biased in favor of females ($\chi^2 = 20.19$, $P < 0.0001$).

Size and growth.—Mean SVL for males ≥ 20 cm SVL (all captures) was 32.0 cm (range, 21.4–37.2; $n = 319$) and was significantly longer ($t = 22.10$, $P < 0.0001$) than that for females ≥ 20 cm SVL at 28.3 cm (range, 20.0–33.8; $n = 497$). However, mean SVL for males decreased almost 2 cm over our study, and female SVL decreased about 1 cm (Fig. 7).

Tail length for males with complete, unregenerated tails averaged 47.6 cm (range, 35.2–55.0 cm; $n = 125$) and was significantly longer ($t = 10.2$, $P < 0.0001$) than that for females at 43.4 cm (range, 31.2–51.0 cm; $n = 204$). However, relative tail length (TL/SVL) was longer in females than males (means: 1.50 vs 1.48; $t = 3.23$, $P = 0.0007$). Tail break frequency data from this study were reported in Hayes et al. (2012).

Mean BM for males was 1,173 g (range, 425–1,710 g; $n = 319$) and was significantly heavier ($t = 21.8$, $P < 0.0001$) than that for females at 869 g (range, 305–1,404 g; $n = 497$). BM was related exponentially to SVL in males ($\log BM = 2.471 \log SVL - 0.657$; $n = 319$, $r = 0.87$, $P < 0.0001$) and females ($\log BM = 2.328 \log SVL - 0.446$; $n = 497$, $r = 0.90$, $P < 0.0001$) for individuals ≥ 20 cm SVL, and these curves were not significantly different between the sexes ($P > 0.05$ for ANCOVA of log-transformed data).

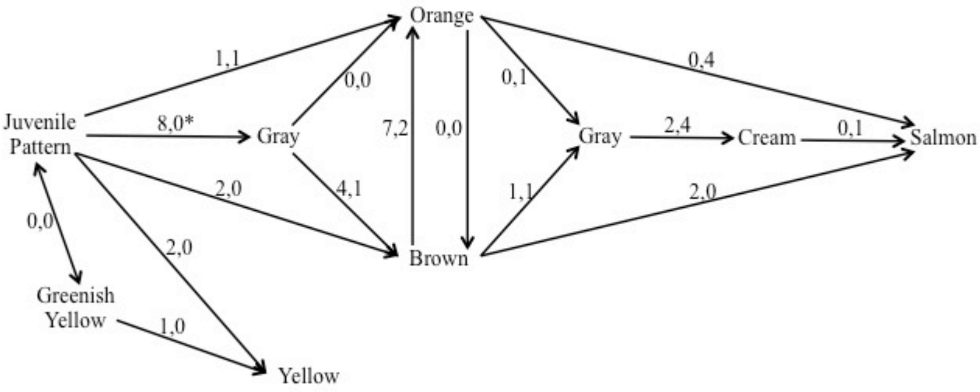

FIGURE 3. Color pattern transitions recorded for recaptured *Cyclura rileyi nuchalis* on Bush Hill Cay ≥ 20 cm SVL at both first and last capture. Numbers at each transition are "females, males" that exhibited the transition. Asterisk indicates suspect gender identification due to difficulty in sexing young adults.

FIGURE 4. Color pattern transition across body sizes (subadult, top; large adult, bottom; all are different individuals) for *Cyclura rileyi nuchalis* on Bush Hill Cay exhibiting the yellow morph. Note the transition from green-yellow to yellow, and the loss of mottling. (Photographed by John B. Iverson and students).

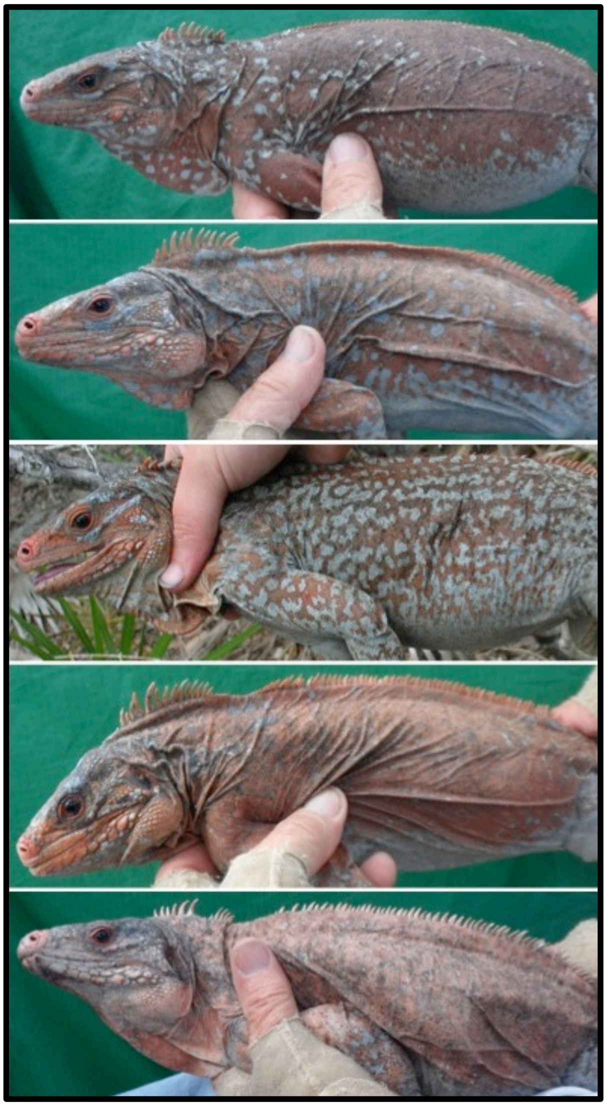

FIGURE 5. Color pattern transition across body sizes (small adult, top; large adult, bottom; all are different individuals) for *Cyclura rileyi nuchalis* on Bush Hill Cay exhibiting (top to bottom) the brown–orange–salmon morph. Note the loss of mottling, and the fading of orange to salmon. (Photographed by John B. Iverson and students).

TABLE 2. Capture information by year for *Cyclura rileyi nuchalis* on Bush Hill Cay. Biomass in kg/ha estimated as the product of estimated population size and mean mass of all captured iguanas in our study (951.6 g), divided by island area. Program MARK cannot estimate numbers for the first and last years of the study.

Year	Total Captures	Total Recaptures	Percent Recaptures	Males	Females	Unsexed	Estimated *n*	Estimated Biomass (kg/ha)
2002	75			36	39			
2003	72	16	22	36	33	3	265	78.8
2004	104	42	40	45	60		322	95.8
2005	106	59	56	38	66	2	255	75.8
2007	96	58	60	36	58		224	66.6
2008	79	65	82	29	44	6	209	62.2
2009	75	61	81	23	45	6	110	32.7
2010	116	103	89	33	76	7	218	64.8
2011	57	51	89	22	32	3	59	17.5
2013	77	70	91	23	49	5		

Mean growth rate (cm SVL/y) was not significantly faster in males ≥ 20 cm SVL (mean = 0.22 cm/y; range, -1.0–3.2 cm/y; $n = 79$) than females ≥ 20 cm SVL (mean = 0.14 cm/y; range, -1.0–2.0 cm/y; $n = 125$, $t = 1.22$, $P = 0.11$). Growth rate was negatively correlated with body size (Fig. 8). For males, the von Bertalanffy model was: SVL = 32.857 $(1 - 0.7883e^{-0.182t})$, for t, time in years post hatching ($n = 64$; mean interval = 5.66 y; range, 2–11 y; $r = 0.90$, $P < 0.0001$). For females it was SVL = 29.030 $(1 - 0.7528e^{-0.198t})$ ($n = 120$; mean interval = 5.95 y; range, 2–11 y; $r = 0.82$, $P < 0.0001$). These growth models suggest that males reach 20 cm SVL (estimated age at maturity, according to Hayes et al. 2004a) at age 3.85 years and females at 4.46 years. This would suggest that females begin nesting in their fifth summer of life.

Coloration.—Of 213 iguanas (133 females, 80 males) recaptured at least once and for which color notes were recorded, 45 (30 females, 15 males) demonstrated changes in color between their first and last capture (mean interval during which color change occurred = 3.31 y; range, 1–9 y). Of these, 14 (13 "females" [gender suspect; see Methods], 1 male) were captured first at SVL < 20 cm with juvenile coloration (i.e., the typical longitudinally striped gray pattern; Fig. 2), but upon final capture as adults had transitioned to adult coloration. The remaining 31 that changed colors as adults (17 females, 14 males) provided a basis for understanding adult color changes (summarized in Fig. 3).

FIGURE 6. Color pattern transition across body sizes (small adult, top; large adult, bottom; all are different individuals) for *Cyclura rileyi nuchalis* on Bush Hill Cay exhibiting (top to bottom) the brown to gray to salmon transition. Note the loss of mottling, and the fading of colors to salmon or cream. (Photographed by John B. Iverson and students).

Two distinct color transition patterns were evident on Bush Hill Cay, each developing as the longitudinal stripes of the juvenile were lost as maturity was reached (though retained in some individuals until 23 cm SVL), and mottling on the body increased initially. The rarer transition pattern (Table 3; Fig. 3) was characterized by the change from the gray juvenile background color to greenish gray to yellowish gray, and eventually to all yellow, with minimal mottling (Fig. 4). This transition took as few as two years based on our recaptures. Among adults ≥ 20 cm SVL, only 13.5% of females and 11.3% of males were yellow when first captured. All of our data indicated that these iguanas remain yellow for the rest of their lives. No yellow iguana (8 males: mean interval between first and last capture = 3.63 y and range, 1–10 y; 12 females: mean interval = 5.75 y and range, 1–11 y) ever changed to another color, although the yellow pattern darkened in some individuals (Fig. 4).

The second identified transition pattern was much more complex, but could be qualitatively described as a loss of the juvenile stripes, leaving a variably mottled gray appearance. This appearance later was suffused with orange or brown, which in some individuals was later lost, leaving a gray background that in a very few individuals washed out to cream or even salmon color (Figs. 5–6). In the gray–brown–orange phases, males tended to be brighter in color; i.e., more likely orange, than gray or brown (65 of 98, 66%, orange in males; 55 of 157, 35%, orange in females).

The direction of color change in our model was somewhat corroborated by comparisons of mean body sizes of individuals exhibiting each color pattern (Table 4). For

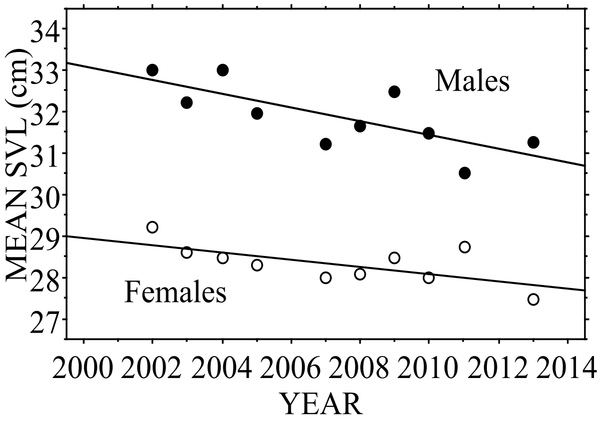

FIGURE 7. Decline in mean snout-vent length (SVL in cm) of adult *Cyclura rileyi nuchalis* on Bush Hill Cay through time. For males: $y = -0.166x + 364.758$, $n = 22–41$ per sample, $r = 0.75$, $P = 0.013$. For females: $y = -0.088x + 204.547$, $n = 32–75$ per sample, $r = 0.67$, $P = 0.036$.

example, cream and salmon males had larger mean body sizes, suggesting that those colors were the latest to develop in life. Unfortunately, the variation in body size among adult females of various colors was minimal, precluding the definition of any patterns.

Population parameters.—Juvenile iguanas were rarely seen or captured on Bush Hill Cay (all authors, pers. obs.). Only 1.17% of all iguana captures (n = 858 total captures) were < 12 cm SVL and only 3.03% were between 12.0 and 19.9 cm SVL. For most of the surveys, the adult sex ratio, whether based on raw capture data or on estimated numbers of males and females, was significantly female-biased (Table 5). The sex ratio based on raw capture data became increasingly female-biased over the course of our study (Fig. 9, top; n = 10, r = 0.76, P = 0.010; proportion male = 29.66 – 0.0146Year). In contrast, the sex ratio based on estimated numbers of males and females from Program MARK did not change significantly during the study (Fig. 9, bottom; n = 8, r = 0.18, P = 0.67).

For males, the best population model from Program MARK included among-year variation in both survival and capture probability estimates. In some recapture intervals (Table 6), annual male survival was estimated to be 100%, whereas in others, estimated survival was only 65–70% (e.g., 2002–2003, 2005–2007, 2010–2011).

For females, two models performed almost equally well – the model with constant female survival estimates and variable capture probabilities (AICc = 1,024.75), and the model with among-interval variation in both survival and capture probability estimates (AICc = 1,026.28). We report both results here. For the model with constant female survival and variable capture probabilities, annualized survival for females was estimated to be 0.892 ± (SE) 0.014 (range, 0.50 to - 1.00). For the second model (Table 6), annualized survival was relatively high (> 87%) during most time

TABLE 3. Frequency of general color morphs among all captured adult *Cyclura rileyi nuchalis* (≥ 20 cm SVL) on Bush Hill Cay, based on their color at first capture. Actual numbers are followed by the expected number (in parentheses) for each color category individually assuming the biased sex ratio of the sample. See text and Figs. 4–6 for color definitions.

Sex	Brown	Orange	Gray	Cream	Salmon	Yellow
Female	53 (38)	55 (73)	52 (46)	3 (7)	0 (2)	22 (21)
Male	9 (24)	65 (47)	24 (30)	8 (4)	3 (1)	12 (13)

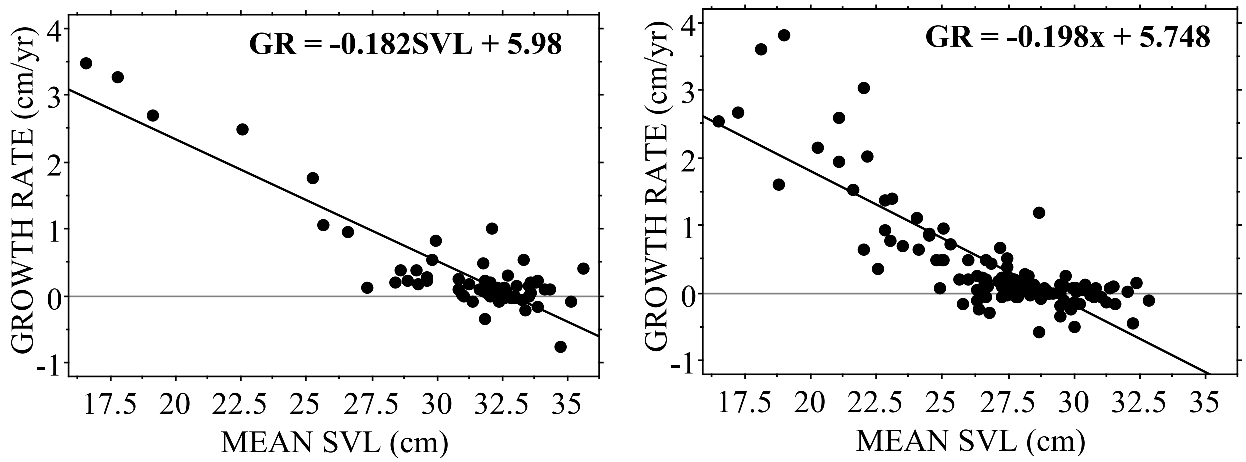

FIGURE 8. Relationship of SVL (in cm; mean of first and last capture) to growth rate (SVL in cm/y) in male (left; r = 0.90, P < 0.0001) and female (right; r = 0.82, P < 0.0001) *Cyclura rileyi nuchalis* on Bush Hill Cay recaptured after > 1 year.

TABLE 4. Mean snout-vent length of *Cyclura rileyi nuchalis* on Bush Hill Cay (for all captures ≥ 20 cm SVL; 318 males, 496 females) for color pattern recorded at capture. ANOVAs for males ($F_{6,115}$ = 9.41, P < 0.0001) and females ($F_{6,179}$ = 14.75, P < 0.0001) were both significant. Letters adjacent to means indicate non-significant differences by Fisher's Least Significant Difference (e.g., juvenile and brown males differed significantly from each other and all other samples).

Male Color	Male SVL	Female Color	Female SVL
Juvenile	23.10	Juvenile	21.13
Brown	29.69	Gray	28.02 B
Orange	31.99 A	Cream	28.31 AB
Gray	32.05 A	Salmon	28.34 AB
Yellow	32.19 AC	Yellow	28.46 AB
Cream	33.05 B	Brown	28.52 A
Salmon	33.50 BC	Orange	28.67 A

intervals. However, survival was substantially lower in the last time interval for which we could estimate survival (only 50% for 2010–2011).

Estimated population size for adult iguanas (≥ 20 cm SVL) on Bush Hill Cay ranged from 59 in 2011 (perhaps biased by the low number of captures, most of them already marked, but surely an underestimate given the 2013 sample of 77) to 322 in 2004 (Table 2). Excluding the lowest estimate, the remaining seven estimates averaged 229. However, there was a significant decline in estimated population sizes during the study period (Fig. 10; *n* = 8, all estimates included; *r* = 0.82, *P* = 0.012; estimated population size = 48779.3 – 24.2Year).

TABLE 5. Adult sex ratios (expressed as proportion of males) of *Cyclura rileyi nuchalis* (≥ 20 cm SVL) from Bush Hill Cay based on raw captures and on population sizes of each sex estimated using capture probabilities from the program MARK analysis. *Indicates sex ratio is significantly different from 1:1 using a chi-square analysis.

Year	Raw captures	Estimated
2002	0.48	--
2003	0.52	0.42*
2004	0.43	0.35*
2005	0.36*	0.22*
2007	0.38*	0.30*
2008	0.40	0.37*
2009	0.34*	0.34*
2010	0.30*	0.31*
2011	0.41	0.44
2013	0.32*	--

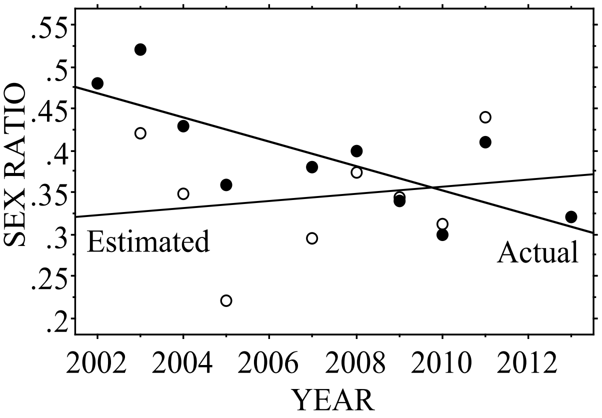

FIGURE 9. Change in the proportion of males in the population of adult *Cyclura rileyi nuchalis* on Bush Hill Cay through time based on raw capture data (Actual, closed circles: n = 10, r = 0.76, P = 0.010; proportion male = 29.66 – 0.0146Year) and on estimated numbers of adult males and females from population models (Estimated, open circles: n = 8, r = 0.18, P = 0.67).

TABLE 6. Annual survival (± SE) of *Cyclura rileyi nuchalis* on Bush Hill Cay based on recapture data analyzed by program MARK. Survival for the last interval in the data (2011–2013) cannot be estimated with this analysis. *SE < 0.0001.

Interval	Males	Females
2002–2003	0.652 ± 0.179	1.000 ± 0*
2003–2004	0.967 ± 0.175	0.872 ± 0.102
2004–2005	0.796 ± 0.161	1.000 ± 0*
2005–2007	0.691 ± 0.065	0.829 ± 0.043
2007–2008	0.996 ± 0.057	0.877 ± 0.084
2008–2009	0.994 ± 0.090	0.942 ± 0.084
2009–2010	1.000 ± 0*	1.000 ± 0*
2010–2011	0.657 ± 0.134	0.501 ± 0.083

Assuming a population estimate of 306 adult iguanas on Bush Hill Cay in 2003 (based on the regression equation for estimated population size; Fig. 10), a total island area of 3.3 ha, and the mean body mass data for all 857 iguana captures on the cay (951.6 g), we conservatively estimated the density of subadults and adults at 95.6/ha and a standing crop biomass of 91.0 kg/ha. However, the method applied to 2011 data, estimated only 113 adults present, a density of only 35.3/ha, and a biomass of only 33.5 kg/ha.

DISCUSSION

Size and growth.—The largest iguana (presumably a male, *n* = 54) reported by Carter and Hayes (2004) from Bush Hill Cay in 1996–1997 was 36.0 cm SVL and 1,650 g BM; however, we recorded a male of 37.2 cm SVL and 1,710 g. Our two largest females measured 33.8 cm SVL and 1,225 g, and 33.0 cm SVL and 1,376 g. The largest SVL reported for *C. rileyi nuchalis* on Fish Cay (the source population) was 31.4 cm and for North Cay was 28.0 cm (presumably males, Hayes et al. 2004a). Carter and Hayes (2004) reported that males were significantly larger than females on Bush Hill Cay, but did not provide body size data by sex. Our data confirm this male-biased dimorphism quantitatively. Males in our study averaged 13.2% longer and 35.0% heavier than females.

Mean body mass of iguanas on Bush Hill Cay during this study (*n* = 857 captures) was 951.6 g (range, 30–1,710 g), compared to a mean of 1,097 g (range, 9.2–1,650 g) for 54 captures in 1996–1997 by Carter and Hayes (2004). Those authors also reported significantly

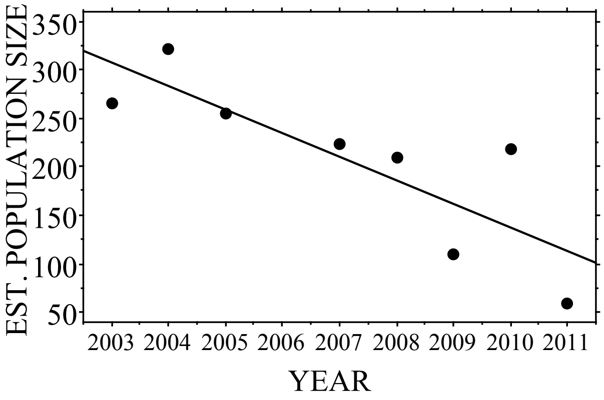

FIGURE 10. Change over time in estimated population size of adult *Cyclura rileyi nuchalis* on Bush Hill Cay based on population models (*n* = 8, *r* = 0.82, *P* = 0.012; estimated population size = 48779.3 – 24.2Year).

lower mean body masses from the natural populations on Fish Cay (459 g) and North Cay (404 g). We concur with Hayes et al. (2004a) that the larger body size on BHC was likely due to reduced intraspecific competition during population growth, although nutritional differences in the diets cannot be ruled out (William Hayes, pers. comm.). However, the 139 g decline (12.7%) in mean body mass in the decade between the mid-1990s and mid-2000s is noteworthy, particularly since the pattern of a decline in body size continued during our study (Fig. 7). It may be that the iguanas that grew to extraordinary sizes during times of low density (i.e., soon after translocation) are now dying and being replaced by individuals that matured during times of high density (i.e., near carrying capacity) and are thus smaller.

Hayes et al. (2004a) reported that *Cyclura rileyi* (all populations) generally reaches sexual maturity at 20 cm SVL and ca. 300 g (at an unknown age), but the precise size at maturity on BHC is unknown. However, based on our growth data, 20 cm SVL was reached on BHC during our study period at ca. 4.5 y in females and ca. 3.9 y in males on average. *Cyclura carinata* is the only other West Indian iguana of similar body size to *C. rileyi*, and it matures at about the same size (18–20 cm SVL); however, despite its more southern (i.e., tropical) distribution, it requires 6–7 years to reach maturity (Iverson 1979). Other species of *Cyclura* are larger and reach maturity from 2–12 years (Table 7 in Iverson et al. 2004b). Translocated populations of *Cyclura* are known to reach maturity more quickly than their source populations (Knapp 2001; Gerber 2007), presumably due to reduced intraspecific competition among the founders, but unfortunately no growth data are available for native populations of *C. rileyi*.

Preliminary observations of the Bush Hill Cay population by Carter and Hayes (2004) found higher frequencies of missing digits in the Bush Hill Cay population (20.4%) compared to either the Fish Cay (12.3%) or the North Cay (14.9%) populations. Bush Hill Cay (51.9%) also had higher frequencies of injured tails than the Fish Cay (24.6%) and North Cay (32.6%) populations in 1996–1997 (Carter and Hayes 2004), and that frequency increased to 60.4% during the period 2002–2010 (Hayes et al. 2012). A meta-analysis of 19 populations of three species of *Cyclura* (including all three *nuchalis* populations) strongly implicated rats as the cause of the elevated rates seen on at least BHC (Hayes et al. 2012).

Iguanas may also suffer indirect competitive effects from rats, via shared limited food resources or through vegetation damage (Towns et al. 2006), and these may intensify during periods of drought or low productivity. We have observed increasing damage to vegetation by rats (e.g., gnawed twigs) and increased encounters with rats (e.g., when they entered live traps intended for iguanas during the day). But unfortunately we have no data on the dynamics of the rat population or primary productivity on BHC. The collection of data such as these would be particularly valuable prior to the removal of the rats.

Coloration.—Ours is the first attempt to quantify color and color changes in any species of *Cyclura*. *Cyclura rileyi* exhibits far more variation in body color than any congener (Schwartz and Carey 1977) and indeed, most other studied lizards (reviewed by Olsson et al. 2013), which is likely related to its insular evolution where background matching of large adults was presumably of little selective value. Furthermore, like many diurnal lizards *C. rileyi* is capable of subtle color changes during the day (darker early, more vivid later), apparently related to light and/or temperature (i.e., "physiological color change"; Cooper and Greenberg 1992; Langkilde and Boronow 2012; Olsson et al. 2013). However, the extraordinary body color variation in *C. rileyi* probably functions primarily in social communication, although the mechanisms are still unknown. We did not quantify color patterns micro-geographically on BHC, although the various color patterns seemed to be distributed randomly across the island. Unfortunately, we did not quantify (or notice) any associations of color among territorial males and nearby females. In addition, since we only visited BHC during May (usually) or June (once), we also cannot address seasonal variation in color on the island.

Hence, although our 12 years of recapture data have clarified the frequencies and general directions of ontogenetic color change in these iguanas, the bases for these changes are completely unknown (e.g., diet: Wikelski unpublished in Hayes et al. 2004b; Costantini et al. 2005), as are their fitness consequences (e.g., Cooper and Greenberg 1992; Rosenblum 2005; Pérez et al. 2012; Olsson et al. 2013; Pérez i de Lanuza et al. 2013). Furthermore, we do not know whether the patterns we have observed mirror those in the founder population on Fish Cay, because few data are available on color morphology (e.g., there is no complete list of all color morphs and their frequencies) and none are available on color change for any population of this species.

Our observations of color patterns on Bush Hill Cay generally agree with those reported for both *C. rileyi rileyi* and *C. rileyi nuchalis* by Hayes and Montanucci (2000), but differ significantly from the colors mentioned by Schwartz and Carey (1977; repeated by Lemm and Alberts 2012) who reported black as a common color (perhaps based on museum animals in fixatives). Hayes and Montanucci (2000) reported that the color patterns of *C. rileyi nuchalis* resemble those of *C. rileyi rileyi* and "Dorsum colors of red, orange, yellow, green, or brown are usually punctuated by darker markings and fine vermiculations. Males generally exhibit more color (red, orange, or yellow) and contrast than females, especially at warmer body temperatures. Juveniles are solid brown or gray, often with a slightly paler mid-dorsal band having faint longitudinal stripes or indistinct darker areas near the middorsal crest. Juveniles lack the brighter coloration and vermiculations of adults, as well as the dorsal chevrons or pale diagonal markings present on juveniles of other taxa." These color notes generally correspond to our observations, although we did not record "red" individuals.

We hope to continue monitoring iguanas from Bush Hill Cay in order to more precisely quantify the various color morphs and their transitions. Similar studies are needed for natural populations of *C. rileyi*, and this species offers a unique possibility to study the fitness correlates of the various color morphs. For example, we calculated the residuals of the SVL-body mass regression of males and females separately to determine any differences in body condition among the six adult and one juvenile color morphs. For females, variation across samples was not quite significant ($F_{6,179}$ = 1.84, P = 0.09), but post hoc tests (Fisher's protected least significant difference, alpha = 5%) identified orange females as significantly heavier than brown females (+8.3 g versus -13.2 g). This may indicate a positive relationship between health and color brightness in females. For males, the variation in size across the color patterns was not significant ($F_{6,115}$ = 0.81, P = 0.57). However, yellow males had the highest mean residual (+30.0 g) and (presumably older) salmon males had the lowest (-25.9 g). These results are clearly inconclusive, but at least suggest that color may have fitness correlates, and is worthy of future study.

Population parameters.—Hayes et al. (2004a) commented on the low incidence of captures and sightings of small (< 12 cm SVL) and large (12.0 to 19.9 cm SVL) juveniles on BHC in 1996–1997. Their frequencies, 1% and 5%, respectively, were similar to those that we found among our captures (1% and 3%, respectively). Natural populations of *C. rileyi nuchalis* on Fish Cay (25%) and North Cay (23%) had much higher frequencies of juveniles (Hayes et al. 2004a, their Table 17.3), as did populations of *C. rileyi cristata* (34%) and most populations of *C. rileyi rileyi* (0% to 57%; mean = 28%). Immature iguanas represented 42% of a sample of 167 *C. carinata* (Fig. 51 in Iverson 1979) prior to the effects of invasive mammals. In the most complete sample year for *C. cychlura inornata* (2002), 43% of 168 iguanas captured on U Cay and 40% of 483 iguanas captured on Leaf Cay were immature (< 25 cm SVL). Hayes et al. (2004a) attributed the low numbers of juveniles on BHC to the presence of rats, as well as the fact that the species is occasionally cannibalistic on other islands (Hayes et al. 2004a). Unfortunately, low numbers of juveniles are typical of most *Cyclura* populations due to introduced, invasive mammals. For example, on an island overrun with exotic mammals, only 5–10% of *C. stejnegeri* were juveniles (Wiewandt 1977).

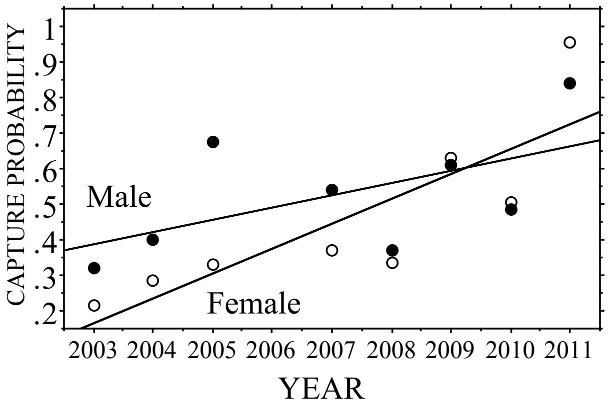

FIGURE 11. Change over time in capture probabilities for male (open circles; n = 8, r = 0.61, P = 0.14; capture probability = 0.034Year – 68.7) and female (closed circles; n = 8, r = 0.84, P = 0.0095; capture probability = 0.070Year – 139.4) *Cyclura rileyi nuchalis* on Bush Hill Cay based on population models.

Hayes et al. (2004a) reported a nearly equal sex ratio (51% male) on Bush Hill Cay in 1996–1997 based on 54 captures. They also found a similar ratio on Fish Cay (51% male) and a slightly male-biased ratio on North Cay (63%). Sex ratios in other species of *Cyclura* are typically even, although Smith and Iverson (2006; ratios reviewed in Table 1) reported a shift from a male-biased ratio to an unbiased ratio in *Cyclura cychlura inornata* as that population grew to carrying capacity following legislative protection.

It is thus quite surprising that we found a strongly female-biased sex ratio (37.5% male), based on 325 first captures of subadults and adults of iguanas from BHC. In addition, as our study progressed, our actual captures became even more female-biased; however, there were no significant changes in the sex ratio based on the estimated number of males and females on Bush Hill Cay from our population models (Table 5). These conflicting observations suggest that the underlying adult sex ratio has likely not shifted significantly during our study, but that the capture probability of males and females diverged over time. Indeed, when we regressed capture probability estimates on time interval (Fig. 11), capture probabilities increased significantly for females (n = 8, r = 0.84, P = 0.0095; capture probability = 0.070Year – 139.4), but not for males, although there was a trend toward an increase (n = 8, r = 0.61, P = 0.14; capture probability = 0.034Year – 68.7). It is perhaps not surprising that capture probabilities increased through time, since our ability to capture these iguanas no doubt also improved with time. However, why our ability to capture males would lag that of females is not clear, although it could reflect gender differences in wariness.

The question remains as to why the sex ratio on Bush Hill Cay would have become so dramatically biased in only a decade? We can offer only three speculative hypotheses. The first is that males may be more susceptible than females to injury and death from the invasive rat population, perhaps due to the year-round territoriality of male iguanas (Hayes et al. 2004a; Lemm and Alberts 2012). Though rats were already present during the 1996–1997 study by Hayes et al. (2004a) and the sex ratio then was balanced, it is likely that the rat population has increased over time. Second, since male *C. rileyi* are so territorial, it may be that the growth of the population toward (or beyond?) carrying capacity has differentially impacted males more than females. Finally, the cay may have been subject to a poaching event between the two studies, and the brighter, more easily captured, territorial males may have been taken preferentially. We have no data to support this last hypothesis, except the decline in the relative number of males, but we are troubled by this possibility.

In May of 1996 and 1997 Hayes et al. (2004a) used a Lincoln-Peterson mark-resighting index and suggested that a population of 299 iguanas resided on BHC (though Carter and Hayes 2004 reported 314 based on the same data). Our early estimates of population size of the iguanas on Bush Hill Cay (265 in 2003, 322 in 2004) are close to these previous estimates; however, there was a decline in estimated population size during our study. In particular, for the most recent year for which we can estimate the population with Program MARK (2011), the estimated size was 59, whereas the estimate was 110 in 2009 and 218 in 2010. We are uncertain at this time whether the observed variance in estimated population sizes is due to some artifact of the population models or variation in the quantity and quality of capture effort (due to variation in weather and/or personnel). Nevertheless, we are concerned that the population appears to be in decline, and our data indicate an average loss of 24 adults per year (Fig. 10). The precipitous decline in survival estimates for both males and females during the 2010–2011 interval is of particular concern. We anticipate making a concerted effort to resurvey the Bush Hill Cay population in 2016 with an experienced crew. The results of that survey should allow us to quantify the rate of decline more definitively.

Carter and Hayes (2004) and Hayes et al. (2004a) estimated the density of iguanas on BHC in 1996–1997 at 95.2/ha, with a standing crop biomass of 104.4 kg/ha. They also reported much lower numbers for the two native populations on Fish Cay (58.9 kg/ha) and North Cay (23.7 kg/ha). Our estimates for the beginning of our study on BHC (95.6/ha and 91.0 kg/ha) were similar to those reported earlier. Thus, the earlier biomass estimates for BHC were among the highest reported for the genus (reviewed in Iverson et al. 2006), matched only by that estimated for *C. cychlura inornata* in the Exumas, which was believed to be near carrying capacity (94.1 kg/ha; Iverson et al. 2006). Assuming that the Bush Hill Cay population was also near carrying capacity in 1996–1997, these data suggest that a standing crop biomass of near 100 kg/ha may be the upper limit for natural populations of this herbivorous genus. Unfortunately, no other populations of *Cyclura* have been reported to be near carrying capacity.

Conclusions.—Our work, and that of Hayes et al. (2004a) and Carter and Hayes (2004), demonstrate the successful translocation of *C. rileyi nuchalis* to Bush Hill Cay. Recent declines in the estimated population, however, suggest that the future outlook for this population bears greater scrutiny. Given the success of this population over its first 30 years, we do not believe that this decline reflects a translocation failure, although data on genetic diversity of the BHC population (given only five founders) would alleviate some remaining concerns. Unfortunately, the introduction of rats to the cay, and the possibility of poaching from this isolated cay, complicate our explanation of the current decline. In any case, we strongly recommend that a rat eradication program be implemented on BHC as soon as possible. Mammal eradication programs have already been demonstrably effective for the recovery of other populations of *Cyclura* (e.g., Mitchell et al. 2002 and Gerber 2007 for *C. carinata*; Day et al. 1998 and Hayes et al. 2004a for *C. rileyi cristata*; Aurora Alifano et al. unpublished for *C. cychlura inornata*; and Wilson 2011 for *C. collei*), and would likely aid in reversing the current decline on BHC.

Given the significant and increasing costs in time and money to establish captive breeding facilities for West Indian iguanas, and the demonstrated success of translocation programs for these lizards (Knapp and Hudson 2004; Table 1), translocations of other endangered island populations of *Cyclura* should be the first strategy explored during the development of their conservation management plans.

Our study also makes it clear that financial support for ongoing monitoring of translocated populations, as well as the founder populations, is essential for long-term conservation of this endangered genus of lizards. As a case in point, if the only existing population of *C. rileyi cristata* had not been monitored (though irregularly), the raccoon and rats introduced there in the mid-1990s would likely have driven that taxon to extinction (Day et al. 1998; Carter and Hayes 2004; Hayes et al. 2004a).

Finally, it should be noted that monitoring of translocations generally focuses only on the relocated species, as has been the case for all *Cyclura* translocations. However, introductions such as these may have broad consequences to the translocation ecosystem, especially considering the possible impacts of a dense population of a large herbivorous species like an iguana (e.g., Schofield 1989; Campbell et al. 1991; Strong and Leroux 2014). We know of no such study associated with any iguana translocation, but urge the undertaking of such work. For example, it is often stated that iguanas are critical seed dispersers in their native ecosystems, and hence, essential to those systems. Yet data demonstrating ecosystem differences with and without iguanas are not yet available.

Acknowledgments.—This work would not have been possible without the continued support by Mrs. Sandra Buckner, The Bahamas National Trust, 7 C's Charters (Bruce Dunham, Sheila Young, and Ron White, and crew members Ian Beaumont, Jason Diller, Aubrey Anne Groeber, Eric Namowicz, Matt Novak, Nikki Overly, Tim Pierce, Steve Schmidt, Will McLean, and Sarah Henry), and the Exuma Cays Land and Sea Park. Annual permits (unnumbered) were issued by The Bahamas Department of Agriculture or The Bahamas Environment Science and Technology Commission. We treated all iguanas humanely and ethically, as outlined in the SSAR Guidelines for Use of Live Amphibians and Reptiles in Field Research (available online only). The financial support of Dr. Ned and Sally Test, the Cope Museum Fund of Earlham College, Iverson's family, and Denison University (Greene Fund, Horizon Fund, Battelle Fund) is greatly appreciated. Finally, the field work could not have been accomplished without the assistance of 64 Earlham College students or alumni (Mark Abbey-Lambertz, Dan Albrecht-Mallinger, Madeline Bachner, Michelle Bahnick, Lenden Bowsman, Corey Bradley, Amanda Burgoon, Sam Campbell-Nelson, Ruthie Carter, Jessica Castleberry, Jordan Cerna, Laura Corichi, Evan Dalton, Eli Darnell, Emma Dixon, Abe Drayton, Max Driffel, Michael Faile, Natsumi Fearnside, Dan Greene, Frances Hall, Kat Hardy, Galen Hartman, Joel Hogle, Alli Hunnicutt, Rachael Jonas-Closs, Stephen Jones, Becca Jordan, Chrysalis Kendall, Kourtney King, Matt Lachuisa, Hannah Lehmann, Diana Lisensky, Laura Lisensky, Lucy Martin, Melissa Mayheux, Colin Meeks, Sarah Muhrer, Kathy Muller, Mollye Nardi, Erika Phelps, Rebecca Prosser, James Rose, Hassan Salem, Sarah Schaack, Kari Schneider, Chaundra Schofield, Jon Shepard, Delphine Sowiak, Joneen Spurlock, Hilary Standish, Danika Stoltz, Julie Tamanini, Alexandra Turnbull, Jen Valiulis, Andrew Vedder, Chris Warren, Emily Warrener, Ryan Welsh, Ann Wildman, Caryn Wixom, David Wolfson, Cameron Young, David Young), 13 Denison University students (Briella Baer, Caitlin Bingaman, Dory Enright, Annie Harmon, Katie Huff, Peter Iverson, Skyler Jordan, Hannah Lugg, Michael McKinney, Lenny Mills, Larissa Rivera, Hallie Sickels, and Sara Wilkes), three post-graduate students (Andrea Aplasca, Dan Benboe, and Kristen Richardson), Earlham staff member Rick Flamm, and Earlham faculty member Amy Mulnix.

LITERATURE CITED

Alberts, A.C. 2007. Behavioral considerations of headstarting as a conservation strategy for endangered Caribbean Rock Iguanas. Applied Animal Behaviour Science 102:380–391.

Alberts, A.C., and J.A. Phillips. 2004. Experimental strategies for the recovery of depleted populations of West Indian Rock Iguanas. Pp. 83–100 *In* Experimental Approaches to Conservation Biology. Gordon, M.S., and S.M. Bartol (Eds.). University of California Press, Berkeley, California, USA.

Alberts, A.C., J.M. Lemm, T.D. Grant, and L.A. Jackintell. 2004. Testing the utility of headstarting as a conservation strategy for West Indian Iguanas. Pp. 210–219 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Alberts, A.C., M.C. Oliva, M.B. Worley, S.R. Telford, Jr., P.J. Morris, and D.L. Janssen. 1998. The need for pre-release health screening in animal translocations: a case study of the Cuban Iguana (*Cyclura nubila*). Animal Conservation 1:165–172.

Anonymous. 2004. Iguana newsbriefs: Stout Iguana conservation. Iguana (Journal of the International Iguana Society) 11:129.

Aplasca, A.C. 2013. Population genetics of the endangered insular Allen Cays Rock Iguana, *Cyclura cychlura inornata*. M.Sc. Thesis, Fordham University, New York, USA. 52 p.

Bradley, K.A., and G.P. Gerber. 2005. Conservation of the Anegada Iguana (*Cyclura pinguis*). Iguana (Conservation, Natural History, and Husbandry of Reptiles) 12:78–85.

Burke, R.L. 1991. Relocations, repatriations, and translocations of amphibians and reptiles: taking a broader view. Herpetologica 47:350–357.

Burton, F.J., and F.F. Rivera-Milán. 2014. Monitoring a population of translocated Grand Cayman Blue Iguanas: assessing the accuracy and precision of distance sampling and repeated counts. Animal Conservation 17 (Supplement 1):40–47.

Campbell, D.G., K.S. Lowell, and M.E. Lightbourn. 1991. The effect of introduced Hutias (*Geocapromys ingrahami*) on the woody vegetation of Little Wax Cay, Bahamas. Conservation Biology 5:536–541.

Carter, R.L., and W.K. Hayes. 2004. Conservation of an endangered Bahamian rock iguana: II. Morphological variation and conservation priorities. Pp. 258–273 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Carter, R.L., W.K. Hayes, and West Indian Iguana Specialist Group. 2000. *Cyclura rileyi* ssp. *nuchalis*. The IUCN Red List of Threatened Species. Version 2014.3. Available from http://www.iucnredlist.org/details/6047/0 [Accessed on 1 December 2014].

Christian, K.A. 1986. Aspects of the life history of Cuban Iguanas on Isla Magueyes, Puerto Rico. Caribbean Journal of Science 22:159–164.

Cooper, W.E., and N. Greenberg. 1992. Reptilian coloration and behavior. Pp. 298–422 *In* Biology of the Reptilia, Volume 18, Physiology E, Hormones, Brain, and Behavior. Gans, C., and D. Crews (Eds.). University of Chicago Press, Chicago, Illinois, USA.

Costantini, D., G. Dell'Omo, S. Casagrande, A. Fabiani, M. Carosi, V. Bertacche, C. Marquez, H. Snell, H. Snell, W. Tapia, and G. Gentile. 2005. Inter-population variation of carotenoids in Galápagos Land Iguanas (*Conolophus subcristatus*). Comparative Biochemistry and Physiology, Part B 142:239–244.

Day, M., W. Hayes, K. Varnham, T. Ross, E. Carey, T. Ferguson, J. Monestine, S. Smith, C. Armstrong, A. Buckle, et al. 1998. Rat eradication to protect the White Cay Iguana. Aliens 8:22–24.

Dellinger, T., and G. von Hegel. 1990. Sex identification through cloacal probing in juvenile Marine Iguanas (*Amblyrhynchus cristatus*). Journal of Herpetology 24:424–426.

Dodd, C.K., and R.A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47:336–350.

Echternacht, A.C., F.J. Burton, and J.M. Blumenthal. 2011. The amphibians and reptiles of the Cayman Islands: conservation issues in the face of invasions. Pp. 129–147 *In* Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Gerber, G. 2004. An update on the ecology and conservation of *Cyclura pinguis* on Anegada. Iguana (Journal of the International Iguana Society) 11:23–26.

Gerber, G. 2007. Turks and Caicos Iguana translocation program, Bahama Archipelago. Re-introduction News 26:53–55.

Germano, J.M., and P.J. Bishop. 2009. Suitability of amphibians and reptiles for translocation. Conservation Biology 23:7–15.

Goodman, R.M., F.J. Burton, and A.C. Echternacht. 2005a. Habitat use of the endangered iguana *Cyclura lewisi* in a human-modified landscape on Grand Cayman. Animal Conservation 8:397–405.

Goodman, R.M., A.C. Echternacht, and F.J. Burton. 2005b. Spatial ecology of the endangered iguana, *Cyclura lewisi*, in a disturbed setting on Grand Cayman. Journal of Herpetology 39:402–408.

Goodyear, N.C., and J. Lazell. 1994. Status of a relocated population of endangered *Iguana pinguis* on Guana Island, British Virgin Islands. Restoration Ecology 2:43–50.

Hayes, W., and R. Montanucci. 2000. Acklins Iguana, *Cyclura rileyi nuchalis*. Pp. 60–62 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Hayes, W.K., R.L. Carter, S. Cyril, Jr., and B. Thorton. 2004a. Conservation of an endangered Bahamian Rock Iguana, I. Population assessments, habitat restoration, and behavioral ecology. Pp. 232–257 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Hayes, W.K., R.L. Carter, M. Wikelski, and J.A. Sonnentag. 2004b. Determinants of lek mating success in male Galápagos Marine Iguanas: behavior, body condition, ornamentation, ectoparasite load, and female choice. Pp. 127–147 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Hayes, W.K., J.B. Iverson, C.R. Knapp, and R.L. Carter. 2012. Do invasive rodents impact endangered insular iguana populations? Biodiversity and Conservation 21:1893–1899.

IUCN. 2013. Guidelines for Reintroductions and other Conservation Translocations. Version 1.0. IUCN Species Survival Commission, Gland, Switzerland.

Iverson, J.B. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bulletin of the Florida State Museum, Biological Sciences 24:175–358.

Iverson, J.B., S.J. Converse, G.R. Smith, and J.M. Valiulis. 2006. Long-term trends in the demography of the Allen Cays Rock Iguana (*Cyclura cychlura inornata*): human disturbance and density-dependent effects. Biological Conservation 132:300–310.

Iverson, J.B., K.N. Hines, and J.M. Valiulis. 2004b. The nesting ecology of the Allen Cays Rock Iguana, *Cyclura cychlura inornata* in The Bahamas. Herpetological Monographs 18:1–36.

Iverson, J.B., G.R. Smith, and L. Pieper. 2004a. Factors affecting long-term growth of the Allen Cays Rock Iguana, in The Bahamas Pp. 176–192 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Knapp, C.R. 2000. Home range and intraspecific interactions of a translocated iguana population (*Cyclura cychlura inornata* Barbour and Noble). Caribbean Journal of Science 36:250–257.

Knapp, C.R. 2001. Status of a translocated *Cyclura* iguana colony in The Bahamas. Journal of Herpetology 35:239–248.

Knapp, C.R., and R.D. Hudson. 2004. Translocation strategies as a conservation tool for West Indian Iguanas. Pp. 199–209 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Knapp, C.R., and C.L. Malone. 2003. Patterns of reproductive success and genetic variability in a translocated iguana population. Herpetologica 59:195–202.

Langkilde, T., and K.E. Boronow. 2012. Hot boys are blue: temperature dependent color change in male Eastern Fence Lizards. Journal of Herpetology 46:461–465.

Langkilde, T., and R. Shine. 2006. How much stress do researchers inflict on their study animals? A case study using the scincid lizard, *Eulamprus heatwolei*. Journal of Experimental Biology 209:1035–1043.

Lazell, J. 1995. Natural Necker. The Conservation Agency Occasional Paper 2:1–28.

Lazell, J. 2002. Restoring vertebrate animals in the British Virgin Islands. Ecological Restoration 20:179–185.

Lemm, J.M., and A.C. Alberts. 2012. *Cyclura*: Natural History, Husbandry, and Conservation of West Indiana Rock Iguanas. Academic Press, San Diego, California, USA.

McCoy, E., and K. Berry. 2008. Using an ecological ethics framework to make decisions about the relocation of wildlife. Science and Engineering Ethics 14:505–521.

Mitchell, N., R. Haeffner, V. Veer, M. Fulford-Gardner, W. Clerveaux, C.R. Veitch, and G. Mitchell. 2002. Cat eradication and the restoration of endangered iguanas (*Cyclura carinata*) on Long Cay, Caicos Bank, Turks and Caicos Islands, British West Indies. Pp. 206–212 *In* Turning the Tide: The Eradication of Invasive Species. Veitch, C.R., and M.N. Clout (Eds.). IUCN SSC Invasive Species Specialist Group, IUCN, Gland, Switzerland, and Cambridge, United Kingdom.

Olsson, M., D. Stuart-Fox, and C. Ballen. 2013. Genetics and evolution of colour patterns in reptiles. Seminars in Cell and Developmental Biology 24:529–541.

Pérez, I., J.D. Anadón, M. Díaz, G.G. Nicola, J.L. Tella, and A. Giménez. 2012. What is wrong with current translocations? A review and a decision-making proposal. Frontiers in Ecology and the Environment 10:494–501.

Pérez i de Lanuza, G., E. Font, and P. Carazo. 2013. Color-assortative mating in a color-polymorphic lacertid lizard. Behavioral Ecology 24:273–279.

Perry, G., and G.P. Gerber. 2011. Conservation of amphibians and reptiles in the British Virgin Islands: status and patterns. Pp. 129–147 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Perry, G., M.C. Wallace, D. Perry, H. Curzer, and P. Muhlberger. 2011. Toe clipping of amphibians and reptiles: science, ethics, and the law. Journal of Herpetology 45:547–555.

Reynolds, R.G. 2011. Status, conservation, and introduction of amphibians and reptiles in the Turks and Caicos Islands, British West Indies. Pp. 377–406 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks. (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Rosenblum, E.B. 2005. The role of phenotypic plasticity in color variation of Tularosa Basin lizards. Copeia 2005:586–596.

Schofield, E. 1989. Effects of introduced plants and animals on island vegetation: examples from the Galápagos Archipelago. Conservation Biology 3:227–238.

Schwartz, A., and M. Carey. 1977. Systematics and evolution in the West Indian iguanid genus *Cyclura*. Studies on the Fauna of Curaçao and Other Caribbean Islands 53:16–97.

Seddon, P.J. 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. Restoration Ecology 18:796–802.

Smith, G.R., and J.B. Iverson. 2006. Changes in sex ratio over time in an endangered iguana (*Cyclura cychlura inornata*). Canadian Journal of Zoology 84:1522–1527.

Strong, J.S., and S.J. Leroux. 2014. Impact of non-native terrestrial mammals on the structure of terrestrial mammal food web of Newfoundland, Canada. PLoS ONE 9(8):e106264. doi:10.1371/journal.pone. 0106264.

Towns, D.R., I.A.E. Atkinson, and C.H Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8:863–891.

White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement:120–138.

Wiewandt, T.A. 1977. Ecology, behavior, and management of the Mona Island Ground Iguana, *Cyclura stejnegeri*. Ph.D. Dissertation, Cornell University, Ithaca, New York, USA. 171 p.

Wilson, B.S. 2011. Conservation of Jamaican amphibians and reptiles. Pp. 273–310 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds). Brill Academic Publishers, Leiden, The Netherlands.

Wilson, B.S., A.C. Alberts, K.S. Graham, R.D. Hudson, R.K. Bjorkland, D.S. Lewis, N.P. Lung, R. Nelson, N. Thompson, J.L. Kunna, et al. 2004. Survival and reproduction of repatriated Jamaican Iguanas: headstarting as a viable conservation strategy. Pp. 220–231 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

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Herpetological Conservation and Biology 11(Monograph 6):154–167.
Submitted: 15 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

MOVEMENTS AND NESTING OF THE LESSER ANTILLEAN IGUANA (*IGUANA DELICATISSIMA*) FROM DOMINICA, WEST INDIES: IMPLICATIONS FOR CONSERVATION

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Abstract.—**The Lesser Antillean Iguana (*Iguana delicatissima*) is endemic to the Lesser Antilles and listed as Endangered according to the IUCN Red List of Threatened Species. Dominica supports the largest population of *I. delicatissima* because of its relatively undisturbed coastal habitat. Though habitats on Dominica are relatively intact, the species is impacted by non-native species, escalating habitat loss and degradation, hunting pressure, and road mortality. To inform and expand management options on the island, we investigated nesting and hatchling-emergence activity at coastal nest sites, post-nesting migrations of females, and the impacts of roads on iguana movements. We also tested the efficacy of a mitigation strategy aimed at reducing road mortality. The nesting season on Dominica is from February to September, though peak activity occurs from April to June. We documented a skewed female sex ratio at coastal sites, along with increases in daily capture rates, during the nesting season. Females make round-trip movements (up to 4,070 m) from inland areas to coastal slopes and are thus vulnerable to vehicular collision. Over 216 days from 2007–2010, we documented 102 iguanas struck by vehicles along the Caribbean coastal road. Most mortalities were females (83%) followed by males (14%) and hatchlings (3%). Mortality rates per day after an awareness campaign and after signs were erected were reduced by almost half. We discuss the utility of using communal nest sites as indicators to assess both the number of breeding females and, indirectly, the potential for hatchling recruitment into the population.**

Abstract.—**De Antillen Leguaan (*Iguana delicatissima*) is een endemische soort van de Kleine Antillen en staat op de IUCN Rode Lijst als bedreigd geclassificeerd. Dominica herbergt de grootste *Iguana delicatissima* populatie vanwege de relatief onverstoorde kusthabitat. Hoewel het leefgebied op Dominica betrekkelijk intact is gebleven, staat de soort onder druk door invasieve diersoorten, toenemende verarming en afkalving van habitat, jachtdruk, en sterfte door het verkeer. Om de situatie in kaart te brengen, en de beheersmogelijkheden op het eiland te vergroten, onderzochten we de nestactiviteit en de bewegingen na het uitkomen van de eieren op de aan de kust gelegen nestgebieden, het migratiegedrag van wijfjes na het nestelen, en de impact van verkeerswegen op leguanenverplaatsingen. We hebben ook de doeltreffendheid getest van een mitigatiestrategie gericht op reducering van verkeerssterfte. Op Dominica wordt genesteld van Februari tot en met September. De meeste activiteit vindt plaats van April tot en met Juni. Gedurende het nestseizoen op de aan de kust gelegen studielocaties registreerden we een sex ratio van meer wijfjes dan mannen, tezamen met een toename in de dagelijkse aantallen wijfjes welke werden afgevangen. Wijfjes maken rondtrekkende bewegingen (tot 4,070 m) van landinwaarts gelegen gebieden naar de hellingen aan de kust en lopen daarmee het gevaar om aangereden te worden. Over een periode van 216 dagen tussen 2007–2010, registreerden wij 102 aangereden leguanen langs de Caribische kustweg. De meeste sterfgevallen waren wijfjes (83%) gevolgd door mannetjes (14%) en pas uitgekomen jongen (3%). Het sterftecijfer werd na een bewustmakingscampagne en het plaatsen van waarschuwingsborden met bijna de helft gereduceerd. We bepraken het nut van het gebruik van nestplaatsen als indicatoren om de aantallen nestelende wijfjes te bepalen, en indirect, het potentieel aan pasgeborenen ter versterking van de populatie.**

Abstract.—**L'Iguane des Petites Antilles (*Iguana delicatissima*) est endémique des Petites Antilles et est classé dans la catégorie En danger par La Liste rouge des espèces menacées de l'UICN. La Dominique abrite la plus importante population de *I. delicatissima* du fait de son habitat côtier relativement indemne de dérangements. Bien que les habitats de la Dominique soient relativement préservés, l'espèce est impactée par des espèces non indigènes, qui augmentent la perte et la dégradation des habitats, ainsi que par la pression de chasse, et la mortalité sur les routes. Afin de recueillir des informations et d'étendre les possibilités de gestion sur l'île, nous avons étudié l'activité de ponte et d'émergence des nouveau-nés sur des sites de ponte côtiers, les migrations des femelles après la nidification, et les impacts des routes sur les déplacements d'iguanes. En Dominique, la ponte se déroule entre février et septembre, bien que le pic d'activité se situe entre avril et juin. Nous avons relevé un sex ratio biaisé envers les femelles sur les sites côtiers, ainsi qu'une augmentation des taux de captures journaliers, pendant la saison de ponte. Les femelles réalisent**

Knapp, Charles R., Lindon Prince, and Arlington James. 2016. Movements and nesting of the Lesser Antillean Iguana (*Iguana delicatissima*) from Dominica, West Indies: implications for conservation. Pp. 154–167 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

des migrations aller-retours (jusqu'à 4,070m) depuis les zones intérieures jusqu'aux pentes côtières et sont donc vulnérables face aux collisions routières. Sur 216 jours entre 2007 et 2010, nous avons relevé 102 iguanes victimes de collisions le long de la route côtière caribbéenne. La majorité des mortalités concernaient les femelles (83%), suivies par les mâles (14%) et les nouveau-nés (3%). Les taux journaliers de mortalité par collision avec des véhicules ont été presque réduits de moitié après une campagne de sensibilisation et la pose de panneaux. Nous discutons de l'utilité de se servir des sites de ponte collectifs comme indicateurs pour estimer le nombre de femelles gestantes et, indirectement, le potentiel de recrutement des nouveau-nés dans la population.

Key Words.—communal nesting; migration; morphology; road mortality; telemetry

INTRODUCTION

The Lesser Antillean Iguana (*Iguana delicatissima*; Fig. 1) is a large species living up to 25 years with a maximum recorded snout-vent length (SVL) of 43.4 cm (Breuil et al. 2010). The iguana once occupied most islands from Anguilla to Martinique in the West Indies. However, based on historical range data, the total population of *I. delicatissima* has most likely declined ≥ 70% since European contact, and the existing population is fragmented (Breuil et al. 2010). Moreover, only three island populations (Îles de Petite Terre, La Désirade, Dominica) are considered relatively stable, while others have been extirpated within the last decade. The proximate drivers for these contemporary extirpations are habitat destruction, hunting, introduction of exotic predators and competitors, and hybridization with Green Iguanas (*I. iguana*). Consequently, the Lesser Antillean Iguana is listed as Endangered according to International Union for Conservation of Nature Red List of Threatened Species criteria (Breuil et al. 2010) and can now be found only on the islands of Anguilla, St. Barthélemy (including the islands of Île Fourchue), St. Eustatius, Guadeloupe (including only the islands of Basse-Terre, Îles de Petite Terre, La Désirade), Dominica, and Martinique (including Îlet Chancel and Ramier; Knapp et al. 2014). Dominica is believed to support the largest single population of *I. delicatissima* due to the extent of available coastal habitat, whereas Les Îles de la Petite Terre supports the highest population density.

The Lesser Antillean Iguana occupies a diverse suite of habitats across its range, including xeric scrub, dry scrub woodland, littoral woodland, mangrove, as well as lower and mid-altitude portions of transitional rainforest. The diversity and condition of these habitats varies by island and iguanas demonstrate unique natural history attributes relative to their environment (see Henderson and Powell 2009 for detailed synopsis of natural history). Therefore, any management program for the Lesser Antillean Iguana must include specific ecological data relative to habitat features. For example, some female *I. delicatissima* inhabiting larger volcanic islands migrate annually from island interiors to nest communally along coastal slopes (Knapp et al. 2014). During these migrations, gravid females are highly vulnerable to vehicular collisions along coastal roads. However, the extent of mortality and its demographic effects are unknown for any population in the Lesser Antilles. Therefore, investigations are crucial to determine the timing and migration routes of nesting females, rates of road mortality, and road attributes that increase the susceptibility to vehicular collision.

The congregation of migrating females at coastal nesting sites provides a cost effective and efficient opportunity to quantify female populations over time. The relationship, however, between non-nesting to nesting populations in an area must be understood for accurate island-wide extrapolations, and to assess the health of coastal habitats. The relative contribution of specific nesting sites to the overall island population is also critical for prioritizing protection for highly influential nesting areas. Furthermore, understanding specific threats while females are at nest sites would refine mitigation strategies.

In an effort to inform conservation management for *I. delicatissima,* we investigated individual morphometrics and sex ratios within and outside the nesting season, post-nesting migrations of females, and the impacts of coastal roads on iguana movements. We also studied nesting ecology and hatchling emergence from the most important nest site identified in the study. Finally, we tested the acute efficacy of a mitigation strategy aimed at

FIGURE 1. The Lesser Antillean Iguana (*Iguana delicatissima*), Dominica. (Photographed by Charles R. Knapp).

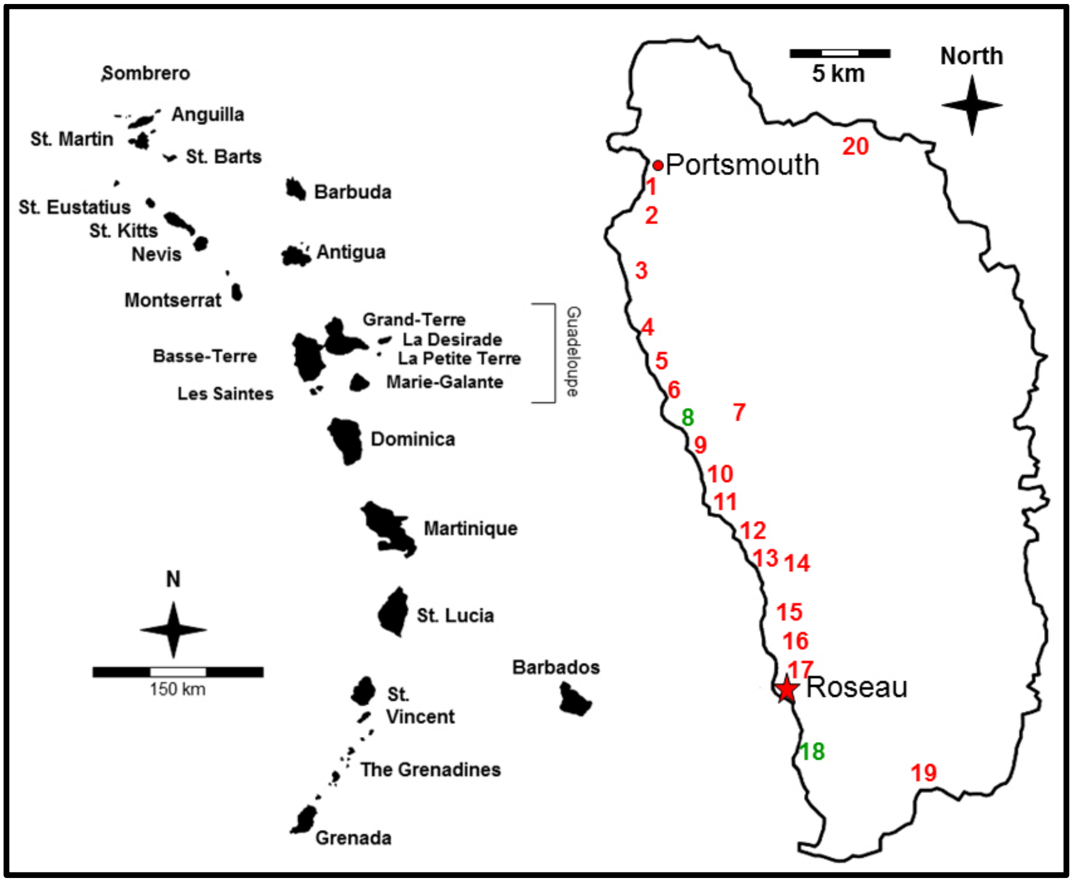

FIGURE 2. Map of Lesser Antilles, West Indies (left) along with capture locations for *Iguana delicatissima* on Dominica (right). Numbers indicate capture locations: (1) Ross University Campus; (2) Picard; (3) South Bioche slope; (4) Colihaut; (5) Coulibistrie Quarry; (6) Coulibistrie; (7) Roche d'Or Estate; (8) Batali Beach; (9) Salisbury; (10) Salisbury/Macoucheri slope; (11) Mero; (12) St. Joseph; (13) Layou; (14) Layou Valley; (15) Hummingbird Inn; (16) Goodwill; (17) Roseau; (18) Champagne Bay; (19) Grand Bay; and (20) Woodford Hill. Green numbers (8 and 18) represent the communal nest sites in this study.

reducing road mortality. Results from this study are not only applicable to I. delicatissima from Dominica but aspects can be applied to conspecific and congeneric populations across the Lesser Antilles.

MATERIALS AND METHODS

***Study area and field seasons*.**—Dominica is one of the largest of the eastern Caribbean islands (48 km long and 24 km wide) with a maximum altitude of 1,447 m. This study was conducted on the Caribbean (leeward) coast, which is characterized primarily by xeric woodland and relatively low rainfall (< 2,000 mm) with a pronounced dry season from February to May. The vegetation is primarily deciduous with leaves falling during the dry season (Malhotra et al. 2007).

We conducted research during two continuous field seasons (April through June; August through September) each year from 2007 to 2009, and from April through June 2010. Our April through June field seasons coincided with female migrations to nest sites and nesting activity while the August through September field seasons coincided primarily with hatchling emergence. We searched for iguanas across the island but the majority of effort, and most captures (18 of 20 sites; Fig. 2), occurred in villages and natural areas on the Caribbean side of the island (see Knapp and Perez-Heydrich 2012). Captures (71%) were concentrated on the coastal slopes of the two recorded communal nest sites at Batali Beach (15°27′01.15″N; 61°26′49.92″W) and Champagne Bay (15°14′48.20″N, 61°22′22.09″W). The Batali Beach site is a Caribbean coastal slope 350 m in length located south of the Batali River. Female iguanas converge on the slope during the nesting season but concentrate most of their nesting in one communal area. The Champagne Bay nesting site is a Caribbean coastal slope 350 m in length located adjacent to the Soufriere-Scott's Head Marine Reserve. Iguanas can be found nesting along the entire slope and not necessarily concentrated at one communal site.

***Morphometrics, tail breaks, and capture history*.**—We captured free-ranging iguanas by noose to record morphometrics including snout-vent length (SVL), tail length (TL) from unbroken tails, body mass (BM), head width (HW), and maximum dorsal spine length. We noted tail breaks and determined sex by cloacal probing for hemipenes. For long-term identification of individual iguanas, we affixed a unique combination of 4-mm colored glass beads through their dorsal crest (Rodda et al. 1988), and injected PIT tags beneath the epidermis on the right dorsolateral side directly anterior to the pelvis. We log-transformed all morphologic variables and compared SVL between sexes using *t*-tests. We used ANCOVA with SVL as a covariate to assess differences between sexes in TL, BM, HW, and maximum dorsal spine length. In analyses where the slopes were not significantly different ($P > 0.05$), interaction terms were deleted and the analyses recalculated to investigate possible differences in intercepts (Sokal and Rohlf 1995). We analyzed data only from iguanas considered adults (≥ 25.0 cm SVL) based on the smallest female confirmed gravid during the study. We used BM data only from females captured during the non-nesting season because most females in the nesting season were captured either gravid, or after having recently oviposited. We compared tail break frequencies by sex, as well as sex ratios of all captures during nesting and non-nesting field seasons using chi-square tests. Daily capture rates were compared between seasons using a *t*-test. Results are reported with ± 1 SD and significance level set at $\alpha = 0.05$ throughout the paper.

Telemetry.—We affixed radio transmitters (Holohil Systems, Inc., Carp, Ontario, Canada; model RI-2C, 11.3 g) using a suture technique (described in Goodman et al. 2009) to the anterior dorsal crest of 9 and 21 female iguanas in 2008 and 2009, respectively. Females were captured after ovipositing at the Batali communal nest site. Transmitter-to-BM ratios ranged from 0.7–1.3%, below the recommended threshold of 7.5% for arboreal lizards (Knapp and Abarca 2009). We tracked females from April to June, and August each year using a hand-held 3-element Yagi directional antenna and a TRX-48S receiver (Wildlife Materials, Inc., Carbondale, Illinois, USA). Only one location per tracking day was recorded for each relocated iguana.

Nesting ecology and hatchlings.—To document nesting activities, we erected an observation blind overlooking the communal nest site at Batali Beach and observed iguana activity for a minimum of one hour every other day from April to June, 2008 and 2009. The communal nesting area is located 20 m from the Caribbean Sea in an exposed portion of the west coastal slope (~ 45°). The slope remains exposed and nearly vegetation-free because of continuous digging by females during the nesting season (Fig. 3). We also observed and documented nesting females opportunistically at the Champagne Bay nesting site over the course of the study.

In order to record patterns and numbers of emerging hatchlings, we constructed a 98 m^2 enclosure of construction plastic surrounding approximately 50% of the main communal nesting area at Batali communal nest site (Fig. 3). The enclosure was erected from August to September in 2008 and 2009. We monitored the enclosure a minimum of six times per day from 0630 to 1830. Hatchlings were either captured by hand or removed from buckets that were sunk along the fence at the bottom of the enclosure. We also monitored the enclosure using camera traps and time-lapse video. Iguanas collected at the enclosure were weighed, measured, marked numerically with white correction fluid, and released outside the enclosure. In order to speed processing time and eliminate possible complications detecting hemipenes, we did not determine sex via probing or permanently mark hatchling iguanas from the enclosure.

Road mortality.—Each field season from April 2008 to June 2010, we drove one of two coastal road segments (north and south) every other day to record locations of road mortalities. The Caribbean coastal road is narrow (~ 4.5 m wide), curves extensively, veers inland for bridge crossings when rivers meet the sea, and passes through natural areas, plantations, smaller villages, and the capital. Land to the east of the road can vary from cliffs to flat topography, while the west side is edged typically by coastal slope or beach. The north segment ranged from the Batali River to Dublanc (11 km). The south segment ranged from the Batali River to Champagne Bay (29 km). Mortalities were also recorded opportunistically when a deceased iguana was spotted while driving regardless of reason. We augmented our records through confirmed reports from the Dominica Forestry, Wildlife and Parks Division. When permissible according to the condition of carcasses, we performed necropsies and recorded sex and SVL for all iguanas, and clutch size, egg length, egg width, and egg mass for

FIGURE 3. Batali communal nest site used by *Iguana delicatissima* on Dominica. The site is enclosed by a drift fence measuring approximately 14 m x 7 m. (Photographed by Charles R. Knapp).

FIGURE 4. Bumper sticker to protect *Iguana delicatissima* distributed on Dominica. The same iguana character was used in the road signs. (Artwork and design by Joel Friesch and John Binns).

gravid females. We analyzed the relationship between SVL and clutch size using least squares regression.

In May 2008, we initiated an awareness campaign focusing on the need to protect iguanas. Until the end of the study, we lectured at schools, presented to the Dominica Forestry, Wildlife and Parks Division officers and at the University of the West Indies Dominica campus, conducted radio and television interviews, and distributed bumper stickers across the island asking people to slow for iguanas (Fig. 4). Preliminary mortality results suggested that the highest concentration of vehicular collisions occurred in the 870 m stretch of road above the communal nest site at Batali Beach. Therefore, on 1 July 2009, road signs asking people to slow for iguanas were erected on the north and south ends of this road segment above the Batali communal nest site. All recorded collisions in this study occurred during the nest migration period (April to July) each year. To control for differences in survey duration from April to July before and after signs were erected, we calculated mortality rates per day before (122 survey days) and after (94 survey days) erecting signs. Rates of collisions pre- and post-signing were evaluated using chi-square tests.

RESULTS

***Morphometrics, tail breaks, and capture history*.**—We captured 1,410 free-ranging iguanas (excluding hatchlings from the enclosure) representing 1,127 individuals. Snout-vent length (t = 1.073, df = 866, P = 0.284) and BM (ANCOVA: $F_{1,213}$ = 3.601, P = 0.059) for adult iguanas in our study did not differ statistically between males and females (Table 1). However, TL (ANCOVA: $F_{1,752}$ = 60.426, $P < 0.001$) and maximum dorsal spine length (ANCOVA: $F_{1,863}$ = 388.147, $P < 0.001$) did differ statistically by sex (Table 1). Slopes for head width were heterogeneous between sexes (ANCOVA: $F_{1,561}$ = 18.032, $P < 0.001$) suggesting that as males grow, HW increases at a higher rate proportionally (Fig. 5). Tail break frequencies between all males (6.0%; 18 of 302 males) and females (4.5%; 37 of 825 females) in the study did not differ statistically (χ^2 = 1.037, df = 1, P = 0.309). Tail break frequencies also did not differ (χ^2 = 2.293, df = 1, P = 0.130) between males (7.3%; 14 of 191 males) and females (4.6%; 31 of 677 females) classified as adults in our study (> 25.0 cm SVL).

Despite accounts of iguanas inhabiting the east (Atlantic) side of Dominica, we only captured two iguanas on the northeast side (Woodford Hill) and one iguana on the southeast side (Grand Bay) despite 176 person hours of searching. Iguanas are less dense on the east side of Dominica and the tall trees make capture difficult. Instead, iguanas were captured at 18 locations on the Caribbean slope at elevations up to 315 m above msl. We did, however, observe a pair of iguanas regularly in the trees of the Picard Gorge (550 m above msl) opposite the parrot viewing overlook on the Syndicate Nature Trail in the Morne Diablotin National Park (reported initially in Malhorta et al. 2007). Sex ratios of captured iguanas differed significantly by season (χ^2 = 28.744, df = 1, $P < 0.001$) with relatively more females (72%, 894 females from 1,246 total captures) being captured in the nesting versus the non-nesting season (51%, 84 females from 164 total captures). Indeed, 63.4% of all 1,410 captures in the study were females from our field seasons that corresponded with nesting (April to June). Captures per day were significantly greater (t = 4.998, df = 157, $P < 0.001$) during the nesting (mean daily captures = 9.6 ± (SD) 3.9 (range, 3–23 daily captures) versus non-nesting (mean daily captures = 5.7 ± (SD) 3.3 (range, 1–12 daily captures) seasons.

***Telemetry*.**—Telemetered female iguanas ranged in SVL from 29.5 to 35.9 cm (mean = 32.7 cm) and in BM from 900 to 1,620 g (mean = 1,174 g), and were tracked from 3 to 119 days post-oviposition (mean = 40 days) in the Batali River Valley. Because of challenges associated with radio-tracking in a narrow valley with steep slopes (e.g., rebounding transmitter signal, inaccessible slopes), only 18 of 30 females were relocated a mean of 11.1 ± 4.3 times (range, 2–17 relocations). Mean distance of last relocation was 1,248 ± 1,077 m (range, 45–4,070 m) from the communal nest site. Mean elevation recorded at last relocation was 87 ± 83 m (range, 12–315 m). Though some females lingered at the communal nest site prior to moving inland, we recorded females returning up the valley at daily rates up to 467 m (1,403 m total distance for the individual tracked over three days). The only female telemetered in both tracking seasons was last relocated within 300 m of the previous year (3,100 m from nest site).

Nesting ecology and hatchlings.—The description of nesting female activity is based on composite observations of more than 50 females, primarily at the

TABLE 1. Means and standard deviations of un-transformed body-size values for *Iguana delicatissima* on Dominica. Ranges are in parentheses and sample sizes in brackets.

	Body mass (g)	**SVL (cm)**	**TL (cm)**	**HW (mm)**	**Max. dorsal spine (mm)**
Males	1,304.5 ± 523.2 (610–3,690) [191]	30.3 ± 3.6 (25.0–42.8) [191]	77.3 ± 6.3 (66.6–97.9) [172]	40.2 ± 5.6 (31.1–58.4) [125]	20.1 ± 3.9 (12.4–28.8) [191]
Females	1,130.8 ± 223.8 (790–1,560) [26]	30.0 ± 2.7 (24.0–38.6) [677]	75.0 ± 4.9 (64.6–90.3) [617]	36.3 ± 3.4 (29.1–47.2) [440]	15.9 ± 2.5 (7.8–27.7) [675]
Hatchlings	15.7 ± 2.1 (8.8–21.8) [1,117]	7.8 ± 0.3 (6.2–8.8) [1,117]	21.3 ± 1.28 (15.0–23.8) [1,117]	—	—

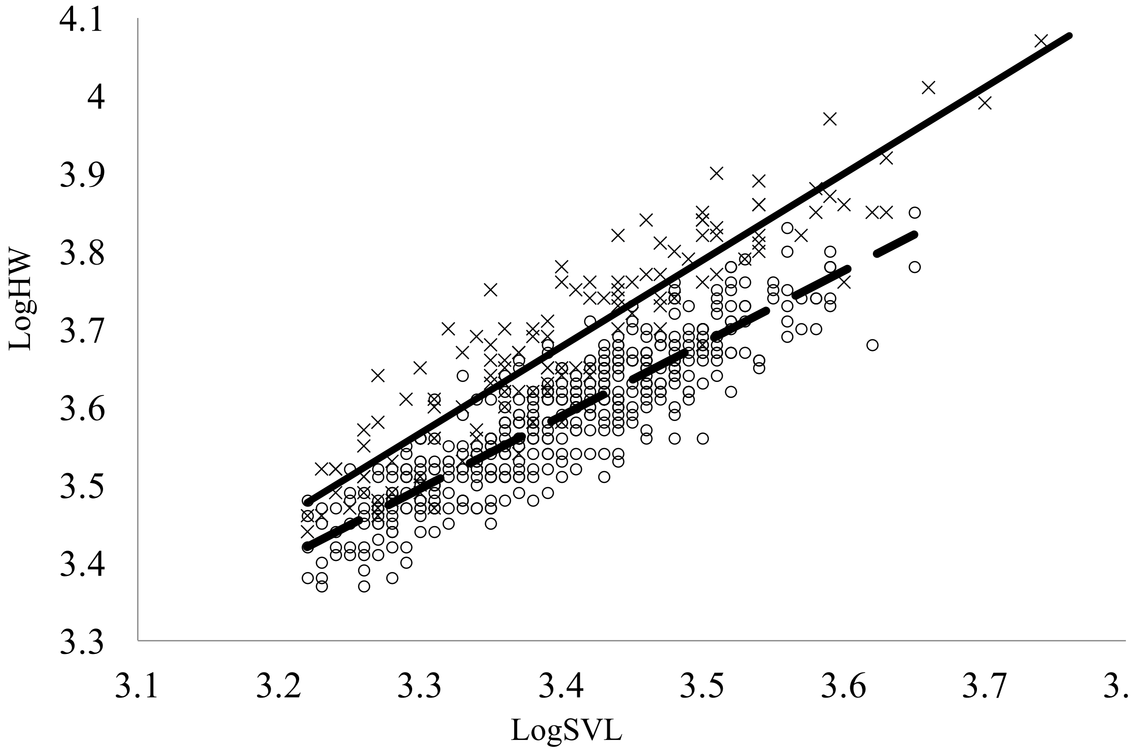

FIGURE 5. Relationship between log-transformed snout-vent length and head width for adult *Iguana delicatissima* from Dominica. Open circles and the dashed trend line represent females. Crosses and the solid trend line represent males.

Batali nest site, over three nesting seasons (2008–2010). Copulation events were observed opportunistically at Batali on 24 April and 5 May 2007, 16 and 25 April 2008, 25 April 2009, and 17 and 20 April 2010. At the Batali communal nest site, nesting activity begins in earnest at the start of April and peaks in mid-May. Although infrequent, recently emerged hatchlings were captured on 3 May and 15 June 2008 at Champagne Bay and Batali Beach, respectively. Additionally, recently emerged hatchlings have been reported in December (Arlington James, pers. obs.). Assuming a three-month incubation period (Breuil et al. 2010), these records suggest that nesting season on Dominica is from February to September.

Hundreds of females converge on communal nest sites from April to June and congregate in trees that retain their foliage (e.g., *Capparis* spp.) during the dry season. As many as 15 female iguanas, with one male, were observed within a 5 m tree-crown diameter at the Batali communal site. At the Batali nest site we captured 76, 102, and 227 females during the 2008, 2009, and 2010 nesting seasons, respectively. Of the 405 adult female iguanas captured during the 2008–2010 nesting seasons, 9.4% (*n* = 34) were recaptures from the previous season, though camera traps confirmed additional marked, uncaptured females in the area. Over the same three-year nesting period, we captured 56, 41, and 69 female iguanas at the Champagne Bay nest site, of which 4.2% (*n* = 7 recaptures of 166 adult females) were recaptures from the previous nesting season.

Female iguanas excavate burrows primarily in the morning and late afternoon, but we have confirmed via camera traps that females can also dig midday. As many as eight iguanas were observed digging at one time. Females are extremely wary while on nesting slopes and flee when minimally disturbed (e.g., view of human observer at distances > 30 m). Exploratory activity and excavation are similar to those described in aggregating Green Iguanas in Panamá (Rand 1968). The soil at the Batali nest site is fine and prone to erosion and collapse so we did not excavate burrows in order to preserve the integrity of the nesting slope. However, we did probe more than 15 burrows and they were all more than 1 m long. Females also nest along beaches and we observed iguana nest excavations resulting in sea turtle eggs being ejected from nests.

Similarly to gravid Green Iguanas that excavate at communal nest sites (Rand 1968), gravid *I. delicatissima* will defend their burrow while in progress, but the aggression fades once spent females exit burrows and finish covering the entrance. Indeed, we did not observe females actively guarding nests from the surface. Spent females left immediately after nest closure and retreated to surrounding trees before migrating back to their activity centers. As with Green Iguanas at the same communal nest site in Panamá (Rand 1968), eggs from previous nesting females are often ejected when late-arriving females excavate new nests. On 31 occasions from 27 April to 30 June 2008, we recorded a total of 160 eggs (range, 0–22 eggs per day) ejected from the site. This total is considered a minimum as ejected eggs were assuredly missed during the season. The constant digging by females and the fragile structure of the slopes can result in rock slides. We recorded two deaths ostensibly as a result of iguanas being hit by falling rocks. We also recorded an iguana trapped by dirt and rocks anterior to its hind legs as it was emerging from its nest burrow. Another iguana was buried headfirst in a burrow with only her tail exposed above the surface. Based on necropsy data from 34 road-killed females, mean clutch size was 12.5 ± 5.2 eggs (range, 4–26 eggs). There was a significant positive relationship between SVL and clutch size ($F_{1,14}$ = 6.152, P = 0.026; Fig. 6). Mean recorded egg mass was 19.6 ± 2.8 g (range, 10.0–23.7 g), mean egg length was 45.3 ± 3.1 mm (range, 31.3–51.8 mm), and mean egg width was 29.5 ± 2.4 mm (range, 24.0–34.5 mm).

At the Batali nest site enclosure, we collected 713 and 548 hatchlings from 17 August to 17 September 2008 and 16 August to 14 September 2009, respectively (Table 1). It is likely that hatchlings escaped, however, as heavy rain events caused breaches in the fence on two occasions each year. Hatchlings typically emerged from the ground between the hours of 0630 and 1000, or between 1300 and 1600. Mean daily emergence rates from the enclosed nest area in 2008 and 2009 were 22.3 ± 15.7 hatchlings (range, 0–58 hatchlings) and 17.8 ± 15.8 hatchlings (range, 1–61 hatchlings), respectively (Fig. 7). The most significant predator of iguana hatchlings is the Dominican Ground Lizard (*Ameiva fuscata*). In the 2008 nesting season, we recorded a minimum of eight predation events involving *A. fuscata* as these lizards patrolled the communal nesting area and entered emergence holes. During the 2008 nesting season, we also observed four snakes (*Alsophis sibonius*), a marine crab (*Grapsus grapsus*), and an American Kestrel (*Falco sparverius*) preying on iguana hatchlings.

Road mortality.—A total of 102 iguanas was recorded killed on roads from 2007 to 2010. Of the 72 iguanas that could be sexed reliably, 83% (*n* = 60) were females, 14% (*n* = 10) males, and 3% (*n* = 2) hatchlings. Most iguanas (57%, *n* = 58) were struck and killed on the 870 m segment of road above the Batali Beach communal nest site. At least 34 (57%) of the 60 females were gravid and migrating to the nest site. The remaining 29 females were assumed to be returning inland after recent coastal nesting activity. This assumption is supported by a marked, non-resident female that was killed eight days after oviposition, the absence of eggs in other females, and the lack of documented road kills outside the nesting season. Mortality rates per day from vehicle collisions

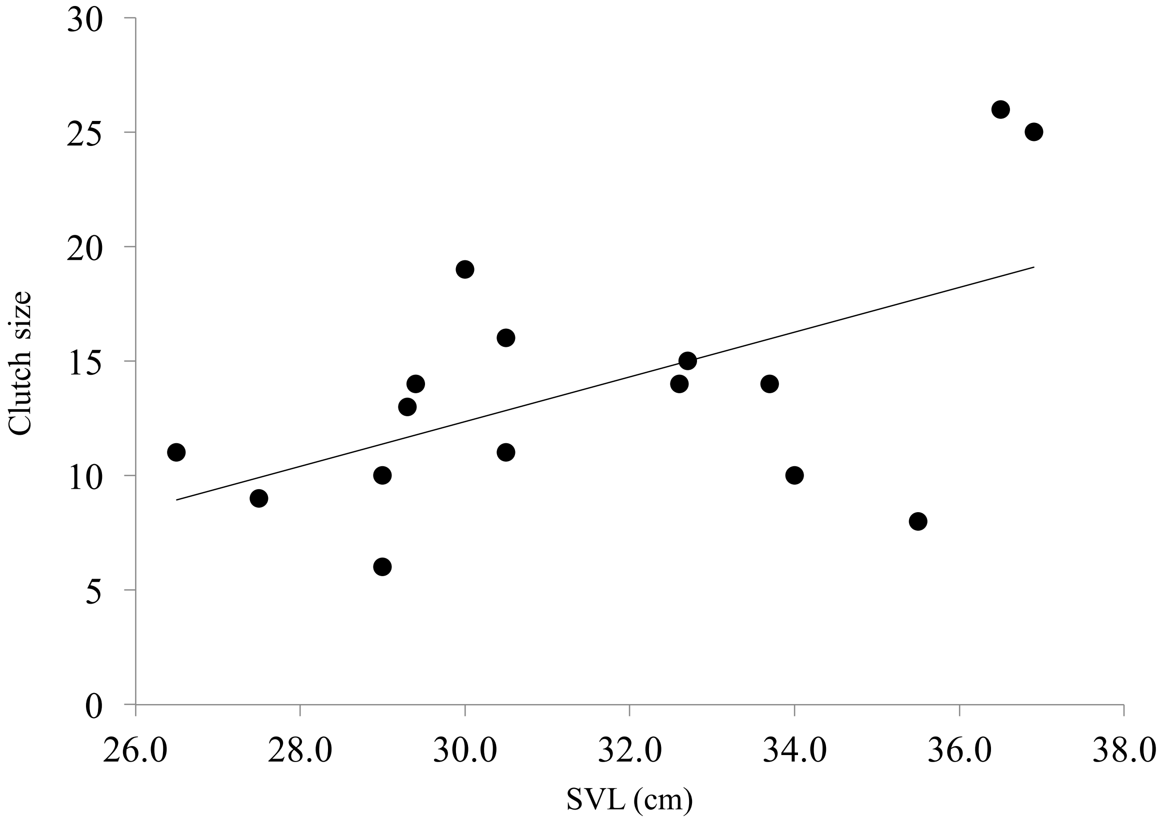

FIGURE 6. Relationship between snout-vent length and clutch size for adult *Iguana delicatissima* from Dominica.

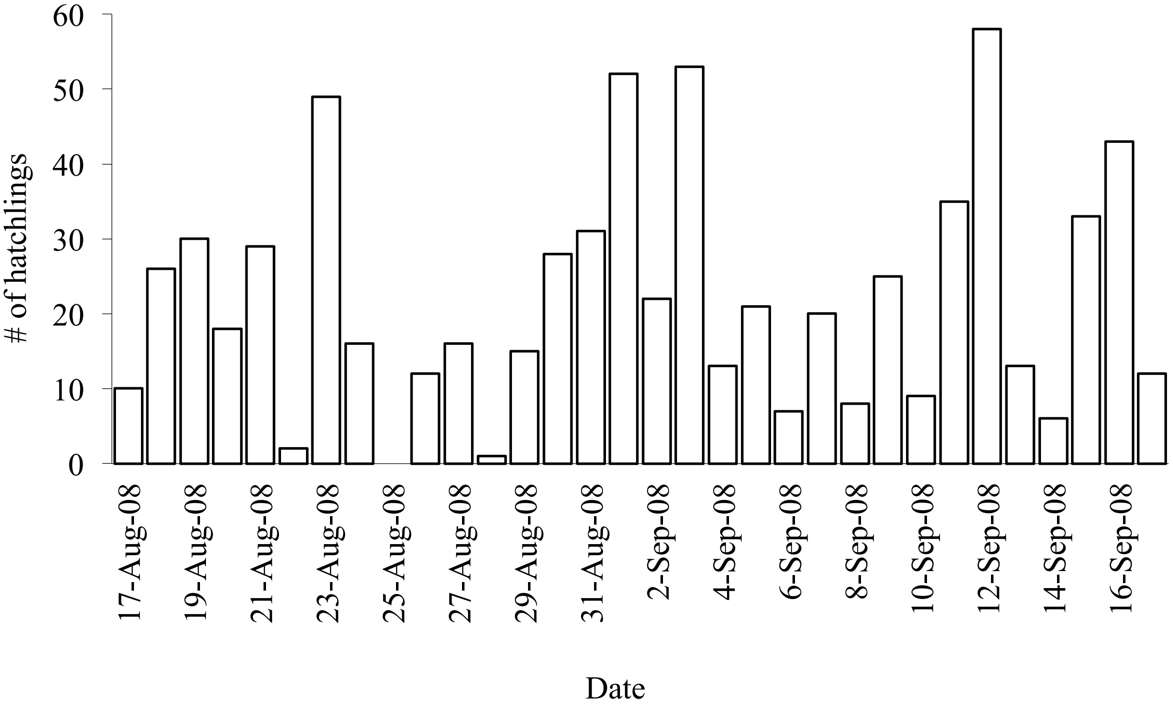

FIGURE 7. Daily emergence of *Iguana delicatissima* hatchlings from 17 August to 17 September 2008 at the Batali communal nest site, Dominica.

after the awareness campaign and signposting were reduced significantly across the island (0.6 versus 0.32 collisions per day; $\chi^2 = 24.863$, df = 1, $P < 0.001$), above the Batali communal nest site (0.35 versus 0.18 collisions per day; $\chi^2 = 12.356$, df = 1, $P < 0.001$), and over the remaining coastal road (0.25 versus 0.14 collisions per day; $\chi^2 = 6.721$, df = 1, $P = 0.009$; Fig. 8).

DISCUSSION

Adult male and female Lesser Antillean Iguanas on Dominica do not differ statistically in SVL or BM, which is unusual (e.g., Wikelski and Trillmich 1997; Beovides-Casas and Mancina 2006; Pasachnik et al. 2012) within the Iguaninae (*sensu* Iguana Taxonomy Working Group of the IUCN SSC Iguana Specialist Group (ITWG) this volume) but may be attributed to an abundance of females in our sample. Male *I. delicatissima* do, however, attain larger maximum body sizes (Table 1). Controlling for SVL, males have longer tails and dorsal spines than females, which is consistent with sexual dimorphism in the congener *I. iguana* (Fitch and Henderson 1977). Longer TL in male iguanas may be influenced by sexual selection. Huyghe et al. (2013) reported that male Common Lizards (*Zootoca vivipara*) with longer tails had a higher probability of mating with females. The difference in tail length of adults could also be attributed to the arboreal ecology of the species. Arboreal lizards tend to have relatively long tails used for balance (Ji et al. 2002). For example, TL represents 75% of total adult body length in the arboreal Oriental Garden Lizard (*Calotes versicolor*) (Ji et al. 2002), while TL represents 72% of total adult length in *I. delicatissma* from Dominica. In contrast, TL represents a smaller percentage of total adult length in ground-dwelling lizards such as the Gila Monster (*Heloderma suspectum*) and Beaded Lizard (*Heloderma horridum*) (32% and 44%, respectively; Gienger and Beck 2007), *Cyclura rileyi nuchalis* (60%; Iverson et al. this volume), and *Liolaemus aparicioi* (66%; Ocampo et al. 2012). The balance benefits of longer tails in large arboreal male *I. delicatissima* may confer advantages in territorial disputes among branches; however, further research is needed to elucidate any sex-specific advantages of greater lengths.

The divergence of HW as adults grow is expected because many male reptiles that exhibit male-male combat demonstrate larger head sizes than females (Alberts et al. 2002; Gienger and Beck 2007). Tail break frequencies for this arboreal species (up to 7.3%) were lower than reported for terrestrial iguana species from other genera such as *Cyclura* (up to 64.5%; reviewed in Hayes et al. 2012) and *Ctenosaura* (up to 51.9%; Pasachnik et al. 2012; Pasachnik 2013) and similar statistically between sexes in this study. The lower break

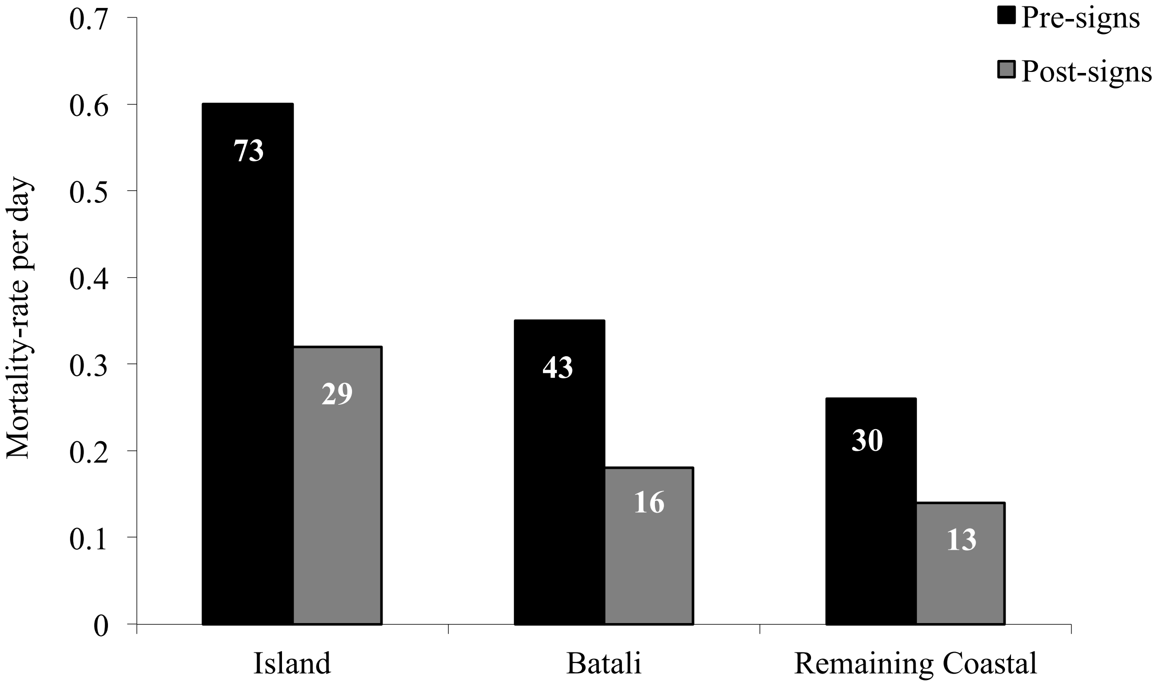

FIGURE 8. Raw mortality rates per day of *Iguana delicatissima* from vehicle collisions before and after the start of an awareness campaign and sign postings above the Batali communal nest site on Dominica. Graph represents data from the entire island, only the 870 m stretch of road above the Batali nest site, and the remaining coastal road. Sample sizes are embedded within the bars.

frequencies may be associated with reduced predation pressure on an arboreal insular iguana species or more resource allocation on the island (Iverson et al. 2004). The lower break frequencies in females may also potentially be attributed to a lack of nest defense in *I. delicatissima* on Dominica. Nest defense in spent females occurs in many other iguana species including *Amblyrhynchus cristatus*, *Brachylophus* spp., *Conolophus pallidus*, *Cyclura* spp., and *I. iguana* (reviewed in Wiewandt 1982; Iverson et al. 2004), and is suspected to elevate tail break frequencies in females (Knapp 2000). Arboreal lizards that experience tail loss may be impacted more significantly because of impaired locomotor abilities such as speed, endurance, momentum, and balance (reviewed in Clause and Capaldi 2006; Maginnis 2006; Bateman and Fleming 2009). Hence, selection may favor a reduction in tail autotomy in arboreal species.

Sex ratios of captured iguanas were skewed significantly toward females in the nesting season. The skewed sex ratio along with increases in daily capture rates during the nesting season were the result of females that migrated from inland areas to coastal sites. With this species, the skewed sex ratios and inflated population numbers during the nesting season, regardless of island, must be considered when analyzing longitudinal population trends (e.g., Lorvelec et al. 2011) as estimates will vary widely depending on the time of year and intra-island location of surveys. Considering these factors, annual female nesting effort at communal sites could be a useful indicator to assess both the number of breeding females and, indirectly, the potential for hatchling recruitment into the population. Moreover, in the absence of labor-intensive monitoring programs, the capacity to assess annual activity and variation in nesting coastal populations provides managers with a simple strategy for assessing trends in Lesser Antillean Iguana populations, assuming that nesting areas can be located and annual survey efforts remain constant.

The potential utility of assessing population trends via communal nesting sites underscores their sensitivity to perturbations. Tourists and livestock can trample communal sites and destroy nest chambers (Breuil 2009). The concentration of nesting females at communal sites also increases their susceptibility to poaching. We observed an excavating female, that was close to the coastal road above the Batali site, taken by a person who only had to step out of his car. At times, coastal slopes on Dominica are used to dump trash and large items such as appliances. The Batali communal nest site was compromised during the 2009 nesting season when items including appliances and tires were discarded down the slope directly above the nest site. Signs were posted at the incipient dumpsite but the activity continued.

Coastal slopes in the Caribbean are also sensitive to extreme weather events such as hurricanes, which undermine their integrity, trigger landslides, or cause severe erosional furrows (Walker et al. 1991). In August 2007, Hurricane Dean struck Dominica causing part of the slope above the Batali communal nesting site to fail, resulting in the loss of hatchlings and nests (Knapp and Valeri 2008). Therefore, preserving the integrity of coastal slopes by enforcing a no dumping policy and constructing coastal roads away from nesting slopes to reduce the potential for landslides must be made a priority for any serious effort at protecting nesting populations of *I. delicatissima*.

Admittedly, redirecting roads may pose a challenge because in tropical island systems such as the Caribbean, road construction and development occurs primarily along coastal areas. Furthermore, construction practices in these systems rarely consider the impacts of development on terrestrial wildlife (Myers et al. 2000; Knapp 2004). Indeed, reptiles are particularly susceptible to the effects of roads, which are unequivocally a major source of mortality for many species and likely pose risks to population viability (Andrews et al. 2008). For example, hundreds of Green Iguanas (*I. iguana*) from Isla de Salamanca in Columbia have been reported killed by vehicles during the breeding season (Harris 1982). On Salamanca, both male and female Green Iguanas were reported on the road, whereas with *I. delicatissima* on Dominica, vehicles kill females disproportionately. This disparity is the result of female migrations to and from nest sites and could prove particularly harmful, especially since disproportionate deaths have the potential to perturb sex ratios, resulting in demographic side effects that destabilize the population (Marchand and Litvaitis 2004).

We identified a < 1 km stretch of road above the Batali nesting site that is responsible for the majority of iguanas (57%) killed by collisions with vehicles. Our ability to identify a relatively short stretch of roadway that is disproportionately responsible for iguana deaths is important and serves as a conservation opportunity. The high costs of physical structures such as overpasses, limits their installations to a few sites and are most likely not realistic for island nations. Other less costly measures (e.g., signposting as in this study) are not effective if installed over long stretches of roads (Malo et al. 2004), therefore our targeted approach using signposting along a < 1 km stretch of road in association with outreach campaigns offers a reasonable chance for success.

Fortunately, the results from our outreach campaign and signposting suggest that these initiatives can play a role in reducing collision mortality. Continuous outreach messaging can be a challenge for some island nations and thus more work is needed to determine the sustained efficacy of a combined campaign of messaging and signs, or signs only. We suspect, however, that without consistent messaging leading up to the nesting season, people will revert back to unsafe and fast driving because female movements are seasonal and easily forgotten. Another mitigation option is the installation of rumble strips on the pavement to remind drivers to reduce speed through sensitive areas.

Based on our extensive search of coastal slopes on the Caribbean side of Dominica, in addition to interviewing people along the coast, the communal nest site at Batali appears to be the most important remaining nesting area on the island. We recorded 713 and 548 hatchlings in 2008 and 2009, respectively, with an additional 160 eggs ejected from nests in 2008. Based on the mean clutch size in this study (12.5 eggs) and estimated eggs ejected (*n* = 160), at least 70 and 57 female iguanas used the area that was enclosed in 2008 and 2009, respectively. However, our enclosures around the nest site included only an estimated 50% of the main site, and 30% of the available nesting area on the entire slope. Factoring the area of the entire slope, and mortality due to vehicle collisions prior to reaching the nest site, we estimate conservatively that 260 female iguanas use, or attempt to use, the Batali nesting slope each year.

The nesting site at Champagne Bay is also important but less concentrated, as females nest intermittently along the 350 m slope. The Champagne Bay nest site is adjacent to a marine protected area, which offers some protection for nesting females. However, the site is a tourist attraction and visitors often walk down the boardwalk and along the slope, thus disrupting nesting activity. Spotting scopes, interpretive graphics, visual barriers, and discussions with guides would enhance the tourist experience during the nesting season and offer further incentive to protect the area.

Telemetry data suggest that female iguanas can make long-distance migrations (recorded up to 4,070 m) from inland areas to coastal nesting sites. Migration of females from normal activity centers to distant nesting sites is typical of iguanids (Wiewandt 1982; reviewed in Iverson et al. 2004). Green Iguanas have been observed migrating up to 3 km to a communal nest site in Panamá (Montgomery et al. 1973; Bock et al. 1989). The most extreme example of female migration (exceeding 10 km to a 1,500 m maximum altitude) includes Galápagos Land Iguanas (*Conolophus subcristatus*) from Fernandina Island in the Galápagos. The costs associated with this long-distance migration are high and estimated to constitute half of the reproductive effort (Werner 1983). The energetic costs associated with nesting migrations on Dominica may influence the frequency of nesting and is worth further scrutiny (see below).

The use of telemetry in this study greatly extended the maximum range of movement recorded previously for *I. delicatissima* (1,800 m; Breuil 2000). All but three of the 18 females from the Batali communal nest site returned and remained within the Batali River Valley. Indeed, the one female tracked in both years made the equivalent round-trip migration and was relocated in the same area as the previous year, suggesting that the valley and coastal slopes are intricately connected. Our relocations underscore the importance of preserving intact migration corridors for females. The three females that exited the Batali River Valley returned to the Coulibistri River Valley immediately north of Batali. Future research will focus on the genetic representation of females at the Batali communal nest site to better understand its relative importance along the Caribbean coast of Dominica.

It is assumed that *I. delicatissima* nests once per season and some have suggested twice per season (Day et al. 2000). We therefore expected more recaptures at the nesting sites of females that nested the previous year. Our low recapture rates of previous nesters (9.4% at Batali and 4.2% at Champagne Bay), and the seemingly lack of alternative nesting areas for females to use, suggest that perhaps reproduction is arrested in some years. Others have reported less-than-annual reproduction in iguanids. Abts (1987) recorded an annual frequency of reproduction in female Common Chuckwallas (*Sauromalus obesus*) to be from 0% to 95% (mean = 52%) while Laurie (1990) reported an annual nesting frequency from 1.0 to 87.9% (mean = 51%) for female Marine Iguanas (*Amblyrhynchus cristatus*). More recently, Iverson et al. (2004) recorded on average only one in three female Allen Cays Rock Iguanas (*Cyclura cychlura inornata*) nest each year. Green Iguanas are considered to nest annually (Bock et al. 1985), or biannually in populations near the equator (Rand and Green 1982). However, Bock et al. (1985) recorded annual return rates to a communal nest site to be only 30–45%. These data combined suggest that less than annual reproduction may be a common life history characteristic in iguanas (Iverson et al. 2004) and warrants additional research.

The Lesser Antillean Iguana faces manifold threats throughout its range and Dominica is one of the last strong-holds for the species. The island of Dominica represents a significant opportunity to conserve *I. delicatissima*, specifically because of the relatively expansive and undisturbed coastline, low human population density, and relatively low development pressure. Currently, Dominica is home to the largest population of *I. delicatissima* (Knapp et al. 2014) and protecting the species there provides a means to connect different landscapes using charismatic species as conservation flagships. Currently on Dominica, parrots are considered a flagship for inland mesic forests, while sea turtles represent beach habitat. The coastal scrub areas, however, lack such a focal species and *I. delicatissima* has charisma and conservation appeal. By being large, conspicuous, and exhibiting interesting behavior, the species has the potential to serve as a flagship (Caro and O'Doherty 1999). Elsewhere, such as in The Bahamas and Galápagos, iguanas are used with variable success to serve as flagship species and support ecotourism (Knapp 2004, 2007). We suspect, based on our experience on Dominica, that the iguana can serve the same purpose if a concentrated effort is made to promote the species. Evidence from this study also suggests that education outreach initiatives can be successful over the short-term, but sustained strategies are needed not only on Dominica but also throughout the Lesser Antilles.

Acknowledgments.—We thank the Dominica Forestry, Wildlife and Parks Division for support and permission (research permit #286) to conduct research on the island. Andy Phillips helped initiate the research. Invaluable assistants include Adam Mitchell, Paul Meier, Philip Shirk, Jacobo Valasco Reyes, and Glenn Gerber. John Binns and Joel Friesch created the artwork and designed the bumper stickers. Elisa Curot-Lodeon and Evert Henningheim provided the French and Dutch translations of the abstract, respectively. The Sunset Bay Club provided comfortable logistical support. San Diego Zoo Global supported all aspects of the study through a Conservation Research Postdoctoral Fellowship. Research was conducted with IACUC approval (#267) from San Diego Zoo Global.

LITERATURE CITED

Abts, M.L. 1987. Environment and variation in life history traits of the Chuckawalla, *Sauromalus obesus*. Ecological Monographs 57:215–232.

Alberts, A.C., J.M. Lemm, A. Perry, L. Morici, and J.A. Phillips. 2002. Temporary alteration of local social structure in a threatened population of Cuban Iguanas (*Cyclura nubila*). Behavioral Ecology and Sociobiology 51:324–335.

Andrews, K.M., J.W. Gibbons, and D.M. Jochimsen. 2008. Ecological effects of roads on amphibians and reptiles: a literature review. Pp. 121–143 *In* Urban Herpetology. Mitchell, J.C., R.E. Jung Brown, and B. Bartholomew (Eds.). Herpetological Conservation 3. Society for the Study for Amphibians and Reptiles, Salt Lake City, Utah, USA.

Bateman, P.W., and P.A. Fleming. 2009. To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. Journal of Zoology 277:1–14.

Beovides-Casas, K., and C.A. Mancina. 2006. Natural history and morphometry of the Cuban Iguana (*Cyclura nubila* Gray, 1831) in Cayo Sijú, Cuba. Animal Biodiversity and Conservation 29:1–8.

Bock, B.C., A.S. Rand, and G.M. Burghardt. 1985. Seasonal migration and nesting site fidelity in the Green Iguana. Pp. 435–443 *In* Migration: Mechanisms and Adaptive Significance. Rankin, M.A. (Ed.). University of Texas Marine Science Institute, Port Aransas, Texas, USA.

Bock, B.C., A.S. Rand, and G.M. Burghardt. 1989. Nesting season movements of female Green Iguanas (*Iguana iguana*) in Panamá. Copeia 1989:214–216.

Breuil, M. 2000. Taxon reports. Lesser Antilles Iguana *Iguana delicatissima* and *Iguana iguana*. West Indian Iguana Specialist Group Newsletter 3(2):11–13.

Breuil, M. 2009. The terrestrial herpetofauna of Martinique: past, present, future. Applied Herpetology 6:123–149.

Breuil, M., M. Day, and C. Knapp. 2010. *Iguana delicatissima*. The IUCN Red List of Threatened Species. Version 2014.3. Available from http://www.iucnredlist.org/details/10800/0 [Accessed on 14 September 2014].

Caro, T., and G. O'Doherty. 1999. On the use of surrogate species in conservation. Conservation Biology 13:805–814.

Clause, A.R., and E.A. Capaldi. 2006. Caudal autotomy and regeneration in lizards. Journal of Experimental Zoology 305A:965–973.

Day, M., M. Breuil, and S. Reichling. 2000. Taxon account: Lesser Antillean Iguana (*Iguana delicatissima*) Pp. 62–67 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A., (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Fitch, H.S., and R.W. Henderson. 1977. Age and sex differences, reproduction, and conservation of *Iguana iguana*. Milwaukee Public Museum Contributions to Biology and Geology 13:1–21.

Gienger, C.M., and D.D. Beck. 2007. Heads or tails? Sexual dimorphism in helodermatid lizards. Canadian Journal of Zoology 85:92–98.

Goodman, R.M., C.R. Knapp, K.A. Bradley, G.P. Gerber, and A.C. Alberts. 2009. Review of radio transmitter attachment methods for West Indian Rock Iguanas (genus *Cyclura*). Applied Herpetology 6:151–170.

Harris, D.M. 1982. The phenology, growth, and survival of the Green Iguana, *Iguana iguana*, in Northern Columbia. Pp. 150–161 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Hayes, W.K., J.B. Iverson, C.R. Knapp, and R.L. Carter. 2012. Do invasive rodents impact endangered insular iguana populations? Biodiversity and Conservation 21:1893–1899.

Henderson, R.W., and R. Powell. 2009. Natural history of West Indian reptiles and amphibians. University of Florida Press, Gainesville, Florida, USA.

Huyghe, K., L.M. San-Jose, M. Peñalver Alcázar, and P.S. Fitze. 2013. An ecomorphological analysis of the determinants of mating success. Biological Journal of the Linnean Society 110:658–664.

Iguana Taxonomy Working Group. 2016. A checklist of the iguanas of the world (Iguanidae; Iguaninae). IUCN SSC Iguana Specialist Group. Pp. 4–46 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Iverson, J.B., K.N. Hines, and J.M. Valiulis. 2004. The nesting ecology of the Allen Cays Rock Iguana, *Cyclura cychlura inornata* in The Bahamas. Herpetological Monographs 18:1–36.

Iverson, J.B., G.R. Smith, S.A. Pasachnik, K.N. Hines, and L. Pieper. 2016. Growth, coloration, and demography of an introduced population of the Acklins Rock Iguana (*Cyclura rileyi nuchalis*) in the Exuma Islands, The Bahamas. Pp. 139–153 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Iverson, J.B., G.R. Smith, and L. Pieper. 2004. Factors affecting long-term growth of the Allen Cays Rock Iguana in The Bahamas. Pp. 176–192 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Ji, X., Q. Qiu, and C.H. Diong. 2002. Sexual dimorphism and female reproductive characteristics in the Oriental Garden Lizard, *Calotes versicolor*, from Hainan, Southern China. Journal of Herpetology 36:1–8.

Knapp, C.R. 2000. Home range and intraspecific interactions of a translocated iguana population (*Cyclura cychlura inornata* Barbour and Noble). Caribbean Journal of Science 36:250–257.

Knapp, C.R. 2004. Ecotourism and its potential impacts on iguana conservation in the Caribbean. Pp. 290–301 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Knapp, C.R. 2007. The potential for iguana-based ecotourism on Andros: a first assessment. The Bahamas Naturalist and Journal of Science 2:10–17.

Knapp, C.R., and J.G. Abarca. 2009. Effects of radio transmitter burdening on locomotor ability and survival of iguana hatchlings. Herpetologica 65:363–372.

Knapp, C.R., and C. Perez-Heydrich. 2012. Using non-conspicuous metrics to examine selected impacts of disturbance on a long-lived reptile. Endangered Species Research 17:193–200.

Knapp, C.R., and S. Valeri. 2008. *Iguana delicatissima* (Lesser Antillean Iguana). Mortality. Herpetological Review 39:227–228.

Knapp, C., M. Breuil, C. Rodrigues, and J. Iverson (Eds.). 2014. Lesser Antillean Iguana, *Iguana delicatissima*: Conservation Action Plan, 2014–2016. IUCN SSC Iguana Specialist Group, Gland, Switzerland.

Laurie, W.A. 1990. Population biology of Marine Iguanas (*Amblyrhynchus cristatus*). I. Changes in fecundity related to a population crash. Journal of Animal Ecology 59:515–528.

Lorvelec, O., M. Pascal, C. Pavis, and P. Feldmann. 2011. Amphibians and reptiles of the French West Indies: inventory, threats, and conservation. Pp. 205–237 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Maginnis, T.L. 2006. The costs of autotomy and regeneration in animals: a review and framework for future research. Behavioral Ecology 17:857–872.

Malhorta, A., R.S. Thorpe, E. Hypolite, and A. James. 2007. A report on the status of the herpetofauna of the Commonwealth of Dominica, West Indies. Applied Herpetology 4:177–194.

Malo, J.E., F. Suárez, and A. Díez. 2004. Can we mitigate animal-vehicle accidents using predictive models? Journal of Applied Ecology 41:701–710.

Marchand, M.N., and J.A. Litvaitis. 2004. Effects of habitat features and landscape composition on the population of a common aquatic turtle in a region undergoing rapid development. Conservation Biology 18:758–767.

Montgomery, G.G., A.S. Rand, and M.E. Sunquist. 1973. Post-nesting movements of iguanas from a nesting aggregation. Copeia 1973:620–622.

Myers, N.R., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Ocampo, M, A. Aguilar-Kirigin, and S. Quinteros. 2012. A new species of *Liolaemus* (Iguania: Liolaemidae) of the Alticolor group from La Paz, Bolivia. Herpetologica 68:410–417.

Pasachnik, S.A. 2013. Growth, reproduction, and diet of Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina*, with notes on the status of the species. Herpetological Conservation and Biology 8:191–198.

Pasachnik, S.A., C.E. Montgomery, L.E. Ruyle, J.P. Corneil, and E.E. Antúnez. 2012. Morphological and demographic analyses of the Black-chested Spiny-tailed Iguana, *Ctenosaura melanosterna*, across their range: implications for populations level management. Herpetological Conservation and Biology 7:399–406.

Rand, A.S. 1968. A nesting aggregation of iguanas. Copeia 1968:552–561.

Rand, A.S., and H.W. Greene. 1982. Latitude and climate in the phenology of reproduction in the Green Iguana. Pp. 142–149 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Rodda, G.H., B.C. Bock, G.M. Burghardt, and S.A. Rand. 1988. Techniques for identifying individual lizards at a distance reveal influences of handling. Copeia 1988:905–913.

Sokal, R.R., and F.J. Rohlf. 1995. Biometry: The Principles and Practices of Statistics in Biological Research. 3rd Edition. W.H. Freeman and Company, New York, New York, USA.

Walker, L.R., D.J. Lodge, N.V.L. Brokaw, and R.B. Waide. 1991. An introduction to hurricanes in the Caribbean. Biotropica 23:313–316.

Werner, D.I. 1983. Reproduction in the iguana *Conolophus subcristatus* on Fernandina Island, Galápagos: clutch size and migration costs. The American Naturalist 121:757–775.

Wiewandt, T.A. 1982. Evolution of nesting patterns in iguanine lizards. Pp. 119–141 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Wikelski, M., and F. Trillmich. 1997. Body size and sexual size dimorphism in Marine Iguanas fluctuate as a result of opposing natural selection: an island comparison. Evolution 51:922–936.

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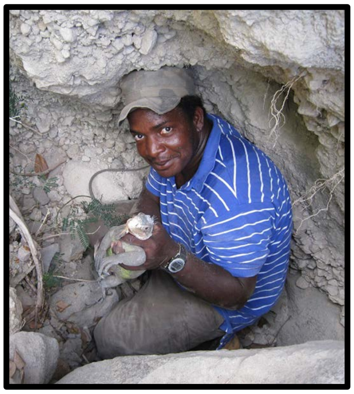

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Herpetological Conservation and Biology 11(Monograph 6):168–176.
Submitted: 18 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

DISTRIBUTION AND NATURAL HISTORY OF THE CAMPECHE SPINY-TAILED IGUANAS (*CTENOSAURA ALFREDSCHMIDTI*)

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Abstract.—**México has one of the greatest reptile diversities of any country in the world, with greater than 50% of species being endemic. Here we present information on the distribution and natural history of the Campeche Spiny-tailed Iguanas, *Ctenosaura alfredschmidti*, along a 70 km transect in southern Campeche, México. We observed 33 and captured 20 (16 adults and four juveniles) of those individuals for use in our analyses. Iguanas were captured primarily from *Haematoxylum* sp. trees at heights between 0.5 and 6.0 m. The sex ratio in this area was 1 M:2.2 F. There was no significant difference in snout-vent length between males and females. However, males were significantly heavier, had significantly longer tibias, and larger heads than females. We observed seven to ten femoral pores on each hind leg of adult *C. alfredschmidti,* with those of the males being more conspicuous than those of the females. The majority of iguanas were observed in lowland deciduous forest habitat, at elevations between 140 and 282 m. Fragmentation and habitat modification was evident across the study area. We estimated approximately 5.1 *Ctenosaura alfredschmidti* individuals/ha in a 1.68 km^2 area across the transect, although abundance is likely under-represented due to the secretive nature of this species. The Biosphere Reserve of Calakmul may serve as a conservation management area for the species. We recommend the status of this species be updated and be protected under Mexican law.**

Resumen.—**México tiene una de las mayores diversidades de reptiles en el mundo, más del 50% de las especies son endémicas. Presentamos información sobre la distribución y la historia natural de las Iguanas de Cola Espinosa de Campeche, *Ctenosaura alfredschmidti*, a lo largo de un transecto de 70 kilómetros al sur de Campeche, México. Observamos 33 y capturamos 20 individuos (16 adultos y cuatro juveniles) para nuestros análisis. Las iguanas fueron capturadas principalmente en árboles de *Haematoxylum* sp., en alturas entre 0.5 y 6.0 m. La proporción de sexos fue 1 M:2.2 H. No hubo diferencia significativa en la longitud hocico-cloaca entre machos y hembras; sin embargo, los machos fueron significativamente más pesados, con tibias significativamente más largas y cabezas más grandes que las hembras. Observamos de siete a diez poros femorales en cada pata trasera de los adultos de *C. alfredschmidti*, en los machos más visibles que en las hembras. La mayoría de las iguanas se observaron en hábitat de bosque caducifolio de tierras bajas, a elevaciones entre 140 y 282 m. La modificación y fragmentación del hábitat fue evidente en toda el área de estudio. Estimamos unos 5.1 individuos/ha de *Ctenosaura alfredschmidti* en un área de 1.68 km^2 a través de nuestro transecto, aunque la abundancia está probablemente subrepresentada debido a la naturaleza secreta de esta especie. La Reserva de la Biosfera de Calakmul puede servir como área de manejo y conservación para la especie. Recomendamos actualizar el estado de esta especie e incluir su protección por las leyes mexicanas.**

Key Words.—biology; distribution; endemic; habitat; natural protected area; México

INTRODUCTION

México is second only to Australia in reptile species richness (P. Uetz. 2013. The Reptile Database. Available from http://www.reptile-database.org [Accessed 3 November 2014]) with 57% of Mexican reptile species being endemic to the country (Flores-Villela and García-Vázquez 2014). In recent decades, various new reptile taxa have been described in México (Dixon and Tipton 2004; Flores-Villela and Canseco-Márquez 2004; Liner 2007; Bezy et al. 2008; Campbell and Flores-Villela 2008; Flores-Villela and Smith 2009; García-Vázquez et al. 2010; Woolrich-Piña and Smith 2012; Bryson et al. 2014). The high species richness holds true for specific groups of reptiles as well, including iguanas. Of the 19 species of true iguanas in México (Iguaninae), 14 (73.6%) are endemic. The spiny-tailed iguanas (*Ctenosaura*) follow a similar trend, with nine of the 11 (81.8%) species occurring in México being endemic (ITWG this volume).

Mexican regulations list seven of the 11 species of *Ctenosaura* as endangered (*C. defensor*), threatened (*C. pectinata*, *C. oaxacana*, *C. similis*, and *C. clarki*), or with special concern ("sujeta a protección especial", *C. acanthura* and *C. hemilopha*). The latter refers to those species that could be threatened, and where recovery and conservation of their populations is promoted (NOM-059-SEMARNAT-2010: NORMA Oficial Mexicana, Protección ambiental-Especies nativas de México de flora

Morales-Mávil, Jorge E., E. Ahmed Bello-Sánchez, and Carlos R. Corona-López. 2016. Distribution and natural history of the Campeche Spiny-tailed Iguanas (*Ctenosaura alfredschmidti*). Pp. 168–176 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo). The remaining species of *Ctenosaura* (*C. conspicuosa*, *C. macrolopha*, *C. nolascensis*, and *C. alfredschmidti*) have not yet been considered for protection under Mexican regulations, due primarily to the fact that little information exists regarding them. In order to better understand the status of these species, update legislation, and create proper management plans, additional information must be gathered.

The Campeche Spiny-tailed Iguana (*Ctenosaura alfredschmidti*) is one such species that is missing vital biological information. The species was described in 1995 from east of Escárcega (Köhler 1995) and later reported from Calakmul, both in southern Campeche, México (Calderon et al. 2003). Though this species has been reported from northern Guatemala (Radachowsky et al. 2003), it is now understood that this was actually *C. defensor* (ITWG this volume). Thus, this species is endemic to the southern region of Campeche, México. The adults are grey-green in color with conspicuous black markings on the back and sides of the abdomen, reddish markings posterior to the black markings on the abdomen, and reddish markings on the back of the neck and throat (Köhler 1995).

Very little additional information is known concerning this species. It is considered Near Threatened according to the IUCN Red List of Threatened Species, though the assessment states that the species nearly meets the criteria to be listed as Critically Endangered and calls for additional information to be gathered (Köhler 2004). In the decade since the Red List assessment, no studies have been conducted to generate these data concerning distribution and natural history. The local government of Campeche promotes and supports studies of reptile species at risk, such as turtles (Berzunza Chio 2010) and crocodiles (Padilla et al. 2010), however iguanas have largely been ignored.

In an effort to collect these vital data for *C. alfredschmidti* we conducted opportunistic visual encounter surveys in southern Campeche, México, between February and July 2010. Our goal was to elucidate aspects of morphology and habitat use. Data presented here will aid in updating the protected status of this species under Mexican law, and in constructing proper conservation management proposals for the species.

MATERIALS AND METHODS

Study site.—Our study site consisted of 1.68 km^2 in southern Campeche, México, on the Yucatán Peninsula near the communities of Escárcega, Matamoros, Libertad, Justicia Social, Silvituc, Constitución, Xpujil, and Calakmul (Fig. 1). The area is characterized by low elevation (< 300 m), an annual rainfall of 100–1,200 mm (Rebolledo Vieyra 2010), and two climatic variants from west to east. Agro-climatic variant type Aw2 is warm and humid with summer rains and mean annual temperature of 22–26° C, occurring near the town of Nueva Conhuas in the western portion of our study area. The second agro-climatic variant, type Aw1(x'), is characterized as having little rain throughout the year, and has a greater influence near Xpujil (Mendoza Vega and Kú Quej 2010) in the eastern portion of our study area. Much of the habitat in this general area is disturbed due to livestock and agricultural fields (beans and corn), new roads, and electric transmission lines. However the area within the Calakmul Biosphere Reserve represents more pristine habitats, including the Balam-ku and Balam-kin Reserves (Lugo-Hubp et al. 1992; Bautista et al. 2005). The predominant vegetation in the area is lowland deciduous forest, tropical low flooded forest, secondary vegetation, farming, and uncovered soil (Palacio et al. 2002; Colchero et al. 2005; Noriega-Trejo and Palacio Aponte 2010) (Fig. 1).

Data collection.—We searched for iguanas, exploring all microhabitats (tree holes, stumps, and logs) along a 70 km long by 24 m wide transect (Fig. 1). We conducted our surveys from February through July 2010. For two weeks each month we searched for eight hours a day, between 0800 and 1600. We sampled the entire transect area twice. We surveyed 24 km along the distance of the transect every month, surveying the same section for two consecutive months. Our total sampling effort was 1,344 person-hours.

We marked each individual by injecting a microchip subcutaneously in the mid-dorsum (RFID, 12 mm, Trovan®, Trovan Ltd., United Kingdom). We photographed each individual before and after capture, and captured all iguanas by hand. We used the initial photographs to identify color patterns and unique marks for future recognition using binoculars (8 x 40). We did not resight or recapture any iguanas. We measured snout-vent length (SVL) to the nearest 0.1 mm, and tail length (TL), tibia length (TBL), head length (HL), and maximum head width (HW) to the nearest 0.1 mm using a tape measure and vernier calipers. We measured head width at the widest part of head, immediately posterior to the eyes, and head length from the tip of the snout to the posterior end of the jaw. We measured total mass (TM) to the nearest 0.1 g using Pesola® spring scales (PESOLA AG, Baar, Switzerland). We determined sex based on external morphology and cloacal probing. We released iguanas at the site of capture after processing. At each site we documented the height of the capture point of each iguana, habitat type, and ambient temperature in the shade approximately 1.5 m off the ground, using a manual weather station (Kestrel 4000, KestrelMeters.com, Birmingham, Michigan, USA).

We determined the difference between juveniles and adults based on the descriptions for *C. defensor* (Lee 2000) and *C. clarki* (Gicca 1982; Pérez-Ramos and Saldaña de la Riva 2002), which are closely related

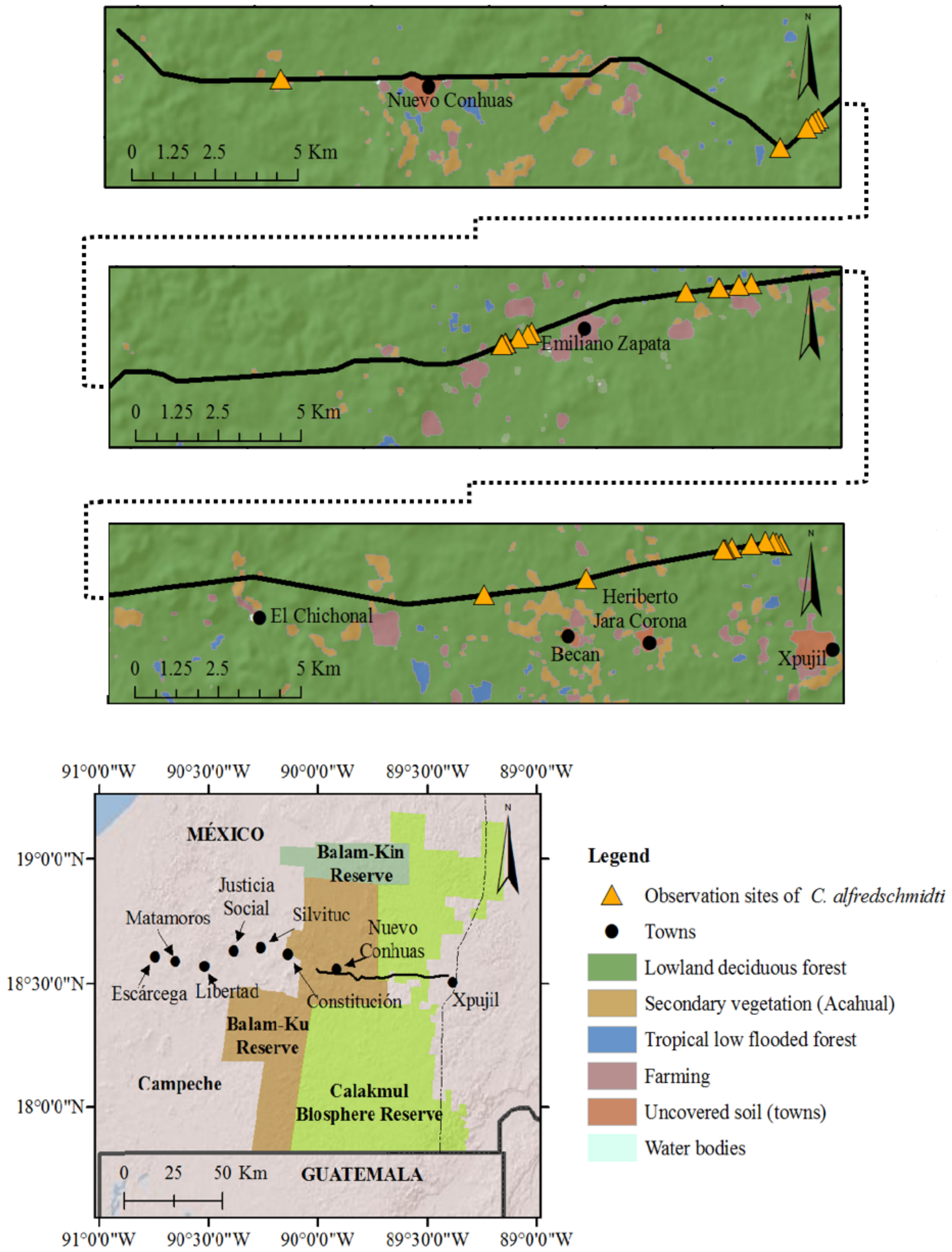

FIGURE 1. Location of transect (black line) and vegetation types along the transect used to survey for *Ctenosaura alfredschmidti* in Campeche, México. The Calakmul Biosphere Reserve is represented by all highlighted areas in the lower map, with the two sections of smaller specific reserves highlighted in two different colors. The upper maps zoom into the transect area and run in consecutive order from west to east moving down the page.

(Köhler et al. 2000; Köhler et al. 2003) and have a similar body size (SVL). We considered individuals with SVL > 90.5 mm to be adults. We identified gravid females by palpating the abdomen of those females that were visibly more robust than others. Developing eggs in the abdominal cavity were clearly identifiable.

Statistical analyses.—We used both parametric and nonparametric tests, depending on data distribution. Assuming a sex ratio of 1:1 we calculated differences between the expected value and the observed using a chi-square test. We compared SVL, HL, HW, TBL, and TM between males and females using *t*-tests. Gravid females were not used in TM analyses. We did not make comparisons of TL due to the high percentage of tail breaks that we encountered. We also compared the number of femoral pores between males and females using a Mann-Whitney U test. Means are presented ± 1 SD. We performed all statistical analysis using Statistica v7.0 for Windows (StatSoft Inc., Tulsa, Oklahoma, USA) with an alpha of 0.05.

RESULTS

We observed 33 individuals in 1.68 km^2 and captured 20 of those, including 16 adults (five males and 11 females) and four juveniles (juvenile mean SVL = 69.8 ± (SD) 14.1 mm (range, 51.9–90.5 mm)). The sex ratio was significantly female-biased (1 M:2.2 F, $\chi^2 = 128.79$, $P < 0.001$). Males were not significantly longer than females ($t = -1.06$, $P > 0.05$), but had significantly longer tibias ($t = -2.56$, $P = 0.022$), and longer ($t = -4.08$, $P = 0.001$) and wider heads than females ($t = -3.61$, $P = 0.003$) (Table 1). Given the high incidence of regenerated tails in adults (80% males and 82% females), TL comparisons were not made. The tail length observed in two adult females that did not have regenerated tails was 120.5 mm and 125.3 mm, and in one adult male was 153.6 mm. Four of the females captured (one on 4 February 2010, two on 22 February 2010, and one on 5 April 2010) were gravid, therefore we did not include them in the TM analysis. Males were significantly heavier than the remaining seven females ($t = -2.15$, $P = 0.050$; Table 1). No difference was found in the number of femoral pores between males and females (left: $U = 42.0$, $P = 0.78$; right: $U = 39.5$, $P = 0.56$). Between seven and 10 femoral pores were found on each leg (mode = eight pores), and the pores in males were more conspicuous than females (Fig. 2).

Thirty-two of the 33 observed iguanas were in lowland deciduous forest that is susceptible to flooding. The remaining individual was recorded from secondary vegetation. No iguanas were observed in farming areas. We observed all iguanas on wide branches (approximately 20 cm in diameter) while basking. Observations occurred at elevations between 140 and 282 m (mean = 222.5 ± 41.7 m), on trees at heights between 0.5 and 6.0 m (mean 2.6 ± 1.6 m); 36.3% ($n = 12$) of individuals were found in *Haematoxylum* sp. trees (*H. campechianum* and *H. brasiletto*) (Fig. 3) and 15.2% ($n = 5$) in felled logs. Between one and two individuals were found in *Cordia dodecandra*, *Thouinia paucidentata*, *Forchhammeria pallida, Caesalpinia gaumeri*, *Vitex*

TABLE 1. Mean and standard deviations of capture height, snout-vent length (SVL), tibia length (TBL), head length (HL), head width (HW), and total mass (TW) in adult *Ctenosaura alfredschmidti* by sex from Campeche, México. Ranges are in parentheses.

	Female (n = 11)	Male (n = 5)	*t*-value	df	*P*
Capture height (m)	2.7 ± 1.9 (0.6–6.0)	1.9 ± 1.1 (0.8–3.5)	0.84	14	0.414
SVL (mm)	147.5 ± 17.7 (120.3–174.4)	156.7 ± 11.4 (142.4–170.0)	-1.06	14	0.306
TBL (mm)	24.5 ± 2.9 (20.3–35.0)	28.3 ± 2.1 (24.7–30.3)	-2.56	14	0.022
HL (mm)	32.1 ± 3.9 (25.9–39.9)	40.9 ± 3.9 (35.6–46.6)	-4.08	14	0.001
HW (mm)	21.3 ± 1.9 (19.1–23.6)	25.8 ± 2.9 (21.4–29.0)	-3.61	13	0.003
TM (g)	107.4 ± 26.9 (60.0–148.0)	143.0 ± 36.7 (105.0–188.0)	-2.15	13	0.050

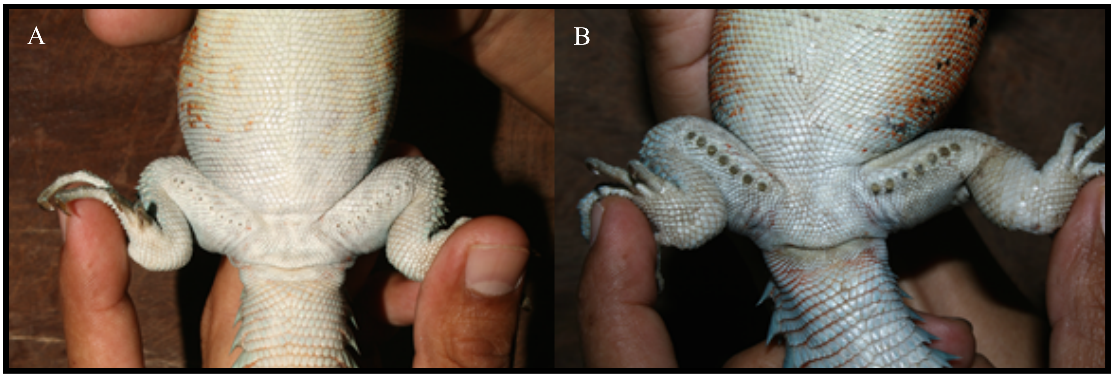

FIGURE 2. Differences in femoral pores between (A) female and (B) male *Ctenosaura alfredschmidti* from Campeche, México. The number or pores is consistent across sexes, but the pores in females are rudimentary. (Photographed by Ahmed Bello).

gaumeri, *Jacquinia macrocarpa*, and *Manilkara zapota*. The remaining iguanas were observed in unidentified trees. Mean perch height was 2.8 ± 2.3 m (range, 0.6–6.0 m) in lowland deciduous forest; the one individual recorded in secondary vegetation was at a perch height of 0.5 m. Gravid females were captured in lowland deciduous forest (three individuals on *Haematoxylum campechianum* and one on *Cordia dodecandra* trees at heights between 0.9 and 5.8 m). We captured iguanas when the average temperature was 33.6° C (27.2–39.7° C) and the average humidity was 53% (36.3–85.7%).

DISCUSSION

Male *Ctenosaura alfredschmidti* were not longer than females, unlike what has been reported for other species in the genus such as: *C. clarki* (Duellman and Duellman 1959), *C. similis* (Fitch and Henderson 1977), *C. pectinata* (Köhler and Streit 1996; Arcos-García et al. 2005), *C. melanosterna* (Pasachnik et al. 2012a), *C. bakeri* (Pasachnik et al. 2012b), and *C. oedirhina* (Pasachnik 2013). *Ctenosaura alfredschmidti* males do however have larger heads than females as has been reported in other iguaninae: *Cyclura rileyi* (Carter and Hayes 2004), *Ctenosaura bakeri* (Gutsche and Streich 2009), *Brachylophus vitiensis* (Morrison et al. 2013). Sexual size dimorphism of the head could be related to a social mating system (Vitt and Cooper 1985; Hews 1990) or sexual selection, for example, larger heads may have an advantage in male-male combat (Carothers 1984; Gier 1997).

The frequency of broken tails observed in *C. alfredschmidti* was extremely high (~ 80%), when compared to congenerics: < 50% in *C. oedirhina* (Pasachnik 2013) and < 40% in *C. bakeri* (Pasachnik et al. 2012b). In addition, there was no sex bias in tail breaks, as there was in *Cyclura cornuta*, with 46% and 27% for males and females, respectively (Pérez-Buitrago et al. 2010). The high degree of tail autotomy could be indicative of predation attempts (Hayes et al. 2012), or allude to a high level of conspecific aggression (Pérez-Buitrago et al. 2010; Davis et al. 2011). Since this species is not hunted for food, human-influenced events are unlikely to be the cause of tail breaks, although this cannot be completely ruled out as humans may attempt to harm this species out of fear.

The female biased sex ratio (1:2.2) observed herein may be an indication that the population in this area is stable, or at least devoid of human hunting pressure as has been confirmed through conversations with locals. A female biased sex ratio is consistent with that found in other stable iguana populations: *C. similis* (1:1.6, Fitch and Henderson 1977), *C. melanosterna* (Cayos Cochinos ESU, 1:1.4, Pasachnik et al. 2012a), *C. oedirhina* (1:1.6, Pasachnik 2013), and *Iguana iguana* (1:2.5, Muñoz et al. 2003). In areas where hunting pressure is known to exist, the reported sex ratio is male biased as gravid females are often targeted for their eggs (Faria et al. 2010; Pasachnik et al. 2012a, b).

The rough density estimate that can be made from our data may also allude to the stability of the population. In the 1.68 km^2 surveyed, 33 observations of individual iguanas were made, or 5.1 individuals/ha. In addition, it can be assumed that the detection rate is low based on the secretive nature of this species. At the upper-end of what has been documented for ctenosaurs, Rioja et al. (2012) reported values for *C. oaxacana* of up to 33.7 individuals/ha in México, and Gómez-Mora et al. (2012) reported values up to 12.3 individuals/ha for *C. pectinata* in Buenavista, Michoacán, México. In comparison, *Ctenosaura quinquecarinata* were estimated at 0.93 individuals/ha on a wildlife refuge in Nicaragua (Robleto 2010), values of *C. similis* ranged from 0.6 to 3.1 individuals/ha in Zamorano, Honduras (Terán Flores 2006), and *C. palearis* were estimated at 0.59 individuals/ha in the Motagua Valley, Guatemala (Cotí and Ariano-Sánchez 2008). Though additional surveys need to be conducted that focus specifically on population and density estimates, it is likely that the density estimates will still fall within the middle of the range of those that have been previously recorded. Habitat alteration (Fig. 4) is likely to be contributing to a reduced encounter rate.

The lowland deciduous forests of Campeche, México that is preferred by *C. alfredschmidti*, are currently undergoing modification to support an increasing human population. Campeche has the second highest level of deforestation in México, with 10.5% of deciduous and

FIGURE 3. Male *Ctenosaura alfredschmidti* basking in *Hemaetoxylum campechianum* tree within sub-deciduous low forest in Campeche, México. (Photographed by Ahmed Bello).

semi-deciduous forest lost (Instituto Nacional de Ecología y Cambio Climático. 2008. Cambio porcentual de la vegetación y uso del suelo 1976–2000. Available from http://www2.inecc.gob.mx/emapas/download/dinamica_1976_2000.pdf [Accessed 5 August 2013]). The primary crops are fruit trees, mainly *Byrsonima crassifolia*, corn, and other grains (Quintana-Morales 2014). The development of new roads and electric transmission lines also contributes to fragmentation of the habitat. This process creates edges with large numbers of felled trees where iguanas were found basking. However, iguanas in these areas are likely to have an increased predation risk given the increased exposure of the individuals.

The increase in crop production presents another possible problem for the iguanas with the corresponding pollution from hydrocarbons and agricultural pesticides. The bioaccumulation of this waste material is known to affect herbivores and insectivores (Morales-Rodríguez and Cobos-Gasca 2005) such as the iguanas. These compounds have been shown to affect reproduction and damage brain tissue in other species, as has been witnessed in the case of some birds and turtles in the Yucatán Peninsula (Morales Rodríguez and Cobos-Gasca 2005; Cobos Gasca et al. 2011).

Nevertheless, these forests still cover a large area, and although the iguanas appear to be represented in low numbers, they have been captured within the Biosphere Reserve of Calakmul (723,185 ha, one of the largest protected areas in México, Fig. 1), which may offer some protection for the long-term persistence of the species. This study provides basic information on *Ctenosaura alfredschmidti* and can be useful for structuring conservation strategies for this species. Long-term monitoring studies focusing on nesting, demographics, foraging, home range, habitat use, and distribution are recommended, while they are still possible. In addition, genetic studies focusing on population structure across the range are vital to understanding the status of the species, particularly in the face of continuing fragmentation. Such studies are important, as environmental officials of the Mexican government (SEMARNAT) promote rescue and translocation programs of wildlife when governmental or private companies propose modification of the environment. In general, authorities should pay special attention to populations of Campeche Spiny-tailed Iguanas, and ensure that individuals are managed properly. Given the data we have presented and what is known about the forest modification in the area, we feel that *Ctenosaura alfredschmidti* should be protected by Mexican Law NOM-059 of SEMARNAT, due to its likely threatened status and potential for continual decline in the near future.

FIGURE 4. Evidence of habitat destruction in the *Ctenosaura alfredschmidti* study site, Campeche, México. (Photographed by Adolfo López Galindo).

Acknowledgments.—We thank Domingo Canales for his invaluable support and the Comisión Federal de Electricidad (CFE) for financial support through the collaboration agreement CFE/UV RRCPTTP-UV-001/07. We also acknowledge the Programa de Fortalecimiento Académico del Posgrado de Alta Calidad I0I0/458/2013 and I0I0/152/2014 C-133/2014 for their support. This study was approved by the institutional guidelines of the Universidad Veracruzana, the Federal Government of México's Secretariat of Environment and Natural Resources (SEMARNAT; official permit #09/GS-2132/05/10). We are grateful for the grant to E.A. Bello-Sanchez (registration 227164) and C.R. Corona-López (registration 197662) from CONACyT for making this work possible.

LITERATURE CITED

Arcos-García, J.L., V.H. Reynoso Rosales, G.D. Mendoza Martínez, and D. Hernández Sánchez. 2005. Sex identification and growth measurement in the Black Iguana (*Ctenosaura pectinata*) in juvenile and newborn stages. Veterinaria México 36:53−62.

Bautista, F., E. Batllori-Sampedro, G. Palacio-Aponte, M. Ortiz-Pérez, and M. Castillo-González. 2005. Integración del conocimiento actual sobre los paisajes geomorfológicos de la Península de Yucatán. Pp. 33–58 *In* Caracterización y Manejo de Suelos en la Península de Yucatán: Implicaciones Agropecuarias, Forestales y Ambientales. Bautista, F., and G. Palacio-Aponte (Eds.). UACAM-UAY-INE, México D.F., México.

Berzunza Chio, J. 2010. Estudio de caso: programa estatal de protección y conservación de la tortuga marina en Campeche. Pp. 342–343 *In* La Biodiversidad en Campeche: Estudio de Estado. Villalobos-Zapata, G.J., and J. Mendoza Vega. (Coord.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Gobierno del Estado de Campeche, Universidad Autónoma de Campeche, El Colegio de la Frontera Sur, México.

Bezy, R.L., K.B. Bezy, and K. Bolles. 2008. Two new species of Night Lizards (*Xantusia*) from México. Journal of Herpetology 42:680−688.

Bryson, R.W., Jr., C.W. Linkem, M.E. Dorcas, A. Lathrop, J.M. Jones, J. Alvarado-Díaz, C.L. Grünwald, and R.W. Murphy. 2014. Multilocus species delimitation in the *Crotalus triseriatus* species group (Serpentes: Viperidae: Crotalinae), with the description of two new species. Zootaxa 3826:475–496.

Calderón, R., J.R. Cedeño-Vásquez, and C. Pozo. 2003. New distributional records for amphibians and reptiles from Campeche, México. Herpetological Review 34:269−272.

Campbell, J.A., and O. Flores-Villela. 2008. A new Long-tailed Rattlesnake (Viperidae) from Guerrero, México. Herpetologica 64:246−257.

Carothers, J.H. 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. American Naturalist 124:244−254.

Carter, R.L., and W.K. Hayes. 2004. Conservation of an endangered Bahamian Rock Iguana, II. Morphological variation and conservation priorities. Pp. 258–273 *In* Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). Iguanas: Biology and Conservation. University of California Press, Berkeley and Los Angeles, California, USA.

Cobos Gasca, V.M., R. Barrientos Medina, and C. Chi Novelo. 2011. Los plaguicidas y su impacto sobre la fauna silvestre de la Península de Yucatán. Bioagrociencias 4:4−9.

Colchero, F., D.A. Conde, C. Manterola, and A. Rivera. 2005. Clasificación de vegetación y uso de suelo para el sur de los estados de Campeche y Quintana Roo. Escala 1:250,000. Extraído del proyecto BJ006: Evaluación y diseño del corredor Sian Ka'an-Calakmul con base en el modelaje espacial del estado de conservación del hábitat de Jaguar (*Panthera onca*) y su relación con la historia de uso de suelo. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), México, D.F., México.

Cotí, P., and D. Ariano-Sánchez. 2008. Ecology and traditional use of the Guatemalan Black Iguana (*Ctenosaura palearis*) in the dry forests of the Motagua Valley, Guatemala. Iguana: Conservation, Natural History, and Husbandry of Reptiles 15:143−149.

Davis, A.K., L.E. Ruyle, and J.C. Maerz. 2011. Effect of trapping method on leukocyte profiles of Black-chested Spiny-tailed Iguanas (*Ctenosaura melanosterna*): implications for zoologists in the field. International Scholarly Research Network Zoology. doi:10.5402/2011/384825

Dixon, J.R., and B.L. Tipton. 2004. *Dryadophis* versus *Mastigodryas* (Ophidia: Colubridae): a proposed solution. Herpetological Review 35:347−349.

Duellman, W.E., and A.S. Duellman. 1959. Variation, distribution, and ecology of the iguanid lizard *Enyaliosaurus clarki* of Michoacan, México. Occasional Papers of the Museum of Zoology, University of Michigan 598:1−11.

Faria, C.M.A., E. Zarza, V.H. Reynoso, and B.C. Emerson. 2010. Predominance of single paternity in the Black Spiny-tailed Iguana: conservation genetic concerns for female-biased hunting. Conservation Genetics 11:1645−1652.

Fitch, H.S., and R.W. Henderson. 1977. Age and sex differences, reproduction, and conservation of *Iguana iguana*. Milwaukee Public Museum Contributions in Biology and Geology 13:1−21.

Flores-Villela, O., and L. Canseco-Márquez. 2004. Nuevas especies y cambios taxonómicos para la herpetofauna de México. Acta Zoológica Mexicana 20:115−144.

Flores-Villela, O., and U.O. García-Vázquez. 2014. Biodiversidad de reptiles en México. Revista Mexicana de Biodiversidad, Suplemento 85:S467−S475.

Flores-Villela, O., and E.N. Smith. 2009. A new species of *Coniophanes* (Squamata: Colubridae), from the coast of Michoacán, México. Herpetologica 65:404−412.

García-Vázquez, U.O., L. Canseco-Márquez, and A. Nieto-Montes de Oca. 2010. A new species of *Scincella* (Squamata: Scincidae) from the Cuatro Ciénegas Basin, Coahuila, México. Copeia 2010:373−381.

Gicca, D.F. 1982. *Enyaliosaurus clarki* (Bailey) Balsas Armed Lizard. Catalogue of American Amphibians and Reptiles 301:1−2.

Gier, P.J. 1997. Iguanid mating systems: ecological causes and sexual selection consequences. Ph.D. Dissertation, University of Oklahoma, Norman, Oklahoma, USA. 162 p.

Gómez-Mora, A., I. Suazo-Ortuño, and J. Alvarado-Díaz. 2012. Distribución, abundancia y uso de hábitat de la Iguana Negra (*Ctenosaura pectinata*) y la Iguana Verde (*Iguana iguana*) en el municipio de Buenavista, Michoacán. Biológicas 14:67−74.

Gutsche, A., and W.J. Streich. 2009. Demography and endangerment of the Utila Island Spiny-tailed Iguana, *Ctenosaura bakeri*. Journal of Herpetology 43:105−113.

Hayes, W.K., J.B. Iverson, C.R. Knapp, and R.L. Carter. 2012. Do invasive rodents impact endangered insular iguana populations? Biodiversity Conservation 21:1893–1899.

Hews, D.K. 1990. Examining hypotheses generated by field measures of sexual selection on male lizards *Uta palmeri*. Evolution 44:1956−1966.

Köhler, G. 1995. Eine neue Art der Gattung *Ctenosaura* (Sauria: Iguanidae) aus dem südlichen Campeche, Mexico. Salamandra 31:1−14.

Köhler, G. 2004. *Ctenosaura alfredschmidti*. The IUCN Red List of Threatened Species. Version 2014.2. Available from http://www.iucnredlist.org/details/44180/0 [Accessed 11 September 2014].

Köhler, G., and B. Streit. 1996. Notes on the systematic status of the taxa *acanthura, pectinata,* and *similis* of the genus *Ctenosaura* (Reptilia: Sauria: Iguanidae). Senckenbergiana Biologica 75:33−43.

Köhler, G., A.J. Gutman, and R. Powell. 2003. Black Iguanas: name and systematics. Iguana (Journal of the International Iguana Society) 10:79−81.

Köhler, G., W. Schroth, and B. Streit. 2000. Systematics of the *Ctenosaura* group of lizards (Reptilia: Sauria: Iguanidae). Amphibia-Reptilia 21:177−191.

Lee, J.C. 2000. A Field Guide to the Amphibians and Reptiles of the Maya World: The Lowlands of México, Northern Guatemala, and Belize. Cornell University Press, Ithaca, New York, USA.

Liner, E.A. 2007. A checklist of the amphibians and reptiles of México. Occasional Papers of the Museum of Natural Science, Louisiana State University 80:1–59.

Lugo-Hubp, J., J. Aceves-Quesada, and R. Espinosa-Pereña. 1992. Rasgos geomorfológicos mayores de la Península de Yucatán. Instituto de Geología 10:143−150.

Mendoza Vega, J., and V.M. Kú Quej. 2010. Clima. Pp. 16−19 *In* La Biodiversidad en Campeche: Estudio de Estado. Villalobos-Zapata, G.J., and J. Mendoza Vega. (Coord.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Gobierno del Estado de Campeche, Universidad Autónoma de Campeche, El Colegio de la Frontera Sur, México.

Morales Rodríguez, M.M., and V.M. Cobos-Gasca. 2005. DDT y derivados en huevos de la Tortuga de Carey *Eretmochelys imbricata* (Linnaeus, 1766), en las costas del estado de Campeche, México. Pp. 237–248 *In* Golfo de México Contaminación e Impacto Ambiental: Diagnóstico y Tendencias. Botello, A.V., J. Rendón-von Osten, G. Gold-Bouchot, and C. Agraz-Hernández (Eds.). 2nd Edition. Universidad Autónoma de Campeche, Universidad Nacional Autónoma de México, Instituto Nacional de Ecología, México.

Morrison, S.F., P. Biciloa, P.S. Harlow, and J.S. Keogh. 2013. Spatial ecology of the critically endangered Fijian Crested Iguana, *Brachylophus vitiensis*, in an extremely dense population: implications for conservation. PLoS ONE 8:e73127. doi:10.1371/journal.pone.0073127

Muñoz, E.M., A.M. Ortega, B.C. Bock, and V.P. Paez. 2003. Demography and nesting ecology of Green Iguana, *Iguana iguana* (Squamata: Iguanidae), in two exploited populations in Depresion Momposina, Colombia. Revista de Biología Tropical 51:229–239.

Noriega-Trejo, R., and Á.G. Palacio Aponte. 2010. Estudios de caso: los bajos inundables de Campeche. Pp. 170–173 *In* La Biodiversidad en Campeche: Estudio de Estado. Villalobos-Zapata, G.J., and J. Mendoza Vega. (Coord.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Gobierno del Estado de Campeche, Universidad Autónoma de Campeche, El Colegio de la Frontera Sur, México.

Padilla, S.E., E. Perera Trejo, M. González Jaúregui, and J.O. Gómez Duarte. 2010. Estudio de caso: el cocodrilo de pantano *Crocodylus moreletii*, en la Reserva de la Biosfera Los Petenes, Campeche. Pp. 344–348 *In* La Biodiversidad en Campeche: Estudio de Estado. Villalobos-Zapata, G.J., and J. Mendoza Vega. (Coord.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Gobierno del Estado de Campeche, Universidad Autónoma de Campeche, El Colegio de la Frontera Sur, México.

Palacio, A., G. Noriega-Trejo, and P. Zamora. 2002. Caracterización físico-geográfica del paisaje conocido como “bajos inundables”. El caso del área natural protegida Balam-kin, Campeche. Investigaciones Geográficas, Boletín del Instituto de Geografía 49:57–75.

Pasachnik, S.A. 2013. Growth, reproduction, and diet of Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina*, with notes on the status of the species. Herpetological Conservation and Biology 8:191–198.

Pasachnik, S.A., C.E. Montgomery, A. Martinez, N. Belal, S. Clayson, and S. Faulkner. 2012b. Body size, demography, and body condition in Utila Spiny-tailed Iguanas, *Ctenosaura bakeri*. Herpetological Conservation and Biology 7:391−398.

Pasachnik, S.A, C.E. Montgomery, L.E. Ruyle, J.P. Corneil, and E.E. Antúnez. 2012a. Morphological and demographic analyses of the Black-chested Spiny-tailed Iguana, *Ctenosaura melanosterna*, across their range: implications for population level management. Herpetological Conservation and Biology 7:399−406.

Pérez-Buitrago, N., A.M. Sabat, and W.O. McMillan. 2010. Spatial ecology of the endangered Mona Island Iguana *Cyclura cornuta stejnegeri*: does territorial behavior regulate density? Herpetological Monographs 24:86–110.

Pérez-Ramos, E., and L. Saldaña de la Riva. 2002. Distribución ecológica del "Nopilchi" *Ctenosaura clarki* (Reptilia: Iguanidae), en las regiones de "Tierra Caliente" y "El Infiernillo", Guerrero-Michoacán, México. Revista Digital Universitaria 3(2). ISSN: 1607–6079.

Quintana-Morales, P.C. 2014. Contexto físico. Pp. 11–23 *In* Acciones de Conservación de la Diversidad Biológica en la Línea de Transmisión Escárcega-Xpujil. González-Christen, A., F. León-Burgos, and D. Canales-Espinosa (Coords.). Comisión Federal de Electricidad and Universidad Veracruzana, México, D.F., México.

Radachowsky, J., R. García-Anleu, and G. Köhler. 2003. First record of *Ctenosaura alfredschmidti* Köhler, 1995 in Guatemala. Salamandra 39:11–13.

Rebolledo Vieyra, M. 2010. Hidrología. Pp. 2–7 *In* La Biodiversidad en Campeche: Estudio de Estado. Villalobos-Zapata, G.J., and J. Mendoza Vega. (Coord.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Gobierno del Estado de Campeche, Universidad Autónoma de Campeche, El Colegio de la Frontera Sur, México.

Rioja, T., A. Carrillo-Reyes, E. Espinoza-Medinilla, and S. López-Mendoza. 2012. Basic ecology of the Oaxacan Spiny-tailed Iguana *Ctenosaura oaxacana* (Squamata: Iguanidae), in Oaxaca, México. Revista de Biología Tropical 60:1613−1619.

Robleto, J. 2010. Estado poblacional de *Ctenosaura quinquecarinata* en el Refugio de Vida Silvestre Río Escalante-Chacocente. M.Sc. Thesis, Universidad Nacional Autónoma de Nicaragua, Managua, Nicaragua. 85 p.

Secretaría de Ecología. 2009. Programa de Conservación y Manejo para la Zona Sujeta a Conservación Ecológica Balam-kin. Gobierno del Estado de Campeche, México.

Terán Flores, M.A. 2006. Densidad poblacional del Garrobo (*Ctenosaura similis*) en cuatro hábitats del Zamorano y su percepción por la comunidad local. B.S. Thesis, Carrera de Desarrollo Socioeconómico y Ambiente, Zamorano, Honduras. 40 p.

Vitt, L.J., and W.E. Cooper, Jr. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. Canadian Journal of Zoology 63:995–1002.

Woolrich-Piña, G.A., and G.R. Smith. 2012. A new species of *Xenosaurus* from the Sierra Madre Oriental, México. Herpetologica 68:551−559.

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Herpetological Conservation and Biology 11(Monograph 6):177–186.
Submitted: 19 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

BIOLOGY AND CONSERVATION OF THE GULF SPINY-TAILED IGUANAS (*CTENOSAURA ACANTHURA*)

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***Abstract.*—Spiny-tailed iguanas are a diverse, taxonomically complex group. There are 11 *Ctenosaura* species in México, nine of which are endemic to the country. This work aims to present information on ecological and biological aspects of the Gulf Spiny-tailed Iguana in the state of Veracruz. *Ctenosaura acanthura* is distributed throughout the coastal plain of the state at altitudes below 500 meters above sea level. Based on 120 captures, males were significantly larger and longer than females, and their heads were wider. We documented that *C. acanthura* consumes a wide variety of food resources (24 species) including both native and ornamental plants, as well as a variety of arthropods. Average clutch size was 27.7 ± 9.1 eggs. There was no relationship between the body length or mass and clutch size. Laboratory incubation took 78.2 ± 6.3 days, at 29–31° C, and the hatching rate was 58.3%. Currently, populations of *C. acanthura* appear stable, due to its ecological plasticity and its presence in all protected areas with tropical forest and wetlands on the plains of Veracruz that we sampled. However, studies of population density, and biological, ecological, physiological, and behavioral research are needed.**

***Resumen*.—Las iguanas de cola espinosa son un grupo diverso y taxonómicamente complejo. Existen 11 especies de *Ctenosaura* en México, nueve de las cuales son endémicas del país. Este trabajo tiene como objetivo presentar información sobre los aspectos ecológicos y biológicos de la iguana de cola espinosa del estado de Veracruz (*Ctenosaura acanthura*). Esta especie se distribuye por toda la llanura costera del estado, en altitudes inferiores a 500 metros sobre el nivel del mar. Basado en 120 capturas, registramos que los machos fueron significativamente más grandes y más pesados que las hembras, y sus cabezas fueron más anchas. Documentamos que *C. acanthura* consume una amplia variedad de recursos alimentarios (24 especies) incluyendo tanto plantas nativas y ornamentales, así como una variedad de artrópodos. El tamaño promedio de la puesta fue 27.7 ± 9.1 huevos. No encontramos relación entre la longitud del cuerpo o masa y el tamaño de la nidada. Realizamos pruebas de incubación en laboratorio y estimamos 78.2 ± 6.3 días, a una temperatura ± 29 a 31° C, y la tasa de eclosión de 58.3%. Actualmente, las poblaciones de *C. acanthura* parecen estables, debido a su plasticidad ecológica y su presencia en todas las áreas protegidas de bosques tropicales y humedales en las llanuras de Veracruz que muestreamos. Sin embargo, se necesitan estudios de densidad de poblaciones, así como de más información biológica, ecológica, fisiológica y conductual.**

Key Words.—distribution; endemism; Iguaninae; México; natural history; protected areas

INTRODUCTION

México has the highest diversity of iguanas (subfamily Iguaninae) of any country, with four out of the eight recognized genera present, and 19 species, representing 43.2% of the world's species. The most diverse genus is *Ctenosaura* (Spiny-tailed Iguanas) which includes 11 of these species (Faria et al. 2010; ITWG this volume). Nine of these are endemic to México (*C. acanthura, C. clarki, C. conspicuosa, C. hemilopha, C. macrolopha, C. nolascensis, C. oaxacana, C. pectinata*, and *C. alfredschmidti*, and one, *C. defensor*, is barely distributed beyond México. Most of these species have small continental ranges or live exclusively on islands; accordingly they have very narrow ecological requirements. However, others are widespread, have more general habits, and occur in many states of the country, like *C. acanthura*, known as the Gulf Spiny-tailed Iguana, Tilcampo, Garrobo, or Chiquipile. It ranges mainly in the state of Veracruz, although it is also found in Llera and Tepehuaje, Tamaulipas, to the southeast to the Isthmus of Tehuantepec, and to the west in San Luis Potosí in the Huasteca region, the Tehuacán Valley in Puebla, and Cuicatlán in Hidalgo (Bailey 1928; Smith and Taylor 1950; Martin 1958; de Queiroz 1995; Köhler et al. 2000; Mendoza-Quijano et al. 2002; Canseco-Márquez and Gutiérrez-Mayén 2010).

Gulf Spiny-tailed Iguanas (Fig. 1) are robust lizards reaching a snout-vent length of 450 mm. Their tails are

Morales-Mávil, Jorge E., Emilio A. Suárez-Domínguez, and Carlos R. Corona-López. 2016. Biology and conservation of the Gulf Spiny-tailed Iguanas (*Ctenosaura acanthura*). Pp. 177–186 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

thick and longer than their bodies, with a series of spiny scales forming rings. The head is triangular and dorsally flattened. Males typically have a dorsal crest formed by long, spiny scales, which are shorter or nonexistent in the females. The tail exhibits black rings. Five to seven femoral pores are present, and in males are up to 2.5 mm in diameter, while in the females they only reach 1 mm diameter (Bailey 1928; Köhler 1993; Canseco-Márquez and Gutiérrez-Mayén 2010).

The body of the males is dark gray, with light stripes or ocelli that are not always present. Their color can also be pale gray, depending on their microhabitat. The hatchlings are green and the juveniles have a light blue color ventrally, with a dark ocellus on the gular region. The transverse stripes on the dorsum are also more evident, with a green background and extending as black rows toward the abdomen. Dark bars are present below the labial region (Bailey 1928; Smith 1935; de Queiroz 1995).

This iguana inhabits the coastal plains of the Gulf of México across many different habitats, including disturbed environments (Suárez-Domínguez et al. 2011). The Mexican Regulation regards this species as Under Special Protection (NOM-059-SEMARNAT-2010: NORMA Oficial Mexicana, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo). It has not yet been evaluated internationally on the Red List of Threatened Species (IUCN. 2014. The IUCN Red List of Threatened Species. Available from http://www.iucnredlist.org [Accessed 5 September 2014]). The information published on this species to date mainly concerns its systematics (Köhler et al. 2000, 2003; Köhler 2004), geographical distribution (Martin 1958; Mendoza-Quijano et al. 2002; Canseco-Márquez and Gutiérrez-Mayén 2010), and behavioral and ecological aspects (Suárez-Domínguez et al. 2004, 2011). It is unknown whether this iguana is present in different protected areas within its distribution, or other conserved unprotected areas. This work presents information on the distribution and ecology of the Gulf Spiny-tailed Iguana in the state of Veracruz, and discusses its current state of conservation and interactions with humans, acknowledging its occurrence, abundance, and role as an indicator of the quality of the habitat.

FIGURE 1. Male Gulf Spiny-tailed Iguana from Catemaco, Veracruz. (Photographed by Jorge E. Morales-Mávil).

METHODS

Study site.—The study was conducted on the coastal plains of Veracruz. Two large plains form the state of Veracruz, one on the north and the other on the south, separated by the foothills of the Trans-Mexican Volcanic Belt, which constitute an important geographic and climate barrier (Soto Esparza and Geissert Kientz 2011). These plains represent 73% of the area of the state (INEGI 1987).

Veracruz is quite diverse in climate: the northern plain has an average annual temperature from 24 to 25° C, and a minimum temperature (annual average) of 13 to 16° C. In the southern plain, the average temperatures are higher, reaching from 25 to above 26° C, with a minimum annual average from 16 to 17° C. The maximum extreme temperature is similar in both plains, oscillating between 27 and 28° C (Soto Esparza and Giddings Berger 2011). The human population is estimated at nearly eight million with an annual growth rate of 2.0% (INEGI, Instituto Nacional de Estadística Geografía e Informática. 2010. Principales Resultados por Localidad (ITER) del Censo de Población y Vivienda 2010. Available from http://www.inegi.org.mx/sistemas/consulta_resultados/iter2010.aspx [Accessed 23 August 2014]).

The vegetation of the plains consists of: (1) tropical evergreen forest; (2) semi-deciduous tropical forest; (3) tropical deciduous forest; (4) palms; (5) savanna; (6) gallery forest or riparian vegetation; (7) mangrove; (8) coastal dune vegetation; (9) pasture; (10) popal-bulrush; and (11) secondary vegetation (Rzedowski 2006). The secondary vegetation in different successional stages, also called *acahual*, constitutes the most widespread vegetation type, which reflects the disturbance of most vegetation types (Castillo-Campos et al. 2011).

Data collection.—Habitats likely to harbor iguanas were systematically sampled by transects, particularly in protected natural areas (state, federal, and Ramsar sites). These protected areas included: Port and City of Veracruz (two transects from June to July 2008), Presa Chicayán (two transects from July to August 2009), Santa Gertrudis Area of Forestal and Faunal Protection (two transects from July to August 2009), Los Tuxtlas Biosphere Reserve (two transects from March to April 2011 and two transects from June to July 2011), Santuario del Loro Huasteco (two transects from July to August 2009), Arroyo Moreno (two transects from June to July 2008), and Ciénega del Fuerte (two transects from July to August 2009 and one transect in March 2010). The Ramsar sites included: mangroves and wetlands of Lake Sontecomapan (two transects from August to September 2011), Alvarado lagoon system (two transects in August 2008), La Mancha and El Llano (one transect in February 2009, one transect from October 2009 to January 2010, and two transects from April to May 2010), the mangroves and wetlands of Tuxpan (two transects from October to November 2011 and three transects from February to March 2012). Transects were also conducted in the wetlands of Coatzacoalcos-Minatitlán (four transects from February to April 2009 and two transects from November to December 2009), Catemaco Lake (two transects from May to June 2010), El Raudal (one transect in June 2010), and areas surrounding Ciudad Cardel (one transect in October 2012). Everywhere, we interviewed local people about human consumption of meat or eggs of iguanas.

For one week each month we inspected each site for eight hours a day, between 0800 and 1600 by foot, boat, or land vehicle. Tree branches and bushes, rock piles, palapa (bungalow) roofs, walls, houses, and abandoned buildings were searched. Iguanas were captured opportunistically and manually with a rod, with a noose, or with the support of *iguaneros* (people dedicated to capturing iguanas for food). UTM coordinates as well as the description of the capture site and microhabitat were noted for each observation. Captured iguanas were measured using a vernier caliper and weighed using field spring scales. Sex was determined by the difference of femoral pore size (present in both sexes but larger in males) and the vertebral row of enlarged spines from base of head to base of tail, being much larger in males (Bailey 1928; Köhler 1993). We measured head width at the widest part of head immediately behind the eyes, and head length from the snout to the angle of the jaw.

***Dietary data*.—**We determined diet using direct observation (n = 26) of feeding in iguanas from Los Tuxtlas, using the animal-focal method with continuous recording (Martin and Bateson 1991) for 30 minutes for each focal or for the time the iguana kept eating. Two people carried out observations separately, each with a focal record. Observations were conducted between October and December 2003 and May to August 2004, at different hours between 0700 and 1900. Other diet records were made from fecal samples (n = 15) obtained from iguanas captured and held captive for two or three days in the La Mancha area. We collected comparative plant materials in the field to use for identification of fecal components. All fecal samples were dried in a desiccation chamber before separation, and identification of the different components (plant and animal) were attempted to order, family, genus, or species.

***Reproductive data*.—**Some gravid females captured in Coatzacoalcos and Sontecomapan between February to April 2009 were held captive within galvanized sheet metal closures (dimensions: 9 x 1.8 x 1.5 m). The enclosures contained a substrate of sand about 50 cm deep where the iguanas were able to nest. The enclosures were conditioned with concrete block shelters and 50 x 70 cm concrete slabs on which to place food, which consisted of fruits and vegetables *ad libitum*, ensuring that all females had access to food. Once the females laid their eggs they were released at their capture site. Eggs were measured, weighed, and transferred to polystyrene boxes (30 x 22 x 25 cm) filled with sand. Eggs were buried in sand with no direct exposure to air. The sand with the eggs was sprinkled regularly to keep it humid during the incubation period. Boxes were covered with a metal mesh cover (fine sieve) and placed on wooden shelves in an incubation room, under ambient temperature between 29 and 31° C and between 60 and 80% humidity. Hatchlings were measured, weighed, and then released in the same capture sites as the females.

***Statistical analyses*.—**We used both parametric and nonparametric tests, depending on the data distribution. Body size using snout-vent length (SVL) and head size of males and females were compared using ANOVA, with an $\alpha = 0.05$. Means are followed by ± 1 SD and range. Relative clutch mass (RCM) was calculated by the clutch mass/gravid female mass quotient (Vitt and Congdon 1978; Cuellar 1984; Castro-Franco et al. 2011). Regression analysis was applied to relate SVL and body mass with clutch parameters. We hypothesized that sex ratio should be 50:50 and we recorded the proportion of males captured per site. A Mann-Whitney U test was used to compare the diet of males and females. We calculated differences between expected value and observed values with a chi-square test.

RESULTS

***Morphometrics and distribution*.—**One hundred twenty adult iguanas (28 males and 92 females) and 13 juveniles were captured. Males were significantly longer than the females: SVL = 239.2 ± (SD) 27.8 mm (range, 194–282 mm) versus non-gravid female SVL = 194.6 ± (SD) 25.7 mm (range, 148–245 mm; F = 18.4, P = 0.0002). Males were also significantly larger compared to non-gravid females in mass: 423.2 ± 120.4 g (range, 206.3–610.0 g) versus 250.5 ± 26.9 g (range, 95.9–371.1 g; F = 15.9, P = 0.0005). Male heads were larger in length: 55.9 ± 9.9 mm (range, 43–68 mm) versus 42.1 ± 1.6 mm (range, 33–49 mm; F = 18.39, P = 0.00023); as well as width: 39.8 ± 6.3 mm (range, 30–50 mm) versus 29.4 ± 4.2 mm (range, 24–35 mm; F = 25.8, P < 0.0001; Fig. 1). The sex ratio (M:F) was 1:3.28 (n = 120), significantly different from a sex ratio of 1:1 (χ^2 = 34.1, P < 0.001).

Gulf Spiny-tailed Iguanas were found in all the protected areas and Ramsar sites explored, as well as the wetlands of Minatitlán-Coatzacoalcos, Raudal, Catemaco,

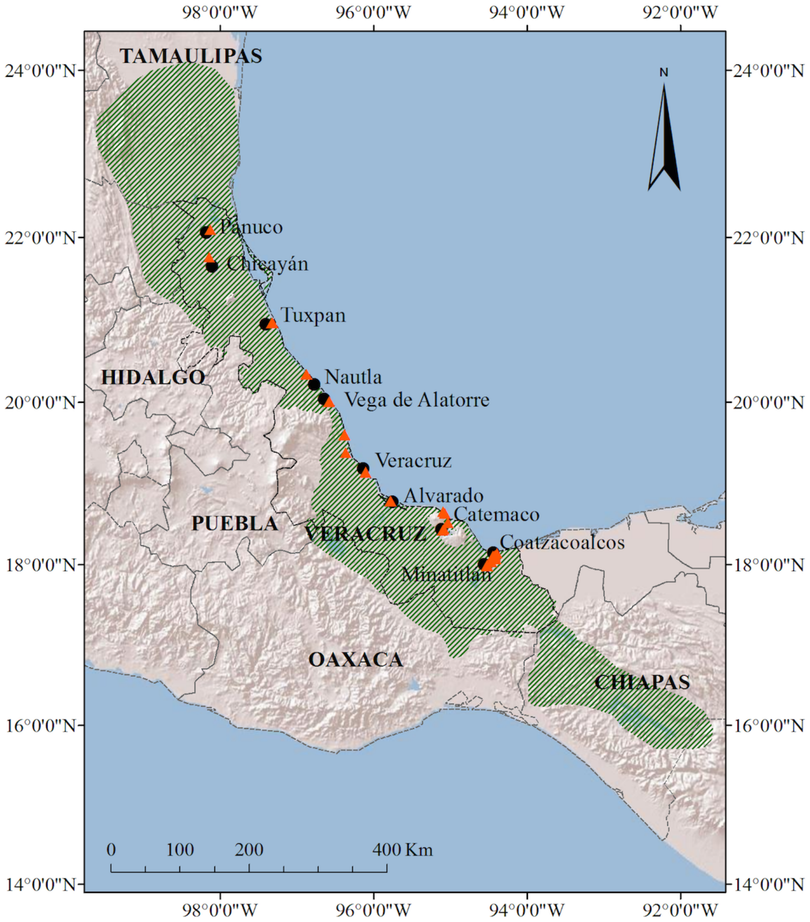

Figure 2. Distribution of Gulf Spiny-tailed Iguanas (*Ctenosaura acanthura*) in the state of Veracruz, México. Green indicates current distribution; red triangles are collecting sites; black dots indicate major cities within the distribution.

and the surroundings of Cardel, in the central part of the state (Fig. 2). Hence, these iguanas were distributed across many different types of vegetation of the coastal plains, including rural, suburban, and even urban environments as in the City and Port of Veracruz, Boca del Río, and Coatzacoalcos cities, where iguanas occur in vacant lots, traffic islands, large gardens, and rooftops.

Table 1. Components identified in the diet of *Ctenosaura acanthura* in Veracruz based on an analysis of scat samples (n = 16).

Taxon	Occurrence percentage
Vegetal components	
Cordia dentata (Boraginaceae)	60
Malvaviscus arboreus (Malvaceae)	40
Nectandra sanguinea (Lauraceae)	20
Xylosma sp. (Salicaceae)	20
Rhacoma urogoga (Celatraceae)	20
Unidentified (Leguminosae)	100
Animal components	
Coleoptera	100
Hymenoptera	100
Crustaceae (Oniscidea)	60

***Diet*.**—From our analysis of 15 fecal samples from adult iguanas (seven males and eight females), we documented nine different components (six plants and three animals) in the diet of *C. acanthura* (Table 1). Also, all samples contained sand and small rocks. No differences were found in the diet of males and females (U = 49.5, P = 0.47). Vertebrate items were not recorded (Table 1). On the other hand, from our observations (n = 26) we recorded 17 components (11 plants and six animals; Table 2). Vertebrate items were not recorded except for the consumption of their own skin.

***Reproductive aspects*.—**Gravid iguanas (n = 26) were captured in February and March; 13 were captured on the margins of the Coatzacoalcos River in mangrove vegetation, secondary vegetation, and pastures, and the other 13 from the community El Real in the Sontecomapan lagoon wetlands consisting of mangrove vegetation, apompal (*Pachira acuatica*), and secondary vegetation.

TABLE 2. Components identified in the diet of *Ctenosaura acanthura* in Veracruz based on direct observations of feeding. Percentage frequencies were calculated separately for animals and plants.

Taxa	Number of items consumed	Percentage of total items consumed	Number of events in which consumption was observed	Frequency of occurrence
Animal components				
Lepidoptera	1	1.52	1	1.89
Orthoptera	1	1.52	1	1.89
Coleoptera	2	3.03	2	3.77
Hemiptera	11	16.67	1	1.89
Diptera	42	63.64	42	79.25
Their own skin	9	13.64	6	11.32
Vegetal components				
Spondias mombin	19	0.83	7	4.58
Pimenta dioica	32	1.41	1	0.65
Anona sp.	43	1.89	7	4.58
Diospyros digyna	52	2.28	4	2.61
Opuntia sp.	90	3.95	5	3.27
Senecio sp.	125	5.49	11	7.19
Sida sp.	128	5.62	5	3.27
Calophyllum sp.	343	15.07	18	11.76
Capsella sp.	427	18.76	31	20.26
Solandra sp.	484	21.27	32	20.92
Passiflora microstipula	533	23.42	32	20.92

The gravid females (n = 26) had an average SVL of 256.1 ± 30.3 mm (range, 215–310 mm) and body mass of 493.1 ± 144.4 g (range, 275–750 g). Clutch size (n = 21) averaged 27.7 ± 9.1 eggs (range, 18–48 eggs), clutch mass (n = 21 clutches, n = 210 eggs) averaged 172.4 ± 61.2 g (range, 90–341 g), and relative clutch mass (RCM; n = 21) averaged 0.358 ± 0.127 (range, 0.156–0.720; CV = 35.5%). Four significant relationships were detected between female morphometrics and clutch measurements: (1) SVL and clutch size ($R^2 = 0.421$, F = 17.45, $P < 0.01$); (2) body mass and clutch size (R^2 = 0.25, F = 8.02, P = 0.009); (3) SVL and clutch mass (R^2 = 0.342, F = 12.49, $P < 0.001$); and (4) body mass and clutch mass ($R^2 = 0.211$, F = 6.42, P = 0.017). Eggs (n = 210) averaged 29.0 ± 2.5 mm (range, 25–33 mm) in length, 20.5 ± 2.1 mm (range, 17–24 mm) in width, 6.0 ± 0.7 g (range, 5.0–7.2 g) in mass. Incubation time averaged 78.2 ± 6.3 days (range, 70–87 days) and 58.3% of the eggs hatched. A positive relationship between female body mass and RCM was found ($R^2 = 0.215$, F = 6.58, $P < 0.017$), but there was no relationship between SVL and RCM (R^2 = 0.0002, F = 0.005, P = 0.944; Table 3). Newly emerged hatchlings (n = 120) had an average SVL = 52.8 ± 3.0 mm (range, 41–58 mm) and mass = 5.1 ± 0.6 g (range, 3.9–6.4 g).

DISCUSSION

The Gulf Spiny-tailed Iguana is distributed all across the coastal plains of the State of Veracruz. *Ctenosaura acanthura* occupies a wide variety of environments, although its primary habitats included: medium evergreen tropical forest, evergreen lowland forest, deciduous forest, and wetlands. However, it has also been found in environments with secondary successional vegetation, including grasslands, croplands, and human settlements (Etheridge 1982; Canseco-Márquez and Gutiérrez-Mayén 2010; Morales-Mávil and Suárez-Domínguez 2010; Suárez-Domínguez et al. 2011).

Among ctenosaurs, *C. acanthura* is medium in size, smaller than the closely related *C. pectinata* (Suazo and Alvarado 1994; Castro-Franco et al. 2011), *C. bakeri* (Köhler 2004), and *C. similis* (Henderson 1973; Mora and Barrantes 1985; Lee 2000). Like other spiny-tailed iguanas, males are larger than females and bear a more prominent mid-dorsal crest: *C. palearis* (Elfström et al. 1994), *C. similis* (Lee 2000), *C. clarki* (Pérez-Ramos and Saldaña de la Riva 2002), *C. macrolopha* (Goldberg 2009), *C. melanosterna* (Pasachnik et al. 2012), *C. bakeri* (Köhler 2004), *C. oedirhina* (Pasachnik 2013), *C. pectinata* (Bailey 1928; Evans 1951), *C. praeocularis* (Hasbún and Köhler 2009), and *C. quinquecarinata* (Bailey 1928).

TABLE 3. Regression analyses (R^2) between reproductive traits and female mass and length of the Gulf Spiny-tailed Iguanas, *Ctenosaura acanthura*. * = Significant.

	Clutch size	Average egg size	Average egg weight	Relative clutch mass (RCM)
Body mass females (n = 26)	$R^2 = 0.250$ $P = 0.009$*	$R^2 = 0.102$ $P = 0.112$	$R^2 = 0.142$ $P = 0.562$	$R^2 = 0.215$* $P = 0.016$
Snout-vent length females (n = 26)	$R^2 = 0.421$* $P < 0.001$	$R^2 = 0.079$ $P = 0.165$	$R^2 = 0.013$ $P = 0.554$	$R^2 = 0.0002$ $P = 0.944$

The diet was based primarily on the consumption of plant parts. Most frequently, iguanas used active foraging, but without traveling long distances. We documented that *C. acanthura* consumed a wide variety of food resources (24 species), including both native plants and ornamental crops and plants from gardens and backyards, as well as a variety of arthropods (Lepidoptera, Orthoptera, Coleoptera, Hemiptera, Diptera). Thus, *C. acanthura* has an omnivorous diet tending toward herbivory (Iverson 1982), a common dietary strategy within the ctenosaur group like *C. pectinata* (Durtsche 2000), *C. hemilopha* (Blázquez and Rodriguez-Estrella 2007), *C. palearis* (Cotí and Ariano-Sánchez 2008), and *C. similis* (Mora 2010). However, vertebrate items were not recorded, which differs from what has been documented for other spiny-tailed iguanas such as *C. similis* (Fitch and Hackforth-Jones 1982; Mora 1991; Krysko et al. 2000), *C. pectinata* (Alvarez del Toro 1982; Suazo and Alvarado 1994), *C. hemilopha* (Blázquez and Rodríguez-Estrella 2007), and *C. oedirhina* (Pasachnik 2013) whose diets included vertebrates such as lizards (including hatchling iguanas), turtle hatchlings, birds, rodents, and even the consumption of carrion in *C. hemilopha* (Blázquez and Rodríguez-Estrella 2007) and *C. similis* (Mora 2010). The consumption of their own skin is a frequent event in iguanines (Blázquez and Rodríguez-Estrella 2007).

The diversity of the diet probably allows *C. acanthura* to occupy a diversity of ecosystems, including disturbed environments (Villanueva-Noriega 2004; Suárez-Domínguez et al. 2011, 2013). Several species of *Ctenosaura* have habits that have allowed them to adjust to environments modified by humans. These lizards regularly share habitats with humans in rural and urban environments, using roofs, galleries, rock walls, and pipes (Burger and Gochfeld 1990; Stephen et al. 2012). We found *C. acanthura* in many different microhabitats: on trees and bushes, in hollow trees, rock piles, pipes, and on roofs and walls of buildings. Indeed, *C. acanthura* living in these disturbed environments exhibit little behavioral or physiological stress (Suárez-Domínguez et al. 2011).

Gravid female *Ctenosaura acanthura* were similar in SVL to those of *C. pectinata* (256.1 ± 30.3 mm vs. 241 ± 2 mm, respectively), but weighed less (493.1 ± 144.4 g vs. 531.1 ± 12.9 g) (López-Ruvalcaba et al. 2012). Relative clutch mass (0.358) was slightly lower than for *C. pectinata* (0.364; Castro-Franco et al. 2011), but with more variation. The significant relationship between RCM values and body mass for females differed from that recorded for *C. pectinata* by Castro-Franco et al. (2011). The average RCM for *C. acanthura* was high among lizards, and was closer to that in snakes (Fitch 1970; Seigel and Fitch 1984; Shine 1992). Clutch size in *C. acanthura* was positively related to female SVL and mass, as has been recorded for many species of reptiles (Fitch 1985; Shine and Greer 1991; Thomson and Pianka 2001). This same relationship was also found in *C. pectinata* (Castro-Franco et al. 2011). Clutch size can be related more to the age of the females than size in some *Ctenosaura* species (Castro-Franco et al. 2011; López-Ruvalcaba et al. 2012), but we do not have age data for our females.

Incubation times of the eggs of *C. acanthura* (mean = 78.2 days) were slightly longer than those reported for *C. pectinata* from Oaxaca (71.2 days, López-Ruvalcaba et al. 2012) or for *C. palearis* (70 days, Elfström et al. 1994). Hatching success for *C. acanthura* was low (58.3%) in comparison to species like *C. pectinata* (80%) with a similar clutch size and incubated under similar conditions (López-Ruvalcaba et al. 2012). However, under different incubation conditions, incubation times for *C. pectinata* were much shorter (Aguirre-Hidalgo 2007) in Chamela, Jalisco (31 days) and Nizanda, Oaxaca (45.6 days). Clutch size in our study of *C. acanthura* (mean = 27.7) was similar to that reported by Corona-López (2010) in two populations of *C. acanthura* from southwestern Veracruz (24.9 ± 6.2 eggs and 32.9 ± 11.7 eggs) and lower than in *C. similis* (sample means = 43–88 eggs, Fitch and Henderson 1978; mean = 62 eggs, Avery et al. 2014) and higher than in *C. oedirhina* (4–7 eggs, Pasachnik 2013), *C. bakeri* (9.3 ± 2.9, range = 9–16, Gutsche and Köhler 2004), or *C. palearis* (11 eggs, Elfström et al. 1994; 6–12 eggs, Cotí and Ariano-Sánchez 2008).

The fact that the Gulf Spiny-tailed Iguana is found in a wide variety of environments, including disturbed sites and human settlements, is probably the reason why females migrate to open, sandy areas in order to nest, as reported by Suárez-Domínguez et al. (2005). However, even though it has not yet been reported for *C. acanthura*, it is possible that some females nest near their home ranges and sacrifice better incubation sites because of a reduction in their predation risk during migrations, as has been suggested for other iguanines (Morales-Mávil et al. 2007).

Age and nutrition of females are known to affect clutch size, hatching success, and hatchling size in lizards (Fitch 1970; Tinkle et al. 1970; Warner et al. 2008; Ford and Seigel 2010; Uller and Olsson 2010). Females of *C. pectinata* older than 4.5 years produce nests with more eggs and larger hatchlings than younger females (Lopez-Ruvalcaba et al. 2012). The newly emerged hatchlings in our study averaged 52.8 mm SVL and 5.1 g body mass, slightly smaller than for *C. macrolopha* (SVL = 55 mm, Goldberg 2009) and *C. pectinata* (55 mm and 5.4 g, Lopez-Ruvalcaba et al. 2012).

Veracruz has a large oil industry as well as agriculture and livestock. Environmental pollution by heavy metals and hydrocarbons is a permanent risk. Environmental contamination by heavy metals is known to affect reproductive success adversely in reptiles (Hopkins et al. 1999; Khan and Law 2005; Hsu et al. 2006). However, Corona-López (2010) demonstrated that females of *C. acanthura* living at a major oil industrial site were not affected in their size and body mass, nor in clutch size or hatch rate, although they did report an effect on the condition of the hatchlings, as nearly 10% of them had deformed tails. However, that could have been the result of extreme temperature during incubation (Shine 2004). In any case, carnivorous species tend to be the most affected reproductively by heavy metals because of bioaccumulation up the food chain. Because *C. acanthura* is omnivorous with a tendency toward herbivory, the pollution effect may be smaller. However, this once again points to the broad ecological plasticity of *C. acanthura* in surviving in highly disturbed environments.

The local people use iguanas for meat or eggs, as they do for related species (Fitch et al. 1982; Stephen et al. 2012). In order to reduce pressure on wild populations of iguanas, the Mexican environmental authorities (The Ministry of Environment and Natural Resources, SEMARNAT) have promoted the establishment of farms by rural people as an alternative to wild capture. However, this approach has only been successful for the Common Green Iguana (*Iguana iguana*). Farms for Gulf Spiny-tailed Iguanas have not been successful because the iguanas are smaller and exhibit more aggressive behavior.

Although Mexican laws currently regard the Gulf Spiny-tailed Iguana as Under Special Protection (Pr; NOM-059-SEMARNAT-2010), it is still harvested by local people. The Pr category includes those species or populations that could potentially be threatened by factors that adversely affect their viability, recommending support for recovery and preservation, or restoration and conservation, of populations and their habitats. This category may include lower risk categories than the classification of the IUCN Red List of Threatened Species. However, for now the population status of *C. acanthura* appears to be stable, presumably due to its ecological plasticity. Furthermore, it is present in all of the protected areas that were sampled with tropical forest in the plains of Veracruz. Nevertheless, additional research is needed to confirm its status at the periphery of the range in Tamaulipas, San Luis Potosí, and Oaxaca.

Acknowledgments.—We received financial support from Fondos Sectoriales of Conacyt- SEMARNAT, (SEMARNAT 2002-co01-0429). This study was approved by the institutional guidelines of the Universidad Veracruzana. Permission for this study was provided by the Federal Government of México's Secretariat of Environment and Natural Resources (SEMARNAT; SEMARNAT No. 9/GS- 2132/05/10). Suárez-Domínguez and Corona-López were supported by CONACYT's grants studies 164464 and 197662.

LITERATURE CITED

Aguirre-Hidalgo, V. 2007. Demography and genetic diversity of the Mexican Black Iguana *Ctenosaura pectinata*. Ph.D. Dissertation, University of Plymouth, Plymouth, Massachusetts, USA.

Alvarez del Toro, M. 1982. Los Reptiles de Chiapas. Publicaciones del Gobierno del Estado de Chiapas, Tuxtla Gutiérrez, Chiapas, México.

Avery, M.L., E.A. Tillman, C. Spurfeld, R.M. Engeman, K.P. Maciejewski, J.D. Brown, and E.A. Fetzer. 2014. Invasive Black Spiny-tailed Iguanas, *Ctenosaura similis*, on Gasparilla Island, Florida, USA. Integrative Zoology 9:590–597.

Bailey, J.W. 1928. A revision of the lizards of the genus *Ctenosaura*. Proceedings of the United States National Museum 73:1–55.

Blázquez, M.C., and R. Rodriguez-Estrella. 2007. Microhabitat selection in diet and trophic ecology of a spiny-tailed iguana *Ctenosaura hemilopha*. Biotropica 39:496–501.

Burger, J., and M. Gochfeld. 1990. Risk discrimination of direct versus tangential approach by basking Black Iguanas (*Ctenosaura similis*): variation as a function of human exposure. Journal Comparative Psychology 104:388–394.

Canseco-Márquez, L., and G. Gutiérrez-Mayén. 2010. Anfibios y Reptiles del Valle de Tehuacán-Cuicatlán. CONABIO, Fundación para la Reserva de la Biosfera Cuicatlán, Benemérita Universidad Autónoma de Puebla, Puebla, México.

Castillo-Campos, G., S. Avendaño Reyes, and M.E. Medina Abreo. 2011. Flora y vegetación. Pp. 163–179 *In* La Biodiversidad en Veracruz: Estudio de Estado. Vol. I. Angón, A.C. (Coord.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Gobierno del Estado de Veracruz, Universidad Veracruzana, Instituto de Ecología, A.C., México.

Castro-Franco, R., M.G. Bustos-Zagal, and F.R. Méndez-De la Cruz. 2011. Variation in parental investment and relative clutch mass of the spiny-tail iguana, *Ctenosaura pectinata* (Squamata: Iguanidae) in central México. Revista Mexicana de Biodiversidad 82:199–204.

Corona-López, C.R. 2010. Concentración de metales pesados en hembras de Iguana Negra (*Ctenosaura acanthura*, Shaw, 1802) y su efecto sobre la tasa de reproducción. M.Sc. Thesis, Instituto de Neuroetología, Universidad Veracruzana, Xalapa, Veracruz, México. 75 p.

Cotí, P., and D. Ariano-Sánchez. 2008. Ecology and traditional use of the Guatemalan Black Iguana (*Ctenosaura palearis*) in the dry forests of the Motagua Valley, Guatemala. Iguana: Conservation, Natural History, and Husbandry of Reptiles 15:143–149.

Cuellar, O. 1984. Reproduction in a parthenogenetic lizard: with a discussion of the optimal clutch size and a critique of the clutch weight/body weight ratio. American Midland Naturalist 111:242–258.

de Queiroz, K. 1995. Checklist and key to the extant species of Mexican iguanas (Reptilia: Iguaninae). Publicaciones Especiales del Museo de Zoología, Universidad Nacional Autónoma de México 9:1–48.

Durtsche, R.D. 2000. Ontogenetic plasticity of food habits in the Mexican Spiny-tailed Iguana, *Ctenosaura pectinata*. Oecologia 124:8–195.

Elfström, B. 1994. The Paleate Spiny-tailed Iguana, *Ctenosaura palearis* Stejneger: distribution and life history. Iguana Times (Journal of the International Iguana Society) 3:2–9.

Etheridge, R.E. 1982. Checklist of the iguanine and Malagasy iguanid lizards. Pp. 7–37 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Evans, L.T. 1951. Field study of the social behavior of the Black Lizard *Ctenosaura pectinata*. American Museum Novitates 1943:1–26.

Faria, C.M.A., E. Zarza, V.H. Reynoso, and B.C. Emerson. 2010. Predominance of single paternity in the Black Spiny-tailed Iguana: conservation genetic concerns for female-biased hunting. Conservation Genetics 11:1645–1652.

Fitch, H.S. 1970. Reproductive cycles in lizards and snakes. Miscellaneous Publications of the Natural History Museum, University of Kansas 52:1–247.

Fitch, H.S. 1985. Variation in clutch and litter size in New World reptiles. Miscellaneous Publications of the Natural History Museum, University of Kansas 76:1–76.

Fitch, H.S, and J. Hackforth-Jones. 1982. *Ctenosaura similis* (Garrobo, Iguana Negra) Pp. 394–396 *In* Costa Rica Natural History. Janzen, D.H. (Ed). The University of Chicago Press, Chicago, Illinois, USA.

Fitch, H.S., and R.W. Henderson. 1978. Ecology and exploitation of *Ctenosaura similis.* University of Kansas Science Bulletin 51:483–500.

Fitch, H.S., R.W. Henderson, and D.M. Hillis. 1982. Exploitation of iguanas in Central America. Pp. 397–417 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Ford, N.B., and R.A. Seigel. 2010. An experimental test of the fractional egg size hypothesis. Herpetologica 66:451–455.

Goldberg, S.R. 2009. Note on reproduction of the Sonoran Spiny-tailed Iguana (*Ctenosaura macrolopha*) (Squamata:Iguanidae). Bulletin of the Chicago Herpetological Society 44:42–43.

Gutsche, A., and G. Köhler. 2004. A fertile hybrid between *Ctenosaura similis* (Gray, 1831) and *C. bakeri* Stejneger, 1901 (Squamata: Iguanidae) on Isla de Utila, Honduras. Salamandra 40:201–206.

Hasbún, C.R., and G. Köhler. 2009. A new species of *Ctenosaura* (Squamata, Iguanidae) from southeastern Honduras. Journal of Herpetology 43:192–204.

Henderson, R.W. 1973. Ethoecological observations of *Ctenosaura similis* (Sauria: Iguanidae) in British Honduras. Journal of Herpetology 7:27–33.

Hopkins, W.A, C. Rowe, and J.D. Congdon. 1999. Elevated trace element concentrations and standard metabolic rate in Banded Water Snakes (*Nerodia fasciata*) exposed to coal combustion wastes. Environmental Toxicology and Chemistry 18:1258–1263.

Hsu, M.J., K. Selvaraj, and G. Agoramoorthy. 2006. Taiwan's industrial heavy metal pollution threatens terrestrial biota. Environmental Pollution 143:327–334.

INEGI, Instituto Nacional de Geografía y Estadística. 1987. Carta Estatal de Regionalización Fisiográfica. Estado de Veracruz. Escala 1:1,000,000. Aguascalientes, México.

Iguana Taxonomy Working Group (ITWG). 2016. A checklist of the iguanas of the world (Iguanidae; Iguaninae). Pp. 4–46 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Iverson, J.B. 1982. Adaptations to herbivory in iguanine lizards. Pp. 60–76 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Khan, M.Z., and F.C.P. Law. 2005. Adverse effects of pesticides and related chemicals on enzyme and hormone systems of fish, amphibians, and reptiles: a review. Proceedings of Pakistan Academy of Sciences 42:315–323.

Köhler, G. 1993. Schwarze Leguane: Freilandbeobachtungen, Pflege, und Zucht. Herpeton Verlag, Offenbach, Germany.

Köhler, G. 2004. Conservation status of spiny-tailed iguanas (genus *Ctenosaura*), with special emphasis on the Utila Iguana (*C. bakeri*). Iguana (Journal of the International Iguana Society) 11:207–211.

Köhler, G., A.J. Gutman, and R. Powell. 2003. Black Iguanas: name and systematics. Iguana (Journal of the International Iguana Society) 10:79–81.

Köhler, G., W. Schroth, and B. Streit. 2000. Systematics of the *Ctenosaura* group of lizards (Reptilia: Sauria: Iguanidae). Amphibia-Reptilia 21:177–191.

Krysko, K., F.W. King, K. Enge, and A. Reppas. 2000. Distribution of the introduced Black Spiny-tailed Iguana (*Ctenosaura similis*) on the southwestern coast of Florida. Florida Scientist 66:74–79.

Lee, J.G. 2000. A Field Guide to the Amphibians and Reptiles of the Maya World. The Lowlands of México, Northern Guatemala, and Belize. Cornell University Press, Ithaca, New York, USA.

López-Ruvalcaba, O.A., J.L. Arcos-García, G.D. Mendoza-Martínez, R. López-Pozos, S.J. López-Garrido, and L. Vélez-Hernández. 2012. Parámetros reproductivos de las hembras de Iguana Negra (*Ctenosaura pectinata*) en condiciones intensivas. Revista Científica 22:65–71.

Martin, P.S. 1958. A biogeography of reptiles and amphibians in the Gomez Farias region, Tamaulipas, México. Miscellaneous Publications, Museum of Zoology, University of Michigan 101:1–102.

Martin, P., and P. Bateson. 1991. La Medición del Comportamiento. Editorial Alianza, Madrid, Spain.

Mendoza-Quijano, F., F. de M. Mejenes-López, and M. Hernández-Aquino. 2002. *Ctenosaura acanthura* (Shaw, 1802), an addition to the known fauna of the Mexican State of Hidalgo. Herpetozoa 15:91–92.

Mora, J.M. 1991. Comparative grouping behavior of juvenile ctenosaurs and iguanas. Journal of Herpetology 25:244–246.

Mora, J.M. 2010. Natural history of the Black Spiny-tailed Iguana (*Ctenosaura similis*) at Parque Nacional Palo Verde, Costa Rica, with comments on the conservation of the genus *Ctenosaura*. Pp. 716–733 *In* Conservation of Mesoamerican Amphibians and Reptiles. Wilson, L.D., J.H. Townsend, and J.D. Johnson (Eds.). Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

Mora, J.M., and G. Barrantes. 1985. Ecología y manejo del Garrobo *Ctenosaura similis* en Costa Rica. Pp. 48 *In* Recursos Naturales y Desarrollo en Costa Rica, Memoria del Simposio. UNA-CONICIT. Navarro, W. (Ed.). Universidad Nacional, Heredia, Costa Rica.

Morales-Mávil, J.E., and E.A. Suárez-Domínguez. 2010. Registro de géneros de vertebrados por municipio. Pp. 53–65 *In* Atlas Regional de Impactos Derivados de las Actividades Petroleras en Coatzacoalcos, Veracruz. Mendoza-Cantú, A. (Ed.). Universidad Nacional Autónoma de México, México, D.F.

Morales-Mávil, J.E., R.C. Vogt, and H. Gadsden-Esparza. 2007. Desplazamientos de la Iguana Verde, *Iguana iguana* (Squamata: Iguanidae) durante la estación seca en La Palma, Veracruz, México. Revista de Biología Tropical 55:709–715.

Pasachnik, S.A. 2013. Growth, reproduction, and diet of Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina*. Herpetological Biology and Conservation 8:191–198.

Pasachnik, S.A., C.E. Montgomery, L.E. Ruyle, J.P. Corneil, and E.E. Antúnez. 2012. Morphological and demographic analyses of *Ctenosaura melanosterna* across its range: implications for population level management. Herpetological Conservation and Biology 7:399–406.

Pérez-Ramos, E., and L. Saldaña de la Riva. 2002. Distribución Ecológica del "Nopilchi" *Ctenosaura clarki* (Reptilia: Iguanidae), en las Regiones de "Tierra Caliente" y "El Infiernillo", Guerrero-Michoacán, México. Revista Digital Universitaria 3(2). ISSN: 1607–6079.

Rzedowski, J. 2006. Vegetación de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, D.F.

Seigel, R.A., and H.S. Fitch. 1984. Ecological patterns of relative clutch mass in snakes. Oecologia 61:293–301.

Shine, R. 1992. Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? Evolution 46:828–833.

Shine, R. 2004. Adaptive consequences of developmental plasticity. Pp. 187–210 *In* Reptilian Incubation: Environment, Evolution, and Behaviour. Deeming, D.C. (Ed.). Nottingham University Press, Nottingham, England.

Shine, R., and A.E. Greer. 1991. Why are clutch sizes more variable in some species than others? Evolution 45:1696–1706.

Smith, H.M. 1935. Miscellaneous notes on Mexican lizards. University of Kansas Science Bulletin 36:119–155.

Smith, H.M., and E.H. Taylor. 1950. An annotated checklist and key to the reptiles of México exclusive of the snakes. United States National Museum Bulletin 199:1–253.

Soto Esparza, M., and D. Geissert Kientz. 2011. Geografía. Pp. 31–34 *In* La Biodiversidad en Veracruz: Estudio de Estado. Vol. I. Angón, A.C. (Coord.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Gobierno del Estado de Veracruz, Universidad Veracruzana, Instituto de Ecología, A.C., México.

Soto Esparza, M., and L.E. Giddings Berger. 2011. Clima. Pp. 35–52 *In* La Biodiversidad en Veracruz: Estudio de Estado. Vol. I. Angón, A.C. (Coord.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Gobierno del Estado de Veracruz, Universidad Veracruzana, Instituto de Ecología, A.C., México.

Stephen, C.L., S. Pasachnik, A. Reuter, P. Mosig, L. Ruyle, and L. Fitzgerald. 2011. Evaluación del Estado, Comercio, y Explotación de las Iguanas de CentroAmérica (Survey of Status, Trade, and Exploitation of Central American Iguanas). Report for the Department of Interior, United States Fish and Wildlife Service, Washington, D.C., USA.

Suárez-Domínguez, E.A., A. González-Romero, J.E. Morales-Mávil, and G. Aguirre-León. 2004. Tamaño del ámbito hogareño y uso de hábitat de hembras de Iguana Negra (*Ctenosaura acanthura*, Shaw, 1802) en la época reproductiva en la zona de la Mancha, Veracruz. M.Sc. Thesis, Instituto de Ecología A.C., Xalapa, Veracruz, México. 107 p.

Suárez-Domínguez, E.A., J.E. Morales-Mávil, R. Chavira, and L. Boeck. 2011. Effects of habitat perturbation on the daily activity pattern and physiological stress of the spiny-tailed iguana (*Ctenosaura acanthura*). Amphibia-Reptilia 32:315–322.

Suárez-Domínguez, E.A., J.E. Morales-Mávil, and C.R. Corona-López. 2013. La iguana de cola espinosa; saurio de los tejados tropicales. La Ciencia y el Hombre 26:12–18.

Suazo, O.I., and D.J. Alvarado. 1994. Iguana Negra: Notas sobre su Historia Natural. Universidad Michoacana de San Nicolás de Hidalgo, USFWS, and Ecotonia, A.C., México.

Thomson, G.G., and E.R. Pianka. 2001. Allometry of clutch and neonate sizes in monitor lizards (Varanidae; *Varanus*). Copeia 2001:443–458.

Tinkle, D.W., H.M. Wilbur, and S.G. Tilley. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55–74.

Uller, T., and M. Olsson. 2010. Offspring size and timing of hatching determine survival and reproductive output in a lizard. Oecologia 162:663–671.

Villanueva-Noriega, M.J. 2004. Patrón de actividad diaria de *Ctenosaura acanthura* (Shaw, 1802) en Montepío, región de Los Tuxtlas, Veracruz, México. Bachelor's Thesis, Universidad Nacional Autónoma de México, México, D.F. 103 p.

Vitt, L.J., and J.D. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. American Naturalist 112:595–608.

Warner, D.A., X. Bonnet, K.A. Hobson, and R. Shine. 2008. Lizards combine stored energy and recently acquired nutrients flexibly to fuel reproduction. Journal of Animal Ecology 77:1242–1249.

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Herpetological Conservation and Biology 11(Monograph 6):187–196.
Submitted: 26 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

CONSERVATION GENETICS OF ROATÁN SPINY-TAILED IGUANAS, *CTENOSAURA OEDIRHINA*

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Abstract.—**Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina*, are assessed as Endangered by the IUCN Red List of Threatened Species and listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Occurring in less than 1% of the available habitat on Roatán, due primarily to hunting pressure, this species faces severe fragmentation. Herein we used a combination of mitochondrial and nuclear DNA to elucidate contemporary levels of genetic diversity and genetic structure across the range of this species. Our results reveal generally low levels of genetic diversity within groups at each site sampled, coupled with moderate to high levels of genetic differentiation among these sites. Although contemporary differentiation among sites is substantial, alleles and haplotypes shared among those sites suggest historical connectivity across Roatán and Barbareta. However, despite past connectivity, our data indicate contemporary disruption of movement among isolated sites, resulting in the high level of observed genetic differentiation. Our data further suggest increased inbreeding within sites, which, coupled with small population size, makes each group more vulnerable to stochastic events and disturbances. In order to manage for the long-term persistence of this species, a captive breeding program may be essential; however, data regarding relatedness within sites and basic reproductive information must be gathered prior to beginning such a program.**

Resumen.—Ctenosaura oedirhina,* o la Iguana de cola espinosa de Roatán, se encuentra listada En Peligro según la lista Roja de la IUCN y bajo el Apéndice II de la Convención Internacional de Especies Amenazadas de Fauna y Flora Silvestres (CITES). Esta especie ocupa menos de 1% del hábitat disponible de la isla de Roatán, debido principalmente a la cacería ilegal, enfrentando así fragmentación severa. A partir de esto, fueron empleados una combinación de marcadores de ADN mitocondrial y nuclear para elucidar los niveles contemporáneos de diversidad y estructura genética a lo largo de su rango de ocupación. Nuestros resultados revelaron bajos niveles de diversidad genética dentro de cada grupo analizado para cada localidad muestreada junto a niveles de diferenciación genética que iban de moderados a elevados entre las localidades muestreadas. Aunque la diferenciación actual entre localidades es sustancial, los alelos y haplotipos compartidos entre localidades sugiere que existió una conectividad histórica entre estas, extendiéndose esta evidencia hasta la isla Barbareta. Sin embargo, independientemente de la conectividad histórica, existe interferencia en el movimiento de las iguanas entre localidades, resultando esto en los niveles elevados de diferenciación genética observada en cada localidad. Ocasionando esto, a la vez, la presencia de varias poblaciones genéticamente aisladas. Adicional a esto, nuestros resultados demuestran una alta señal de endogamia dentro de las localidades muestreadas, la cual, junto a los pequeños números poblacionales, ocasiona que las poblaciones en Roatán sean más vulnerables a disturbios en el hábitat y eventos estocásticos. Por consiguiente, el manejo de esta población a largo plazo para su conservación pudiera requerir de la implementación de un programa de reproducción en cautiverio. Sin embargo, información sobre los niveles de parentesco para cada localidad e información básica sobre reproducción debe ser colectada antes de iniciar un programa de esa categoría.

Key Words.—endangered; fragmentation; Honduras; *palearis* clade; population genetics

INTRODUCTION

Fragmentation of natural habitats is one of the greatest threats to biodiversity, as it often results in a decrease in overall habitat availability, and changes the quality and configuration of the habitat (Ehrlich and Ehrlich 1970; Soulé 1983). Species living within fragmented habitats often suffer from reduced population sizes and decreased migration potential. From a genetic perspective, fragmentation can result in lower diversity within each fragment, increased differentiation among fragments, increased levels of inbreeding, lower evolutionary potential, and an overall higher risk of extinction. The degree to which fragmentation affects a species is dependent upon initial migration patterns and genetic subdivision, and the cumulative diversification that may occur through genetic drift and inbreeding following further population subdivision (Crnokrak and Roff 1999; Frankham et al. 2010; Allendorf and Luikart 2013). Understanding the effect that habitat fragmentation has on a given species is thus of immense conservation concern. When dealing with endangered species, often already having small populations, the risk of extinction is all the more elevated in fragmented landscapes.

Pasachnik, Stesha A. and Stephen Hudman. 2016. Conservation genetics of Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina*. Pp. 187–196 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

In theory, recolonization events can counter the effects of fragmentation and prevent extinction. However, when anthropogenic causes are at play, recolonization rarely exceeds population decline and extirpation continues (e.g., Bolger et al. 1997). Corridors are often suggested as a means of increasing migration and recolonization events, however, understanding the effectiveness of corridors is complex. Studies have shown that various taxa respond differently to corridors (Wiens 1997). Reptiles in particular have demonstrated difficulty adapting to corridor use, depending on habitat quality (e.g., Boudejemandi et al. 1999). In addition to habitat quality, other factors may play a role in preventing migration in general or while using corridors. When dealing with species that are subject to harvesting, the amount of protection afforded across a landscape may play a larger role in determining the degree of isolation than the habitat itself. In other words, if harvesting cannot be prevented in areas between fragments, the quality of the habitat becomes less important (e.g., Goode et al. this volume).

Species that have inherently small populations due to range restrictions, such as those occurring on small islands, will be increasingly affected by fragmentation, as they do not have the ability to expand or shift their ranges (Frankham 1998). Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina* (de Queiroz 1987), exemplify a narrow-range insular endemic whose population may be suffering the effects of human-mediated fragmentation. These iguanas are endemic to Roatán, Barbareta, and a few satellite cays located within the Bay Islands, Honduras (McCranie et al. 2005; Pasachnik 2013). This species has been recognized as the second most vulnerable reptile species in Honduras (Wilson and McCranie 2003), is Endangered by the International Union for Conservation of Nature (IUCN; Pasachnik et al. 2010), and listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; species in which trade must be controlled in order to avoid utilization incompatible with their survival; Pasachnik and Ariano 2010). Although the Honduran government designated *C. oedirhina* as in need of protection in 1994 (Pasachnik et al. 2010), virtually no protection is actually afforded to this species by the government. Instead, the protection that is given comes largely from grassroots efforts within the local community, by prohibiting habitat destruction and harvesting on private property.

Goode et al. (this volume) showed that this species is found in almost all habitat types on the island, but that their distribution is largely influenced by the amount of protection afforded to them. Of the approximate 160 km^2 expanse of Roatán, *C. oedirhina* is found only in small pockets across the island (less than 1% by area), where hunting is prevented by grassroots efforts (Goode et al. this volume). The objective of our research was to understand the genetic structure of this species, within and among its remaining populations. We used mtDNA and microsatellite data to evaluate contemporary levels of genetic diversity within and among sample sites across the distribution of *C. oedirhina*. We also evaluated patterns of spatial genetic structure to understand the level to which habitat fragmentation and harvesting may be associated with disrupted connectivity among populations of *C. oedirhina*. Any patterns revealed by our analyses will shed light on the condition of this species and can be used to develop informed strategies directed at best management practices for its long-term survival.

MATERIALS AND METHODS

Study site.—Roatán is the largest and middle island of the Bay Islands and is located approximately 48 km north of mainland Honduras. A series of hills run along the spine of the island, reaching 235 m at the highest point (McCranie et al. 2005). The Bay Islands, and Roatán in particular, are becoming an increasingly popular tourist destination. From 1985 to 2013, the urban areas of the island increased from 0.95 km^2 to 14.50 km^2, and the sandy beach areas decreased from 3.28 km^2 to 0.38 km^2 (Aiello 2007; Goode et al. this volume). A consequence of this increased development has been an influx of people from the mainland, who bring with them the custom of consuming iguana meat. Thus, harvesting seems to be increasing on Roatán as the population from the mainland grows (Pasachnik et al. 2012). Hence, though habitat destruction is increasing, *C. oedirhina* is most affected by the local level of protection afforded to them more than habitat type availability (Goode et al. this volume). The exact study locations are not recorded herein due to the status of this species. If desired, additional information concerning these locations may be requested from the authors.

Field collection.—We collected DNA samples from 108 individuals across the geographic range of *C. oedirhina* on the islands of Roatán and Barbareta, Honduras, during 2010 and 2011 (Fig. 1, Table 1). We took a digital photograph upon capture and snout-vent length, tail length, sex, and mass were recorded. In addition, we gave each individual a unique mark, with PIT tags, bead tags (Rodda et al. 1998), and paint, to avoid re-sampling. We drew a 0.3 ml sample of blood from the caudal vein of each individual and stored it in an EDTA buffer (Longmire et al. 1992) for molecular analysis. In order to prevent infection, we disinfected the puncture site with ethanol before the blood was drawn and sealed it with a topical adhesive afterward.

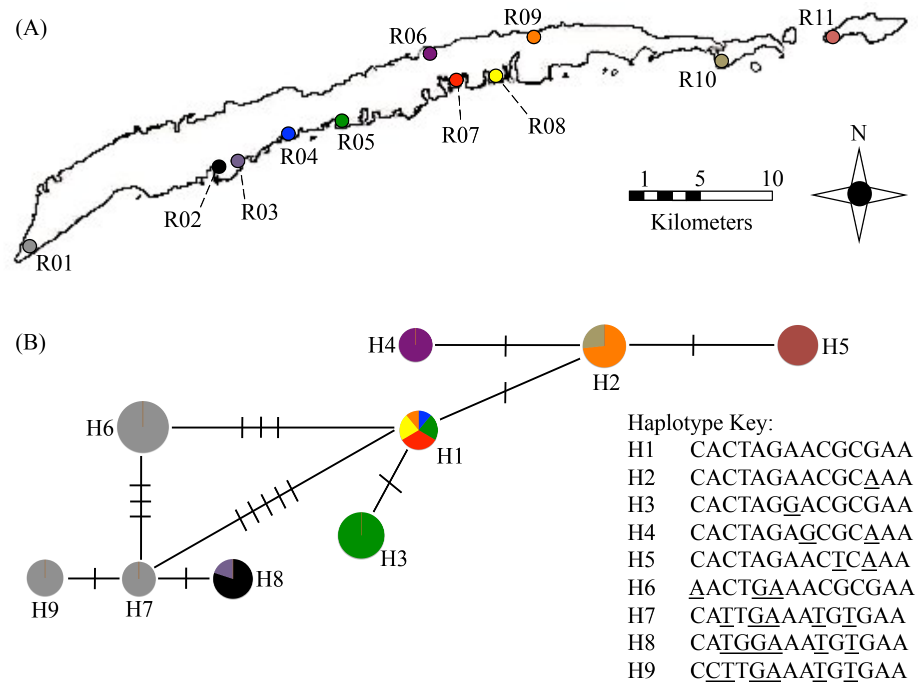

FIGURE 1. (A) Sampling sites for *Ctenosaura oedirhina* distributed across Roatán (R01–R10) and Barbareta (R11), Honduras. Site numbers correspond to those presented in Table 1 and each site is color-coded. (B) A mtDNA haplotype network constructed from a 674 bp region of the ND4 gene. Pie charts represent the nine individual haplotypes (H1–H9) and color codes represent proportional contribution of individuals from each sample site to the total number of observations of a haplotype (e.g., H1 was observed at R04, R05, R07, R08, and R09). The size of each pie chart is scaled to indicate the proportional contribution of each haplotype to the total sample. Haplotype identities are based on 12 single nucleotide polymorphisms included in the key.

***DNA sequencing*.**—We extracted total genomic DNA (gDNA) by tissue digestion in cell lysis buffer (10 mM Tris, 100 mM EDTA, 2% SDS, pH = 8.0) with proteinase K (Invitrogen, Inc., Grand Island, New York, USA), treatment with RNase A (Qiagen, Inc., Valencia, California, USA), ammonium acetate precipitation of proteins, and alcohol precipitation of DNA before suspension in TLE buffer (10 mM Tris, 0.1 mM EDTA, pH = 8.0). We confirmed gDNA quality by agarose gel electrophoresis and quantified gDNA concentration using an ND-1000 spectrophotometer (NanoDrop Technologies, Inc., Wilmington, Delaware, USA). We diluted each sample to a concentration of ~10 ng/µl for use as template in polymerase chain reaction (PCR).

***Mitochondrial DNA analysis*.**—We assessed mitochondrial DNA variation by amplifying 675 bp of NADH dehydrogenase subunit 4 using primers ND4 (5’–

TABLE 1. Sample sites, number of samples collected in 2010 and 2011 (N), number of sequences used to estimate haplotype diversity (n_S), number of samples used to estimate microsatellite allele frequencies (n_M), and the average number of individuals successfully genotyped (n_G) per sample location for *Ctenosaura oedirhina* across its range in Honduras. Descriptive statistics are provided for the full microsatellite data set (12 Loci; P = proportion polymorphic loci, H_O = Observed Heterozygosity, H_E = Expected Heterozygosity, k = average number of alleles per locus, and k_E = the effective number of alleles per locus), and rarefied allelic richness (Â), gene diversity (G = H_E), and inbreeding coefficients (F_{IS}) are provided for two reduced data sets (10 loci and 8 loci).

	Sample Sizes				12 Loci					10 Loci					8 Loci				
Sample Site	N	n_S	n_M	n_G	P	H_O	H_E	k	k_E	k	Â	H_O	G	F_{IS}	k	Â	H_O	G	F_{IS}
R01	43	35	41	39.8	0.75	0.33	0.42	4.0	2.5	4.6	2.6	0.40	0.42	0.24	5.3	3.0	0.50	0.53	0.05
R02	9	8	7	6.9	0.75	0.35	0.40	2.8	2.2	3.2	2.8	0.42	0.52	0.15	3.5	3.0	0.52	0.53	0.02
R03	2	2	2	2.0	0.50	0.42	0.25	1.7	1.5										
R04	1	1																	
R05	22	22	15	14.5	0.83	0.37	0.42	3.3	2.3	3.8	2.8	0.45	0.51	0.22	4.3	3.1	0.59	0.56	0.05
R06	1	1	1	1.0	0.25	0.25	0.13	1.3	1.3										
R07	2	2	2	2.0	0.58	0.33	0.30	1.9	1.8										
R08	2	2																	
R09	12	10	10	9.8	0.83	0.44	0.45	3.8	2.6	4.3	3.1	0.53	0.50	0.21	4.9	3.6	0.62	0.66	0.07
R10	6	4	5	4.8	0.58	0.33	0.36	2.8	2.3	3.2	2.8	0.39	0.52	0.20	3.8	3.6	0.62	0.49	0.21
R11	10	8	9	8.8	0.58	0.26	0.32	2.9	2.4	3.3	3.2	0.31	0.57	0.07	3.9	3.0	0.52	0.39	0.24
Grand Mean	10.0	8.6	10.2	9.95	0.63	0.34	0.34	2.7	2.1	3.7	2.9	0.42	0.51	0.18	4.3	3.2	0.52	0.57	0.09

CAC CTA TGA CTA CCA AAA GCT CAT GTA GAA GC –3'; Sites et al. 1996) and ND4R1 (5'– CGA AAC ACC TCT CGG TTT GC –3'; Pasachnik et al. 2009). We conducted amplifications in a total volume of 15 µl using 3.0 µl 5X PCR buffer, 1.2 µl 8 mM dNTPs, 0.75 µl of 10 mM forward primer, 0.75 µl of 10 mM reverse primer, 0.15 µl Taq polymerase, 5.15 µl ddH$_2$O, and 4.0 µl gDNA template. PCR cycling was performed by denaturing at 94° C for 3 min., followed by 30 cycles of 94° C for 30 s, 50° C for 30 s, 72° C for 90 s, and a final extension at 72° C for 5 min. We verified PCR success by gel electrophoresis, and purified successful reactions using ExoSap (exonuclease I/shrimp alkaline phosphatase; New England BioLabs, Ipswich, Massachusetts, USA). We performed sequencing reactions using the original PCR primers. We assembled forward and reverse sequences for each template using GENEIOUS R6 (v6.1.8; BioMatters, Inc., San Francisco, California, USA). We corrected incongruent base calls manually by examining the electropherograms for the forward and reverse reads. We verified alignment for the 90 sequences representing nine haplotypes identified herein (Accession Numbers: KM883205-KM883213) using GENEIOUS R6 with the aid of 12 published sequences representing five haplotypes (Accession Numbers: GU331999-GU332001 and GU906221-GU906222), which were also used to augment our estimates of haplotype diversity. We differentiated haplotypes and characterized molecular diversity (number of haplotypes, haplotype diversity, and nucleotide diversity) within and among sample sites using DnaSP v5 (Librado and Rozas 2009).

Nuclear DNA analysis.—We assessed nuclear DNA variation using 12 microsatellite loci from the genome of *Ctenosaura melanosterna* known to successfully amplify in the genome of *C. oedirhina* (Stewart et. al 2012). We amplified all loci using the touchdown PCR conditions given in Stewart et al. (2012) and labeled PCR products for individual loci with one of four fluorescent dyes (6-FAM, NED, PET, or VIC). We subsequently combined markers into three multiplexes, which we separated by electrophoresis using an ABI 3130XL Genetic Analyzer (Applied Biosystems, Grand Island, New York, USA). We calibrated fragment sizing with the LIZ 500 (-250) or GeneScan600 size standard and implemented them using the microsatellite plugin for GENEIOUS R6 (v6.1.8; BioMatters).

Of the 12 microsatellite markers targeted for analysis, two loci (*Ctme217*, *Ctme220*) were monomorphic across all sample sites, and each of the other loci had a fixed allele in at least one sample site. For markers that were polymorphic among sample sites, we found no consistent deviations from Hardy-Weinberg equilibrium (MCMC permutation test using 1,000 batches of 10,000 dememorization steps followed by 10,000 iterations in GenePop v 4.2; Raymond and Rousset 1995) when using the Dunn-Sidak stepwise Bonferroni correction (Sokal and Rohlf 1995). Notably, however, markers *Ctme212* and *Ctme216* showed significant heterozygote deficiency at two sites (R01 and R05), and marker *Ctme427* showed significant heterozygote deficiency at two sites (R01 and R11). Although not significant after Dunn-Sidak correction, markers *Ctme212* and *Ctme216* were fixed (five of nine sites for each) or demonstrated heterozygote deficiency ($P < 0.05$ at four of nine sites for each) across all sample sites. Further, genetic diversity at three sites is characterized using fewer than five individuals (R03, R06, and R07). We therefore made descriptions of genetic diversity and analyses of population differentiation and spatial genetic structure using a data set based on eight polymorphic loci and including six sample sites.

For those loci in Hardy-Weinberg and linkage equilibrium, we estimated rarefied allelic richness (Â; Petit and Mousadik 1998; Leberg 2002), gene diversity ($G = H_E$; Nei 1987) and the inbreeding coefficient (F_{IS}) using FSTAT v2.9.3 (Goudet 1995). We characterized each site sampled by taking the average over loci for each estimate of genetic diversity (Table 1).

We estimated genetic differentiation among sample sites in three ways. First, we used GENEPOP v3.4 (Raymond and Rousset 1995; Rousset 2008) to test for genotypic differentiation between each pair of sites (MCMC permutation test using 1,000 batches of 10,000 dememorization steps followed by 10,000 iterations in GenePop v4.2; Raymond and Rousset 1995) followed by the stepwise Bonferronni procedure (Sokal and Rohlf 1995). Second, we examined spatial genetic structure among sample sites using the clustering algorithm STRUCTURE (v2.3; Pritchard et al. 2000). We modeled the genetic structure of *C. oedirhina* on Roatán using an empirically determined allele frequencies parameter ($\lambda = 0.727$), under an admixture model with correlated allele frequencies. We allowed k to vary from two to six, and our strategy resulted in four potentially informative groups based on the method of Evanno et al. (2005). Third, we calculated F_{ST} (Weir and Cockerham 1984) and examined this statistic as a function of geographic distance to summarize spatial patterns of pairwise population differentiation over the entire study area. We used the statistical package R (R Development Core Team, Vienna, Austria) to implement 10,000 iterations of Mantel's permutation test (Mantel 1967) to determine the pattern of genetic isolation with respect to geographic distance (isolation-by-distance).

Finally, we used a Bayesian clustering algorithm implemented in BayesAss v3.0 (Wilson and Rannala 2003) to detect the signature of recent movement among sampled sites on Roatán. We used five replicate runs (each with a different seed) with a burn-in of 10^6 iterations, sampling for 10^7 iterations, and data collection every 10^3 steps during sampling. We empirically determined values for the migration (m), allele

TABLE 2. Observed haplotype distribution and haplotype frequencies for a 675 base region of subunit four of NADH dehydrogenase at 11 *Ctenosaura oedirhina* sample sites on Roatán and Barbareta in the Bay Islands of Honduras.

Sample Site	Haplotype								
	H1	H2	H3	H4	H5	H6	H7	H8	H9
R01						28	2		5
R02								8	
R03								2	
R04	1								
R05	2		20						
R06				1					
R07	3								
R08	2								
R09	1	11							
R10		4							
R11					11				
Frequency	0.09	0.15	0.20	0.01	0.11	0.28	0.02	0.10	0.05

frequencies (a), and inbreeding (f) switching proposals such that acceptance rates were between 20% and 40%, as suggested by Rannala (2007). We estimated the mean signature of movement between sample sites by taking the average of the off-diagonal values, which represents the proportion of the individuals sampled at each site thought to be of migrant ancestry.

RESULTS

Mitochondrial DNA analysis.—We observed nine haplotypes characterized by 12 single nucleotide polymorphisms among the 11 sites sampled. Genetic variation within sample sites was characterized by k = 0–1.24 nucleotide differences (median = 0), resulting in haplotype diversities (H_d) from 0–0.346 (median = 0) and nucleotide diversities (π) from 0–0.0019 (median = 0). In contrast to the relatively low within-site measures, global measures of genetic diversity revealed differentiation among sites: $k_T = 3.061$, $H_{dT} = 0.838$, and $\pi_T = 0.0047$. Each sample site was characterized by one to three haplotypes (Fig. 1, Table 2) with variable signal of site differentiation (range = 0–1; Table 3), but generally high pairwise differentiation (mean $F_{ST} = 0.951$; Hudson et al. 1992).

Nuclear data analysis.—Genetic diversity was generally low across sample sites. The full data set (i.e., the 12 locus data set) revealed 1.3–2.6 effective alleles per locus (mean = 2.09; Table 1) and a proportion of polymorphic loci ranging from 0.25 to 0.83 (mean = 0.63; Table 1). Accordingly, expected heterozygosity was generally low across the study site (range = 0.13–0.45, mean = 0.34; Table 1). The reduced microsatellite data set (i.e., the eight locus set) revealed substantial subdivision among populations. Most population pairs demonstrated significantly different allele frequencies, with the notable exceptions of the R09–R10 pair ($P > 0.10$, Fisher's Combined Probability across loci) and the R02–R09 pair ($P > 0.05$, Fisher's Combined Probability across loci).

Analysis of genetic structure revealed that the six sample sites included in this analysis formed four genetic clusters (Fig. 2). Site R01, at the west end of the study area, formed a single cluster. Sites R02 and R05 formed a second cluster, and Sites R09 and R10 formed a third cluster. Finally, Site R11, at the east end of the study area formed a distinct cluster. Notably, all individuals demonstrated some level of admixture among the four genetic groups, but the signal of differentiation is nevertheless substantial (Fig. 2).

Global genetic differentiation, based on the 8-locus data set, was moderate ($F_{ST} = 0.128$) with pairwise estimates of F_{ST} ranging from 0.036 (Sites R09 and R10; Table 4) to 0.176 (Sites R01 and R11; Table 4). The level of genetic differentiation, however, is independent of geographic distance (Mantel Test; $r = 0.10$, $P > 0.05$; Fig. 3), suggesting a broad-scale lack of connectivity between the sites sampled.

TABLE 3. Estimates of F_{ST} for *Ctenosaura oedirhina* across its range in Honduras based on haplotype data analyzed using DnaSP; sites R04 and R06 are excluded because they are represented by only one sequence.

	R01	R02	R03	R05	R07	R08	R09	R10
R01	—							
R02	0.83	—						
R03	0.83	0.00	—					
R05	0.81	0.99	0.99	—				
R07	0.77	1.00	1.00	0.91	—			
R08	0.77	1.00	1.00	0.91	0.00	—		
R09	0.81	0.99	0.99	0.91	0.91	0.91	—	
R10	0.83	1.00	1.00	0.96	1.00	1.00	0.00	—
R11	0.87	1.00	1.00	0.97	1.00	1.00	0.92	1.00

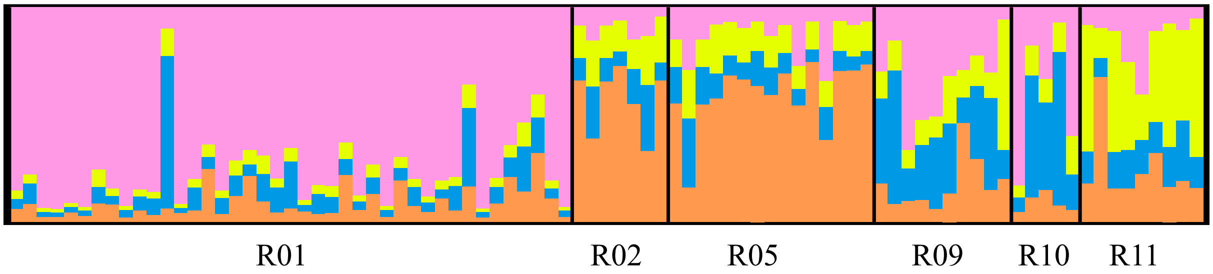

Figure 2. STRUCTURE results showing genetic clusters for *Ctenosaura oedirhina* by color (K= 4). Each vertical bar represents an individual, with colors corresponding to the proportional assignment of its multi-locus genotype. Sample sites share some portion of genetic information across the range of the species (Roatán and Barbareta, Honduras) as indicated by the shared colors between sites, but are distinct by the predominant color (pink, orange, blue, or yellow) that identifies each group.

Bayesian estimates of gene flow among sample sites were generally positive (range = 0.009–0.130) but not discernable from zero based on 95% credible limits (Table 5). Mean estimates of gene flow were qualitatively higher between sample sites on Roatán proper (m = 0.049) than from Roatán to Barbareta or Barbareta to Roatán (m = 0.037 and m = 0.027, respectively).

Discussion

We used mtDNA (ND4) and microsatellite data to assess genetic structure for *Ctenosaura oedirhina* occupying 11 sample sites distributed across the islands of Roatán and Barbareta located within the Bay Islands, Honduras. Our analyses revealed generally low levels of genetic variation within populations for both the mtDNA and microsatellite data sets. Both data sets suggest historical connectivity among sample sites on Roatán and Barbareta, as revealed by the sharing of some ND4 haplotypes among sites coupled with the signal of historical admixture among sites in the microsatellite data. Nevertheless, the signature of past connectivity is overwhelmed by that of contemporary erosion of genetic diversity and disruption of movement among sample sites. In other words, though each sample site is characterized by low estimates of genetic diversity (i.e., few alleles per locus and low gene diversity, low nucleotide and haplotype diversity), the moderately high level of differentiation indicates that the genetic constitution of each group is different, thus global genetic diversity is reasonably high. Such a pattern has likely resulted from small population sizes and increased rates of genetic drift as a consequence of fragmentation (Allendorf and Luikart 2013). Our data, therefore, elucidate a high degree of spatial structuring that is consistent with strong barriers to movement as suggested by a moderately high global F_{ST} and lack of correlation between genetic and geographic distances. This suggests that the sample sites comprise a set of isolated genetic units that are subdivided into groups, largely defined by impassable intervening areas. Given that this species is already an endangered narrow-range insular endemic, further subdivision and isolation is increasingly threatening.

The level of isolation observed between groups of *C. oedirhina* across Roatán proper is consistent with that observed between populations separated by significant barriers to dispersal. For example, measures of genetic differentiation among islands (based on microsatellite data) of *Conolophus* spp. (Tzika et al. 2008), *Varanus komodoensis* (Ciofi and Bruford 1999), and *Cyclura cychlura cychlura* (Colosimo et al. 2014) were significant and qualitatively similar to those observed among samples sites for *C. oedirhina* across Roatán. In each of those cases, however, there was little signature of within-island genetic structuring, as can be observed

Table 4. Multilocus estimates of F_{ST} based on the 8-locus microsatellite data set for *Ctenosaura oedirhina* across its range in Honduras.

	R01	R02	R05	R09	R10
R01	—				
R02	0.17	—			
R05	0.17	0.04	—		
R09	0.08	0.07	0.12	—	
R10	0.05	0.14	0.15	0.04	—
R11	0.18	0.11	0.13	0.09	0.14

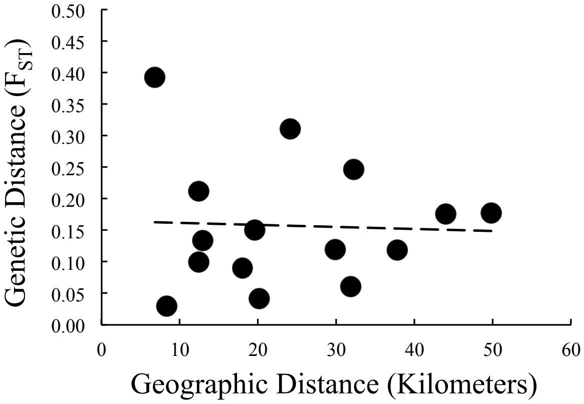

Figure 3. The relationship between genetic distance (F_{ST}) and linear geographic distance (km) for *Ctenosaura oedirhina* suggests that differentiation among groups of spiny-tailed iguanas on Roatán is not a function of distance-limited dispersal (Mantel Test, $r = 0.10$, $P > 0.05$).

TABLE 5. Estimates of migration (m ± 1 SD) for *Ctenosaura oedirhina* from the sample site indicated in the row title to the sample site indicated in the column title. The diagonal (in bold) represents the proportion of microsatellite variation of non-migrant origin; estimates of m are based on the 8-locus data set.

	R01	R02	R05	R09	R10	R11
R01	**0.95 ± 0.02**	0.01± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
R02	0.03 ± 0.03	**0.71 ± 0.03**	0.13 ± 0.06	0.08 ± 0.05	0.03 ± 0.03	0.03 ± 0.03
R05	0.03 ± 0.02	0.11 ± 0.05	**0.79 ± 0.05**	0.04 ± 0.03	0.02 ± 0.02	0.02 ± 0.02
R09	0.11 ± 0.06	0.05 ± 0.05	0.06 ± 0.05	**0.71 ± 0.04**	0.03 ± 0.02	0.04 ± 0.03
R10	0.09 ± 0.05	0.04 ± 0.04	0.04 ± 0.04	0.07 ± 0.05	**0.72 ± 0.04**	0.04 ± 0.03
R11	0.03 ± 0.03	0.04 ± 0.04	0.04 ± 0.03	0.05 ± 0.04	0.03 ± 0.02	**0.81 ± 0.06**

on Roatán. Such genetic differentiation among sample sites might be explained by strong social interactions, philopatry, or limited dispersal capabilities (Allendorf and Luikart 2013). However, given the extremely small size of Roatán, and direct estimates of habitat utilization, it is clear that connectivity among sample sites is disrupted by disturbance (i.e., increased poaching pressure) rather than being an artifact of the biology of *C. oedirhina* or natural vicariance. In an extensive analysis of habitat utilization, Goode et al. (this volume) have shown that stable densities of iguanas only occur in areas afforded protection from poaching, though additional suitable areas are available. Further, the lack of correlation between genetic and geographic distance coupled with a moderately high global F_{ST} (= 0.128) strongly suggest that there are limited corridors between populations, and that genetic diversity is locally and independently governed within sample sites.

The consequences of disrupted connectivity between elements of a putative metapopulation can be severe. Decreased local population size, genetic drift, and the resulting potential inbreeding depression contribute to the erosion of genetic diversity (Crnokrak and Roff 1999). Our data reveal evidence of small population sizes, consistent with ecological work by Goode et al. (this volume), and locally decreased genetic diversity within sample sites on Roatán. Indeed, estimates of gene diversity (H_E; Nei 1987) on Roatán are consistently lower than those reported for sample sites on the same island. For example, estimates for groups of *C. cychlura cychlura* on Andros Island ranged from 0.44 to 0.70 (Colosimo et al. 2014) and estimates for *Sphenodon punctatus* (Moore et al. 2008) ranged from 0.73 to 0.78, which are 10–44% higher than the estimates observed for *C. oedirhina*. The estimates observed for *C. cychlura cychlura* and *Sphenodon punctatus* are consistent with estimates taken from Marine Iguanas (*Amblyrhynchus cristatus*) occurring on a subset of the Galápagos Islands (Fernandina, San Cristóbal, and Santiago; Steinfartz et al. 2009) comprising larger samples, and taken from larger islands with lower human population densities. Although, the samples sizes reported here are smaller than those reported in Steinfartz et al. (2009), they are consistent with those reported by Colosimo et al. (2014). Hence, it is unlikely that the erosion of genetic diversity on Roatán is solely explained by sampling error and underestimates of these metrics.

Our data, coupled with the ecological work by Goode et al. (this volume) suggest that groups of Roatán Spiny-tailed Iguanas are negatively impacted by fragmentation resulting from anthropogenic pressures. Groups characterized at individual locations appear to have been historically connected given that haplotypes and alleles are shared among sampling locations across the island. Although these data suggest that the population of *C. oedirhina* on Roatán may have once been large and panmictic, individuals can now only be found in a few locations and in relatively low numbers (Goode et al. this volume). This has resulted in the current subdivisions, which appear to be evolving independently. The result is an increase in signal of local inbreeding (see F_{IS} in Table 1) and an apparent erosion of local genetic diversity. Given that this subdivision is likely relatively recent for *C. oedirhina*, the signal of inbreeding is relatively low at this moment; however, the reduced genetic variation and reduced gene flow among groups will quickly elevate the degree of inbreeding and likely make each population more vulnerable to environmental changes (increased temperature, altered precipitation, infectious diseases), demographic stochasticity (random changes in life expectancy or reproductive output), and continued human-related disturbances (Frankham et al. 2010).

As global measures of genetic diversity (i.e., genetic differentiation) are relatively high, augmenting exchange between groups might be a useful conservation strategy for maintaining population viability. That is, though each sample group holds limited genetic diversity, the groups combined hold higher diversity, as each group has different genetic variants. Therefore, exploring options for moving individuals among sites or maintaining a captive breeding program that facilitates exchange may be worthwhile. In many instances captive programs have prevented extinction, such as with the Jamaican Rock Iguana, *Cyclura collei* (see Wilson et al. this volume). That being said, such management strategies should not be entered into lightly and careful organization and monitoring must be in place before and during the process (see Alberts 2004).

Baseline data concerning the level of within-group relatedness and overall reproductive output would provide insight into the potential for local adaptation, and overall potential for a successful breeding program on Roatán. In general, captive breeding programs should consider economic constraints, biological suitability (i.e., which species can be raised and bred), and potential for success during the planning process (Allendorf and Luikart 2013). Considering these potential limitations, managers should look closely at sites R01, R05, R09, and R11 as potential sources for breeding stock or locations for captive breeding programs. Taken together, these sites represent a cross-section of the highest population densities (Goode et al. this volume) and extant genetic variation (based on the 12 locus data set) on Roatán and the eastern island (site R11; Barbareta). Indeed, Barbareta may be an ideal location for a captive breeding effort as it is privately owned and protected, thus limiting the required economic input for successful program development. Many iguana species breed successfully in captivity, particularly when within their native range. For example, *C. bakeri*, the sister species to *C. oedirhina,* had a successful breeding facility in place for many years, in its native range (Stesha Pasachnik, pers. obs.). Thus, it seems likely that *C. oedirhina* would respond similarly to such a program. Nevertheless, experimental evidence regarding mate-choice dynamics and inbreeding and outbreeding factors should be considered prior to establishing such a program. If deemed reasonable, a captive breeding program could have benefits beyond rescuing within-population genetic diversity. Headstarting individuals in a captive breeding program may also have a substantial positive impact on population growth.

Goode et al. (this volume) showed that this species is a generalist. Thus, reintroduction should result in increased local recruitment and decreased negative impacts of inbreeding. Captive breeding may also provide the added benefit of increased effective fecundity because eggs would be protected from harvesting for human consumption, a common practice in Central America (Pasachnik et al. 2012, 2014). A successful captive breeding program could also facilitate education and outreach initiatives, involving local inhabitants of Roatán in the protection of their endemic species. Although captive breeding has a high potential for success, such a program must be viewed as a temporary means of management and not the sustainable solution. Rather, if captive breeding is implemented, efforts must be directed concurrently toward formal, legislated, habitat protection as well as the establishment of protected, high-quality dispersal corridors. Establishing protected habitat corridors has a high potential to facilitate connectivity between isolated groups, thus ensuring gene flow between populations and establishing a self-sustaining metapopulation with the capacity to respond to short- and long-term ecological dynamics, as was likely the case historically.

Acknowledgments.—This study would not have been possible without the help of many field assistants, especially Mikel Belcaries and Ashley Goode; the Instituto Nacional de Conservación y Desarrollo Forestal, Áreas Protegidas y Vida Silvestre for permitting (DICTAMEN-DVS-ICF-054-2010 and 064-2011) and the Kanahua facility, in particular Andrea Martinez, for aid in acquiring permits and on the ground support; the multitude of local residents who allowed us to work on their property; John Sahrmann and Jessica Plaggenberg for assistance in the lab; and grants from the International Iguana Foundation and Mohamed bin Zayed Species Conservation Fund.

LITERATURE CITED

Aiello, D. 2007. Coast to coral: evaluating terrestrial development's relationship to coral ecosystem condition in Roatán, Honduras. M.Sc. Thesis, College of Arts and Sciences of Ohio University, Athens, Ohio, USA. 120p.

Alberts, A. 2004. Conservation strategies for West Indian Rock Iguanas (genus *Cyclura*): current efforts and future directions. Iguana (Journal of the International Iguana Society) 11:212–223.

Allendorf, F.W., and G. Luikart. 2013. Conservation and the genetics of populations. Wiley-Blackwell Publishing, Hoboken, New Jersey, USA.

Bolger, D.T., A.C. Alberts, R.M. Sauvajot, P. Potenza, C. McCalvin, D. Tran, S. Mazzoni, and M.E. Soule. 1997. Response of rodents to habitat fragmentation in coastal southern California. Ecological Applications 7:552–563.

Boudjemadi, K., J. Lecomte, and J. Clobert. 1999. Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. Journal of Animal Ecology 68:1207–1224.

Ciofi, C., and M.W. Bruford. 1999. Genetic structure and gene flow among Komodo Dragon populations inferred by microsatellite loci analysis. Molecular Ecology 8:S17–S30.

Colosimo, G., C.R. Knapp, L.E. Wallace, and M.E. Welch. 2014. Inferred vs realized patterns of gene flow: an analysis of population structure in the Andros Island Rock Iguana. PLoS ONE 9:e106963. doi:10.1371/journal.pone.0106963

Crnokrak, P., and D.A. Roff. 1999. Inbreeding depression in the wild. Heredity 83:260–270.

de Queiroz, K. 1987. A new Spiny-tailed Iguana from Honduras, with comments on relationships within Ctenosaura (Squmata: Iguania). Copeia 1987:892–902.

Ehrlich, P.R., and A.H. Ehrlich. 1970. Population Resources Environment: Issues in Human Ecology. W.H. Freeman, San Francisco, California, USA.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14:2611–2620.

Frankham, R. 1998. Inbreeding and extinction: island populations. Conservation Biology 12:665–675.

Frankham, R., J.D. Ballou, and D.A. Briscoe. 2010. Conservation Genetics. 2nd Edition. Cambridge University Press, New York, New York, USA.

Goode, A.B.C., S.A. Pasachnik, and T.L. Maple. 2016. Habitat utilization of Roatán Spiny-tailed Iguanas (*Ctenosaura oedirhina*) and its implications for conservation. Pp. 79–89 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Goudet, J. 1995. Fsat version 1.2: a computer program to calculate F-statistics. Journal of Heredity 6:485–486.

Hudson, R.R., M. Slatkin, and W.P. Maddison. 1992. Estimation of levels of gene flow from DNA sequence data. Genetics 132:583–589.

Leberg, P. 2002. Estimating allelic richness: Effects of sample size and bottlenecks. Molecular Ecology 11:2445–2449.

Librado, P., and J. Rozas. 2009. DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. Bioinformatics 25:1451–1452.

Longmire, J.L., G.F. Gee, C.L. Hardekopf, and G.A. Mark. 1992. Establishing paternity in whooping cranes (*Grus americana*) by DNA analysis. The Auk 109:522–529.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27:209–220.

McCranie, J.R., L.D. Wilson, and G. Köhler. 2005. Amphibians and Reptiles of the Bay Islands and Cayos Cochinos, Honduras. Bibliomania, Salt Lake City, Utah, USA.

Moore, J.A., H.C. Miller, C.H. Daughtery, and N.J. Nelson. 2008. Fine-scale genetic structure of a long-lived reptile reflects recent habitat modification. Molecular Ecology 17:4630–4641.

Nei, M. 1987. Molecular Evolutionary Genetics. Columbia University Press, New York City, New York, USA.

Pasachnik, S.A. 2013. Growth, reproduction, and diet of Roatán Spiny-tailed Iguanas, *Ctenosaura oedirhina*. Herpetological Conservation and Biology 8:191–198.

Pasachnik, S.A., and D. Ariano. 2010. CITES Appendix II listing of the *Ctenosaura palearis* clade. Reptile and Amphibian Conservation and Natural History 17:136–139.

Pasachnik, S.A., D. Ariano-Sánchez, J. Burgess, C.E. Montgomery, and G. Köhler. 2010. *Ctenosaura oedirhina*. The IUCN Red List of Threatened Species. Version 2015.2. Available from http://www.iucnredlist.org/details/44191/0 [Accessed on 14 June 2015].

Pasachnik, S.A., J.A. Danoff-Burg, E.A. Pineda, and J. Corneil. 2014. Local knowledge and use of the Critically Endangered *Ctenosaura melanosterna* in the Valle de Aguán, Honduras. Herpetological Conservation and Biology 9:436–447.

Pasachnik, S.A., B.M. Fitzpatrick, T.J. Near, and A.C. Echternacht. 2009. Gene flow between an endangered endemic iguana, and its wide spread relative, on the island of Utila, Honduras: When is hybridization a threat? Conservation Genetics 10:1247–1254.

Pasachnik, S.A., C.E. Montgomery, L.E. Ruyle, J.P. Corneil, and E.E. Antunez. 2012. Morphological and demographic analyses of *Ctenosaura melanosterna* across its range: implications for population level management. Herpetological Conservation and Biology 7:399–406.

Petit R., and A. El Mousadik. 1998. Identifying populations for conservation on the basis of genetic markers. Conservation Biology 12:844–855.

Pritchard J.K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–959.

Rannala B. 2007. BayesAss Edition 3.0 User's Manual. Available from http://www.rannala.org/?page_id=245

Raymond M., and F. Rousset. 1995. An exact test for population differentiation. Evolution 49:280–1283.

Rodda, G.H., B.C. Bock, G.M. Burghardt, and A.S. Rand. 1988. Techniques for identifying individual lizards at a distance reveal influences of handling. Copeia 1988:905–913.

Rousset, F. 2008. GenePop 4.0 for Windows and Linux. Molecular Ecology Resources 8:103–106.

Sites, J.W., S.K. Davis, T. Guerra, J.B. Iverson, and H.L. Snell. 1996. Character congruence and phylogenetic signal in molecular and morphological data sets: a case study in the living iguanas (Squamata, Iguanidae). Molecular Biology and Evolution 13:1087–1105.

Sokal R.R., and F.J. Rohlf. 1995. Biometry. W.H. Freeman and Company, New York City, New York, USA.

Soulé, M.E. 1983. What do we really know about extinction? Pp. 111–124 *In* Genetics and Conservation. A Reference for Managing Wild Animal and Plant Populations. Schonewald-Cox, C.M., S.M. Chambers, B. MacBryde, and W.L. Thomas (Eds). Benjamin/Cummings, Menlo Park, California, USA.

Steinfartz, S., S. Glaberman, D. Lanterbecq, M.A. Russello, S. Rosa, T.C. Hanley, C. Marquez, H.L. Snell, H.M. Snell, G. Gentile, et al. 2009. Progressive colonization and restricted gene flow shape island-dependent population structure in Galápagos Marine Iguanas (*Amblyrhynchus cristatus*). BMC Evolutionary Biology 9:297–315.

Stewart, E.S., S.A. Pasachnik, C.E. Montgomery, and S.P. Hudman. 2012. Characterization of 22 polymorphic microsatellite loci for the Black-chested Spiny-tailed Iguanas (*Ctenosaura melanosterna*) and cross-amplification success in four other *Ctenosaura* species. Conservation Genetics Resources 4:47–50.

Tzika, A.C., S.F.P Rosa, A. Fabiani, H.L. Snell, H.M. Snell, C. Marquez, W. Tapia, K. Rassmann, G. Gentile, and M.C. Milinkovitch. 2008. Population genetics of Galápagos Land Iguana (genus *Conolophus*) remnant populations. Molecular Ecology 17:4943–4952.

Weir, B.S., and C.C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370.

Wiens, J.A. 1997. Metapopulation dynamics and landscape ecology. Pp. 43–62 *In* Metapopulation Biology. Ecology, Genetics, and Evolution. Hanski, I., and M.E. Gilpin (Eds). Academic Press, San Diego, California, USA.

Wilson, B., T.D. Grant, R. van Veen, R. Hudson, D. Fleuchaus, O. Robinson, and K. Stephenson. 2016. The Jamaican Iguana (*Cyclura collei*): a report of 25 years of conservation effort. Pp. 237–254 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Wilson G.A., and B. Rannala. 2003. Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163:1177–1191.

Wilson, L.D., and J.R. McCranie. 2003. The conservation status of the herpetofauna of Honduras. Amphibian and Reptile Conservation 3:6–33.

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Herpetological Conservation and Biology 11(Monograph 6):197–213.
Submitted: 2 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

NESTING MIGRATIONS AND REPRODUCTIVE BIOLOGY OF THE MONA RHINOCEROS IGUANA, *CYCLURA STEJNEGERI*

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Abstract.—**We studied the nesting migrations and reproductive ecology of the endangered Mona Rhinoceros Iguana *Cyclura stejnegeri* at three localities from 2003 to 2006. Female movements while seeking a nesting site ranged from 0.3 to 12.8 km, were mostly erratic. Time elapsed between mating and oviposition averaged 30 ± 5 days, while the nesting period lasted four weeks (July to early August). Nest site fidelity by females in consecutive years was 50%, although non-resident females at one study site used the same beach 72% of the time. Clutch size averaged 14 eggs and was positively correlated with female snout-vent length (SVL). Egg length was the only egg size variable correlated negatively with female size. Incubation temperatures averaged 32.8° C (2005) and 30.2° C (2006) and fluctuated up to 9° C. Overall hatching success from 2003–2005 was 75.9%. Some nests failed as a result of flooding of the nest chamber and in one case a nest was destroyed by feral pigs. Hatchling sex ratio was close to 1:1 for all individual nests and all hatchlings collected throughout the study. Hatchling morphometrics (SVL, body mass) were not related to female size. Egg predation by pigs was low compared to previous reports from the 1970s, which reached levels of up to 100% in some years. The dramatic increase in hatching success may be the result of fencing the most important iguana nesting areas in 1985, an initiative that is maintained until now, to prevent feral pig incursions.**

Resumen.—**Del 2003 al 2006 estudiamos la migraciones asociadas a la búsqueda de sitios para la anidación y la ecología reproductiva de la iguana *Cyclura stejnegeri* en tres localidades de Isla de Mona. Las distancias recorridas por las hembras durante la búsqueda de sitios para anidar fluctuaron entre 0.3 y 12.8 km con desplazamientos en su mayoría erráticos. El tiempo promedio entre el apareamiento y la ovoposición fue de 30 ± 5 días y la época de anidación duró cuatro semanas entre julio y agosto. Las hembras mostraron fidelidad al sitio de anidaje en un 50% de los casos, aunque el 72% de hembras no residentes en una playa retornaron a la misma en años consecutivos. El promedio de huevos por nidada fue de 14 y estuvo positivamente correlacionado con el tamaño (longitud hocico-cloaca, SVL) de la hembra. De las dimensiones de los huevos, solo el largo del huevo estuvo negativamente correlacionado con el tamaño de la hembra. Las temperaturas de incubación promedio fueron de 32.8° C (2005) y 30.2° C (2006) con fluctuaciones hasta de 9° C. Algunos nidos fueron destruidos debido a las fuertes lluvias que inundaron la cámara del nido y solo un nido fue destruido por cerdos silvestres. La proporción sexual de los neonatos fue de 1:1 para los nidos individuales y para todos los neonatos colectados en el estudio. La morfometría de los neonatos (SVL, peso) no estuvo relacionada con el tamaño de la madre. La depredación de nidos por cerdos fue baja comparada con los años setenta cuando podía alcanzar valores hasta del 100% en algunos años. El incremento sustancial en el éxito de eclosión puede ser el resultado de la instalación de cercas en 1985 en algunas áreas de anidaje para evitar la depredación de nidos por parte de cerdos silvestres.**

Key Words.—Caribbean Iguanine; lizard; nesting ecology; reproductive success; rock iguana

INTRODUCTION

Caribbean Ground Rock Iguanas (11 species, eight subspecies; ITWG this volume) of the genus *Cyclura* are among the most endangered lizards in the world (Alberts 2000). Factors affecting most of the populations of these species include habitat degradation, illegal pet trade, and negative interactions with exotic animals (Alberts 2000). Current actions to augment some *Cyclura* populations include captive breeding and headstarting initiatives (Alberts 2007; Pérez-Buitrago et al. 2008; Burton and Rivera-Milán 2014), translocations (Knapp 2000, 2001; Knapp and Hudson 2004; Wilson et al. 2004), and eradication/control of feral animal species (Mitchell et al. 2002; Donlan et al. 2003; Campbell et al. 2004; Hayes et al. 2004; Gerber 2007). However, knowledge of *Cyclura* biology is relatively poor due to the remoteness of islands on which some species live, and/or the lack of financial/logistic resources to study these long-lived lizards (Iverson et al. 2004).

Pérez-Buitrago, Néstor, Alberto M. Sabat, and W. Owen McMillan. 2016. Nesting migrations and reproductive biology of the Mona Rhinoceros Iguana, *Cyclura stejnegeri*. Pp. 197–213 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Knowledge of the reproductive biology of the genus *Cyclura* is a critical component to the evaluation of their population trends, but studies addressing their reproduction have been limited to descriptions of basic aspects such as timing of nesting and hatching, clutch size, egg and hatchling dimensions, and hatching success based on relatively small sample sizes and over short periods of time (but see Iverson et al. 2004; Knapp et al. 2006). This information has been used to analyze life-history trait patterns among species/populations (Wiewandt 1982; Iverson et al. 2004), but its utility in developing population viability models that may be used to guide specific conservation actions is limited. Moreover, there are still several aspects of reproduction in *Cyclura* that are poorly documented, such as details of their nesting migrations. From a conservation perspective, knowledge of the factors that may be reducing the availability of nesting areas and/or reducing hatching success rates is critical.

In this study we document the reproductive biology of the Mona Rhinoceros Iguana (*Cyclura stejnegeri*) using radio-telemetry and mark-recapture techniques. During three reproductive seasons (2003–2005), we documented nest timing, clutch size, egg dimensions, hatchling size, reproductive effort, and the nesting migrations undertaken by females to reach nesting sites. In addition, we compared the spatial variation in clutch size and hatching success across study sites. We also evaluate the effect of management actions taken by the Department of Natural Resources of Puerto Rico (DRNA-PR) in 1982 on reproductive success. These actions included fencing some nesting areas to prevent feral pig incursions and creating areas free of vegetation to increase available nesting habitat.

MATERIALS AND METHODS

***Study site*.**—Mona Island is located in the middle of the Mona channel, between the Dominican Republic and Puerto Rico. It is an oceanic island with a subtropical dry forest climate (Ewel and Whitmore 1973). Most of the island's perimeter is characterized by vertical cliffs 45 m in height that also delimit the largest habitat type of the island (93%), the relatively undisturbed limestone rocky "plateau". On Mona Island, there are three different types of iguana nesting habitat. First, on the plateau, a unique habitat type not extensively represented (1%) is the depressions called "bajuras". The "bajuras" are the only zones on the plateau with a relatively continuous accumulation of clay soil suitable for iguana nesting. Secondly, in the southwestern region of the island, there is a large sandy/limestone coastal plain that offers iguanas another area suitable for nesting (Wiewandt 1977; Haneke 1995). These coastal plain areas were fenced in 1985 by the DRNA-PR to minimize feral pig incursions and thus reduce egg predation. However, a large part of the coastal plain was planted with exotic species such as *Casuarina equisetifolia* and *Swietenia mahogany* (Diaz 1984; Cintrón and Rogers 1991), thus reducing the availability of appropriate and contiguous nesting sites. Nonetheless, it still constitutes an estimated 74% of all nesting habitat available on the island. Currently, there are small sunny and sandy areas that apparently have not been affected by human activity recently, as well as areas that were cleared by the DRNA-PR in 1992 to provide additional suitable zones for nesting females. In addition to the nesting areas located in the southwestern coastal plain, there are a few narrow (< 150 m wide) beaches available that represent the third type of open area available for iguana nesting.

This study was conducted at three locations of Mona Island representing two of the three nesting habitats described above. The Lighthouse site is located near the eastern coast of Mona Island on its limestone plateau, lacks human disturbance and does not contain well-defined nesting areas (Fig. 1). The second area, Sardinera Beach, is located in the southwestern coastal plain near the site of the DRNA-PR facilities, and is a highly disturbed area close to the zones in which the native vegetation was replaced by exotic tree species. The third study site, Pájaros Beach, is a narrow but elongated beach in the southeast where the predominant vegetation type is "cliff forest" (Cintrón and Rogers 1991). This area has a small camping facility used by tourists approximately 30% of the year, and contains some open zones appropriate for nesting.

***Field data collection*.**—From 2003 to 2005 we captured female iguanas at the three study sites using nets. Most capture effort was concentrated during April, June–July, and October–November. For each captured iguana, we recorded the snout-vent length (SVL) to the nearest 1 mm, body mass (BM) to the nearest 0.1 kg, tail length (TL) and tail breaks to the nearest 1 mm. If sex was externally unclear, we determined it by probing (Schaeffer 1934; Dellinger and Von Hegel 1990). We marked iguanas externally with a unique combination of color beads attached to the dorsal crest (Rodda et al. 1988) and internally with a passive integrated transponder (PIT) tag (AVID®).

We collected data on nesting ecology using two methods. First, we captured a subset of 21 females (nine in Sardinera, eight in Pájaros, and four in the Lighthouse) prior to the nesting seasons and outfitted them with 15 g collar radio transmitters (model R1-2D, Holohil Systems, Ltd., Ontario, Canada) with a battery life expectancy of 18 months (Goodman et al. 2009). We radio-tracked these females before the nesting season (April–March) to obtain information about their space use (i.e., home range) and activity patterns not associated with mating or nesting. We monitored females daily in June (mating period) to attempt to observe copulations and then we tracked them during the nesting season (July–August) to document their movement patterns while seeking nesting sites (nesting migrations). During each monitoring session, we recorded the female's position using WAAS enabled Magellan GPS units, the activity in which the animal was engaged as defined by Wiewandt (1977; i.e., seeking, digging, filling, and nest guarding), and the time of day. Battery life of some radio transmitters allowed us to monitor some females for more than one nesting season. The second method we used to study nesting ecology involved capturing "unknown" females that arrived at our focal nesting sites at Pájaros and Sardinera from elsewhere. We captured and processed (as described above) these females either when they were gravid and seeking a place for nesting, or immediately after oviposition and were back-filling or guarding their nests.

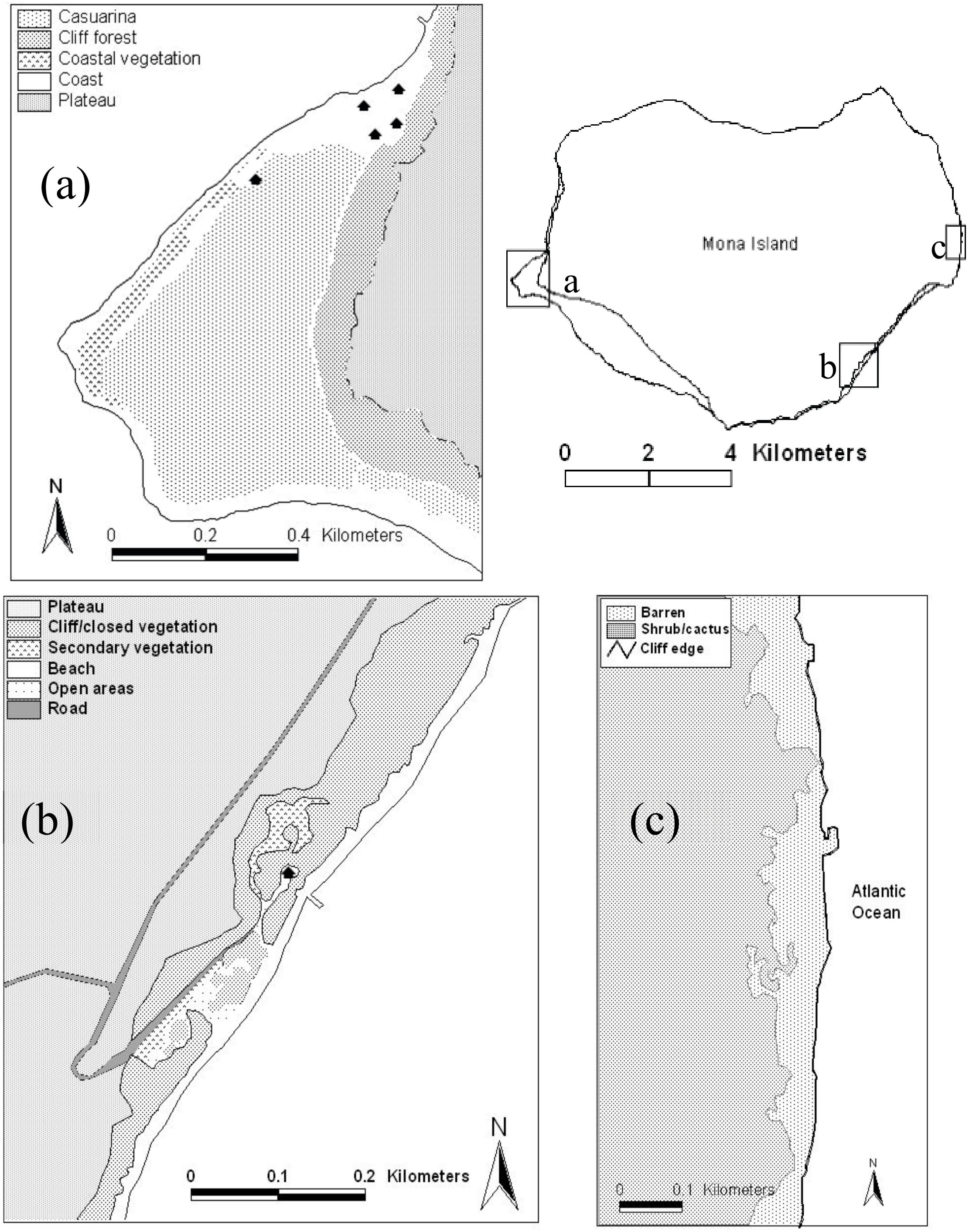


FIGURE 1. Schematic maps of Mona Island and the three study areas for *Cyclura stejnegeri*: (A) Sardinera [DRNA-PR facilities represented by up-right black arrows]; (B) Pájaros; and (C) the Lighthouse with major vegetation/terrain features shown for each.

To mark egg chamber locations, we drove away females engaged in filling the nest and we buried a piece of wood or rock tied to a nylon cord at the level of the first egg. The other end of the cord remained outside the nest, attached to a fixed item above the ground in a manner such that the nesting iguana could not remove it when she returned to continue back-filling and guarding the nest. This method allowed us to effectively locate nests during the hatching period in October–November and to document the hatching success of these nests.

During 2004 and 2005, we estimated the reproductive output of 15 gravid females that were seeking a nesting site or had just oviposited. We captured and measured (SVL, body mass) these females, and we counted and measured (length and width to the nearest 0.1 mm, mass to the nearest 0.1 g) their eggs within 24 h after being laid by temporarily removing them from the nest chambers. In addition, we noted egg aspect (collapsed, turgid) and numbered them with a marker pen. This protocol allowed us to estimate reproductive parameters and reproductive output following Iverson et al. (2004). Specifically, we calculated relative clutch size (RCS: the ratio of clutch size to body mass measured before nesting x 100), relative egg mass (REM: the ratio of mean egg mass in the clutch to the female's body mass measured before nesting x 100), and relative clutch mass (RCM: the ratio of total clutch mass to the female's body mass measured before nesting x 100; Iverson et al. 2004). Sometimes, several iguanas construct nests within a small area, confounding nest chambers. To avoid this, we only used information from nests for which we were certain of the female's identity.

Approximately 75–78 days after nesting, when hatchling emergence was expected (Wiewandt 1977), we installed a circular aluminum fence (4 m diameter and 0.6 m height) using as the center point the estimated position of the nest chamber, to collect the hatchlings upon emergence. After 85 days we opened the nests using the nylon cord as a guide. If eggs were still inside of the nest, we refilled the nest, or we collected the individuals that had already hatched and left the remaining eggs buried. We removed and opened eggs that failed to complete the incubation process after 95 days of incubation to determine whether they contained embryos or were infertile (no visible embryo detected). We measured (SVL and tail length to the nearest 0.1 cm, body mass to the nearest 0.1 g) hatchlings obtained from each nest and determined sex by probing (Schaeffer 1934; Dellinger and Von Hegel 1990). In 2003 and 2004, we permanently marked 154 of the collected hatchlings with PIT tags placed in the lateral part of the tail, 3 cm behind the pelvic bone. Most of the PIT-tagged hatchlings were released into the wild after a month in captivity, but 30 individuals per year were retained in captivity at the Mona head-starting program facility.

In 2005 and 2006, we placed eight temperature data loggers (HOBO temp, Onset Computer Corporation, Bourne, Massachusetts, USA) each year in nest chambers. The data loggers were placed adjacent to the first eggs detected. In addition, we recorded environmental temperature at each site by placing temperature loggers 0.5 and 1.0 m above the ground near each nest, suspended in open areas exposed to direct sunlight.

During the 2006 hatching season (October–November), we conducted censuses every other day to record "escape holes" associated with nests (holes that hatchlings make to escape from the nest chamber) in all of the nesting areas in the southwestern coastal plain (including Sardinera) and in the small beaches located on the south and east sides of the island (sites not part of the three focal areas in this study). We identified potential nesting areas by inspecting satellite images (IKONOS, 2 m pixel resolution, 2001) for open, vegetation-free sites followed by field corroboration of these areas. The sites surveyed comprised 74% of the total area available for nesting on the island, according to Haneke (1995).

Statistical analysis.—We made comparisons between reproductive parameters (clutch size and egg mass) only on data from Sardinera and Pájaros because the number of nests successfully monitored at the Lighthouse was low, and the number of eggs was sometimes impossible to measure in the Lighthouse area because nest chambers were located in deep rocky crevices. There were no differences in female size (t = 0.91, P = 0.37, n = 29), clutch size (t = 1.92, P = 0.07, n = 26), or hatchling morphometrics (SVL t = -1.63, P = 0.11, body mass t = 1.23, P = 0.22; n = 34 nests) between the Sardinera and Pájaros sites, so we pooled this information for all subsequent analyses. For females monitored for more than one year, we included only the first year's data on clutch size and egg morphometrics to avoid non-independent sampling. Means ± one standard deviation (SD) are reported. We performed all statistical analyses using STATISTICA v5.5 (Kernel release 2000, StatSoft Inc., Tulsa, Oklahoma, USA) and we used α = 0.05 to assign significance. For testing the directionality of a female's movements during the nesting period, we used the Rayleigh test (Batschelet 1981) as calculated in the Animal Movement extension analysis of ArcView v.3.2 (Hooge et al. 1999). For this analysis, we only included the locations recorded after radio-marked females moved out of the boundaries of their home ranges during the nesting season.

RESULTS

Mating activity and nesting frequency.—We observed four copulations of radio-collared females between 16 and 30 June, two in 2003, and two in 2004.

These females laid their eggs between 24 and 35 days (mean = 30 ± 5) after mating. The nesting seasons of 2004 and 2005 spanned from 5 July to 9 August, with a peak in nesting activity between 17 and 29 July (Fig. 2). Nesting females had a mean SVL = 48.5 ± (SD) 4.4 cm (range, 34.4–57.7 cm; *n* = 62). The smallest nesting female detected (SVL of 34.4 cm, body mass of 2.3 kg) had been captive reared in the headstart facility for 2.7 years before release, and was 4.7 years old. Mid-size wild mature females (SVL < 45 cm) were scarce in the monitored areas, and when present they were very shy and avoided us. However, their relative rareness could also be because they are poorly represented in the population (e.g., see Fig. 3). The nine radio-collared or marked females resident at Pájaros or Sardinera that we monitored over two or more consecutive nesting seasons nested each year. However, of 25 non-resident females (i.e., females that probably lived on the plateau year-round and migrated for nesting) captured at the Pájaros nesting sites in 2004, only 18 (72%) were also detected nesting in 2005.

Nesting migrations and nest site fidelity.—Females were categorized into three groups based on their movements prior to nesting: (1) females that stayed in their home range and nested within it; (2) females that temporarily abandoned their usual home range but returned and nested within it; and (3) females that left their home range, returned, but left again to nest outside it. Some of the females in this third category had areas that appeared suitable for nesting within their home ranges, but chose not to use them. Most females appeared to perform exploratory movements outside of their home ranges irrespective of where they nested (Table 1).

Radio-collared females nested in areas that were between 0 km (when females remained and nested inside their home ranges) to 930 m (mean = 279 ± 271 m, *n* = 19) from the center of their home ranges. However, actual movements taken to reach the final nesting site were variable and longer, with a maximum displacement of 12.8 km (mean = 2.4 ± 2.3 km, range = 0.3–12.8, *n* = 21). All females returned to their established home ranges after nesting, after having spent between 1 and 16 days (mean = 9 ± 9 days, *n* = 18) away.

Of the 11 radio-tracked females that we monitored for more than one nesting season, only four (two from the Lighthouse and two from Sardinera) moved in a specific direction to reach the same nesting spot used the previous year (all angle counts between 4–6, all angular concentration $R > 0.85$, all Rayleigh values $z > 4.2$, and all $P < 0.02$; $n = 4$). However, if the site was already occupied by another iguana, females started moving erratically. All other radio-tracked iguanas moved randomly, abandoning and returning to their home ranges at least once. The Rayleigh test of directionality failed to detect a specific bearing during the path (all angle counts between 4–9, all angular concentration $R > 0.23$, all Rayleigh values $z < 0.35$, and all $P > 0.27$; $n = 14$).

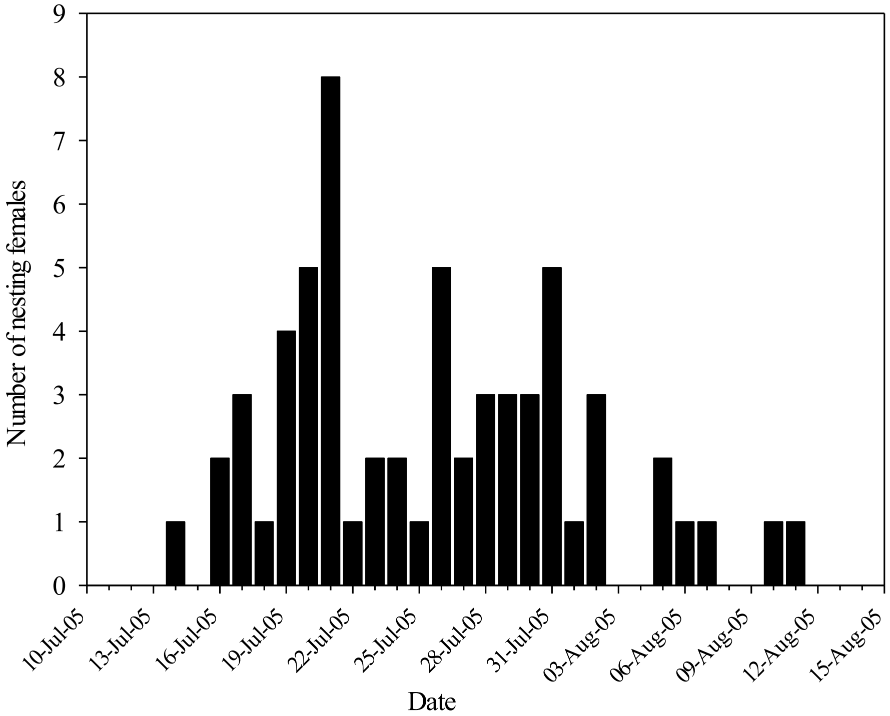


FIGURE 2. The number of nests of Mona Rhinoceros Iguanas recorded per day during the 2005 nesting season at Pájaros beach.

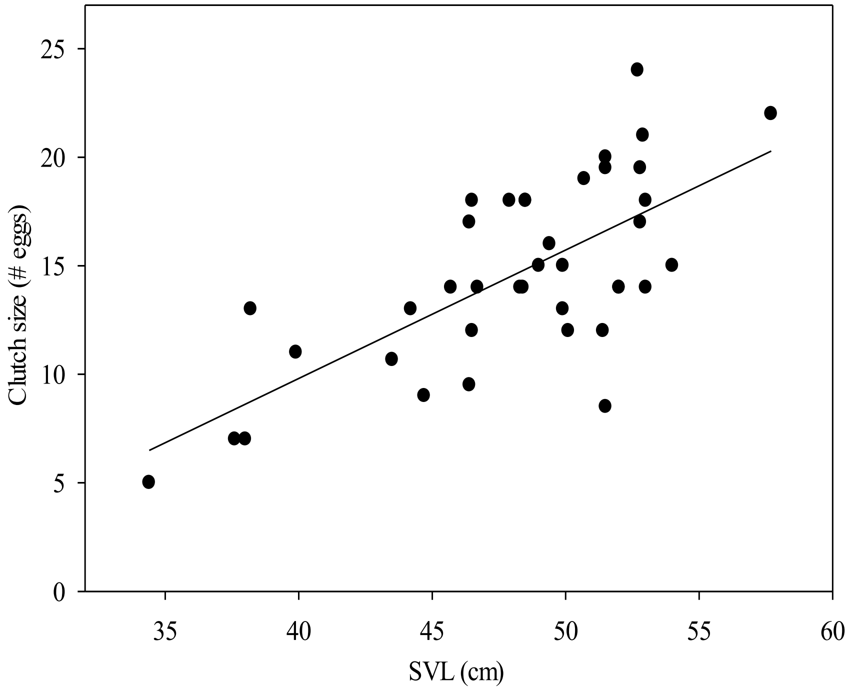


FIGURE 3. Relationship between female snout-vent length (SVL) and clutch size in the Mona Rhinoceros Iguana ($r^2 = 0.48$, $P < 0.001$, $n = 39$).

TABLE 1. Nest site availability and general movement patterns performed by Mona Rhinoceros Iguana females during the 2003–2005 nesting seasons. Note that although most of the females had potential nesting sites in their home range, most of them left and did not use those sites.

Behavior description	Radio-marked	Not radio-marked[1]
Never left the usual home range area and nested inside it.	5 (18.5%)	0 (n/a)
Left the usual home range but returned and nested inside it.	7 (25.9%)	6 (27.3%)
Left the home range, returned, and left again to nest outside of the usual home range.	15 (55.6%)	16 (72.7%)
% of females with available nest sites inside their home range.	19 (70.0%)	18 (80.0%)
Number of females.	27	22

[1] Resident females in the study area that were never radio-collared but for which sporadic data were collected about their home range outside of the nesting season.

For females that we monitored more than one year (with or without a radio transmitter), nest site fidelity was variable. Thirteen (52%, $n = 25$) nested the second year within 7 m of their previous nest site, while the other 12 (48%, $n = 25$) nested in areas up to 400 m away. One of the females at the Lighthouse nested in the same spot (a limestone crevice) within her home range for three consecutive years.

Clutch size and egg size.—Clutch size (CS) varied from four to 24 eggs (mean = 14.1 ± 5.0, $n = 61$; Table 2) and was positively related to female SVL ($r^2 = 0.48$, $P < 0.001$, $n = 39$; Fig. 3). Egg length (EL) averaged 76.4 ± 6.1 mm (range = 60.1–90.1, $n = 268$) and egg width (EW) 45.1 ± 3.1 mm (range = 35.4–48.6, $n = 268$). Egg mass (EM) averaged 85.0 ± 16.6 g (range = 39.4–110.5, $n = 268$). EL and EW were positively correlated with egg mass ($r^2 = 0.61$, $P < 0.001$, EM = 0.316(EL) + 49.16, $n = 254$; and $r^2 = 0.42$, $P < 0.001$, EM = 0.164(EW) + 31.225, $n = 254$). In addition, EL and EW were positively correlated with each other ($r^2 = 0.21$, EL = 0.73(EW) + 0.723, $P = 0.001$, $n = 254$). Egg length was negatively correlated with female SVL ($r^2 = 0.31$, $P = 0.02$, $n = 17$; Fig. 4), although EW and EM were not ($r^2 = 0.41$, $P = 0.43$, $n = 17$; $r^2 = 0.15$, $P = 0.12$, $n = 17$, respectively; Fig. 4). Egg elongation (Mean clutch EL / mean clutch EW) averaged 1.68 ± 0.09 (range = 1.46–1.85, $n = 17$) and was not correlated with female SVL ($r^2 = 0.22$, $P > 0.40$, $n = 17$).

We found an atypical nest from a female (SVL = 54.1 cm) that contained eggs that were unusually small (EL = 60.1 ± 4.4 mm; EW = 41.1 ± 3.6 mm) and much lighter in mass (53.8 ± 12.2 g) compared with the average egg size. This nest had a hatching success of 64.7% (29.4% were infertile eggs and 5.9% embryos failed to complete development). Hatchlings from this nest were smaller in size (SVL mean = 10.4 ± 0.2 cm) and much lighter (body mass = 47.2 ± 3.6 g) than hatchlings that emerged from normal eggs (SVL mean = 11.6 ± 0.4 cm; hatchling body mass = 69.4 ± 0.1 g).

Reproductive output parameters.—Clutch mass (CM), which ranged from 470 to 1,700 g (1,190 ± 290 g), was not significantly related to female size ($r^2 = 0.01$, $P = 0.07$, $n = 15$). Relative egg mass (REM) averaged 1.68 ± 0.51 (range = 0.59–2.44, $n = 15$) and was negatively related to female SVL ($r^2 = 0.39$, $P < 0.008$, $n = 15$) and clutch size ($r^2 = 0.70$, $P = 0.001$, $n = 14$). Relative clutch size (RCS) averaged 0.26 ± 0.04 (range = 0.18–0.35) and was not related to female size ($r^2 = 0.01$, $P = 0.67$, $n = 15$). Relative clutch mass (RCM) averaged 22.56 ± 5.47 (range = 7.16–29.29) and was not related to female size ($r^2 = 0.09$, $P = 0.23$, $n = 15$).

Incubation.—Incubation period (to emergence) averaged 82.7 ± 4.1 days (range = 74–93) and did not vary significantly among years (2003–2005; $F_{2,41} = 54$, $P < 0.59$). We obtained only nine data sets (one Lighthouse, three in Pájaros, three in Sardinera, and two environmental) for temperature profiles during the incubation period. Mean temperatures in nest chambers from two nests in Pájaros and Sardinera in 2005 were 32.8 ± 1.6° C (maximum range = 25.9–36.5; Fig. 5A, 5B). The lowest temperatures recorded during the last four weeks of the incubation period were associated with heavy rains and cold days, with little sun that caused nest temperatures to drop. Temperatures from a nest located in a limestone crevice at the Lighthouse averaged 32.6 ± 2.0° C (range = 27.1–34.8; Fig. 5C) and were similar to temperatures in sand nests. However, hatching success for this nest was 0% due to flooding of the chamber that killed all embryos at a very late stage of development.

In 2006, temperatures from three data loggers were lower (30.2 ± 0.8° C, maximum range = 26.7–32.2) than in 2005. Two nests in 2006 always had temperatures above the mean air temperature during the incubation period (Fig. 5E, 5F), but one nest exhibited the lowest nest chamber temperature recorded, averaging 28.8 ± 1.1° C (range = 26.7–31.4). This nest was in a locality that experienced only between four and six hours of sun exposure daily (Fig. 5D). Despite the low solar exposure, hatching success was 79.2% in a clutch of 24 eggs, and was the longest incubation period recorded during the study (93 days).

TABLE 2. Comparison of nesting ecology parameters for the Mona Rhinoceros Iguana results from Wiewandt (1977) and this study.

Attribute	Wiewandt 1977	This study
Nesting period	Two weeks in July (most in a week); Earliest nesting date: July 25; Latest nesting date: 1 August.	Four weeks (peak between 18–30 July); Earliest nesting date: July 5; Latest nesting date: 10 August.
Nesting frequency	Indirect evidence that females nest every year (based on appearance of gravid females).	Females nest every year.
Females migrations	Reported up to 6.5 km. No further details given.	Described in detail (see text).
Nest architecture	Length: 1.1 m ($n = 7$, range = 0.6–1.5 m); Width: 21 x 15 cm; Depth: 54 cm ($n = 31$, range = 30–76).	Not documented.
Clutch parameters	Mean clutch size = 12, range = 5–12, $n = 37$.	Mean clutch size = 14.1 ± 5.0, range = 4–24, $n = 61$.
Egg morphology	Mean length = 78 mm, range = 74–82; Mean width = 51 mm, range = 46–56; Mean mass = 88 g, range = 82–93; $n = 18$.	Mean length = 76.4 ± 6.1 mm, range = 60.1–90.1; Mean width = 45.1 ± 3.1 mm, range = 35.4–48.6; Mean mass = 85.0 ± 16.6 g, range = 39.4–110.5; $n = 268$.
Incubation temperatures	29–31° C. Two days monitoring.	2005: Mean = 32.8° C, range = 25.9–36.5; 2006: Mean = 30.2° C, range = 26.7–32.2.
Incubation period	Mean 83 days, range = 78–89 days, $n = 8$.	Mean 82.7 ± 4.1 days, range = 74–93, $n = 43$.
Hatching success	79% ($n = 451$ eggs)	Mean = 75.9 ± 34.4%, range = 0–100, $n = 860$ eggs; 61 clutches (multi-year: 2003–2006).
Hatchling morphology	Mean SVL = 11.9 ± 0.5 cm, range = 10.5–12.7; Mean body mass = 70 g, range = 60–92; $n = 65$ hatchlings.	Mean SVL = 11.6 ± 0.5 cm, range = 10.0–12.9; Mean body mass = 68.9 ± 9.6 g, range = 41.6–97.2; $n = 423$ hatchlings from 36 nests; sex ratio 1:1.

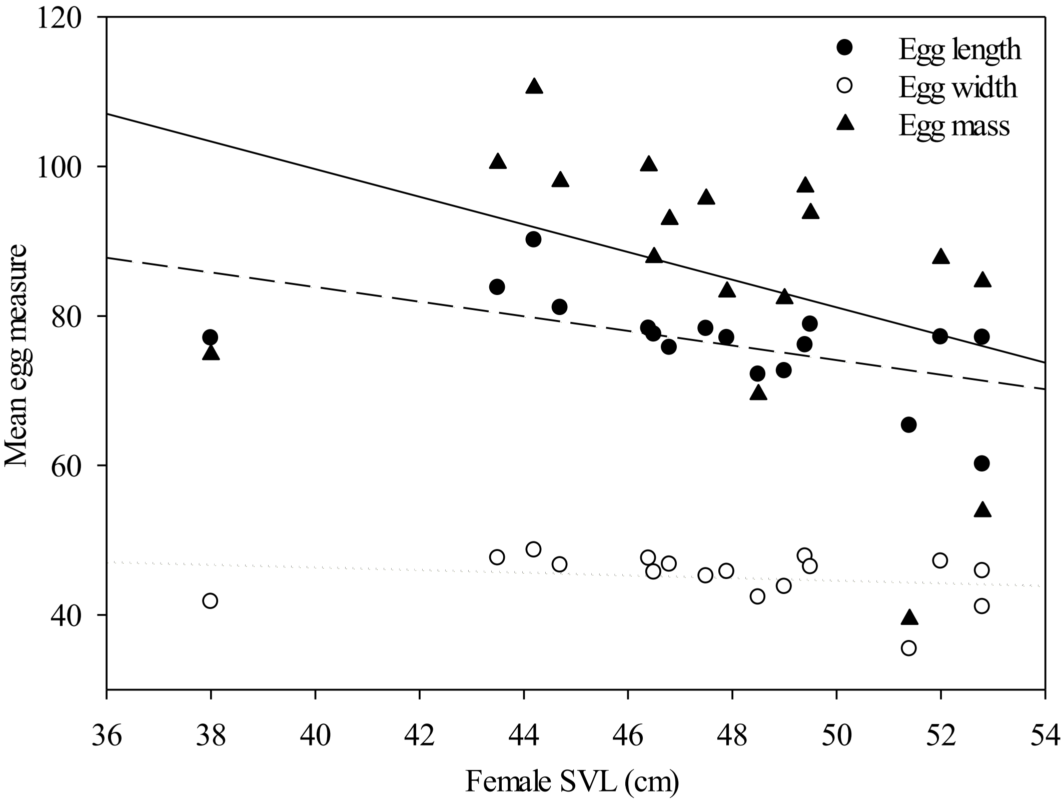


FIGURE 4. Relationship between female snout-vent length (SVL) and mean egg length, width, and egg mass in the Mona Rhinoceros Iguana. Mean egg length is measured in mm (solid circles), mean egg width measured in mm (open circles), and egg mass measured in g (triangles). Only egg length was negatively correlated with female SVL (r^2 = 0.31, P = 0.02, n = 17).

Hatching success.—Overall hatching success for the four years 2003 to 2006 fluctuated from 0 to 100% (mean = 75.9 ± 34.4, n = 61). Neither hatching success nor the proportion of infertile eggs was related to female SVL (r^2 = 0.11, P = 0.11, n = 22; r^2 = 0.11, P = 0.13, n = 22; respectively). Hatching success within nests varied from 0–100% in 2004 and 2005, but in 2003 it varied from 40–100% and in 2006 from 70–100%. On average, the percentage of infertile eggs per nest was 8.6 ± 18.5% (range = 0–100%, n = 61) and the percentage of embryos that failed to complete development was 16.0 ± 31.8% (range = 0–100%, n = 61). Nests with zero hatching success and with embryos that failed to develop were nests that experienced chamber inundation due to heavy rains in 2004 and 2005. All four of these nests were from the Lighthouse area and they were located in limestone crevices. Of all the nests at the three study sites, feral pigs (*Sus scrofa*) depredated only one. This nest was located in a small depression (2 m in diameter) filled with soil in the Lighthouse area and the bottom of the egg chamber was only 25 cm below the surface.

Hatchling morphometrics.—Hatchling SVL averaged 11.6 ± 0.5 cm and body mass averaged 68.9 ± 9.6 g (n = 423). There was a positive relationship between mean egg mass and mean hatchling mass per nest (r^2 = 0.94, n = 8, P = 0.000057). In addition, there was a positive relationship between mean egg length and mean hatchling SVL per nest (r^2 = 0.79, n = 8, P = 0.002). We also found a positive relationship between mean egg mass and hatchling SVL per nest (r^2 = 0.91, n = 8, P = 0.0002). Neither hatchling SVL nor body mass were related to the SVL of the female that laid them (r^2 = 0.14, P = 0.26, n = 23; r^2 = 0.05, P = 0.49, n = 23). The sex ratio of all hatchlings collected was not significantly different from 1:1 (χ^2 = 0.02, P = 0.88, n = 403 hatchlings). Overall sex ratio in each clutch also did not differ significantly from 1:1 (all χ^2 < 0.25, P > 0.08, n = 22).

Nest abundance in the coastal nesting sites.—The escape-hole surveys we conducted in 2006 yielded 680 nests along 8.6 ha of the southwestern coastal plain, which included Pájaros beach and other small beaches in the south portion of the island, and resulted in a density of 0.007 nests/m^2. Eleven sites with a total area of 0.5 ha within the larger 8.6 ha monitored area exhibited nest densities that were much higher, averaging 0.107 ± 0.064 nests/m^2 (range = 0.026–0.232). Some of these sites correspond to managed areas within the *Casuarina* matrix that were cleared of vegetation, while others correspond to natural, undisturbed nesting sites. We found no differences in nest densities between the high-density managed and natural nesting sites (U = 12, z = -0.55, P = 0.58, n = 11). We found 49% of the 680 nests with escape-holes in these 11 locations, despite that they only comprised 5.8% of the surveyed area. The other 51% of the nests we located in the remaining 94.2% of the surveyed area.

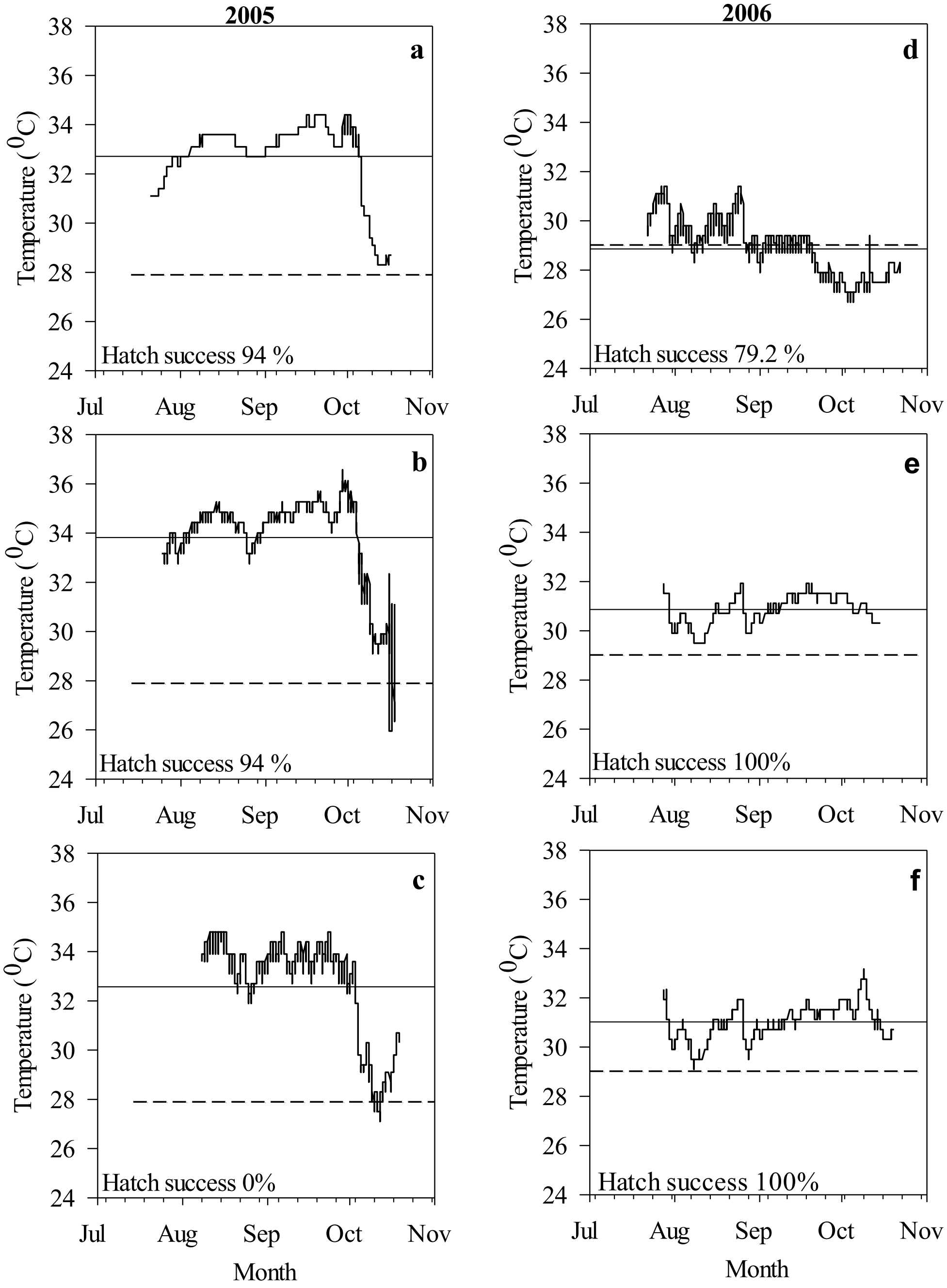


FIGURE 5. Nest chamber temperature profiles and hatching success of six nests for Mona Rhinoceros Iguanas monitored in 2005 or 2006. Dashed line represents the mean environmental temperature 0.5 m above the ground in an adjacent sunny and sandy exposed area during the incubation period. For more details see Results section. Horizontal solid lines are means across entire incubation period.

DISCUSSION

Wiewandt (1977) was the first to document the basic aspects of the nesting ecology of the Mona Rhinoceros Iguana. Wiewandt, however, did not capture iguanas, particularly breeding females, to avoid disrupting their nesting behavior. Thus, his findings were based on direct observations of aspects such as nesting phenology, clutch size, egg size, and hatch timing. In general, the major differences between Wiewandt's data and ours are for nesting period and clutch size (Table 2). Wiewandt recorded a nesting period of only two weeks in July, while we found that nesting can take place over a period of four weeks. Wiewandt measured a mean clutch size of 12 ± 3.9 eggs (range = 5–19), which is significantly lower than the mean clutch size of 14.1 ± 5.0 eggs (range = 4–24) we found in this study ($t = 2.23$, $P = 0.028$, $n = 98$). In addition, hatching success reported by Wiewandt (1977) in undisturbed nests was 79%, whereas in this study it was 75.9% over our four-year study period (Table 2).

Mating and nesting period.—Despite the limited number of mating observations, ours is the first study to record the time elapsed between mating and nesting for the Mona Rhinoceros Iguana (i.e., 30 ± 5 days). Although we cannot be sure whether the matings resulted in fertilizations of eggs and/or were the only copulation those females attained, females laid eggs a month after copulating, which is the expectation based on the mating-nesting timing for the species and has also been considered typical among *Cyclura* (Wiewandt 1982; Iverson et al. 2004).

For iguanas, the major determinants of nesting phenology (mating, nesting, and hatching) are related to climate (i.e., temperature and moisture). Climate may have strong effects on the seasonal activity patterns, incubation duration, hatchling emergence, and food abundance. Typically, iguanid species lay eggs during the period in which ambient temperatures are closer to the optimal incubation temperatures, and the hatch time coincides with the period of highest food availability for the hatchlings (Wiewandt 1982).

The only previous information on nesting frequency for this genus comes from *C. cychlura inornata* (Iverson et al. 2004). In that species, nesting frequency appears to be related to female size, with large females nesting on an annual basis but younger females only nesting every two or three years. In this study, we also found that large females nest on an annual basis, but the general lack of young adults in Mona precludes definitive conclusions about nesting frequency by smaller females. It has been suggested that nesting frequency in iguanines follows a latitudinal gradient (Wiewandt 1982). Species occurring at high latitudes have to confront a higher degree of environmental uncertainty that may compromise optimal female conditions for successful reproduction (i.e., via low food availability prior to the reproductive season), and for at least some other species reproducing on an annual basis is not the rule, as occurs in *Sauromalus* from the Gulf of Mexico (Wiewandt 1982; Abts 1987).

In this study, we documented a 4.7 year-old headstarted female to have the smallest size (34.4 cm SVL and 2.3 kg) reported thus far for a nesting female in her first reproductive season, similar to captive female *C. cornuta* in the Dominican Republic (Ottenwalder 2000). Previously, the smallest breeding female had been an individual with a SVL of 38.0 cm and 2.1 kg, estimated to be six or seven years old (Wiewandt 1977). Captive-reared Mona Rhinoceros Iguanas grow at similar rates as their wild mid-sized counterparts (Pérez-Buitrago et al. 2008), so we believe that it is likely that wild females also mature at four or five years of age.

Nesting migrations.—Natal homing, the phenomenon by which a female returns to nest in the place where she hatched, has been widely documented for many reptiles, including marine and freshwater turtles (Bowen et al. 1994; Freedberg et al. 2005), some crocodilians, and some lizards (Hein and Whitaker 1997; Jenssen 2002; Russell et al. 2005). In theory, natural selection favors this behavior because it allows a female to nest in locations that have been previously successful for incubation (Freedberg and Wade 2001), but it requires the environment to be predictable and a net gain in fitness when natal homing is exhibited.

It is unclear if iguanas show natal homing, although nesting migrations from home ranges to the nest sites have been documented (see Iverson et al. 2004 and references therein). Reported distances traveled fluctuated between 30 m in *C. cychlura inornata* (Iverson et al. 2004) and 15 km in *Conolophus subcristatus* (Werner 1982) and appear to be dependent on island size. For the Mona Rhinoceros Iguana, the previous record for linear distance traveled by a female iguana was 6.5 km, based on a casual observation of a marked female (Wiewandt 1977). We found a large variation in the linear distances traveled by females before nesting (mean = 279 ± 271 m, range = 0–930 m, $n = 19$), and also in the length of the erratic and tortuous paths of females, which reached a maximum value of 12.8 km (mean = 2.4 ± 2.1 km). In this study, most females left (even those with available nesting sites in their home ranges), if only temporarily, shifting directions many times and passing by many potential nesting sites before ovipositing either within their home ranges or in other nesting areas outside their home ranges. Ignoring suitable nesting sites to nest far away from established centers of activity has been interpreted as a "sign" of natal homing (Wiewandt 1982). However, the irregular paths followed by most female Mona Rhinoceros Iguanas are not supportive of the natal homing hypothesis, which predicts that females would move in a direct manner, such as in a straight line when the terrain allows. Specificity in travel directions has been documented for other reptile species showing natal homing, including turtles (Avens et al. 2003; Nagelkerken et al. 2003), and also seems to be the case for Galápagos Land Iguanas (*Conolophus subcristatus*), which migrate up to 10 km to an area located in a volcano caldera that appears to have the best conditions for nesting/incubation on the island (Werner 1983). Most females in this study moved erratically and only four radio-tracked females followed specific bearings. Additional indirect evidence of the lack of natal homing for the Mona Rhinoceros Iguana comes from captive-raised females that did not nest in the places where they were released or where they were hatched (García et al. 2007), as well as their erratic movement patterns, which differed from the constant bearings followed by hatchlings during the natal dispersal phase (Pérez-Buitrago and Sabat 2007).

Our observations suggest a high degree of behavioral plasticity, including the ability to navigate in a specific direction, but also the capacity to explore unfamiliar zones to find a suitable nesting site and then return to their usual centers of activity. The ability to find a suitable nesting site would be strongly selected for iguanas on Mona Island, where most sandy communal nesting sites are confined to the coastal plain, the "bajuras", and to a much lower extent, very discrete crevices with soil on the plateau. In addition, the strong female-female competition in some communal nesting areas would be an additional factor prompting the development of optimal mechanisms for navigation that allow females to find less crowded nesting sites.

We also detected strong evidence of site fidelity on a coarse scale (i.e., regional, such as the southwestern beach) by re-capturing 72% of non-resident iguanas over two consecutive years on Pájaros beach. Once an iguana finds an optimal nesting beach she appears to be able to return to it in successive years. This is important for iguanas living in the interior of the island, far from the nesting areas located on the coastal plain or the "bajuras". However, at a finer scale (within a local site), our data suggest low nest site fidelity, which perhaps only occurs incidentally, and/or is dependent on competition with other gravid/spent females. Competition may also be the reason why some females change nesting sites, particularly for young females, as was observed for one young female that traveled the longest distance (12.8 km; Fig. 6C). This female moved through many communal nesting areas where a high density of females could have prevented her from successfully acquiring a nesting site. For larger, stronger, more experienced females, tolerating competition in densely populated nesting aggregations may be related to benefits such as the soft sandy soils (due to the use of these sites in previous years) and vegetation-free areas that may facilitate digging and assure optimal incubation temperatures for eggs (Wiewandt 1982).

At the rocky Lighthouse study area, where good nesting sites were scarce and scattered, we detected females laying eggs inside their home ranges in limestone crevices where sufficient accumulation of reddish clay soil made nesting possible. One of these females used the same crevice within its home range for three consecutive years with an overall hatching success of 80%, while others migrated away from their usual home ranges following specific paths first, but eventually switching directions many times, perhaps because other females were already nesting there.

The extent of the importance of nesting in limestone crevices for the population as a whole is unclear, but should be considered in future studies. Moreover, hatching successes at these sites appeared to be highly dependent on the amount of rain during the incubation period, since flooding of the nest chamber can result in the embryo death. However, there are difficulties in identifying and gaining access to nests in limestone crevices for monitoring.

***Clutch size and egg size*.**—We found that Mona Rhinoceros Iguanas laid a mean of 14 eggs, similar to what has been reported for *C. cornuta cornuta* (in captivity) from the Dominican Republic, but higher than the 12 eggs/clutch previously reported for the species (Wiewandt 1977). The discrepancy between Wiewandt´s (1977) data and our values may be due to the fact that in his nest surveys, he detected four nests with only six eggs and he did not detect any nests with as many eggs as we did (24 eggs/clutch). The difference in clutch size is likely due to the difference in body size between the studies. As documented for reptiles in general, larger individuals/species are generally able to produce larger clutches. We confirmed this pattern, one that also holds true across other species/populations of *Cyclura* (Iverson et al. 2004 and references therein). *Cyclura pinguis* and *C. stejnegeri* are the largest members of the genus and also have the largest clutch sizes, a character that has been considered ancestral (Iverson et al. 2004) based upon the currently accepted phylogeny for *Cyclura* iguanas (Malone et al. 2000).

Within iguanine species, egg mass (EM) is generally not related to female size as found in this study, although there is a reported positive relationship across species of *Cyclura* (Iverson et al. 2004). However, EM was highly variable on Mona Island with two females laying very small eggs. One case involved the smallest female detected in this study, whereas the other was a very old (perhaps unhealthy) female. For egg length (EL), we found that smaller females tended to produce longer eggs, a trait that allows small females (possibly constrained by a small pelvic opening) to produce eggs with a large mass (Iverson et al. 2004). However, egg elongation (Mean clutch EL / mean clutch EW) was not correlated with female size, which contrasted with what

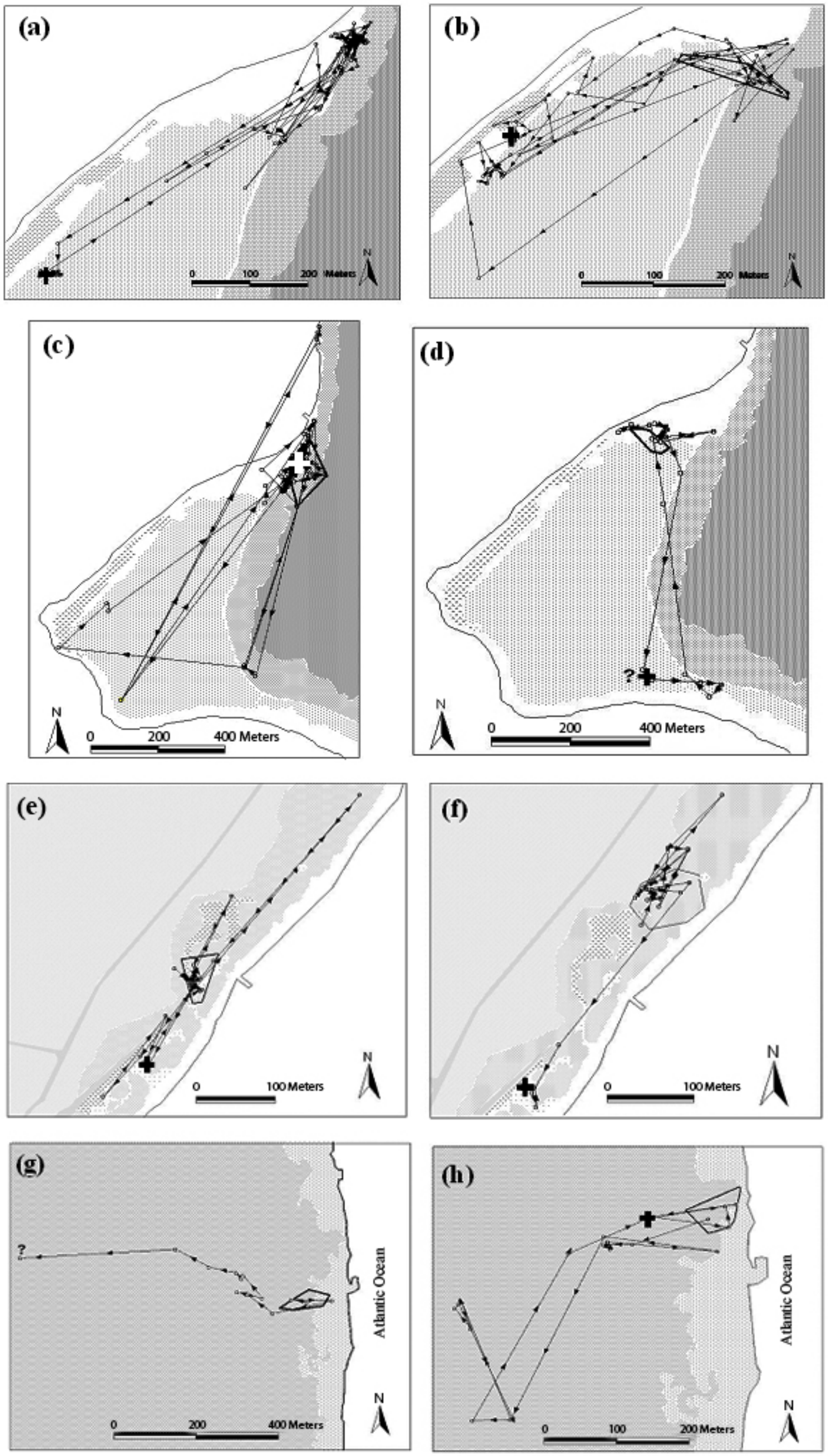


FIGURE 6. Nesting movements of four female Mona Rhinoceros Iguanas. Nesting locations were recorded at Sardinera (A, B, C, D), two at Pájaros (E, F), and two at the Lighthouse (G, H). Thick line polygons represent the home ranges of these females during the non-reproductive period. Nest sites, or suspected nest locations, are represented by a white (C) or black cross. Map legends for each study site are in Figure 1. The radio signal of the female represented in map G was lost at the position indicated by the question mark. All maps except F and G show the movements back to the home range after nesting.

was found in the smaller-sized *Cyclura cychlura inornata* (Iverson et al. 2004). *C. cychlura inornata* begins laying eggs at a SVL of only 26–27 cm and a body mass of 0.75 kg, while the Mona Rhinoceros Iguana first nests at 34.4 cm SVL and 2.3 kg. The smaller size and correspondingly constrained pelvic opening of *C. cychlura inornata* may explain why Iverson et al. (2004) found a negative relationship between egg elongation and female size, a relationship that does not exist in the Mona Rhinoceros Iguana.

Relative egg mass (REM) was lower (1.68 ± 0.50%) in this study than previously inferred (2.21%) from Wiewandt's data by Iverson et al. (2004). The discrepancy may be a result of the smaller clutch size reported by Wiewandt and the smaller egg mass data used for estimating REM by Iverson et al. (2004). The REM value we report here for the Mona Rhinoceros Iguana is the lowest for any *Cyclura* species. Given that the Mona Rhinoceros Iguana is one of the largest members of the genus, this suggests that having a large body size may result in a reduction in reproductive output per individual offspring. On the other hand, the lack of relationship between RCM and body size may imply that females are allocating a constant proportion of energy to their clutches, as reported for *C. cychlura inornata* (Iverson et al. 2004).

Consistent with reported patterns in lizards, including other iguanas and *Cyclura* specifically, we found that hatchling size (SVL and body mass) was positively related to egg size (Boylan 1984; Van Marken Lichtenbelt and Albers 1993; Alberts et al. 1997; Iverson et al. 2004; Knapp et al. 2006). The lack of a relationship between hatchling size and female size that we found has been previously documented for other *Cyclura* (Iverson et al. 2004; Knapp et al. 2006). The relationship between hatchling and egg size is in accordance with optimal egg size theory that postulates that both egg and hatchling sizes are maximized at a point at which there is not a reduction in fitness caused by a reduction in offspring number (Congdon and Gibbons 1987). Thus, hatchling size appears to be more "resilient" to environmental factors than other reproductive parameters such as clutch size and egg size. This can vary among populations of a single species across different environmental settings, including island size (Iverson et al. 2004; Knapp et al 2006).

Incubation temperatures.—Despite the fact that the mean incubation temperature we report is similar to the previous records of incubation temperatures for other *Cyclura* (*C. cychlura inornata*: 31.4° C, Iverson et al. 2004; *C. cychlura cychlura*: 32.8° C, Knapp 2000; and *C. ricordii*: 30–31° C, Ottenwalder 2000), we found larger temperature fluctuations than previously reported – up to 9° C in one monitored nest and up to 6° C in others. This large variation was caused by consecutive rainy or cloudy days that lowered nest chamber temperatures during the last weeks of the incubation period. Interestingly, despite these fluctuations, hatching success was high in the monitored nests (except in one case in which all full-term embryos died by drowning). This suggests that fertilized eggs are highly resilient to severe drops in temperature late in the incubation period and fluctuations in oxygen in nest chambers (Iverson et al. 2004). This is further corroborated by a nest (Fig. 5D) which exhibited mean temperatures that were lower than the environmental temperature through the incubation period, and only had temperatures higher than 30° C for short periods. In addition, the temperature recorded in the only nest located in a limestone crevice that was monitored did not differ from nests located in the more typical spots with a sandy substrate.

Hatching success.—The overall hatching success rate across the three years (76%) was similar to that reported by Wiewandt (1977) of 79% and other *Cyclura* species such as *C. carinata* (78%, Iverson 1979), *C. collei* (76%, Vogel 1994), *C. cychlura inornata* (81%, Iverson et al. 2004), *C. nubila caymanensis* (92%, Gerber 2000a), *C. nubila nubila* (85%, Christian 1986), and *C. pinguis* (84%, Gerber 2000b), as well as other island iguanid species such as *Conolophus* (87%, Snell and Tracy 1985) and *Amblyrhynchus* (88%, Rauch 1988). Complete failure of fertilized eggs to develop occurred only at the Lighthouse, and was the result of either flooding due to heavy rains, or predation by pigs (one nest). Neither of these factors caused mortality at the other two study sites located on the coast. Obviously, the sandy coastal plain offers more suitable areas for nesting, and if heavy rains occur, sand allows water to drain rapidly, preventing anoxic or high CO_2 conditions in the egg chamber. On the other hand, Wiewandt (1977) observed that hatching success in iguana nests could be dramatically affected by pig predation and hypothesized that the amount of rain in the 3–4 months before nesting could be a factor for the inter-annual variation in egg loss to pigs or flooding, which varied from 0–100% across four monitored localities. It is possible that years with heavy rains increase vegetation resources for pigs and thus reduces levels of egg predation during those years (Wiewandt 1977). However, pig access is restricted at Pájaros and Sardinera. At Pájaros, the beach is limited by vertical cliffs and has only one access trail that is used daily by the DRNA-PR staff and periodically by tourists, probably rendering the area unattractive to feral pigs. At Sardinera, and along the southwest coastal plain, the DRNA-PR installed a fence in 1985 (following one of the major recommendations made by Wiewandt 1977) that is still maintained to exclude pigs from the sandy areas that run parallel to the beach to reduce pig predation on turtle and iguana nests. Even though it has not been formally quantified, this management action appears to have had a very strong positive impact on hatching success for turtles (Carlos Diez, pers. comm.) and as we report here, also for iguanas.

Nest abundance at coastal nesting sites.—The number of nests detected in the southwestern coastal plain and other beaches in 2006 was 680. In 1994, Haneke (1995) surveyed iguana nests in the same coastal localities and only found 159 nests with escape holes. In part, we attribute this dramatic increase in the number of nests between 1994 and 2006 to the management initiative conducted by the DRNA-PR in 1992 which cleared three 50m x 50m areas within the *Casuarina* matrix to increase the availability of suitable nesting areas. Other factors that may have contributed to the increase in nests in the coastal areas are that in 1998 the island was hit by Hurricane Georges which downed many *Casuarina* trees bordering the pine plantation, and also in 1998 the DRNA-PR initiated a non-systematic initiative of killing *Casuarina* trees in the same areas. These two factors have resulted in the creation of new open areas appropriate for nesting. We have shown that most females moved in erratic paths and thus they were probably able to discover these new areas and use them. We speculate that before these "new" nests sites were available, iguanas were forced to nest in suboptimal sites, such as the soils covered by *Casuarina* leaves or in the rocky sites on the plateau.

Wiewandt (1977) suggested that of the total surface area of Mona Island, only 1% (55.4 ha) was suitable for iguanas to nest. Of this area, only about 9 ha are located in the coastal portion of the island, which implies that most of the available nesting areas are located in the plateau depressions. However, hatching success in the plateau depressions is likely to be very low because dry years, although optimal for egg development, may induce high predation rates by pigs due to low resource abundance, whereas wet years, although bad for eggs due to the risk of nests flooding, apparently have low levels of pig predation (Wiewandt 1977). Nests in the sandy soils of the coastal plain do not flood even during wet years. Also, since 1982 the southwestern coastal plain has been fenced to prevent pig incursions, and the other beaches are not very accessible to pigs because vertical cliffs surround them. Thus, the coastal nesting sites account for most of the yearly hatchling production. Haneke (1995) suggested that in 1994 the bulk of the hatchlings were produced in the coastal sites and for that year, it represented the total hatchling production, since all 110 nests in the plateau depressions were completely depredated by pigs. The four-fold increase in the number of nests in the coastal area, followed by an increase in the area available for nesting, strongly suggests that good nest sites are limited on Mona and may therefore have been a potential factor constraining population growth. It also implies that removing the *Casuarina* plantation will increase the number of iguanas that are able to nest in optimal sites and result in an increase in the overall reproductive output of the population.

Acknowledgments.—This research was funded by the Center for Applied Tropical Ecology and Conservation (grant NSF HRD-0206200) of the University of Puerto Rico, Rio Piedras Campus. Logistic support and research permits were provided by the Natural Resources Department of Puerto Rico (DRNA-PR) and we are particularly grateful to Alberto Álvarez, Carlos Diez, Miguel García, and the staff of the Endangered Species Division of the DRNA-PR. The DRNA-PR Mona Island staff (rangers, biologists, and technicians) helped us in many ways while conducting this project. Particularly, we are very grateful to Gaspar Pons, Miguel Nieves, Miltón Pérez, José Jimenez, Miguel Bonet, and Reynaldo Pagan. Many people helped us in the field, mainly Alberto Álvarez, Johanna Delgado, John Bendon, Stephany Boven, Raissa Menendez, Maria José Andrade, Jessica Castro, Carlos Toledo, Marcela Zalamea, Marina Rujas, Manuel Correa, and Keysa Rosas. We also want to thank Pilar Angulo-Sandoval and Brian C. Bock for reviewing early versions of this manuscript.

LITERATURE CITED

Abts, M.L. 1987. Environmental and variation in life history traits of the Chuckwalla, *Sauromalus obesus*. Ecological Monographs 57:215–232.

Alberts, A. (Ed.). 2000. West Indian Iguanas: Status Survey and Conservation Action Plan. IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Alberts, A.C. 2007. Behavioral considerations of headstarting as a conservation strategy for endangered Caribbean Rock Iguanas. Applied Animal Behaviour Science 102:380–391.

Alberts, A.C., A.M. Perry, J.M. Lemm, and J.A. Phillips. 1997. Effects of incubation temperature and water potential on growth and thermoregulatory behavior of hatchling Cuban Rock Iguanas (*Cyclura nubila*). Copeia 1997:766–776.

Avens, L., J. Braun-McNeill, S. Epperly, and J. Lohmann. 2003. Site fidelity and homing behavior in juvenile Loggerhead Sea Turtles (*Caretta caretta*). Marine Biology 143:211–220.

Batschelet, E. 1981. Circular Statistics in Biology. Academic Press, New York City, New York, USA.

Boylan, T. 1984. Breeding the Rhinoceros Iguana *Cyclura c. cornuta* at Sydney Zoo. International Zoo Yearbook 23:144–148.

Bowen, B.W., T.A. Conant, and S.R. Hopkins-Murphy. 1994. Where are they now? The Kemp's Ridley headstart project. Conservation Biology 8:853–856.

Burton, F.J., and F.F. Rivera-Milán. 2014. Monitoring a population of translocated Grand Cayman Blue Iguanas: assessing the accuracy and precision of distance sampling and repeated counts. Animal Conservation 17:40–47.

Campbell, K., C.J. Donlan, F. Cruz, and V. Carrión. 2004. Eradication of feral goats *Capra hircus* from Pinta Island, Galápagos, Ecuador. Oryx 38:328–333.

Christian, K.A. 1986. Aspects of the life history of Cuban Iguanas on Isla Magueyes, Puerto Rico. Caribbean Journal of Science 22:159–164.

Cintrón, B., and L. Rogers. 1991. Plant communities of Mona Island. Acta Científica 5:10–64.

Congdon, J.D., and J.W. Gibbons. 1987. Morphological constraint on egg size: a challenge to optimal egg size theory? Proceedings of the National Academy of Sciences 84:4145–4147.

Dellinger, T., and G. von Hegel. 1990. Sex identification through cloacal probing in juvenile Marine Iguanas (*Amblyrhynchus cristatus*). Journal of Herpetology 24:424–426.

Diaz, D.C. 1984. Recovery Plan for the Mona Iguana *Cyclura stejnegeri*. Natural Resources Department, San Juan, Puerto Rico.

Donlan, C.J., B.R. Tershy, K. Campbell, and F. Cruz. 2003. Research for requiems: the need for more collaborative action in eradication of invasive species. Conservation Biology 17:1850–1851.

Ewel, J.J., and J.L. Whitmore. 1973. The ecological life histories zones of Puerto Rico and U.S. Virgin Islands. United States Department of Agriculture Forestry Research Paper ITF-18:1–72.

Freedberg, S., and M.J. Wade. 2001. Cultural inheritance as a mechanism for population sex-ratio bias in reptiles. Evolution 55:1049–1055.

Freedberg, S., M.A. Ewert, B.J. Ridenhour, M. Neiman, E. Craig, and C.E. Nelson. 2005. Nesting fidelity and molecular evidence for natal homing in the freshwater turtle, *Graptemys kohnii.* Proceedings of the Royal Society B 272:1345–1350.

García, M.A., N. Pérez-Buitrago, A.O. Álvarez, and P.J. Tolson. 2007. Survival, dispersal, and reproduction of headstarted Mona Island Iguanas, *Cyclura cornuta stejnegeri*. Applied Herpetology 4:357–363.

Gerber, G. 2000a. Lesser Caymans Iguana. Pp. 41–44 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Gerber, G. 2000b. Conservation of the Anegada Iguana, *Cyclura pinguis*: Field Research Report. Unpublished report to British Virgin Islands National Park Trust. 48 pp.

Gerber, G. 2007. Turks and Caicos Iguana translocation program, Bahama Archipelago. Re-introduction News 26:53–55.

Goodman, R.M., C.R. Knapp, K.A. Bradley, G.P. Gerber, and A.C. Alberts. 2009. Review of radio transmitter attachment methods for West Indian Rock Iguanas (genus *Cyclura*). Applied Herpetology 6:151–170.

Haneke, B. 1995. A study of Mona Rock Iguana (*Cyclura cornuta stejnegeri*) nesting sites on Mona Island, Puerto Rico. Iguana Times (Journal of the International Iguana Society) 4:61–71.

Hayes, W.K., R.L. Carter, S. Cyril, Jr., and B. Thornton. 2004. Conservation of an endangered Bahamian Rock Iguana, I. Population assessments, habitat restoration, and behavioral ecology. Pp. 232–257 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Hein, E.W., and S.J. Whitaker. 1997. Homing in the Eastern Fence Lizards (*Sceloporus undulatus*) following short distance translocation. Great Basin Naturalist 57:348–351.

Hooge, P.N., B. Eichenlaub, and E. Solomon. 1999. The Animal Movement Program. USGS, Alaska Biological Science Center. Anchorage, Alaska, USA.

ITWG (Iguana Taxonomy Working Group). 2016. A checklist of the iguanas of the world (Iguanidae; Iguaninae). Pp. 4–46 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Iverson, J.B. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bulletin of the Florida State Museum, Biological Sciences 24:175–358.

Iverson, J.B., K.N. Hines, and J.M. Valiulis. 2004. The nesting ecology of the Allen Cays Rock Iguana, *Cyclura cychlura inornata* in The Bahamas. Herpetological Monographs 18:1–36.

Jenssen, T.A. 2002. Spatial awareness by the lizard *Anolis cristatellus*: Why should a non-ranging species demonstrate homing behavior? Herpetologica 58:364–371.

Knapp, C.R. 2000. Exuma Island Iguana. Pp. 32–34 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Knapp, C.R. 2001. Status of the translocated *Cyclura* iguana colony in The Bahamas. Journal of Herpetology 35:239–248.

Knapp C.R., and R.D. Hudson. 2004. Translocation strategies as a conservation tool for West Indian Iguanas: evaluations and recommendations. Pp. 199–209 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Knapp, C.R., J.B. Iverson, and A.K. Owens. 2006. Geographic variation in nesting behavior and reproductive biology of an insular iguana (*Cyclura cychlura*). Canadian Journal of Zoology 84:1566–1575.

Malone, C.L., T. Wheeler, J.F. Taylor, and S.K. Davis. 2000. Phylogeography of the Caribbean Rock Iguana (*Cyclura*): implications for conservation and insights on the biogeographic history of the West Indies. Molecular Phylogenetics and Evolution 17:269–279.

Mitchell, N.C., R. Haeffner, V. Veer, M. Fulford-Gardner, W. Clerveaux, C.R. Veitch, and G. Mitchell. 2002. Cat eradication and the restoration of endangered iguanas (*Cyclura carinata*) on Long Cay, Caicos Bank, Turks and Caicos Islands, British West Indies. Pp. 206–212 *In* Turning the Tide: The Eradication of Invasive Species. Veitch, C.R., and M.N. Clout (Eds.). IUCN SSC Invasive Species Specialist Group, IUCN, Gland, Switzerland.

Nagelkerken, I., L.P.J.J. Pors, and P. Hoetjes. 2003. Swimming behaviour and dispersal patterns of headstarted Loggerhead Turtles *Caretta caretta.* Aquatic Ecology 37:183–190.

Ottenwalder, J. 2000. Rhinoceros Iguana. Pp. 22–27 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Pérez-Buitrago, N., and A. Sabat. 2007. Natal dispersal, home range, and habitat use of hatchlings of the Mona Island Iguana (*Cyclura cornuta stejnegeri*). Applied Herpetology 4:365–376.

Pérez-Buitrago, N., M.A. García, A. Sabat, J. Delgado-Acevedo, A. Álvarez, W.O. McMillan, and S.M Funk. 2008. Do headstart programs work? Survival and body condition in headstarted Mona Island Iguanas *Cyclura cornuta stejnegeri*. Endangered Species Research 6:55–65.

Rauch, N. 1988. Competition of Marine Iguana females (*Amblyrhynchus cristatus*) for egg-laying sites. Behaviour 107:91–106.

Rodda, G.H., B.C. Bock, G.M. Burghardt, and A.S. Rand. 1988. Techniques for identifying individual lizards at a distance reveal influences of handling. Copeia 1988:905–13.

Russell, A.P., A.M. Bauer, and M.K. Johnson. 2005. Migration in amphibians and reptiles: an overview of patterns, and orientation mechanisms. Pp. 151–203 *In* Migration of Organisms: Climate, Geography, Ecology. Elewa, A.M.T. (Ed.). Springer-Verlag, Heidelberg, Germany.

Schaeffer, W.H. 1934. Diagnosis of sex in snakes. Copeia 1934:181.

Snell, H.L., and R. Tracy. 1985. Behavioral and morphological adaptations by Galápagos Land Iguanas (*Conolophus subcristatus*) to water and energy requirements of eggs and neonates. American Zoologist 25:1009–1018.

Van Marken Lichtenbelt, W., and K. Albers. 1993. Reproductive adaptations of the Green Iguana on a semiarid island. Copeia 1993:790–798.

Vogel, P. 1994. Evidence of reproduction in a remnant population of the endangered Jamaican Iguana, *Cyclura collei* (Lacertilia, Iguanidae). Caribbean Journal of Science 30:234–241.

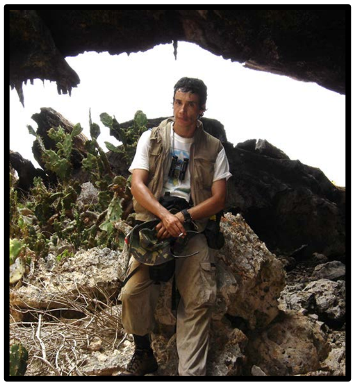
Werner, D.I. 1982. Social organization and ecology of Land Iguanas, *Conolophus subcristatus*, on Isla Fernandina, Galápagos. Pp. 342–365 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Werner, D.I. 1983. Reproduction in the iguana *Conolophus subcristatus* on Fernandina Island, Galápagos: clutch size and migration costs. The American Naturalist 121:757–775.

Wiewandt, T.A. 1977. Ecology, Behavior, and Management of the Mona Island Ground Iguana, *Cyclura stejnegeri*. Ph.D. Dissertation, Cornell University, Ithaca, New York, USA. 338 p.

Wiewandt, T.A. 1982. Evolution of nesting patterns in iguanine lizards. Pp. 119–141 *In* Iguanas of the World: Their Behavior, Ecology, and Conservation. Burghardt, G.M., and A.S. Rand (Eds.). Noyes Publications, Park Ridge, New Jersey, USA.

Wilson, B.S., A.C. Alberts, K.S. Graham, R.D. Hudson, R.K. Bjorkland, D.S. Lewis, N.P. Lung, R. Nelson, N. Thompson, J.L. Kunna, et al. 2004. Survival and reproduction of repatriated Jamaican Iguanas. Pp. 220–231 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.



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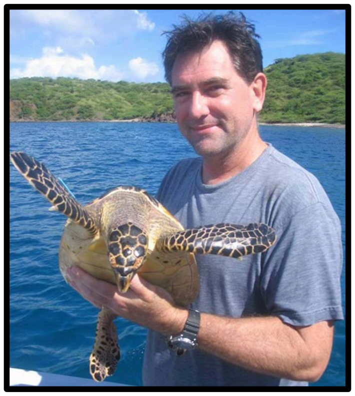

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Herpetological Conservation and Biology 11(Monograph 6):214–221.
Submitted: 15 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

EFFECTS OF TOURISM ON BODY SIZE, GROWTH, CONDITION, AND DEMOGRAPHY IN THE ALLEN CAYS IGUANA, *CYCLURA CYCHLURA INORNATA*, ON LEAF CAY, THE BAHAMAS

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Abstract.—**The feeding of wildlife by ecotourists has become increasingly popular, but its effects are not well studied. The endangered Allen Cays Iguana is known to occur naturally on only two small cays in the northern Exuma Islands (The Bahamas). One of those cays, Leaf Cay (4 ha) has an easily accessible beach to which up to 150 people converge each day to feed the iguanas. However, iguanas from other parts of the cay rarely ever see an ecotourist. This study investigated the differences in body size, growth, body condition, and demography of the iguanas on opposite sides of Leaf Cay. Iguanas on the human-impacted side of the cay were larger, grew faster, and weighed more (relative to body length), but had similar survival rates as those without human interaction. Capture sex ratios did not differ between sides of the cay and were generally not different from a 1:1 ratio. Although these data might be interpreted as positive impacts of supplemental feeding, when viewed with previously published differences in behavior and blood chemistry, the long-term effects of these feeding activities are of potential concern.**

Key Words.—ecotourism; feeding; Rock Iguana; The Bahamas

INTRODUCTION

The impacts of ecotourism on ecosystems are relatively under-studied compared to recent increases in such activities. For example, increased recreational use of nature preserves or other natural areas can have diverse direct and indirect negative impacts on local ecosystems (Boyle and Samson 1985; Garber and Burger 1995; Rodríguez-Prieto and Fernandez-Juricic 2005; Kangas et al. 2010; Wells et al. 2012). Iguanas are one group that might be impacted, both positively and negatively, by ecotourism (Knapp 2004).

One common activity associated with some so-called ecotourism is the feeding of wildlife (Orams 2002). Natural trophic subsidies can have myriad effects on food webs (see review in Polis et al. 1997). Human supplementation or subsidization of food in a variety of contexts has been shown to increase reproduction but decrease adult survivorship in birds (Arcese and Smith 1988; see review of effects on bird populations in Robb et al. 2008), increase body and liver condition in fish (Dempster et al. 2011), increase the abundance of coyotes (Rose and Polis 1998; Fedriani et al. 2001), and increase body mass in Grey Foxes (Harrison 1997). Thus it is no surprise that anthropogenic supplementation of food associated with ecotourism may be expected to have impacts on the species being fed, as well as other species in the community.

Among lizards, approved feeding of Komodo Dragons (*Varanus komodoensis*) by tourists induced a numerical response by the lizards, and increased their density at feeding sites while feeding was conducted (Walpole 2001). In another large lizard, the use of human food waste by *Varanus varius* resulted in larger lizards and more male-biased sex ratios at such subsidized sites, at least in the short-term (Jessop et al. 2012). In both of these cases, the studies did not last long enough to evaluate potential longer-term effects of the supplementation.

The Allen Cays Rock Iguana (*Cyclura cychlura inornata*) is endemic to two islands in The Bahamas (Leaf Cay and U Cay) (Fig. 1), and is listed as Endangered by the IUCN Red List of Threatened Species. These two cays are a popular destination for tourists, yachtspeople, and locals, because the iguanas associated with the main beaches have become acclimated to supplemental feeding. Whereas this feeding was only occasional back in the 1980s (Iverson et al. 2006), it is now done daily, and by large numbers of people. The main beach on Leaf Cay has particularly extensive contact with humans, with the daily arrival of 3–5 powerboats carrying as many as 150 people each day to feed the iguanas (Fig. 2; Iverson et al. 2006). This feeding activity has resulted in an unnatural concentration of iguanas on the feeding beach. For example, in 2008 when we sampled 289 iguanas on Leaf Cay (ca. 50% of the subadult and adult population on the cay), 68% of the captured iguanas were present on or immediately adjacent to the feeding beach which comprises only 2% of the total island area.

Smith, Geoffrey R., and John B. Iverson. 2016. Effects of tourism on body size, growth, condition, and demography in the Allen Cays Iguana, *Cyclura cychlura inornata*, on Leaf Cay, The Bahamas. Pp. 214–221 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

However, based on our mark-recapture censuses, iguanas on the opposite side of Leaf Cay (4 ha total area) apparently never visit the feeding beach. Hence, this situation allows a direct comparison to be made of fed versus unfed iguanas in the same genetically homogeneous population (Aplasca 2013). We investigated this system in order to examine the impact of tourist feeding on the body size, growth, condition, and demography of the iguanas. The long-term nature of our study allowed for in-depth analysis of these parameters relative to the development of the tourism industry (Iverson et al. 2004b). Specifically, we compared data from Leaf Cay over a 14-year period for subadult and adult iguanas on the feeding beach versus iguanas from other parts of the island away from the beach to determine the possible effects of supplemental feeding by humans.

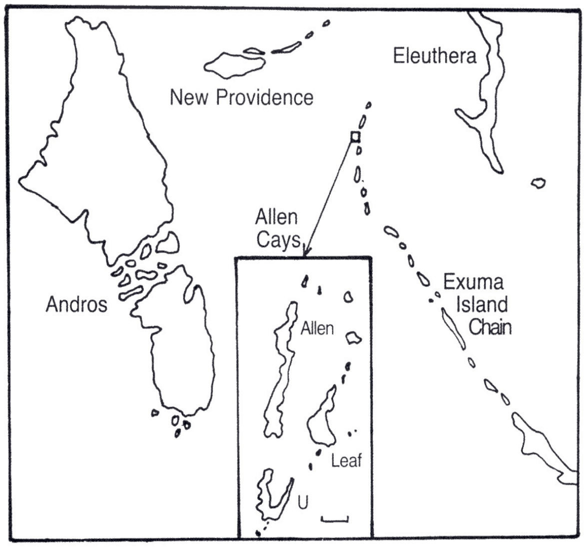

FIGURE 1. Map of study island for Allen Cays Iguanas in the Exumas Islands, The Bahamas. Scale in inset is 200 m.

FIGURE 2. Tourists feeding Allen Cays Iguanas on the main beach on Leaf Cay, The Bahamas. (Photographed by Hannah Lugg).

MATERIALS AND METHODS

This study began in 2000 and involved nearly annual sampling through 2013 (see full study site description and general methods in Iverson et al. 2004b). Sample dates included: 19–21 and 23 May 2000; 9–10 and 13–14 May, and 15 June–11 July 2001; 15–17 and 20 May, and 15 June–13 July 2002; 14–15, 17, and 19 May 2003; 11–13 and 16 May 2004; 13–16 May 2005; 11–13 and 16 May 2008; 17–19 May 2009; 12–14 May 2010; 16–17 and 19 May 2011; and 16–18 and 21 May 2013. Data within each year were considered a separate sample. Iguanas were captured by a team of up to 15 workers using dip nets, nooses, baited live traps, or by hand. Individuals were identified by unique toe clip combinations and PIT tags. Snout-vent length (SVL) and tail length (TL) were measured to the nearest mm, and body mass (BM) was measured to the nearest 5 g. Juveniles < 20 cm SVL were aged by their size cohort following Iverson et al. (2004a), and subsequently aged by the time interval until their recapture. Iguanas were released immediately after processing in the general area where they were captured.

For this study we only included data from iguanas that had been repeatedly (and only) captured on the feeding beach (i.e., fed, with high human interaction) or on other parts of the cay (non-fed, with minimal human interaction). Data from males and females were analyzed separately. Means are given ± 1 standard error (SE).

We calculated the mean SVL of the 10 largest males and the 10 largest females captured from each side of the island during each survey visit (if fewer than 10 individuals were captured for any category of iguanas in any year, we used all individuals captured). We used an ANCOVA on these mean SVLs with site as a factor and year as the covariate for each sex separately.

To test for differences in growth between fed and non-fed sites, we employed two approaches. The first test employed ANCOVA (SVL) or ANOVA (BM) of growth rate (GR; [final SVL or BM – initial SVL or BM]/interval between initial and final capture; cm yr^{-1} or g yr^{-1}) with site and sex as factors and mean SVL for the interval between first and last capture as covariate for SVL growth rate (mean SVL was not a significant co-variate for BM growth rate). The second approach used regression of log-transformed data from actual age versus SVL for all captures. We used ANCOVA to compare these regressions by site, separately by sex.

We used two approaches to compare body condition (i.e., body mass relative to body length) of iguanas from the feeding beach versus residents from the opposite side of the cay. First, residuals from the SVL–BM regression (log transformed) for the last capture for each individual (Jakob et al. 1996; Schulte-Hostedde et al. 2005) was analyzed for each sex separately (male equation: logBM = -1.37 + 2.97 logSVL, $n = 161$, $r^2 = 0.74$, $P < 0.0001$; female equation: logBM = -1.44 + 2.99 logSVL, $n = 152$, $r^2 = 0.79$, $P < 0.0001$). Second, we compared body condition using Fulton's K (Cone 1989; Stevenson and Woods 2006). Considerable controversy surrounds the use of the first of these (García-Berthou 2001; Green 2001; but see Schulte-Hostedde et al. 2005), but it does produce values with dimensions that are biologically interpretable; whereas Fulton's K is dimensionless (Cone 1989). Using both approaches (assuming corroborated results) would provide increased confidence in our interpretations.

We calculated sex ratios for each year's sample using only subadults and adults ≥ 20 cm SVL. We also submitted our capture/recapture matrix (only for subadult or adult iguanas ≥ 20 cm SVL) to Program MARK to obtain annualized survival estimates and capture probabilities using the Cormack-Jolly-Seber method (White and Burnham 1999), separately for males and females. In all cases, the model including annual variation in both survival estimates and capture probabilities was the best model or the second best model with AICc values very close to the best model. We thus present the results of the models including variation in both survival estimates and capture probabilities. We used paired t-tests to compare survival estimates and capture probabilities between the feeding beach and the rest of the cay for males and females separately.

RESULTS

***Body size*.**—The mean SVL of the largest males was greater for the feeding beach than the rest of Leaf Cay (Fig. 3A; Site effect: $F_{1,19} = 96.4$, $P < 0.0001$). For both sites, the mean SVL of the largest males captured each year declined over the course of the study (Fig. 3A; Year effect: $F_{1,19} = 6.4$, $P = 0.021$; Mean $\text{SVL}_{\text{feeding beach}} = 51.3 - 0.12[\text{Year}]$; Mean $\text{SVL}_{\text{Rest of Leaf Cay}} = 59.8 - 0.26[\text{Year}]$). The interaction term between site and year was not significant, indicating that the slopes were not significantly different.

The mean SVL of the largest females was significantly greater at the feeding beach than for the rest of Leaf Cay (Fig. 3B; Site effect: $F_{1,19} = 200.6$, $P < 0.0001$). As with males, mean SVL of the largest females captured each year decreased significantly over the course of our study (Fig. 3B; Year effect: $F_{1,19} = 5.1$, $P = 0.036$; Mean $\text{SVL}_{\text{feeding beach}} = 37.8 - 0.042[\text{Year}]$; Mean $\text{SVL}_{\text{Rest of Leaf Cay}} = 49.3 - 0.21[\text{Year}]$). The interaction term between site and year was not significant, indicating that the slopes were not significantly different.

***Growth rate*.**—Mean growth rate in SVL was greater for iguanas from the feeding beach than for iguanas from the rest of Leaf Cay (1.03 ± (SE) 0.05 cm yr^{-1} [range, -0.4–3.75 cm yr^{-1}; $n = 232$] versus 0.26 ± 0.05 cm yr^{-1} [range, -0.9–1.75 cm yr^{-1}; $n = 83$]; $F_{1,309} = 133.0$, $P < 0.0001$). Overall, males grew significantly faster than females (1.14 ± 0.07 cm yr^{-1} [$n = 162$] versus 0.49 ± 0.04 cm yr^{-1} [$n = 153$]; $F_{1,309} = 72.6$, $P < 0.0001$). There was a significant sex by site interaction: the effect of the feeding beach was greater in males than in females (Table 1; $F_{1,309} = 23.8$, $P < 0.0001$). For all iguanas, growth rate declined with mean individual SVL ($F_{1,309} = 30.7$, $P < 0.0001$). There was a significant sex by mean SVL interaction ($F_{1,309} = 14.9$, $P = 0.0001$), with females reaching asymptotic growth at smaller sizes than males.

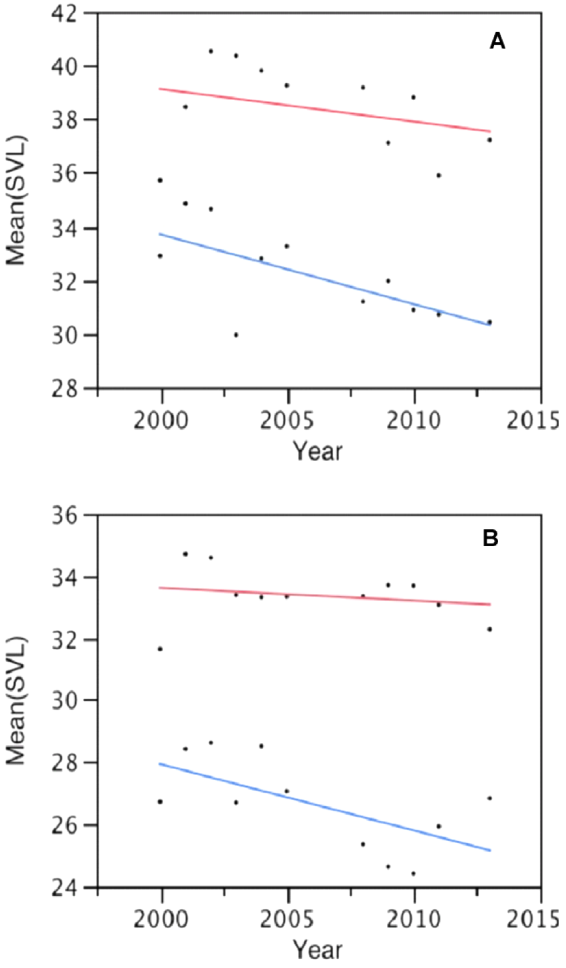

FIGURE 3. Mean snout-vent length (SVL in cm) of the largest (A) male and (B) female *Cyclura cychlura inornata* for yearly samples on Leaf Cay, The Bahamas, from 2000 to 2013 for iguanas from the feeding beach (red) and the rest of the cay (blue).

TABLE 1. Mean growth rates in snout-vent length (SVL) and body mass for male and female *Cyclura cychlura inornata* from the feeding beach and the rest of Leaf Cay, The Bahamas. Means are given ± 1 SE. Sample size (*n*) is given in parentheses.

	Feeding beach	Rest of cay
SVL		
Male	1.50 ± 0.07 cm y^{-1} (114)	0.29 ± 0.06 cm y^{-1} (48)
Female	0.57 ± 0.04 cm y^{-1} (118)	0.22 ± 0.07 cm y^{-1} (35)
BM		
Male	184.3 ± 14.4 g y^{-1} (104)	-10.6 ± 18.8 g y^{-1} (32)
Female	32.5 ± 4.8 g y^{-1} (104)	-7.5 ± 11.4 g y^{-1} (26)

Mean BM growth rate was much greater in iguanas from the feeding beach than iguanas from other areas, where BM change was negative (i.e., lost mass over time) on average (108.4 ± 7.3 g yr^{-1} [$n = 208$] versus -9.2 ± 13.9 g yr^{-1} [$n = 58$]; $F_{1,262} = 55.7$, $P < 0.0001$). Overall, males gained mass faster than females (138.5 ± 10.7 g yr^{-1} [$n = 136$] versus 24.5 ± 11.6 g yr^{-1} [$n = 130$]; $F_{1,262} = 22.3$, $P < 0.0001$). There was a significant sex by site interaction such that there was no significant difference in BM growth rate in females between the feeding beach site and the rest of the cay, whereas there was a larger difference for males from the two locations (Table 1; $F_{1,262} = 24.3$, $P < 0.0001$).

For males, logSVL was greater for iguanas from the feeding beach than the rest of the cay (Site effect: $F_{1,408} = 35.4$, $P < 0.0001$). LogSVL increased linearly with logAge ($F_{1,408} = 601.6$, $P < 0.0001$). There was a significant interaction between logAge and site such that males from the feeding beach showed a greater increase in body size as they aged compared to males from the rest of Leaf Cay (Fig. 4A; site x logAge effect: $F_{1,408} = 18.9$, $P < 0.0001$; $\text{logSVL}_{\text{feeding beach}} = 0.96 + 0.46[\text{logAge}]$, $n = 365$; $\text{logSVL}_{\text{rest of Leaf Cay}} = 1.06 + 0.32[\text{logAge}]$, $n = 47$).

Female iguanas from the feeding beach had a greater mean logSVL compared to females from the rest of the cay (Site effect: $F_{1,464} = 59.9$, $P < 0.0001$). LogSVL increased linearly with logAge ($F_{1,464} = 1108.1$, $P < 0.0001$). There was a significant interaction between logAge and site such that females from the feeding beach showed a greater increase in body size as they aged compared to females from the rest of Leaf Cay (Fig. 4B; site x logAge effect: $F_{1,464} = 9.2$, $P = 0.0026$; $\text{logSVL}_{\text{feeding beach}} = 1.06 + 0.32$ logAge [$n = 396$]; $\text{logSVL}_{\text{rest of Leaf Cay}} = 1.08 + 0.27$ logAge [$n = 72$]).

Body condition.—In general, iguanas from the feeding beach on Leaf Cay weighed more at a given body length than iguanas from the other parts of the cay. Male iguanas from the feeding beach had significantly greater logSVL–logBM residuals ($F_{1,159} = 15.8$, $P < 0.0001$) and Fulton's K values ($F_{1,159} = 16.2$, $P < 0.0001$) than males from the rest of Leaf Cay (Table 2). Females from the feeding beach had greater mean logSVL–logBM residuals than did females from the rest of Leaf Cay (Table 2; $F_{1,150} = 8.7$, $P = 0.0037$). Fulton's K for females was also significantly greater on the feeding beach than on the rest of Leaf Cay (Table 2; $F_{1,150} = 5.8$, $P = 0.017$).

Sex ratio.—The mean proportion of captures that were males for the feeding beach site was 0.46 ± 0.01 and for the rest of Leaf Cay was 0.50 ± 0.04. For the vast majority of our surveys, the capture sex ratio did not differ significantly from 1:1 for either the feeding beach or the rest of Leaf Cay (Table 3). The proportion of captures that were male did not differ between the feeding beach and the rest of the cay (paired *t*-test on proportion males in each survey: $t_{10} = 1.3$, $P = 0.24$).

The proportion of captures that were male on the feeding beach tended to increase but this trend was not significant ($n = 11$, $r^2 = 0.23$, $P = 0.13$). For the rest of Leaf Cay, there was no relationship between the survey year and the proportion of captured iguanas that were male ($n = 11$, $r^2 = 0.026$, $P = 0.63$).

Demography.—The mean number of captures per individual was 4.80 for males on the feeding beach, 5.61 for females on the feeding beach, 3.27 for males from the rest of the cay, and 2.92 for females from the rest of the cay. The proportion of total captures that came from the feeding beach did not change over the course of the study (mean = 0.83 ± 0.02; $n = 11$, $r^2 = 0.18$, $P = 0.20$).

Annual survival rates did not differ for males or females between the feeding beaches and the rest of the cay (Table 4; $t_9 = -0.28$, $P = 0.79$). Capture probabilities for both males and females were higher on the feeding beach than on the rest of the cay (Table 5; $t_9 = -1.7$, $P = 0.11$).

TABLE 2. Estimates of body condition (residuals of logBM on logSVL regression and Fulton's K) for resident male and female *Cyclura cychlura inornata* from the feeding beach and the rest of Leaf Cay, The Bahamas. Means are given ± 1 SE. Sample size (*n*) is given in parentheses.

	Males		Females	
	Feeding Beach (114)	Rest of Cay (48)	Feeding Beach (118)	Rest of Cay (35)
Residuals	0.023 ± 0.012	-0.056 ± 0.011	0.009 ± 0.006	-0.029 ± 0.012
Fulton's K	0.042 ± 0.001	0.034 ± 0.001	0.036 ± 0.001	0.033 ± 0.001

DISCUSSION

Human interactions, presumably as a direct result of supplemental feeding, have apparently had significant impacts on size, growth, and body condition (but not demography) of iguanas on Leaf Cay. From 2000 through 2013, there has been a decrease in maximum body size in both females and (especially) males. We hypothesize that this decline is in large part due to removal of large, and potentially more aggressive and dangerous males, by tour operators or poachers. A shift in the sex ratios from male-dominated to equality on Leaf Cay over a similar period of time also supports this hypothesis (see Smith and Iverson 2006). This is further corroborated by our

TABLE 3. Number of resident males and females of Allen Cays Iguanas captured on the feeding beach and the rest of the cay for each survey on Leaf Cay, The Bahamas. *indicates the observed sex ratio was significantly different from 1:1.

	Feeding beach		Rest of Leaf Cay	
Year	Males	Females	Males	Females
2000	43	62	4	7
2001	73	102*	42	25*
2002	83	113*	41	38
2003	62	63	11	10
2004	75	87	19	25
2005	56	72	14	13
2008	63	68	14	13
2009	50	60	3	8
2010	65	56	8	7
2011	44	55	9	3
2013	41	49	10	10

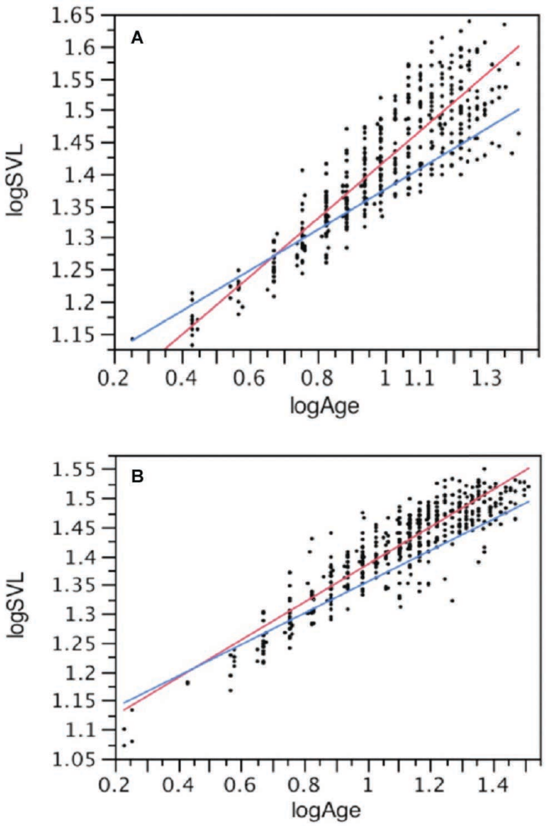

FIGURE 4. Growth rate of *Cyclura cychlura inornata* on Leaf Cay, The Bahamas, based on snout-vent lengths (SVL in cm) at known ages. Males (top) and females (bottom) at the feeding beach (red) and the rest of the cay (blue).

TABLE 4. Annual survival estimates for male and female *Cyclura cychlura inornata* from the feeding beach and the rest of Leaf Cay, The Bahamas. Estimates are given ± 1 SE; *indicates SE < 0.0001.

	Males		Females	
Interval	Feeding beach	Rest of cay	Feeding beach	Rest of cay
2001–2002	1.000*	1.000*	1.000*	1.000*
2002–2003	0.999 ± 0.032	1.000*	0.973 ± 0.026	0.872 ± 0.094
2003–2004	0.830 ± 0.050	0.838 ± 0.118	0.956 ± 0.033	1.000*
2004–2005	0.919 ± 0.052	0.925 ± 0.165	0.884 ± 0.043	0.683 ± 0.131
2005–2008	0.907 ± 0.024	1.000*	0.940 ± 0.018	1.000*
2008–2009	0.909 ± 0.047	1.000*	0.997 ± 0.027	0.726 ± 0.242
2009–2010	0.905 ± 0.054	0.406 ± 0.109	0.997 ± 0.057	0.682 ± 0.276
2010–2011	0.822 ± 0.071	1.000*	0.862 ± 0.087	1.000*

TABLE 5. Capture probabilities for resident male and female *Cyclura cychlura inornata* from the feeding beach and the rest of Leaf Cay, The Bahamas. Estimates are given ± 1 SE.

	Males		Females	
Year	Feeding beach	Rest of cay	Feeding beach	Rest of cay
2000	0.971 ± 0.028	0.750 ± 0.216	0.933 ± 0.032	0.750 ± 0.153
2001	0.862 ± 0.043	0.865 ± 0.056	0.879 ± 0.034	0.769 ± 0.083
2002	0.738 ± 0.054	0.250 ± 0.065	0.627 ± 0.051	0.295 ± 0.086
2003	0.851 ± 0.046	0.380 ± 0.093	0.862 ± 0.039	0.622 ± 0.103
2004	0.738 ± 0.060	0.353 ± 0.090	0.762 ± 0.050	0.524 ± 0.125
2005	0.857 ± 0.050	0.353 ± 0.090	0.761 ± 0.050	0.306 ± 0.104
2008	0.697 ± 0.061	0.101 ± 0.050	0.719 ± 0.053	0.333 ± 0.142
2009	0.843 ± 0.054	0.372 ± 0.130	0.624 ± 0.063	0.333 ± 0.148
2010	0.763 ± 0.073	0.496 ± 0.140	0.678 ± 0.076	0.200 ± 0.115

discovery of large iguanas on at least six cays (up to 60 km distant) that were initially marked as residents on Leaf Cay. The decline of body size in iguanas on other parts of the island may be the result of the larger individuals there relocating to the feeding beach. However, it may also be the consequence of the population approaching carrying capacity or a long-term trend in some other factor (e.g., climate, primary productivity). One potential test of these hypotheses would be to examine these patterns on the much less visited nearby U Cay.

The feeding of iguanas by tourists appears to increase growth in the iguanas on Leaf Cay and also to improve their body condition. The larger body size of females from the feeding beach also likely increased their reproductive output since clutch size and reproductive frequency are positively related to female body size (Iverson et al. 2004a). Considering only these traits, one might argue that supplemental feeding by tourists has had a positive impact on the iguanas on Leaf Cay. However, other studies on the effects of ecotourism on the *C. cychlura inornata* on Leaf Cay suggest negative impacts on the individual iguanas. For example, the items consumed by iguanas on the Leaf Cay beach contained such things as trash and non-native foods, as well as sand (Hines 2011). One consequence of the altered diet was the consumption of foods with higher water content, resulting in hardened feces (Hines 2011), especially if such foods are consumed with sand (see Fig. 1 in Knapp et al. 2013), that may cause cloacal prolapse and possibly death (Hines et al. 2010).

In addition, *C. cychlura inornata* from Leaf Cay are less wary of humans than other islands where they are not fed (Hines 2011), potentially making it easier to poach these iguanas. Furthermore, large iguanas on the feeding beach, especially males, may also become more aggressive as they become entrained to human presence (pers. obs.), thus making them a threat to ecotourists, and potentially subject to removal by tour operators or poachers. These iguanas on Leaf Cay and other visited cays also showed no differences in hormonal stress responses to those from islands not visited by tourists (Knapp et al. 2013). Romero and Wikelski (2002) also found no difference in stress hormone levels between Galápagos Marine Iguanas (*Amblyrhynchus cristatus*) from areas visited by humans and areas not visited by humans (but see French et al. 2010 who found increased stress hormone levels in *A. cristatus* in visited populations compared to non-visited populations). Iguanas on Leaf Cay and other visited cays had increased endoparasite loads and more loose feces compared to those on cays not regularly visited by humans (Knapp et al. 2013). Fed iguanas also had higher blood glucose levels (presumably due to an artificial diet high in sugar), higher uric acid levels in the blood (presumably due to unnatural consumption of animal protein), and higher serum cholesterol and triglycerides (males only) (Knapp et al. 2013). Supplemental feeding has been shown to increase testosterone in lizards (e.g., *Sceloporus graciosus*, Ruiz et al. 2010), which could have implications for aggression and other aspects of lizard behavior. Thus, while individuals may grow faster as a consequence of feeding by tourists, other aspects of their biology appear to be negatively affected, even though the consequences may be delayed for many years.

One alternative explanation for many of our results is that the habitat and environmental conditions may be better on the feeding beach than the rest of the cay, independent of the feeding that is taking place on the island. While this is a possibility, we unfortunately did not start to monitor the capture locations of individual iguanas until tourist feeding on Leaf Cay had already increased. Thus, we have no direct evidence to address this issue. However, indirect evidence suggests a predominant role of supplemental feeding in explaining our results. First, survival rates did not significantly differ between the beach and the rest of the cay. Second, data comparing the diets, endoparasites, blood chemistry, and behavior of Leaf Cay iguanas to conspecifics on islands without feeding suggest a clear impact of the feeding on individual *C. cychlura inornata* (Hines 2011; Knapp et al. 2013). Third, it is our impression that habitat quality on Leaf Cay is variable, but this variation in quality is not systematically distributed such that the “better” habitat is associated with the feeding beach.

At this time, it is not clear how the mixed effects of ecotourist visits to Leaf Cay on individual iguanas described above will translate into long-term demographic responses. Based on the lack of significant differences in capture sex ratios between the feeding beach and the rest of the cay, as well as the lack of consistent differences in survivorship between these two areas, there appear to be limited demographic effects of supplemental feeding for these iguanas, at least so far. Given the long-lived nature of *Cyclura*, even our 13-year study may not be sufficiently long to detect impacts on the demography of this population. Continued monitoring of these long-lived lizards will be necessary to fully understand such impacts. In addition, continued monitoring of other populations of *C. cychlura inornata* on cays without high levels of human visitation are needed to help discern the true impacts of ecotourism on the Allen Cay Iguanas of Leaf Cay.

We echo the recommendations of Knapp et al. (2013) concerning supplemental feeding by tourists on Leaf Cay and other cays that support *Cyclura*. Namely, we do not recommend stopping tourist visits nor do we recommend a cessation of supplemental feeding. Rather, we encourage the tour operators to modify their feeding procedures, perhaps by changing the food that they provide the tourists (see Knapp et al. 2013). We also agree with Knapp et al. (2013) in calling for some cays or populations of *Cyclura* to be protected from extensive, organized tourist visits and supplemental feeding. Such protected cays and populations would allow comparisons to be made between fed and unfed populations, as well as a hedge in the event that the long-term effects of tourism and supplemental feeding endanger *Cyclura* populations.

Acknowledgments.—This work would not have been possible without the continued support by Mrs. Sandra Buckner, The Bahamas National Trust, The Bahamas Department of Agriculture, Bahamas Environment, Science and Technology Commission, 7 C's Charters (Bruce Dunham, Sheila Young, and Ron White and crew members Ian Beaumont, Jason Diller, Aubrey Anne Groeber, Eric Namowicz, Matt Novak, Nikki Overly, Tim Pierce, Steve Schmidt, Will McLean, and Sarah Henry), and the Exuma Cays Land and Sea Park. The financial support of Dr. Ned and Sally Test, the Cope Museum Fund of Earlham College, Iverson's family, and Denison University (Greene Fund, Horizon Fund, Battelle Fund) is greatly appreciated. Finally, the field work could not have been accomplished without the assistance of 73 Earlham College students or alumni (Mark Abbey-Lambertz, Dan Albrecht-Mallinger, Madeline Bachner, Michelle Bahnick, Lenden Bowsman, Corey Bradley, Amanda Burgoon, Sam Campbell-Nelson, Ruthie Carter, Jessica Castleberry, Jordan Cerna, Laura Corichi, Evan Dalton, Eli Darnell, Amelie Davis, Emma Dixon, Abe Drayton, Max Driffel, Kori Engdahl, Michael Faile, Natsumi Fearnside, Brendan Gallagher, Dan Greene, Frances Hall, Kat Hardy, Galen Hartman, Kirsten Hines, Joel Hogle, Alli Hunnicutt, Rachael Jonas-Closs, Stephen Jones, Becca Jordan, Chrysalis Kendall, Kourtney King, Matt Lachuisa, Hannah Lehmann, Diana Lisensky, Laura Lisensky, Lucy Martin, Melissa Mayheux, Colin Meeks, Katie Mier, Sarah Muhrer, Kathy Muller, Mollye Nardi, Stesha Pasachnik, Erika Phelps, Lynne Pieper, Rebecca Prosser, Leslie Pulver, James Rose, Hassan Salem, Sarah Schaack, Kari Schneider, Chaundra Schofield, Jon Shepard, Delphine Sowiak, Joneen Spurlock, Hilary Standish, Danika Stoltz, Julie Tamanini, Alexandra Turnbull, Jen Valiulis, Andrew Vedder, Chris Warren, Emily Warrener, Ryan Welsh, Ann Wildman, Caryn Wixom, David Wolfson, Cameron Young, and David Young), 13 Denison University students (Briella Baer, Caitlin Bingaman, Dory Enright, Annie Harmon, Peter Iverson, Katie Huff, Skyler Jordan, Hannah Lugg, Michael McKinney, Lenny Mills, Larissa Rivera, Hallie Sickels, and Sara Wilkes), three post-graduate students (Andrea Aplasca, Dan Benboe, and Kristen Richardson), Earlham staff member Rick Flamm, and Earlham faculty member Amy Mulnix.

LITERATURE CITED

Aplasca, A.C. 2013. Population genetics of the endangered insular Allen Cays Rock Iguana, *Cyclura cychlura inornata*. M.Sc. Thesis, Fordham University, New York City, New York, USA. 52 p.

Arcese, P., and J.N.M. Smith. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. Journal of Animal Ecology 57:119–136.

Boyle, S.A., and F.B. Samson. 1985. Effects of nonconsumptive recreation on wildlife: a review. Wildlife Society Bulletin 13:110–116.

Cone, R.S. 1989. The need to reconsider the use of condition indices in fishery science. Transactions of the American Fisheries Society 118:510–514.

Dempster, T., P. Sanchez-Jerez, D. Fernandez-Joven, J. Bayle-Sempere, R. Nilsen, P.-A. Bjørn, and I. Uglem. 2011. Proxy measures of fitness suggest coastal fish farms can act as population sources and not ecological traps for wild gadoid fish. PLoS ONE 6(1):e15646. doi:10.1371/journal.pone.0015646

Fedriani, J.M., T.K. Fuller, and R.M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography 24:325–331.

French, S.S., D.F. DeNardo, T.J. Greives, C.R. Strand, and G.E. Demas. 2010. Human disturbance alters endocrine and immune response in the Galápagos Marine Iguana (*Amblyrhynchus cristatus*). Hormones and Behavior 58:792–799.

Garber, S.D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. Ecological Applications 54:1151–1162.

García-Berthou, E. 2001. On the misuse of residuals in ecology: testing regression residuals vs. analysis of covariance. Journal of Animal Ecology 70:708–711.

Green, A.J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? Ecology 82:1473–1483.

Harrison, R.L. 1997. A comparison of Grey Fox ecology between residential and undeveloped rural landscapes. Journal of Wildlife Management 61:112–122.

Hines, K.N. 2011. Effects of ecotourism on endangered Northern Bahamian Rock Iguanas (*Cyclura cychlura*). Herpetological Conservation and Biology 6:250–259.

Hines, K.N., C.R. Knapp, T.T. Zachariah, J.B. Iverson, and G.R. Smith. 2010. *Cyclura cychlura inornata*. Paraphimosos and prolapsed cloaca. Herpetological Review 41:77–78.

Iverson, J.B., S.J. Converse, G.R. Smith, and J.M. Valiulis. 2006. Long-term trends in the demography of the Allen Cays Rock Iguana (*Cyclura cychlura inornata*): human disturbance and density-dependent effects. Biological Conservation 132:300–310.

Iverson, J.B., K.N. Hines, and J.M. Valiulis. 2004a. The nesting ecology of the Allen Cays Rock Iguana, *Cyclura cychlura inornata* in The Bahamas. Herpetological Monographs 18:1–36.

Iverson, J.B., G.R. Smith, and L. Pieper. 2004b. Factors affecting long-term growth of the Allen Cays Rock Iguana in The Bahamas. Pp. 176–192 *In* Iguanas: Biology and Conservation. Alberts, A.C, R. Carter, W. Hayes, and E. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Jakob, E.M., S.D. Marshall, and G.W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

Jessop, T.S., P. Smissen, F. Scheelings, and T. Dempster. 2012. Demographic and phenotypic effects of human mediated trophic subsidy on a large Australian lizard (*Varanus varius*): meal ticket or last supper? PLoS One 7(4):e34069. doi:10.1371/journal.pone.0034069

Kangas, K., M. Luoto, A. Ihantola, E. Tomppo, and P. Siikamäki. 2010. Recreation-induced changes in boreal bird communities in protected areas. Ecological Applications 20:1775–1786.

Knapp, C.R. 2004. Ecotourism and its potential impact on iguana conservation in the Caribbean. Pp. 290–301 *In* Iguanas: Biology and Conservation. Alberts, A.C, R. Carter, W. Hayes, and E. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Knapp, C.R., K.N. Hines, T.T. Zachariah, C. Perez-Heydrich, J.B. Iverson, S.D. Buckner, S.C. Halach, C.R. Lattin, and L.M. Romero. 2013. Physiological effects of tourism and associated food provisioning in an endangered iguana. Conservation Physiology 1:1–12.

Orams, M.B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. Tourism Management 23:281–293.

Polis, G.A., W.B. Anderson, and R.D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Robb, G.N., R.A. McDonald, D.E. Chamberlain, and S. Bearhop. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6:476–484.

Rodríguez-Prieto, I., and E. Fernandez-Juricic. 2005. Effects of direct human disturbance on the endemic Iberian frog *Rana iberica* at individual and population levels. Biological Conservation 123:1–9.

Romero, L.M., and M. Wikelski. 2002. Exposure to tourism reduces stress-induced corticosterone levels in Galápagos Marine Iguanas. Biological Conservation 108:371–374.

Rose, M.D., and G.A. Polis. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79:998–1007.

Ruiz, M., S.S. French, G.E. Demas, and E.P. Martins. 2010. Food supplementation and testosterone interact to influence reproductive behavior and immune function in *Sceloporus graciosus*. Hormones and Behavior 57:134–139.

Schulte-Hostedde, A.I., B. Zinner, J.S. Millar, and G.J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology 86:155–163.

Smith, G.R., and J.B. Iverson. 2006. Changes in sex ratio over time in the endangered iguana *Cyclura cychlura inornata*. Canadian Journal of Zoology 84:1522–1527.

Stevenson, R.D., and W.A. Woods. 2006. Condition indices for conservation: new uses for evolving tools. Integrative and Comparative Biology 46:1169–1190.

Walpole, M.J. 2001. Feeding dragons in Komodo National Park: a tourism tool with conservation complications. Animal Conservation 4:67–73.

Wells, F.H., W.K. Lauenroth, and J.B. Bradford. 2012. Recreational trails as corridors for alien plants in the Rocky Mountains, USA. Western North American Naturalist 72:507–533.

White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation for populations of marked animals. Bird Study 46(Suppl.):120–138.

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Herpetological Conservation and Biology 11(Monograph 6):222–236.
Submitted: 19 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

THE BIOGEOGRAPHY OF THREATENED INSULAR IGUANAS AND OPPORTUNITIES FOR INVASIVE VERTEBRATE MANAGEMENT

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***Abstract.*—Iguanas are a particularly threatened group of reptiles, with 61% of species at risk of extinction. Primary threats to iguanas include habitat loss, direct and indirect impacts by invasive vertebrates, overexploitation, and human disturbance. As conspicuous, charismatic vertebrates, iguanas also represent excellent flagships for biodiversity conservation. To assist planning for invasive vertebrate management and thus benefit threatened iguana recovery, we identified all islands with known extant or extirpated populations of Critically Endangered and Endangered insular iguana taxa as recognized by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. For each island, we determined total area, sovereignty, the presence of invasive alien vertebrates, and human population. For the 23 taxa of threatened insular iguanas we identified 230 populations, of which iguanas were extant on 185 islands and extirpated from 45 islands. Twenty-one iguana taxa (91% of all threatened insular iguana taxa) occurred on at least one island with invasive vertebrates present; 16 taxa had 100% of their population(s) on islands with invasive vertebrates present. Rodents, cats, ungulates, and dogs were the most common invasive vertebrates. We discuss biosecurity, eradication, and control of invasive vertebrates to benefit iguana recovery: (1) on islands already free of invasive vertebrates; (2) on islands with high iguana endemicity; and (3) for species and subspecies with small total populations occurring across multiple small islands. Our analyses provide an important first step toward understanding how invasive vertebrate management can be planned effectively to benefit threatened insular iguanas.**

***Résumé.*—Les iguanes constituent un groupe de reptiles particulièrement menacé avec 61% des espèces en voie d'extinction. Les menaces principales qui pèsent sur les iguanes sont la disparition de leur habitat, les impacts directs et indirects lies à la présence d'espèces exotiques, l'exploitation excessive, et les dérangements liés aux activités anthropiques. La grande taille des iguanes leur confère un charisme qui constitue un atout important dans le contexte de la conservation de la biodiversité. Dans le cadre de la conservation des espèces menacées d'iguanes au travers de l'élaboration d'un plan destiné à limiter les impacts des vertébrés exotiques, nous avons identifié toutes les îles sur lesquelles il existent ou ont existé des populations d'iguanes appartenant à des taxons caractérisés comme En danger et En danger critique d'extinction suivant les critères adoptés par l'Union Internationale de la Conservation de la Nature (UICN) dans le cadre de la Liste rouge des espèces menacées. Pour chaque île les éléments suivant ont été détaillés: surface totale, souveraineté du territoire, présence d'espèces exotiques envahissantes, population humaine. Pour 23 taxons d'iguanes menacés de zones insulaires, nous avons identifié 230 populations dont la présence actuelle est encore confirmée sur 185 îles et l'absence constatée sur 45 autres îles autrefois peuplées. Au total 21 taxons d'iguanes (91% de tous les taxons d'iguanes des zones insulaires) se trouvent au moins sur une île recelant également la présence de vertébrés exotiques envahissants; 16 taxons ont 100% de leur population sur des îles sur lesquelles la présence d'espèces de vertébrés exotiques envahissants a été confirmée. Les rongeurs, les chats, les ongulés, et les chiens sont les espèces de vertébrés exotiques les plus communément rencontrées. La discussion porte sur les activités relatives à la biosécurité, l'éradication, et le contrôle des espèces de vertébrés exotiques qui pourraient contribuer à la conservation des iguanes: (1) sur les îles encore indemnes de la présence d'espèces de vertébrés exotiques; (2) sur les îles qui présentent un taux d'endémisme élevé en ce qui concerne les iguanes; (3) appartenant à des espèces et sous-espèces dont les populations sont faibles et distribuées sur de multiples petites îles. Notre analyse constitue une importante première étape dans la compréhension de la façon doivent être gérées les espèces de vertébrés exotiques dans le cadre d'actions destinées à la conservation des espèces d'iguanes des zones insulaires.**

***Resumen.*—Las iguanas son un grupo de reptiles particularmente amenazado con 61% de las especies en peligro de extinción. Dentro de las principales amenazas se encuentran la pérdida de hábitat, los impactos directos e indirectos por vertebrados exóticos invasores, la sobreexplotación, y el disturbio humano. Las iguanas son especies carismáticas y a la vez emblemáticas para la conservación de la biodiversidad. Con el fin de ayudar a la planificación del manejo de**

Tershy, Bernie, Kelly M. Newton, Dena R. Spatz, Kirsty J. Swinnerton, John B. Iverson, Robert N. Fisher, Peter Harlow, Nick D. Holmes, and Donald A. Croll. 2016. The biogeography of threatened insular iguanas and opportunities for invasive vertebrate management. Pp. 222–236 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

vertebrados exóticos invasores para el beneficio de la recuperación de iguanas amenazadas, se identificaron todas las islas con poblaciones de iguanas existentes o extirpadas En Peligro Crítico y En Peligro, documentadas en la Lista Roja de Especies Amenazadas de la Unión Internacional para la Conservación de la Naturaleza (UICN). Para cada isla, se determinó la superficie total, la soberanía, la presencia de vertebrados exóticos invasores, y la población humana. Para los 23 taxones de iguanas insulares amenazadas, se identificaron 230 poblaciones en las que iguanas estaban presentes en 185 islas y extirpadas de 45 islas. Veintiún taxones (91% del total amenazados) se localizaron en al menos una isla con presencia de vertebrados invasores y 16 taxones tenían 100% de su poblaciones en islas con presencia de vertebrados invasores. Los roedores, gatos, ungulados, y perros fueron los vertebrados invasores más comunes. Discutimos la bioseguridad, la erradicación, y el control de vertebrados invasores para beneficiar la recuperación de las iguanas: (1) en las islas sin presencia de vertebrados invasores; (2) en las islas con alta endemismo de iguanas; y (3) para las especies y subespecies con pequeñas poblaciones localizadas en múltiples islas pequeñas. Nuestros análisis proporcionan un importante primer paso hacia la comprensión de cómo el manejo de los vertebrados exóticos invasores se puede planificar mediante acciones efectivas de conservación para el beneficio de las iguanas insulares amenazadas.

Key Words.—endangered species; global conservation planning; invasive species; island conservation

INTRODUCTION

Of the 10,038 reptiles, lizards comprise the largest group (56%) with 5,634 species (Pincheira-Donoso et al. 2013). Species experts using the International Union for Conservation of Nature (IUCN) Red List of Threatened Species criteria have assessed 1,916 species of lizards worldwide and determined that 265 (14%) are Critically Endangered (CR) or Endangered (EN) (IUCN 2014. The IUCN Red List of Threatened Species. Available from http://www.iucnredlist.org [Accessed 15 July 2014]). The true iguanas (Iguanidae; Iguaninae), with 44 extant taxa (Iguana Taxonomy Working Group (ITWG) this volume), represent a unique group of lizards, many of which are highly endangered. Iguanas are generally large, primarily herbivorous lizards that occur in the tropics and subtropics. They are effective at colonizing islands, with 28 species endemic to islands (64% of all iguana species; ITWG this volume). Like many insular species (Ricketts et al. 2005), insular iguanas tend to be more threatened than continental taxa with 65% of assessed taxa Extinct (EX), CR or EN compared to 45% for continental taxa.

Primary threats to all iguanas are habitat loss, direct and indirect impacts by invasive vertebrates, overexploitation, and human disturbance (Gibbons 1984; Lemm and Alberts 2012). As with many insular species, iguanas on islands are particularly vulnerable to threats from invasive vertebrates. Cats, dogs, and mongoose present the most direct threat to iguanas and can directly reduce iguana populations through predation on eggs, young, and adults (Iverson 1978; García et al. 2001; Wilson et al. this volume). As early as 1984, cats were identified as the “single most important factor responsible for the decline in *Brachylophus*” in Fiji (Gibbons 1984). Herbivores such as goats, rabbits, cattle, and donkeys can directly impact iguanas (e.g. Fijian Iguanas) through competition for food resources, and indirectly through habitat destruction and subsidizing predator populations (Gibbons 1984). Rodents, pigs, and other omnivores can impact iguanas both directly and indirectly through many of the above mechanisms (Wiewandt and García 2000; Hayes et al. 2004, 2012; Towns et al. 2006).

Fortunately, these threats can often be mitigated (Alberts 2000; Knapp et al. 2011; Lemm and Alberts 2012). Successful eradications of invasive vertebrates from islands have resulted in demonstrable, positive conservation benefits to bird, mammal, reptile, invertebrate, and plant species (Croll et al. 2005; Towns 2008; Lavers et al. 2010; Keitt et al. 2011), including several iguana species (Day et al. 1998; Mitchell et al. 2002; Hayes et al. 2004; Gerber 2007; Jones et al. 2016). This action, in combination with other conservation solutions such as the establishment of legal protected areas, and translocation or re-introduction have been identified as conservation actions that can help improve the recovery potential for CR and EN iguanas (Knapp and Hudson 2004; Iverson et al. this volume). As conspicuous charismatic vertebrates, iguanas also represent excellent flagships for conservation of other island taxa (Knapp 2007).

A logical first step in developing recovery plans to offset the threats of invasive alien species (IAS) on insular iguanas includes understanding the distribution of iguana populations, the island-specific invasive vertebrate threats to each population, and the physical and socio-political characteristics of each island. This information is an important foundation that conservation planners can use to assess the feasibility of different options for invasive vertebrate management, and where that effort may yield the greatest benefit (e.g., Margules and Pressey 2000; Myers et al. 2000; Brooks et al. 2006). To aid with planning and prioritization of future IAS management scenarios, we conducted a systematic review (Spatz et al. 2014) and generated a database of: (1) all known current and historical breeding islands for the world’s Critically Endangered (CR) and Endangered (EN) insular endemic iguanas as recognized by the IUCN Red List of Threatened Species; (2) basic physical and socio-political attributes of each island, including geographic location, island size, human population size, and gross national income; and (3) the presence and extent of invasive alien vertebrates on each island. We then used these data to identify islands and discuss scenarios with the greatest potential for implementing programs that reduce the threat of invasive vertebrates and benefit iguana recovery, including: (1) islands free of invasive vertebrates; (2) islands with high iguana endemicity; and (3) species and subspecies with small total populations occurring across multiple small islands.

MATERIALS AND METHODS

Threatened insular iguana distributions.—We used the taxonomy and threat status designations of the IUCN Red List of Threatened Species (IUCN. 2014. *op. cit.*) to identify 23 primarily insular endemic iguana taxa recognized as Critically Endangered (CR) or Endangered (EN; Table 1). This database included one EN species, Black-chested Spiny-tailed Iguana (*Ctenosaura melanosterna*), that breeds on both the continental mainland and islands of Honduras. Where available, the independent IUCN assessment of a subspecies was used instead of the nominate species assessment. Eight iguana taxa with insular populations listed by the ITWG (this volume) that have not been assessed by the IUCN, 11 insular endemic iguana taxa assessed as Vulnerable (VU) or Near Threatened (NT) by the IUCN, three insular and continental taxa assessed as Least Concern (LC) and the Common Green Iguana (*Iguana iguana*) were not included in the analyses (Appendix 1). However, given the overall vulnerability of insular iguanas to invasive vertebrates, the principles and concepts described here likely also apply to many if not all of these other species.

To identify each insular breeding population for each taxon, we conducted a systematic review of 90+ separate sources of literature and online databases (as detailed in Spatz et al. 2014), and consulted with experts (see Acknowledgments). A single taxon on a single island was considered one population, even if multiple discrete sub-populations or colonies existed on the island. Identified breeding populations were grouped into two status categories: extant (includes potentially extant), or extirpated (Spatz et al. 2014). We excluded from the analysis cases where the data did not allow us to determine iguana breeding status or island location, and where small numbers of iguanas were present but known not to be breeding. Detailed distribution data were further developed, including IAS present, in consultation with experts knowledgeable about these islands and included members of the IUCN SSC Iguana Specialist Group. We have presented some of these data in the Threatened Island Biodiversity Database developed by Island Conservation, University of California Santa Cruz Coastal Conservation Action Lab, BirdLife International, and IUCN Invasive Species Specialist Group (hereafter TIB Partners). Due to the sensitivity of locations of select taxa, this public website does not display all distribution data used in the analyses (TIB Partners. 2014. Threatened Island Biodiversity Database. Available from http://tib.islandconservation.org [Accessed version 2014.1]). Each island with an extant or extirpated threatened iguana taxon (hereafter: threatened insular iguana island or TII island) was linked to the Global Island Database (UNEP-WCMC 2013) via a unique identification number and spatial reference for each island.

Threatened insular iguana island attributes.—We determined sovereignty of TII islands using United Nations Member States designations (United Nations. 2014. Member States of the United Nations. Available from http://www.un.org/en/members/ [Accessed 15 July 2014]). We determined area of TII islands using the Global Island Database (UNEP-WCMC 2013). We used the most recent human population census data (through 2012) from government reports and public websites to estimate the number of human inhabitants on each TII island (see Spatz et al. 2014 for details). Due to differences in the precision of these estimates, we pooled data into ordinal categories of 0, 1–100, 101–1,000, > 1,000, or unknown. For each island, we determined 2013 gross national income (GNI) per capita (in USD; categorized into high, upper middle, lower middle, and low income levels (The World Bank. 2013. GNI per capita, Atlas method (current US$). Available from http://data.worldbank.org [Accessed 26 August 2014]).

Invasive species threats.—We focused on invasive alien mammals (cats, dogs, mongoose, rodents, and ungulates) as well as invasive populations of the Common Green Iguana, *Iguana iguana* (hereafter: invasive vertebrates; TIB Partners. 2014. *op. cit.*), whose presence could have direct or indirect impacts on threatened insular iguanas. We did not include the invasive North American Raccoon (*Procyon lotor*) as distributional data for this species is vague; however, we recognize this species can represent a severe threat (see Hayes et al. 2004). For each TII island, we conducted a systematic review of 90+ sources of literature and online databases to determine if the island has (or had) invasive vertebrates present (see details in Spatz et al. 2014). We also identified successful eradications of invasive vertebrates where appropriate. TII islands were considered invasive-free if invasive vertebrates were known to be completely absent. TII islands were considered to have invasive vertebrates if one or more invasive vertebrate taxa were confirmed or suspected to be present. For islands where invasive vertebrate status was unknown, we took a precautionary approach and considered at least one invasive vertebrate present. Means throughout the paper are presented with ± 1 standard deviation (SD).

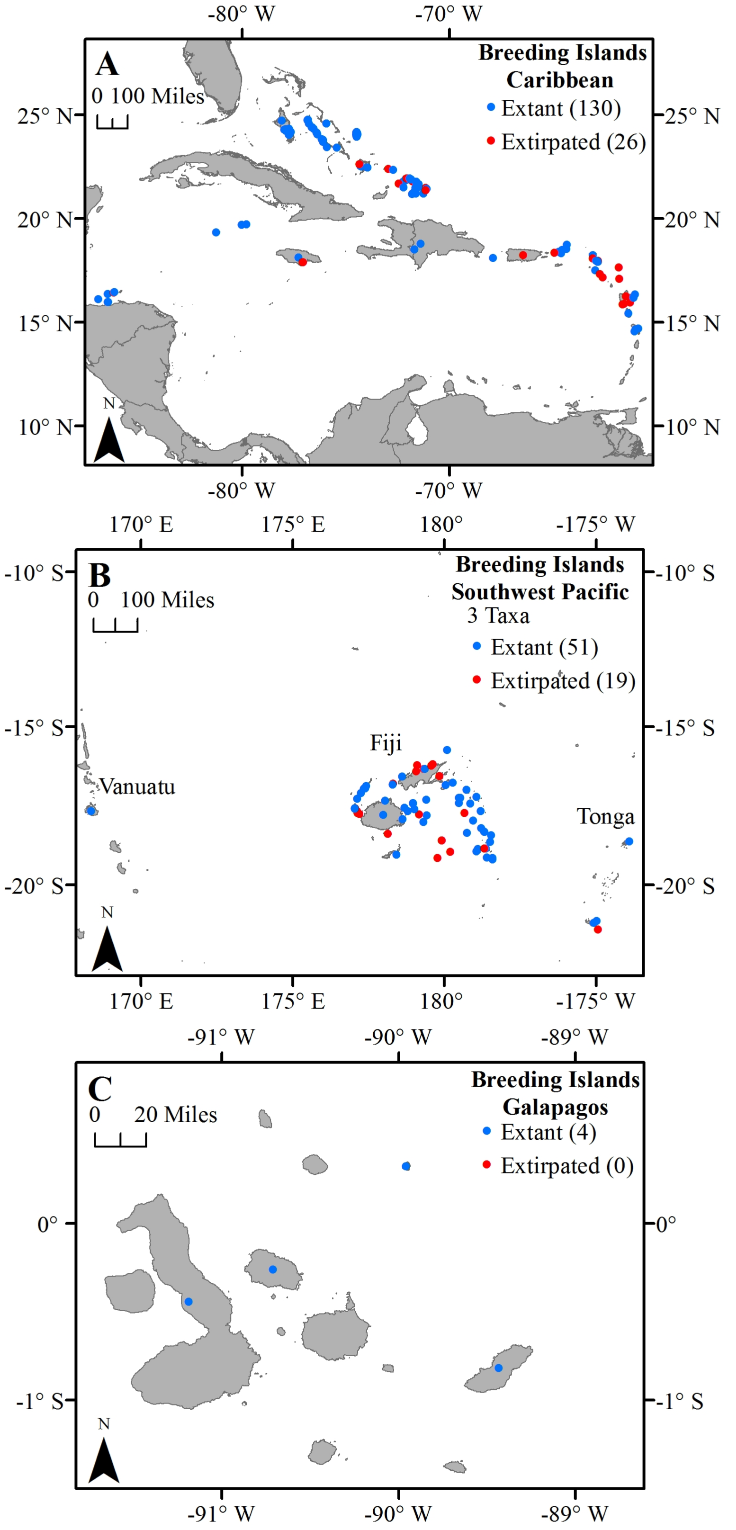

FIGURE 1. Islands where threatened insular iguana taxa are extant (blue dots) or have been extirpated (red dots) within: (A) the Caribbean region; (B) southwest Pacific; and (C) Galápagos Islands. Seven islands were excluded: three lacked sufficient breeding information and four because iguana populations were recorded as not breeding.

RESULTS

Threatened insular iguana distributions.—For the 23 threatened insular iguana taxa (12 CR, 11 EN), we identified extant or extirpated populations on 230 islands. In addition, seven islands were excluded from this total: three lacked sufficient breeding information and four because iguana populations were recorded as not breeding (Fig. 1). Of these 230 islands, iguanas were extant on 185 islands and extirpated from 45 islands, with extirpated iguana populations representing nine taxa (Table 1).

Extant breeding populations of iguana taxa identified in this review were located on a mean = 8.04 ± (SD) 9.62 islands (range, 1–38 islands; median = 2; Fig. 2). Twelve taxa (52%) currently breed on 1–2 islands (17 islands total), seven of which (30% of all threatened insular iguanas) were extant on a single island. In contrast, eight taxa (35%) currently breed on 10 or more islands. Island characteristics between threatened insular iguanas with extant (*n* = 185) and extirpated (*n* = 45) populations differed, with extant islands less likely to be inhabited by humans (45.4% versus 80%), and smaller in size (median of 1.8 versus 23.6 km^2).

Threatened insular iguana island attributes.—All TII islands were located either in the Caribbean region (including Greater Antilles, Lesser Antilles, The Bahamas, Turks and Caicos Islands, and Honduras; 68%), eastern Pacific (Galápagos Islands; 2%), or in the southwest Pacific (30%). The total area of these islands ranged from 0.00024–76,480 km^2 (Fig. 3), although most threatened insular iguana taxa on larger islands are known to have very localized and restricted distributions (e.g., Hispaniola, Jamaica). These islands occurred within 16 sovereign countries that were designated as high income (*n* = 144 islands; 63%), upper middle income (*n* = 78; 34%), lower middle income (*n* = 7; 3%), including Hispaniola (for Ricord’s Iguana), which includes Haiti (low income) and the Dominican Republic (upper middle income). Almost half of all TII islands are uninhabited (47.8%) and 51% of populated islands (20.4% of all islands) are home to fewer than 1,000 people (Fig. 4).

Invasive vertebrate species threats.—Of the 230 islands with threatened insular iguana populations, 173 (75%) had one or more invasive vertebrate taxa present, 28 islands (12%) had an unknown status for all vertebrate groups (thus assessed conservatively in this analysis as having invasive vertebrates present), and 29 islands were invasive vertebrate-free. Twenty-one iguana taxa (91% of all threatened insular iguana taxa) occurred on at least one island with invasive vertebrates present; 16 taxa (70% of all insular threatened iguana taxa) had 100% of their population(s) on islands with invasive vertebrates present or unknown (Table 1). Of the 173 islands with threatened insular iguanas and invasive vertebrates, rodents were the most prevalent (88%), followed by cats (62%), ungulates (60%), and dogs (51%). Invasive Common Green Iguanas were present on 17 islands (7.4%), eight of which had extirpated populations of threatened insular iguana taxa (*Iguana delicatissima*, *Cyclura carinata carinata*, and *Cyclura pinguis*).

Seventy-five populations of 12 taxa occur on islands with invasive vertebrates but without human habitation (Fig. 5). Seven threatened insular iguana taxa occurred on 29 islands entirely free of invasive vertebrates; four of these islands underwent invasive vertebrate eradication programs to achieve this outcome, and one additional island may also be free of invasive vertebrates pending confirmation of eradication (Table 2). Invasive vertebrate eradication programs have been successful on another five TII islands (Table 2; Island Conservation, University of California Santa Cruz Coastal Conservation Action Laboratory, IUCN SSC Invasive Species Specialist Group, University of Auckland, and Landcare Research New Zealand. 2014. Database of Island Invasive Species Eradications. Available from http://diise.islandconservation.org [Accessed 19 September 2014]), however these programs did not remove all invasive species present (e.g., cats removed but not rodents). These islands therefore were considered as having invasives present in our analyses. Of the twelve threatened insular iguana taxa currently breeding on a single island or on only two islands (17 islands in total; Table 1), 10 taxa currently breed only on islands with invasive vertebrates present, six of which breed on uninhabited islands or islands with < 1,000 inhabitants (Table 1).

DISCUSSION

Insular populations of threatened iguanas represent challenges and opportunities for implementing conservation strategies. One such opportunity is invasive vertebrate management (both eradication and control), which is a well-established strategy to recover threatened species (Lavers et al. 2010), but its application has been limited for iguanas. Invasive vertebrate eradication from islands is an effective and proven tool, and is being increasingly applied to aid in the recovery of a variety of threatened insular taxa (Jones et al. 2016); worldwide about 20 successful eradications are achieved each year (Keitt et al. 2011). Our analysis identifies clear opportunities to benefit threatened insular iguana populations, and inform strategies for identifying and prioritizing islands for invasive vertebrate management. We recognize that the list of islands for each threatened insular iguana species in our analysis may represent a minimum for those that breed on small cays, and this number may increase as new information is gathered and

TABLE 1. Known breeding populations of Critically Endangered and Endangered iguanas (Iguanidae: Iguaninae) on islands used in this analysis. [a]The number of islands extant is likely an underestimate for *Cyclura cychlura cychlura* or other species (Charles Knapp, pers. comm.). [b]Population estimates obtained from IUCN Red List assessments (ITWG this volume). [c]Includes both insular and continental populations.

Taxa	**Common Name**	**IUCN Status**	**# Islands Extant (median island size km^2)**	**# Islands Extirpated (median island size km^2)**	**Total Iguana Population Estimate[b]**	**% Total Islands with Invasive Species (% w/ unknown invasive species)**	**% Total Islands with > 1000 People**
Amblyrhynchus cristatus mertensi	San Cristóbal Marine Iguana	EN	2 (574.3)	0 (na)	Unknown	100%	50%
Amblyrhynchus cristatus nanus	Genovesa Marine Iguana	EN	1 (16.6)	0 (na)	1,500	0	0
Brachylophus bulabula	Central Fijian Banded Iguana	EN	12 (66.8)	2 (24.5)	6,000 +	100% (7%)	50%
Brachylophus fasciatus	Lau Banded Iguana	EN	27 (13.0)	12 (18.5)	Unknown	100% (3%)	15%
Brachylophus vitiensis	Fijian Crested Iguana	CR	12 (6.2)	5 (1.6)	Unknown	100%	12%
Conolophus marthae	Pink Land Iguana	CR	1 (4,738.6)	0 (na)	192	100%	100%
Ctenosaura bakeri	Utila Spiny-tailed Iguana	CR	1 (48.7)	0 (na)	< 5,000	100%	100%
Ctenosaura melanosterna	Black-chested Spiny-tailed Iguana	EN	2 (1.7)	0 (na)	< 5,000[c]	100%	0
Ctenosaura oedirhina	Roatán Spiny-tailed Iguana	EN	2 (61.0)	1 (0.9)	< 2,500	67%	33%
Cyclura carinata	Turks and Caicos Rock Iguana	CR	38 (0.7)	10 (24.2)	~ 30,000	69%	8%
Cyclura collei	Jamaican Rock Iguana	CR	1 (11,025.9)	2 (3.4)	Unknown	100%	33%
Cyclura cychlura cychlura	Andros Rock Iguana	EN	16[a] (5.6)	0 (na)	2,000–5,000	100% (50%)	18%
Cyclura cychlura figginsi	Exuma Rock Iguana	CR	14 (0.2)	0 (na)	< 1,300	100% (7%)	0
Cyclura cychlura inornata	Allen Cays Rock Iguana	EN	9 (0.04)	0 (na)	< 500	33% (11%)	0
Cyclura lewisi	Grand Cayman Blue Rock Iguana	EN	1 (209.8)	0 (na)	443	100%	100%
Cyclura nubila caymanensis	Sister Islands Rock Iguana	CR	2 (39.3)	0 (na)	1,200–1,500	100%	50%
Cyclura pinguis	Anegada Rock Iguana	CR	6 (1.5)	2 (4,592.5)	< 200	100%	25%
Cyclura ricordii	Ricord's Rock Iguana	CR	2 (38,249.0)	0 (na)	2,000–4,000	100%	50%
Cyclura rileyi cristata	Sandy Cay Rock Iguana	CR	1 (0.2)	0 (na)	150–200	0	0
Cyclura rileyi nuchalis	Acklins Rock Iguana	EN	4 (0.9)	1 (24.7)	> 13,000	60% (20%)	0
Cyclura rileyi rileyi	San Salvador Rock Iguana	CR	14 (0.1)	0 (na)	< 1,000	79% (57%)	0
Cyclura stejnegeri	Mona Rhinoceros Iguana	EN	1 (57.0)	0 (na)	1,500–2,000	100%	0
Iguana delicatissima	Lesser Antillean Iguana	EN	16 (1.1)	10 (129.9)	< 20,000	100% (31%)	58%

shared. These islands represent potential opportunities for threatened insular iguana conservation, particularly for those that: (1) are free of invasive vertebrates; (2) have high iguana endemicity; and (3) have species and subspecies with small total populations occurring across multiple small islands.

Prior studies have found that successful conservation actions, including invasive vertebrate management, are directly related to the absence of human populations, compliance with management policies, and country income levels (James et al. 1999; Andrade and Rhodes 2012; Glen et al. 2013). Our analysis demonstrates that islands harboring threatened insular iguanas are concentrated in high and middle income countries (97% of TII islands), which suggests some capacity and resources to restore, protect, and manage these islands. For successful invasive species eradication, island size is also an important limiting factor and can directly influence cost and feasibility (Howald et al. 2007; Keitt et al. 2011). For example, Santiago Island (Ecuador), home to the Galápagos Marine Iguana (*Amblyrhynchus cristatus mertensi*), is uninhabited by humans but is nearly four times larger (585 km²) than the largest successful rodent eradication known to date (Macquarie Island, Australia, 128 km^2) and thus may not be a feasible candidate for rodent eradication currently. Human population size also plays a dominant role in the feasibility and success of conservation actions on islands (e.g., James et al. 1999; Ratcliffe et al. 2009; Oppel et al. 2011), and to date most successful invasive vertebrate eradications have occurred on islands with few or no human inhabitants (Glen et al. 2013). Feasibility of any invasive vertebrate eradication will ultimately require expert consideration of the social, logistical, and ecological circumstances for individual islands (Dawson et al. 2015).

Maintaining the invasive vertebrate-free status of islands lacking such species represents a high priority and cost-effective strategy to ensure the persistence of threatened insular iguana populations. We identified 29 islands inhabited by threatened insular iguanas, representing seven taxa that are on islands currently free of invasive vertebrates. The invasive vertebrate-free status of four of these 29 islands was achieved through eradication programs. Maintaining the faunal integrity of islands is an especially high priority for Genovesa Marine Iguanas (*Amblyrhynchus cristatus nanus*; Galápagos) and Sandy Cay Rock Iguanas (*Cyclura rileyi cristata*; The Bahamas), both occurring naturally on only a single island (see Hayes et al. this volume). Understanding potential reinvasion risks and implementing effective biosecurity plans are critical steps to protecting these and other islands inhabited by threatened species of iguanas. For several species, initiatives are already in place including strict biosecurity protocols within the Galápagos (Parque

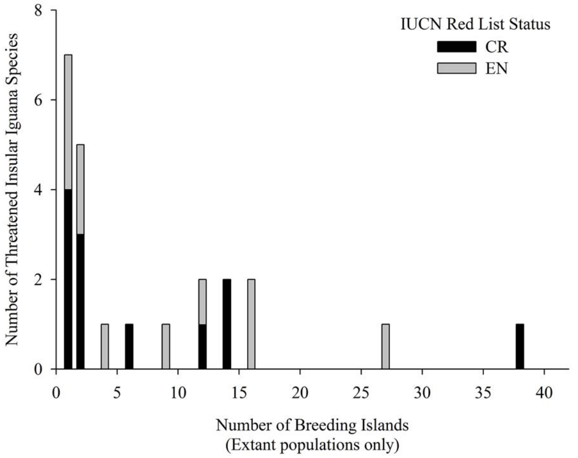

FIGURE 2. Relative endemism of extant threatened insular iguana taxa assessed by IUCN Red List of Threatened Species Criteria (CR: Critically Endangered; EN: Endangered).

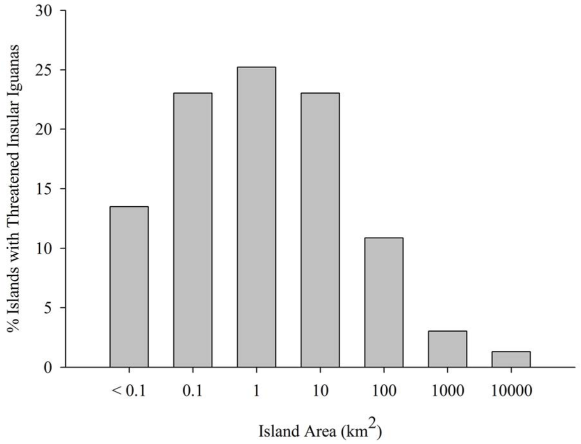

FIGURE 3. Percentage of islands with threatened insular iguana taxa by island size.

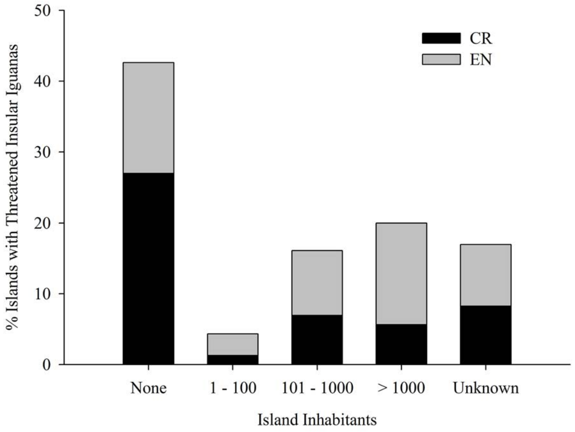

FIGURE 4. Percentage of threatened insular iguana populations relative to island human inhabitants.

Nacional Galápagos 2008), a voluntary code of conduct in St. Lucia (Government of St. Lucia 2012), and ongoing projects to maintain Sandy Cay (British Virgin Islands) as rat-free, and to prevent the spread of invasive Common Green Iguanas within the Cayman Islands (Thomas 2014).

Iguanas inhabiting only one or two islands represent a clear conservation priority given these are the only locations where these species occur. However, many of these islands are large in size and densely populated by humans, making whole-island invasive vertebrate management infeasible. Iguanas may also not occupy the entire island, making island-wide action unnecessary. In total, eight threatened insular iguana taxa were identified as breeding on islands where ≥ 50% of the islands that they occupied had > 1,000 people (Table 1). On such islands, sub-island conservation action is clearly a more appropriate strategy. The Jamaican Iguana (*Cyclura collei*) and the Grand Cayman Blue Rock Iguana (*Cyclura lewisi*) have both been recovered from near-extinction through an intensive recovery program that included localized invasive cat, dog, and mongoose (Jamaica only) control combined with an effective head-starting program (Wilson 2011; Wilson and Stephenson 2014; Wilson et al. this volume). Predator exclusion fences to protect endemic reptiles are also being considered for several larger inhabited islands in the Caribbean (St. Croix USVI, St. Lucia). Similarly, invasive vertebrate management for seabirds on large, inhabited islands offers analogous insights for iguanas, including invasive vertebrate impacts at a local scale (Jones et al. 2011), predator-proof exclusion fences (e.g., Burns et al. 2012, Young et al. 2013), and assisted colonization (Carlile et al. 2012).

One island that should be assessed further for whole-island invasive vertebrate management (i.e., eradication) to protect single island endemics is Mona Island in Puerto Rico. Mona Island is large (~ 57 km^2) and uninhabited. Invasive species eradication would remove the primary threat to the island endemic Mona Rhinoceros Iguana, *Cyclura stejnegeri* (1500–2000 individuals), plus a host of other unique biota including seven additional endemic reptiles. Invasive cats prey on hatchlings and juveniles, while pigs and goats degrade habitat, destroy nests, and compete with iguanas for food (Weiwandt and García 2000; García et al. 2001; García and Gerber this volume). While invasive vertebrate eradication on Mona Island is within the scope defined by other successful eradications, site-specific considerations need to be addressed to better understand the feasibility of a potential eradication program. Improving our understanding of rodents as potential threats to Mona Rhinoceros Iguanas, and indeed all threatened insular iguana species, is important given that effects have been observed elsewhere (Hayes et al. 2012). A management plan needs to be developed for

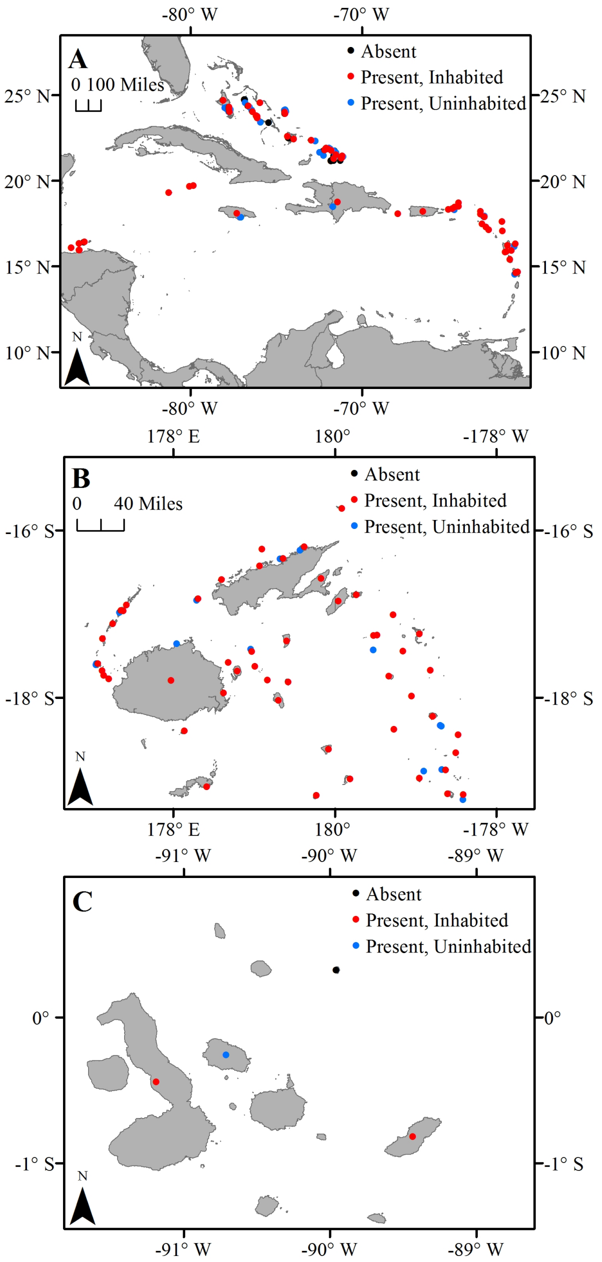

FIGURE 5. Islands where threatened insular iguana taxa occur in the absence of invasive vertebrates (black dots), with invasive vertebrates on uninhabited islands (blue dots) or with invasive vertebrates on inhabited islands (red dots) within: (A) the Caribbean region; (B) Fiji (islands in Tonga and Vanuatu were excluded from the scale of this map, but all have invasive species and are inhabited); and (C) the Galápagos Islands. Islands with invasive vertebrates include both present and unknown status.

the island that considers how to remove invasive animals given its complex limestone topography, reflects the views of some of the stakeholders (i.e., hunters), and considers trapping methods that avoid impacting native non-target species (e.g., see Jolley et al. 2012). Given that the iguana is only known from Mona Island, invasive vertebrate eradication will be critical to ensuring the long-term persistence of the species.

Similarly, the eradication of cats from Yaqaga Island (Fiji) is urgently required if the population of Fijian Crested Iguanas (*Brachylophus vitiensis*) inhabiting the island are to survive. In December 2009, a dead half-eaten Fijian Crested Iguana (likely killed by a cat) was found on the 9.7 km^2 human-inhabited and mongoose-free island of Yaqaga in Northwestern Fiji. To our knowledge, this discovery represents the first record of this species in living memory on the island. Extensive field surveys in January 2010, February 2011, and July 2014 located just four iguanas in an isolated pocket of forest in the center of the island. Researchers assumed its extreme rarity was due to the large number of feral cats on the island. In 2011 and 2012, 16 feral cats were trapped and removed from this island but complete eradication has not been completed.

Our analysis suggests that 75 populations of 12 taxa (56%) of threatened insular iguanas occur on islands with invasive vertebrates, yet lack human habitation and are less than 10 km^2 in size. These represent high value, low-cost conservation opportunities because of their small size, reduced social issues, and relatively simple eradication strategies. Taxa such as Exuma Rock Iguanas (*Cyclura cychlura figginsi*) in The Bahamas fit these criteria, representing a total population of < 2,000 individuals inhabiting 13 small cays (< 5 km^2 with < 10 people) with confirmed or unknown invasives. The 2012 eradication of invasive mice (*Mus musculus*) from Allen Cay in The Bahamas (6 ha), which was conducted to protect Allen Cays Rock Iguana habitat (*C. cychlura inornata*) and Audubon's Shearwaters (*Puffinus lherminieri*), provides insights how to undertake such programs. This project took approximately one year to plan and conduct, and required ~ $56,000 USD (2013) in operational costs to implement the eradication.

To increase cost-efficiency, reduce reinvasion risk, and improve iguana population resilience, eradication programs for iguanas inhabiting multiple small islands in close proximity can be defined and managed as 'eradication units' (Savidge et al. 2012). Additionally, to maximize the long-term efficacy of eradication programs as they pertain to rodents, eradication units are best assessed by incorporating both anthropogenic (level of visitor traffic and thus risk of introducing rodents) and natural reinvasion risk (proximity to adjacent islands from which rodents can swim; Harris et al. 2012). Assessing an optimal set of islands can also be strengthened by using a return on investment approach (Donlan et al. 2014).

With the exception of islands where threatened insular iguanas have been extirpated, this analysis does not attempt to identify islands from which invasive vertebrates could be eradicated in order to support translocated populations of iguanas. While 13 known translocations of Rock Iguanas (*Cyclura* sp.) have been implemented successfully (Iverson et al. this volume), translocation or reintroduction to invasive vertebrate-free islands is an under-utilized tool for iguana conservation (Knapp and Hudson 2004). In particular, small cays provide a unique opportunity for a programmatic

TABLE 2. Threatened insular iguana islands which have undergone a successful invasive mammal eradication. Eradication data from the Database of Island Invasive Species Eradications (*op. cit.*) and references therein.

Taxa	Island Name	Invasive Species Eradicated	Invasive Species Remaining
Amblyrhynchus cristatus mertensi	Santiago, Ecuador	*Sus scrofa* (2000), *Equus asinus* (2004), *Capra hircus* (2006)	*Mus musculus*, *Rattus rattus*
Brachylophus vitiensis	Monuriki, Fiji	*Capra hircus* (2011), *Rattus exulans* (to be confirmed)	None (pending rodent eradication confirmation)
	Yadua Taba, Fiji	*Capra hircus* (2003)	*Rattus exulans*
Conolophus marthae	Isabela, Ecuador	*Equus asinus* (restricted range 2005), *Capra hircus* (in progress)	*Mus musculus, Rattus rattus, Canis familiaris, Felis catus, Sus scrofa, Bos taurus*
Cyclura carinata	Bay Cay, Turks and Caicos	*Rattus rattus* (2002)	None
	Long Cay, Turks and Caicos	*Felis catus* (1999)	*Rattus rattus*, *Mus musculus*
Cyclura cychlura inornata	Allen Cay, The Bahamas	*Mus musculus* (2012)	None
Cyclura pinguis	Guana, British Virgin Islands	*Capra hircus* (1991)	*Rattus* sp., *Felis catus, Canis familiaris*, *Ovis aries*
Cyclura rileyi cristata	White (Sandy) Cay, The Bahamas	*Rattus rattus* (1998), *Mus musculus* (1998), *Procyon lotor* (1997 incursion prevented)	None
Cyclura rileyi rileyi	Low Cay, The Bahamas	*Rattus rattus* (2000)	None

approach toward iguana conservation. Invasive vertebrate eradications followed by iguana translocations, nest site enhancement, captive-breeding and release, and head-starting should be considered when developing management plans for iguana species. Of the 46 islands from which iguanas have been extirpated, 33% are less than 5 km^2 in size with < 1,000 inhabitants, and all but one have invasive species (10 of which represent two iguana taxa in Fiji). If habitat is appropriate, these islands may represent potential relocation islands.

Prioritizing invasive vertebrate management to benefit iguanas should also take into account the timing, scope, and severity of the threats posed by these invasive vertebrates on individual islands, and highlight islands where eradication has the potential to mitigate the most severe threats (e.g., see Brooke et al. 2007 for an example with eradication to benefit threatened birds). For example, the interaction of the Pacific Rat (*Rattus exulans*) within the ecological context of iguanas in the Pacific is poorly understood. The Pacific Rat arrived in Fiji with the first Austronesian humans about 3,300 years ago (Roberts 1991), and is probably found on every island in Fiji. In the absence of other invasive vertebrates, *R. exulans* appears to have little or no effect on Pacific iguana populations, thus lowering the priority of eradications of this species to protect iguanas. For example, the Fijian island with the densest population of iguanas also has a large population of *R. exulans* (Morrison et al. 2013). Opportunities that offer the highest conservation return on investment would also require an assessment of the timing, scope, and severity of other threats, such as impacts from climate change, habitat loss, over-exploitation, and human disturbance. That is, on which islands can eradication of invasive vertebrates remove the primary threat to iguanas? However, even for cases where other threats are projected as more severe than invasive vertebrates, such as habitat loss or projected sea level rise, invasive vertebrate management may still be an achievable option and may offer a pathway to improve population resilience (e.g., Heller and Zavaleta 2009).

Our analyses provide an important first step in identifying the potential of invasive vertebrate management as a conservation action for threatened insular iguanas. A logical second step would be to assess potential islands suitable for iguana translocation or relocation from which invasive vertebrates could be eradicated. In addition, overlaying information relevant to land ownership, protected area status, cost, and complexity of action would help further prioritize sites for threatened insular iguana conservation through actions such as protecting invasive-free islands, within-island invasive vertebrate management such as fencing and control, and invasive vertebrate eradication.

Acknowledgments.—We thank the expert contributors to the Threatened Island Biodiversity Database regarding threatened iguanas and invasive species on their breeding islands, including Aarijana Barun, Robert Powell, Charles Knapp, Clive Petrovic, David Wiedenfeld, Glenn Gerber, Graham Reynolds, Jim Goetz, Kevin de Queiroz, Michel Breuil, Numi Mitchell, Natalia Collier, Oliver Lorvelec, Paul Watler, Renata Platenberg, Ron Carter, Stesha Pasachnik, Sandra Buckner, Tommy Hall, Victor Hugo Reynoso, William Hayes, and Wes Jolley. We recognize invaluable support from local field teams, including but not limited to Pita Biciloa, Jone Niukula, Dick Watling, Nunia Thomas, Clare Morrison, Alivereti Naikatini, Tamara Osborne, Tuverea Tuamoto, Sialesi Rasalato, Marika Tuiwawa. We thank the dedicated team at UC Santa Cruz who helped collect and compile data for this project: Erin McCreless, Lauren Smith, Leslie Hart, Kai Kopecky, Sarah Sampson, Kevin Davidson, Alec Scott, Tess Braun, Tanya Gemperle, Erin Pickett, Michael Dittman, John Harley, and Dean Roblee. In addition, research supporting this study was funded by the Packard Foundation, the National Fish and Wildlife Foundation, the Friends of Long Marine Lab, the Dr. Earl H. Myers and Ethel M. Myers Oceanographic and Marine Biology Trust, International Iguana Foundation, Taronga Conservation Science Initiative, CEPF – Conservation International, Mohamed bin Zayed Species Conservation Fund, BirdLife International, University of the South Pacific, and NatureFiji-MareqetiViti.

LITERATURE CITED

Alberts, A. 2000. West Indian Iguanas: Status Survey and Conservation Action Plan. IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Andrade, G.S., and J.R. Rhodes. 2012. Protected areas and local communities: an inevitable partnership toward successful conservation strategies? Ecology and Society 17:14.

Brooks, T.M., R.A. Mittermeier, G.A.B. da Fonseca, J. Gerlach, M. Hoffmann, J.F. Lamoreux, C.G. Mittermeier, J.D. Pilgrim, and A.S.L. Rodrigues. 2006. Global biodiversity conservation priorities. Science 313:58–61.

Brooke, M. de L., G.M. Hilton, and T.L.F. Martins. 2007. Prioritizing the world's islands for vertebrate-eradication programmes. Animal Conservation 10:380–390.

Burns, B., J. Innes, and T. Day. 2012. The use and potential of pest-proof fencing for ecosystem restoration and fauna conservation in New Zealand. Pp. 65–90 *In* Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes? Somers, M.J., and M.W. Hayward (Eds.). Springer, New York City, New York, USA.

Carlile, N., D. Priddel, and J. Madeiros. 2012. Establishment of a new, secure colony of endangered Bermuda Petrel *Pterodroma cahow* by translocation of near-fledged nestlings. Bird Conservation International 22:46–58.

Croll, D.A., J.L. Maron, J.A. Estes, E.M. Danner, and G.V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. Science 307:1959–1961.

Dawson, J., S. Oppel, R.J. Cuthbert, N. Holmes, J.P. Bird, S.H.M. Butchart, D.R. Spatz, and B. Tershy. 2015. Prioritizing islands for the eradication of invasive vertebrates in the United Kingdom Overseas Territories. Conservation Biology 29:143–153.

Day, M., W. Hayes, K. Varnham, T. Ross, E. Carey, T. Ferguson, J. Monestine, S. Smith, C. Armstrong, A. Buckle, A. Alberts, and S. Buckner. 1998. Rat eradication to protect the White Cay Iguana. Aliens 8:22–24.

Donlan, C.J., G.M. Luque, and C. Wilcox. 2014. Maximizing return on investment for island restoration and species conservation. Conservation Letters. doi:10 .1111/conl.12126

García, M., and G.P. Gerber. 2016. Conservation and management of *Cyclura* iguanas in Puerto Rico. Pp. 61–67 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

García, M., C. Diez, and A. Alvarez. 2001. The impact of feral cats on Mona Island wildlife and recommendations for their control. Caribbean Journal of Science 37:107–108.

Gerber, G. 2007. Turks and Caicos Iguana translocation program, Bahama Archipelago. Re-introduction News 26:53–55.

Gibbons, J. 1984. Iguanas of the South Pacific. Oryx 18:82–91.

Glen, A.S., R. Atkinson, K.J. Campbell, E. Hagen, N.D. Holmes, B.S. Keitt, J.P. Parkes, A. Saunders, J. Sawyer, and H. Torres. 2013. Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? Biological Invasions 15:2589–2603.

Government of St. Lucia. 2012. Voluntary Code of Conduct for Saint Lucia's Tourism Sector with Species Reference to Invasive Alien Species (IAS). Mitigating the Threats of Invasive Alien Species in the Insular Caribbean Workshop, Project No. GFL / 2328–2713–4A86, GF–1030–09–03.

Harris, D.B., S.D. Gregory, L.S. Bull, and F. Courchamp. 2012. Island prioritization for invasive rodent eradications with an emphasis on reinvasion risk. Biological Invasions 14:1251–1263.

Hayes, W., R. Carter, S. Cyril, Jr., and B. Thornton. 2004. Conservation of an endangered Bahamian Rock Iguana, I. Population assessments, habitat restoration, and behavioral ecology. Pp. 232–257 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Hayes, W.K., R.A. Escobar, S.K. Fry, E.M. Fortune, J.A. Wasilewski, D.M. Tuttle, K.S. West, J.B. Iverson, S.D. Buckner, and R.L. Carter. 2016. Conservation of the endangered Sandy Cay Rock Iguanas (*Cyclura rileyi cristata*): invasive species control, population response, pirates, poaching, and translocation. Pp. 106–120 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Hayes, W.K., J.B. Iverson, C.R. Knapp, and R.L. Carter. 2012. Do invasive rodents impact endangered insular iguana populations? Biodiversity and Conservation 21:1893–1899.

Heller, N.E., and E.S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation 142:14–32.

Howald, G., C.J. Donlan, J.P. Galván, J.C Russell, J. Parkes, A. Samaniego, Y. Wang, D. Veitch, P. Genovesi, M. Pascal, et al. 2007. Invasive rodent eradication on islands. Conservation Biology 21:1258–1268.

Iverson, J.B. 1978. The impact of feral cats and dogs on populations of the West Indian Rock Iguana, *Cyclura carinata*. Biological Conservation 14:63–73.

Iverson, J.B., G.R. Smith, S.A. Paschnick, K.N. Hines, and L. Pieper. 2016. Growth, coloration, and demography of an introduced population of the Acklins Rock Iguana (*Cyclura rileyi nuchalis*) in the Exuma Islands, The Bahamas. Pp. 139–153 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Iguana Taxonomy Working Group (ITWG). 2016. A checklist of the iguanas of the world (Iguanidae; Iguaninae). Pp. 4–46 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

James, A.N., M.J.B. Green, and J.R. Paine. 1999. A global review of protected area budgets and staff. WCMC Biodiversity Series No. 10. WCMC–World Conservation Press, Cambridge, United Kingdom.

Jolley, W.J., K.J. Campbell, N.D. Holmes, D.K. Garcelon, C.C. Hanson, D. Will, B.S. Keitt, G. Smith, and A.E. Little. 2012. Reducing the impacts of leg hold trapping on critically endangered foxes by modified traps and conditioned trap aversion on San Nicolas Island, California, USA. Conservation Evidence 9:43–49.

Jones, H.P., N.D. Holmes, S.H.M. Butchart, B.R. Tershy, P.J. Kappes, I. Corkery, A. Aguirre-Muñoz, D.P. Armstrong, E. Bonnaud, A.A. Burbidge, and et al. 2016. Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113:4033–4038.

Jones, H.P., D.R. Towns, T. Bodey, C. Miskelley, J.C. Ellis, M. Rauzon, S. Kress, and M. Mckown. 2011. Recovery and restoration on seabird islands. Pp. 317–357 *In* Seabird Islands: Ecology, Invasion, and Restoration. Mulder, C.P.H, D.R. Towns, W.B. Anderson, and P.J. Bellingham (Eds.). Oxford University Press, Oxford, United Kingdom.

Keitt, B., K. Campbell, A. Saunders, M. Clout, Y. Wang, R. Heinz, K. Newton, and B. Tershy. 2011. The Global Islands Invasive Vertebrate Eradication Database: a tool to improve and facilitate restoration of island ecosystems. Pp. 74–77 *In* Island Invasives: Eradication and Management. Veitch D.R., M.N. Clout, and D. Towns (Eds.). IUCN, Gland, Switzerland.

Knapp, C.R. 2007. Potential for iguana-based ecotourism on Andros: a first assessment. Bahamas Naturalist and Journal of Science 2:10–17.

Knapp, C.R., and R.D. Hudson. 2004. Translocation strategies as a conservation tool for West Indian Iguanas: evaluations and recommendations. Pp. 199–209 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Knapp, C.R., J.B. Iverson, S. Buckner, and S. Cant. 2011. Conservation of amphibians and reptiles in The Bahamas. Pp. 53–87 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Lavers, J.L., C. Wilcox, and C.J. Donlan. 2010. Bird demographic responses to predator removal programs. Biological Invasions 12:3839–3859.

Lemm, J.M., and A.C. Alberts. 2012. *Cyclura*: Natural History, Husbandry, and Conservation of West Indian Rock Iguanas. Academic Press, San Diego, California, USA.

Margules, C.R., and R.L. Pressey. 2000. Systematic conservation planning. Nature 405:243–53.

Mitchell, N., R. Haeffner, V. Veer, M. Fulford-Gardner, W. Clerveaux, C.R. Veitch, and G. Mitchell. 2002. Cat eradication and the restoration of endangered iguanas (*Cyclura carinata*) on Long Cay, Caicos Bank, Turks and Caicos Islands, British West Indies. Pp. 206–212 *In* Turning the Tide: The Eradication of Invasive Species (Proceedings of the International Conference on Eradication of Island Invasives). Veitch, C.R., and M.N. Clout (Eds.). IUCN, Gland, Switzerland.

Morrison, S.F., P. Biciloa, P.S. Harlow, and J.S. Keogh. 2013. Spatial ecology of the critically endangered Fijian Crested Iguana, *Brachylophus vitiensis*, in an extremely dense population: implications for conservation. PLoS ONE 8(9):e73127. doi:10.1371/journal.pone.0073127

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Oppel, S., B.M. Beaven, M. Bolton, J. Vickery, and T.W. Bodey. 2011. Eradication of invasive mammals on islands inhabited by humans and domestic animals. Conservation Biology 25:232–240.

Parque Nacional Galápagos. 2008. Protocolos para Viajes de Campo y Campamentos en las Islas Galápagos. Parque Nacional Galápagos, Ecuador. Available from http://www.galapagospark.org/documentos/protocolos_campo_galapagos.pdf

Pincheira-Donoso, D., A.M. Bauer, S. Meiri, and P. Uetz. 2013. Global taxonomic diversity of living reptiles. PloS One 8:e59741. doi:10.1371/journal.pone.0059741

Ratcliffe, N., M. Bell, T. Pelembe, D. Boyle, R. Benjamin, R. White, B. Godley, J. Stevenson, and S. Sanders. 2009. The eradication of feral cats from Ascension Island and its subsequent recolonization by seabirds. Oryx 44:20.

Ricketts, T.H., E. Dinerstein, T. Boucher, T.M. Brooks, S.H.M. Butchart, M. Hoffmann, J.F. Lamoreux, J. Morrison, M. Parr, J.D. Pilgrim, et al. 2005. Pinpointing and preventing imminent extinctions. Proceedings of the National Academy of Sciences 102:18497–18501.

Roberts, M. 1991. Origin, dispersal routes, and geographic distribution of *Rattus exulans*, with special reference to New Zealand. Pacific Science 45:123–30.

Savidge, J.A., M.W. Hopken, G.W. Witmer, S.M. Jojola, J.J. Pierce, P.W. Burke, and A.J. Piaggio. 2012. Genetic evaluation of an attempted *Rattus rattus* eradication on Congo Cay, U.S. Virgin Islands, identifies importance of eradication units. Biological Invasions 14:2343–2354.

Spatz, D.R., K.M. Newton, R. Heinz, B. Tershy, N.D. Holmes, S.H.M. Butchart, and D.A. Croll. 2014. The biogeography of globally threatened seabirds and island conservation opportunities. Conservation Biology 28:1282–1290.

Thomas, S. 2014. Island restoration in the Caribbean UK Overseas Territories. Invasive alien species management strategies workshop: learning and sharing best practices between northern islands protected areas. CAR-SPAW-RAC St Martin, French West Indies, 12–14 May 2014. Available from http://www.car-spaw-rac.org/IMG/pdf/RSPB_St_Martin_IAS_workshop.pdf

Towns, D.R. 2008. Eradications as reverse invasions: lessons from Pacific Rat (*Rattus exulans*) removals on New Zealand islands. Biological Invasions 11:1719–1733.

Towns, D.R., I.A.E. Atkinson, and C.H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8:863–891.

UNEP-WCMC. 2013. Global Islands Database. United Nation's Environmental Program. Cambridge, United Kingdom.

Wiewandt, T., and M. García. 2000. Mona Island Iguana: *Cyclura cornuta stejnegeri*. Pp. 27–31 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Wilson, B.S. 2011. Conservation of Jamaican amphibians and reptiles. Pp. 273–310 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds). Brill Academic Publishers, Leiden, The Netherlands.

Wilson, B., and K. Stephenson. 2014. The Jamaican Iguana Pilot Final Report for the 'Mitigating the Threat of Invasive Alien Species in the Insular Caribbean Project'. Jamaican Iguana Recovery Group, University of the West Indies, Mona Campus, Jamaica.

Wilson, B., T.D. Grant, R. Van Veen, R. Hudson, D. Fleuchaus, O. Robinson, and K. Stephenson. 2016. The Jamaican Iguana (*Cyclura collei*): a report on 25 years of conservation effort. Pp. 237–254 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

Young, L.C., E.A. VanderWerf, M.T. Lohr, C.J. Miller, A.J. Titmus, D. Peters, and L. Wilson. 2013. Multi-species predator eradication within a predator-proof fence at Ka'ena Point, Hawai'i. Biological Invasions 15:2627–2638.

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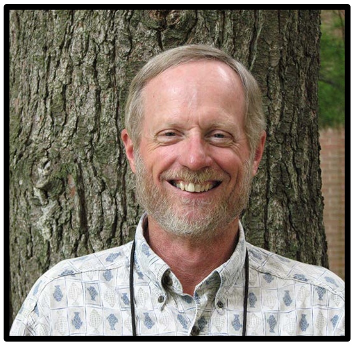
KIRSTY J. SWINNERTON holds a Ph.D. in Biodiversity Conservation from the University of Kent, United Kingdom, and is the Caribbean Program Manager for Island Conservation, a US-based non-profit organization dedicated to saving island species from extinction through the removal of invasive vertebrates. Her particular interest is in the recovery of critically endangered species through invasive species management, captive-breeding, reintroduction, translocation, and management of wild populations, and she has been involved in several iconic projects such as for the Mauritius Pink Pigeon and the Hawaiian Po'ouli. Her focus on island endemic taxa has taken her through the Mascarenes, Hawaii, Fiji, and to Puerto Rico where she now lives full-time. She is a fellow of the Zoological Society of London and has been a member of the IUCN SSC Iguana Specialist Group since 2011, actively developing a Caribbean regional program to support the recovery of West Indian Rock Iguanas and the Lesser Antillean Iguana through invasive vertebrate removal. (Photographed by Sandra Buckner).



JOHN B. IVERSON holds a Ph.D. in Biology from the University of Florida and is Biology Research Professor at Earlham College in Richmond, Indiana. Because of his interests in the natural history, ecology, and evolution of iguanas and turtles, he is currently on the steering committees (and founding member) of the IUCN SSC Iguana Specialist Group, and the Tortoise and Freshwater Turtle Specialist Group. He has been involved with the Turtle Survival Alliance since its inception in 2001 (currently a board member), and serves on the board of the Turtle Conservation Fund. He has been active in several herpetological societies, serving as editor and president of the Herpetologists' League. He has maintained long-term field research sites since 1980 for Rock Iguanas in the Exumas in The Bahamas, and since 1981 for turtles at the Crescent Lake National Wildlife Refuge in western Nebraska. His hobby is restoring a 76-acre woodlot/cornfield (now in a conservation easement) to a mature hardwood forest. (Photographed by Deanna McCartney).

ROBERT N. FISHER has worked with a wide range of reptile and amphibian species for over two decades, both across the Pacific Basin on islands and widely across southern California. His main areas of research have been in reptile and amphibian conservation biology, biogeography, natural history, systematics, and evolution, and today his research interests focus on critically endangered species, biodiversity, and the impacts of various drivers of population change (i.e., invasive species and landscape level fires). Captive breeding and reintroduction experiments are being conducted too with the goal of increasing species resiliency. He has a Ph.D. in Biology from University of California, Davis, and is a Supervisory Research Ecologist with the U.S. Geological Survey in San Diego, California. (Photographed by Kim Lovich).

PETER S. HARLOW has worked professionally with a wide range of reptile and amphibian species for over three decades, mostly in Australia but also in southern Africa, Indonesia, USA, Canada, and Fiji. His main areas of research have been in reptile and amphibian ecology, physiology, and conservation biology, and today his research interests include invasive species ecology, *in situ* conservation, restoration ecology, captive breeding, and reintroduction. He has a Ph.D. in Biology from Macquarie University, Australia, and is the manager of the herpetofauna division at Taronga Zoo in Sydney, Australia. (Photographed by Joe Wasilewski).

NICK HOLMES works for Island Conservation, a non-government organization with a mission of preventing extinctions by removing invasive species from islands. Prior to Island Conservation, Nick managed the Kauai Endangered Seabird Recovery Project at the Pacific Cooperative Studies Unit at the University of Hawaii, working to improve the recovery outcome for Newell's Shearwaters, Hawaiian Petrels and Band-rumped Storm-petrels. Nick earned his Ph.D. from the University of Tasmania, Australia. (Photograph supplied by Nick Holmes).

DONALD A. CROLL holds a Ph.D. from Scripps Institution of Oceanography, University of California and is a Professor in the Ecology and Evolutionary Biology Department at the University of California, Santa Cruz. His primary research encompasses two main themes: the impacts of introduced species on island ecosystems and the ecology of large, highly mobile, marine predators. The first theme seeks to use predator introductions and removals as whole ecosystem experiments to understand the direct (e.g., trophic cascades) and indirect (e.g., nutrient subsidies) impact of introduced species on island ecosystems. The second theme seeks to understand the interaction between: (1) the physiological, behavioral, and life history characteristics of marine vertebrate predators; (2) physical and biological oceanographic processes; and (3) the distribution, abundance, and behavior of prey species as a means to develop and implement feasible conservation measures. Concurrent with his academic career, Dr. Croll co-founded Island Conservation with Dr. Bernie Tershy, a nonprofit conservation organization dedicated to preventing extinctions and protecting natural ecological and evolutionary processes. (Photograph supplied by Don Croll).

APPENDIX 1. Insular iguana taxa listed by the ITWG (this volume) not included in the analyses. *Includes islands outside native range.

Taxa	Common Name	IUCN Status	Breeding Location
Amblyrhynchus cristatus albemarlensis	Isabela Marine Iguana	VU	Insular
Amblyrhynchus cristatus cristatus	Fernandina Marine Iguana	VU	Insular
Amblyrhynchus cristatus hassi	Santa Cruz Marine Iguana	VU	Insular
Amblyrhynchus cristatus sielmanni	Pinta Marine Iguana	VU	Insular
Amblyrhynchus cristatus venustissimus	Española Marine Iguana	VU	Insular
Conolophus pallidus	Barrington Land Iguana	VU	Insular
Conolophus subcristatus	Galápagos Land Iguana	VU	Insular
Ctenosaura conspicuosa	San Esteban Spiny-tailed Iguana	Not Assessed	Insular
Ctenosaura nolascensis	Nolasco Spiny-tailed Iguana	VU	Insular
Ctenosaura pectinata	Guerreran Spiny-tailed Iguana	Not Assessed	Insular and Continental
Ctenosaura similis	Common Spiny-tailed Iguana	LC	Insular and Continental
Ctenosaura similis similis	Common Spiny-tailed Iguana	Not Assessed	Insular
Ctenosaura similis multipunctata	Providence Spiny-tailed Iguana	Not Assessed	Insular
Cyclura cornuta	Hispaniolan Rhinoceros Iguana	VU	Insular
Cyclura nubila nubila	Cuban Rock Iguana	VU	Insular
Dipsosaurus dorsalis	Common Desert Iguana	LC	Insular and Continental
Dipsosaurus catalinensis	Santa Catalina Desert Iguana	Not Assessed	Insular
Iguana iguana	Common Green Iguana	Not Assessed	Insular* and Continental
Sauromalus ater	Common Chuckwalla	LC	Insular and Continental
Sauromalus hispidus	Spiny Chuckwalla	NT	Insular
Sauromalus klauberi	Catalina Chuckwalla	Not Assessed	Insular
Sauromalus slevini	Slevin's Chuckwalla	Not Assessed	Insular
Sauromalus varius	Piebald Chuckwalla	Not Assessed	Insular

Herpetological Conservation and Biology 11(Monograph 6):237–254.
Submitted: 30 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

THE JAMAICAN IGUANA (*CYCLURA COLLEI*): A REPORT ON 25 YEARS OF CONSERVATION EFFORT

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Abstract.—**Considered extinct by the late 1940s, the Jamaican Iguana (*Cyclura collei*) was re-discovered in 1970, and its existence confirmed in 1990. The 1970 re-discovery went largely unnoticed; in contrast, the 1990 "re-discovery" spawned a successful international recovery effort. Here we summarize results of that 25-year *C. collei* recovery effort. We also assess the project's achievement of overall objectives, and offer some recommendations for ensuring the long-term persistence of the species.**

Early interventions such as protecting nesting sites and collecting hatchlings for captive breeding and headstarting likely averted the extinction of *C. collei*. Subsequent conservation activities have focused on recovering the remnant population, securing protection for the Hellshire Hills, and establishing a re-introduced population on the Goat Islands. Biological interventions such as nest site protection and headstarting have been demonstrably effective. Most notably, the number of nesting iguanas in the core population increased at least six-fold between 1991 and 2013.

Unfortunately, habitat protection initiatives have met with far less success. Illegal tree cutting for charcoal production continues to degrade Hellshire's remnant forest, and enforcement of existing laws remains an elusive goal. Despite the declaration of the Portland Bight Protected Area (PBPA) in 1999, inclusive of the iguana's entire Hellshire Hills refuge and both Goat Islands, the area continues to be considered for large-scale development projects promoted by the government. A recent (2013) plan to develop a large Chinese-funded port facility and industrial complex in the PBPA is the most worrisome proposal yet presented, and would cripple the iguana's prospects for future survival.

Key Words.—headstarting; invasive species control; reintroduction; re-discovered species; reptile conservation; Rock Iguana

INTRODUCTION

Historical perspective: 1600s to 1990.—The endemic Jamaican Iguana (*Cyclura collei*) was once common along the coastal plains and hills of southern Jamaica (Sloane 1725), but was considered rare or absent on the mainland near the end of the 1800s, presumably due to a combination of over-harvesting, habitat loss, and the introduction of non-native mammalian predators such as the Indian Mongoose (*Herpestes javanicus* [=*auropunctatus*]) (Woodley 1971, 1980; Vogel et al. 1996; Grant et al. 2013). The iguana was considered extinct after a small population disappeared around 1948 from Great Goat Island, located off the western side of the Hellshire peninsula, apparently due to the introduction of the mongoose from the mainland in the mid-1920s (Lewis 1944; Woodley 1980). The species was re-discovered in the Hellshire Hills in 1970 (Woodley 1971, 1980), and again in 1990 (Alberts 1993; Vogel et al. 1996). Those re-discoveries represented the only records of the species on the mainland of Jamaica in the 20th century.

The 1970 re-discovery, the retrieval of a specimen killed by a pig hunter's dog, went largely unnoticed by local and international scientific and conservation communities. This was perhaps unsurprising. Locally, Jamaica lacked a resident herpetologist, and lizards are generally loathed by most Jamaicans. Furthermore, no environmental lobby or environmental NGO existed at the time in Jamaica, and efforts to combat the "global extinction crisis" were in their infancy. For example, the world's large zoos were only beginning to develop support for *in situ* conservation efforts, and the field of conservation biology did not yet exist. So, in the early 1970s, financial and institutional support from a global conservation community – so critical in most species recovery efforts today – was simply not available to take up the iguana's cause.

A second chance: 1990–2014.—In contrast to the quiet and largely ignored 1970 re-discovery, the 1990 re-discovery generated enormous local and international interest, and galvanized a successful recovery effort that continues today (Alberts 2000; Vogel et al. 1996; Wilson 2011). The 1990

Wilson, Byron, Tandora D. Grant, Rick van Veen, Rick Hudson, Dawn Fleuchaus, Orlando Robinson, and Kimberly Stephenson. 2016. The Jamaican Iguana (*Cyclura collei*): a report on 25 years of conservation effort. Pp. 237–254 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

re-discovery was different for two reasons. First, Jamaica had a resident herpetologist at the time, in the late Dr. Peter Vogel, then a Lecturer in the Department of Life Sciences, at The University of the West Indies, Mona (UWI). Second, the period 1970–1990 witnessed an international awakening to the global extinction crisis, formalized by the genesis of a new discipline, conservation biology (Soulé 1986). These developments led to a myriad of new funding opportunities, conservation positions, and diverse institutions eager to engage in conservation research and recovery efforts. Notably, the world's universities and major zoos began supporting conservation efforts aimed at averting extinctions (e.g., Hudson and Alberts 2004).

Following the 1990 re-discovery, Dr. Vogel and other local stakeholders formed the Jamaican Iguana Research and Conservation Group (JIRCG). With considerable technical and financial support from international partners, the JIRCG (re-named in 2006 as the Jamaican Iguana Recovery Group [JIRG]) implemented emergency actions (primarily nest site protection and diversion of charcoal burners away from the critical nesting areas) that likely prevented an otherwise certain extirpation of the remnant population. Also crucial, the nucleus of iguanas for a captive program for breeding and headstarting was collected between 1991 and 1993. Undeniably, 1990–1993 was a most critical period for the Jamaican Iguana (Vogel et al. 1996).

Subsequent conservation activities have focused on recovery efforts for the remnant population, securing protection for the Hellshire Hills, and establishing a reintroduced population on the Goat Islands (Wilson et al. 2004; Wilson 2011; Grant et al. 2013). This report represents an update and summary of research and conservation activities carried out over the 1990–2014 period. In addition to presenting recent conservation results, we also examine the extent to which overall project objectives have been achieved, and submit some recommendations aimed at ensuring the survival of this iconic species and the threatened "hotspot within a hotspot" for which it serves as a flagship species (e.g., Alberts 2000; Wilson and Vogel 2000; Lewis et al. 2011).

International significance for global iguana conservation.—Retrospectively, the Jamaican Iguana re-discovery generated an impressive collective impact on iguana conservation, and on reptile conservation in general. Following the exciting "re-discovery" news emanating from Jamaica in 1990, the U.S. zoo herpetological community selected Caribbean lizards for its fledgling reptile conservation programs and *Cyclura* species naturally emerged as a leading priority. The Jamaican Iguana presented a compelling cause around which to rally zoo support. Soon a small cadre of participating zoos was directing much needed financial, technical, and logistical support to the JIRCG's field research and conservation efforts. Over the next several years, that U.S.-based group managed to raise funds not only for the Jamaican Iguana program, but also channeled critical support to the Anegada and Grand Cayman Blue Iguana recovery programs that were also in their infancy. Zoo staff drew upon their media expertise to publicize this captivating "second chance, re-discovery to recovery" story, which helped attract the attention of the global conservation donor community and also galvanized involvement from additional zoos. In the 1990s, the Jamaican Iguana story was featured in numerous popular magazines, newspapers, and even prompted sponsorship from Nike, Inc. to create wear-resistant iguana vests for the first radio-tracking study (Hudson and Alberts 2004).

In 1993, local and international groups convened a workshop in Kingston, Jamaica, that brought most of the existing Caribbean iguana and conservation expertise together for the first time. Assistance from IUCN, International Union for Conservation of Nature, was enlisted to conduct a Population and Habitat Viability Assessment (PHVA), and a recovery plan was generated that outlined immediate action steps to recover the iguana (JIRCG 1993). This PHVA was the first for a lizard and only the second of many future analyses for reptile species. Alliances forged during the workshop soon led to the formation of the IUCN SSC West Indian Iguana Specialist Group in 1996, that later (2000) expanded its mandate to include all iguana genera. The Iguana Specialist Group (ISG) is today recognized as a global strategic leader for prioritizing iguana research, developing recovery programs, and mobilizing conservation action.

A second major iguana conservation group emerged in 2001, the International Iguana Foundation (IIF), in response to the paucity of financial resources available for iguana programs. With leadership from many of the zoos that had supported iguana conservation since the early 1990s, the nonprofit IIF quickly developed a revenue stream from previously unavailable sources that allowed improved planning and action for core-supported species, including *C. collei*. A small grants program has awarded proposals benefitting over 20 iguana species throughout their range. In the 13 years since inception, the IIF has raised close to two million USD, nearly all of which has been directed toward iguana conservation, research, and education programs in host countries (Hudson 2006).

MATERIALS AND METHODS

Preamble.—Primary field methods (e.g., mark-release, headstarting) have been detailed elsewhere (Vogel 1994; Vogel et al. 1996; Wilson et al. 2004) and are not repeated here. Rather, we restrict our discussion to methods or approaches that were either novel (e.g., deployment of "Judas Iguanas") or significantly modified (e.g., headstarting and captive protocols), or that otherwise warrant special mention (e.g., predator trapping).

Study site.—The Hellshire peninsula, located ~ 20 km west of the capital city of Kingston, consists of low-lying limestone hills covered in dry tropical forest. Boasting some sections that may never have been cut, the Hellshire Hills have arguably retained the largest intact (old growth) dry tropical forest in the region (McLaren et al. 2011). This remaining core of primary forest supports a rich collection of endemic plant and animal species, and encompasses the entire current range of the Jamaican Iguana (Vogel et al. 1996; Wilson and Vogel 2000; Wilson 2011). The Hellshire Hills is regarded as a "hotspot within a hotspot" (Lewis et al. 2011) – an exceptionally important biodiversity area within one of Earth's recognized biodiversity hotspots, the insular Caribbean (Myers et al. 2000; Mittermeier et al. 2005). The area is considered an Important Bird Area (Wege and Anadon-Irizarry 2008), a Key Biodiversity Area by the Critical Ecosystem Partnership Fund, and is listed by the Alliance for Zero Extinction as one of roughly 600 important sites worldwide that is facing an imminent extinction (see Ricketts et al. 2005; Grant 2014). Until the Jamaican government withdrew the application at the end of 2013, local agencies and major government stakeholders had worked for 15 years to declare the PBPA a UNESCO Biosphere Reserve (United Nations Educational, Scientific and Cultural Organization; Serju 2014).

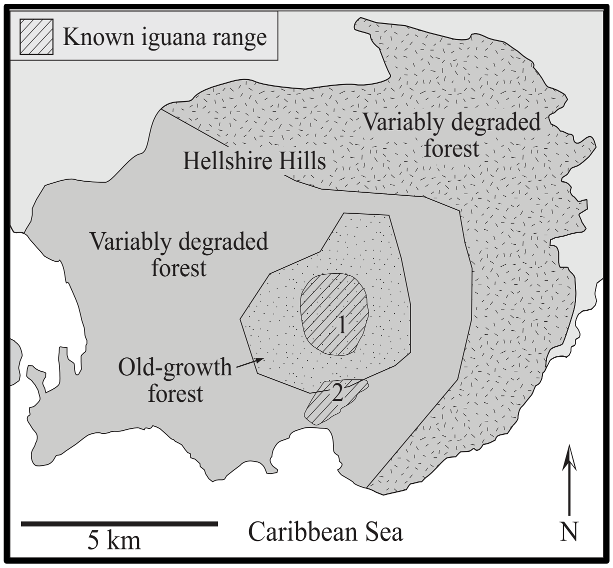

FIGURE 1. Habitat map of Hellshire Hills, Jamaica, with inset showing known area of occurrence for the Jamaican Iguana. (1) Main population; (2) Small subpopulation of one wild male individual and ~ 12 headstart individuals released in 2007. Note that habitat designations labeled here are transitory due to on-going loss and degradation of the Hellshire Hills forest; areas coded as "Variably Degraded" represent mosaics of degraded and highly degraded habitat, including those currently under assault from illegal tree cutting activities associated with the production of charcoal. Note also that the eastern portion (stippling) is more highly degraded, whereas the western portion (no stippling) contains larger tracts of recovering forest.

Although Jamaican Iguana surveys and field research have been conducted throughout the Hellshire Hills, conservation and research efforts have focused on the main population discovered in 1990. That core population is restricted to the most isolated and least disturbed section of the forest, ~ 12.5 km^2 in the south-central portion of the peninsula (Fig. 1).

Population monitoring.—Our primary index of iguana abundance is the number of females using the two main communal nesting areas that were identified during surveys in 1990 (Vogel 1994; Vogel et al. 1996). Those sites were monitored intensively in 1991 and a count of nesting females was obtained (Vogel 1994); that assessment provides the best, indeed the only window into the demographic past of *C. collei*. Our analysis of population trends is based on referencing those 1991 data as a baseline and examining comparable data obtained for the period 2004–2013.

In addition to trapping efforts focused on female iguanas during the nesting season, observational and mark-recapture data were collected throughout other seasons. In particular, a live-trapping grid designed for predator control (see below) proved useful in augmenting behavioral observations and focused trapping efforts. Additional observational and capture data were obtained using camera traps (2008–2013) and in the context of radio-telemetry studies.

Nest site monitoring: annual counts of nesting females.—Nest site monitoring consisted of daily observations during the nesting season (mid-May through June), using hides constructed adjacent to the main communal nesting areas (see Vogel 1994). The primary goal of nest site monitoring was to determine the number and location of nests within the primary, historically monitored nesting sites. The identity of nesting females was determined either by external marks (color-coded beads, paint marks) or after capture (primarily using baited cage traps) from their implanted transponders, although not all nesting individuals were captured or identified in a given year. Ultimately, an annual tally of nesters (nesting confirmed, or individual captured gravid in vicinity) was generated for the same communal nesting areas for which baseline data were collected in 1991.

Indexing annual productivity: enumeration of hatchlings.—Obviously, the number of females depositing nests may not translate into population productivity if those nests are unsuccessful. Therefore, the number of hatchlings resulting from an annual nesting effort represents a better indicator of population viability. However, overall hatching success (the number of hatchlings produced) is influenced by multiple factors, including the number of females nesting, the size and fecundity of those females, and hatching success per nest.

In addition, the annual count of hatchlings is necessarily dependent on our ability to capture recently emerged individuals, and harvesting efficiency is influenced by environmental conditions, availability of human resources, seasonal preparation, and luck, all of which have been subject to variation. For example, nest site fencing rings were either damaged or efforts compromised by tropical storms and hurricanes, especially during the years 2004 (Ivan), 2005 (Dennis and Emily), 2007 (Dean), and 2008 (Gustav). Predators also occasionally damaged nest site fencing rings and hatchlings sometimes escaped through emergence holes dug under surround barriers. As a consequence, our measures of annual productivity include a substantial margin of error, but nevertheless provide a useful minimum index of overall productivity.

The only changes in hatchling collection protocol implemented in recent years (2005–2013) were improvements to the system of fencing used to protect nesting areas and facilitate the collection of hatchlings. The current system consists of using polyethylene "poultry curtain" as fencing, secured on the bottom interior with strips of rubber hosing staked into the substrate (Fig. 2). This method minimizes soil disturbance and erosion potential, and permits rapid repair or re-erection of fencing following storms. Hollow tubes and shade structures are placed within enclosures to facilitate harvesting and provide hatchlings with protection from direct sunlight and avian predators. Notably, nest site fencing rings have been erected increasingly early in recent years (currently ~ mid-August), as annual nesting has been initiated earlier.

Headstart-release and captive population.—The methods employed in the headstart-release program, including field collection of hatchlings, captive rearing, health screening, and repatriation, are detailed in Wilson et al. (2004). Some headstarting protocols were modified based on discussion and analysis during the Species Recovery Plan workshop held in 2006 (Grant et al. 2013) and those changes are appropriate to detail here. Modifications incorporated in recent years include: (1) collecting 40 wild hatchlings per year (up from 20) with a female bias; (2) improvements in diet and other aspects of husbandry; (3) optimizing occupation of the available (captive) space; and (4) the construction of additional rearing enclosures. Blood samples for genetic analysis are now primarily collected in the field from as many annual hatchlings as possible, both those that are transferred to Kingston's Hope Zoo for headstarting and those released after initial morphometric processing. All hatchlings were marked with implanted transponders or occasionally by toe-clipping when transponders were in short supply. An annual health screening of the entire captive colony now occurs in the spring before scheduled releases and prior to follicle advancement.

FIGURE 2. Nest site surround (4 x 6 x 0.8 m) for capturing hatchling Jamaican Iguanas at the "Upper Nest Site", Hellshire Hills. (Photographed by Rick Van Veen).

The *ex situ* U.S. zoo assurance colony has been managed according to methodologies developed for the sustainability of small captive populations by the Association of Zoos and Aquariums (AZA), and is based on the most sound genetic and demographic models available (Grant 2012).

Distribution surveys: deployment of Judas Iguanas.—To assess the population's full geographic range, surveys and associated research work have been conducted outside of the species' current (known) range of occupancy. Unfortunately, the rugged terrain and lack of water sources render ground surveys in interior Hellshire problematic, and result in a high ratio of effort to coverage (Woodley 1971). As a consequence, logistical obstacles have historically limited the number and scope of survey efforts in Hellshire's interior forest.

To enhance our chances of detecting new subpopulations or isolated individuals outside the known area of occurrence, we tested a new and promising survey strategy. Specifically, we adapted the "Judas Goat" approach (see Campbell and Donlan 2005; Campbell et al. 2005) and released zoo-reared iguanas outfitted with radio transmitters into areas east and west of the core population. Just as Judas Goats can be used to detect individuals at low density or to confirm the completion of an eradication campaign, we aimed to employ Judas Iguanas to detect scattered individuals or confirm absence.

Because iguanas interact socially (e.g., sexually, antagonistically, etc.), we assumed (based on prior experience with monitored releases) that radio-tagged animals released into novel areas would likely encounter and interact with any resident iguanas. Thus, Judas Iguanas could provide a mechanism for detecting wild iguanas under exceedingly low-density conditions in large expanses of rugged terrain. Evidence of wild iguana(s) can either be confirmed directly (observations of individuals or sign noted during radio-tracking) or indirectly; for example, males often bear the consequences

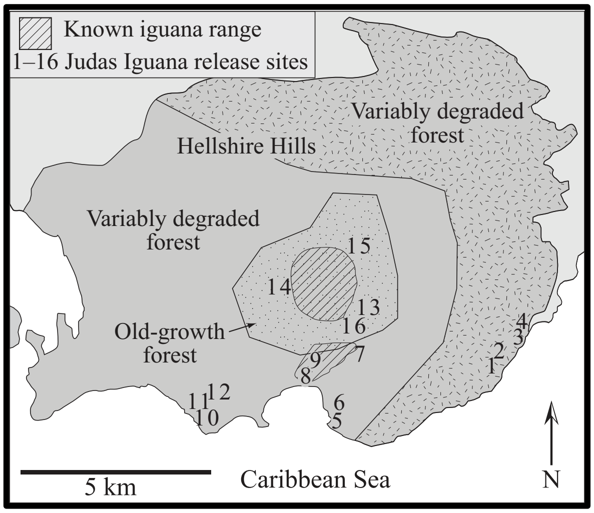

FIGURE 3. Locations of 16 Judas Jamaican Iguana releases in the Hellshire Hills, Jamaica. See Fig. 1 for a description of the "Variably Degraded" habitat designation.

(scars) of agonistic encounters, so evidence of recent fighting in a Judas male would indicate the presence of another male iguana.

We released a total of 14 Judas Iguanas (9 males, 5 females) outfitted with Holohil PD-2 radio transmitters (Holohil Systems Ltd., Ontario, Canada) spread among nine sites during 2008 and 2009. The 14 individuals ranged between five to 16 y, weighed between 900 and 3,450 g, and were radio-tracked for up to 189 d. Two individuals (both males) were re-captured and later deployed on another Judas mission; hence, Judas releases were conducted at 16 different locations within nine focal areas (Fig. 3).

Predator control.—We initiated a program to reduce impacts from non-native mammalian predators in May 1997. That mongoose-focused effort began with 20 live cage traps (32 x 12 x 10 cm) placed along a loop trail passing through the two primary (communal) iguana nesting areas (see Fig. 4). Traps were baited with salted fish and the effort was sporadically operational until January 1998, at which point trapping was conducted during every week of the year, with traps being open and operational ~ three days per week. In this early phase of predator control (1997–1999) traps were checked daily and inactivated for the several days of the week during which a worker was not present to conduct daily checks.

Due to on-going concern about high levels of mongoose predation and the apparent success of removal trapping in reducing mongoose abundance (see Lewis et al. 2011, and discussion below), a decision was made in 1999 to leave traps open and operational on a continuous basis, with traps being checked every 2–3 days, minimally, to release any iguanas captured unintentionally. With the singular exception of a several-week period during the early 2000s, this trapping regime has been operating every day since June 1999, and continues to the present (September 2014).

The trap-removal effort was expanded to include the deployment of up to ~ 300 traps, including stations established along new trapping trails that added a "Western Loop" in 2011–2012 and an "Eastern Loop" in 2013–2014. The combined trapping ring now surrounds the original (1997) trapping loop and increased the size of the predator-controlled area by over two-fold (Fig. 4). Beginning in the early-mid 2000s, the original traps (32 x 12 x 10 cm) were replaced with larger traps (80 x 30 x 25 cm). Larger traps enhance the potential for capturing larger invasive alien species (IAS) (e.g., cats and small dogs) and also reduce the risk of injury to native species such as the iguana and the Jamaican Coney. In addition to our primary use of live mesh box traps (above) we periodically deployed wire snares for larger IAS (e.g., pigs, dogs) and also experimented with leg-hold traps targeting cats.

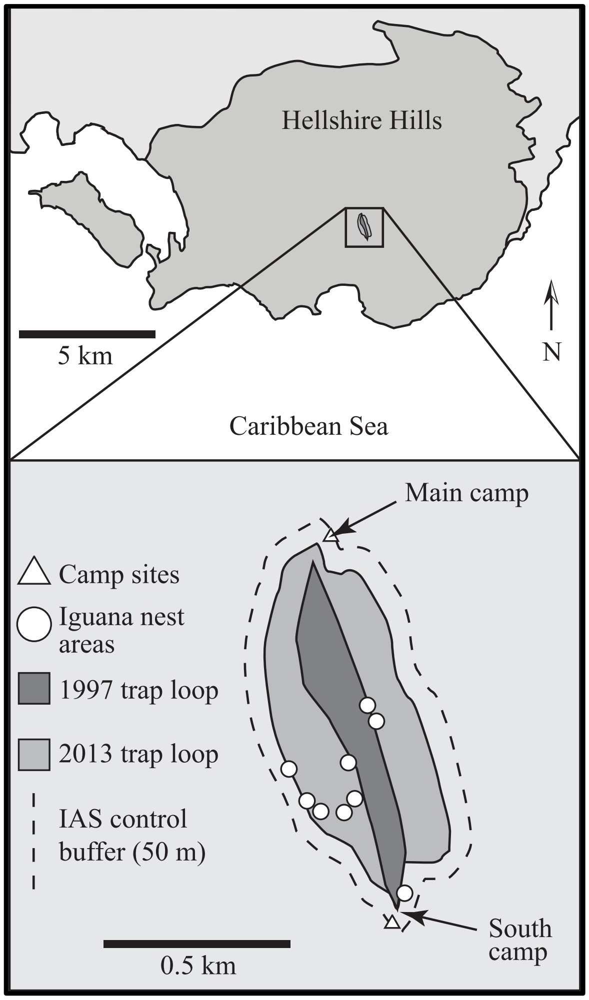

FIGURE 4. Core Jamaican Iguana area in the Hellshire Hills showing original (1997) invasive alien species (IAS) trapping loop coverage (dark grey) and more recent 2012–2014 trap loop expansion (lighter grey) with a 50 m buffer control area (dashed line).

Construction of artificial nesting sites.—In 2005, iguanas began nesting in a small vegetable garden (~ 2.5 x 1.5 m) at the main field station, demonstrating the potential utility of creating artificial nesting areas to compensate for the scarcity of suitable soil deposits in the species' current area of occupancy (Fig. 5A). In addition, significant crowding had become apparent at one of the two main communal nesting sites by 2009, as evidenced by nesting iguanas excavating previously deposited nests, resulting in reproductive failure for some early nesting individuals. To accommodate the increasing number of nesting iguanas, we constructed an artificial nesting site in 2011–2012 (Fig. 5B) located ~ 40 m south of the "Upper Nest Site", the more productive of the two main communal nesting areas (Vogel 1994). Due to the paucity of soil in Hellshire, we imported soil (by foot trail) from a site ~ 2 km north of the nesting area, drawing from an abandoned charcoal kiln in a slightly degraded section of the forest. Thus, the soil contained some charcoal residue but was viewed as acceptable, given the alternatives (local soil depletion or the introduction of potential pathogens or non-native plants via importation of soil from a more distant location).

RESULTS

Population trends: nesting females and hatchlings at core, monitored sites.—The number of iguanas nesting at the core communal nesting sites has increased dramatically over the past two decades (Fig. 6). A maximum of nine females was observed in the vicinity of the two communal nesting areas in 1991, with six confirmed as having nested at those sites (Vogel 1994). In 2013, 53 females were documented as nesting or observed gravid in those same areas, representing a six-fold increase since conservation activities were initiated. In addition, 10 nests were recorded at nearby locations (within ~ 1 km of the main nesting areas), nearly all of which were deposited by repatriated headstarters. Two of these nesting areas did not exist in 1991 (the artificial nesting sites), and another two were probably not active in the preceding decades. Allowing these "new", primarily headstart nests to be included in our overall tally yields a 2013 total of 63 nesters in the core area, suggesting a seven-fold increase since 1991.

We cannot say for certain that iguanas are not nesting outside of our area of conservation focus, especially given the large number of headstarters that have been released into the core nesting area (*n* = 137 females as of 2015). However, the potential for successful nesting outside of the core, predator-controlled area seems remote due to egg and hatchling mortality attributable to IAS predators. For example, camera trap data verified 100% mongoose predation on 14 nests deposited outside of the predator-controlled zone during 2011–2012 (Rick van Veen, unpubl. data). As a consequence, nests not protected from mongoose predation in particular are unlikely to make a substantial contribution to future recruitment. Accordingly, the monitored communal nesting areas within the predator-controlled area probably account for most, if not all of the species' annual productivity.

The number of hatchling iguanas harvested has increased steadily since conservation and monitoring activities were initiated in 1991 (Fig. 7). And while some of this increase may be attributable to improved harvesting efficiency, the overall trend is clearly the product of increasing numbers of nesting females (see Fig. 6).

Distribution surveys: deployment of Judas Iguanas.—We released 14 individual Judas Iguanas; two of the large males were recaptured and released at second locations, resulting in 16 Judas Iguana releases to nine general locations. Twelve (eight male, four female)

FIGURE 5. (A) "Stumpy" (headstarted Jamaican Iguana released in 2001) nesting in a small vegetable garden at field station "South Camp", Hellshire Hills, in 2006. This inadvertent, artificial nesting area was constructed in 2005, and as of 2010 was supporting annual nesting by up to three Jamaican Iguanas. (B) Artificial nesting site constructed adjacent to the "Upper Nest Site". A nest excavation hole can be seen in the lower left portion of the image. (Photographed by Rick Van Veen).

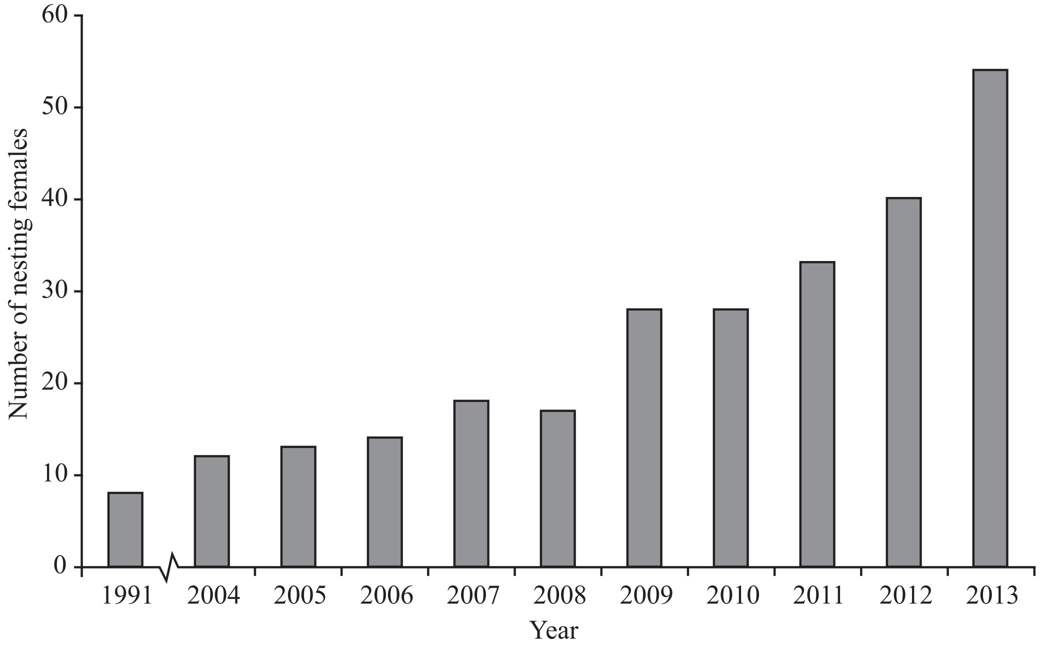

FIGURE 6. Estimated number of nesting females per year (= number of confirmed nests plus gravid female Jamaican Iguanas observed at monitored communal nesting sites in the Hellshire Hills between 1991 and 2013).

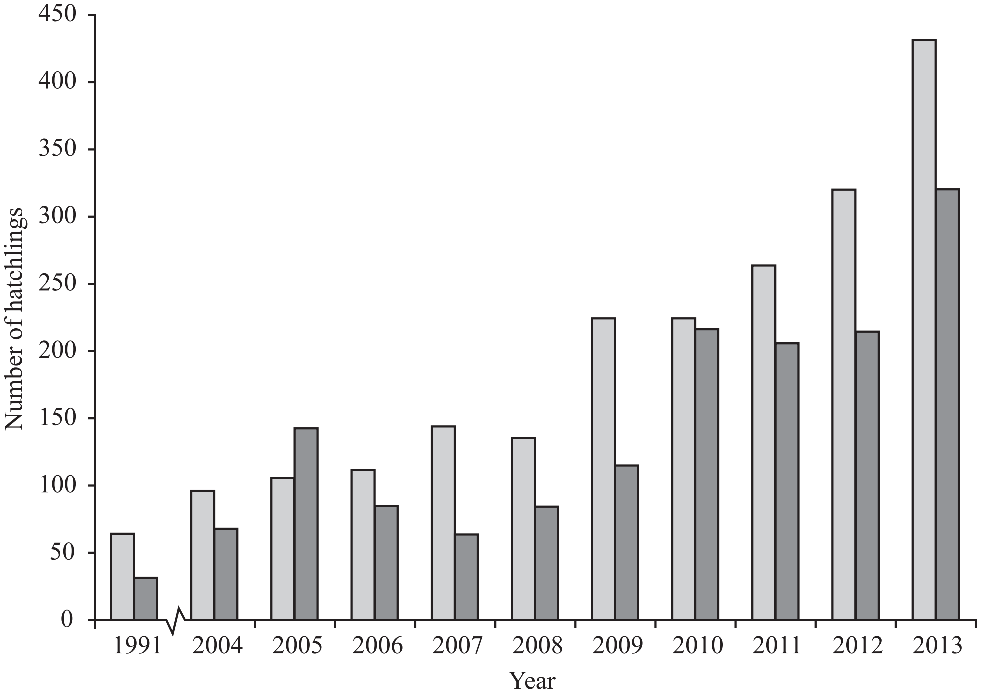

FIGURE 7. Number of captured/enumerated hatchling Jamaican Iguanas in the Hellshire Hills (dark grey) and predicted total number of hatchlings (light grey). Predicted numbers of hatchlings were based on the number of females nesting, and assumed an average successful clutch size of eight hatchlings per female. Although *C. collei* is known to produce clutches of up to 20, many of the recent (headstart) females were small and would have produced smaller clutches.

releases were in 2008 (7 February to 12 August) and four (three male, one female) in 2009 (5 May to 28 July). In all, we recorded 197 waypoints (sightings or confirmed locations) during subsequent radio-tracking efforts. With the exception of Judas Iguanas that entered the core iguana area and interacted with (known) resident iguanas, none of the Judas Iguanas appear to have contacted other iguanas. Associated ground surveys also failed to reveal any iguana sign outside of the known area of occupancy.

Using Judas Iguanas to assist in survey efforts shows considerable promise, albeit at significant risk to the individual iguanas deployed. For example, iguanas released in degraded forest near Hellshire's periphery are exposed to increased predation risk from IAS; Judas Iguanas released in eastern Hellshire were frequently chased by dogs and may explain the loss of at least one large male (Judas Iguana release #1). Various IAS were noted in the vicinity of all Judas release sites. Although only one of the six small iguanas (< 1,200 g) was a confirmed victim of predation, the remaining five were classified as "lost", but under circumstances suggesting that they were also victims of IAS predation.

Females, regardless of age or size, appeared to find a safe refuge and made only small forays from those locations. Large males on the other hand, were quite mobile, with all of the largest (> 2,000 g) males moving large distances. For example, Judas Iguana release #15 was released on the edge of the known iguana distribution, and after making several large forays returned to within the known iguana range. Another large male Judas Iguana was released to the east of the core area in the vicinity of a wild (unknown identity) male iguana; that Judas Iguana left his release site and was found some weeks later, 6.5 km away in a housing estate outside of the Hellshire forest (Judas Iguana release #7). That individual was captured and later released within the known iguana range where it was monitored until it lost its transmitter several weeks later.

Headstart and release.—In the initial years after the 1990 re-discovery, the majority of eggs/hatchlings observed in the Hellshire Hills were collected for headstarting at the Hope Zoo (1991–1994). For several years afterward (1995–2000), only a small number of hatchlings were headstarted, due to space and financial restrictions at the Hope Zoo, as well as a focus on other components of the recovery effort. Iguanas were released back to Hellshire beginning in 1996 with a pair of young adults, and repatriations have continued on a nearly annual basis ever since (Table 1). As released iguanas created space at the captive facility, the program aimed to collect 20 hatchlings per year through 2006.

To date, a total of 565 iguanas have lived some portion of their life at the Hope Zoo. Overall, iguana health at the headstart facility has been very good (Lung et al. 2002; Nancy Lung, pers. comm.), with only a very small percentage being lost to disease, trauma, or congenital defects. 16% have died or were reported as missing before being released. Most of the missing animals were believed to have been lost via cage breaches from hurricane damage or wear, and are assumed dead because of the abundance of non-native predators in the neighborhood surrounding the Hope Zoo.

During the annual health screen all captive iguanas are examined physically and measured for growth. At the time of the Species Recovery Planning (SRP) meeting in 2006 (Grant et al. 2013), available growth data indicated that most iguanas reached 1–2 kg in size between ages 6–8 years old, and some when as young as 4–5 years (additional details will be published elsewhere). Slow but consistent improvements in husbandry at the Hope Zoo have been accomplished over the years, resulting in improved (increased) growth rates. It was recommended by the SRP that if iguanas were afforded consistent access to high quality food, ample sunlight (cages kept clear of vine cover), numerous hides and visual barriers to separate conspecifics, and were housed at lower densities, their growth rates would increase (based on data from congeneric programs). With a density of 4–6 iguanas per cage and a female bias of up to 3:1 to minimize competition, most iguanas should be larger than one kg in the spring before their sixth birthday.

Further, if all cage space was optimized and additional cages constructed, the program could incorporate 40 new hatchlings and anticipate the release of 40 older headstarters per year. Collection in the field for this target began in 2007. Although husbandry recommendations have not been followed consistently, there has been improvement, particularly in the last several years. For example, only eight iguanas remained captive beyond their sixth birthday as of the release in March 2014. To date, a total of 278 headstarters (141 males, 137 females) have been repatriated back into Hellshire (Table 1).

During the first years of releases (1996–2001), the size at which an iguana would be safe from feral cat and mongoose predation was unknown. Ultimately, animals were released between 1,000–2,850 g (Wilson et al. 2004). In Anegada, where cats are the main predator, radio-tracked headstarted Anegada Iguanas were released between 414–2,050 g. While no strong correlation between size and survival was found during the first two years post-release, the smallest iguanas did not survive, suggesting that 400 g was still a vulnerable size class (Bradley and Gerber 2006). In the more remote release sites on Grand Cayman, iguanas are released at 2–3 years old, because native snakes are the main predator (Burton 2012). Most Jamaican Iguanas are not radio-tracked after release so their fate is unknown unless they are opportunistically observed or captured in cage traps in Hellshire, either caught incidentally in traps intended for mongoose or those intentionally set for recapture data (e.g., during nesting). However, during the Judas Iguana effort, a 900 g male released outside the predator-controlled area was found one month later under a bush with its intestines pulled through a 2.5 cm abdominal hole, characteristic of mongoose predation (Rick van Veen, pers. obs.). Since 2009, all non-Judas iguanas have been released in the core, predator-controlled area, and all were larger than 900 g.

***Off-island,* ex situ *program*.**—As a further hedge against catastrophic loss in the wild, 24 iguanas were exported in two groups of 12 between 1994 and 1996 to establish a collectively managed *ex situ* captive population in U.S. zoos (Central Florida, Sanford, Florida; Fort Worth, Texas; Gladys Porter, Brownsville, Texas; Indianapolis, Indiana; San Diego, California; Sedgwick County, Wichita, Kansas) (Grant 2012). Because zoos had previous experience breeding other *Cyclura* species, the exportation was expected to create a long-term sustainable reservoir of wild genetic diversity and provide an off-island assurance colony in the event of a decline or loss of the Jamaica-based population. In addition, iguanas in the U.S. population promote education and awareness, and generate funding and support for the ongoing recovery effort in Jamaica. Iguanas were paired according to their clutch assignments, which were determined initially by nest emergence in the field and later supported by microsatellite data (Davis 1996). However, allelic diversity was examined at only four loci in this preliminary analysis, so additional study will be required to characterize kinship and diversity within the *ex situ* population as a whole. Because the remnant wild population was so small and isolated for many years, relatedness in the U.S. captive group has probably been underestimated. Genetic analyses currently in progress are focused on retention and potential skew of diversity in

TABLE 1. Captive Jamaican Iguanas headstarted, released, and captive-bred at the Hope Zoo, Kingston, and U.S. zoos. Iguana numbers are in the format: Males.Females.Unknown sex (Total). *Two females confiscated from a zoo in St. Elizabeth have an unknown hatch date but were at least 10 years old in 2012.

Hatch Year	Transferred to Hope Zoo	Captive-Bred Hatches: Hope Zoo	Exported to the U.S.	Captive-Bred Hatches: U.S.	Year of Release	Released to Hellshire
UNK*	0.2 (2)					
1991	13.14.4 (31)		4.2 (6)			
1992	5.8 (13)		3.3 (6)			
1993	22.18 (40)		2.4 (6)			
1994	12.16.1 (29)		3.3 (6)			
1995	5.3 (8)					
1996	2.5 (7)				1996	1.1 (2)
1997	*none*				1997	3.3 (6)
1998	5.5 (10)				1998	5.7 (12)
1999	3.2 (5)				1999	4.3 (7)
2000	1.2 (3)				2000	*none*
2001	10.8 (18)	0.0.1 (1)			2001	6.7 (13)
2002	7.12 (19)			0.0.1 (1)	2002	*none*
2003	16.13 (29)				2003	5.4 (9)
2004	7.12 (19)	2.1.1 (4)			2004	0.2 (2)
2005	11.9 (20)				2005	7.9 (16)
2006	6.14 (20)			9.12.3 (24)	2006	*none*
2007	23.15.1 (39)				2007	9.9 (18)
2008	22.18 (40)				2008	13.7 (20)
2009	11.17.1 (29)				2009	7.14 (21)
2010	23.29 (52)				2010	8.4 (12)
2011	14.26.3 (43)				2011	8.9 (17)
2012	14.32 (46)			3.3 (6)	2012	7.12 (19)
2013	8.34.1 (43)			9.7.2 (18)	2013	30.22 (52)
2014	12.16 (28)			0.0.24 (24)	2014	15.14 (29)
2015	*to be determined*				2015	13.10 (23)
TOTAL	252.330.11 (593)	2.1.2 (5)	12.12 (24)	21.22.30 (73)		141.137 (278)

the wild population, especially due to the influence of the headstart-release program (Mark Welch, pers. comm.).

In the first decade of the recovery program, *C. collei* proved to be more reluctant to breed in captivity than other *Cyclura* species. A single hatchling was discovered in one of the headstart cages at the Hope Zoo in 2001, representing the first captive breeding for the species. That hatchling was smaller than the average seen in the wild and did not live beyond one month. In 2004, a second group of four hatchlings was discovered in the headstart facility, three of which thrived and have since been released. Despite attempts to improve the Hope Zoo's two exhibit cages to promote breeding with visual barriers, soil suitable for digging burrows, and hides, the pairs have not reproduced and have at times seriously injured each other during agonistic encounters. It is likely that breeding is disrupted by the stress of numerous exhibit visitors and/or iguanas should be separated except during the breeding season or housed in much larger enclosures. In the successful Grand Cayman captive facility, pairs of iguanas are kept together year-round only in pens that are substantially larger than those available at the Hope Zoo (Fred Burton, pers. comm.).

Captive breeding in the U.S. first occurred at the Indianapolis Zoo in 2002, although the single hatchling died before completely exiting the shell. In 2006, the same dam and sire produced 20 hatchlings, in addition to four hatchlings produced by a second dam. Zoo staff concluded that mimicking Jamaica's seasonal environmental parameters such as photoperiod, temperature, and humidity, as well as reducing the animal's contact with humans, were the keys to reproductive success (Searcy et al. 2009). Unfortunately, since the death of that sire, the females have not reproduced successfully with their new mate. In 2004, Zoo Miami joined the AZA *Cyclura* program and three iguanas were transferred there, followed by two more in 2009. Two of the females in Miami produced a total of six hatchlings in 2012, 10 in 2013, and 16 in 2014. Second-generation dams at the San Diego Zoo Institute for Conservation Research and the Sedgwick County Zoo also produced one and seven hatchlings, respectively, in 2013, and eight hatchlings were produced in 2014 at Sedgwick. 63% of the clutches hatched in August, 25% in September, and 13% in October, which is similar to seasonality in Jamaica.

Almost all female iguanas in the U.S. have laid infertile eggs, and most have done so annually. Copulation is not always observed (including when clutches are successful) and it is unclear whether the lack of reproduction is behavioral, environmental, or a combination of both. The youngest dams to reproduce in the U.S. were second-generation females at 6.5 years old, and either 6.5- or 7.5-year old headstarters at the Hope Zoo. The oldest dam to reproduce was 20.5 years old in Miami (2014); she was 18.5 years old when her first successful clutch was laid. It is unknown how long Jamaican Iguanas can live or remain reproductively active, but a related species (*Cyclura lewisi)* has lived to at least 69 years of age, and although that individual never sired offspring, it was observed to have healthy sperm upon death (Barbara Durrant, pers. comm.). Six of the original 1991 hatch year iguanas are still captive (two in the U.S., four at the Hope Zoo), one of which has reproduced successfully. Two of the oldest females known from the original (early 1990s) nesting group were still alive and nesting in 2012 and 2013, suggesting a minimum reproductive age of at least 27 years.

Non-native predator control.—Beginning with 20 traps in 1997, and ultimately expanding the effort to include ~ 300 traps by 2014, our live cage trap program resulted in the removal of well over 1,500 non-native (IAS) predators, primarily mongooses (> 90%) based on > 350,000 trap days (one trap open for 24 h = one trap day). Larger IAS (e.g., wild pigs and dogs) have been removed by whatever means were available in the field, including the use of wire snares.

Early predator control efforts (1997–1998) indicated that local mongoose density could be reduced rapidly by implementing a trap-removal program. An initial capture rate of seven mongooses per 100 trap days (1 trap day = 1 trap open for 1 d) was reduced by more than an order of magnitude (to 0.25 per 100 trap days) after initial clearance (Lewis et al. 2011). Current trapping efforts result in the removal of > 150 mongooses per annum, primarily males, and the core area is considered clear of resident mongooses but serves as a sink for individuals dispersing or making extra-territorial forays.

Although feral cats were trapped and removed with some regularity, they are not as easily trapped as mongooses. Some cats avoid cage traps, such that other trapping techniques are required for their removal (Tolson 2000; Nogales et al. 2004). For example, we trapped and removed only 17 cats between November 2012 and October 2013, compared to 156 mongooses during that same one-year period. Dogs represent an occasional, recurrent threat that can result in significant demographic impacts because they are the only predators capable of killing adult iguanas. When dogs have come into and remained in the core iguana area, removal attempts have been initiated. For example, around 10 dogs were removed during the 2004–2013 period, primarily using snares.

Incidental take of native wildlife.—As anticipated, our trapping efforts resulted in some incidental take of non-target species. In 17 years of live box trapping (> 350,000 trap days) we documented only two instances of injury or death to iguanas. Reporting those unfortunate occurrences is important and provides an opportunity to inform future predator control efforts. In one case, a dog mauled a trapped iguana from outside of the trap, resulting in the loss of part of the iguana's tail and several toes; that individual was taken to the Hope Zoo for recovery and was later returned to its territory in the Hellshire Hills. One death occurred when a predator tampered with the trap, moving and exposing it to direct sunlight, which led to the death of the trapped iguana. Leg-hold trapping trials also resulted in the death of one iguana, bringing the project's 17-year total to two instances of non-target, threatened species loss.

Other non-target casualties of the trapping program included a few birds, land crabs, and hermit crabs. Importantly, we did not record any injuries or losses to other threatened species, such as the Jamaican Coney or the Jamaican Boa; individuals of those species were all released unharmed after capture.

DISCUSSION

Current distribution.—Our delineation of the current range of *C. collei* is based on observations (> 2,500) of individuals and sign (e.g., scat, trails), and represents the confirmed area of occupancy (Fig. 1). Although the existence of unknown satellite individuals or subpopulations is a possibility, available information suggests this is unlikely and that the core population under conservation management is the only remaining wild population of the Jamaican Iguana. This remnant population is restricted to a small area of (~ 1.18 km^2), with a second, minor concentration consisting almost exclusively of headstarters occupying a smaller area (~ 0.22 km^2) to the south of the main population (Fig. 1).

This core iguana zone is located in the middle of what is considered Hellshire's highest quality old growth forest – an area of around 12.5 km^2, or about 10% of Hellshire's total area. Overall, a total area of less than 1.5 km^2 appears to support essentially the entire (certainly over 90%) presumed remaining *C. collei* population. Unless the area of occupancy can be expanded significantly or a second population established in an additional location, the Jamaican Iguana will always be considered Critically Endangered by the IUCN Red List of Threatened Species (Grant et al. 2010; Baillie and Butcher 2012).

Survey efforts in 1990 in the Hellshire Hills also identified a small subpopulation located ~ 3 km west of the main population. Two active holes and one iguana were sighted, suggesting a small concentration consisting of only a few individuals (Vogel et al. 1996). Subsequent survey efforts in western Hellshire (1999, 2008) failed to detect any sign of resident iguanas, and complementary efforts employing Judas Iguanas also failed to reveal any sign of the species. Accordingly, the western subpopulation is assumed extirpated. However, survey work in wider Hellshire, and attempts to locate iguanas in western Hellshire in particular, have not been exhaustive, so additional effort is warranted. While informative, our Judas Iguana efforts also did not cover the entirety of the Hellshire Hills, so the deployment of additional Judas Iguanas to the west and elsewhere is recommended.

Population status.—Though influenced by variation in harvesting success, the number of hatchlings enumerated annually has increased regularly and dramatically over the years, in concert with the increasing size of the nesting population (see Figs. 6 and 7). Also notable has been the use of artificial nesting sites, with up to three females making annual use of a small abandoned vegetable garden site, and two nests known at the large newly created site since 2012. This represents a significant enhancement of nesting potential, and an approach that could be further exploited to increase productivity in the core area and to expand the current distribution of iguanas. Considering the high failure rate of rock hole nests documented by camera traps, the limited availability of optimum nesting soil in Hellshire is likely to restrict future iguana population growth.

Between 1991 and the early 2000s the core nesting population consisted of perhaps a dozen older adult animals. For example, 11 females were recorded as nesting in 1999 (JIRCG, unpublished data), a number very close to the nine documented as nesting (or observed gravid in the area) in 1991 (Vogel 1994). Up through 2003, no new (young adult) wild recruits had been observed. The first such wild recruit (PIT-tagged and released as a hatchling, and survived to adulthood) to the nesting population was documented in 2008 for a female that hatched in 2004, and may have been the first wild recruit in over a decade, as well as the youngest female known to have nested successfully. Also by 2004, headstarters were beginning to comprise a significant proportion of the nesting population (28%). By 2013, headstarters comprised ~ 80% of the nesting population, with remnants of the original (1990s) cohort and a small number of recent wild recruits making up the remainder (Fig. 8).

The recruitment of new wild females into the nesting population has been far less dramatic than the accelerated enlistment resulting from the repatriation of headstarters. We know of only four females that matured in the wild and nested successfully, but this is significant and presumably reflects improved juvenile survival prospects owing to predator control. However encouraging, the small number of wild recruits underscores the persistence of high mortality on hatchling and juvenile iguanas, and the population's dependence on continued predator control efforts and sustained headstart releases.

Implications of Global Climate Change.—Jamaica's recent climate history has followed global and Caribbean trends of warmer temperatures, increased frequency of rainfall extremes and storm events, and rising sea levels (CSGM 2012). Mean annual temperatures are projected to increase by 2.8–4.3° C for the region that includes the Hellshire Hills, and the current drying trend is predicted to be most extreme (28–52% annual decrease) in the eastern part of the island. Increased temperatures have already been implicated in tropical lizard extirpations (Sinervo et al. 2010), and decreased rainfall negatively impacts lizard populations by reducing growth rates and productivity through a reduction in food and moisture availability (e.g., Tanaka and Tanaka 1982; Vogel 1984; Holmgren et al. 2001). Tropical storms and hurricanes can have immediate and delayed effects on species and habitats (e.g., Lugo 2008; Zimmerman et al. 2014).

This climate change scenario is not encouraging, and could have negative consequences for the iguana in the present century. Obvious mitigation measures include eliminating tree cutting and halting the construction of new roads or other developments in Hellshire. In addition, conserving coastal mangroves will help maintain the quality of coastal habitats that served as iguana habitat before the species became restricted to the rugged limestone interior. Such coastal habitats contain abundant nesting habitat (e.g., sandy soils) and represent prime areas into which a recovering iguana population could expand. Rather than presenting another stumbling block to the iguana's recovery, the specter of climate change should catalyze more definitive action to combat illegal tree cutting and other threats to Hellshire, and perhaps even improve environmental conditions in the short term.

Assessing project efficacy: addressing major threats to the iguana's persistence.—Woodley (1971) was the first to articulate clearly the major threats to the iguana's survival: (1) non-native mammalian predators; (2) illegal tree cutting and production of charcoal; and (3) large-scale development projects. Woodley (1971) also formalized the concept of restoring the Goat Islands through IAS eradications and selected species introductions. Those same major threats, as well as the Goat Islands restoration proposal, were reiterated in the original conservation strategy for the species (Vogel et al. 1996), and have been highlighted in all subsequent management or recovery plans for the species (e.g., NEPA 2003; Grant et al. 2013). Appropriately then, we briefly summarize progress in mitigating those well-known threats, and also report on developments relating to the long-awaited re-establishment of an iguana population on the Goat Islands – an effort that is "arguably the most decisive single action that can be taken to safeguard the species from extinction" (Wilson 2011).

Threat (I): IAS predators. Our predator control program has been effective at reducing the density of the mongoose in particular, and in combination with headstarting, appears to have been responsible for the remarkable population growth of the Jamaican Iguana. We therefore advocate similar control programs to recover threatened (prey) species in cases where resources are available for *in situ* conservation efforts. And while the cost and effort required for implementing a trap-removal program can be considerable, an appropriately scaled effort can be incorporated into an existing *in situ* conservation program with little additional cost. The work required to maintain a trap-removal campaign is not appealing to all field personnel, which perhaps accounts for the paucity of previous control efforts, even in cases where IAS predators have been identified as the leading cause of a species' endangerment. Appropriately conducted live cage trapping (with targeted removal) not only reduces the impact of IAS, but can also provide a useful technique for monitoring populations of threatened species.

Although live cage trapping has proven to be extremely effective in reducing the density of the mongoose, feral cats remain a serious problem in Hellshire. Current cage trapping efforts are effective at removing some but not all cats, and those that remain represent a significant threat to young iguanas and other threatened wildlife species. Our limited use of leg-hold traps targeting cats was effective, but also resulted in the incidental death of an iguana. Hence, in the absence of a significant increase in resources and trained personnel to deploy and check traps regularly, a sustained leg-hold trapping campaign is beyond the project's current capacity; this, owing to the high risk to non-target species during both the day (e.g., iguana) and at night (e.g., Jamaican Coney). However, pulsed leg-hold trapping efforts conducted over discrete time periods could be extremely effective, especially if conducted by expert trappers during optimal season(s). Overall, we advocate the continued use of live cage traps, especially given their utility in monitoring the iguana population

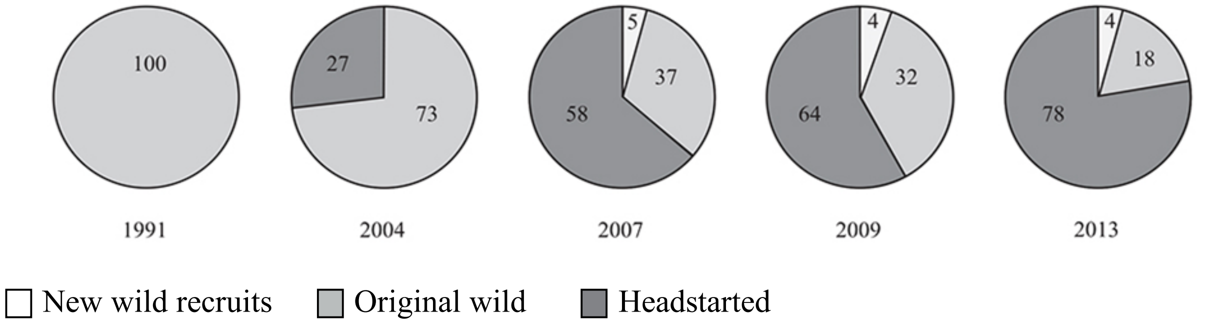

FIGURE 8. Changes (shown as percentages) in the composition of nesting Jamaican Iguanas in the Hellshire Hills between 1991 and 2013. Data include only females accurately identified and do not reflect numbers of estimated nesters in Figure 6.

(e.g., > 350 captures in 2013), and the relatively low risk posed to non-target species. In addition, current cage trapping efforts could be improved through camouflaging or burying traps, or by the use of other techniques known to enhance the success of trapping efforts targeting feral cats (e.g., pre-baiting, use of attractants). Finally, emerging technologies for taxon-specific toxicants or bio-control agents should be consulted as an obvious component of any adaptive conservation plan for the Jamaican Iguana.

Threat (II): Charcoal burning. Illegal tree cutting associated with charcoal production continues to degrade remaining intact portions of the Hellshire forest, and the prospects for active enforcement of existing laws seem as elusive in 2014 as ever before, despite Hellshire and the Goat Islands being included in the recently (1999) declared PBPA. Not surprisingly, both of the entities that were delegated management authority for the PBPA submitted management plans that included measures to protect the remaining Hellshire forest from tree cutting associated with charcoal production. To date, unfortunately, protection and enforcement efforts on the part of the delegated managers have ranged from woefully inadequate to altogether absent. In 2012, chain saws were heard from the field station ("South Camp") for the first time in the project's history, and in 2013 active charcoal kilns within 1 km of the core iguana area were documented from a helicopter (Fig. 9; van Veen et al. 2014). Though both incidents were reported to the authorities, no effective action was ever taken. Similarly, reports of commercial-scale charcoal production elsewhere in Hellshire have failed to elicit effective enforcement response from the relevant management authorities (Fig. 9).

Threat (III): Large-scale development projects. Despite the declaration of protected status for the PBPA in 1999, inclusive of the iguana's entire remaining Hellshire habitat and both of the Goat Islands, the area continues to be considered for large-scale development projects promoted by the Jamaican government – projects that would result in massive habitat loss and degradation, and likely lead to the iguana's extinction in the wild.

Development, primarily for housing, has continued on the eastern side of Hellshire since the 1960s. Fortunately, government plans (also dating back to the 1960s) to construct a large community in the center of Hellshire never came to fruition, and development has generally been restricted to the vicinity of roads created decades ago. But proposals for large-scale tourism along Hellshire's isolated, central beaches have surfaced with some regularity in recent decades. Those beaches fringe the iguana's remaining habitat, and even modest development along the coast would likely doom the iguana due to the construction of access roads and the resulting influx of both people and IAS predators (see Iverson 1978).

The "Goat Islands Project": Biodiversity refuge or Chinese mega-port?—The rehabilitation of the Goat Islands through IAS eradications and the re-introduction of the iguana has long been viewed as perhaps the only hope for ensuring the persistence of the species in the wild. This is the view shared by local experts in Jamaica and by international conservation and iguana researchers (e.g., the IUCN SSC Iguana Specialist Group). First articulated in the "Woodley Report" (1971), the Goat Islands restoration project has: (1) appeared in every subsequent species recovery plan for the iguana (e.g., Vogel et al. 1996; Grant et al. 2013); (2) been featured in various management plans for the PBPA; and (3) is listed as a high priority objective in the Jamaican government agency's National Strategy and Action Plan on Biodiversity (NEPA 2003). The overall restoration effort would include re-introduction of several other threatened endemic species (e.g., Jamaican Coney, Jamaican Skink,

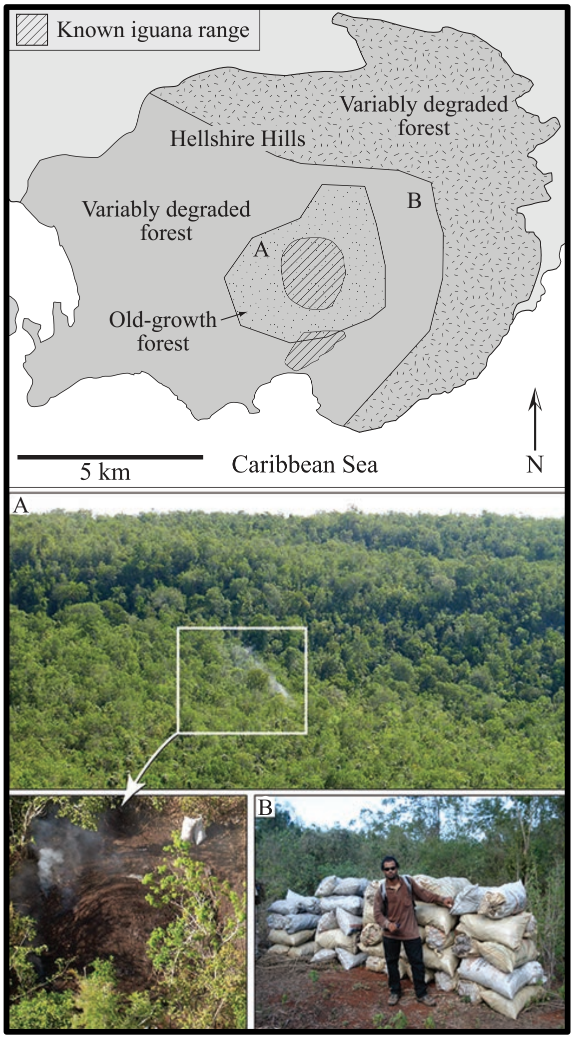

FIGURE 9. Active charcoal kiln less than one km from the core Jamaican Iguana area in western Hellshire in 2013 (A), and evidence of commercial charcoal production in eastern Hellshire in 2011 (B). See Fig. 1 for a description of the "Variably Degraded" habitat designation. (Photographed by Jeremy Francis (A) and Machel Emanuel (B)).

Jamaican Boa, and Blue-tailed Galliwasp). Removing IAS predators such as the mongoose from the islands would also benefit threatened migrating and resident bird species in the area (Island Conservation, Report to the Urban Development Corporation 2007). This restoration would have constituted the most significant single conservation intervention ever achieved in the Caribbean region and could have generated significant ecotourism benefits.

Unfortunately, recent development proposals have threatened the implementation of this obvious, long-acknowledged conservation imperative. The islands themselves are under government control/ownership, and their use and future is assigned to the Urban Development Corporation (UDC). The UDC is a quasi-government (i.e., government-appointed board) entity and is responsible for the management and development of the island's government-owned properties. In spite of lobbying by the JIRG and international conservation organizations (including the IUCN) over many years, the UDC was ultimately not willing to support initiatives aimed at creating a biodiversity reserve on the Goat Islands; rather, various plans to develop or sell/lease the islands were apparently considered, often surfacing after a change in the elected government and the resulting change in the composition of the UDC Board.

The most recent proposal involves the sale or lease of the Goat Islands and adjacent lands, possibly including sections of western Hellshire, to a state-run Chinese development company, China Harbour Engineering Company (CHEC; Goldenberg 2014; Grant 2014; Moore 2014). There have been reports in the international media that CHEC's parent company, China Communications and Construction Company (CCCC) is currently black-listed by the World Bank under its Fraud and Corruption Sanctioning Policy (Sri Lanka Guardian 2014; The World Bank 2011; Conniff 2014). CCCC appears on the list of firms barred from World Bank-financed contracts (The World Bank. 2014. Debarred and Cross-Debarred Firms and Individuals. Available from http://web.worldbank.org/external/default/main?theSitePK=84266&contentMDK=64069844&menuPK=116730&pagePK=64148989&piPK=64148984 [Accessed 25 September 2014]). Both Jamaica and China have received "unfavorable" ratings on the International Corruption Perception Index (Transparency International. 2014. Corruption Perception Index Available from http://www.transparency.org/research/cpi/overview [Accessed 29 August 2014]; see Boxill et al. 2007).

Although few specific details about the planned development have been announced (as of September 2014), the CHEC plans would apparently involve the conversion of the Goat Islands and its surrounding mangroves and coral reefs, into a massive transshipment port capable of accommodating the "New Panamax" ships in anticipation of the expanded Panama canal and proposed Nicaraguan canal (also a Chinese consortium development impacting protected areas; Hance 2014). Portions of the Hellshire mainland to the east and northeast of the Goat Islands would be incorporated into repackaging facilities and other industrial components of this port and the island's planned "logistics hub" initiative. If allowed to proceed, this project would completely destroy the Goat Islands, and the associated impacts on adjacent Hellshire would be severe. At the time of writing, NEPA has issued a license to CHEC for initial geotechnical investigation in the area and survey work has begun (see http://www.savegoatislands.org). Ultimately, this development would likely precipitate a cascade of extinctions and cripple the island's largest "protected" ecosystem.

RECOMMENDATIONS

(1) Continue current* in situ *and* ex situ *conservation efforts.—*Cyclura collei* is regarded as "conservation dependent", and in the absence of current management interventions (e.g., predator control, headstarting) the remnant population would likely be extirpated in the near future, perhaps within decades. Accordingly, continuation of high priority objectives for field and captive management (Grant et al. 2013) will be necessary to safeguard the species in the short term.

(2) Initiate Goat Islands restoration and iguana re-introduction program.—Long considered the only realistic hope for the Jamaican Iguana's persistence in the wild, this rehabilitation project should be commenced with urgency – especially given the unchecked threats to the iguana's remnant habitat in the Hellshire Hills.

(3) Enforce existing laws (e.g., Forestry Act, NRCA Act) in Hellshire Forest Reserve.—This is a government mandate, and is the single most important and conspicuously absent component of the recovery effort.

(4) Construct additional nesting sites in the predator-controlled core iguana zone.—The proven success of artificially constructed nesting sites, together with increasing competition for nesting access at existing (natural) areas, suggest that the construction of additional artificial nests would improve nesting success and further accelerate population growth.

(5) Conduct additional surveys to delimit the iguana's area of occupancy.—As an on-going exercise, surveys outside of the core area should be continued in an effort to detect previously unknown individuals or subpopulations, and to assess the possible establishment of repatriated headstarters that migrated away from their original release sites in the core area.

Acknowledgments.—This paper is dedicated to the memories of the late Peter Vogel and Edwin Duffus; without their early work this contribution would not have been possible. We also express major thanks to the Hellshire field team of Mark Gold, Leon Samson, Dennis Smith, and Kenroy Williams; they do the hard yards and represent the front line of defense for the iguana. We also thank the numerous volunteers who have assisted in the field or with health screening of the captive population, especially Dr. Nancy Lung and others from the Fort Worth Zoo, as well as representatives from the Audubon Nature Institute and the Dutch Iguana Foundation.

We are especially grateful to Diana McCaulay and Danielle Andrade at the Jamaica Environment Trust for editorial review. For recent financial support (2004–2013) we thank the Beneficia Foundation, Conservation International, Disney Worldwide Conservation Fund, Fresno Chaffee Zoo, Global Environment Facility (via the MTIASIC project), Houston Zoo Naturally Wild Conservation Fund, International Iguana Foundation, International Iguana Society, Mohamed bin Zayed Conservation Fund, and Zoo Miami. We also acknowledge the early financial supporters and members of the AZA Jamaican Iguana Species Survival Plan.

LITERATURE CITED

Alberts, A.C. 1993. The most endangered lizard in the world: the Jamaican Iguana, *Cyclura collei*. Vivarium 5:12–14.

Alberts, A. (Ed.). 2000. West Indian Iguanas: Status Survey and Conservation Action Plan. IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Baillie, J.E.M., and E.R. Butcher. 2012. Priceless or Worthless? The World's Most Threatened Species. Zoological Society of London, United Kingdom.

Boxill, I., R. Lewis, A. Russell, and A. Bailey. 2007. Political culture of democracy in Jamaica: 2006. Latin American Public Opinion Project, Vanderbilt University, Nashville, Tennessee, USA.

Bradley, K.A., and G.P. Gerber. 2006. Release of headstarted iguanas in Anegada, British Virgin Islands. Re-introduction News 25:14–16.

Burton, F.J. 2012. *Cyclura lewisi*. The IUCN Red List of Threatened Species. Version 2014.3. Available from http://www.iucnredlist.org/details/44275/0 [Accessed on 14 September 2014].

Campbell, K., and C.J. Donlan. 2005. Feral goat eradications on islands. Conservation Biology 19:1362–1374.

Campbell, K., G.S. Baxter, P.J. Murray, B.E. Coblentz, C.J. Donlan, and V. Carrion. 2005. Increasing the efficacy of Judas goats by sterilization and pregnancy termination. Wildlife Research 32:737–743.

Climate Studies Group, Mona (CSGM). 2012. State of the Jamaican climate 2012: information for resilience building (full report). Produced for the Planning Institute of Jamaica (PIOJ), Kingston, Jamaica.

Conniff, R. 2014. Jamaica to hand over heart of its largest protected area to black-listed Chinese conglomerate. Strange Behaviors. Available from https://strangebehaviors.wordpress.com/2014/04/22/jamaica-to-hand-over-heart-of-its-largest-protected-area-to-blacklisted-chinese-conglomerate/

Davis, S. 1996. Genetic studies of the Jamaican Iguana. Iguana Times (Journal of the International Iguana Society) 5:57.

Goldenberg, S. 2014. Iconic Jamaican Iguana under threat from $1.5bn Chinese port project – Development will destroy Jamaica's biggest nature reserve and fragile coastal areas, conservationists warn. The Guardian. Available from http://www.theguardian.com/environment/2014/may/23/jamaican-iguana-nature-reserve-china-port-project

Grant, T.D. 2012. Population analysis and breeding plan, Jamaican Iguana (*Cyclura collei*), Rock Iguana *Cyclura* Program, AZA Red Program. San Diego Zoo Institute for Conservation Research, San Diego, California, USA.

Grant, T.D. 2014. Biosphere Reserve to transshipment port: travesty for Jamaica's Goat Islands. IRCF Reptiles and Amphibians Conservation and Natural History 21:37–43.

Grant, T.D., R. Gibson, and B.S. Wilson. 2010. *Cyclura collei*. The IUCN Red List of Threatened Species. Version 2014.3. Available from http://www.iucnredlist.org/details/6027/0 [Accessed on 14 September 2014].

Grant, T., L. Pagni, and B. Wilson (Eds.). 2013. Jamaican Iguana: Species Recovery Plan, 2006–2013. IUCN SSC Iguana Specialist Group, IUCN, Gland, Switzerland.

Hance, J. 2014. The Gran Canal: will Nicaragua's big bet create prosperity or environmental ruin? Global Forest Reporting Network. Available from http://news.mongabay.com/2014/0827-gfrn-hance-nicaragua-canal.html

Holmgren, M., M. Scheffer, E. Ezcurra, J.R. Gutiérrez, and G.M.J. Mohren. 2001. El Niño effects on the dynamics of terrestrial ecosystems. Trends in Ecology and Evolution 16:89–94.

Hudson, R.D. 2006. The International Iguana Foundation: providing critical support to endangered iguanas. Herpetological Review 37:402–403.

Hudson, R.D., and A.C. Alberts. 2004. The role of zoos in the conservation of West Indian Iguanas. Pp. 274–289 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Iverson, J.B. 1978. The impact of feral cats and dogs on a population of the West Indian Rock Iguana*, Cyclura carinata*. Biological Conservation 14:63–73.

Jamaican Iguana Research and Conservation Group (Eds.). 1993. Population and Habitat Viability Assessment for the Jamaican Iguana (*Cyclura collei*). IUCN SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota, USA.

Lewis, C.B. 1944. Notes on *Cyclura*. Herpetologica 2:93–98.

Lewis, D.S., R. van Veen, and B.S. Wilson. 2011. Conservation implications of Small Indian Mongoose (*Herpestes auropunctatus*) predation in a hotspot within a hotspot: the Hellshire Hills, Jamaica. Biological Invasions 13:25–33.

Lugo, A.E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. Austral Ecology 33:368–398.

Lung, N.P., B.L. Raphael, J.C. Ramer, and T. Reichard. 2002. West Indian Rock Iguana conservation: the importance of veterinary involvement. Proceedings of the American Association of Zoo Veterinarians 2002:234–238.

McLaren, K., M. Lévesque, M. Sharma, B. Wilson, and M.A. McDonald. 2011. From seedlings to trees: using ontogenetic models of growth and survivorship to assess long-term (> 100 years) dynamics of a neotropical dry forest. Forest Ecology and Management 262:916–930.

Mittermeier, R.A., P.R. Gil, M. Hoffmann, M. Pilgrim, T. Brooks, C.G. Mittermeier, J. Lamoreux, G.A.B. da Fonseca (Eds.). 2005. Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. University of Chicago Press, Chicago, Illinois, USA.

Moore, R. 2014. Saving Goat Islands, Jamaica. National Geographic NewsWatch. Available from http://newswatch.nationalgeographic.com/2014/04/22/saving-goat-islands-jamaica/

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Proceedings of the National Academy of Sciences 102:18497–18501.

NEPA. 2003. National Strategy and Action Plan on Biological Diversity in Jamaica. National Environment and Planning Agency, Kingston, Jamaica.

Nogales, M., A. Martin, B.R. Tershy, C.J. Donlan, D. Weitch, N. Puerta, B. Wood, and J. Alonso. 2004. A review of feral cat eradication on islands. Conservation Biology 18:310–319.

Ricketts, T.H., E. Dinerstein, T. Boucher, T.M. Brooks, S.H.M. Butchart, M. Hoffmann, J.F. Lamoreux, J. Morrison, M. Parr, J.D. Pilgrim, et al. 2005. Pinpointing and preventing imminent extinctions. Proceedings of the National Academy of Sciences 102:18497–18501.

Searcy, R., L. Villers, R. Reams, J. Wyatt, III, and J. Pilarski. 2009. Captive reproduction of the Jamaican Iguana (*Cyclura collei*). Zoo Biology 28:343–349.

Serju, C. 2014. Bight betrayal – Environmentalists angered as gov't pulls back on biosphere recognition for Portland protected area. Jamaica Gleaner. Available from http://jamaica-gleaner.com/gleaner/20140106/lead/lead1.html

Sinervo, B., F. Mendez-de-la-Cruz, D.B. Miles, B. Heulin, E. Bastiaans, M. Villagran-Santa Cruz, R. Lara-Resendiz, N. Martinez-Mendez, M.L. Calderon-Espinosa, R.N. Meza-Lazaro, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–899.

Sloane, H. 1725. A Voyage to the Islands of Madeira, Barbados, Nieves, St. Christophers, and Jamaica with Natural History of the Herbs and Trees, Four-footed Beasts, Insects, Reptiles, etc. of the Last of Those Islands. Vol II. London, United Kingdom.

Soulé, M.E. 1986. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Inc. Sunderland, Massachusetts, USA.

Sri Lanka Guardian. 2014. World Bank banned China Harbour Engineering Company. Available from http://www.srilankaguardian.org/2014/02/world-bank-banned-china-harbour.html

Tanaka L.K., and S.K. Tanaka. 1982. Rainfall and seasonal changes in arthropod abundance on a tropical oceanic island. Biotropica 14:114–123.

The World Bank. 2011. World Bank applies 2009 debarment to China Communications Construction Company Limited for fraud in Philippines roads project. Available from http://www.worldbank.org/en/news/press-release/2011/07/29/world-bank-applies-2009-debarment-to-china-communications-construction-company-limited-for-fraud-in-philippines-roads-project

Tolson, P. 2000. Control of introduced species. Pp. 86–89 *In* West Indian Iguanas: Status Survey and Conservation Action Plan. Alberts, A. (Ed.). IUCN SSC West Indian Iguana Specialist Group, IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Van Veen, R., B. Wilson, T. Grant, and R. Hudson. 2014. Where to now? An uncertain future for Jamaica's largest endemic vertebrate. Oryx 48:169–171.

Vogel, P. 1984. Seasonal hatchling recruitment and juvenile growth of the lizard *Anolis lineatopus*. Copeia 1984:747–757.

Vogel, P. 1994. Evidence of reproduction in a remnant population of the endangered Jamaican Iguana, *Cyclura collei* (Lacertilia: Iguanidae). Caribbean Journal of Science 30:234–241.

Vogel, P., R. Nelson, and R. Kerr. 1996. Conservation strategy for the Jamaican Iguana, *Cyclura collei*. Pp. 395–406 *In* Contributions to West Indian Herpetology: A Tribute to Albert Schwartz. Powell R., and R.W. Henderson (Eds.). Society for the Study of Amphibians and Reptiles Contributions to Herpetology 12, Ithaca, New York, USA.

Wege, D.C., and A. Anadon-Irizarry (Eds.). 2008. Important Bird Areas in the Caribbean: Key Sites for Conservation. Birdlife Conservation Series No. 15, Birdlife International, Cambridge, United Kingdom.

Wilson, B.S. 2011. Conservation of Jamaican amphibians and reptiles. Pp. 273–310 *In* Conservation of Caribbean Island Herpetofaunas. Volume 2: Regional Accounts of the West Indies. Hailey, A., B.S. Wilson, and J.A. Horrocks (Eds.). Brill Academic Publishers, Leiden, The Netherlands.

Wilson, B.S., and P. Vogel. 2000. A survey of the dry forest herpetofauna of the Hellshire Hills, Jamaica, including the re-discovery of the Blue-tailed Galliwasp (*Celestus duquesneyi* Grant). Caribbean Journal of Science 36:244–249.

Wilson, B.S., A.C. Alberts, K.S. Graham, R.D. Hudson, R.K. Bjorkland, D.S. Lewis, N.P. Lung, R. Nelson, N. Thompson, J.L. Kunna, et al. 2004. Survival and reproduction of repatriated Jamaican Iguanas: headstarting as a viable conservation strategy. Pp. 220–231 *In* Iguanas: Biology and Conservation. Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.

Woodley, J.D. 1971. Hellshire Hills Scientific Survey, 1970. Research Report No. 1. Department of Zoology, University of the West Indies, Mona, Kingston, Jamaica.

Woodley, J.D. 1980. Survival of the Jamaican Iguana, *Cyclura collei*. Journal of Herpetology 14:45–49.

Zimmerman, J.K., J.A. Hogan, A.B. Shiels, J.E. Bithorn, S.M. Carmona, and N. Brokaw. 2014. Seven-year responses of trees to experimental hurricane effects in a tropical rainforest, Puerto Rico. Forest Ecology and Management 332:64-74.

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TANDORA D. GRANT received a bachelor's degree in Biochemistry and Molecular Biology from the University of California, Santa Cruz. Currently a Research Coordinator at the San Diego Zoo Institute for Conservation Research, her work has focused primarily on conservation recovery strategies for Caribbean iguanas, San Clemente Loggerhead Shrike, and the San Diego Coast Horned Lizard. Tandora serves as Program Officer for the IUCN SSC Iguana Specialist Group (ISG), as well as Red List Authority evaluating the conservation status for all iguana species. She is the Species Coordinator and Population Management Advisor for the AZA Species Survival Plans for Jamaican and Grand Cayman Blue Iguanas. Having developed studbooks for these species, she assesses genetic and demographic statistics to determine optimum captive breeding pairs and release candidates. She is incorporating molecular data in this analysis to further define the fitness of reintroduced populations and guide management actions. Most recently, she developed websites for the ISG, International Iguana Foundation, and the Save Goat Islands site providing information opposing development in Jamaican Iguana habitat. (Photographed by Jeffrey Lemm).

RICK VAN VEEN has worked with iguanas for more than a decade. He is an avid herpetologist, interested in natural history, ecology, invasive species ecology and management, conservation biology, and *in situ* conservation. He has worked with a diverse range of wildlife including crocodiles, sea turtles, frogs, snakes, macropods (kangaroos and wallabies), bats, seals, and penguins. He is also interested in feral animal management and has experience controlling exotic populations of pigs, cats, rats, mongoose, and dogs. Rick holds a Bachelor's of Zoology/Botany degree in Conservation Biology and Land Management from James Cook University, Townsville, Australia. Currently, he is a Ph.D. student at the University of the West Indies, Kingston, Jamaica, studying the ecology and conservation of the remaining wild population of the critically endangered Jamaican Iguana, *Cyclura collei*. Most recently, Rick has been working in Fiji with native Pacific Iguanas (*Brachylophus* sp.) and conducting eradication trials on the recently introduced invasive Common Green Iguana (*Iguana iguana*). (Photographed by Tandora Grant).

Rick Hudson earned a bachelor's degree in Biology from the University of Richmond in 1977 and began his career at the Fort Worth Zoo in 1980, where he has spent the past 34 years, first as Curator in the herpetology department, then moving to conservation and science in 2000. He was active in mobilizing reptile conservation programs under the Association of Zoos and Aquariums (AZA) and chaired their Lizard Advisory Group and Rock Iguana Species Survival Plan for many years. He also co-chaired the AZA Crocodile Advisory Group and the Field Conservation Committee. A long-time champion for West Indian Iguanas (*Cyclura*), most notably the Jamaican Iguana, Rick helped organize the Iguana Specialist Group in 1997 and served that group in a leadership capacity for many years. In 2001, he led the organization of the International Iguana Foundation (IIF) to provide sustainable funding to critical iguana conservation programs and today serves as their Executive Director. Since forming, the IIF has raised nearly $2 million for iguana conservation and supports programs throughout the Caribbean, Central America, and Fiji. (Photographed by John Binns).

Dawn Fleuchaus began her career as a zookeeper over 20 years ago. She received her Bachelor of Arts in Biology and Biological Aspects of Conservation from the University of Wisconsin, Milwaukee (1993). She developed skills in animal observation and handling at the Racine Zoo overseeing large cats, wolves, hoofstock, birds, and a variety of herps and small mammals. For the past 16 years, Dawn has worked as a Zookeeper and Area Supervisor at the Milwaukee County Zoo. She worked for a number of years in the small mammals building, then as the animal hospital area supervisor. She has been Area Supervisor of the North America and Australia areas for the past 11 years. She has been a member of the American Association of Zookeepers, the Association of Zoos and Aquariums, and the International Marine Animal Trainers Association. Through the generous support of the Milwaukee County Zoo and the Zoological Society of Milwaukee, Dawn has work with the Jamaican Iguana Recovery Group since 2002. Her annual fieldwork includes assisting in behavioral monitoring, morphometric data collection, and blood sampling. (Photographed by Kimberly Stephenson).

Orlando Robinson received a bachelor's degree in 1994 in Botany and Zoology from the University of the West Indies, Jamaica, and a master's degree in Natural Resource Management from the Universidad Nacional Pedro Henriquez Ureña, Santo Domingo, Dominican Republic, in 1999. He has been with Hope Zoo since August 2000, where he started as the Assistant Curator and a year later as the Curator. During his tenure at the Hope Zoo, he has seen various management changeovers from management by the central government to that of a non-governmental organization. Orlando's major role as curator has been the strategic development of the Hope Zoo's master plan with special emphasis on strengthening conservation, research, and education programmes both locally and internationally, through involvement with various stakeholders. His involvement with the Jamaica Iguana Recovery Group has been through the headstart programme where he oversees the husbandry of the captive-reared population, including the collection of biometric data. (Photographed by Nancy Lung).

Kimberly Stephenson received a bachelor's degree in Zoology and Environmental Physics from the University of the West Indies, Mona, and is currently a Ph.D. student whose work seeks to model the impact of climate change on arthropods and small reptiles in the dry limestone forest of the Hellshire Hills. As a graduate student, she conducts research through two research groups based at UWI, the Climate Studies Group, Mona (CSGM) and the Jamaican Iguana Recovery Group (JIRG). Her work with the CSGM has assessed climate across the Caribbean region using a number of observed and modeled data sources, and she currently assists with managing JIRG field operations in the Hellshire Hills. (Photographed by Dawn Fleuchaus).

Herpetological Conservation and Biology 11(Monograph 6):255–264.
Submitted: 13 September 2014; Accepted: 12 November 2015; Published: 12 June 2016.

GENETIC TOOLS FOR ASSISTING SUSTAINABLE MANAGEMENT AND CONSERVATION OF THE SPINY-TAILED IGUANA, *CTENOSAURA PECTINATA*

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***Abstract.*—The System of Management Units for the Conservation of Wildlife (Sistema de Unidades de Manejo para la Conservación de la Vida Silvestre, SUMA), regulated by the Mexican Ministry of Environment and Natural Resources, seeks the correct management and sustainable use of wildlife. The main tool used by SUMA is wildlife management units (UMAs) that harbor wildlife for several purposes (e.g., production, education, research, conservation, and exhibition). *Ctenosaura pectinata,* a threatened Mexican endemic spiny-tailed iguana, is legally managed through UMAs, some of them harboring individuals that were unwanted pets or confiscations of unknown origin. Facilities may become overcrowded, as iguanas cannot be returned to the wild without knowledge of their origins. This may lead to irresponsible or accidental releases of individuals or their captive-born offspring into the wild; a potential source of genetic contamination to local populations. To promote proper management of captive individuals and to evaluate their potential reintroduction into the wild, we created and tested a distribution-wide database to identify the origin of 24 confiscated individuals harbored in two UMAs in México. We compiled mtDNA and microsatellite data derived from previous studies, including 341 individuals from 49 localities. We applied two Bayesian methods for population genetic assignment using the database as a baseline. In several cases, it was possible to narrow down the potential geographic region of origin when considering mtDNA together with the microsatellite data. The database is potentially a useful resource for authorities and conservation organizations.**

***Resumen.*—El Sistema de Unidades de Manejo para la conservación de la Vida Silvestre (SUMA), regulado por la Secretaría del Medio Ambiente y Recursos Naturales en México, busca el manejo correcto y el uso sustentable de la vida silvestre. El instrumento principal que usa SUMA son las unidades de manejo de vida silvestre (UMAs) que albergan vida silvestre con diferentes propósitos (e.g., producción, educación, investigación, conservación, y exibición). La iguana negra *Ctenosaura pectinata* es una especie amenazada y endémica de México que es manejada a través de UMAs, algunas de las cuales albergan iguanas que fueron mascotas indeseadas o decomisadas, de origen desconocido. Las instalaciones pueden llegar a superpoblarse al no poder regresar las iguanas a su hábitat sin saber de dónde vienen. Esto puede llevar a liberaciones irresponsables o escapes de individuos o su descendencia nacida en cautiverio, constituyendo así una fuente potencial de 'contaminación genética' para las poblaciones locales. Para promover el manejo adecuado de los individuos en cautiverio y evaluar la posibilidad de su liberación en su hábitat, creamos una base de datos que cubre la distribución entera de la especie, para identificar el sitio de origen de 24 individuos confiscados y albergados en dos zoológicos en México. Recopilamos datos de DNA mitocondrial y microsatelital derivados de estudios previos que incluyen 341 individuos de 49 localidades. Empleamos dos métodos bayesianos de asignación genética de poblaciones usando la base de datos como referencia. En algunos casos fue posible reducir el número de potenciales regiones geográficas de origen cuando se usa la información mitocondrial y microsatelital conjuntamente. La base de datos es potencialmente un recurso útil para las autoridades y organizaciones involucradas en la conservación de la especie.**

Key Words.—Garrobo de Roca; genetic assignment; Guerreran iguanas; México; microsatellites; mtDNA; wildlife management units.

INTRODUCTION

Conservation genetics involves the application of evolutionary and molecular genetics to biodiversity conservation (Frankham 2010). Among other applications, conservation genetics contributes to: (1) resolving taxonomic uncertainties; (2) defining evolutionary divergent units that require separate management; (3) managing to minimize inbreeding, loss of genetic diversity, and extinction risk; (4) obtaining important information for species conservation (e.g., demographic parameters and history, mating system, gene flow, parentage, etc.); and (5)

Zarza, Eugenia, Víctor H. Reynoso, and Brent C. Emerson. 2016. Genetic tools for assisting sustainable management and conservation of the spiny-tailed iguana, *Ctenosaura pectinata*. Pp. 255–264 *In* Iguanas: Biology, Systematics, and Conservation. Iverson, J.B., T.D. Grant, C.R. Knapp, and S.A. Pasachnik (Eds.). Herpetological Conservation and Biology 11(Monograph 6).

forensics (Frankham 2010). Conservation genetics takes advantage of molecular and analytical techniques to quantify and understand the distribution and dynamics of genetic diversity. One such analytical approach is genetic population assignment. This consists of assigning reference populations as possible origins of individuals on the basis of multilocus genotypes (Piry et al. 2004; Latch et al. 2006). This procedure has been widely used in conservation genetics of iguanas and other organisms to understand patterns of migration (Paetkau et al. 2004; Lanterbecq et al. 2010; Colosimo et al. 2014; Wang 2014), to identify hybrid individuals (Pierpaoli et al. 2003; Barilani et al. 2005; Vähä and Primmer 2006), to address illegal species trading, hunting and fishing (Frantz et al. 2006; Wasser et al. 2008; Nielsen et al. 2012; Gentile et al. 2013), to identify past translocations and inform repatriation of individuals (Tzika et al. 2008), and to identify the origin of captive individuals to inform release of species to their habitat (Russello et al. 2007). Baseline information on the genetic composition and structure of the species populations is thus required to obtain reliable results.

Here we apply genetic population assignment methods to identify potential source populations of captive individuals of unknown origin, of the threatened spiny-tailed iguana, *Ctenosaura pectinata*. We aim to improve management of captive individuals and to advise on their potential release into the wild. In the following we summarize background information and the outcomes of evolutionary and molecular genetic studies on *C. pectinata*. The latter of which provide the baseline genetic information for this study.

Ctenosaura pectinata.—Our model species is one of the nearly 500 reptilian species endemic to México (Flores-Villela and García-Vazquez 2014). It is found from 0 to 1,000 m above sea level within the tropical lowlands along the Pacific coast and in the Río Balsas basin in central México, with populations also on the Marías and Isabel islands in the Pacific Ocean. It is found primarily in the seasonally dry tropical deciduous forest (SDTDF), but it can also be found in thorny forests, grasslands, oak forest, mangrove, and coastal dunes, and is sometimes associated with human settlements (Suazo and Alvarado 1994). This species exhibits sexual dimorphism, with males bearing a dorsal spiny crest and being generally bigger than females, reaching up to one meter in total length. They show ontogenetic color change, with hatchlings being green and becoming darker when adults (Köhler 2002), who exhibit a vast range in coloration (Fig. 1).

Currently, Mexican Law NOM-059-ECOL-2010 (SEMARNAT 2010) lists *C. pectinata* as threatened ('amenazada'), meaning that it may be at risk of extinction in the short or medium term, if action to mitigate threats is not taken. This species is economically and culturally important for some rural communities, as they are used as food, traditional medicine, pets, and their skin is used to produce handicrafts. The traditional practice of hunting gravid female *C. pectinata* just before they lay their eggs is particularly threatening because it leads to rapid population decline (Aguirre-Hidalgo 2007). This is aggravated by the predominance of single paternity, which makes the species susceptible to rapid loss of genetic variation (Faria et al. 2010). Additionally, the anthropogenic transformation of 71% of the original area of the SDTDF in México, and the protection of only 0.2% of the remaining area (Portillo-Quintero and Sánchez-Azofeifa 2010) challenge the survival of this species.

Ctenosaura pectinata is comprised of nine cryptic mtDNA lineages: North A, North B, North C, North D,

FIGURE 1. Examples of color variation in *Ctenosaura pectinata* across its geographic distribution in México. (Photographed by Víctor H. Reynoso and Eugenia Zarza).

Colima, Balsas, Guerrero, Oaxaca and South (Zarza et al. 2008, 2011). Genetic distances (Tamura and Nei 1993) between these lineages range from 4.11 to 11.57% (Zarza et al. 2008). The deepest genetic distance occurs between overlapping clades from the Central Western Coast of México (North and Colima clades). Further, multilocus studies uncovered two microsatellite genotypic clusters that are geographically discordant with the distribution of four mtDNA lineages (i.e., North C, North D, Colima, and Balsas; Zarza et al. 2011). Several processes might account for this discordance. Differences in effective population size between mtDNA and nuclear markers could lead to faster lineage sorting of maternal lineages than of nuclear markers, resulting in the observed discordance. However, after correcting for effective population size, Zarza et al. (2011) could not entirely account for the differences in genetic structure. The observed pattern is consistent with historic secondary contact and hybridization of once genetically distinct lineages. Previously isolated lineages of other taxa have come into secondary contact in central western México (Devitt 2006), suggesting that introgressive hybridization might not be a rare process in the evolution of species in this region.

These recently described genetic clusters within *C. pectinata* have restricted distributions and divergent evolutionary histories, however when individuals from different clusters come into contact they may mate and produce fertile offspring (Zarza et al. 2008, 2011). Accidental or intentional introductions could lead to mating of individuals with different genetic backgrounds and thus introgression. While recent research suggests that introgression can sometimes have adaptive outcomes (Kronforst 2012; Pardo-Diaz et al. 2012), it can also lead to a loss of local adaptation and outbreeding depression (Gentile et al. 2013). Conservation strategies that utilize genetic information alongside the biology of the species and its threats are urgently needed to protect the unique evolutionary history, adaptations, and ecological role of *C. pectinata*.

The Mexican Ministry of Environment and Natural Resources (SEMARNAT) implemented the System of Management Units for the Conservation of Wildlife (Sistema de Unidades de Manejo para la Conservación de la Vida Silvestre, SUMA), that aims to reach a balance between wildlife conservation and the needs of the people. Within this system, Wildlife Management Units (UMAs) function as breeding, research, education, and training centers among other things (SEMARNAT, Sistema de Unidades de Manejo para la Conservación de la Vida Silvestre. Available from http://www.semarnat.gob.mx/temas/gestion-ambiental/vida-silvestre/sistema-de-unidades-de-manejo [Accessed 1 December 2015]). For example, all zoos and iguana breeding facilities (iguanarios) are UMAs. SUMA guidelines discourage the inclusion of animals from geographic regions outside of where a given UMA is located, however this is not always adhered to. Some UMAs harbor individuals that were unwanted pets or confiscations, lacking origin information. In some cases these facilities become overcrowded or unsuitable, and irresponsible or accidental releases of individuals or their captive-born offspring could occur. This could in turn result in genetic contamination of local populations through interbreeding between individuals with different genetic backgrounds, leading to outbreeding depression.

To promote proper management of *C. pectinata* captive individuals, and to provide information for their potential release into the wild, we created a genetic database using data generated by previous studies (Zarza et al. 2008, 2011; Faria et al. 2010). We then tested the utility of our database for genetic population assignment, which consists of assigning reference populations as possible origins of individuals on the basis of multilocus genotypes (Piry et al. 2004; Latch et al. 2006). We focused on *C. pectinata* individuals held in two UMA zoos in México and applied two Bayesian clustering approaches. This is a direct application of a large-scale genetic survey that could serve as a model in other vertebrate species facing similar threats.

MATERIALS AND METHODS

Field and laboratory work.—We created a geo-referenced database comprised of microsatellite genotypes for 341 individuals across eight loci, and mtDNA sequence data (ND4) for 317 individuals, collected across 49 sites covering the entire distribution of *C. pectinata* and part of the distribution of *C. acanthura*, which appears nested within *C. pectinata* (see Zarza et al. 2008). We excluded localities in northern México where *C. pectinata* and *C. hemilopha* co-occur and hybridize (Zarza Franco 2008) to avoid the inclusion of *C. hemilopha* alleles that may confound population genetic assignment. Previous molecular and evolutionary studies detail the protocols used to purify, genotype, sequence, and analyze these samples (Zarza et al. 2008, 2009, 2011; Zarza Franco 2008; Faria et al. 2010).

To test the utility of our database for population assignment we collected 0.15 ml blood samples from the caudal vein of *C. pectinata* individuals harbored in the Zoológico de Morelia, Morelia, Michoacán (*n* = 15; 100% of the population in the zoo) and in Zoológico Zoochilpan in Chilpancingo, Guerrero (*n* = 9; approximately 50% of the adult population in the zoo), in 2006. Iguanas were captured by hand or by noosing. We applied the same laboratory and analytical procedures to these 24 samples as those that were used for the reference database, and provide a brief summary below.

We extracted genomic DNA using a modified salt precipitation protocol (Aljanabi and Martinez 1997). We PCR amplified and sequenced a 561 bp fragment of the mitochondrial ND4 gene using the primers ND4, ND4Rev (Arèvalo et al. 1994), ND4F1 (Zarza et al. 2008) and ND4R623 (Hasbún et al. 2005) with conditions described in Zarza et al. (2008). We genotyped the captive samples with twelve microsatellite markers. We individually PCR amplified loci Pec01, Pec03, Pec20, Pec21, Pec24, Pec25, Pec89, TNB1 with conditions described by Zarza et al. (2009). We PCR amplified locus Cthe37 using protocols described by Blázquez et al. (2006). We PCR amplified loci Pec16 and Pec73 (Zarza et al. 2009) together with Cthe12 (Blázquez et al. 2006) in a multiplex reaction described in Zarza et al. (2011). We combined the PCR products of the 12 loci in two different mixes that allow loci to be distinguished according to fluorescent dye and allele size (Zarza et al. 2011). The two mixes were run independently in an automated ABIprism 3730 and peaks were visualized with GeneMapper software version 4.0 (Applied Biosystems, Foster City, California, USA).

Data analyses.—We took a phylogenetic tree estimation approach to infer the mtDNA haplotype relationships of the zoo individuals. The analyses included all the haplotypes currently known for *C. pectinata* available from GeneBank plus the haplotypes of the confiscated individuals. We aligned the mtDNA sequences with MUSCLE (Edgar 2004). We searched for the best tree with maximum likelihood inference and performed 1,000 bootstrap replicates with RAxMLv8 (Stamatakis 2014) to assess the statistical support for each node.

We performed genetic population assignment of individuals based on microsatellite frequencies with two Bayesian clustering approaches that do not require *a priori* grouping of individuals: BAPS (Corander and Marttinen 2006; Corander et al. 2008) and STRUCTURE (Pritchard et al. 2000; Hubisz et al. 2009). These methods allow individuals to be of mixed ancestry, proportionally assigning an individual genome to clusters defined while minimizing Hardy-Weinberg and linkage disequilibrium (Latch et al. 2006).

We ran simulations with STRUCTURE v2.3.2 under the admixture model assigning a uniform prior for the parameter Alpha (degree of admixture) and estimating the allele frequency parameter (Lambda) assuming correlated allele frequencies and without taking into account knowledge on locality. We ran preliminary analyses including the entire dataset (i.e., 341 individuals) plus the 24 individuals of unknown origin, under K = 2 – K = 10 for one million MCMC iterations and 10 replicates. Likelihood values plateaued after K = 4, with some K = 4 – K = 6 runs giving alternative but biologically meaningful clustering

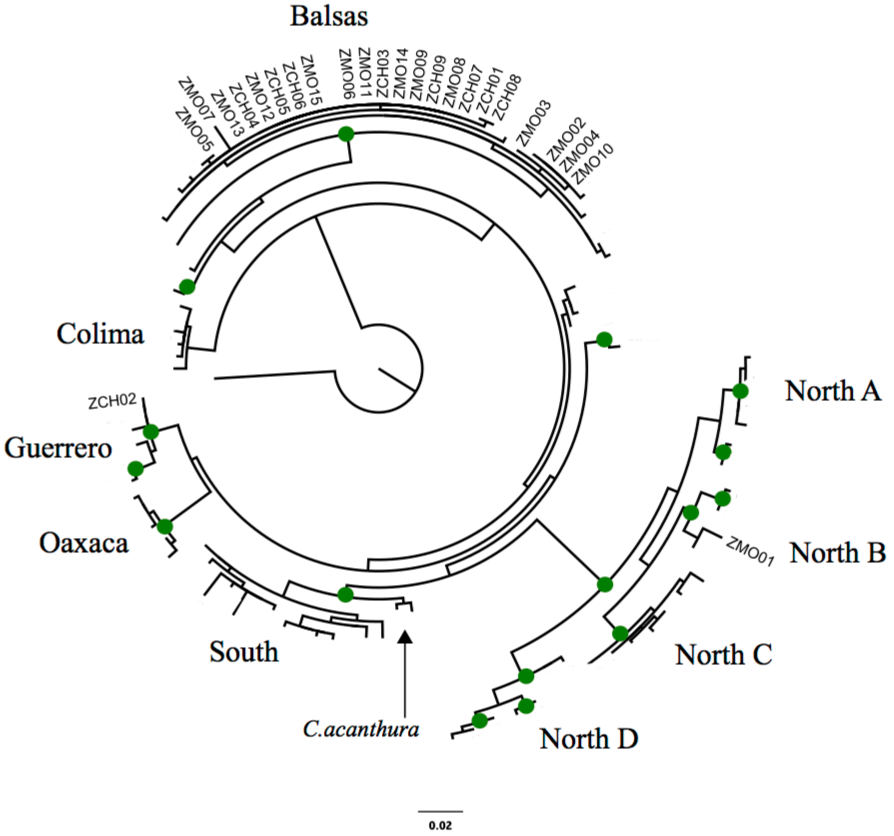

FIGURE 2. Maximum likelihood tree showing the relationship of *Ctenosaura pectinata* mtDNA haplotypes sampled in wild populations (unlabeled tips) and each captive individual (labeled tips). Statistically supported nodes (bootstrap > 80%) are marked with green circles. Haplotypes of captive individuals are labeled as ZM- (Zoológico de Morelia) and ZCH- (Zoológico Zoochilpan). Clade names correspond to those used in Zarza et al. (2008).

patterns (e.g., concordance with the distribution of some mtDNA clades, presence of geographical barriers). However, in the very north and very south of the distribution, clustering was not consistent among all the runs for each K, perhaps as a result of isolation by distance (Frantz et al. 2006). This will be further investigated in a future publication. As the zoo samples were consistently not assigned to any of these 'problematic' regions, we removed the most northern and southern localities (Sinaloa, Oaxaca, and Veracruz samples) and worked with a reduced data set (Fig. 2; supplementary material available on request) and the captive individuals, however the entire database is available upon request. This allowed us to investigate potential substructure in the central coastal and inland area of the distribution with the benefit of reduced computation time required for the assignment. We performed ten iterations for each value of K (K = 2 – K = 4) with one million MCMC replicates after a burn-in period of 100,000. We chose the most likely K using the Evanno et al. (2005) method. For each confiscated and wild individual, we averaged their proportion of ancestry (Q value) among the results of the ten iterations under the most likely K. This served to genetically characterize each locality and to compare its composition with the proportion of ancestry of the confiscated individuals and infer their potential origin. Previous studies have employed Q values between 0.75 and 0.90 to assign individuals to a population (Vähä and Primmer 2006; Schwartz and Karl 2008; Wilkinson et al. 2011; Winkler et al. 2011). In these studies, individuals with lower Q values were assigned to different hybrid categories. We used a stringent value of Q = 0.9 as the threshold for population assignment.

Additionally, we applied the trained clustering

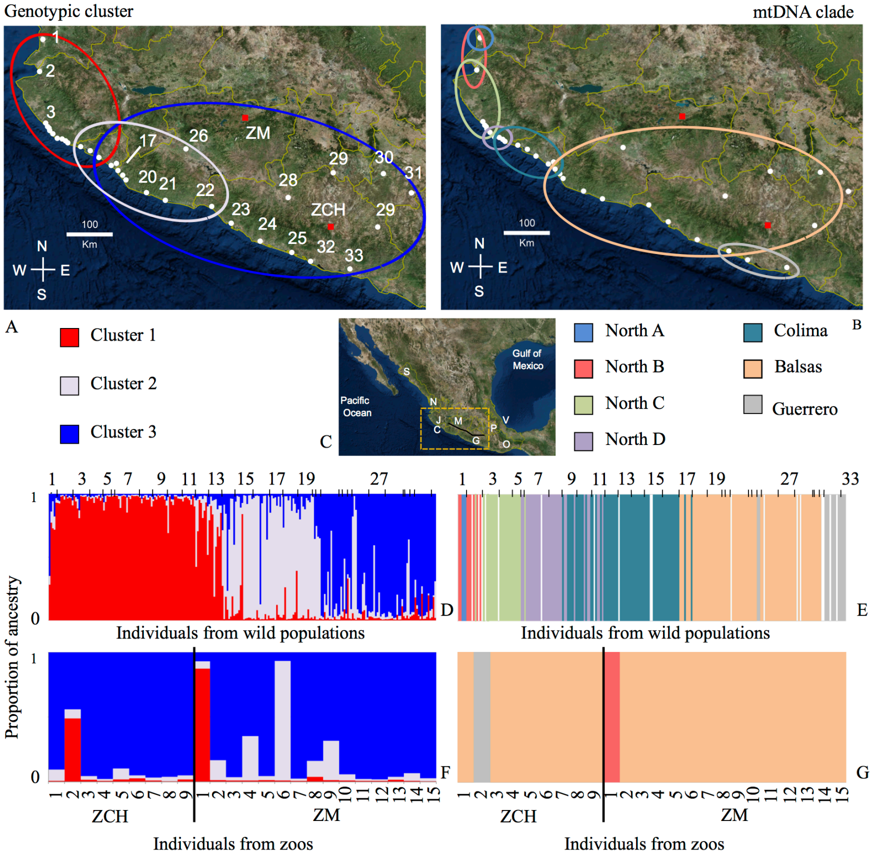

FIGURE 3. Geographic setting, sampling, and genetic population assignment of *C. pectinata* captive individuals from México. (A) Geographic distribution (ovals) of genotypic clusters inferred with STRUCTURE, and wild individual sampling localities (white dots). For simplicity only some localities are numbered. The location of Zoológico de Morelia (ZM) and Zoológico Zoochilpan (ZCH) are marked as red squares. Details of localities are listed in supplementary material available on request. (B) mtDNA clade distribution and sampling localities as in A. (C) Map of México with state names relevant for this study (S: Sinaloa; N: Nayarit; J: Jalisco; C: Colima; M: Michoacán; G: Guerrero; O: Oaxaca; P: Puebla; V: Veracruz), reduced data set geographic area (yellow square, as highlighted in A and B) and location of the Balsas Depression (black line). (D) STRUCTURE plot showing three clusters in the wild populations reduced dataset, each bar represents an individual's proportion of ancestry (Q value). For simplicity only some localities are numbered. (E) Bar plot showing mtDNA haplotype clade of each individual collected in wild populations; white bars are missing data. For simplicity only some localities are numbered. (F) Proportion of ancestry of the confiscated individuals harbored in two UMA zoos. (G) mtDNA haplotype of confiscated individuals harbored in zoos. In Fig. F and E, individuals collected in Zoológico Zoochilpan are shown on the left side of the black line (ZCH 1–9); individuals collected in Zoológico de Morelia are shown on the right side of the black line (ZM 1–15). Map sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, the GIS User Community, INEGI, and CONABIO.

algorithm implemented in BAPS v6 (Corander et al. 2008), which uses baseline populations that include individuals of known origin to perform population assignment of individuals of unknown origin. To create the training data set, we combined microsatellite genotypes and mtDNA clade information of the 341 reference individuals, where each mtDNA clade was coded as diploid data with one unknown allele. We then input genotype and mtDNA information of the confiscated individuals to perform the assignment to any of the baseline populations. We performed five replicates and confirmed assignment consistency and likelihood variation among runs.

RESULTS

Individuals of unknown origin carried mtDNA haplotypes of the clades North B, Balsas, or Guerrero (Fig. 2). The STRUCTURE analyses suggest that there are three genetic clusters in the reduced dataset (Fig. 3A). These clusters are found from the state of Nayarit to Guerrero on the Pacific lowlands and the Balsas Depression (Fig. 3A, 3C). Ten of the 15 individuals harbored at Zoológico de Morelia were assigned to clusters 1, 2, or 3, with Q > 0.90 of ancestry, and three more individuals would have been assigned if we had used a less stringent, but acceptable threshold (Q > 0.80; Table 1). With this method alone it was not possible to pinpoint a specific locality due to the inherent genetic homogeneity of the genetic clusters. However, given the geographic discordance between mtDNA and nuclear markers, when using both types of information, it is possible to narrow down the potential localities of origin. For example individual ZM01 has an mtDNA haplotype that is only found in localities 1 and 2 (Fig. 3B, 3E, 3G) with a genotype matching that of individuals in those localities. This interpretation is consistent with the outcome of BAPS, which assigns this individual to locality 2 (Table 1). Similarly, individual ZM06 has an mtDNA haplotype belonging to the Balsas clade, which is widespread in central México (localities 17–30; Fig. 3B), with its genotype belonging to cluster 2. This narrows down the possible localities of origin to sites where the combination of individuals with cluster 2 genotypes and Balsas clade mtDNA haplotypes occurs (i.e., localities 17–21 and 25–26; Fig. 3A). BAPS assigns this individual to localities 21 and 30 with equal probability. The assignment to locality 30 is probably due to a relatively low number of individuals collected in this locality (*n* = 3).

Individuals ZM04 and ZM09 show mixed ancestry with around 0.34 of their genome belonging to cluster 2 and around 0.64 to cluster 3 (Table 1). Although in the wild there are individuals with mixed ancestry, there are no localities with a high number of individuals with the above-described combination of ancestry, only some individuals collected in localities 22–26 and 30 (Fig. 3;

TABLE 1. Genetic population assignment of *Ctenosaura pectinata* individuals harbored in UMA zoos, in México, based on: (1) their proportion of ancestry (Q value) estimated with STRUCTURE (Clusters 1–3); (2) mtDNA clade they belong to as inferred with RAxML; and (3) locality number of origin assigned with BAPS. Cluster 1 is depicted in red, Cluster 2 in pink, and Cluster 3 in blue, and shown in Fig. 2A, 2D, and 2F. ZCH = samples collected in Zoochilpan Zoo; ZM = samples collected in Zoológico de Morelia.

Sample	Cluster 1 ancestry	Cluster 2 ancestry	Cluster 3 ancestry	mtDNA clade	BAPS assigned locality
ZM01	0.87	0.06	0.07	North B	2
ZM02	0.01	0.15	0.83	Balsas	26, 27
ZM03	0.01	0.03	0.96	Balsas	27, 28
ZM04	0.01	0.34	0.65	Balsas	22
ZM05	0.01	0.03	0.96	Balsas	28
ZM06	0.01	0.92	0.07	Balsas	21, 30
ZM07	0.01	0.02	0.98	Balsas	27
ZM08	0.04	0.12	0.84	Balsas	25, 26
ZM09	0.01	0.31	0.68	Balsas	21
ZM10	0.01	0.05	0.94	Balsas	22
ZM11	0.01	0.01	0.98	Balsas	27
ZM12	0.01	0.01	0.98	Balsas	26, 27
ZM13	0.02	0.02	0.96	Balsas	27
ZM14	0.01	0.06	0.93	Balsas	26, 27
ZM15	0.01	0.02	0.97	Balsas	26, 27
ZCH01	0.01	0.09	0.91	Balsas	27
ZCH02	0.49	0.07	0.44	Guerrero	33
ZCH03	0.02	0.03	0.96	Balsas	27
ZCH04	0.01	0.01	0.98	Balsas	27
ZCH05	0.02	0.08	0.90	Balsas	27
ZCH06	0.03	0.02	0.95	Balsas	26, 27
ZCH07	0.01	0.02	0.97	Balsas	22, 27
ZCH08	0.01	0.03	0.96	Balsas	26, 27
ZCH09	0.02	0.03	0.95	Balsas	27

supplementary material available on request). BAPS assigns ZM04 to locality 22 whereas ZM09 is assigned to locality 21 and 27. The latter individual carries a Balsas clade mtDNA haplotype (i.e., Genbank accession number EU246769; supplementary material available on request) that is not found in locality 21. Therefore, it is not clear if ZM09 originated in captivity or in the wild.

Eight of the sampled individuals harbored in Zoológico Zoochilpan were assigned to cluster 3 (Q > 0.90; Table 1; Fig. 3). Only one individual showed mixed ancestry and was assigned to cluster 1 and 3 with mtDNA haplotype belonging to the Guerrero clade. Cluster 1 and 3 do not have areas of overlap in nature that we know of. BAPS assigned this individual to locality 33 (Table 1). None of the genotyped individuals from locality 33 or from anywhere else in the wild showed this pattern and proportion of mixed ancestry, thus it is likely that this individual is a hybrid that originated in captivity. However, it is uncertain if the hybridization occurred in Zoochilpan. In general, the locality assignments with BAPS are consistent with the STRUCTURE cluster assignment.

DISCUSSION

The genetic database created and tested herein includes the genotype and mtDNA haplotype of hundreds of individuals sampled throughout the geographic distribution of *C. pectinata*. This database has proved useful in narrowing down potential areas of origin of confiscated individuals. BAPS allowed for assignment at the locality level that was consistent with cluster assignment performed with STRUCTURE. In other words, the locality assigned by BAPS was within the cluster assigned by STRUCTURE. Most of the individuals were assigned when setting a high threshold (i.e., Q > 0.90), or a slightly less stringent threshold (Q > 0.80). However, it was more challenging to assign individuals to specific localities when the individual demonstrated admixture or when there are several admixed wild populations. Indeed, previous studies have pointed out that population assignment with any method is less accurate when levels of gene flow between localities reflect an F_{ST} value of 0.05 or less (Latch et al. 2006; Vähä and Primmer 2006).

The strength of our study comes from the range-wide sampling and multilocus approach that allowed for the characterization of the geographic structure of this species throughout its more than 1,000 km long distribution. To further explore the utility of the database, more individuals with known origin and different levels of admixture should be used to verify the robustness of their genetic assignment.

Our results have direct implications for the management of captive populations. We show that UMA zoos in México do harbor individuals from various origins, sometimes having a genetic composition that is native to areas far away from the location of the UMA. It has been shown that even largely differentiated genotypic clusters (Zarza et al. 2011) and even *Ctenosaura* species (Gutsche and Köhler 2008; Zarza Franco 2008; Pasachnik et al. 2009) can exchange genes when in contact. Thus accidental or intentional releases may have unforeseen consequences in the local populations. Until the effects of hybridization and introgression on the adaptation of different genetic clusters are studied, translocation and releases should be avoided.

With the creation of a database including nuclear genotypes and mtDNA data, we aim to provide a resource for Mexican authorities and conservation organizations to identify the origin of confiscated individuals to either return the individuals to their area of origin or to place them in a UMA within a genetically similar area (Schwartz and Karl 2008). Genetic population assignment methods have assisted in determining the origin of confiscated Galápagos iguanas using mtDNA (Gentile et al. 2013). However, in the case of *C. pectinata*, given the discordant geographic distribution between maternally and paternally inherited markers, it is not possible to rely on mtDNA sequences alone to assign individuals to their population of origin. The use of maternally and bi-parentally inherited markers helps to discriminate among possible localities of origin and to improve genetic assignment as has been carried out in other iguana species (Tzika et al. 2008; Lanterbecq et al. 2010; Colosimo et al. 2014). The compiled database will also be useful in inferring the origin of the individuals introduced in non-natural ranges, e.g., USA and Grenada (Townsend et al. 2003; VHR pers. obs.). With this information, locations of illegal trade could be detected and special efforts made to stop poaching for the pet trade (Wasser et al. 2008).

Future genetic work, aided with new sequencing technologies, should aim to detect adaptive genomic variation associated with particular ecological or morphological traits (Allendorf et al. 2010; Angeloni et al. 2012). This will serve to identify regions under selection and associated single nucleotide polymorphisms. Recent conservation genomic developments suggest that genetic markers associated with genes under selection are especially powerful for population genetic assignment given their high degree of genetic differentiation (Nielsen et al. 2012).

Acknowledgments.—Samples were collected under the permits SEMARNAT SGPA/DGV/03563/06, 08239, 02934 to VHR, SGPA/DGVS. Thanks to Laura Briseño from Zoológico de Morelia and José de Jesús Rivas Obé from Zoológico Zoochilpa for providing access to the iguanas harbored in Zoos. This project was funded through a scholarship awarded to EZ by CONACyT (National Council of Science and Technology in

México) as part of her Ph.D. studies at the University of East Anglia, United Kingdom, and grant IN206911–3, Programa de Apoyo a la Investigación e Innovación Tecnológica, UNAM, to VHR.

LITERATURE CITED

Aguirre-Hidalgo, V. 2007. Demography and genetic diversity of the Mexican Black Iguana *Ctenosaura pectinata*. Ph.D. Dissertation, University of Plymouth, School of Biological Sciences, Plymouth, United Kingdom. 143 p.

Aljanabi, S.M., and I. Martinez. 1997. Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. Nucleic Acids Research 25:4692–4693.

Allendorf, F.W., P.A. Hohenlohe, and G. Luikart. 2010. Genomics and the future of conservation genetics. Nature Reviews Genetics 11:697–709.

Angeloni, F., N. Wagemaker, P. Vergeer, and J. Ouborg. 2012. Genomic toolboxes for conservation biologists. Evolutionary Applications 5:130–143.

Arèvalo, E., S.K. Davis, and J.W. Sites. 1994. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in Central México. Systematic Biology 43:387–418.

Barilani, M., S. Deregnaucourt, S. Gallego, L. Galli, N. Mucci, R. Piombo, M. Puigcerver, S. Rimondi, J.D. Rodríguez-Teijeiro, S. Spanò, et al. 2005. Detecting hybridization in wild (*Coturnix c. coturnix*) and domesticated (*Coturnix c. japonica*) quail populations. Biological Conservation 126:445–455.

Blázquez, M.C., R. Rodríguez Estrella, and A. Munguía Vega. 2006. Characterization of 10 microsatellite loci in the spiny-tailed iguana *Ctenosaura hemilopha*. Molecular Ecology Notes 6:753–755.

Colosimo, G., C.R. Knapp, L.E. Wallace, and M.E. Welch. 2014. Inferred vs. realized patterns of gene flow: an analysis of population structure in the Andros Island Rock Iguana. PLoS ONE 9(9): e106963. doi:10.1371/journal.pone.0106963

Corander, J., and P. Marttinen. 2006. Bayesian identification of admixture events using multilocus molecular markers. Molecular Ecology 15:2833–2843.

Corander, J., P. Marttinen, J. Sirén, and J. Tang. 2008. Enhanced Bayesian modeling in BAPS software for learning genetic structures of populations. BMC Bioinformatics 9:539.

Devitt, T.J. 2006. Phylogeography of the Western Lyre Snake (*Trimorphodon biscutatus*): testing arid land biogeographical hypotheses across the Nearctic-Neotropical transition. Molecular Ecology 15:4387–4407.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32:1792–1797.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14:2611–2620.

Faria, C.M.A., E. Zarza, V.H. Reynoso, and B.C. Emerson. 2010. Predominance of single paternity in the Black Spiny-tailed Iguana: conservation genetic concerns for female-biased hunting. Conservation Genetics 11:1645–1652.

Flores-Villela, O., and U.O. García-Vazquez. 2014. Biodiversidad de reptiles en México. Revista Mexicana de Biodiversidad 85:S467–S475.

Frankham, R. 2010. Challenges and opportunities of genetic approaches to biological conservation. Biological Conservation 143:1919–1927.

Frantz, A.C., J.T. Pourtois, M. Heuertz, L. Schley, M.C. Flamand, A. Krier, S. Bertouille, F. Chaumont, and T. Burke. 2006. Genetic structure and assignment tests demonstrate illegal translocation of Red Deer (*Cervus elaphus*) into a continuous population. Molecular Ecology 15:3191–3203.

Gentile, G., M. Ciambotta, and W. Tapia. 2013. Illegal wildlife trade in Galápagos: molecular tools help the taxonomic identification of confiscated iguanas and guide their rapid repatriation. Conservation Genetics Resources 5:867–872.

Gutsche, A., and F. Köhler. 2008. Phylogeny and hybridization in *Ctenosaura* species (Sauria, Iguanidae) from Caribbean Honduras: insights from mitochondrial and nuclear DNA. Zoosystematics and Evolution 84:245–253.

Hasbún, C.R., A. Gómez, G. Köhler, and D.H. Lunt. 2005. Mitochondrial DNA phylogeography of the Mesoamerican spiny-tailed lizards (*Ctenosaura quinquecarinata* complex): historical biogeography, species status, and conservation. Molecular Ecology 14:3095–3107.

Hubisz, M.J., D. Falush, M. Stephens, and J.K. Pritchard. 2009. Inferring weak population structure with the assistance of sample group information. Molecular Ecology Resources 9:1322–1332.

Köhler, G. 2002. Schwarzleguane: Lebensweise, Pflege und Zucht. Herpeton Verlag, Offenbach, Germany.

Kronforst, M.R. 2012. Mimetic butterflies introgress to impress. PLoS Genetics 8:e1002802. doi:10.1371/journal.pgen.1002802

Lanterbecq, D., S. Glaberman, M.N. Vitousek, S. Steinfartz, E. Benavides, M. Wikelski, and A. Caccone. 2010. Genetic differentiation between marine iguanas from different breeding sites on the island of Santa Fé (Galápagos Archipelago). Journal of Heredity 101:663–675.

Latch, E.K., G. Dharmarajan, J.C. Glaubitz, and O.E. Rhodes, Jr. 2006. Relative performance of Bayesian clustering software for inferring population substructure and individual assignment at low levels of population differentiation. Conservation Genetics 7:295–302.

Nielsen, E.E., A. Cariani, E. Mac Aoidh, G.E. Maes, I. Milano, R. Ogden, M. Taylor, J. Hemmer-Hansen, M. Babbucci, L. Bargelloni, et al. 2012. Gene-associated markers provide tools for tackling illegal fishing and false eco-certification. Nature Communications 3:851. doi:10.1038/ncomms1845

Paetkau, D., R. Slade, M. Burden, and A. Estoup. 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. Molecular Ecology 13:55–65.

Pardo-Diaz, C., C. Salazar, S.W. Baxter, C. Merot, W. Figueiredo-Ready, M. Joron, W.O. McMillan, and C.D. Jiggins. 2012. Adaptive introgression across species boundaries in *Heliconius* butterflies. PLoS Genetics 8:e1002752. doi:10.1371/journal.pgen.1002752

Pasachnik, S.A., B.M. Fitzpatrik, T.J. Near, and A.C. Echternacht. 2009. Gene flow between and endangered endemic iguana, and its wide spread relative, on the island of Utila, Honduras: when is hybridization a threat? Conservation Genetics 10:1247–1254.

Pierpaoli, M., Z.S. Birò, M. Herrmann, K. Hupe, M. Fernandes, B. Ragni, L. Szemethy, and E. Randi. 2003. Genetic distinction of wildcat (*Felis silvestris*) populations in Europe, and hybridization with domestic cats in Hungary. Molecular Ecology 12:2585–2598.

Piry, S., A. Alapetite, J.-M. Cornuet, D. Paetkau, L. Baudouin, and A. Estoup. 2004. GENECLASS2: a software for genetic assignment and first-generation migrant detection. Journal of Heredity 95:536–539.

Portillo-Quintero, C.A., and G.A. Sánchez-Azofeifa. 2010. Extent and conservation of tropical dry forests in the Americas. Biological Conservation 143:144–155.

Pritchard, J.K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–959.

Russello, M.A., C. Hyseni, J.P. Gibbs, S. Cruz, C. Marquez, W. Tapia, P. Velensky, J.R. Powell, and A. Caccone. 2007. Lineage identification of Galápagos tortoises in captivity worldwide. Animal Conservation 10:304–311.

Schwartz, T.S., and S.A. Karl. 2008. Population genetic assignment of confiscated Gopher Tortoises. The Journal of Wildlife Management 72:254–259.

SEMARNAT. 2010. NOM-059-SEMARNAT-2010. Diario Oficial de la Federación, Jueves 30 de Diciembre.

Stamatakis, A. 2014. RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics:btu033. doi:10.1093/bioinformatics/btu033

Suazo, O.I., and D.J. Alvarado. 1994. Iguana Negra: Notas Sobre su Historia Natural. Universidad Michoacana de San Nicolás Hidalgo, Michoacán, and Fish and Wildlife Service, Ecotonia A.C., México.

Tamura, K., and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10:512–526.

Townsend, J.H., K.L. Krysko, and K.M. Enge. 2003. The identity of spiny-tailed iguanas, *Ctenosaura*, introduced to Florida, USA (Squamata: Sauria: Iguanidae). Herpetozoa 16:67–72.

Tzika, A.C., S.F.P. Rosa, A. Fabiani, H.L. Snell, H.M. Snell, C. Marquez, W. Tapia, K. Rassmann, G. Gentile, and M.C. Milinkovitch. 2008. Population genetics of Galápagos Land Iguana (genus *Conolophus*) remnant populations. Molecular Ecology 17:4943–4952.

Vähä, J.-P., and C.R. Primmer. 2006. Efficiency of model-based Bayesian methods for detecting hybrid individuals under different hybridization scenarios and with different numbers of loci. Molecular Ecology 15:63–72.

Wang, J. 2014. Estimation of migration rates from marker-based parentage analysis. Molecular Ecology 23:3191–3213.

Wasser, S.K., W. Joseph Clark, O. Drori, E. Stephen Kisamo, C. Mailand, B. Mutayoba, and M. Stephens. 2008. Combating the illegal trade in African Elephant ivory with DNA forensics. Conservation Biology 22:1065–1071.

Wilkinson, S., C. Haley, L. Alderson, and P. Wiener. 2011. An empirical assessment of individual-based population genetic statistical techniques: application to British pig breeds. Heredity 106:261–269.

Winkler, K.A., B. Pamminger-Lahnsteiner, J. Wanzenböck, and S. Weiss. 2011. Hybridization and restricted gene flow between native and introduced stocks of Alpine Whitefish (*Coregonus* sp.) across multiple environments. Molecular Ecology 20:456–472.

Zarza, E., R.T. Pereyra, V.H. Reynoso, and B.C. Emerson. 2009. Isolation and characterization of polymorphic microsatellite markers in the Black Spiny-tailed Iguana (*Ctenosaura pectinata*) and their cross-utility in other *Ctenosaura*. Molecular Ecology Resources 9:117–119.

Zarza, E., V.H. Reynoso, and B.C. Emerson. 2008. Diversification in the northern neotropics: mitochondrial and nuclear DNA phylogeography of the iguana *Ctenosaura pectinata* and related species. Molecular Ecology 17:3259–3275.

Zarza, E., V.H. Reynoso, and B.C. Emerson. 2011. Discordant patterns of geographic variation between mitochondrial and microsatellite markers in the Mexican Black Iguana (*Ctenosaura pectinata*) in a contact zone. Journal of Biogeography 38:1394–1405.

Zarza Franco, G.E. 2008. Phylogeography and genetic analysis of secondary contact zones of *Ctenosaura pectinata* and related species. Ph.D. Dissertation, University of East Anglia, Norwich, United Kingdom. 147 p.

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