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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**

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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).

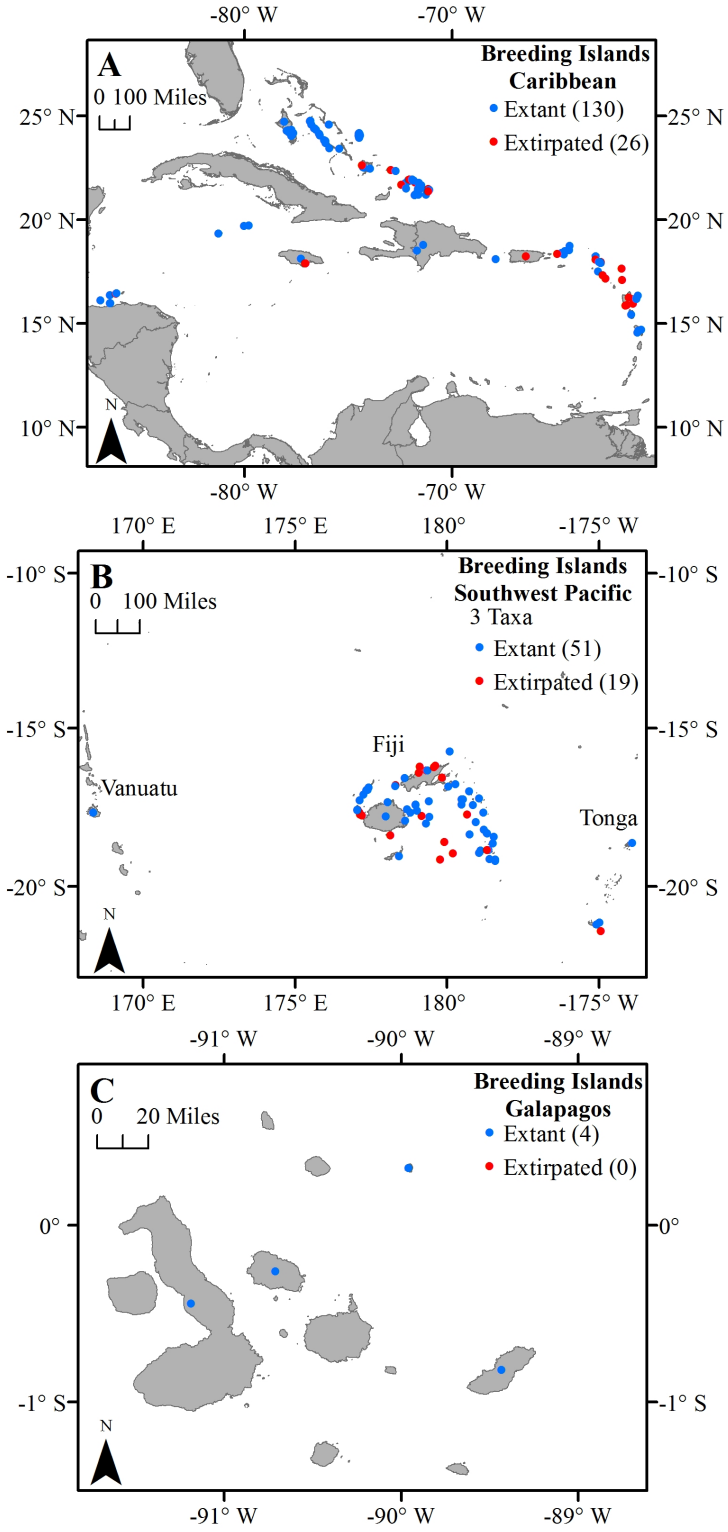

FIGURE 1. Islands where threatened insular iguana taxa are extant (blue dots) or have been extirpated (red dots) within: (A) the Caribbean region; (B) southwest Pacific; and (C) Galápagos Islands. Seven islands were excluded: three lacked sufficient breeding information and four because iguana populations 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

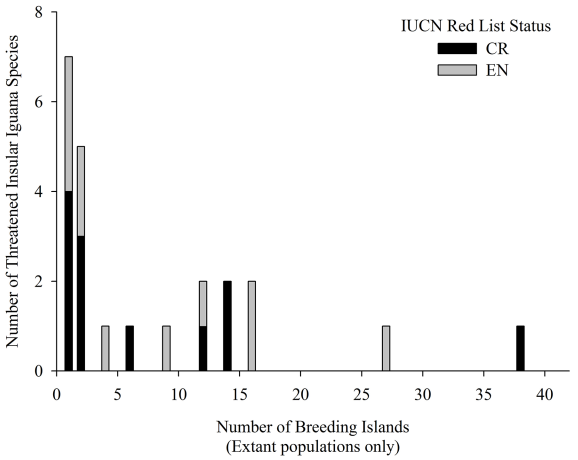

FIGURE 2. Relative endemism of extant threatened insular iguana taxa assessed by IUCN Red List of Threatened Species Criteria (CR: Critically Endangered; EN: Endangered).

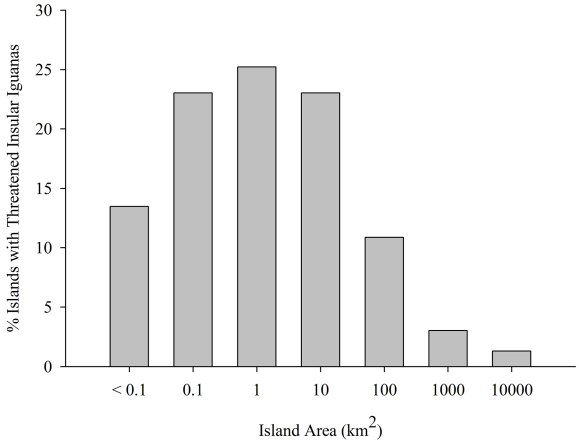

FIGURE 3. Percentage of islands with threatened insular iguana taxa by island size.

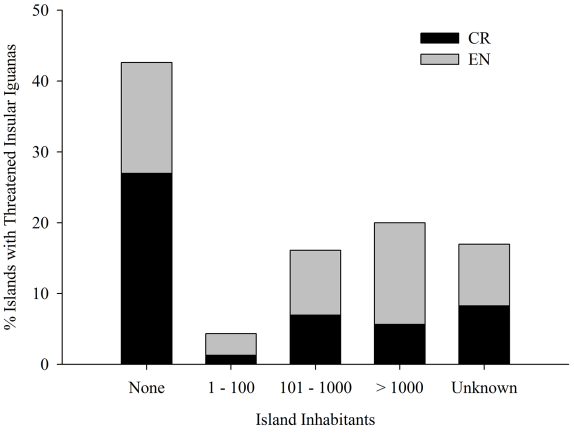

FIGURE 4. Percentage of threatened insular iguana populations relative to island human inhabitants.

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

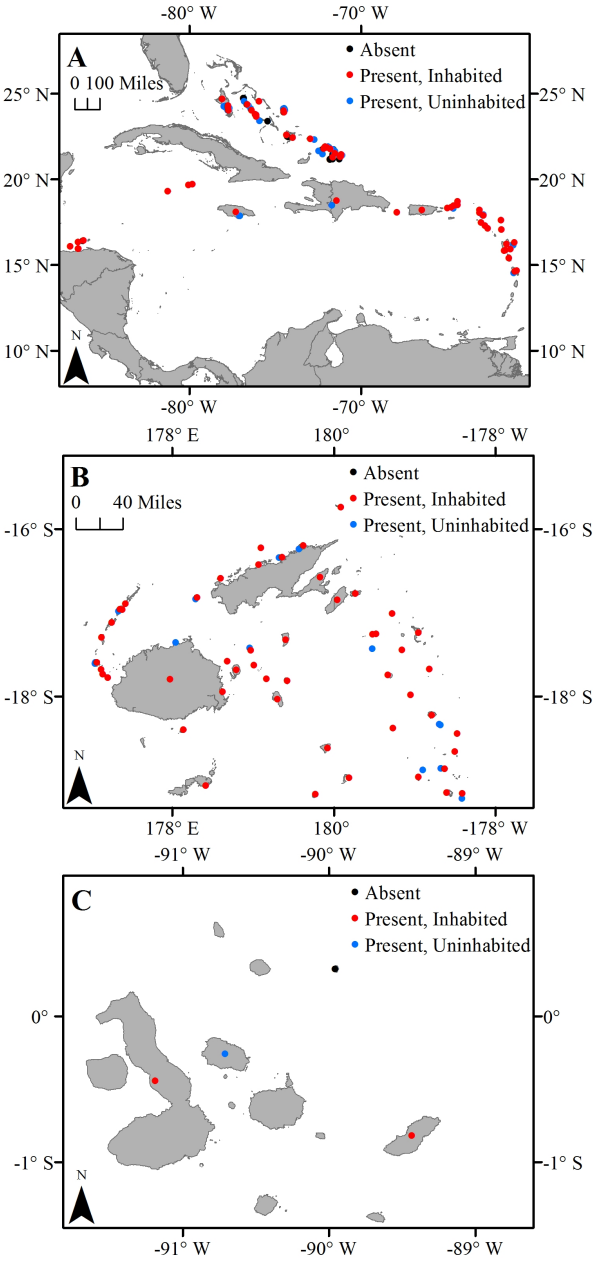

FIGURE 5. Islands where threatened insular iguana taxa occur in the absence of invasive vertebrates (black dots), with invasive vertebrates on uninhabited islands (blue dots) or with invasive vertebrates on inhabited islands (red dots) within: (A) the Caribbean region; (B) Fiji (islands in Tonga and 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.

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KELLY M. NEWTON holds a master's degree in Ocean Sciences from the University of California, Santa Cruz. Kelly's current research focus is on the integration of multiple long-term monitoring datasets to assess the impacts of invasive species eradications on islands. In addition, she developed and maintains multiple databases focused on the ecology and conservation of islands. She helped to create the Threatened Island Biodiversity Database, a global database of threatened island species at risk from invasive species. In addition, she helped to create the Database of Island Invasive Species Eradications, a global database of all current and historic vertebrate eradications on islands. (Photographed by Meisha Key).

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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