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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

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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 $\geq$ 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.

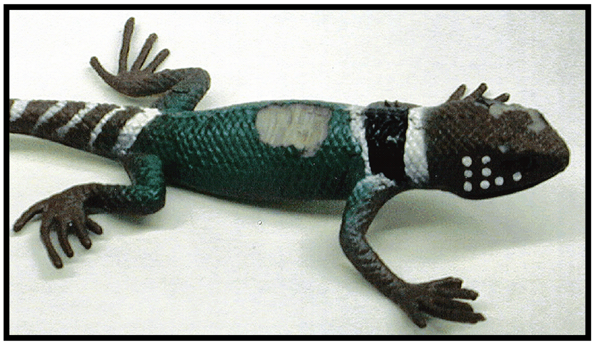

FIGURE 3. Bite marks, presumably from Black Rat (*Rattus rattus*), on a rubber lizard similar in size (6–7 cm snout-vent length) to a hatchling Sandy Cay Rock Iguana (*Cyclura rileyi cristata*), placed on Sandy Cay, Exuma Cays, The Bahamas. (Photographed by William K. Hayes).

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

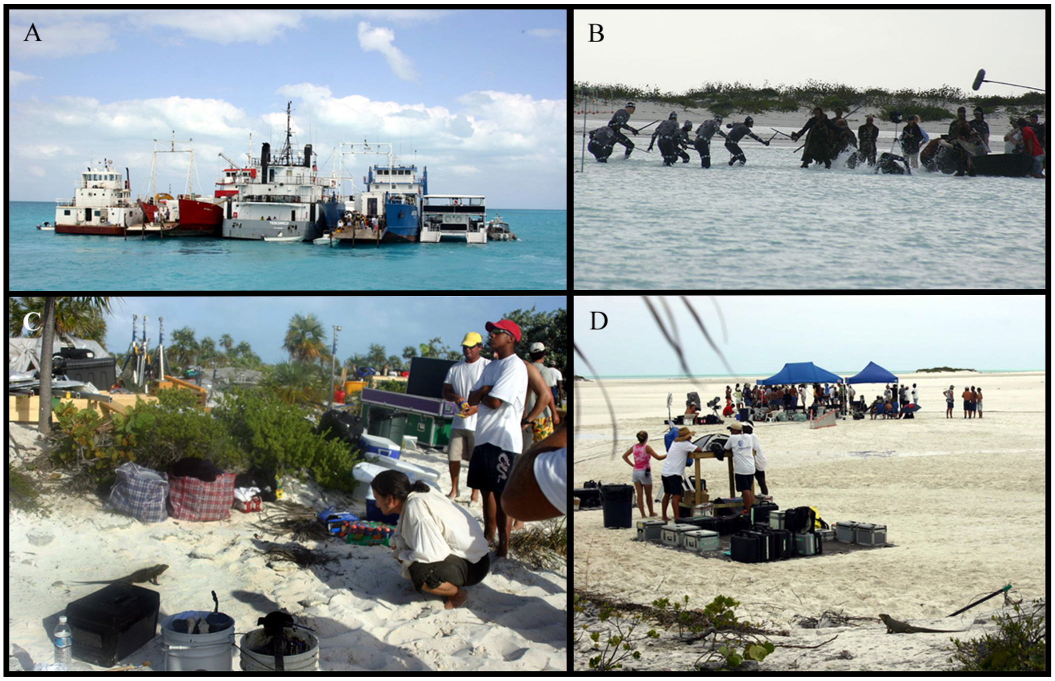

FIGURE 4. Images from the cinema production of portions of Episodes Two and Three of the Disney film series *Pirates of the Caribbean*, filmed on Sandy Cay, southern Exuma Cays, The Bahamas. (A) Support barges required to reduce impact on the cay; (B) cinematic fight scene; and (C and D) Sandy Cay Rock 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.

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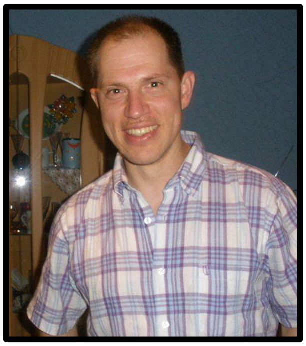
William K. Hayes serves as a Professor of Biology and the Director of the Center for Biodiversity and Conservation Studies at Loma Linda University, Loma Linda, California. He earned his B.S. and M.Sc. degrees in Biology at Walla Walla University, Walla Walla, Washington, where he first began studying 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).

Ricardo A. Escobar III is an Assistant Professor of Biology and the Director of the Undergraduate Environmental Sciences program at Loma Linda University, Loma Linda, California. He majored in biology at La Sierra University, La Sierra, California, and studied the movement ecology and behaviors of Common Green Iguanas in Costa Rica as a thesis topic for his M.Sc. in Biology at Loma Linda University. He is currently studying the biogeography, phylogenetics, and movement ecology of West Indian boas for his doctoral dissertation at Loma Linda University. Prior to his current position, he worked as a biologist for the California Department of Fish and Game for six years, conducting surveys on endangered animals and plants, including butterflies, frogs, small mammals, and raptors as part of the Multiple Species Habitat Conservation Plan for Western Riverside County, California. (Photographed by Edgar M. Fortune).



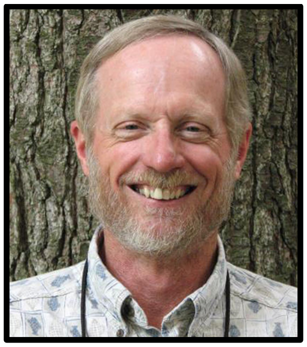
Shawn K. Fry grew up in the Pacific Northwest, where he developed an engaging interest in herpetology. He earned his B.S. in Biology in 1996 at Walla Walla University, Walla Walla, Washington. He then studied the Sandy Cay Rock Iguana for his M.Sc. thesis at Loma Linda University, Loma Linda, California, 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).

Edgar M. Fortune is a naturalist and conservationist with over 30 years of experience in the zoo industry. He is the Founder and President of Global Insular Conservation Society (GICS), a non-profit organization focused on fragile island ecosystems and their native flora and fauna. GICS uses sound, scientific research to support conservation of indigenous species. He attended Northeast Louisiana University and the University of Washington, where he majored in zoology. Edgar has always had a special interest in the flora and fauna of the Caribbean and is focusing his efforts on sustaining those isolated ecosystems. He has written and co-authored several articles about his work on behalf of the Sandy Cay Rock Iguana. (Photographed by Ricardo A. Escobar III).

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 Conners).

Donald M. Tuttle is the founder and CEO of Jadora International LLC, a global leader in sustainable forest ecosystem management. After attending the University of Washington in Seattle, he owned and operated Rain City, a haven for confiscated exotic and endangered species, from 1996–2006. Prior to and during this time he assisted with assorted zoological and community education projects of the Smithsonian Institution and the California Academy of Sciences in Central America, the West Indies, and Southeast Asia. He also founded the Insular Species Conservation Society, which has supported several research projects in The Bahamas. From 2006–2008, he served as a Major Gifts Officer for the Woodland Park Zoo, Seattle, Washington. Driven by a sense of mission, he founded Jadora in 2008 with the conviction that it is possible to preserve the world's forests while developing a sustainable green economy and improving the livelihoods of local communities. (Photographed by Joe Wasilewski).

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).