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GROWTH, COLORATION, AND DEMOGRAPHY OF AN INTRODUCED POPULATION OF THE ACKLINS ROCK IGUANA (*CYCLURA RILEYI NUCHALIS*) IN THE EXUMA ISLANDS, THE BAHAMAS

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***Abstract*.—In 1973, five Acklins Rock Iguanas (*Cyclura rileyi nuchalis*) from Fish Cay in the Acklins Islands, The Bahamas, were translocated to Bush Hill Cay in the northern Exuma Islands. That population has flourished, despite the presence of invasive rats, and numbered > 300 individuals by the mid-1990s. We conducted a mark-recapture study of this population from May 2002 through May 2013 to quantify growth, demography, and plasticity in coloration. The iguanas from Bush Hill Cay were shown to reach larger sizes than the source population. Males were larger than females, and mature sizes were reached in approximately four years. Although the sex ratio was balanced in the mid-1990s, it was heavily female-biased throughout our study. Juveniles were rare, presumably due to predation by rats and possibly cannibalism. The estimated population size declined by > 60% over the course of our study. The causes could not be precisely identified, but predation by and competition with rats, and possibly poaching, were likely responsible. We strongly recommend the eradication of rats to prevent further loss of iguanas. Iguanas from Bush Hill Cay are polymorphic in color, with adults exhibiting two major color transition patterns: a yellow body color with minimal mottling (10–15% of individuals), and a brown or orange background with gray or blue-gray mottling that variably fades in some individuals. Even though there is evidence that this was a successful translocation, recent declines in the estimated population size suggest that the future of this population is uncertain and will require continued monitoring.**

Key Words.—color polymorphism; conservation; density; introduction; rats; sex ratio; translocation

INTRODUCTION

The translocation of individuals of threatened or endangered species to new areas or to previously occupied areas has been a controversial conservation strategy (e.g., McCoy and Berry 2008; Seddon 2010; Perez et al. 2012). Some reviews suggest that translocations and reintroductions of amphibians and reptiles are generally not successful (e.g., Dodd and Seigel 1991); however, others suggest that this is not always the case or that generalizations across taxa are not useful (e.g., Burke 1991). Indeed, a more recent review of amphibian and reptile translocations has found an increase in success rates for such translocations in more recent years (Germano and Bishop 2009).

Despite the many differences of opinion and given the increasing anthropogenic impacts on the natural world, translocations of organisms will, by necessity, become a much more frequent conservation management strategy. The International Union for Conservation of Nature (IUCN) first developed rudimentary international guidelines in 1998, and then in 2013 published their formal guidelines for reintroductions and translocations (IUCN 2013). Setting aside these controversies, it remains that many translocations (both authorized and unauthorized) have been done, and hence assessing the success and value of these actions is of great conservation importance, falling on the shoulders of field biologists.

Multiple translocations or reintroductions have been conducted with populations of Rock Iguanas (genus *Cyclura*) as they often have narrow and threatened ranges (e.g., Knapp and Hudson 2004). In some cases, the reintroduction of headstarted juveniles has been attempted, with good evidence of success (e.g., *C. collei*: Wilson et al. 2004, Wilson 2011; *C. lewisi*: Echternacht et al. 2011; *C. nubila*: Alberts et al. 1998, 2004; *C. pinguis*: Gerber 2004, Bradley and Gerber 2005, Perry and Gerber 2011; see also reviews in Alberts and Phillips 2004, Alberts 2007). In addition, translocations of "colonies" of Rock Iguanas to previously unoccupied areas or islands have occurred, either as part of a

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conservation program or as an independent act of private citizens or unknown persons (Table 1). In many of these cases, it appears that successful, self-maintaining populations of *Cyclura* have been created (Table 1), as Rock Iguanas appear to have life history traits that facilitate successful translocation (Knapp and Hudson 2004), such as density-dependent individual (Knapp 2001) and population growth (Iverson et al. 2006).

However, in several cases, little about the ecology and natural history of these translocated populations is known, particularly as they relate to the natural source population. Understanding these details is vital to the persistence of the population, if not the species as a whole. For the best studied translocated iguana population to date, Knapp has examined the demography and spatial ecology of the translocated population of *Cyclura cychlura inornata* on Alligator Cay, The Bahamas (Knapp 2000, 2001; Knapp and Malone 2003). In addition, Goodman et al. (2005a, b) have examined habitat use and spatial ecology in captive-bred *C. lewisi* released in a botanical park on Grand Cayman as part of a reintroduction program (see also Burton and Rivera-Milán 2014).

Here we examine the growth, color patterns, and demography of an introduced population of the endangered Acklins Rock Iguana, *Cyclura rileyi nuchalis* in The Bahamas. Hayes et al. (2004a) reported that five individual *Cyclura rileyi nuchalis* were introduced to Bush Hill Cay within the Exuma Cays Land and Sea Park from Fish Cay in the Acklins Islands (~ 350 km SE of Bush Hill Cay) in 1973 (see also Hayes and Montanucci 2000). Very little is known about the ecology and natural history of this species and subspecies in its native range (but see Hayes and Montanucci 2000; Carter and Hayes 2004; Hayes et al. 2004a). Nevertheless, the population on Bush Hill Cay has flourished and now inhabits nearly every square meter of the island. Unfortunately, the island also supports a large population of rats (Hayes et al. 2004a, 2012). While this introduction was not part of an authorized conservation or management project, we believe it can serve as an informative translocation "experiment," shedding light on similar situations.

MATERIALS AND METHODS

Study species and site.—*Cyclura rileyi nuchalis* is listed as Endangered on the IUCN Red List of Threatened Species (Carter et al. 2000), is strictly

TABLE 1. Known translocations of Rock Iguanas (*Cyclura*), arranged by approximate declining latitude of source population.

Taxon	Location	Founders/Source	Status	References
C. cychlura inornata	Alligator Cay, The Bahamas	8 juveniles from Leaf Cay (1988, 1990)	75–90 (1999)	Knapp 2000, 2001; Knapp and Malone 2003
	Flat Rock Reef Cay, The Bahamas	< 10 from U and Leaf Cays (1996)	> 200 (2013)	Iverson, unpublished; Aplasca 2013
	Guana Cay, Little San Salvador, The Bahamas	11 from Leaf Cay (2005)	Reproducing	Hines, unpublished
C. cychlura figginsi	Pasture Cay, central Exumas, The Bahamas	16 from Leaf Cay S. Exumas (2002, 2006)	> 20 (2014)	Knapp and Hudson 2004; Knapp, pers. comm.
C. rileyi nuchalis	Bush Hill Cay, The Bahamas	5 from Fish Cay (1973)	> 200 (2013)	Hayes et al. 2004a; this study
C. rileyi rileyi	Low Cay, San Salvador, The Bahamas	14 from Green Cay (2005)	12 (2012); no reproduction	Hayes et al. this volume
C. carinata	Six Hills, French, Bay, and Middle Cays, TCI	18–82 from Big & Little Ambergris Cays, TCI (2002–2003)	"extremely successful"	Gerber 2007; Reynolds 2011
	Long Cay, Caicos, TCI	800 from Big Ambergris Cay, TCI (2000)	"established"	Mitchell et al. 2002; Reynolds 2011
C. nubila nubila	Isla Magueyes, Puerto Rico	"a few" from Cuba (mid-1960s)	167 (mid-1980s)	Christian 1986; Knapp and Hudson 2004
C. lewisi	Northeastern Grand Cayman (GC)*	405 captive headstarted, Grand Cayman (2004–2012)	> 40	Goodman et al. 2005a, b; Echternacht et al. 2011; Burton and Rivera-Milán 2014
C. pinguis	Guana Island, BVI	8 from Anegada (1984–1986)	100 (2002); > 300 (2004)	Goodyear and Lazell1994; Anonymous 2004; Perry and Gerber 2011
	Necker Island, BVI	4 from Guana Island, BVI (1995)	"successful"	Lazell 1995, 2002; Perry and Gerber 2011
	Norman Island, BVI	12 from Guana Island (2000s)	unknown	Perry and Gerber 2011

*Reintroduction

protected by The Bahamas under the "Wild Animals Protection Act" of 1968 and the "Wildlife Conservation and Trade Act" of 2004, and is listed on Appendix I (the most restrictive category) of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). *Cyclura rileyi nuchalis* is native to Long Cay (the type locality), Fish Cay, and North Cay in the Acklins Islands, The Bahamas, although it has been extirpated (by unknown causes) from Long Cay (Hayes et al. 2004a). In January of 1973, G.C. Clough released 11 Bahaman Hutias (*Geocapromys ingrahami*) from East Plana Cay in the southeastern Bahamas to Little Wax Cay in the Exuma Islands (immediately adjacent to Bush Hill Cay). It was apparently on the same trip that Clough also collected five iguanas from Fish Cay. According to Oris Russell (pers. comm. to Richard Franz), in 1973 Clough brought the iguanas to him on New Providence and Russell released them on Bush Hill Cay. The descendants of those five individuals constitute the population that we have studied for the past 12 years. Bush Hill Cay (BHC; 3.3 ha) lies within the Exuma Cays Land and Sea Park near the northern limit. Its precise location is withheld for conservation purposes. The lowland portion of the island is dominated by a palm forest (*Coccothrinax argentata*) on a primarily sand substrate. The upland (to 13.4 m elevation) is primarily rocky coppice vegetation. Field work was performed on BHC on sunny to partly cloudy days during periods when iguanas were active (e.g., 0900 to 1800) on 21–22 May 2002 (4 hours; 15 persons), 20–21 May 2003 (9 hours; 14 persons), 17–18 May 2004 (8 hrs; 13 persons), 17–18 May 2005 (11 hours; 16 persons), 26–27 June 2007 (15 hrs; 12 persons), 17–18 May 2008 (14 hrs; 16 persons), 23–24 May 2009 (15 hrs; 15 persons), 17–18 May 2010 (15 hrs; 15 persons), 22–23 May 2011 (12 hrs; 17 persons), and 22–23 May 2013 (11 hrs; 18 persons). Iguanas were captured by hand, dipnet, noose, or live trap.

Protocol.—Processing methods followed those of Iverson et al. (2004a). Snout-vent length (SVL in mm), tail length (TL in mm), tail condition (with lengths in mm of any regenerated segments), and body mass (BM in grams) were measured on each capture. Body and limb injuries were also recorded.

Missing digits and regenerated tails (some forked; see Hayes et al. 2012) were common for iguanas on BHC. We incorporated the information on the extent of missing digits (e.g., toe completely missing) into our marking system based on toe clips (no PIT tags used), such that only one or two toes (and only one per limb) were typically clipped by us (Langkilde and Shine 2006; Perry et al. 2011). When used in combination with notes about body size, scars, regenerated tails, sex, and color, accurate identification of individuals was possible, even when additional digits disappeared between captures (presumably through intraspecific aggression and/or mauling by rats).

FIGURE 1. Ventral view of pelvic region of male (top) versus female (bottom) *Cyclura rileyi nuchalis* on Bush Hill Cay illustrating secondary sexual differences in femoral pore and proximal tail morphology (larger pores and obvious hemipenial bulges evident in males). (Photographed by John B. Iverson).

Lizards were sexed initially by cloacal probing (Dellinger and Hegel 1990) until we were confident that differences in the external morphology of the cloacal region accurately reflected the animal's sex (Fig. 1). However, we were not confident in our sexing of juveniles and smaller subadults by either probing or external morphology, and thus those individuals were excluded from relevant analyses.

Iguanas from Bush Hill Cay exhibit striking variation in body and head coloration (Figs. 2–6). Hence, brief notes on body color were also recorded for each individual at each capture. For consistency, particularly given subtle changes in color depending on lizard body temperature (warmer: colors brighter), all color determinations were made by author JBI. Body color in subadults and adults was scored on two qualitative dimensions: presence of gray to blue-gray mottling (generally noted as obviously mottled versus little or no mottling), and general body color (see below). Juveniles bear a distinctly different pattern from adults, being basically gray with dorsal and dorsolateral longitudinal stripes (Fig. 2, top), and were simply color-scored as "juvenile". Many, but not all lizards were photographed during each capture event.

Von Bertalanffy growth models were calculated from our recapture data using SVL only at first and last capture (Fabens 1965), but excluding recapture intervals of only one year or less. Curves were anchored by the mean size of five first-year iguanas (9.56 cm) estimated to be 0.83 years of age when captured in May.

We submitted our capture/recapture matrix (only for subadult or adult iguanas ≥ 20 cm SVL; size at maturity according to Hayes et al. 2004a) to Program MARK (Available from http://warnercnr.colostate.edu/~gwhite/mark/mark.htm) to obtain annualized survival estimates and capture probabilities (White and Burnham 1999), separately for males and females. All other statistics (two-tailed *t*-tests, least-squares regression analysis, ANOVA) were calculated with Statview™ software (formerly Abacus Concepts, Berkeley, California, USA).

FIGURE 2. Body size transition in color pattern from juveniles (ca. 16 cm SVL, top two photographs) to subadults (ca. 20 cm SVL, bottom two photographs) for *Cyclura rileyi nuchalis* on Bush Hill Cay; all images from different individuals. Note the retention of juvenile striping anteriorly in the third individual, but loss in the fourth. (Photographed by John B. Iverson and students).

RESULTS

Over our 11-year study period we captured 337 individual iguanas (122 males, 203 females, 12 unsexed juveniles) a total of 862 times (i.e., 525 recaptures; Table 2). The mean number of recaptures was 2.61 for males (range, 1–8 recaptures; n = 80) and 2.39 for females (range, 1–7 recaptures; n = 133). Mean recapture interval from first to last capture was 4.8 y (range, 1–11 y) for males and 5.5 for females (range, 1–11 y). The sex ratio (203 females, 122 males) was significantly biased in favor of females ($\chi^2 = 20.19$, $P < 0.0001$).

Size and growth.—Mean SVL for males ≥ 20 cm SVL (all captures) was 32.0 cm (range, 21.4–37.2; n = 319) and was significantly longer ($t = 22.10$, $P < 0.0001$) than that for females ≥ 20 cm SVL at 28.3 cm (range, 20.0–33.8; n = 497). However, mean SVL for males decreased almost 2 cm over our study, and female SVL decreased about 1 cm (Fig. 7).

Tail length for males with complete, unregenerated tails averaged 47.6 cm (range, 35.2–55.0 cm; n = 125) and was significantly longer ($t = 10.2$, $P < 0.0001$) than that for females at 43.4 cm (range, 31.2–51.0 cm; n = 204). However, relative tail length (TL/SVL) was longer in females than males (means: 1.50 vs 1.48; $t = 3.23$, $P = 0.0007$). Tail break frequency data from this study were reported in Hayes et al. (2012).

Mean BM for males was 1,173 g (range, 425–1,710 g; n = 319) and was significantly heavier ($t = 21.8$, $P < 0.0001$) than that for females at 869 g (range, 305–1,404 g; n = 497). BM was related exponentially to SVL in males (logBM = 2.471logSVL – 0.657; n = 319, $r = 0.87$, $P < 0.0001$) and females (logBM = 2.328logSVL – 0.446; n = 497, $r = 0.90$, $P < 0.0001$) for individuals ≥ 20 cm SVL, and these curves were not significantly different between the sexes ($P > 0.05$ for ANCOVA of log-transformed data).

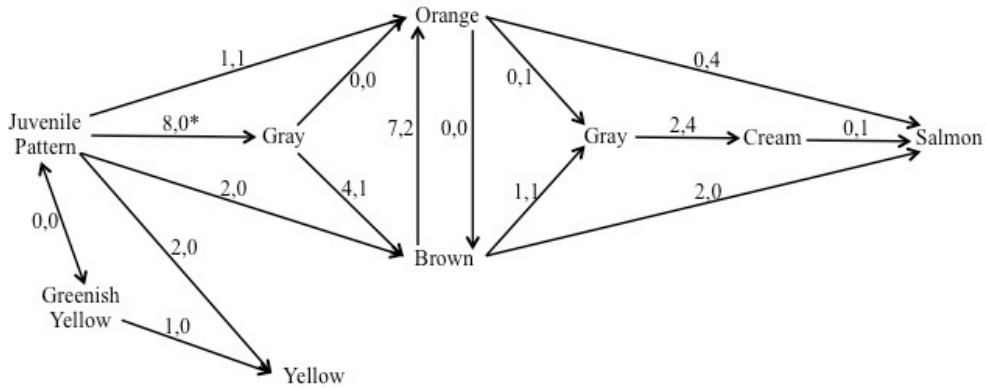

FIGURE 3. Color pattern transitions recorded for recaptured *Cyclura rileyi nuchalis* on Bush Hill Cay ≥ 20 cm SVL at both first and last capture. Numbers at each transition are "females, males" that exhibited the transition. Asterisk indicates suspect gender identification due to difficulty in sexing young adults.

FIGURE 4. Color pattern transition across body sizes (subadult, top; large adult, bottom; all are different individuals) for *Cyclura rileyi nuchalis* on Bush Hill Cay exhibiting the yellow morph. Note the transition from green-yellow to yellow, and the loss of mottling. (Photographed by John B. Iverson and students).

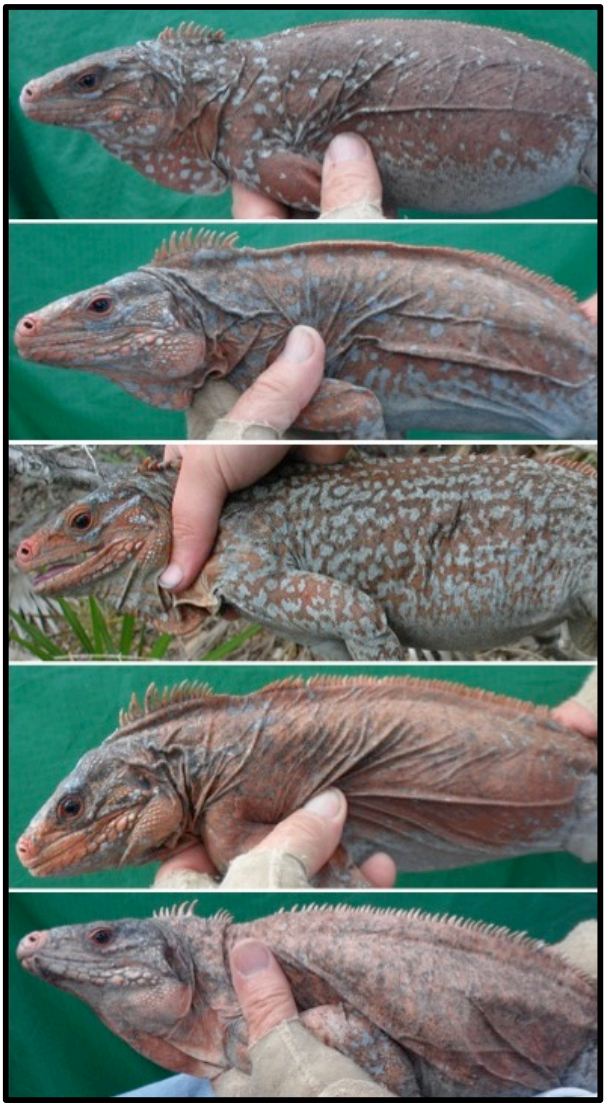

FIGURE 5. Color pattern transition across body sizes (small adult, top; large adult, bottom; all are different individuals) for *Cyclura rileyi nuchalis* on Bush Hill Cay exhibiting (top to bottom) the brown–orange–salmon morph. Note the loss of mottling, and the fading of orange to salmon. (Photographed by John B. Iverson and students).

TABLE 2. Capture information by year for *Cyclura rileyi nuchalis* on Bush Hill Cay. Biomass in kg/ha estimated as the product of estimated population size and mean mass of all captured iguanas in our study (951.6 g), divided by island area. Program MARK cannot estimate numbers for the first and last years of the study.

Year	Total Captures	Total Recaptures	Percent Recaptures	Males	Females	Unsexed	Estimated *n*	Estimated Biomass (kg/ha)
2002	75			36	39			
2003	72	16	22	36	33	3	265	78.8
2004	104	42	40	45	60		322	95.8
2005	106	59	56	38	66	2	255	75.8
2007	96	58	60	36	58		224	66.6
2008	79	65	82	29	44	6	209	62.2
2009	75	61	81	23	45	6	110	32.7
2010	116	103	89	33	76	7	218	64.8
2011	57	51	89	22	32	3	59	17.5
2013	77	70	91	23	49	5		

Mean growth rate (cm SVL/y) was not significantly faster in males ≥ 20 cm SVL (mean = 0.22 cm/y; range, -1.0–3.2 cm/y; n = 79) than females ≥ 20 cm SVL (mean = 0.14 cm/y; range, -1.0–2.0 cm/y; n = 125, t = 1.22, P = 0.11). Growth rate was negatively correlated with body size (Fig. 8). For males, the von Bertalanffy model was: SVL = 32.857 ($1 - 0.7883e^{-0.182t}$), for t, time in years post hatching (n = 64; mean interval = 5.66 y; range, 2–11 y; r = 0.90, P < 0.0001). For females it was SVL = 29.030 ($1 - 0.7528e^{-0.198t}$) (n = 120; mean interval = 5.95 y; range, 2–11 y; r = 0.82, P < 0.0001). These growth models suggest that males reach 20 cm SVL (estimated age at maturity, according to Hayes et al. 2004a) at age 3.85 years and females at 4.46 years. This would suggest that females begin nesting in their fifth summer of life.

Coloration.—Of 213 iguanas (133 females, 80 males) recaptured at least once and for which color notes were recorded, 45 (30 females, 15 males) demonstrated changes in color between their first and last capture (mean interval during which color change occurred = 3.31 y; range, 1–9 y). Of these, 14 (13 "females" [gender suspect; see Methods], 1 male) were captured first at SVL < 20 cm with juvenile coloration (i.e., the typical longitudinally striped gray pattern; Fig. 2), but upon final capture as adults had transitioned to adult coloration. The remaining 31 that changed colors as adults (17 females, 14 males) provided a basis for understanding adult color changes (summarized in Fig. 3).

FIGURE 6. Color pattern transition across body sizes (small adult, top; large adult, bottom; all are different individuals) for *Cyclura rileyi nuchalis* on Bush Hill Cay exhibiting (top to bottom) the brown to gray to salmon transition. Note the loss of mottling, and the fading of colors to salmon or cream. (Photographed by John B. Iverson and students).

Two distinct color transition patterns were evident on Bush Hill Cay, each developing as the longitudinal stripes of the juvenile were lost as maturity was reached (though retained in some individuals until 23 cm SVL), and mottling on the body increased initially. The rarer transition pattern (Table 3; Fig. 3) was characterized by the change from the gray juvenile background color to greenish gray to yellowish gray, and eventually to all yellow, with minimal mottling (Fig. 4). This transition took as few as two years based on our recaptures. Among adults ≥ 20 cm SVL, only 13.5% of females and 11.3% of males were yellow when first captured. All of our data indicated that these iguanas remain yellow for the rest of their lives. No yellow iguana (8 males: mean interval between first and last capture = 3.63 y and range, 1–10 y; 12 females: mean interval = 5.75 y and range, 1–11 y) ever changed to another color, although the yellow pattern darkened in some individuals (Fig. 4).

The second identified transition pattern was much more complex, but could be qualitatively described as a loss of the juvenile stripes, leaving a variably mottled gray appearance. This appearance later was suffused with orange or brown, which in some individuals was later lost, leaving a gray background that in a very few individuals washed out to cream or even salmon color (Figs. 5–6). In the gray–brown–orange phases, males tended to be brighter in color; i.e., more likely orange, than gray or brown (65 of 98, 66%, orange in males; 55 of 157, 35%, orange in females).

The direction of color change in our model was somewhat corroborated by comparisons of mean body sizes of individuals exhibiting each color pattern (Table 4). For

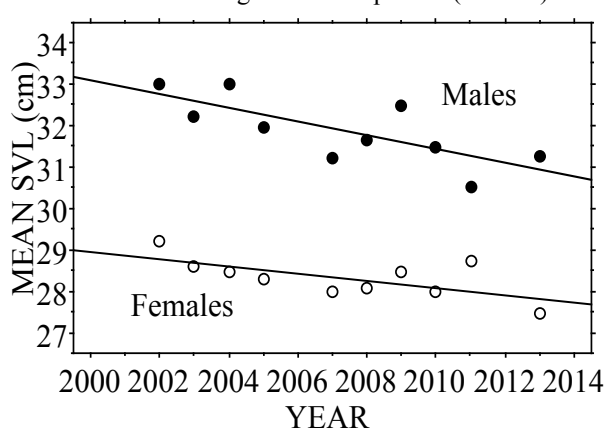

FIGURE 7. Decline in mean snout-vent length (SVL in cm) of adult *Cyclura rileyi nuchalis* on Bush Hill Cay through time. For males: y = -0.166x + 364.758, n = 22–41 per sample, r = 0.75, P = 0.013. For females: y = -0.088x + 204.547, n = 32–75 per sample, r = 0.67, P = 0.036.

example, cream and salmon males had larger mean body sizes, suggesting that those colors were the latest to develop in life. Unfortunately, the variation in body size among adult females of various colors was minimal, precluding the definition of any patterns.

Population parameters.—Juvenile iguanas were rarely seen or captured on Bush Hill Cay (all authors, pers. obs.). Only 1.17% of all iguana captures (n = 858 total captures) were < 12 cm SVL and only 3.03% were between 12.0 and 19.9 cm SVL. For most of the surveys, the adult sex ratio, whether based on raw capture data or on estimated numbers of males and females, was significantly female-biased (Table 5). The sex ratio based on raw capture data became increasingly female-biased over the course of our study (Fig. 9, top; n = 10, r = 0.76, P = 0.010; proportion male = 29.66 – 0.0146Year). In contrast, the sex ratio based on estimated numbers of males and females from Program MARK did not change significantly during the study (Fig. 9, bottom; n = 8, r = 0.18, P = 0.67).

For males, the best population model from Program MARK included among-year variation in both survival and capture probability estimates. In some recapture intervals (Table 6), annual male survival was estimated to be 100%, whereas in others, estimated survival was only 65–70% (e.g., 2002–2003, 2005–2007, 2010–2011).

For females, two models performed almost equally well – the model with constant female survival estimates and variable capture probabilities (AICc = 1,024.75), and the model with among-interval variation in both survival and capture probability estimates (AICc = 1,026.28). We report both results here. For the model with constant female survival and variable capture probabilities, annualized survival for females was estimated to be 0.892 ± (SE) 0.014 (range, 0.50 to -1.00). For the second model (Table 6), annualized survival was relatively high (> 87%) during most time

TABLE 3. Frequency of general color morphs among all captured adult *Cyclura rileyi nuchalis* (≥ 20 cm SVL) on Bush Hill Cay, based on their color at first capture. Actual numbers are followed by the expected number (in parentheses) for each color category individually assuming the biased sex ratio of the sample. See text and Figs. 4–6 for color definitions.

Sex	Brown	Orange	Gray	Cream	Salmon	Yellow
Female	53 (38)	55 (73)	52 (46)	3 (7)	0 (2)	22 (21)
Male	9 (24)	65 (47)	24 (30)	8 (4)	3 (1)	12 (13)

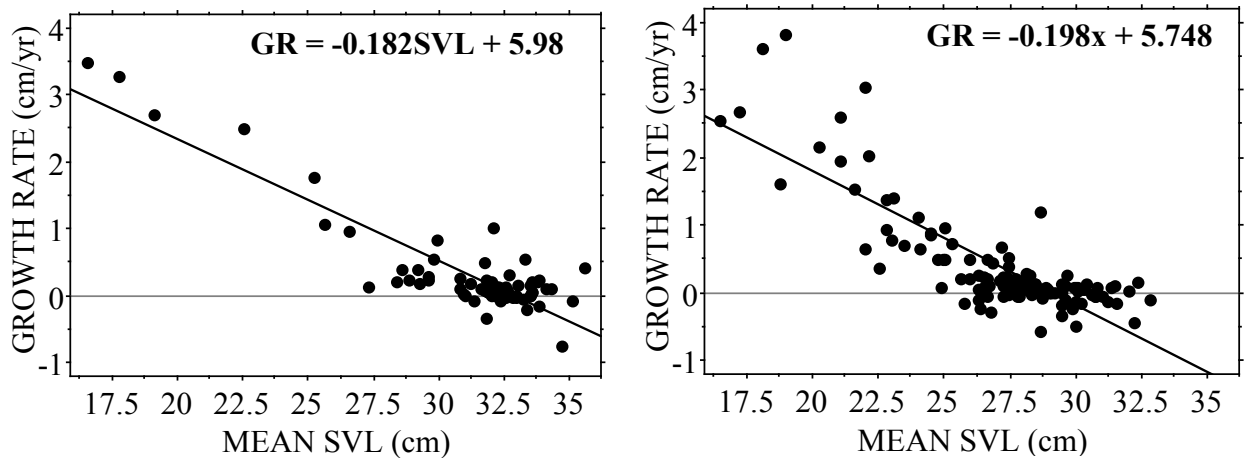

FIGURE 8. Relationship of SVL (in cm; mean of first and last capture) to growth rate (SVL in cm/y) in male (left; r = 0.90, P < 0.0001) and female (right; r = 0.82, P < 0.0001) *Cyclura rileyi nuchalis* on Bush Hill Cay recaptured after > 1 year.

TABLE 4. Mean snout-vent length of *Cyclura rileyi nuchalis* on Bush Hill Cay (for all captures ≥ 20 cm SVL; 318 males, 496 females) for color pattern recorded at capture. ANOVAs for males ($F_{6,115}$ = 9.41, P < 0.0001) and females ($F_{6,179}$ = 14.75, P < 0.0001) were both significant. Letters adjacent to means indicate non-significant differences by Fisher's Least Significant Difference (e.g., juvenile and brown males differed significantly from each other and all other samples).

Male Color	Male SVL	Female Color	Female SVL
Juvenile	23.10	Juvenile	21.13
Brown	29.69	Gray	28.02 B
Orange	31.99 A	Cream	28.31 AB
Gray	32.05 A	Salmon	28.34 AB
Yellow	32.19 AC	Yellow	28.46 AB
Cream	33.05 B	Brown	28.52 A
Salmon	33.50 BC	Orange	28.67 A

intervals. However, survival was substantially lower in the last time interval for which we could estimate survival (only 50% for 2010–2011).

Estimated population size for adult iguanas (≥ 20 cm SVL) on Bush Hill Cay ranged from 59 in 2011 (perhaps biased by the low number of captures, most of them already marked, but surely an underestimate given the 2013 sample of 77) to 322 in 2004 (Table 2). Excluding the lowest estimate, the remaining seven estimates averaged 229. However, there was a significant decline in estimated population sizes during the study period (Fig. 10; n = 8, all estimates included; r = 0.82, P = 0.012; estimated population size = 48779.3 – 24.2Year).

Assuming a population estimate of 306 adult iguanas on Bush Hill Cay in 2003 (based on the regression equation for estimated population size; Fig. 10), a total island area of 3.3 ha, and the mean body mass data for all 857 iguana captures on the cay (951.6 g), we conservatively estimated the density of subadults and adults at 95.6/ha and a standing crop biomass of 91.0 kg/ha. However, the method applied to 2011 data, estimated only 113 adults present, a density of only 35.3/ha, and a biomass of only 33.5 kg/ha.

TABLE 5. Adult sex ratios (expressed as proportion of males) of *Cyclura rileyi nuchalis* (≥ 20 cm SVL) from Bush Hill Cay based on raw captures and on population sizes of each sex estimated using capture probabilities from the program MARK analysis. *Indicates sex ratio is significantly different from 1:1 using a chi-square analysis.

Year	Raw captures	Estimated
2002	0.48	--
2003	0.52	0.42*
2004	0.43	0.35*
2005	0.36*	0.22*
2007	0.38*	0.30*
2008	0.40	0.37*
2009	0.34*	0.34*
2010	0.30*	0.31*
2011	0.41	0.44
2013	0.32*	--

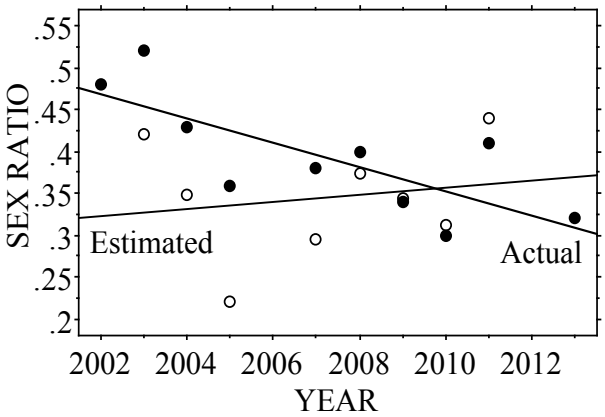

FIGURE 9. Change in the proportion of males in the population of adult *Cyclura rileyi nuchalis* on Bush Hill Cay through time based on raw capture data (Actual, closed circles: n = 10, r = 0.76, P = 0.010; proportion male = 29.66 – 0.0146Year) and on estimated numbers of adult males and females from population models (Estimated, open circles: n = 8, r = 0.18, P = 0.67).

TABLE 6. Annual survival (± SE) of *Cyclura rileyi nuchalis* on Bush Hill Cay based on recapture data analyzed by program MARK. Survival for the last interval in the data (2011–2013) cannot be estimated with this analysis. *SE < 0.0001.

Interval	Males	Females
2002–2003	0.652 ± 0.179	1.000 ± 0*
2003–2004	0.967 ± 0.175	0.872 ± 0.102
2004–2005	0.796 ± 0.161	1.000 ± 0*
2005–2007	0.691 ± 0.065	0.829 ± 0.043
2007–2008	0.996 ± 0.057	0.877 ± 0.084
2008–2009	0.994 ± 0.090	0.942 ± 0.084
2009–2010	1.000 ± 0*	1.000 ± 0*
2010–2011	0.657 ± 0.134	0.501 ± 0.083

DISCUSSION

Size and growth.—The largest iguana (presumably a male, n = 54) reported by Carter and Hayes (2004) from Bush Hill Cay in 1996–1997 was 36.0 cm SVL and 1,650 g BM; however, we recorded a male of 37.2 cm SVL and 1,710 g. Our two largest females measured 33.8 cm SVL and 1,225 g, and 33.0 cm SVL and 1,376 g. The largest SVL reported for *C. rileyi nuchalis* on Fish Cay (the source population) was 31.4 cm and for North Cay was 28.0 cm (presumably males, Hayes et al. 2004a). Carter and Hayes (2004) reported that males were significantly larger than females on Bush Hill Cay, but did not provide body size data by sex. Our data confirm this male-biased dimorphism quantitatively. Males in our study averaged 13.2% longer and 35.0% heavier than females.

Mean body mass of iguanas on Bush Hill Cay during this study (n = 857 captures) was 951.6 g (range, 30–1,710 g), compared to a mean of 1,097 g (range, 9.2–1,650 g) for 54 captures in 1996–1997 by Carter and Hayes (2004). Those authors also reported significantly

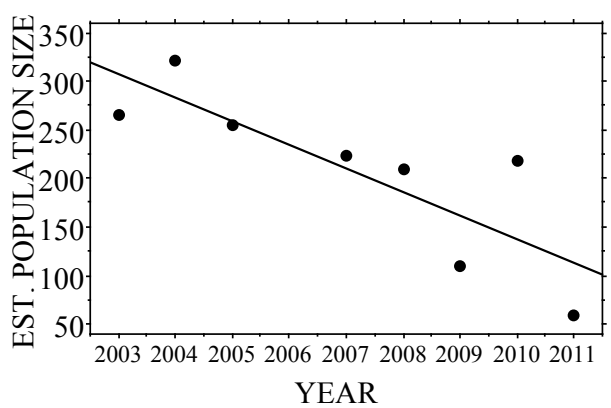

FIGURE 10. Change over time in estimated population size of adult *Cyclura rileyi nuchalis* on Bush Hill Cay based on population models (n = 8, r = 0.82, P = 0.012; estimated population size = 48779.3 – 24.2Year).

lower mean body masses from the natural populations on Fish Cay (459 g) and North Cay (404 g). We concur with Hayes et al. (2004a) that the larger body size on BHC was likely due to reduced intraspecific competition during population growth, although nutritional differences in the diets cannot be ruled out (William Hayes, pers. comm.). However, the 139 g decline (12.7%) in mean body mass in the decade between the mid-1990s and mid-2000s is noteworthy, particularly since the pattern of a decline in body size continued during our study (Fig. 7). It may be that the iguanas that grew to extraordinary sizes during times of low density (i.e., soon after translocation) are now dying and being replaced by individuals that matured during times of high density (i.e., near carrying capacity) and are thus smaller.

Hayes et al. (2004a) reported that *Cyclura rileyi* (all populations) generally reaches sexual maturity at 20 cm SVL and ca. 300 g (at an unknown age), but the precise size at maturity on BHC is unknown. However, based on our growth data, 20 cm SVL was reached on BHC during our study period at ca. 4.5 y in females and ca. 3.9 y in males on average. *Cyclura carinata* is the only other West Indian iguana of similar body size to *C. rileyi*, and it matures at about the same size (18–20 cm SVL); however, despite its more southern (i.e., tropical) distribution, it requires 6–7 years to reach maturity (Iverson 1979). Other species of *Cyclura* are larger and reach maturity from 2–12 years (Table 7 in Iverson et al. 2004b). Translocated populations of *Cyclura* are known to reach maturity more quickly than their source populations (Knapp 2001; Gerber 2007), presumably due to reduced intraspecific competition among the founders, but unfortunately no growth data are available for native populations of *C. rileyi*.

Preliminary observations of the Bush Hill Cay population by Carter and Hayes (2004) found higher frequencies of missing digits in the Bush Hill Cay population (20.4%) compared to either the Fish Cay (12.3%) or the North Cay (14.9%) populations. Bush Hill Cay (51.9%) also had higher frequencies of injured tails than the Fish Cay (24.6%) and North Cay (32.6%) populations in 1996–1997 (Carter and Hayes 2004), and that frequency increased to 60.4% during the period 2002–2010 (Hayes et al. 2012). A meta-analysis of 19 populations of three species of *Cyclura* (including all three *nuchalis* populations) strongly implicated rats as the cause of the elevated rates seen on at least BHC (Hayes et al. 2012).

Iguanas may also suffer indirect competitive effects from rats, via shared limited food resources or through vegetation damage (Towns et al. 2006), and these may intensify during periods of drought or low productivity. We have observed increasing damage to vegetation by rats (e.g., gnawed twigs) and increased encounters with rats (e.g., when they entered live traps intended for iguanas during the day). But unfortunately we have no data on the dynamics of the rat population or primary productivity on BHC. The collection of data such as these would be particularly valuable prior to the removal of the rats.

Coloration.—Ours is the first attempt to quantify color and color changes in any species of *Cyclura*. *Cyclura rileyi* exhibits far more variation in body color than any congener (Schwartz and Carey 1977) and indeed, most other studied lizards (reviewed by Olsson et al. 2013), which is likely related to its insular evolution where background matching of large adults was presumably of little selective value. Furthermore, like many diurnal lizards *C. rileyi* is capable of subtle color changes during the day (darker early, more vivid later), apparently related to light and/or temperature (i.e., "physiological color change"; Cooper and Greenberg 1992; Langkilde and Boronow 2012; Olsson et al. 2013). However, the extraordinary body color variation in *C. rileyi* probably functions primarily in social communication, although the mechanisms are still unknown. We did not quantify color patterns micro-geographically on BHC, although the various color patterns seemed to be distributed randomly across the island. Unfortunately, we did not quantify (or notice) any associations of color among territorial males and nearby females. In addition, since we only visited BHC during May (usually) or June (once), we also cannot address seasonal variation in color on the island.

Hence, although our 12 years of recapture data have clarified the frequencies and general directions of ontogenetic color change in these iguanas, the bases for these changes are completely unknown (e.g., diet: Wikelski unpublished in Hayes et al. 2004b; Costantini et al. 2005), as are their fitness consequences (e.g., Cooper and Greenberg 1992; Rosenblum 2005; Pérez et al. 2012; Olsson et al. 2013; Pérez i de Lanuza et al. 2013). Furthermore, we do not know whether the patterns we have observed mirror those in the founder population on Fish Cay, because few data are available on color morphology (e.g., there is no complete list of all color morphs and their frequencies) and none are available on color change for any population of this species.

Our observations of color patterns on Bush Hill Cay generally agree with those reported for both *C. rileyi rileyi* and *C. rileyi nuchalis* by Hayes and Montanucci (2000), but differ significantly from the colors mentioned by Schwartz and Carey (1977; repeated by Lemm and Alberts 2012) who reported black as a common color (perhaps based on museum animals in fixatives). Hayes and Montanucci (2000) reported that the color patterns of *C. rileyi nuchalis* resemble those of *C. rileyi rileyi* and "Dorsum colors of red, orange, yellow, green, or brown are usually punctuated by darker markings and fine vermiculations. Males generally exhibit more color (red, orange, or yellow) and contrast than females, especially at warmer body temperatures. Juveniles are solid brown or gray, often with a slightly

paler mid-dorsal band having faint longitudinal stripes or indistinct darker areas near the middorsal crest. Juveniles lack the brighter coloration and vermiculations of adults, as well as the dorsal chevrons or pale diagonal markings present on juveniles of other taxa." These color notes generally correspond to our observations, although we did not record "red" individuals.

We hope to continue monitoring iguanas from Bush Hill Cay in order to more precisely quantify the various color morphs and their transitions. Similar studies are needed for natural populations of *C. rileyi*, and this species offers a unique possibility to study the fitness correlates of the various color morphs. For example, we calculated the residuals of the SVL-body mass regression of males and females separately to determine any differences in body condition among the six adult and one juvenile color morphs. For females, variation across samples was not quite significant ($F_{6,179}$ = 1.84, P = 0.09), but post hoc tests (Fisher's protected least significant difference, alpha = 5%) identified orange females as significantly heavier than brown females (+8.3 g versus -13.2 g). This may indicate a positive relationship between health and color brightness in females. For males, the variation in size across the color patterns was not significant ($F_{6,115}$ = 0.81, P = 0.57). However, yellow males had the highest mean residual (+30.0 g) and (presumably older) salmon males had the lowest (-25.9 g). These results are clearly inconclusive, but at least suggest that color may have fitness correlates, and is worthy of future study.

Population parameters.—Hayes et al. (2004a) commented on the low incidence of captures and sightings of small (< 12 cm SVL) and large (12.0 to 19.9 cm SVL) juveniles on BHC in 1996–1997. Their frequencies, 1% and 5%, respectively, were similar to those that we found among our captures (1% and 3%, respectively). Natural populations of *C. rileyi nuchalis* on Fish Cay (25%) and North Cay (23%) had much higher frequencies of juveniles (Hayes et al. 2004a, their Table 17.3), as did populations of *C. rileyi cristata* (34%) and most populations of *C. rileyi rileyi* (0% to 57%; mean = 28%). Immature iguanas represented 42% of a sample of 167 *C. carinata* (Fig. 51 in Iverson 1979) prior to the effects of invasive mammals. In the most complete sample year for *C. cychlura inornata* (2002), 43% of 168 iguanas captured on U Cay and 40% of 483 iguanas captured on Leaf Cay were immature (< 25 cm SVL). Hayes et al. (2004a) attributed the low numbers of juveniles on BHC to the presence of rats, as well as the fact that the species is occasionally cannibalistic on other islands (Hayes et al. 2004a). Unfortunately, low numbers of juveniles are typical of most *Cyclura* populations due to introduced, invasive mammals. For example, on an island overrun with exotic mammals, only 5–10% of *C. stejnegeri* were juveniles (Wiewandt 1977).

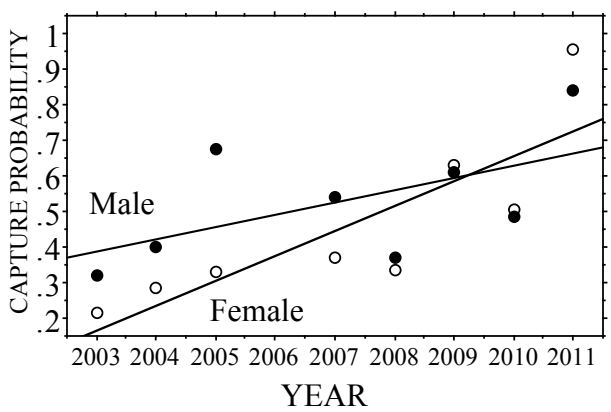

FIGURE 11. Change over time in capture probabilities for male (open circles; n = 8, r = 0.61, P = 0.14; capture probability = 0.034Year – 68.7) and female (closed circles; n = 8, r = 0.84, P = 0.0095; capture probability = 0.070Year – 139.4) *Cyclura rileyi nuchalis* on Bush Hill Cay based on population models.

Hayes et al. (2004a) reported a nearly equal sex ratio (51% male) on Bush Hill Cay in 1996–1997 based on 54 captures. They also found a similar ratio on Fish Cay (51% male) and a slightly male-biased ratio on North Cay (63%). Sex ratios in other species of *Cyclura* are typically even, although Smith and Iverson (2006; ratios reviewed in Table 1) reported a shift from a male-biased ratio to an unbiased ratio in *Cyclura cychlura inornata* as that population grew to carrying capacity following legislative protection.

It is thus quite surprising that we found a strongly female-biased sex ratio (37.5% male), based on 325 first captures of subadults and adults of iguanas from BHC. In addition, as our study progressed, our actual captures became even more female-biased; however, there were no significant changes in the sex ratio based on the estimated number of males and females on Bush Hill Cay from our population models (Table 5). These conflicting observations suggest that the underlying adult sex ratio has likely not shifted significantly during our study, but that the capture probability of males and females diverged over time. Indeed, when we regressed capture probability estimates on time interval (Fig. 11), capture probabilities increased significantly for females (n = 8, r = 0.84, P = 0.0095; capture probability = 0.070Year – 139.4), but not for males, although there was a trend toward an increase (n = 8, r = 0.61, P = 0.14; capture probability = 0.034Year – 68.7). It is perhaps not surprising that capture probabilities increased through time, since our ability to capture these iguanas no doubt also improved with time. However, why our ability to capture males would lag that of females is not clear, although it could reflect gender differences in wariness.

The question remains as to why the sex ratio on Bush Hill Cay would have become so dramatically biased in only a decade? We can offer only three speculative hypotheses. The first is that males may be more susceptible than females to injury and death from the invasive rat

population, perhaps due to the year-round territoriality of male iguanas (Hayes et al. 2004a; Lemm and Alberts 2012). Though rats were already present during the 1996–1997 study by Hayes et al. (2004a) and the sex ratio then was balanced, it is likely that the rat population has increased over time. Second, since male *C. rileyi* are so territorial, it may be that the growth of the population toward (or beyond?) carrying capacity has differentially impacted males more than females. Finally, the cay may have been subject to a poaching event between the two studies, and the brighter, more easily captured, territorial males may have been taken preferentially. We have no data to support this last hypothesis, except the decline in the relative number of males, but we are troubled by this possibility.

In May of 1996 and 1997 Hayes et al. (2004a) used a Lincoln-Peterson mark-resighting index and suggested that a population of 299 iguanas resided on BHC (though Carter and Hayes 2004 reported 314 based on the same data). Our early estimates of population size of the iguanas on Bush Hill Cay (265 in 2003, 322 in 2004) are close to these previous estimates; however, there was a decline in estimated population size during our study. In particular, for the most recent year for which we can estimate the population with Program MARK (2011), the estimated size was 59, whereas the estimate was 110 in 2009 and 218 in 2010. We are uncertain at this time whether the observed variance in estimated population sizes is due to some artifact of the population models or variation in the quantity and quality of capture effort (due to variation in weather and/or personnel). Nevertheless, we are concerned that the population appears to be in decline, and our data indicate an average loss of 24 adults per year (Fig. 10). The precipitous decline in survival estimates for both males and females during the 2010–2011 interval is of particular concern. We anticipate making a concerted effort to resurvey the Bush Hill Cay population in 2016 with an experienced crew. The results of that survey should allow us to quantify the rate of decline more definitively.

Carter and Hayes (2004) and Hayes et al. (2004a) estimated the density of iguanas on BHC in 1996–1997 at 95.2/ha, with a standing crop biomass of 104.4 kg/ha. They also reported much lower numbers for the two native populations on Fish Cay (58.9 kg/ha) and North Cay (23.7 kg/ha). Our estimates for the beginning of our study on BHC (95.6/ha and 91.0 kg/ha) were similar to those reported earlier. Thus, the earlier biomass estimates for BHC were among the highest reported for the genus (reviewed in Iverson et al. 2006), matched only by that estimated for *C. cychlura inornata* in the Exumas, which was believed to be near carrying capacity (94.1 kg/ha; Iverson et al. 2006). Assuming that the Bush Hill Cay population was also near carrying capacity in 1996–1997, these data suggest that a standing crop biomass of near 100 kg/ha may be the upper limit for natural populations of this herbivorous genus. Unfortunately, no other populations of *Cyclura* have been reported to be near carrying capacity.

Conclusions.—Our work, and that of Hayes et al. (2004a) and Carter and Hayes (2004), demonstrate the successful translocation of *C. rileyi nuchalis* to Bush Hill Cay. Recent declines in the estimated population, however, suggest that the future outlook for this population bears greater scrutiny. Given the success of this population over its first 30 years, we do not believe that this decline reflects a translocation failure, although data on genetic diversity of the BHC population (given only five founders) would alleviate some remaining concerns. Unfortunately, the introduction of rats to the cay, and the possibility of poaching from this isolated cay, complicate our explanation of the current decline. In any case, we strongly recommend that a rat eradication program be implemented on BHC as soon as possible. Mammal eradication programs have already been demonstrably effective for the recovery of other populations of *Cyclura* (e.g., Mitchell et al. 2002 and Gerber 2007 for *C. carinata*; Day et al. 1998 and Hayes et al. 2004a for *C. rileyi cristata*; Aurora Alifano et al. unpublished for *C. cychlura inornata*; and Wilson 2011 for *C. collei*), and would likely aid in reversing the current decline on BHC.

Given the significant and increasing costs in time and money to establish captive breeding facilities for West Indian iguanas, and the demonstrated success of translocation programs for these lizards (Knapp and Hudson 2004; Table 1), translocations of other endangered island populations of *Cyclura* should be the first strategy explored during the development of their conservation management plans.

Our study also makes it clear that financial support for ongoing monitoring of translocated populations, as well as the founder populations, is essential for long-term conservation of this endangered genus of lizards. As a case in point, if the only existing population of *C. rileyi cristata* had not been monitored (though irregularly), the raccoon and rats introduced there in the mid-1990s would likely have driven that taxon to extinction (Day et al. 1998; Carter and Hayes 2004; Hayes et al. 2004a).

Finally, it should be noted that monitoring of translocations generally focuses only on the relocated species, as has been the case for all *Cyclura* translocations. However, introductions such as these may have broad consequences to the translocation ecosystem, especially considering the possible impacts of a dense population of a large herbivorous species like an iguana (e.g., Schofield 1989; Campbell et al. 1991; Strong and Leroux 2014). We know of no such study associated with any iguana translocation, but urge the undertaking of such work. For example, it is often stated that iguanas are critical seed dispersers in their native ecosystems, and hence, essential to those systems. Yet

data demonstrating ecosystem differences with and without iguanas are not yet available.

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