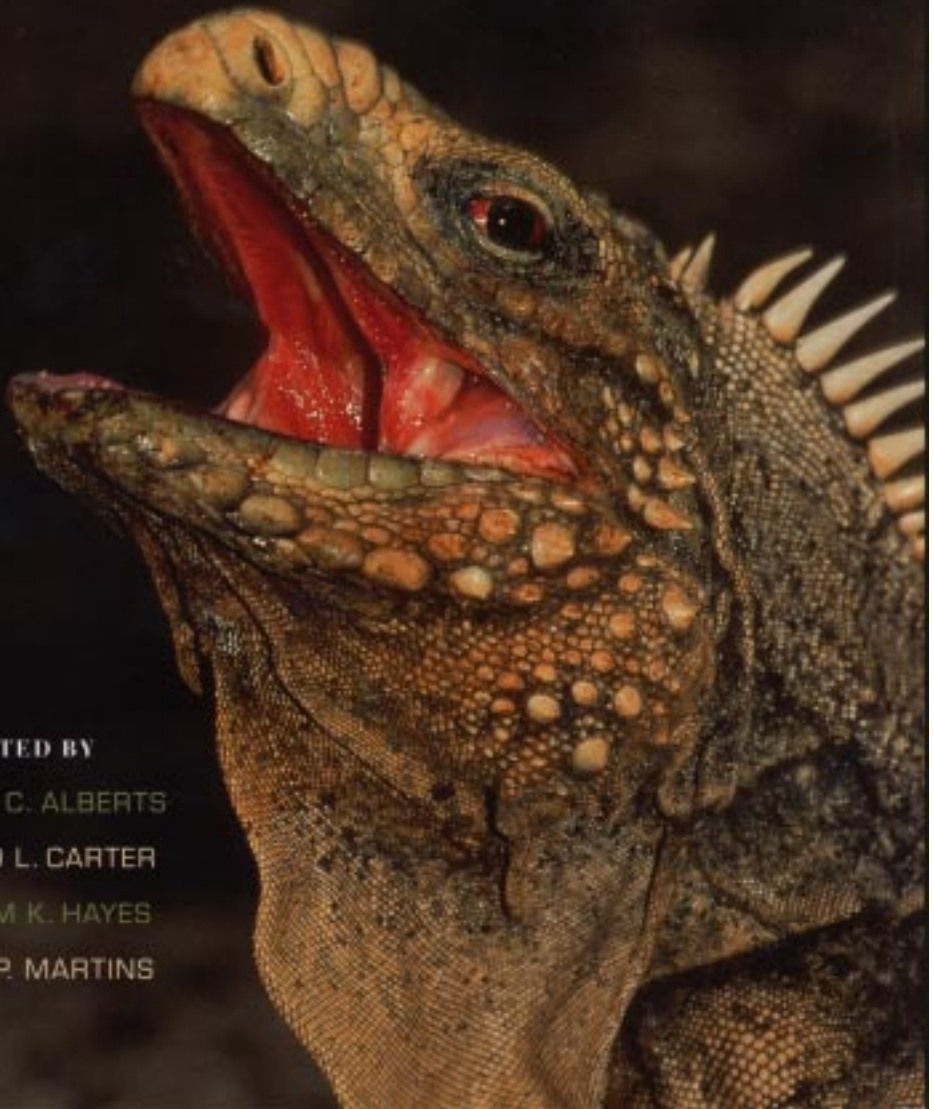


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IGUANAS

BIOLOGY AND CONSERVATION



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Conservation of an Endangered Bahamian Rock Iguana, II

MORPHOLOGICAL VARIATION AND CONSERVATION PRIORITIES

Ronald L. Carter and William K. Hayes

GIVEN THE PRECARIOUS STATUS of two of the three subspecies of the San Salvador iguana (*Cyclura rileyi*) in the wild (Hayes et al., this volume), consideration should be given to treating these three subspecies as separate management units. The phenetic analysis by Schwartz and Carey (1977) provided the current taxonomy of *Cyclura*, which recognizes the subspecies of *C. rileyi*. Their conclusions were derived largely from assessment of morphological characters, primarily scale counts. More recently, Hollingsworth (1998) and Malone et al. (2000) proposed interspecific relationships based on modern phylogenetic analyses of morphological and mitochondrial DNA (mtDNA) variation, respectively, and both studies found support for the specific status of *C. rileyi*. However, because of the lack of mtDNA differentiation within *C. rileyi* (Malone et al., 2000), Malone and Davis (this volume) question the need for managing the three subspecies as separate entities. Although more detailed genetic analyses in our lab remain uncompleted, we have collected morphological data that, in addition to our ecological data (Hayes

et al., this volume), may shed some light on this important question.

In this chapter, we address two major areas that relate to the conservation of *C. rileyi*. First, we present findings on morphological variation between and within the three subspecies. We consider several aspects of morphology, including body size, frequency of injuries, femoral pore counts, and head scalation. Although subject to phylogenetic constraints, population differences in body size and injury rates often reflect differences in, and sometimes adaptation to, local ecology. Within a population, temporal variation in these measures can be expected to track environmental change. Thus, morphological study may offer insights on the relative health of a population. Differences in femoral pore and head-scale counts, in contrast, generally reflect phylogeny (although sometimes ontogeny or sexual dimorphism) rather than ecology, and therefore are useful for taxonomic purposes (e.g., Snell et al., 1984; Hollingsworth, 1998). Using these characters, we employ discriminant analyses to evaluate the possible taxo-

nomic distinctiveness of the three subspecies. Second, we offer specific conservation recommendations that take into consideration our major findings from both our population assessments and behavioral ecology studies (Hayes et al., this volume), in addition to the morphological data presented here.

MORPHOLOGICAL VARIATION

METHODS

CAPTURE AND DATA COLLECTION

Between 1993 and 1999, we captured, marked, and measured snout-vent length (SVL), head length, and tail length of 484 iguanas (75 *C. r. cristata*, 198 *C. r. nuchalis*, 211 *C. r. rileyi*) as described in Hayes et al. (this volume). We noted damage to toes and tail, measured tail regeneration if present, and counted the number of femoral pores on both legs. Close-up photos of the head (35 mm color slides), both dorsal and lateral angles, were obtained for most lizards. Although taken primarily for identification purposes, these photos were later used for scale counts. Even though coloration differences are conspicuous between some populations, we did not undertake a formal study of this trait. Several ecological features of individual populations were considered in the analyses of body size and injuries. These included size of cay, population size, iguana density, number of plant species, and presence of rats (see Hayes et al., this volume).

DATA TREATMENT AND ANALYSES

Statistical tests were conducted using SPSS for Windows (release 8.0, 1997; SPSS Inc., Chicago, Illinois), with $\alpha = 0.05$. Both parametric and nonparametric tests were conducted depending on the data properties. For some data, log transformations were required prior to analyses. In some cases, we report parametric tests of data that failed to meet parametric assumptions, but when possible, we used nonparametric alternatives to confirm suitability of the parametric tests. For multivariate tests,

effect sizes (proportion of variance explained by an independent variable) are indicated in some cases by η^2 .

RESULTS AND DISCUSSION

BODY SIZE VARIATION

Our analyses of the relationship between body mass and SVL revealed several patterns of variation. The strong correlation between body mass and SVL was best explained by a power regression equation ($\text{mass} = 0.049 \text{ SVL}^{2.908}$; $r^2 = 0.94$). An analysis of covariance (ANCOVA) model ($\log \text{mass} = \text{sex} \times \text{subspecies} \times \log \text{SVL}$) revealed that the relationship between mass and SVL (a measure of body condition) was similar for males and females ($P = 0.77$, $\eta^2 = 0.00$) but differed significantly among the three subspecies ($F_{2,433} = 18.47$, $P < 0.001$, $\eta^2 = 0.08$): *C. r. nuchalis* was leaner than the other two subspecies. When the ANCOVA was restricted only to adult iguanas (≥ 20 cm SVL), the same patterns emerged, again showing *C. r. nuchalis* to be leaner than the other subspecies ($F_{2,366} = 22.71$, $P < 0.001$, $\eta^2 = 0.11$; figure 18.1). Another ANCOVA model ($\log \text{mass} = \text{sex} \times \text{season} \times \log \text{SVL}$), restricted to captures of adult *C. r. rileyi* in March, May–June, and November 1995 ($n = 36$, 32, and 10, respectively), revealed a significant interaction between sex and season ($F_{2,71} = 4.87$, $P = 0.01$, $\eta^2 = 0.12$), arising because males were heavier than females in March, whereas females were heavier than males in May–June (November samples were too small for comparison). The significant main effect of season ($F_{2,71} = 8.70$, $P = 0.016$, $\eta^2 = 0.05$) indicated that iguanas, regardless of sex, were heaviest in March and leanest in November (figure 18.1).

These data are consistent with the conclusions of Iverson (1979) and Auffenberg (1982a)—based on analyses of fat bodies and diet, respectively, for *C. carinata*—that iguanas feed most heavily in spring and less heavily in the summer (when time and energy are devoted to reproduction) and winter (when food resources are least available). However, the extent to which relative hydration influences body condition remains to

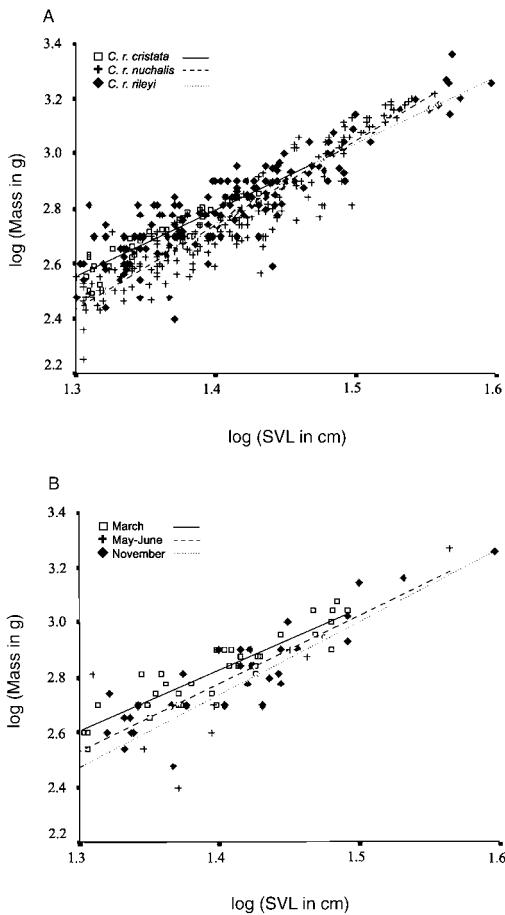


FIGURE 18.1. Relationships between log body mass (g) and log snout-vent length (SVL, cm) in (A) adults of three subspecies of *Cyclura rileyi* and (B) adults of *C. r. rileyi* captured in March, May–June, and November 1995.

be investigated and represents a potentially confounding factor.

Among the eleven populations comprising the three subspecies, there were significant differences in mean body mass (one-way ANOVA: $F_{10,445} = 67.14$, $P < 0.001$, $\eta^2 = 0.60$) and mean SVL (one-way ANOVA: $F_{10,470} = 26.23$, $P < 0.001$, $\eta^2 = 0.36$), with the largest iguanas occurring on Low Cay and in the translocated population, and the smallest occurring on Manhead and White Cays (table 18.1). Iguanas from the translocated population attained significantly larger body size than those from their source population on Fish Cay (Scheffe post-hoc comparison, $P < 0.001$). A similar phenomenon was reported

by Knapp (2001a) for a translocated population of *C. cyclura inornata* in the Exumas and may result from reduced competition for food and thermoregulatory sites. Iverson (2001) and Iverson et al. (this volume) noted that individuals of *C. c. inornata* on sparsely populated Allens Cay in the northern Exumas were substantially larger than those on two adjacent, densely populated cays. He proposed that the extraordinary growth may be a result of reduced competition, the presence of unique food plants (e.g., morning glory [*Ipomoea pes-caprae*]), or the possible inclusion of significant animal protein (nesting Audubon's shearwaters [*Puffinus lherminieri*]) in their diet. We additionally suggest that more energy can be allocated to growth when social interactions are fewer (compare Christian et al., 1986; Wikelski et al., 2001) on sparsely populated islands.

Spearman correlation analyses among the eleven populations indicate that both maximum SVL and mean body mass were independent of cay size, population size, iguana density, and number of plant species (all $P > 0.20$). The reasons for population differences in body size remain unclear to us. However, we suspect that variation in quantity and quality of food has a substantial influence on growth rate, maximum body size, and population density (e.g., Iverson, 1979, this volume; Knapp, 2001a; Tracy, this volume; Wikelski and Carbone, this volume). More detailed analyses of vegetation on these cays should be informative.

Body size dimorphism is fairly distinct in *C. rileyi*. As in most iguanas, males attain a larger size (25.4 cm SVL and 683 g; $n \geq 245$ for each mean) than females (22.5 cm SVL and 474 g; $n \geq 198$ for each mean), with females averaging only 89% of the SVL and 69% of the body mass of males. An ANCOVA model (head length = sex \times subspecies \times SVL) showed that males also have significantly larger heads than do females ($F_{1,458} = 19.30$, $P < 0.001$, $\eta^2 = 0.04$). No differences in head size dimorphism were apparent among the subspecies ($P = 0.16$, $\eta^2 = 0.01$). Sexual dimorphism in head size exists in most iguanas studied to date and may arise from

TABLE 18.1
Body Size and Ecological Variables for Iguanas Sampled from All Known Populations of Cyclura rileyi cristata, C. r. nuchalis, and C. r. rileyi

TAXON	CAY	MASS (KG)			SVL (CM)			ECOLOGICAL VARIABLES				
		N	MEAN ± SE	RANGE	MEAN ± SE	RANGE	AREA (ha)	POP SIZE (N)	DENSITY (N/ha)	PLANT SPECIES	RATS	
<i>C. r. cristata</i>	White	75	0.371 ± 0.025	0.037–0.760	20.1 ± 0.5	10.2–28.0	14.9	136	9.1	20+	Present	
<i>C. r. nuchalis</i>	Fish	57	0.465 ± 0.026	0.020–0.830	23.8 ± 0.7	9.0–31.4	73.9	9484	128.3	50+	Absent	
	North	87	0.378 ± 0.014	0.046–0.660	22.4 ± 0.4	11.1–28.0	51.7	3036	58.7	50+	Absent	
	Transloc popn	54	1.097 ± 0.048	0.030–1.650	29.8 ± 0.6	9.2–36.0	3.3	314	95.2	47	Absent	
<i>C. r. rileyi</i>	Gaulin	3	0.650 ± 0.029	0.600–0.700	24.4 ± 0.9	22.8–25.8	1.6	Recently extirpated	—	10	Absent	
<i>C. r. rileyi</i>	Goulding	35	0.557 ± 0.046	0.033–1.100	23.1 ± 0.9	9.3–31.0	2.9	116	40.0	16+	Absent	
	Green	86	0.589 ± 0.020	0.100–0.900	23.4 ± 0.5	8.0–31.1	5.1	130	25.5	10	Absent	
	Guana	15	0.665 ± 0.139	0.050–1.200	26.2 ± 1.8	12.1–35.2	1.6	30	18.8	42	Present	
	Low	16	1.481 ± 0.098	0.750–2.300	34.2 ± 0.9	26.3–39.5	10.8	42	3.9	31	Present	
	Manhead	25	0.292 ± 0.028	0.109–0.500	21.3 ± 0.7	16.0–27.0	3.3	38	11.5	15	Absent	
	Pigeon	31	0.603 ± 0.042	0.100–1.050	24.7 ± 0.7	12.5–31.0	7.8	70	9.0	7	Present	

Sources: Ecological variables from Hayes et al. (this volume).

Notes: Excludes a very small population on the main island of San Salvador that could not be sampled. Data are from 1993 to 1998. Differences in lower bound of body size range generally reflect success in the capture of young iguanas and time of year of sampling (some populations were not visited during fall hatching season).

intrasexual selection (e.g., male-male interactions), intersexual selection (via female choice), differential allocation of energy for reproduction, or resource partitioning (Hayes et al., this volume). At present, we lack data to identify the cause(s) of head size dimorphism in *Cyclura*.

INJURIES

We observed a range of injuries, including missing toes, tail fractures, loss of a portion of the tail, frequent penetration by cactus spines, missing nuchal spines, missing feet ($n = 2$), missing portions of the snout ($n = 2$), and damage to or loss of an eye ($n = 2$). One iguana showed fractures of the ribs and spine that had healed, but this resilient individual was handicapped by lower limb paralysis. Injuries to toes and tails were most frequent (table 18.2). We restricted our analyses to counts of missing digits (frequency and number of digits lost), missing portions of the tail (frequency, either missing or inferred from regeneration), and length (cm) of tail regeneration.

For toe injuries (table 18.2), there were significant differences between the three subspecies ($\chi^2_2 = 28.47$, $P < 0.001$) and among the eleven populations ($\chi^2_{10} = 53.1$, $P = 0.001$), but ecological explanations for the differences were unclear. The proportion of all iguanas with missing digits was 24.9%, and all five populations above this value were of *C. r. rileyi*. Because high rates of toe injury were evident on cays composed largely of both sandy (Pigeon) and rocky habitats (Green, Goulding), substrate differences probably do not account for population differences. Although hermit crabs (*Coenobita clypeatus*), which are particularly dense on San Salvador's cays (W. Hayes and R. Carter, unpubl. data), might contribute to the high rate of digit loss in *C. r. rileyi*, Pigeon Cay has few (if any) hermit crabs. The high proportion of Low Cay iguanas with missing digits (75%) may be related to the skin disease detected by Auffenberg (1982b), although the mean number of lost toes is higher now than was observed in 1982 (3.1, $n = 16$; and 1.2, $n = 13$, respectively). Excluding Gaulin Cay because of small sample size, Spearman corre-

lation analyses revealed that the frequency of toe loss among populations was independent of cay size, population size, and iguana density (table 18.2; all $P > 0.054$). However, there was a weak and possibly spurious relationship between toe loss and number of plant species ($r_s = -0.70$, $P = 0.024$). Frequency of toe loss was similar for rat-infested ($n = 4$) and rat-free ($n = 6$, excluding Gaulin) cays (table 18.2; Mann-Whitney U test, exact one-tailed $P = 0.31$).

Among all iguanas, males (30.5% of 262 iguanas) were more likely to have missing toes than were females (19.4% of 201 iguanas; $\chi^2_1 = 7.38$, $P = 0.007$), presumably as a consequence of more frequent or more intense agonistic behavior. The proportion of iguanas with missing toes increased with age class (5.0%, 10.4%, and 28.5% for 20 juveniles, 67 subadults, and 390 adults, respectively; $\chi^2_2 = 14.35$, $P = 0.001$), suggesting that toe loss accumulates gradually as iguanas age. The average number of toes lost (table 18.2) shows patterns similar to the frequency data, except that there was no relationship with number of plant species ($P = 0.062$).

For tail injuries (table 18.2), there were no differences between the subspecies ($P = 0.36$), but there were significant differences among the populations ($\chi^2_{10} = 34.3$, $P < 0.001$). The proportion of all iguanas suffering a tail injury was 35.8%, similar to that reported in some *Cyclura* (e.g., *C. carinata carinata*, *C. cyclura cyclura*, *C. pinguis*, *C. cornuta stejnegeri*), but greater than that of others (e.g., <15% in *C. cyclura figginsii*, *C. cyclura inornata*), as reviewed by Iverson et al. (this volume). Populations exceeding this value included three *C. r. rileyi* populations (Guana, Low, and Pigeon Cays), the translocated population of *C. r. nuchalis*, and the single *C. r. cristata* population. All of these populations coexist with rats except for the translocated population, although we suspect rats may be present there as well. Consequently, iguanas on confirmed rat-infested cays had a higher frequency of tail breaks than those on rat-free cays (49.3% and 31.8%, respectively; Mann-Whitney $U = 3.0$, exact one-tailed $P = 0.034$). Although rats might be able to sever the tail of juvenile iguanas, we

TABLE 18.2
Descriptive Statistics for *Iguanas* Sampled Showing Injuries

TAXON	CAY	MISSING DIGIT(S)			INJURED TAIL		TAIL REGENERATION		
		N	PERCENTAGE	NUMBER (MEAN ± S.E.)	N	PORTION MISSING (%)	PERCENTAGE OF INJURED	REGROWTH (cm) (MEAN ± S.E.)	RATS
<i>C. r. cristata</i>	White	75	16.0	0.23 ± 0.07	75	42.7	90.6	5.9 ± 0.8	Present ¹
<i>C. r. nuchalis</i>	Fish	57	12.3	0.16 ± 0.06	57	24.6	85.7	6.8 ± 1.1	Absent
	North	87	14.9	0.26 ± 0.08	86	32.6	96.4	7.9 ± 0.5	Absent
	Transloc popn	53	20.4	0.37 ± 0.12	54	51.9	89.3	7.4 ± 1.0	Absent
<i>C. r. rileyi</i>	Gaulin	3	33.3	0.33 ± 0.33	3	0.0	—	—	Absent
	Goulding	35	34.3	0.74 ± 0.21	35	22.9	87.5	8.0 ± 2.0	Absent
	Green	86	33.7	0.76 ± 0.16	84	22.6	63.2	6.4 ± 1.2	Absent
	Guana	15	13.3	0.20 ± 0.14	15	40.0	83.3	6.3 ± 1.9	Present
	Low	16	75.0	3.06 ± 0.69	16	50.0	37.5	4.2 ± 1.2	Present ¹
	Manhead	19	21.1	0.32 ± 0.17	22	36.4	62.5	5.5 ± 1.5	Absent
	Pigeon	31	51.6	0.94 ± 0.24	31	64.5	80.0	7.4 ± 0.8	Present
Totals		478	24.9	0.52 ± 0.06	478	35.8	82.5	6.9 ± 0.3	

¹ Recently eradicated.

doubt they could do much damage to adult tails and concur with others (e.g., Vitt et al., 1974; Iverson, 1979; Jaksic and Greene, 1984; Iverson et al., this volume) that explanations other than predation (i.e., social interactions) should be considered for causes of tail loss. Spearman correlation analyses revealed that the frequency of tail loss among populations (excluding Gaulin Cay) was independent of cay size, population size, iguana density, and number of plant species (all $P > 0.15$).

Males (38.3% of 262 iguanas) and females (31.2% of 202 iguanas) were equally likely to suffer tail injury ($P = 0.11$). Tail breaks were reported with equal frequency in males and females of most *Cyclura* studied to date (*C. c. carinata*, *C. c. cyclura*, *C. c. figginsi*, *C. c. inornata*), but males experienced disproportionately high breakage in *C. c. stejnegeri* and *C. pinguis* (reviewed by Iverson et al., this volume). In our analyses, the frequency of tail injury was similar for all size classes (35.0%, 37.9%, and 35.5% for 20 juveniles, 66 subadults, and 391 adults, respectively; $P = 0.93$). This finding implies that the majority of tail losses occur when iguanas are young. If adults were equally likely to lose their tails, then adults would have a greater cumulative frequency of tail loss than younger age classes, as the primary evidence of such injuries (regeneration) persists through life. However, there are survival and social costs associated with tail loss (e.g., Iverson, 1979; Fox et al., 1990; Wilson, 1992) that are not reflected in our data. If young with lost tails have lower survivorship, then tail loss in adult iguanas could be more frequent than suggested by our data.

For those iguanas that have lost a portion of their tail ($n = 141$), 82.5% showed regeneration (table 18.2). This proportion was consistent among the populations, sexes, and size classes. The mean length of regenerated tissue was 6.9 ± 0.3 cm ($n = 141$), and likewise was similar among the populations, sexes, and size classes. The maximum regeneration length was 17.3 cm. Iverson (1979) concluded that tail regeneration appears to be rapid in both juvenile and adult *C. c. carinata*. Healing of the tail sometimes re-

sulted in distinct bifurcation ($n = 5$) or trifurcation ($n = 1$) of regenerated portions, as noted for *C. c. carinata*, and is presumably the result of incompletely severed tails (Iverson, 1979).

FEMORAL PORE COUNTS

The number of femoral pores differed significantly among the three taxa (one-way ANOVA, $F_{2,467} = 113.4$, $P < 0.001$, $\eta^2 = 0.33$; table 18.3). Scheffé post-hoc comparisons indicate that each taxon differed significantly from the others. Within *C. r. nuchalis*, the three populations differed significantly (one-way ANOVA, $F_{2,186} = 6.81$, $P = 0.001$, $\eta^2 = 0.07$), with counts on North Cay higher than those on Fish Cay or in the translocated population. The founders of the translocated population originated from Fish Cay (Hayes et al., this volume), and the mean counts from these cays were indistinguishable, although variance in the translocated population was lower. Within *C. r. rileyi*, the six populations (excluding that on Gaulin) also varied significantly (one-way ANOVA, $F_{2,200} = 2.53$, $P = 0.03$, $\eta^2 = 0.06$), but Scheffé post-hoc comparisons detected no pairwise differences among cays (all $P > 0.085$). For the entire data set, the count of femoral pores was similar for males and females ($P = 0.43$).

HEAD SCALATION CHARACTERS

Undergraduate student Melissa Andres conducted head scale counts based on careful review of 35 mm color slides taken of 223 specimens captured in the field. The photos were close-up shots of iguana heads (usually one dorsal view and one lateral view) intended originally for identification purposes. A summary of these counts, based on scale names in Smith (1995), is presented in table 18.3. Unfortunately, complete scale counts were not available for most iguanas because of limited photo quality (lighting, angle, and focus), skin conditions that obscured some features (ecdysis remnants, soil or food residues, and scarring), and the application of conservative criteria to data collection. Tests for sexual dimorphism within individual populations having sufficient samples (White Cay for *C. r. cristata*;

all three populations of *C. r. nuchalis*; Green Cay for *C. r. rileyi*) showed only one character to be dimorphic (RN [defined in table 18.3] for two populations of *C. r. nuchalis*; Mann-Whitney two-tailed $P < 0.05$ for both), but with opposite patterns on each cay.

One-way ANOVAs followed by Scheffé post-hoc comparisons were used to separately compare variance between the three subspecies, and variance within *C. r. nuchalis* and *C. r. rileyi*, in scalation features. Although much of the data failed to meet the assumptions of parametric tests, nonparametric Kruskal-Wallis ANOVAs conducted on the same data sets yielded identical results. The analyses (table 18.3) showed that means for twelve of the thirteen scalation characters differed significantly among the three subspecies. Seven of these characters differed significantly between taxa but not across populations within taxa. Thus, a combination of these characters might lead to reliable diagnosis. One character, number of infralabials to eye center (IL), revealed the close affinity of the translocated *C. r. nuchalis* population (7.1 ± 0.1) to its source population on Fish Cay (7.1 ± 0.1). Both of these populations differed significantly from North Cay (6.4 ± 0.1 ; Scheffé $P < 0.001$).

DISCRIMINANT ANALYSES

Stepwise discriminant function analysis (DFA), which is robust to violations of parametric assumptions (McGarigal et al., 2000), was conducted to further evaluate distinctiveness of the three taxa using counts of femoral pores and select head scales. Differences in these characters are generally regarded as nonadaptive and, therefore, are suitable for phylogenetic evaluation (e.g., Snell et al., 1984; Hollingsworth, 1998). The predictor variables included number of femoral pores (FP), in addition to most head scalation characters (BF and PF in table 18.3 were excluded due to small samples). Because of missing data for many characters, only a subset of iguanas was available for the analysis. The final model, which included sixty-eight iguanas and six predictors (FP, BP, NA, SP, ST, BL; see table 18.3 for their definitions and values), re-

veals a high degree of distinctiveness between the three subspecies (Wilks's $\lambda = 0.173$, $\chi^2_{12} = 100.8$, $P < 0.001$). *Cyclura r. cristata* ($n = 11$) was correctly classified 100% of the time. *C. r. nuchalis* ($n = 26$) was correctly assigned 84.6% of the time (twenty-two cases), and was incorrectly classified as *C. r. rileyi* in four cases (15.4%). *C. r. rileyi* ($n = 31$) had the lowest percentage of correct predictions (twenty-five cases; 80.6%) and was incorrectly classified as *C. r. nuchalis* in four cases (12.9%) and as *C. r. cristata* in two cases (6.5%). Characters FP and SP provided the greatest discrimination. A canonical plot of the discriminant function (DF) scores for individual iguanas shows clustering (figure 18.2). Whereas *C. r. cristata* and *C. r. nuchalis* are clearly distinct from each other, *C. r. rileyi* shows intermediate characters.

Principal components analysis was also conducted on the correlation matrix of the six characters identified by the final DFA model. Three principal components (PC) were extracted (using Varimax rotation), with factor loadings shown in table 18.4. PC1 is composed largely of characters BP, NA, and SP; PC2 is composed largely of characters FP and ST; and PC3 is largely made up of character BL. None of these components showed sexual dimorphism. The factor scores of each individual iguana are plotted in figure 18.3, where clustering of the three subspecies is evident, with *C. r. rileyi* exhibiting intermediate scores. DFA of the factor scores again revealed a high degree of distinctiveness among the three taxa (Wilks's $\lambda = 0.194$, $\chi^2_6 = 104.8$, $P < 0.001$). However, the proportion of iguanas correctly assigned was somewhat lower than that achieved with DFA of original data. *C. r. cristata* ($n = 11$) was correctly classified 90.9% of the time (ten cases) and was incorrectly grouped with *C. r. rileyi* in one case. *C. r. nuchalis* ($n = 26$) was correctly assigned 84.6% of the time (twenty-two cases) and was incorrectly classified as *C. r. rileyi* in four cases (15.4%). *C. r. rileyi* ($n = 31$) was correctly classified 77.4% of the time (twenty-four cases) and was incorrectly classified as *C. r. nuchalis* in five cases (16.1%) and as *C. r. cristata* in two cases (6.5%).

TABLE 18.3
Comparisons of Femoral Pore Counts and Scalation Differences for Populations of Cyclura rileyi cristata, C. r. nuchalis, and C. r. rileyi

CHARACTER	<i>C. r. cristata</i>				<i>C. r. nuchalis</i>				<i>C. r. rileyi</i>				P		
	N	MEAN	S.E.	RANGE	N	MEAN	S.E.	RANGE	N	MEAN	S.E.	RANGE	THREE SSP.	C _m	C _r
FP: Total number of femoral pores	72	42.6 ^a	0.3	35-49	189	47.1 ^b	0.2	41-55	209	43.6 ^c	0.2	35-51	0.000	0.001	0.030
BF: Scales bordering frontal	5	6.4	0.4	5-7	25	6.4	0.2	4-8	28	6.5	0.1	5-8	0.807	0.884	0.741
BP: Scales between prefrontals (minimum)	14	1.9 ^a	0.1	1-2	47	0.6 ^b	0.1	0-1	54	1.1 ^c	0.1	0-2	0.000	0.415	0.005
CS: Chin shields to eyecenter	18	6.6 ^a	0.2	5-8	115	6.0 ^b	0.1	5-7	74	6.1 ^b	0.1	5-8	0.004	0.958	0.348
IC: Scale rows between infralabials and chin shields below eyecenter	19	2.6 ^a	0.1	2-3	117	2.0 ^b	~0	1-3	82	2.1 ^c	0.1	1-3	0.000	0.150	0.000
IL: Infralabials to eyecenter	19	6.7	0.2	5-8	110	6.9	0.1	5-8	76	6.7	0.1	5-8	0.044	0.000	0.316
NA: Scale rows between nasals and first zygous scale	14	0.9 ^a	0.1	0-1	43	1.6 ^b	0.1	0-4	61	0.9 ^a	0.1	0-3	0.000	0.288	0.084
PF: Scale rows between prefrontals and frontal (minimum)	2	5.5 ^a	0.5	5-6	25	4.1 ^b	0.1	3-5	12	4.3 ^b	0.1	4-5	0.000	0.851	0.588
RN: Scales touching rostral between nasals and supralabials	18	2.0 ^a	0.0	2-2	99	1.4 ^b	0.1	1-2	70	1.7 ^c	0.1	1-2	0.000	0.345	0.000

SL: Supralabials to eyecenter	19	7.4 ^a	0.2	6-9	104	6.9 ^b	0.1	6-8	68	6.7 ^c	0.1	6-8	0.000	0.446	0.356
SN: Total number of supranasals and postnasals	20	5.0 ^{ab}	0.3	4-7	108	4.8 ^a	0.1	4-6	71	5.5 ^b	0.1	4-8	0.000	0.069	0.573
SP: Scales between supranasals and prefrontals (minimum)	15	2.1 ^a	0.1	1-3	68	1.0 ^b	~0	1-2	69	1.3 ^c	0.1	1-2	0.000	0.382	0.734
ST: Supralabials to triangular scale at mouth corner	16	7.2 ^a	0.1	6-8	80	7.0 ^{ab}	0.1	6-8	56	6.7 ^b	0.1	6-10	0.013	0.508	0.382
BL: Sublabial isolated anteriorly from other sublabials (presence or absence in individuals)	19		Present: 1 (5%) Absent: 18 (95%)		114	Present: 45 (39%) Absent: 69 (61%)			80	Present: 25 (31%) Absent: 55 (69%)			0.012 ¹	—	—

Notes: Probability levels (*P*, based on one-way ANOVAs unless otherwise indicated) are shown for subspecific differences (comparison of three taxa) and for population differences within *C. r. nuchalis* (three populations) and *C. r. rileyi* (up to six populations). For characters having a significant main effect, means that differ significantly from those of other subspecies are indicated by different superscripts (a, b, or c; Scheffé post-hoc contrasts).

¹ χ^2 test.

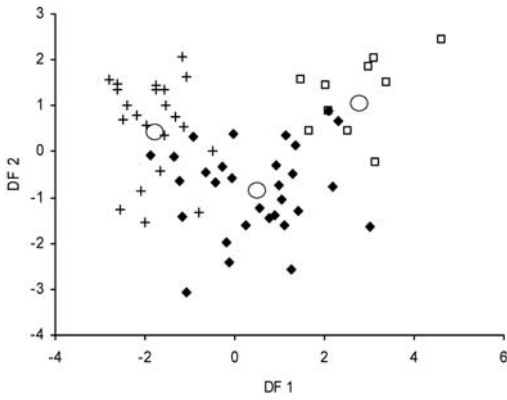


FIGURE 18.2. Canonical plot of the discriminant function (DF) scores for each individual of the three subspecies of *Cyclura rileyi* (□, *C. r. cristata*, $n = 11$; +, *C. r. nuchalis*, $n = 26$; ◆, *C. r. rileyi*, $n = 31$). Open circles denote group centroids for the three taxa.

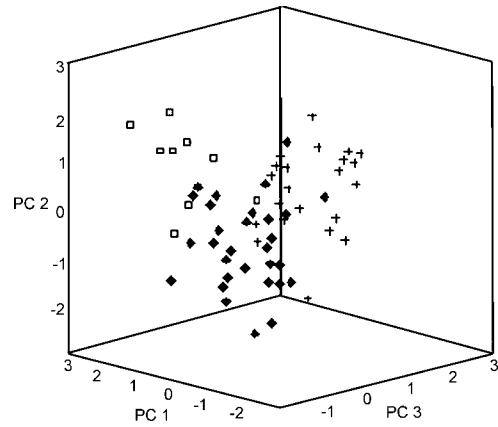


FIGURE 18.3. Three-dimensional plot of the principal component (PC) scores for each individual of the three subspecies of *Cyclura rileyi* (□, *C. r. cristata*, $n = 11$; +, *C. r. nuchalis*, $n = 26$; ◆, *C. r. rileyi*, $n = 31$). Each of the three principal components represents one or more scalation characters, as summarized in table 18.4 and defined in table 18.3.

TABLE 18.4

Factor Loadings of Each Character
for the Three Principal Components

CHARACTER	FACTOR LOADINGS		
	PC1	PC2	PC3
FP	-0.149	0.687	0.404
BP	0.829	0.040	0.084
NA	-0.669	0.052	-0.076
SP	0.773	0.046	-0.249
ST	0.125	0.837	-0.201
BL	0.030	-0.001	0.902
Variance explained (%)	29.5	19.7	18.2

Notes: Principal Components (PC) extracted (with Varimax rotation) from the correlation matrix of scalation characters taken from adult *Cyclura rileyi*. For each PC, the characters with the highest factor loadings (>0.60) are in bold. Total variance extracted was 67.4%. Characters are defined in table 18.3.

Of the three components, PC1 provided the greatest discrimination.

These analyses suggest subspecific and population differences that warrant a formal study involving more complete scale counts. The addition of other scalation characters and molec-

ular data to the DF would increase the likelihood of complete diagnosis of the three taxa. Schwartz and Carey (1977), who provided the current taxonomy of this group, thought that *C. r. cristata* might be sufficiently distinct from the other two forms to warrant specific status. Our data here lend some support to this idea. Schwartz and Carey (1977) also remarked that *C. r. cristata* has characters intermediate between *C. cyclura*, which likewise occurs on the Great Bahama Bank, and the other forms of *C. rileyi* that are isolated on separate banks.

CONSERVATION PRIORITIES

A unifying goal in conservation biology is to identify and conserve genetically important, naturally occurring populations, thus allowing the dynamic process of evolution to continue unaffected by human factors as much as possible. Unfortunately, present-day anthropogenic pressures make this goal virtually unattainable, especially for populations endemic to insular ecosystems, which are particularly vulnerable to invasive species and habitat degradation. A more practical goal is to preserve and manage ecosystems. To achieve this, conservation programs

are often directed toward umbrella or keystone species, because the preservation of an individual species requires protection of its habitat and other aspects of ecosystem function. We believe that many species of *Cyclura* qualify as umbrella species; additional ecological studies will reveal their potential as a keystone species.

Here we recommend the implementation of a series of conservation initiatives and new research foci that ideally will move *C. rileyi* from crisis management to full remediation and recovery from endangered status. This task will require carefully prioritized planning, the cooperative efforts of many private and governmental entities, and must be data driven. We suggest that a research-based approach to conservation is most beneficial in the long term and that *C. rileyi* can serve as a model species for developing conservation plans for other West Indian iguanas.

CLARIFICATION OF SYSTEMATIC RELATIONSHIPS

Advances in DNA sequencing, informatics, and family tree analysis have helped to answer the contentious question of what units of life to preserve. Divergent and often conflicting definitions of species and subspecies and the unequal application of these concepts across taxa have complicated conservation efforts. The evolutionarily significant units (ESU) category was created to identify units in nature that, if saved, would help preserve biodiversity, evolutionary processes, and ecosystems (Ryder, 1986; Moritz, 1994, 1999). ESU criteria were developed to help prioritize the use of limited conservation resources. Criteria for ESU designation are debated and range from absence of gene flow to the more commonly accepted criterion of mtDNA sequence-based reciprocal monophyly. For taxa that do not meet the stringent conditions of strong phylogenetic branches, Moritz (1999) has suggested a lesser category: a management unit (MU). Management units can be distinguished by different alleles being more common in one MU than in another.

Malone et al. (2000) recently examined the phylogeographic relationships of *Cyclura* using

a mtDNA ND4 to a leucine transfer RNA (tRNA) sequence and suggested conservation priorities among the species based largely on ESU criteria, with the goal of preserving as much biodiversity as possible. Their results support a southeast-to-northwest pattern of island divergence for the genus, the phylogenetic basal status of *C. pinguis* and *C. collei*, and the more recent establishment of *C. rileyi* in the Bahamas. These findings have profound implications for establishing conservation priorities among West Indian iguana taxa and support the ranking of *C. pinguis* and *C. collei* as priority species because of their ancient divergence and imperiled status (Alberts, 2000). Malone et al. (2000) further questioned the appropriateness of subspecific recognition within *C. rileyi*, based on their findings of no haplotypic differences among the subspecies.

Recognition of each of the three subspecies of *C. rileyi* as ESUs may be debatable, depending on the criteria used. However, the subspecies certainly do not meet the stringent ESU criterion of reciprocal monophyly for mtDNA sequences (Moritz, 1999). The second ESU criterion, often used for populations that are separated by a significant genetic distance, has not been formally evaluated at the population level. We concur with Malone et al. (2000) that final resolution of the taxonomic status of *C. rileyi* should be determined by analysis of more rapidly diverging nuclear markers, such as microsatellites. In our lab, we have used random amplified polymorphic DNA (RAPD) as a first-level survey tool and have initiated microsatellite studies. Even though these assays are incomplete, preliminary results from RAPD bands indicate the absence of gene flow between island populations and band-sharing differences that, if confirmed by microsatellites, will inform the discussion. Discriminant analyses of our morphological data, although based on a limited number of characters, suggest that a suite of morphological features exist that, with additional data and further analysis, will allow for complete diagnosis of one or more of the three subspecies and possible elevation to a higher conservation priority.

Given the historic and present isolation of the subspecies (each more than 100 km apart and possibly on their own evolutionary trajectory) and the apparent morphological differences, we believe these populations to be at least important conservation MUs, if not emerging ESUs. Although we advocate ESU priority-setting criteria for determining the use of limited conservation resources, we believe it would be premature and unfortunate to alter conservation planning by declaring *C. rileyi* as a single ESU based solely on mtDNA and limited microsatellite samples. Clearly, further genetic analysis is needed to understand more fully this taxon's evolutionary past, current levels of diversity, and potential for adaptive change in the future.

Apart from questions of a population's ESU status and the amount of genetic diversity between populations (MU status), there are additional reasons to direct conservation activities toward *C. rileyi* populations. By doing so, we emphasize the need to save and manage ecosystems rather than species. These iguanas are ideally suited as umbrella species, and conservation efforts to save them will provide protection for many additional species of plants and animals. For example, several cays that harbor iguanas host some of the largest and most diverse seabird communities in the Bahamas, and these urgently need protection. Furthermore, we believe that iguana conservation in general is heuristically and esthetically valuable at local, national, and regional levels, and needs the full support of all stakeholders.

FORMAL PROTECTION OF EXISTING POPULATIONS

The greatest immediate threat to *C. rileyi* is that existing populations or habitats will become further diminished in size or quality. At present, only the translocated population in the northern Exumas is afforded formal protection within the National Park system managed by the Bahamas National Trust (BNT). Although some of the cays supporting iguanas are privately owned (see Hayes et al., this volume), others are Crown Land (public lands owned by the nation and not

presently granted to anyone) that deserve consideration for inclusion within the National Park system.

We urgently recommend protection of *C. rileyi* populations by the creation of three national park units. First, and perhaps most important, the addition of White Cay as a satellite unit to the existing Exumas Land and Sea Park (or another recently proposed Exumas park) would benefit *C. r. cristata*. Second, at least two disjunct regions of San Salvador Island should be designated as a new national park to protect *C. r. rileyi*, including the northern cays of Grahams Harbor that host iguanas (Gaulin and Green Cays) and dense colonies of seabirds (Gaulin, Catto, and White Cays), and the interior cays within the southern portion of Great Lake that harbor iguanas (Pigeon Cay) and dense rookeries of herons and cormorants (Cormorant Cay and adjacent islets). This new park would protect not only iguanas, but also the most diverse and possibly the largest remaining seabird and waterbird colonies in the entire archipelago (W. Hayes, unpubl. data). The remaining cays that support *C. r. rileyi* are privately owned, but their purchase by BNT warrants consideration. Third, Fish and North Cays in the Acklins Bight should be incorporated within a new national park for the benefit of *C. r. nuchalis* and other sensitive fauna, including conch, sharks, bonefish, and the flock of flamingos that regularly forage there. This new park should include other nearby cays that appear suitable for translocation of new iguana populations. In collaboration with the IUCN Iguana Specialist Group, we have presented these ideas to the Bahamian government and the BNT (Carey et al., 2001), and urge timely enactment of these recommendations. The desire and commitment of the BNT to protect the iguanas and their habitats was expressed as early as 1983 in a document submitted to the Bahamas government (S. Buckner, pers. comm.).

To enforce protection of these populations, we recommend instituting a system of wardens, as implemented for other national parks, and placing informational signs on protected cays similar

to those already posted on Green Cay by the International Iguana Society. The signs should serve notice that the iguanas are protected by national and international law and warn against bringing animals (e.g., dogs, cats) to the cays. Seasonal restrictions on visitation of the cays should also be considered, to protect iguana and seabird nests, which are especially vulnerable to disturbance (e.g., trampling, overheating). An educational program, as discussed below, would increase vigilance by local residents.

CONTINUED RESEARCH

Conservation efforts have become increasingly focused and publicly recognized for a number of taxa, including West Indian iguanas. The effectiveness of individual programs depends on many factors, including the relative rarity of the species, the quality and quantity of remaining habitat, the levels of funding and intervention required to preserve a species, and political issues that may benefit or impede the program. The basic biology of the organism—arguably the most important factor—is often the least appreciated and most neglected facet of recovery programs. Although our research has provided important and useful data on the biology of *C. rileyi*, we are far from fully understanding how iguanas interact with their environment. As a result, we cannot provide reliable estimates of the minimum viable population and area needed to sustain the species. Because *C. rileyi* populations vary considerably in demography, habitat diversity, behavioral ecology, and levels of threat from invasive species and habitat degradation, this species is ideally suited for research on the relationships between behavioral ecology, life history, and local adaptation.

INVASIVE SPECIES CONTROL, HABITAT RESTORATION, AND MONITORING

In addition to habitat protection, conservation management often involves habitat restoration and enrichment. Further study is needed to better understand the nutritional and nesting requirements of iguanas and the direct or indirect impact of rats and other invasive species. Al-

though we have undertaken considerable effort on several cays to control invasive species and restore nesting habitat (Hayes et al., this volume), continued monitoring will be essential to evaluate the success of our efforts and detect new threats. The methods of rodenticide delivery appear to work, and should be applied to other populations that still coexist with rats. Although there is no available means to control the *Cactoblastis* moths that are decimating *Opuntia* cacti on San Salvador's offshore cays, the loss of vegetation important for food and cover could be ameliorated by the planting of alternative plant species. The removal of invasive Australian pine (*Casuarina*) is also needed on several cays. We anticipate that complete removal of *Casuarina* from White Cay would greatly reduce the number of falcons that visit the island and use the trees as hunting perches during migration and winter. Our methods of estimating population size will allow us to continue accurate monitoring and should be suitable for surveys of other iguana populations.

ESTABLISHMENT OF NEW POPULATIONS

Reintroductions of either wild-captured or captive-headstarted iguanas may be useful for supplementing existing populations (when outbreeding depression can be avoided), creating new populations, and selectively augmenting genetic diversity within existing or new populations (e.g., Knapp and Hudson, this volume; Welch et al., this volume). We urgently recommend the initiation of translocation projects to benefit all three subspecies of *C. rileyi* and suggest the following three approaches. First, because *C. r. cristata* is presently confined to a single cay, one or more additional cays must be found that are (or can be rendered) suitable for a translocated population. Nearby Leaf Cay appears to be ideal, except that the dense rat population must first be extirpated and permission granted by the owner. Other cays in the southern Exumas should be considered as well. Because of the great difficulty in locating and capturing adult females, we suggest that hatchlings (or older juveniles) be translocated unless

a captive headstarting program can be established as an intermediate step. Second, for *C. r. rileyi*, we recommend the restocking of recently extirpated cays with individuals from nearby cays (e.g., Green to Gaulin, Low to High, Guana to Barn, and Manhead to Cut). Furthermore, we recommend establishment of a new population on the main island via translocation of individuals from Goulding Cay to the relatively undisturbed area east of Storrs Lake. To maximize genetic diversity, individuals from other populations could be released as well (but see Welch et al., this volume). Radiotracking translocated individuals will be essential to determine how far they might wander from the relative safety of this remote area. As a third approach, we recommend the translocation of *C. r. nuchalis* from North Cay and Fish Cay to six unoccupied, smaller, nearby cays in the Acklins Bight. Using these islands, we hope to investigate experimentally the relative success of translocation at different times (before versus after the mating season) and under different conditions (into occupied versus unoccupied habitats).

As a final consideration, all of the cays in the Acklins Bight are low elevation (see Hayes et al., this volume) and therefore subject to inundation by storm surges and rising sea levels. Obviously, long-range considerations are important for conservation planning. We suspect that the historic loss of populations on the six smaller cays resulted from previous storms, and we should not assume that North Cay and Fish Cay are invulnerable to similar events in the future. Thus, although the small population introduced to the northern Exumas occupies an island with greater relief (see Hayes et al., this volume), we need to search for yet another safe haven within the Acklins-Crooked-Long Cay island group.

ESTABLISHMENT OF HEADSTART PROGRAMS

For political and logistical reasons, no headstart programs exist for any of the Bahamian iguanas. Because of the success of headstart programs with other iguanas (Hudson, 2000a; Alberts et al., this volume; Wilson et al., this volume), we strongly recommend that such programs be ini-

tiated for the Bahamian species. Specifically, we recommend establishing captive rearing facilities for *C. r. rileyi* at the Gerace Research Center (formerly Bahamian Field Station) on San Salvador Island and for *C. r. cristata* at a yet to be identified facility on Great Exuma. To safeguard against the introduction of exotic disease and reduce pressure on natural populations from commercial herpetoculturists, we urge that captive propagation and/or rearing of *C. rileyi* be conducted solely in the Bahamas.

DEVELOPMENT AND IMPLEMENTATION OF EDUCATIONAL PROGRAMS

Education will be central to the full recovery of *C. rileyi*. As our work with *C. rileyi* progresses, we plan to devote a greater proportion of our time to conservation education. Although we have engaged college students in our research activities and have sponsored one Bahamian student for Ph.D. studies at Loma Linda University, California, general interest in careers in conservation appears limited by few employment opportunities in the Caribbean region. However, working with younger students has been more encouraging. Our recent work with San Salvador school children through the local Boy Scouts chapter and their involvement in habitat restoration (Hayes et al., this volume) was especially well received. Currently we are working with the Disney Corporation through their conservation grants program to develop hands-on learning modules that will engage preteens and teens in conservation problem-solving activities. These modules will include practical activities that demonstrate, among other things, the tools ecologists use to study animals (e.g., radiotelemetry) and the impact humans have on iguana and seabird populations (e.g., loss of eggs due to trampling and overheating). These projects are in addition to the general lectures we offer that heighten awareness and appreciation of iguanas and the fragile ecosystems of the Bahamas. Although our efforts are focused locally on the island groups where we work, we recognize the need for a broader emphasis on conservation education throughout the islands. Success will be

measured ultimately by the degree to which the Bahamian people become invested in conservation activities, taking full ownership of the process of protecting and managing their national treasures.

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