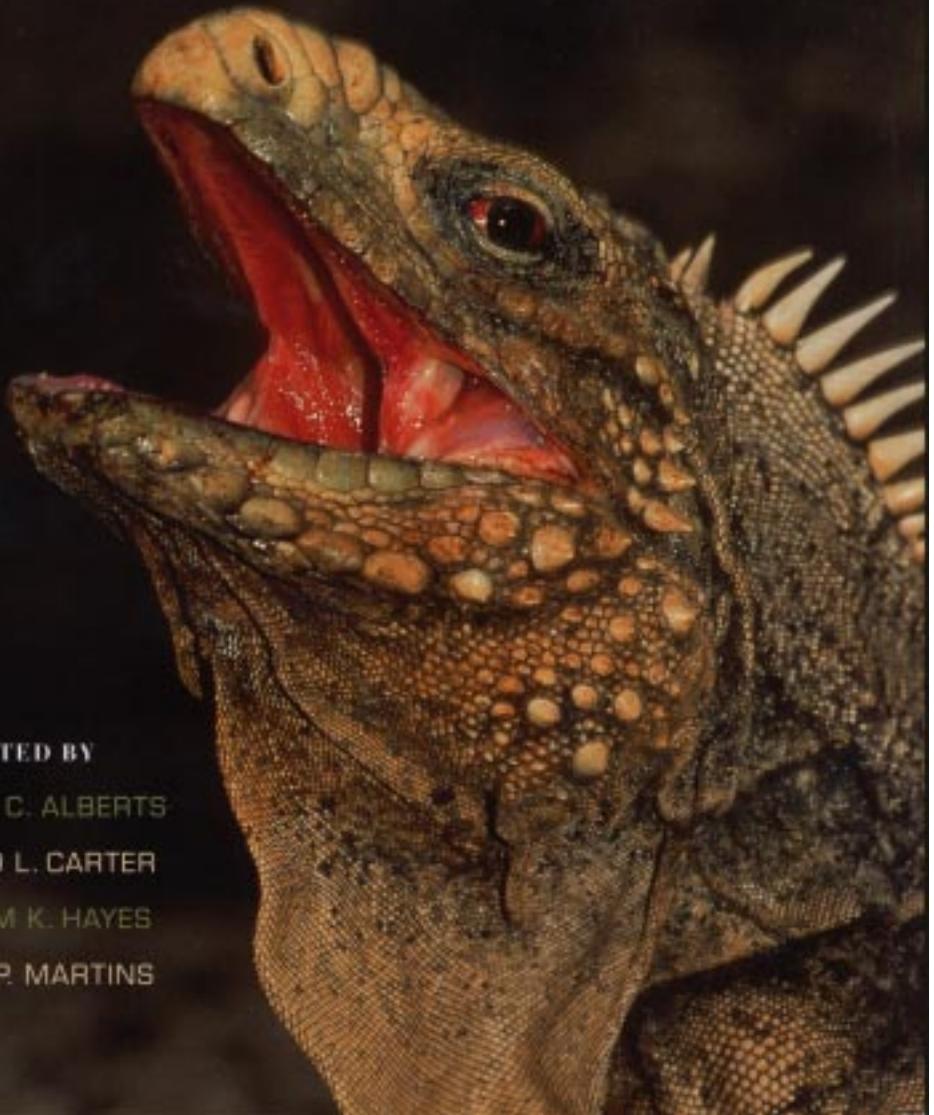


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BIOLOGY AND CONSERVATION



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Behavior and Ecology of Rock Iguanas, II

POPULATION DIFFERENCES

Ahrash N. Bissell and Emília P. Martins

POPULATION DIFFERENCES in morphology and behavior may reflect evolutionary changes that can ultimately lead to further divergence and speciation (Mayr, 1970). Although differences in morphology, behavior, and genetics have been found within several lizard species, these differences are usually far less than the differences found among species (e.g., Wiens, 1997; Martins et al., 1998). Recent studies, however, have shown that genetic (Welch, 1997; Welch et al., this volume) and behavioral (Martins and Lamont, 1998) differences among populations of *Cyclura* iguanas can be substantial. In this chapter, we present new and more thorough data on population differences in *C. carinata* behavior, morphology, and ecology and discuss how differences of this sort may be important in the conservation of endangered species.

Iguanas are as complex behaviorally as many bird and mammal species; they have large brains and multifaceted social and foraging behaviors (e.g., Brattstrom, 1974; Burghardt, 1977a,b, this volume; Ryan, 1982). The West Indian genus *Cyclura* is of particular interest because it exhibits an unusual diversity of social behavior. As

an example, territoriality is by far the most common form of social behavior in lizards and seems to be the evolutionarily primitive condition for the group as a whole (Martins, 1994). Most of the three hundred or so species of *Anolis* lizards are territorial to one extent or another, with males using visual displays to defend their territories against intruders. In contrast, among the eight species of *Cyclura*, some are territorial, whereas others live in large aggregations or social groups (e.g., see review in Martins and Lamont, 1998) comparable to the aggregations of green iguanas found in Central America (Burghardt, 1977b; Dugan, 1982a). Thus, *Cyclura* exhibits remarkable diversity of social behavior across the genus.

Moreover, both the structure and use of communicative displays differ among populations in this genus (Martins and Lamont, 1998). Like many lizards, *Cyclura* utilizes a complex communicative display called the *headbob*, in which a lizard raises and lowers its head in a series of ritualized motions (Carpenter and Ferguson, 1977; Iverson, 1979). Headbobs are used in both aggressive and courtship interactions (Iverson, 1979; Dugan, 1982b; Martins and Lacy, this

volume). As in other lizard species, headbob display structure differs among each of the several *Cyclura* species for which this behavior has been measured (Martins and Lamont, 1998). Moreover, populations within some *Cyclura* species exhibit variation in both the structure and use of communicative displays. For example, a natural population of Cuban iguanas, *C. nubila*, has been found to produce displays that are one headbob longer but one second shorter (an overall faster display) than an introduced population of this species in Puerto Rico (Martins and Lamont, 1998). These observed differences among *Cyclura* populations are potentially large enough to impede communication among individuals from different populations.

Although there are clear morphological differences among species of *Cyclura* (which are the basis for most species categorizations), population differences in morphology have not been as well documented. Iverson (1979) measured adult weight and snout-vent length (SVL) for male and female *C. carinata* on four islands and found substantial variation both among and within the island populations, although the differences were not analyzed statistically. Size and weight are important indicators of social status and health, respectively (Iverson, 1979; also shown for *C. cornuta stejnegeri*: Wiewandt, 1977), and may have an impact on the resulting social dynamics of different island populations.

In this study, we collected behavioral and morphological measures of iguanas in fourteen different *C. carinata* populations in the Turks and Caicos Islands (TCI). We focused on *C. carinata* because of their unusual social behavior, including the formation of large groups of up to twenty individuals and the use of an apparent “appeasement” display (directed by smaller iguanas toward larger animals, resulting in decreased aggression by the larger animal: e.g., Iverson, 1979; Martins and Lacy, this volume). The study populations were located on separate islands in Chalk Sound (figure 8.1), a protected body of water within the large island of Providenciales. The islands within Chalk Sound were

formed approximately three thousand years ago when the Caribbean Sea rose to its present levels (Colquhoun, 1983; Carew, 1997). Thus, any differences observed in behavior or morphology are likely to be due to relatively recent divergence or to phenotypic plasticity resulting perhaps from differences in the size or ecology of different islands. In this study, we explored population differences in behavior and morphology in detail; when possible, we related these behavioral variables to environmental differences among islands to see if there was any evidence for possible selective differences among island environments.

METHODS

Data were collected from April–June, 1998 (during the mating season) on twelve populations (A–L) on separate islands within Chalk Sound. We grouped islands into clusters based on geographical proximity to each other (figure 8.1). Animals on islands that are closer geographically are more likely to be genetically similar, due to both history and any interisland migration. We visited the islands randomly with respect to day of the week and time of day; all islands were visited at least twice in the morning and twice in the afternoon. There was very little variation in temperature or precipitation over the course of the study period (mean diurnal temperature = 31.1 ± 0.01 °C).

MORPHOLOGY

We captured fifty-five iguanas on island A, and up to twenty iguanas on each of the remaining study islands B–L (we caught every animal on islands with fewer than twenty individuals). We measured SVL, head width, and weight of each captured iguana, calculating averages for each island using only measurements taken from adult animals. We also marked each iguana with colored beads strung on a wire through the nuchal crest, so that we could identify individuals from a distance, and used probes to determine their sex.

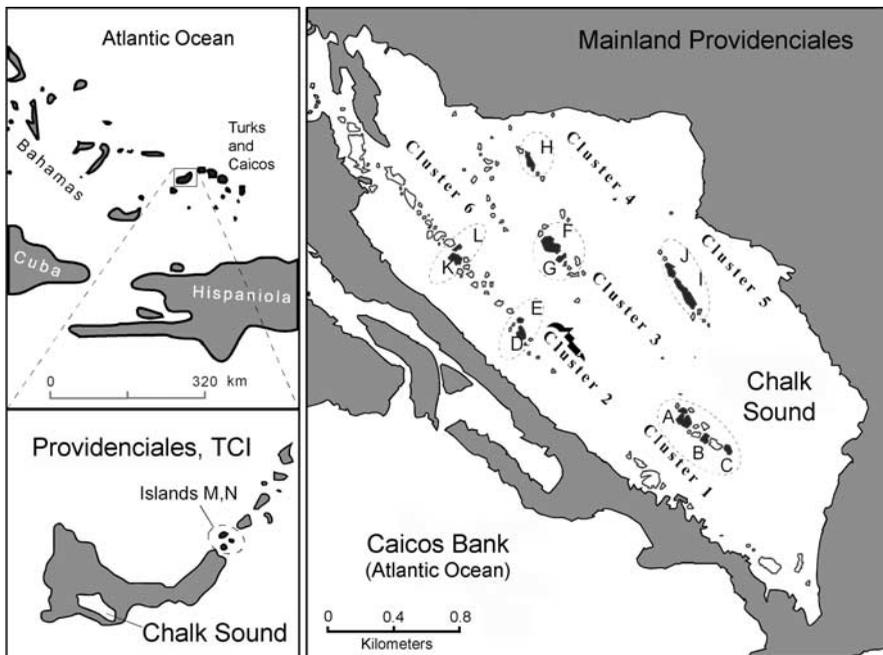


FIGURE 8.1. Map of study area showing location of twelve islands (and associated clusters) in Chalk Sound and two islands (M and N) to the north of Providenciales (not included in present study). Other islands also had iguana populations, but most were uninhabited. Also shown is the location of the Turks and Caicos Islands (TCI) in the Atlantic Ocean.

BEHAVIOR

At each island within Chalk Sound, we walked in such a way as not to cover the same ground twice while we searched for iguanas (to avoid sampling the same individual more than once a day). We made hand-written notes to record the behavior of each animal we encountered (both marked and unmarked) for up to thirty minutes before moving on. Observations were conducted only at peak activity times (Iverson, 1979) to insure that time of day and temperature had as little effect as possible on the resulting data. We noted the age (juvenile or adult), sex, and identity of the focal animal whenever possible. Many of the animals (all animals on islands A–E and H) were individually marked and sexed when taking morphological measurements (see above). Large unmarked males were also easily sexed on the basis of size and crest-spine lengths. Note, however, that some of the unmarked animals classified as females are likely to have been juvenile males.

We continuously recorded each occurrence of a headbob display and the numbers and sexes of any other iguanas (excluding very small animals that were clearly juveniles) observed within 3 m of the displaying animal (number of neighbors). For our purposes, we defined headbob display broadly, including any series of up-and-down motions of the head, regardless of the context in which it was produced (see Martins and Lacy, this volume, for more complete description of display structure and contextual use). We did not include nods (a slow, single raising and lowering of the head), shudderbobs (rapid up-and-down motions generally associated with courtship and produced while the animal is in locomotion), or postural displays that did not involve headbobs. For statistical analyses, we summed the number of displays given by each iguana during each observation session (one to four sessions per individual) and then divided by the actual duration of the session to obtain display rates (per hour) for each individual.

We used the total number of neighbors during an observation session as a measure of local iguana density that might affect the number of displays produced during a particular observation session. Although island-wide density might also play a role, we only briefly report these estimates because they are likely to be much less accurate. For small islands (B, C, D, E, G, J, L), where all or nearly all iguanas were captured, island-wide density estimates are simply the total number of animals divided by the island area. For larger islands, where a subset of animals was captured, island density was estimated from two separate trips to the island as $N_e = CM/R$, where C is the total number of animals seen, M is the number of animals that was marked on the first trip to the island, and R is the number of marked animals that was observed during the second visit.

ENVIRONMENT

We measured vegetation diversity and height on each island within Chalk Sound using a point-transect method (O'Leary et al., 1994). We ran one transect along the longest axis of each island and ran cross-transects every 50 m or half of the longest distance; thus, the number of transects varied from two to six, depending on the size of the island. Every 4 m along a transect, we measured the height of the vegetation, and we identified and counted all plant species within a 1-m circle at that same point. We used the species data to calculate a Shannon-Wiener index of vegetation diversity, H' (Begon et al., 1996). Finally, we estimated island area by measuring the perimeter of each island using a compass and a tape measure, plotting the measurements onto graph paper, and estimating the total area using Image Tool (UTHSCSA, 1996).

STATISTICAL ANALYSIS

We began by using multiple regression procedures in SAS (SAS Institute, 1990) to test for differences among islands and island clusters (islands were nested within island clusters) in each of the measured variables. We included sex as a factor when considering other behavioral and morphological variables, and included transect

as a factor when considering vegetation height. Islands with sample sizes of fewer than five for either morphological or behavioral variables were not included in these analyses. We also estimated island averages for each variable and used these to calculate Pearson product-moment correlation coefficients among variables.

RESULTS

We recorded between twelve and forty-two focal animal observation sessions on each of the twelve islands during a total of 112 hours of observation. There were only minor differences among sexes ($t_{279} = 1.63$, not significant [NS]) and islands (males: $F_{10,151} = 1.36$, NS; females: $F_{9,111} = 1.15$, NS) in the duration of the observation sessions. Males on different islands averaged from 4.1 to 16.5 displays/hour, and there were significant differences among islands and island clusters in this measure (table 8.1, figure 8.2). In contrast, female display frequencies were not significantly different among islands or island clusters (table 8.1). Overall, females averaged 5.19 displays/hour, which was significantly less than the 7.51 displays/hour given by males ($t_{270,49} = 2.41$, $P < 0.05$). The number of neighbors ranged from 1.1 to 2.3 animals, which varied significantly among islands but not among island clusters (table 8.1), and there was little difference between sexes in the number of neighbors ($t_{272} = 0.08$, NS).

Results were similar for all morphological measures (table 8.2), probably because of the close relationship among them (all pairwise comparisons: $P < 0.01$; lowest $r = 0.700$). Thus, we focus on iguana mass as an indicator of size for all subsequent analyses. Average iguana mass on different islands ranged from 0.32 to 1.09 kg for males versus 0.40–0.54 kg in females and was significantly variable among both islands and island clusters (table 8.2). Across all islands, male iguanas (0.78 kg) were significantly heavier on average than females (0.45 kg; $F_{1,177} = 277.48$, $P < 0.001$), although the difference in weight between the sexes varied among island clusters (table 8.2).

TABLE 8.1
*Mean Values and Sample Sizes of Behavioral Characteristics
 for the Twelve Chalk Sound Islands Studied*

ISLAND (CLUSTER)	N (M/F)	DISPLAYS/HOUR		NUMBER OF NEIGHBORS
		MALES	FEMALES	
A (1)	14/6	4.1 (1.36)	5.9 (4.85)	2.3 (0.20)
B (1)	9/3	7.4 (2.08)	1.7 (0.88)	1.0 (0.04)
C (1)	0/12	—	2.6 (0.62)	1.1 (0.06)
D (2)	2/0	5.4 (1.84)	—	1.0 (0)
E (2)	4/0	13.4 (4.35)	—	1.0 (0)
F (3)	23/18	6.8 (1.26)	5.8 (1.85)	1.9 (0.14)
G (3)	16/13	8.8 (2.09)	8.5 (2.52)	1.8 (0.14)
H (4)	25/12	2.3 (0.72)	1.0 (0.74)	1.6 (0.10)
I (5)	14/13	16.5 (3.42)	6.4 (2.27)	1.9 (0.17)
J (5)	18/12	7.1 (1.84)	5.0 (1.31)	1.7 (0.11)
K (6)	27/15	7.5 (1.58)	6.3 (1.61)	1.9 (0.11)
L (6)	10/17	13.4 (4.64)	4.8 (1.91)	1.9 (0.23)
Average	14.7/12.1	8.4 (1.30)	4.8 (0.74)	1.6 (0.13)
Islands	—	$F_{4,147}$ 3.98 ¹	$F_{4,109}$ 0.64	$F_{5,264}$ 5.23 ¹
Clusters	—	$F_{4,147}$ 5.96 ¹	$F_{4,109}$ 1.77	$F_{4,264}$ 2.17

Notes: Numbers in parentheses are one standard error. —, No data. Results are shown at the bottom for multivariate regression analyses of each of the variables among islands and island clusters. Islands with sample sizes < 5 were not included in the analyses.
¹P < 0.001.

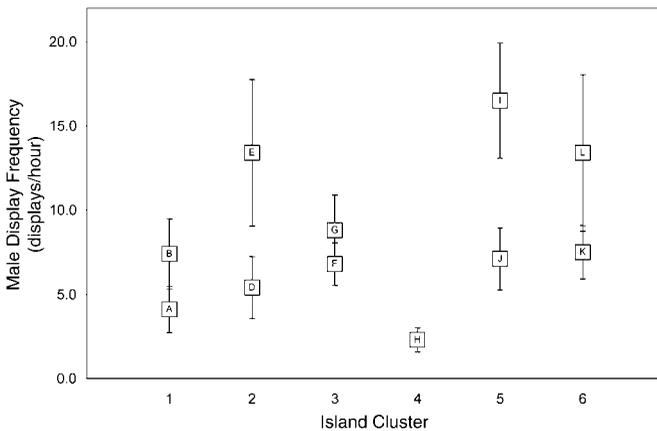


FIGURE 8.2. Average number of displays/hour produced by males on different islands (indicated within the square marker) and island clusters (indicated on the x axis). Error bars indicate one standard error.

TABLE 8.2
Mean Values and Sample Sizes of Morphological Characteristics of Each Iguana Population on the Twelve Chalk Sound Islands Studied

ISLAND (CLUSTER)	N (M/F)	MASS (kg)		SVL (mm)		HEAD WIDTH (mm)	
		MALES	FEMALES	MALES	FEMALES	MALES	FEMALES
A (1)	34/21	0.72 (0.022)	0.48 (0.016)	258.8 (2.76)	224.7 (3.03)	36.8 (0.58)	30.1 (0.41)
B (1)	3/10	0.89 (0.035)	0.53 (0.054)	262.3 (3.20)	222.0 (6.00)	40.9 (2.03)	31.4 (0.53)
C (1)	4/2	0.32 (0.073)	0.4 (0.023)	193.0 (7.02)	214.3 (5.85)	28.2 (2.90)	28.5 (0.74)
D (2)	—	—	—	—	—	—	—
E (2)	—	—	—	—	—	—	—
F (3)	14/6	0.66 (0.043)	0.45 (0.048)	244.4 (5.19)	217.8 (4.25)	34.8 (1.06)	28.2 (0.75)
G (3)	6/12	0.80 (0.035)	0.4 (0.019)	261.0 (2.74)	221.0 (1.67)	38.8 (1.58)	29.3 (0.23)
H (4)	9/11	0.70 (0.057)	0.39 (0.014)	245.2 (7.31)	218.4 (2.59)	36.3 (1.46)	27.8 (0.50)
I (5)	9/11	0.94 (0.051)	0.54 (0.038)	274.1 (4.80)	242.8 (5.67)	39.8 (1.08)	30.8 (0.82)
J (5)	7/7	0.70 (0.091)	0.54 (0.028)	251.4 (11.20)	228.0 (3.75)	34.8 (1.98)	29.8 (0.44)
K (6)	11/9	1.09 (0.054)	0.51 (0.045)	278.3 (4.23)	241.2 (4.07)	41.9 (1.04)	31.2 (0.44)
L (6)	4/16	1.03 (0.050)	0.43 (0.018)	282.0 (1.68)	231.4 (3.00)	43.0 (0.88)	30.0 (0.64)
Average	10.1/10.5	0.79 (0.070)	0.47 (0.019)	257.8 (2.27)	226.7 (1.50)	37.4 (0.46)	30.0 (0.21)
Islands	—	F _{2,83} 6.55 ²	F _{4,94} 4.37 ²	F _{2,83} 4.91 ¹	F _{4,94} 3.32 ¹	F _{2,83} 5.88 ²	F _{4,94} 2.39
Clusters	—	F _{4,83} 13.47 ²	F _{4,94} 3.12 ¹	F _{4,83} 5.17 ²	F _{4,94} 9.39 ²	F _{4,83} 4.33 ²	F _{4,94} 5.05 ²
Sex by Islands		F _{2,177} 3.96 ¹		F _{2,179} 0.52		F _{2,179} 1.88	
Sex by Clusters		F _{4,177} 7.09 ²		F _{4,179} 1.02		F _{4,179} 2.80	

Notes: Numbers in parentheses are one standard error. —, No data. Results are shown at the bottom for multivariate regression analyses of each of the variables among islands and island clusters. Islands with sample sizes < 5 were not included in the analyses.

¹ P < 0.05.

² P < 0.001.

TABLE 8.3
*Mean Values of Island Area and Vegetation Characteristics for
 the Twelve Chalk Sound Islands Studied*

ISLAND (CLUSTER)	AREA (HECTARES)	IGUANA DENSITY	VEGETATION	
			AVERAGE HEIGHT (m)	DIVERSITY (H)
A (1)	0.667	90.6	0.94 (0.081)	2.02
B (1)	0.216	78.0	1.09 (0.117)	2.05
C (1)	0.167	103.0	0.54 (0.105)	1.38
D (2)	0.133	117.4	0.87 (0.122)	1.81
E (2)	0.047	22.5	1.09 (0.203)	2.08
F (3)	0.654	63.3	1.03 (0.087)	2.39
G (3)	0.169	103.1	1.14 (0.126)	2.50
H (4)	0.209	27.8	0.73 (0.107)	1.50
I (5)	0.816	108.4	1.27 (0.080)	2.55
J (5)	0.315	126.6	1.13 (0.130)	2.32
K (6)	0.549	101.2	1.46 (0.125)	2.60
L (6)	0.194	44.4	1.27 (0.166)	2.72
Islands	—	—	$F_{5,505}$ 5.23 ¹	$F_{5,23}$ 7.03 ¹
Clusters	—	—	$F_{23,505}$ 1.50	$F_{6,23}$ 1.10

Notes: Numbers in parentheses are one standard error. —, No data. Results are shown at the bottom for multivariate regression analyses of each of the variables among islands and island clusters. Islands with sample sizes < 5 were not included in the analyses.

¹ $P < 0.001$.

Vegetation height ranged from 0.54 to 1.46 m and vegetation diversity (H') ranged from 1.38 to 2.72. Both vegetation height and diversity were significantly different among island clusters but not among all of the islands individually (table 8.3). There was significant variation in average vegetation height among the vegetation transects (range: 0.29–1.79 m) on each island as well ($F_{23,505} = 1.895$, $P < 0.01$).

Finally, we examined island environmental effects on iguana morphology and behavior

(table 8.4). On islands with greater vegetation diversity, both males and females displayed more often (figure 8.3). Although vegetation height and diversity are highly positively correlated, only male iguanas displayed more often on islands with taller vegetation (figure 8.4). In contrast, the number of neighbors was positively correlated with female but not male display rates. In addition to displaying more often, males weighed more on islands with increased vegetative diversity and taller vegetation (table 8.4).

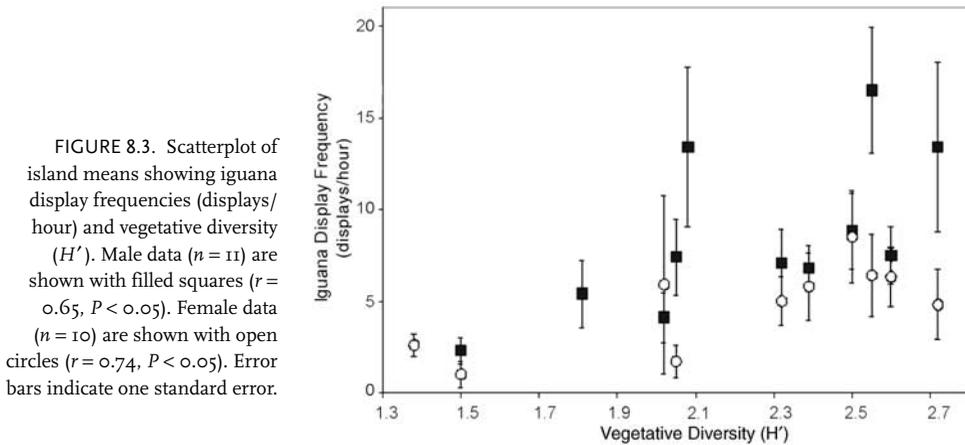
TABLE 8.4
Correlation Coefficients for Each Pairwise Comparison of Island Habitat Characteristics
and Iguana Morphology and Behavior

	ISLAND AREA	VEGETATION HEIGHT	VEGETATION DIVERSITY	MALE MASS WEIGHT	FEMALE MASS WEIGHT	MALE DISPLAYS/HOUR	FEMALE DISPLAYS/HOUR	NUMBER OF NEIGHBORS
Island area	1.000	0.358	0.403	0.241	0.527	0.094	0.448	0.718 ²
Vegetation height		1.000	0.930 ²	0.907 ²	0.584	0.643 ²	0.593	0.417
Vegetation diversity			1.000	0.776 ²	0.421	0.650	0.741 ¹	0.554
Male weight				1.000	0.445	0.601	0.336	0.375
Female weight					1.000	0.307	0.148	0.081
Male displays/hour						1.000	0.404	-0.026
Female displays/hour							1.000	0.689 ¹
Number of neighbors								1.000

Notes: Sample sizes ranged from 10 to 12 islands, depending on the comparison being made.

¹ $P < 0.05$.

² $P < 0.01$.



Although one might have expected island size to affect the vegetative composition of these islands, island area was not correlated with either vegetative diversity or vegetation height. Island-wide iguana density was also not correlated with any of the other behavioral, morphological, or ecological variables. Only the number of neigh-

bors (local density) was positively correlated with island size (table 8.4).

DISCUSSION

Among populations of *C. carinata*, we found substantial variations in body size, the number

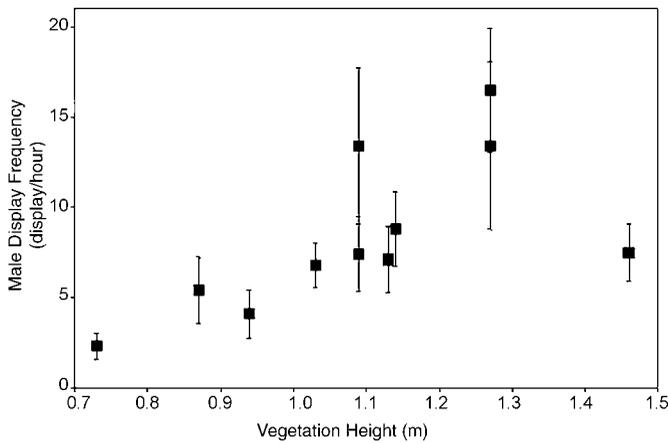


FIGURE 8.4. Scatterplot of island means showing male iguana display frequencies (displays/hour) with vegetation height (m) ($r = 0.64$, $P < 0.05$). Error bars indicate one standard error.

of neighbors within 3 m, and the frequency with which headbob displays were used. These differences are evident both at the level of island clusters and that of individual islands, indicating that interisland migration and other geographic factors may be important components of the population differences we found. In addition, some population differences seem to be related, at least in part, to differences in island ecology, including vegetative height, diversity, and the local density of iguanas.

The behavioral and morphological differences we observed in these iguana populations are large on an absolute scale. For example, male display frequencies varied between two and sixteen headbobs/hour on different islands. Similarly, large population differences were found in the details of headbob display structure for different islands (average number of headbobs per display ranged from seven to eighteen; Martins and Lacy, this volume). Although such differences are large enough to have a considerable impact on the abilities of animals from different populations to communicate, they may also be the result of differences in island ecology or social composition.

Male iguanas displayed more often on islands with taller vegetation (figure 8.4), and higher vegetative diversity was correlated with both increased male and female display frequencies (figure 8.3). Display behavior seems to have evolved in response to habitat conditions in other rep-

tiles (e.g., anoles: Fleishman, 1988a,b; snakes: Senter, 1999). For example, terrestrial snakes use a horizontal defensive display pattern, whereas arboreal snakes use a vertical pattern; this difference in display structure is thought to be the result of selection by predators to maximize the visibility of the snakes (Senter, 1999). Future studies testing whether taller vegetation and higher local density directly affect display frequencies in *Cyclura* may help clarify the conditions under which we might expect the animals to behave differently both as individuals and as members of complex social groups. Such studies could also provide useful tools for headstart and other programs involved in the conservation and captive management of these iguanas.

Male iguanas also weigh more on islands with taller and more diverse vegetation. Taller plants and greater plant diversity reflect better growth conditions on these islands (Correll and Correll, 1982). Food is probably a limiting resource for *C. carinata* in the wild (Iverson 1979, 1982). *C. carinata* will often eat one species of plant for several days and then abruptly switch to a different food source (Iverson, 1979; Auffenberg, 1982a). This type of feeding behavior is thought to be a behavioral mechanism by which animals can maximize the diversity of food they eat to obtain sufficient quantities of essential nutrients from generally nutrient-poor vegetation (Auffenberg, 1982a). Thus, islands with taller and more diverse vegetation may have higher

quality forage and present more opportunities for the iguanas to browse on different types of plants with different critical nutrients.

Much of what makes any species unique is its behavior. In animals such as iguanas with highly diverse behavior, we should thus be very concerned with preserving the behavioral uniqueness of populations (Stone et al., 1994; Clemmons and Buchholz, 1997; Gosling and Sutherland, 2000). Without this diversity of behavior, most animals would be far less successful in their abilities to survive and reproduce and to adapt to changing environmental conditions (Regal, 1983). Five of the eight recognized *Cyclura* species (Sites et al., 1996) are listed as either endangered or critically endangered by the IUCN—the World Conservation Union, due primarily to habitat loss and the introduction of exotic predators (Iverson, 1978; Hudson, 1996; Alberts, 2000). In many cases, headstart programs (e.g., Alberts et al., this volume; Wilson et al., this volume) and translocation (Knapp and Hudson, this volume) are being considered as conservation management tools for *Cyclura* iguanas. If animals from different populations are behaviorally distinct (and perhaps becoming genetically distinct), this information must be known before animals from different groups are combined for conservation purposes.

It is difficult to make many practical recommendations without further information about the behavior of the species of interest. We need to study the communication, social, and foraging behaviors of all eight species of *Cyclura* and also determine how these types of behavior vary

from population to population. We need information on the effects of different social environments and conservation strategies on the development of normal adult social behavior, as well as on the lizards' survival and reproduction. Future studies of these issues for *C. carinata* should investigate the plastic responses of individual iguanas to different environments, the reproductive success of iguanas from morphologically and behaviorally distinct populations in different social situations, and the consequences of individual variation in behavioral traits. Studies of *Cyclura* offer an unusual opportunity to test theoretical issues related to population divergence, especially for behavioral diversity, while working towards the long-term preservation of the unique characteristics of these endangered iguanas.

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