MORPHOLOGY AND HABITAT USE AMONG INSULAR POPULATIONS

OF THE LIZARD *ANOLIS LEMURINUS* FROM THE

CAYOS COCHINOS ARCHIPELAGO

OF HONDURAS

by

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ABSTRACT

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In Honduras, *Anolis lemurinus* is distributed along the Atlantic versant of the mainland and on the Caribbean island system consisting of the Bay Islands and Cayos Cochinos archipelagos. In the Cayos Cochinos, *A. lemurinus* occurs on the two largest islands, Cayo Mayor and Cayo Menor, which are separated by less than 1km. A previous study using genetic (amplified fragment-length polymorphisms) and morphometric (mass and SVL) data suggested that populations of *A. lemurinus* in the Cayos Cochinos did not differ from each other (Klutsch et al. 2007).

Despite the extremely close proximity of Cayo Mayor and Cayo Menor populations, I hypothesized that they might differ in morphology and habitat use due to

noticeable differences in the abiotic and biotic environment between islands. I sampled lizards from both islands, measuring 12 morphometric variables, 9 environmental and habitat use variables, and 3 physiological variables. Principal Component and Discriminant analyses revealed that populations of males could be distinguished based on morphology. No such differences were found for females, although sample sizes for females may ave been too low for statistical inference. Moreover, correlation and regression analyses revealed that space use and upper thermal tolerance is related to dewlap size in males. Observed differences in habitat use and morphology can perhaps be explained by differences in population density, community composition, and forest structure among islands.

TABLE OF CONTENTS

Chapter   Page

LIST OF ILLUSTRATIONS

LIST OF TABLES

CHAPTER 1

INTRODUCTION

1.1 Islands as Natural Laboratories

The "central paradigm of island biogeography," as first put forth by Wallace
(1902), is that islands provide "natural experiments" by which scientists may tease apart
evolutionary processes in a simplified context (Whittaker and Fernandez-Palacios, 2007;
Losos and Ricklefs 2009). Islands display many characteristics that make them prime for
evolutionary biology research. In addition to being incredibly numerous, they are
generally small, comparatively simple in both biotic and abiotic components, and
intrinsically quantifiable (Whittaker and Fernandez-Palacios, 2007; Losos and Ricklefs
2009).

To date, the vast majority of studies of insular biota have concentrated on
comparisons of endemic species and multi-species radiations (Schluter 2000). These
species, even when sister-taxa and found within a single archipelago, often have been
isolated for tens of thousands, and in many cases hundreds of thousands, of years. While
studies of endemics are undoubtedly useful in some sense, they have an often overlooked
drawback—determining the selective mechanisms that have resulted in the speciation of
populations that have been isolated for long periods of geological time becomes

increasingly difficult due to problems associated with attributing present ecological conditions to past divergence (Huey and Bennett 1987). Although studies that examine multi-species insular radiations are not lacking (for a discussion of these see Schluter 2000), few studies of island biota have taken an in-depth ecological approach in studying island populations of a single species (Whittaker and Fernandez-Palacios, 2007). By examining multiple populations of one species (or several closely related species) that have been recently isolated on islands which vary in their ecological conditions, we may reasonably assume that observed differences between these populations are—at least in part—related to these conditions (Garland et al. 1991).

1.2 The Study System

In this study, I focused on insular populations of a single species of lizard. This species, *Anolis lemurinus* (Figure 1.1), occurs on mainland Central America and on two groups of Caribbean islands off the northern coast of Honduras—the Cayos Cochinos and Islas de la Bahia (Wilson and Hahn 1973; Kohler 2003; Figure 1.2). Although generally referred to separately for ease of discussion, these archipelagos should be considered part of a single system as they are biologically (they share similar floras and faunas), geographically (no two islands are more than 100 km apart), and geologically (they were formally part of the Cordillera de Dios of Honduras) related (Wilson and Hahn 1973; Birmingham et al. 1998; McCranie et al. 2005).

The Islas de la Bahia are composed of three islands, Utila, Roatan, and Guanaja (area = 49.3 km^2, 155.9 km^2, and 55.4 km^2, respectively), which sit an average of 55 km from the mainland (McCranie et al. 2005).

The Cayos Cochinos (Figure 2, inset) are composed of two larger islands, Cayo Menor and Cayo Mayor (area = 0.64 km^2 and 1.67 km^2, respectively), and 13 smaller coral cays. Cayo Menor and Cayo Mayor together make up more than 97% of the archipelago's land-mass, and are separated by approximately 1km. They sit about 18 km from mainland Honduras (McCranie et al. 2005).

The Cayos Cochinos and Islas de la Bahia lye on the continental shelf, and geologic evidence suggests that they were mountain peaks in the Cordillera de Dios (uplifted during the collision of the North American and Caribbean plates), and were connected to Honduras via a coastal plain approximately eight to twelve thousand years ago (Bermingham et al. 1998; McCranie et al. 2005). Presumably they were isolated as a result of coastal flooding associated with glacial melt at the end of the Wisconsin glacial period (Bermingham et al. 1998). Since that time, it appears the biota of the Bay Islands and Cayos Cochinos have diverged to a large extent from that of the mainland (with 12 endemic species of squamate reptiles alone), a particularly surprising fact given the close geographic (and temporal) proximity they share with mainland populations (McCranie et al. 2005). The occurrence of such a large number of endemic species on these small islands suggests that gene flow between mainland and island populations has been minimal. Prevailing ocean currents may supply an explanation for this pattern. Currents

Figure 1.1. A male *A. lemurinus* from Cayo Menor.
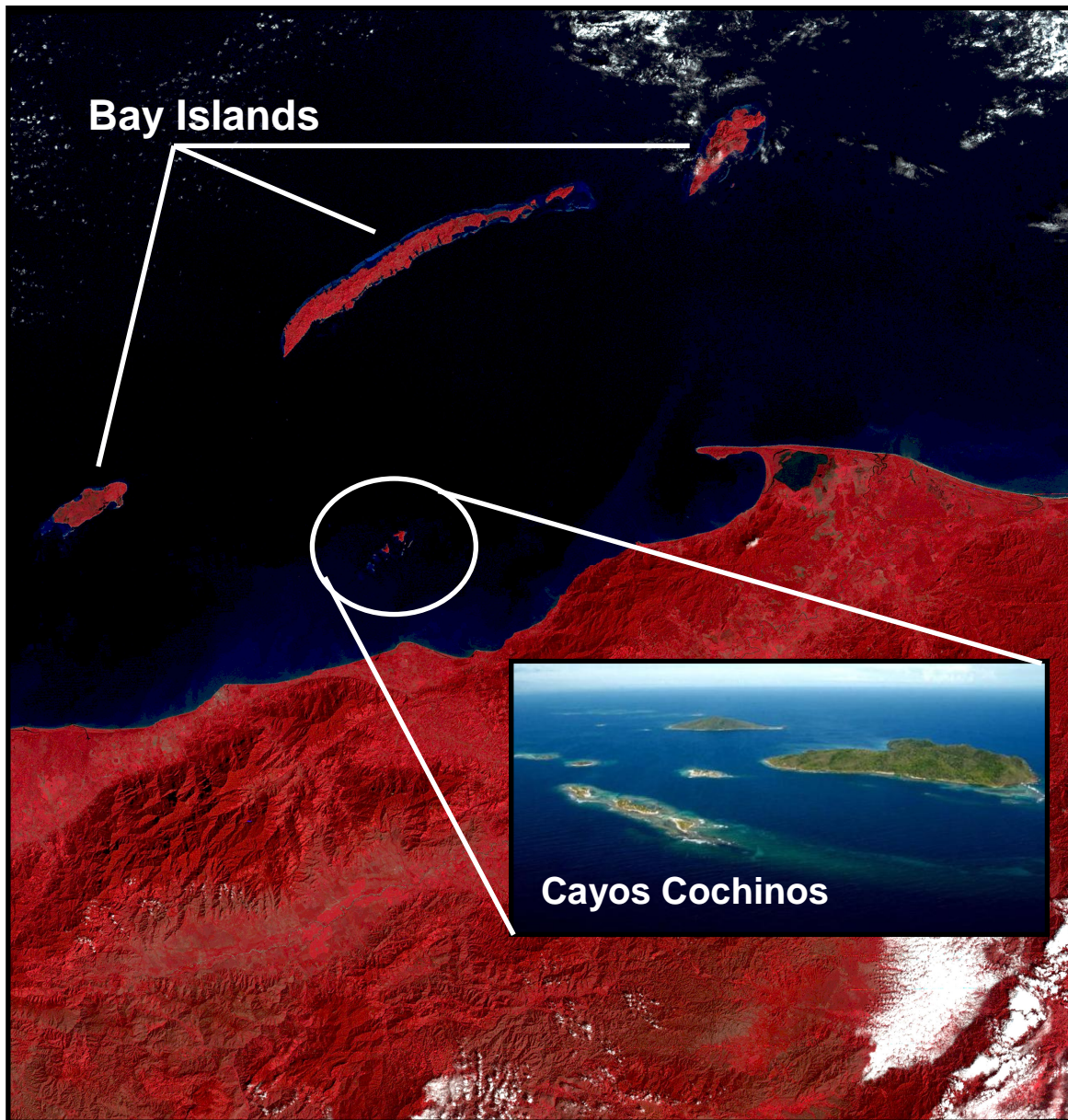
Figure 1.2. The Bay Islands and Cayos Cochinos (inset) of Honduras.

in this region flow strongly from west to east (Shrives pers. comm.), while potential colonizers can only come from the south. Therefore, the tendency for organisms rafting from mainland Honduras would be to miss the islands enitrely, and be swept west towards Belize and the Yucatan Peninsula.

1.3 The Study Species

Anolis represents one of the most species-rich genera of vertebrate on the planet, and presumably at least part of this diversity is due to an increased tendency for these lizards—endowed to them by an innate evolutionary plasticity (the basis of which is not entirely understood)—to radiate throughout island archipelagos (Williams 1983; Thorpe et al. 2008; Pinto et al. 2008). The genus *Anolis* is composed of approximately 400 lizard species that are distributed throughout the southeastern United States and Latin America, with nearly half of these occurring on Caribbean islands (Pough et al. 2004; Pinto et al. 2008).   Due to the large number of *Anolis* species found in the Caribbean and the fact that several studies have demonstrated that anoline lizards evolve in predictable ways on islands (e.g. Williams 1972, 1983; Roughgarden 1987, 1989, 1995; Butler and Losos 2002), species in this genus serve as model organisms to elucidate evolutionary processes driving species radiations (Roughgarden et al. 1983; Williams 1972, 1983; Schluter 2000).

Anolis lemurinus is widely distributed on the Pacific and Atlantic versants of mainland Central America, with insular populations on Cayo Menor and Cayo Mayor in the Cayos Cochinos, and on Utila and Roatan in the Bay Islands (Kohler 2003; McCranie

et al. 2005). Until recently, virtually nothing was known of the variation that exists between these populations.

Using amplified fragment length polymorphisms (AFLP), Klutsch et al. (2007) examined three phylogeographic hypotheses for *A. lemurinus* in the Islas de la Bahia and Cayos Cochinos. These authors supported a "stepping stone" model of archipelago colonization with little to no ongoing gene flow between the Cayos Cochinos and Bay Islands, or between island populations and mainland Honduras (Figure 1.3). According to their analysis, *A. lemurinus* independently colonized Utila and Roatan after first arriving in the Cayos Cochinos. Their observations, as well as those of other authors (e.g. Kohler 2003, McCranie et al. 2005) suggest that populations in the Bay Islands are somewhat divergent in general ecology and morphology from those in the Cayos Cochinos, and thus appear to be in the midst of a radiation event. The data acquired by Klutsch et al. (2007) also suggested, however, that populations in the Cayos Cochinos (i.e. on Cayo Menor and Cayo Mayor) seemed to display a metapopulation structure, and were more-or-less genetically and morphologically indistinguishable from each other and from mainland populations. Unfortunately, Klutch et al. (2007) only examined coarse aspects of morphology such as snout-to-vent-length (SVL) and mass, while ignoring potential differences in behavior and habitat use.
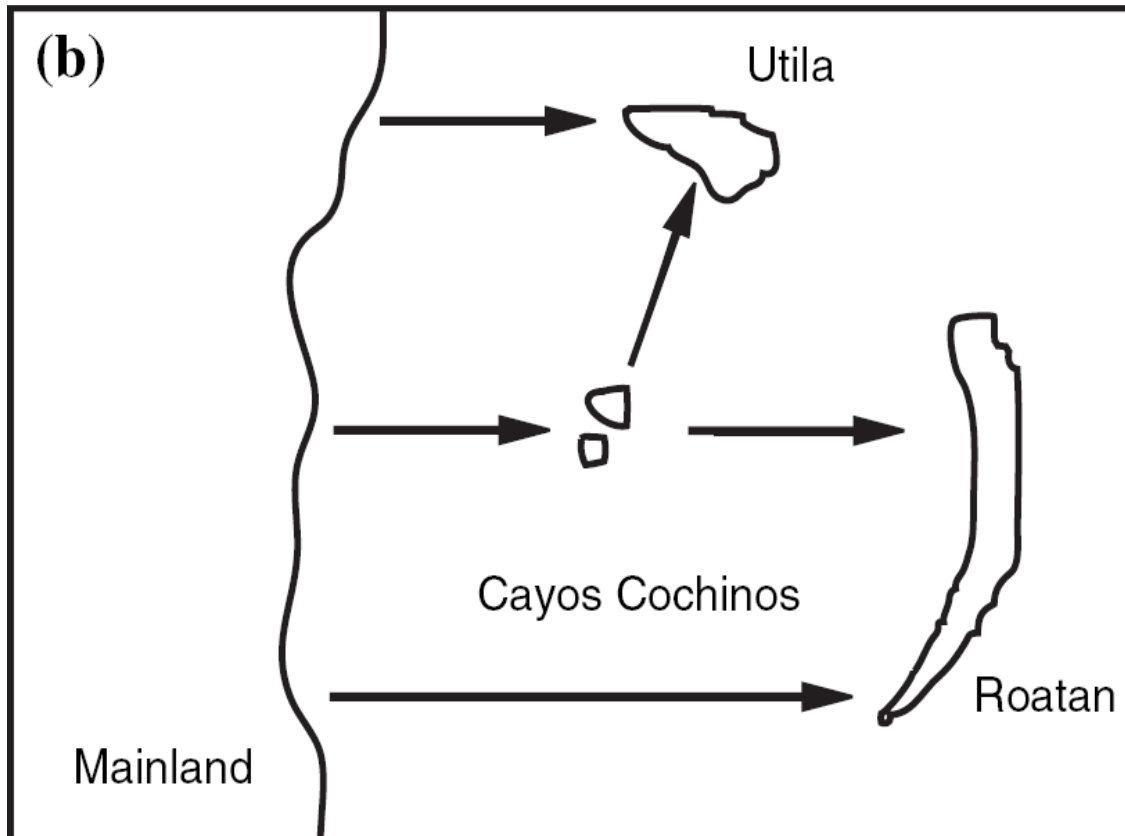
Figure 1.3. Using AFLP data, Klutsch et al. (2007) supported a stepping stone colonization model (their hypothesis "b") for *A. lemurinus* in the Cayos Cochinos and Bay Islands (adapted from Klutsch et al. 2007).

1.4 An Examination of Cayos Cochinos Populations

Anolis lemurinus habitat on Cayo Mayor and Cayo Menor (Figure 1.4b and 1.4c, respectively) appear to differ from habitat on the mainland (Figure 1.4a). On the mainland, *A. lemurinus* occurs in mesic broad-leafed forests, while in the Cayos Cochinos they occur in hotter, drier oak forests (Savage 2002; Klutsch pers. comm.; Logan pers. obs.).

Within the Cayos Cochinos, vegetation types and distribution differ between islands. For example, an invasive palm (*Attalea sp.*) that has noticeably altered the understory vegetation on Cayo Mayor, does not occur on Cayo Menor (Birmingham et al. 1998). Additionally, several mammal and snake species, including *Rattus rattus*, *Dasyprocta punctata*, *Agouti paca*, *Leptophus mexicanus*, and *Oxybelis aeneus*, occur on Cayo Mayor but are absent from Cayo Menor (Birmingham et al. 1998). *R. rattus*, as well as *L. mexicanus* and *O. aeneus* (arboreal snake species), may serve as major predators of anoles on Cayo Mayor.

In addition to habitat differences among island and mainland populations, *A. lemurinus* coexists in the Cayos Cochinos with only a single congener, *A. allisoni* (Bermingham et al. 1998; McCranie et al. 2005), whereas on the Atlantic versant of mainland Honduras *A. lemurinus* can occur sympatrically with as many as five other *Anolis* species (Kohler 2003).

Due to these differences, and because gene flow between mainland and island populations has been minimal, this system offers an opportunity to examine the
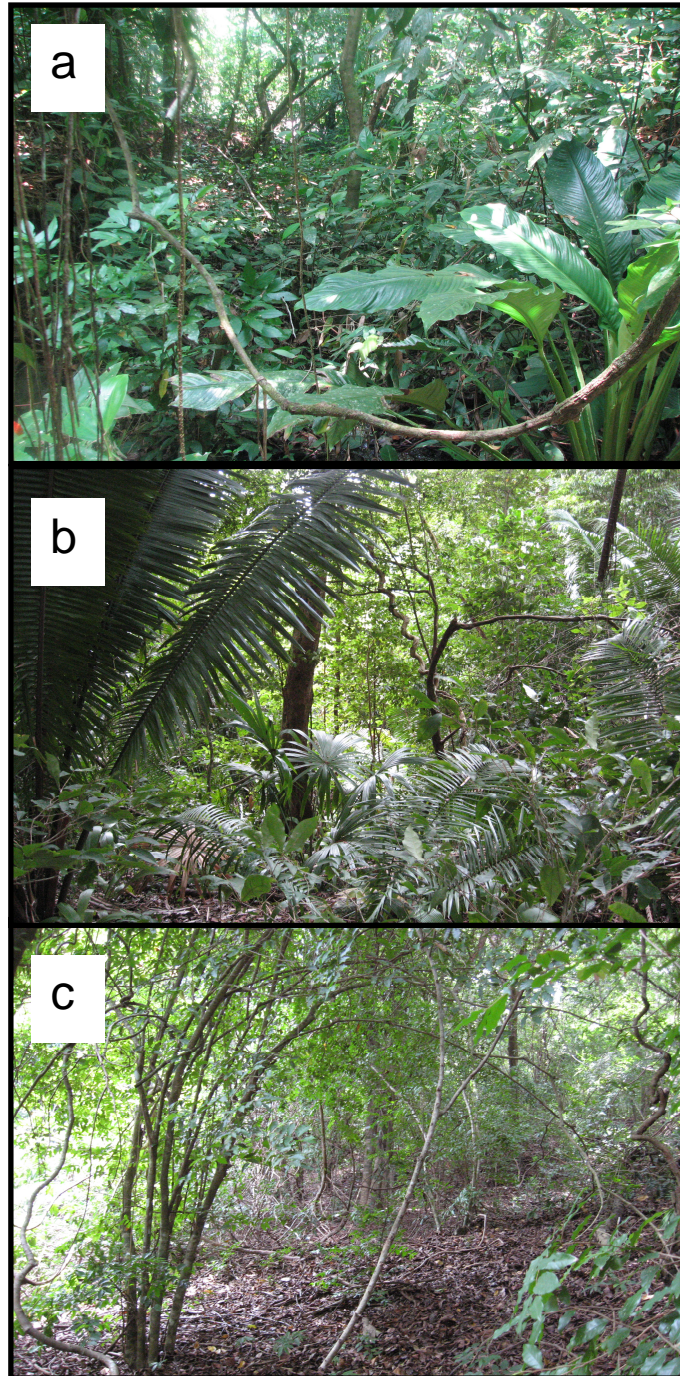
Figure 1.4. *A. lemurinus* habitat on (a) mainland Honduras (Parque Nacional Pico Bonito), (b) Cayo Cochino Mayor, and (c) Cayo Cochino Menor.

ecological correlates of organisms exposed to differing abiotic and biotic environmental conditions after a geologically recent colonization event.

In this study, I compared aspects of habitat use and morphology of *A. lemurinus* on the islands of Cayo Menor and Cayo Mayor in the Cayos Cochinos archipelago of Honduras.

CHAPTER 2

MATERIALS AND METHODS

2.1 Data Acquisition

Anolis. lemurinus populations on Cayo Menor and Cayo Mayor were sampled from 26 June 2008 to 19 August 2008 under UT-Arlington IACUC protocol #A08.023. My base of operations was the Honduran Coral Reef Foundation Biological Field Station on Cayo Menor. I was only able to visit Cayo Mayor for one day each week, resulting in a total of 17 sampling days on Cayo Menor and 8 sampling days on Cayo Mayor over the course of the eight-week study. Lizards were captured using the standard "noosing" technique, outlined in Southerland (1996).

On Cayo Menor all lizards were taken back to the Honduran Coral Reef Foundation's "dry lab" to process. Capture locations were flagged and all individuals were returned to their respective capture locations within 12 hours of processing. On Cayo Mayor, lizards were processed in the field and released soon after at capture locations. On both islands, to avoid repeat sampling of individuals, each lizard was marked on its ventral surface with a streak of white out, and no single location was sampled more than twice (once initially, and a second time when a sample of lizards was returned to a particular location). Given the high perch/territory affinity of the study species, this method provided for a low probability of re-sampling bias.

The types of variables measured included morphometric, habitat, micro-meteorological, and physiological.

I measured the morphometric variables of mass, snout-to-vent length (SVL), tail length, jaw (mandible) length, jaw width, hind limb length, forelimb length, pelvic girdle width, pectoral girdle width, inter-limb length, dewlap diameter, toe pad width, and toe pad length. Mass was measured using a 10 gram capacity Pesola® brand spring scale and other morphometric variables were measured with dial calipers.

I measured the environmental variables of perch height, perch width, perch dead or alive, density of vegetation within cubic meter of perch, canopy cover, distance from nearest open environment (defined as a 5m^2 or larger break in canopy cover), distance from nearest emergent tree (defined as a tree whose crown reached at least the bottom of the forest canopy), ambient temperature at perch site, wind-speed at perch site, solar radiation at perch site, humidity at perch site, and slope orientation. GPS coordinates, elevation, time of capture, observed behavior, and sex (determined from an examination of dewlap size and presence/absence of a hemipenal bulge at the base of the tail) were also recorded.

Perch height, distance from nearest open environment, and distance from nearest emergent tree were measured with a metric tape measure. Dial calipers were used to measure perch widths ranging from 0 to 15cm, and diameter tape was used to measure perch widths greater than 15cm. Canopy cover was estimated using a concave spherical densiometer manufactured by Forest Densiometers Company. Ambient temperature,

13

humidity, and wind-speed were measured using a Kestrel® brand portable weather station. Solar radiation was measured using a Mannix® brand UV light meter.

Ambient temperature, wind-speed, and solar radiation at each perch site were used to calculate the Grey Body Temperature Index (GBTI). Using biophysical temperature equilibration equations (Roughgarden et al., 1983; Roughgarden, 1995), GBTI classifies a perch site by estimating the temperature that a grey, five gram lizard-shaped object would achieve if allowed to come to thermal equilibrium at that perch site.

I measured the physiological variables of "panting temperature" (for the Cayo Menor population), and field-active internal (cloacal) body temperature for both Cayo Menor and Cayo Mayor populations. Panting temperature (a metric of upper thermal tolerance) was obtained after a 24 hour acclimation period by placing a lizard in a plastic chamber, exposing it to direct sunlight, and recording the internal body temperature at which the lizard began to gape for evaporative cooling (Roughgarden et al., 1983; Roughgarden, 1995).

2.2 Data Analysis

The number of individuals in different size classes differed among islands, and it was therefore necessary to size-correct all morphometric data prior to analysis (unless the analyses themselves were dependent on variation in body size). Because the first component of a morphometric Principal Component Analysis (PC1) explained most of the variance due to body size, all morphometric data (log-transformed to satisfy the linearity and normality assumptions of Principal Component Analysis) were regressed

against this component and residuals were obtained for further analysis (all morphometric variables referred to as "size-corrected" were manipulated in this manner). For the same reason, analyses of patterns in overall body-size were performed using PC1 as a surrogate measure. Additionally, due to the behaviorally and sexually dimorphic nature of *A. lemurinus*, all analyses were performed on males and females separately, and female morphology was not examined in detail due to small sample sizes. Finally, males were not compared with females due to large differences in sample size among sexes.

Several methods were used to look for overall differences in morphology, distribution, and physiology among island populations. First, t-tests with a Bonferroni correction (to correct for inflated family-wise error; Sokal and Rohlf 1995) were used to compare each variable. Second, Principal Component Analysis on the correlation matrix of log-transformed morphometric variables for males was performed to examine patterns of variance among islands. Third, discriminant analyses (using the direct method on correlation matrices) were performed on environmental and size-corrected morphometric variables for males and females to see whether these variables could explain variation in, and be used to distinguish among, populations. For discriminant analyses, *a priori* groups (prior probabilities) were determined based on the number of lizards sampled from each island. Lastly, body condition among populations of males was examined using the residuals from a regression of log-transformed mass on log-transformed SVL.

Correlations between morphometric variables, panting temperature, and space use were examined using Pearson's method, while multiple regression was used to explore patterns of space use among populations (i.e. which environmental and morphometric

15

variables significantly predict variation in the Gray Body Temperature Index; see below).

Multiple regression was also used to examine relationships between environmental and morphometric variables within populations.

All statistical analyses were performed using the software package SYSTAT 11[®].

Ambient temperature (T_e), wind-speed (v), and solar radiation (Q_{tot}) data were included in the following biophysical model (taken from Roughgarden 1981) in order to calculate the Grey Body Temperature Index (GBTI):

$$GBTI = \frac{\alpha_{GB}\beta_{sol}Q_{tot}}{4F_{WH}\varepsilon\sigma(T_e + 273)^3 + h_c} + T_e$$

Where:

α_{GB} = Grey body solar absorptivity

β_{sol} = Orientation constant

Q_{tot} = Total solar radiation (direct and reflected) (W/m^2)

F_{WH} = Whole body diffuse radiation view factor

ε = Emissivity

σ = Stefan Boltzmann constant (Wm^{-2}k^{-4})

T_e = Operative temperature (℃)

h_c = Heat transfer coefficient (Wm^{-2}c^{-1})

The heat transfer coefficient (h_c) was calculated using the following equation for heat transfer:

$$H_c = \frac{1.5ak_{air}}{(m/1000)^{1/3}} \left(\frac{(\rho v m/1000)^{1/3}}{\mu} \right)^b$$

Where:

$a =$ Empirically determined intercept in the log-log plot of Nusselt vs. Reynolds number for the *Re* number range 4 - 4000

$K_{air} =$ Thermal conductivity of air at 25°C ($Wm^{-1}c^{-1}$)

$m =$ Mass (g)

$\rho =$ Density of air at 25°C (kg/m^3)

$v =$ Wind speed (m/s)

$\mu =$ Dynamic viscosity of air at 25°C ($kg\ m^{-1}s^{-1}$)

$b =$ Empirically determined slope in the log-log plot of Nusselt vs. Reynolds number for the Re number range 4 – 4000

After combining constants and explicitly including h_c to reduce the GBTI equation to its simplest form, the final model becomes:

$$GBTI = \frac{0.3288Q_{tot}}{1.958 \times 10^{-7} (T_e + 273)^3 + \left[1.3913 \left(\frac{5.85 \times 10^{-6}v)^{1/3}}{1.84 \times 10^{-5}} \right)^{0.466} \right]} + T_e$$

Where: Q_{tot}, T_e, and v are solar radiation, ambient temperature, and wind speed, respectively, measured at the perch sites of individual lizards.

CHAPTER 3

RESULTS

3.1 Summary Statistics

Tables 3.1 displays means ± standard errors for all morphometric variables

included in analyses. Table 3.2 displays means ± standard errors for all environmental

(habitat and micro-meteorological) and physiological variables included in analyses.

While males differed significantly among islands in elevation (n = 96, t = 2.983, P <

0.019), size-corrected mass (n = 96, t = -4.125, P < 0.001), and size-corrected dewlap

diameter (n = 96, t = 3.704; P < 0.002), females did not differ in any variable measured (n

= 54, all P's > 0.05).

Although detection probability may have differed among sexes (see Buckland et

al. 2001), sex ratios on both islands appeared to be biased towards males, with 59% males

on Cayo Mayor and 68% males on Cayo Menor.

3.2 Principle Component Analysis

Because males only differed in morphological variables (with the exception of

elevation, but see discussion), Principal Component Analysis was performed on male

morphometric variables only. All morphometric variables loaded strongly positive on

Table 3.1. Means ± standard errors of morphometric variables for selected populations of *Anolis lemurinus*.

	Cayo Menor		Cayo Mayor	
Variable	**♂ (n=55)**	**♀ (n=25)**	**♂ (n=41)**	**♀ (n=29)**
Mass (g)	5.56 ± 0.22	6.37 ± 0.21	4.62 ± 0.17	5.21 ± 0.14
SVL (mm)	60.93 ± 1.03	64.27 ± 0.59	58.19 ± 0.95	60.61 ± 0.57
Dewlap Length (mm)	15.14 ± 0.64	5.18 ± 0.19	16.12 ± 0.71	5.32 ± 0.12
Jaw Length (mm)	16.77 ± 0.24	17.62 ± 0.15	16.37 ± 0.21	16.97 ± 0.15
Jaw Width (mm)	10.00 ± 0.14	10.38 ± 0.11	9.74 ± 0.13	10.10 ± 0.07
Forelimb Length (mm)	18.98 ± 0.32	19.91 ± 0.27	18.85 ± 0.32	19.27 ± 0.16
Hind limb Length (mm)	32.66 ± 0.47	33.91 ± 0.29	31.30 ± 0.46	32.69 ± 0.25
Inter-limb Length (mm)	22.15 ± 0.44	23.62 ± 0.33	21.10 ± 0.42	22.01 ± 0.40
Pectoral Girdle Width (mm)	7.41 ± 0.15	7.77 ± 0.12	7.22 ± 0.15	7.38 ± 0.08
Pelvic Girdle Width (mm)	5.11 ± 0.09	5.78 ± 0.10	4.93 ± 0.08	5.38 ± 0.09
Toe Pad Length (mm)	2.92 ± 0.07	2.91 ± 0.08	2.87 ± 0.07	2.87 ± 0.06
Toe Pad Width (mm)	1.68 ± 0.05	1.66 ± 0.05	1.53 ± 0.03	1.57 ± 0.04

Table 3.2. Means ± standard errors of environmental and physiological variables for selected populations of *Anolis lemurinus*.

Variable	Cayo Menor		Cayo Mayor	
	♂ (n=55)	♀ (n=25)	♂ (n=41)	♀ (n=29)
Perch height (cm)	89.28 ± 8.22	73.91 ± 9.85	94.45 ± 9.74	78.55 ± 8.75
Perch width (mm)	68.64 ± 11.33	46.98 ± 5.32	128.08 ± 21.46	87.23 ± 17.57
Proportion of vegetation within m^3	0.11 ± 0.03	0.09 ± 0.02	0.10 ± 0.02	0.09 ± 0.02
Percent canopy cover	97.47 ± 0.19	97.71 ± 0.18	97.26 ± 0.18	98.08 ± 0.27
Distance to nearest emergent tree (cm)	38.75 ± 6.56	54.74 ± 14.05	32.78 ± 10.23	39.55 ± 11.37
Distance to nearest open environment (m)	28.06 ± 3.61	32.26 ± 4.16	22.27 ± 4.24	17.76 ± 3.85
Elevation (m)	77.37 ± 5.59	78.36 ± 8.20	97.45 ± 3.75	93.15 ± 4.89
Ambient temperature (C)	28.02 ± 0.20	28.00 ± 0.22	28.36 ± 0.12	28.43 ± 0.14
Percent humidity	89.52 ± 0.83	90.06 ± 1.17	89.30 ± 0.74	90.09 ± 0.90
Solar radiation	16.61 ± 1.49	14.13 ± 1.49	20.83 ± 2.65	17.41 ± 2.64
Wind speed (m/sec)	0.15 ± 0.03	0.15 ± 0.04	0.17 ± 0.04	0.19 ± 0.04
Grey Body Temperature Index (C)	27.49 ± 0.57	28.00 ± 0.22	28.36 ± 0.12	28.43 ± 0.14
Field-active body temperature (C)	28.35 ± 0.22	28.49 ± 0.25	28.72 ± 0.16	28.84 ± 0.19
Panting temperature (C)	33.16 ± 0.49	32.99 ± 0.87	_____	_____
Evaporative water loss (g/m^2/h)	7.53 ± 0.74	6.95 ± 1.86	_____	_____

PC1 (component loadings > 0.745), which explained 76.98% of the variance. PC2 is characterized by weakly positive and negative loadings for all morphometric variables, and explained 5.26% of the variance (Table 3.3). Although there is some noise, males from either island appear to separate along both components (Figure 3.1).

PCA was not performed on females because neither morphometric nor environmental variables significantly differed among populations (see section 3.1).

3.3 Discriminant Analysis

A discriminant function derived from all size-corrected morphometric and environmental variables was correct 85% of time in classifying male *A. lemurinus* based on island of occurrence. Twenty nine of 36 individuals were classified correctly as coming from Cayo Mayor, and 39 of 44 individuals were classified correctly as coming from Cayo Menor. The discriminant function explained 45% of the variance among individuals (Wilks' Lambda = 0.547; P < 0.01).

When environmental variables were removed from the analysis and the discriminant function was derived from only size-corrected morphometric variables, it was correct 77% of the time in classifying males based on island of occurrence. Twenty nine of 41 individuals were classified correctly as coming from Cayo Mayor, and 45 of 55 individuals were classified correctly as coming from Cayo Menor. The discriminant function explained 26% of the variance among individuals (Wilks' Lambda = 0.739; P < 0.006).

Table 3.3. **Component loadings for morphometric PCA on all males. All morphometric variables were log-transformed prior to analysis.**

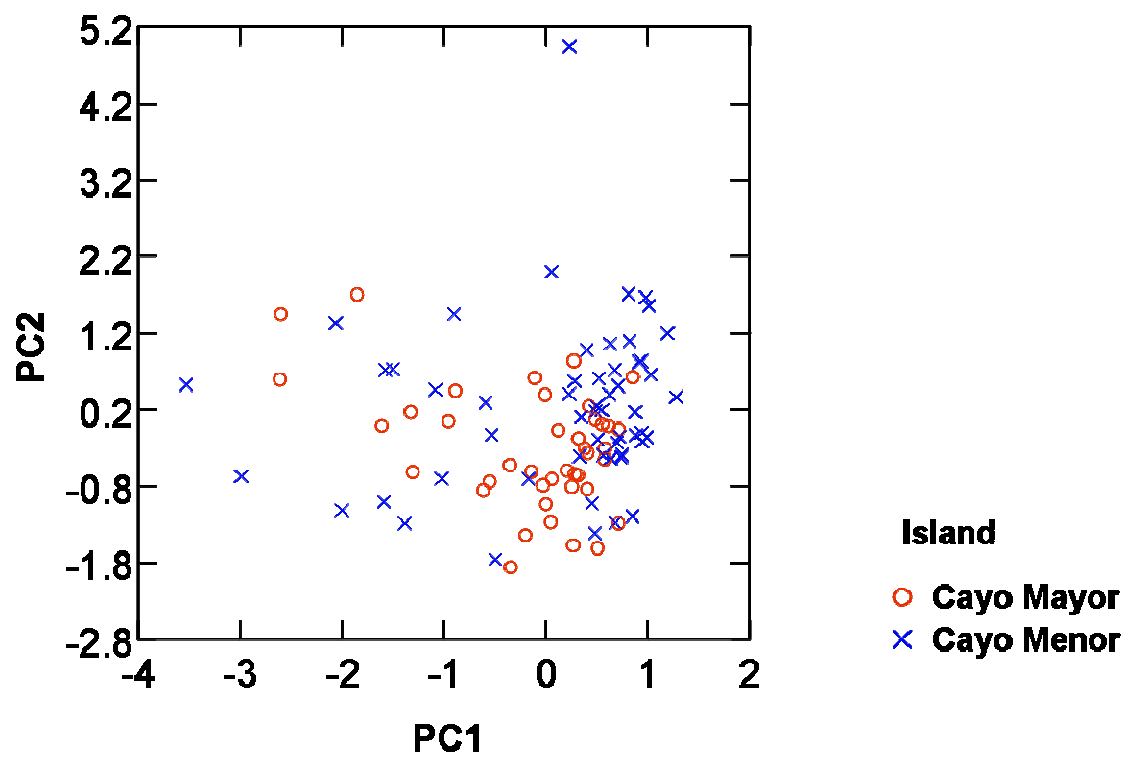| Variable	Principal Component	
	1	**2**
Mass	0.953	0.114
SVL	0.969	0.049
Hind limb length	0.950	-0.070
Forelimb length	0.779	-0.374
Inter-limb length	0.865	0.130
Jaw length	0.938	-0.041
Jaw width	0.933	0.120
Pelvic girdle width	0.762	0.141
Pectoral girdle width	0.911	-0.160
Toe pad width	0.746	0.542
Toe pad length	0.854	-0.137
Dewlap diameter	0.829	-0.281
% variance explained	**76.98**	**5.26**

Figure 3.1. Morphometric PCA scatter plot for factor scores of Cayo Mayor and Cayo Menor males.

When size-corrected morphometric variables were removed from the analysis and the discriminant function was derived from only environmental variables, it was correct 67% of the time in classifying males based on island of occurrence. Twenty of 36 individuals were classified correctly as coming from Cayo Mayor and 32 of 42 individuals were classified correctly as coming from Cayo Menor. The discriminant function explained 18% of the variance among individuals (Wilks' Lamda = 0.823; P < 0.181).

A discriminant function derived from all size-corrected morphometric and environmental variables was correct 85% of the time in classifying females based on island of occurrence. Twenty of 28 individuals were classified correctly as coming from Cayo Mayor and 16 of 20 individuals were classified correctly as coming from Cayo Menor. The discriminant function explained 50% of the variance among individuals (Wilks' Lambda = 0.504; P < 0.241).

When environmental variables were removed from the analysis and the discriminant function was derived from only size-corrected morphometric variables, it was correct 70% of the time in classifying females based on island of occurrence. Twenty one of 29 individuals were classified correctly as coming from Cayo Mayor and 17 of 25 individuals were classified correctly as coming from Cayo Menor. The discriminant function explained 21% of the variance among individuals (Wilks' Lambda = 0.786; P < 0.430).

When size-corrected morphometric variables were removed from the analysis and the discriminant function was derived from only environmental variables for 20 females

on Cayo Menor and 28 females on Cayo Mayor, it was correct 75% of the time in classifying individuals based on island of occurrence. Twenty four of 28 individuals were classified correctly as coming from Cayo Mayor and 12 of 20 individuals were classified correctly as coming from Cayo Menor. The discriminant function explained 31% of the variance among individuals (Wilks' Lambda = 0.687; P < 0.077).

3.4 Male morphology

At a given body size, island of occurrence was a significant predictor of male mass (ANCOVA with PC1 as a covariate; $F_{1,92}$ = 15.005, P < 0.001; Figure 3.2) and dewlap diameter (ANCOVA with PC1 as a covariate; $F_{1,92}$ = 13.600, P < 0.001; Figure 3.3) with males on Cayo Menor having greater mass and smaller dewlaps. Cayo Menor males were also in better body condition (ANOVA, $F_{1,94}$ = 5.327, P < 0.024; Figure 3.4).

When data from males on both islands were pooled and all environmental variables were used together in a multiple regression to predict size-corrected male dewlap diameter, the slope of the regression was not significant (P < 0.265, R^2 = 0.141). When environmental predictors for size-corrected dewlap diameter were analyzed separately for each island, none of the environmental variables were significant predictors for either Cayo Mayor or Cayo Menor males (all P's > 0.05).

When data for males from both islands were pooled and all environmental variables were used as predictors for PC1 (a surrogate measure for body size), the slope of the regression was not significant (P < 0.055, R^2 = 0.203). The same analysis was
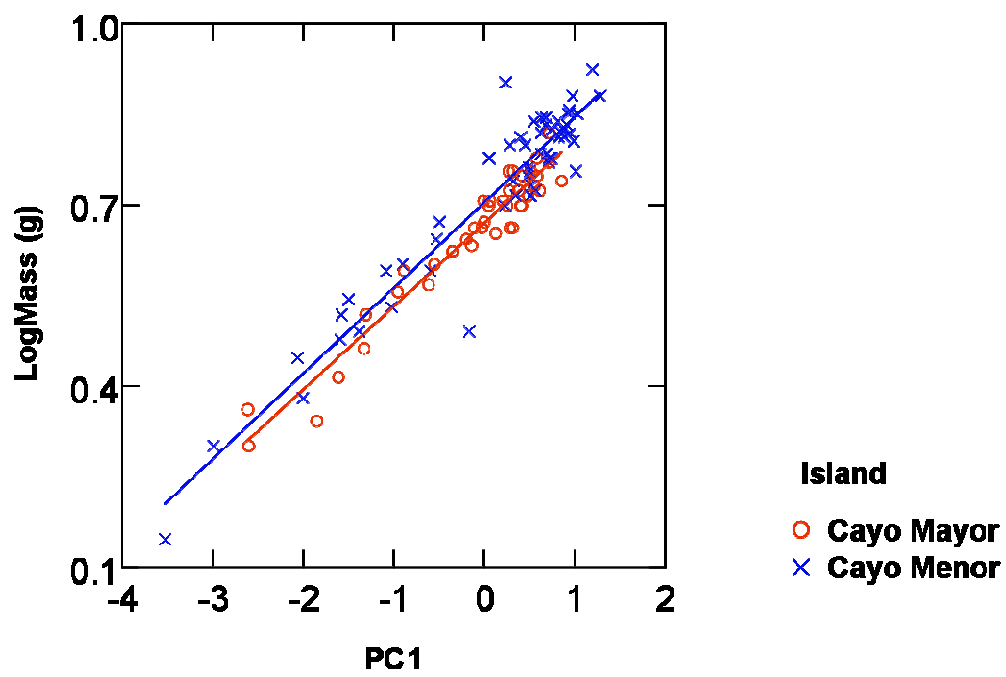
Figure 3.2. Log-transformed mass as a function of body size (PC1) for Cayo Mayor and Cayo Menor males.
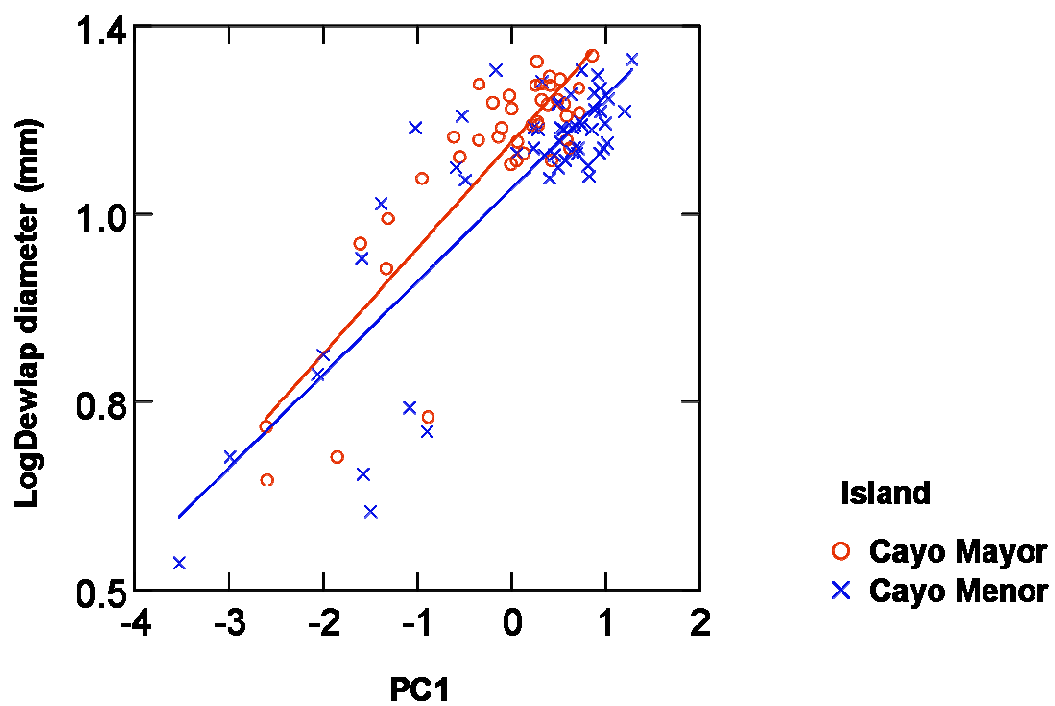
Figure 3.3. Log-transformed dewlap diameter as a function of body size (PC1) for Cayo Mayor and Cayo Menor males.
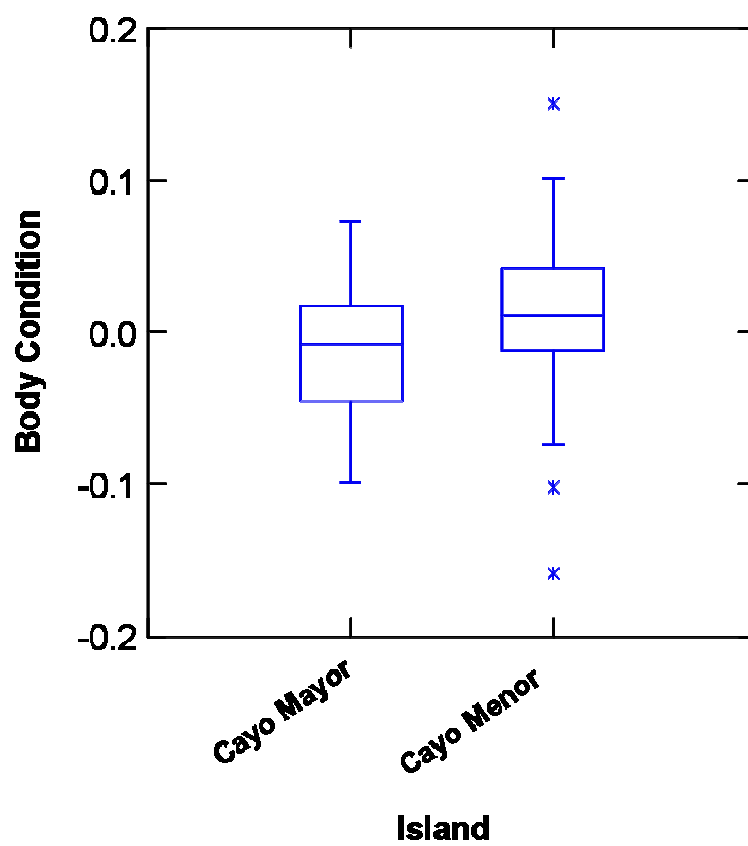
Figure 3.4. Density display for body condition among males of Cayo Mayor and Cayo Menor (body condition indexed as SVL-corrected mass).

conducted using mass as the dependent variable, and the slope of the regression was not significant ($P < 0.638$, $R^2 = 0.212$).

3.5 Physiology and Space Use

Among size-corrected morphometric and environmental variables, only dewlap diameter was positively correlated with upper thermal tolerance (panting temperature) in Cayo Menor males ($n = 12$, $r = 0.823$, $P < 0.002$; Figure 3.5). None of the environmental or morphological variables measured were correlated with upper thermal tolerance in Cayo Menor females ($n = 7$, all r's < 0.300, all P's >0.05).

Variance in GBTI was significantly different among populations of males (hypothesis test for equality of two variances; $n = 91$, $P < 0.001$; Figure 3.6), and therefore analyses aimed at determining the environmental correlates of GBTI were performed separately for each island (Sokal and Rohlf 1995). For environmental variables measured on both Cayo Mayor and Cayo Menor males, only humidity was a significant predictor of GBTI (P's < 0.010). Only the slope of the regression for Cayo Menor was significant, however (GBTI = 31.911 - 0.184*humidity – 0.005*perch height – 0.002*perch width + 0.250*vegetation within cubic meter + 0.139*canopy cover – 0.003*distance to nearest emergent tree – 0.003*distance to nearest open environment – 0.002*elevation; $R^2 = 0.668$, $F_{8,35} = 8.788$, $P < 0.001$). Humidity was significantly correlated with ambient temperature on both islands (r's < -0.780, P's < 0.001), which is a component of GBTI.
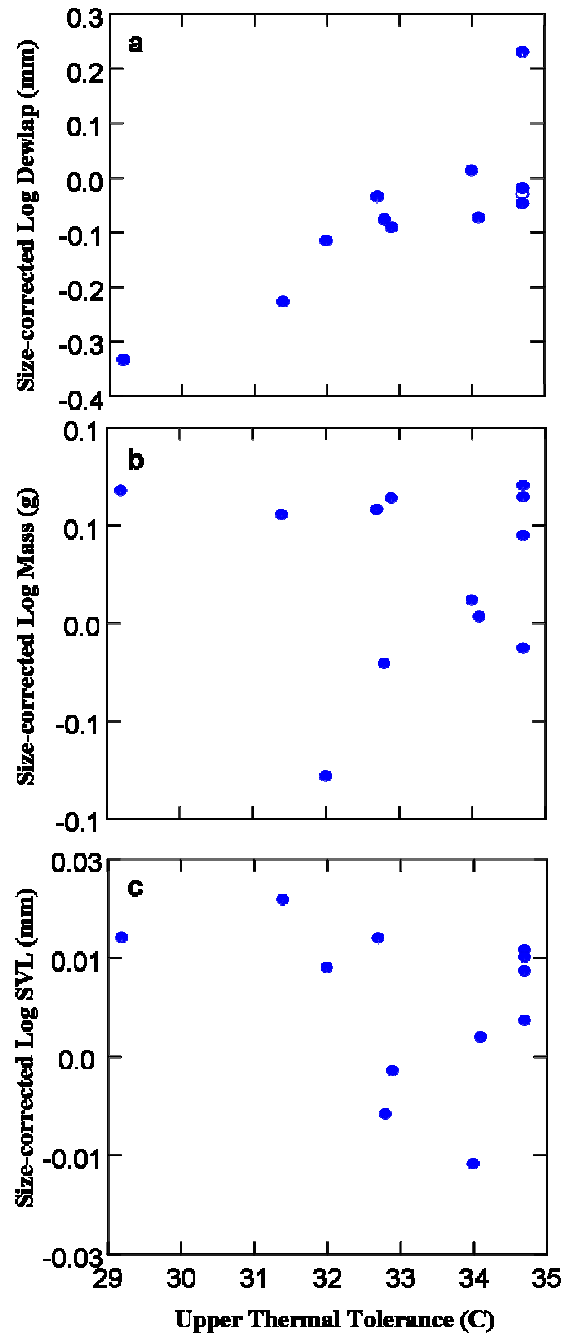
Figure 3.5. Upper thermal tolerance was significantly correlated with (a) size-corrected dewlap diameter, but not with (b) size-corrected mass, or (c) size-corrected SVL.
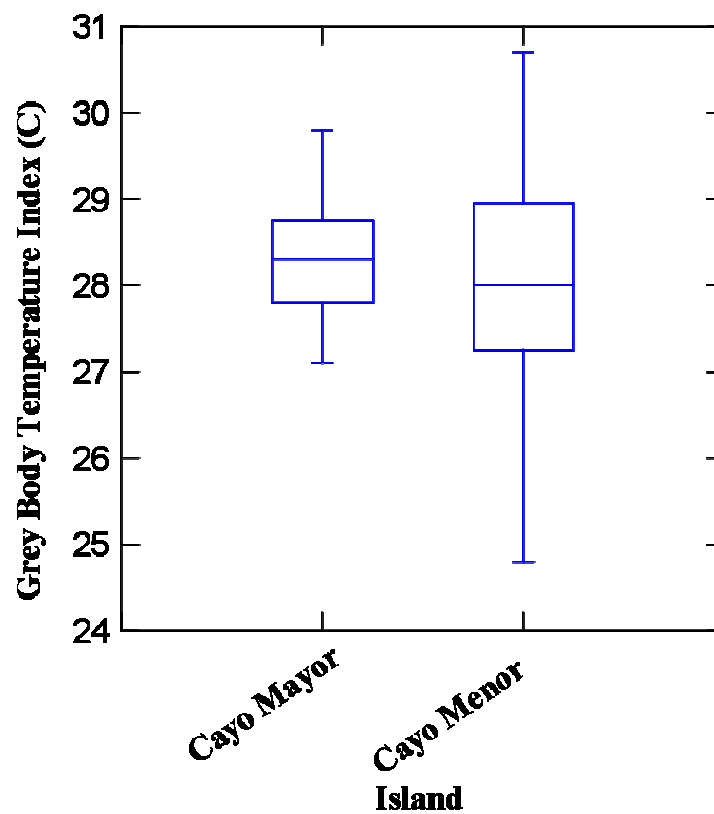
Figure 3.6. Density display for values of the Grey Body Temperature Index (GBTI) among males of Cayo Mayor and Cayo Menor.

Among size-corrected morphometric variables for Cayo Mayor males, pectoral girdle width ($P < 0.027$) and dewlap diameter ($P < 0.025$) were significant predictors of GBTI, and the slope of the regression was significant (GBTI = 28.238 + 0.399*mass + 13.432*SVL – 1.126*hind limb – 0.591*forelimb – 1.683*interlimb + 0.231*jaw length + 2.493*jaw width + 2.671*pelvic girdle + 11.404*pectoral girdle + 0.665*toe pad + 3.484*dewlap; $R^2 = 0.494$, $F_{11,28} = 2.481$, $P < 0.027$). There was also a loose positive correlation between GBTI and size-corrected dewlap diameter for Cayo Mayor males (n = 40, r = 0.490, $P < 0.002$; Figure 3.7a). This pattern did not exist for Cayo Menor males (n = 51, r = 0.156, $P < 0.274$; Figure 3.7b).

Among size-corrected morphometric variables for Cayo Menor males, hind limb length was a significant predictor of GBTI ($P < 0.043$) although the slope of the regression was not significant ($P < 0.062$).

Humidity ($P < 0.001$), percent canopy cover ($P < 0.036$), and distance to nearest emergent tree ($P < 0.025$) were all significant predictors of GBTI when environmental data was pooled for all females, and the slope of the regression was significant (GBTI = 21.575 – 0.108*humidity – 0.001*perch height + 0.001*perch width – 1.418*vegetation within cubic meter + 0.176*canopy cover – 0.004*distance to nearest emergent tree – 0.005*distance to nearest open environment – 0.001*elevation; $R^2 = 0.626$, $F_{8,39} = 8.146$, $P < 0.001$).

Of size-corrected morphometric variables, SVL ($P < 0.047$), jaw length ($P < 0.031$), jaw width ($P < 0.015$), pectoral girdle width ($P < 0.004$), and toe pad length ($P <$
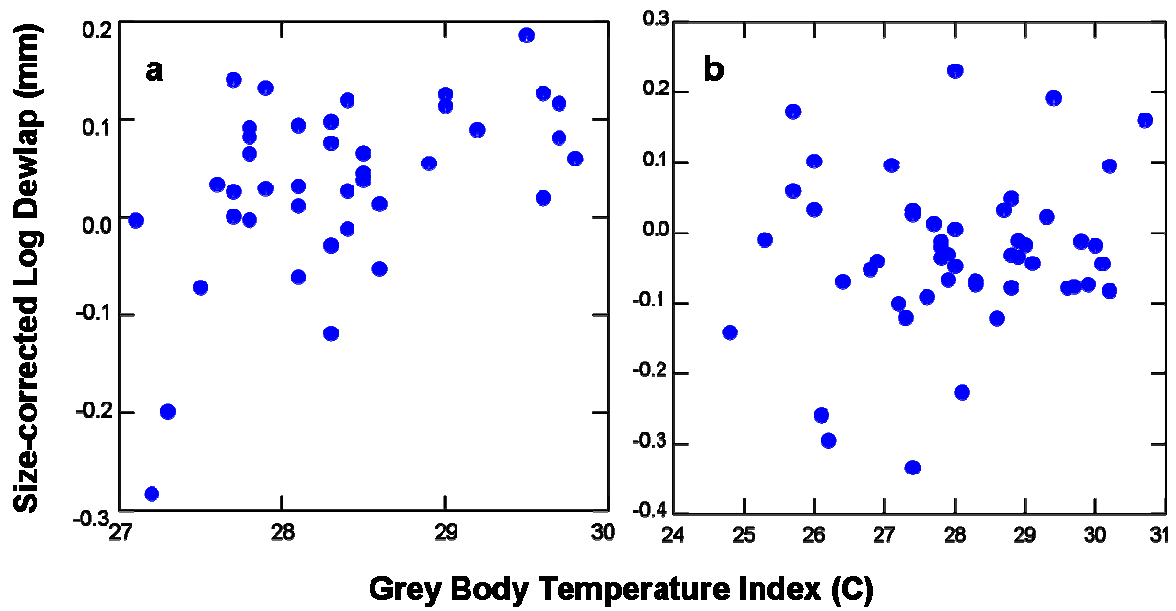
Figure 3.7. The Grey Body Temperature Index was positively correlated with size-corrected log dewlap diameter in (a) Cayo Mayor males, but not in (b) Cayo Menor males.

0.007) were significant predictors of GBTI when all females were pooled, and the slope was significant (GBTI = 28.179 − 9.227*mass + 31.668*SVL + 0.956*hind limb + 1.430*forelimb + 27.343*jaw length + 28.228*jaw width + 5.302*pelvic girdle + 19.802*pectoral girdle + 1.818*toe pad width + 11.808*toe pad length + 0.617*dewlap; $R^2 = 0.531$, $F_{11,40} = 3.443$, $P < 0.003$).

Field-active body temperatures were significantly different from GBTI for both Cayo Mayor (n = 40, t = -3.264, P < 0.003) and Cayo Menor (n = 51, t = 2.578, P < 0.014) males. Field-active body temperatures for Cayo Mayor females did not significantly differ from GBTI (n = 29, t = 1.881, P < 0.071), while body temperatures for Cayo Menor females did (n = 23, t = 2.424, P < 0.025).

CHAPTER 4

DISCUSSION

4.1 Are *Anolis lemurinus* Populations in the Cayos Cochinos Different?

Although sample sizes were probably too small to detect differences in morphology and habitat use among females, male *A. lemurinus* from the Cayos Cochinos appear to differ in several characteristics. Despite the fact that Cayo Mayor and Cayo Menor populations are less than 1km apart and Klutsch et al. (2007) considered them to be genetically and morphologically indistinguishable, Principal Component and Discriminant analyses (on size-corrected morphometric data) reveal that populations can be distinguished based on male morphology.

The first two axes of a Principle Component analysis combined to explain more than 80% of the variation inherent in the male morphometric data, and males appeared to separate along both PC1 and PC2 (suggesting that they group differently in morphospace). Moreover, a discriminant function derived from morphometric data for males was successful at predicting whether an individual came from Cayo Mayor or Cayo Menor. [Although the discriminant function derived from both environmental and morphometric variables was the most successful at discriminating among islands, the interpretation of the function itself—a linear combination of the input variables— becomes difficult due to the unclear relationships among those variables]. A discriminant

function derived from only male environmental variables, on the other hand, could not successfully classify males based on island of origin.

The results of the Principal Component and Discriminant analyses, taken together, suggest that Klutsch et al. (2007) were incorrect in their assertion that Cayos Cochinos populations were morphologically indistinguishable, and highlight the importance of more detailed morphological data when making among-island comparisons.

4.2 Male Mass, Dewlap Size, and Body Condition

Morphometric analyses reveal that Cayo Mayor and Cayo Menor males—when corrected for body size—differ in mass, dewlap diameter, and body condition in a peculiar way. Males on Cayo Mayor are smaller in mass and in worse body condition, but have larger dewlaps relative to males on Cayo Mayor. This pattern is intriguing, as one would expect larger lizards to have larger dewlaps, all else remaining equal. Elevation was a significant predictor of dewlap size among males of both islands, but this was most likely a relict of the fact that most lizards sampled on Cayo Mayor were at a higher elevation (due to logistic constraints). Nevertheless, there are several potential explanations for dewlap and body size patterns among males.

One hypothesis that could explain the mass-dewlap-body condition pattern involves life-history tradeoffs that might be predicted to arise from increased levels of intraspecific competition. Although abundance data was not collected during the study

period, it was fairly obvious that *A. lemurinus* on Cayo Mayor were much more abundant per unit area than those from Cayo Menor. On Cayo Mayor, as many as a dozen males could be sampled within a $10m^2$ area, whereas nearly a hectare was needed to sample the same number of males on Cayo Menor.

Males of most *Anolis* species are highly territorial (often with extremely high site-fidelity) and are known to spend much time and energy defending territories from other males (Fox et al. 2003). They often accomplish this through visual displays that include "push-ups," head-bobbing, and dewlap extension (Fox et al. 2003). It seems reasonable to assume, then, that males with larger dewlaps would be more successful at defending their territories and driving away other males. Thus, as a result of increased exposure to conspecifics, Cayo Mayor males might possess some mechanism allowing them to divert energy from growth and fat storage to dewlap production. As such, this mechanism would also explain why Cayo Mayor males are in worse body condition and smaller in size-corrected mass. This hypothesis, of course, would be a proximate cause of increased dewlap size, and if it were true one would predict that from season to season dewlap size, mass, and body condition would fluctuate in parallel with population density.

Perhaps a more parsimonious hypothesis for variation among islands in mass, body condition, and dewlap size could be that density-dependent selection is influencing selection on body size and dewlap size independently (Calsbeek 2009). It is possible that a high population density could result in increased resource overlap among individuals in terms of both habitat use and prey availability. The former could result in selection for larger dewlaps and the latter in decreased mass and body condition.

Mass and body condition aside, several hypotheses have been put forth to explain patterns in dewlap size among *Anolis* lizards. The "sexual selection" hypothesis (Fitch and Hillis 1984) suggests that males living in seasonal environments should have larger dewlaps relative to those from aseasonal environments, due to comparatively short breeding seasons. In other words, females should select males with larger dewlaps when the period of time in which they have to mate is reduced. Fitch and Hillis (1984) found support for this hypothesis after noticing a correlation between rainfall patterns (i.e. length of the rainy season) and dewlap size in anoles from Central America (males from areas with shorter rainy periods tended to have larger dewlaps). This hypothesis is unlikely to explain differences in dewlap size among Cayos Cochinos populations, however, because they occur in the same geographic location and thus their environments do not differ in seasonality.

A second hypothesis that has been proposed to explain patterns in dewlap size is known as the "species recognition" hypothesis (Rand and Williams 1970) which posits that the dewlap size of a species should diverge from that of sympatric species in order to reduce interspecific mating events. Since the *Anolis* communities of Cayo Mayor and Cayo Menor are identical (*A. lemurinus* and *A. allisoni* on both islands), this hypothesis is unlikely to explain dewlap size patterns in the Cayos Cochinos.

A third hypothesis for patterns in dewlap size involves the relationship between habitat structure and the effectiveness of visual communication, and can be termed the "habitat illumination" hypothesis (Losos and Chu 1998). Because dewlaps are used as visual cues (and larger dewlaps are generally more visible), the "habitat illumination"

hypothesis predicts that dewlaps should be larger for species that live in darker habitats. Anecdotally, the habitat where *A. lemurinus* occurs on Cayo Mayor does appear to be dimmer than on Cayo Menor, although incident solar radiation and canopy cover do not differ among islands.

A fourth dewlap size hypothesis involves the apparent function of dewlap display as a predator deterrence mechanism (Vanhooydonck et al. 2009). In the Cayos Cochinos, the primary predators of *Anolis* lizards are likely snakes and birds. Birds appear to occur in similar abundance on both islands (Birmingham et al. 1998), although *Oxybelis aeneus* and *Leptophus mexicanus* (arboreal snakes that specialize on lizard prey) occur solely on Cayo Mayor (McCranie et al. 2005). *Dryadophis melanolomus* and *Leptodeira septentrionalis* both occur on Cayo Menor, but *D. melanolomus* is a ground dwelling predator and *L. septentrionalis* seems to occur at an extremely low abundance (McCranie et al. 2005; Montgomery and Green pers. comm.). Moreover, although mammals are not known to be dominant predators of anoles, *Rattus rattus* likely adds to predation pressure on anoles from Cayo Mayor (no mammal species are known from Cayo Menor). Increased predation pressure on Cayo Mayor, then, might provide an explanation for why males on that island have comparatively larger dewlaps.

4.3 Patterns in Physiology and Space Use

When examining ectotherm populations, studies often use internal body temperatures to quantify space as a resource axis, as body temperatures are a function of abiotic variables that often differ among microhabitats (Roughgarden 1995). This is an

40

inherently flawed method, however, because differences in size, shape, texture, and color (among other things) that occur between sexes, populations, and individuals in different size classes may cause consistent biases in internal body temperature. Thus variation in body temperature among individuals may not represent parallel variation in microhabitat use (Roughgarden 1995). To correct for this bias, I used ambient temperature, wind speed, and solar radiation data collected at the perch site of each lizard to estimate the Grey Body Temperature Index (GBTI) of each perch site. Technically speaking, the GBTI of a perch site is the temperature that a five gram lizard-shaped grey object would achieve if allowed to come to thermal equilibration at that site (Roughgarden 1981). By quantifying each individual's position in space using a standardized metric, GBTI permitted me to compare microhabitat use among populations irrespective of potential differences in morphology, physiology, and behavior that occur among individuals.

Although mean GBTI did not differ among islands for males or females, it did differ among males in two primary ways. First, on Cayo Mayor, pectoral girdle width and dewlap diameter significantly predicted GBTI, while on Cayo Menor none of the morphometric variables predicted GBTI. From this, it appeared that males from Cayo Mayor used microhabitat in a way that was dependent upon their morphology. This suggested that space use covaried with other aspects of male ecology on Cayo Mayor, but not on Cayo Menor.

Interestingly, Cayo Mayor males showed lower variance in GBTI, which indicated a narrower range of space use among individuals. This pattern is difficult to interpret, however, since if males were at a higher abundance on Cayo Mayor one would

expect them to display *higher* variance in space use as more individuals would be forced into sub-optimal habitat due to competition for space (Huey and Slatkin 1976). On the other hand, abundance patterns might explain why space use is related to aspects of morphology on Cayo Mayor but not Cayo Menor, as males with larger dewlaps are predicted to be better able to compete for space (Vanhooydonck et al. 2005).

For females, several environmental variables (such as humidity and canopy cover) were significant predictors of GBTI. This is not surprising, however, as most of the environmental variables measured correlate with one or more of the components of GBTI in a predictable manner (e.g. a low value for canopy cover will necessarily result in a higher value for incident solar radiation). Several morphometric variables were also significant predictors for GBTI in Cayo Mayor and Cayo Menor females, suggesting that the way in which females exploit microhabitat is related to aspects of their morphology.

An unexpected pattern was discovered when upper thermal tolerance was compared with size-corrected dewlap diameter among males on Cayo Menor (thermal tolerance data was not collected for Cayo Mayor males). Males with larger size-corrected dewlaps had higher upper thermal tolerance relative to males with smaller size-corrected dewlaps. The cause of this relationship is unclear, although it is most likely not a direct one. Perhaps higher thermal tolerance is simply a side-effect of higher levels of some hormone (e.g. testosterone) which is meant to increase dewlap size (Tokarz 2002). It might also be plausible that males with larger dewlaps spend more time in the open defending prime territories or attempting to attract females, and this exposure has resulted in higher upper thermal tolerances. Additionally, the dewlaps of anoles are often viewed

as ornamentation, and there are many examples of species that use ornamentation to signal the presence of beneficial underlying characteristics to the opposite sex (see Grether 1996; Moller and Nielsen 1997). Dewlap size has been shown to predict other aspects of performance (such as bite force and jumping ability) in many *Anolis* species (Vanhooydonck et al. 2005; Lailvaux and Irschick 2007), and it is therefore plausible that increased dewlap size could indicate increased thermal tolerance (assuming higher upper thermal tolerance is a *beneficial* characteristic) as well. Lastly, since panting temperature was used as an index of upper thermal tolerance, there could simply be a behavioral tendency for more dominant males (i.e. males with larger dewlaps relative to other males of the same body size) to wait longer before panting. If this were the case, the observed pattern would have nothing to do with an intrinsic ability for males with larger dewlaps to tolerate higher temperatures.

4.4 Conclusions and Suggestions for Future Research

It is perhaps not surprising that I found differences among two populations of lizards that occur on separate islands. Nevertheless, they are separated geographically by less than 1 km (McCranie et al. 2005), were isolated as recently as eight thousand years ago (Bermingham et al. 1998), and were considered genetically and morphologically indistinguishable by previous workers (Klutsch et al. 2007).

Male *A. lemurinus* among islands in the Cayos Cochinos archipelago differ in their use of microhabitat (as indexed by GBTI), and in ecologically important aspects of morphology such as mass and dewlap size. Despite the acquisition of detailed micro-

meteorological and habitat use data, the reasons for these differences are still obscure. The problem is particularly confusing, as the lizards on Cayo Mayor that have larger dewlaps also are smaller in mass and in worse body condition. Data on abundance and intraspecific interactions (i.e. ethological data) may help to further refine hypotheses aimed at explaining this pattern.

Sample sizes were not large enough to reveal differences among female *A. lemurinus* in the Cayos Cochinos (n = 25 and 29 on Cayo Menor and Cayo Mayor, respectively). Nevertheless, many analyses approached statistical significance and thus populations of females probably differ in both morphology and habitat use, although definite conclusions are not possible at present.

More data is needed to fully understand the relationship between dewlap size and upper thermal tolerance. In order to understand why lizards with larger dewlaps have higher thermal tolerances, several questions should be investigated: First, are dewlap size and thermal tolerance mechanistically intertwined, or do they both share the same relationship with some unknown variable (e.g. testosterone concentrations)? How is dewlap size related to lower thermal tolerance? How do relative dewlap size and thermal tolerance interact to shape the fitness surface of males? In other words, if relative dewlap size is kept constant, do males with higher thermal tolerances have higher fitness? How is upper thermal tolerance related to habitat use and mating success (i.e. can females identify a male with higher upper thermal tolerance)?

Lastly, *A. lemurinus* is sympatric with the Caribbean species *A. allisoni* on both Cayo Mayor and Cayo Menor (Kohler, 2003; McCranie et al., 2005). Although

anecdotal evidence suggests that there may be differences in habitat affinity, thermal tolerance, and within-island distribution between these two species (Montgomery and Green pers. comm.), there is no data to support this hypothesis, and their ecological relationships in the Cayos Cochinos remain unknown. Comparing the ecology of *A. lemurinus* and *A. allisoni* may reveal patterns governing faunal assemblage and suggest hypotheses pertaining to interspecific competition and the effects of phylogenetic history on local adaptation (Roughgarden 1995; Schluter 2001; Jezcova et al. 2009). Finally, an examination of interactions between *A. lemurinus* and *A. allisoni* may help to explain the differences in morphology and habitat use seen among *A. lemurinus* populations.

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BIOGRAPHICAL INFORMATION

The author is originally from Chicago, IL where he barely graduated from high school in 2001. In 2005, he received his A.S. in Biological Sciences from the College of Lake County in Grayslake, IL and in 2007 he received his B.A. in Zoology from Southern Illinois University at Carbondale. This manuscript represents the culmination of his M.S. in Biology from the University of Texas at Arlington, in 2009.

The author's research interests sit broadly within the field of evolutionary ecology, although he has a specific interest in the thermal biology and community ecology of insular ectotherms.