Revista Chilena
de Historia Natural
a SpringerOpen Journal

RESEARCH   **Open Access**

Morphometric variation in island and mainland populations of two lizard species from the Pacific Coast of Mexico

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Abstract

Background: Body size exerts a strong influence on the physiology, morphology, ecology, and evolution of other life history traits in vertebrates. We compared the morphometry and allometry of two lizard species (*Anolis nebulosus* and *Aspidoscelis lineattissima*) occurring on mainland and island populations on the Pacific Coast of Mexico in order to understand the effect of an insular environment on body size and other morphometric structures.

Results: Results showed that both males and females of *A. nebulosus* from San Pancho Island were larger in body size than those from the mainland. Moreover, males of *A. lineattissima* from Cocinas Island exhibited larger forms of most measured morphometric traits than those from the mainland, whereas females from both island and mainland populations did not differ in body size or in other morphometric traits analyzed. Multivariate allometric coefficients of males and females of *A. nebulosus* from island and mainland populations showed a lower percentage of positive allometries than in *A. lineattissima*, probably because the former species is highly sedentary. Island populations of both species exhibit male-biased sexual dimorphisms in body size and size-adjusted morphometric traits. In contrast to the mainland population, morphometric comparisons of body size-adjusted traits showed that male *A. lineattissima* were larger than females only in head length, head width, forearm length, and tibia length, whereas in *A. nebulosus*, sexual dimorphism was observed just in HL.

Conclusions: This study supports the hypothesis (island rule) that vertebrates on islands are larger than those of conspecifics on the mainland. In addition, sexual dimorphism observed between males and females of both species and populations could be associated with allometric growth (positive or negative) from some morphometric structures, as well as differences in the growth rates of these organisms.

Keywords: Allometry; *Anolis nebulosus*; *Aspidoscelis lineattissima*; Islands; Evolution; Sexual dimorphism

Background

Phenotypic responses in organisms at different spatial and temporal scales reflect a wide range of factors, such as interspecific interactions, resource availability, climate, and other environmental variations (Michaud and Echternacht 1995; Meiri 2010). Thus, a careful study of the phenotype can provide insights on the evolutionary trajectories of morphometric characteristics among populations and species (Sinervo et al. 1991; Michaud and Echternacht 1995; Meiri 2010). In many groups of vertebrates, including lizards, the phenotypic responses may be related to body size at sexual maturity, and this in turn with other life history characteristics, such as size at sexual maturity, clutch size or brood size, size at hatching, and other features (Michaud and Echternacht 1995; Meiri 2010). Therefore, morphometric and allometric analysis is a fundamental tool in the study of evolutionary ecology, systematics, taxonomy, and comparative biology (Meiri 2010).

In general, allometry relates morphometric variables (e.g., width and length of the skull, limb length, body weight, and volume) with body size of individuals (Feldman and Meiri 2013). In lizards specifically, body size is associated allometrically with a variety of reproductive traits (e.g., sexual maturity, egg size, size at hatching, and clutch frequency: Ramírez-Bautista and Vitt 1997; Meiri et al. 2012), aspects of sexual selection (sexual dimorphism,

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territoriality; Anderson and Vitt 1990), niche divergence both between sexes of a single species and across species (Mc Arthur and Levins 1967), and foraging ecology (e.g., active vs. ambush foraging; Meiri 2010). Variations in these characteristics have been interpreted as expressions of phenotypic plasticity or reaction norms (Stearns 1992). Thus, comparative studies among populations and species on life history characteristics have received considerable attention by evolutionary ecologists putting forward hypotheses about differences in the evolution of body size in lizards on island and mainland environments (Feldman and Meiri 2013). For example, Tinkle and Ballinger (1972) showed that variation in food resource availability and thermal constraint among *Sceloporus undulatus* populations influences growth rate, survival, age, and size at maturity in different populations. Other studies have shown that in *Anolis* species, allometric trajectories of the head, digital lamellae count, and other morphometric characteristics reflect sexual dimorphism between males and females and, therefore, ecological niche divergence (diet, habitat use, and microhabitat; Losos et al. 2003). These divergences are present both among populations of the same species and across species (Andrews 1976, 1979). Variation in habitat (e.g., islands vs. mainland environments) promotes variation in population body size, growth rate, age at maturity, and other characteristics of life history and ecology of lizard species (Meiri 2007, 2010). Interpretations of the functional significance of these population-specific variations facilitated the development of several hypotheses or theories collectively known as the island rule (Foster 1964). In general, this rule predicts that patterns of allometric trajectories or scaling relationships in body proportions of species on islands are different as compared with mainland sites, and this arises due to life in an insular environment relatively poor in competitors and predators (Meiri 2010).

Morphometric and ecological comparisons among populations, both of a single species and across multiple species, suggest that the island rule occurs in all vertebrate groups that inhabit islands with arboreal or terrestrial habits (Novosolov et al. 2013). However, some authors note that not all groups, including at least some lizards, follow the pattern of the rule (Meiri 2007, 2010). Consequently, this study is grounded on the hypothesis that populations of island environments have diverged on a large scale in shape and size, regardless of the habits (arboreal and terrestrial) of lizards. The aim of this study was to compare the morphometry and allometry of two lizard species that inhabit the same vegetation community on islands as compared with nearby mainland sites. We selected two species, the arboreal *Anolis nebulosus* and the terrestrial *Aspidoscelis lineattissima*, for study due to their locally high abundance and occurrence on both island and mainland environments from the Pacific Coast of Mexico. In addition, we asked the following questions: 1) Do populations on islands exhibit a larger body size than those from mainland populations? 2) Is there variation in other morphometric characteristics, within and across species between these two sites? 3) Are there differences in the expression of sexually dimorphic traits between males and females of each species between island and mainland populations?

Methods
Study area
Fieldwork was conducted on islands in Chamela Bay on the Mexican coast of the Pacific Ocean, as well as nearby mainland sites in the Municipality of La Huerta, Jalisco, Mexico (Comisión Nacional de Áreas Naturales Protegidas 2008). We sampled *A. nebulosus* on San Pancho Island (SPI; 19° 32′ 0.45″ N, 105° 05′ 2.61″ W; Figure 1) and at the Biological Field Station Chamela (BFSCH), Universidad Nacional Autónoma de México (UNAM) (19° 31′ 31.8″ N, 105° 03′ 44.5″ O; Figure 1). Studies of *A. lineattissima* were conducted on Cocinas Island (CI; 19° 32′ 8.07″ N, 105° 06.5′ 8.40″ O; Figure 1) and the mainland town of Xametla (19° 32′ 5.15″ N, 105° 04′ 9.53″ O; Figure 1).

The BFSCH population is located about 1,800 m from Chamela Bay while Xametla is located about 500 m from the coast (Figure 1). The dominant vegetation types of BFSCH are tropical dry forest, patches of deciduous forest, and desert scrub (Trejo-Vázquez 1988). In Xametla, the major vegetation types are tropical dry forest and coastal dunes (Trejo-Vázquez 1988). SPI is located 500 m from the mainland and has a total area of 2.4 ha, and its dominant vegetation types are tropical dry forest and desert scrub. CI is about 3 km from the mainland, has a total area of 26.2 ha, and is primarily covered by tropical dry forest and coastal dunes (Trejo-Vázquez 1988).

Fieldwork
We conducted fieldwork during each of six time periods, three during the dry season, and three during the rainy season. Each sample period lasted 16 days, with 3 to 4 days of fieldwork at each individual site. Surveys during the dry season occurred in December 2011 and March and December 2012; rainy season surveys took place in June, August, and October 2012. In order to observe the status of lizard populations, we established three study plots of 30×60 m^2 at each site. Each plot was arranged parallel to others at the same site and separated from adjacent plots by 10 m. Using the mark-recapture method (Ramírez-Bautista 1995), we obtained information on body size and morphometric characteristics for individuals of both *A. nebulosus* and *A. lineattissima*. At each
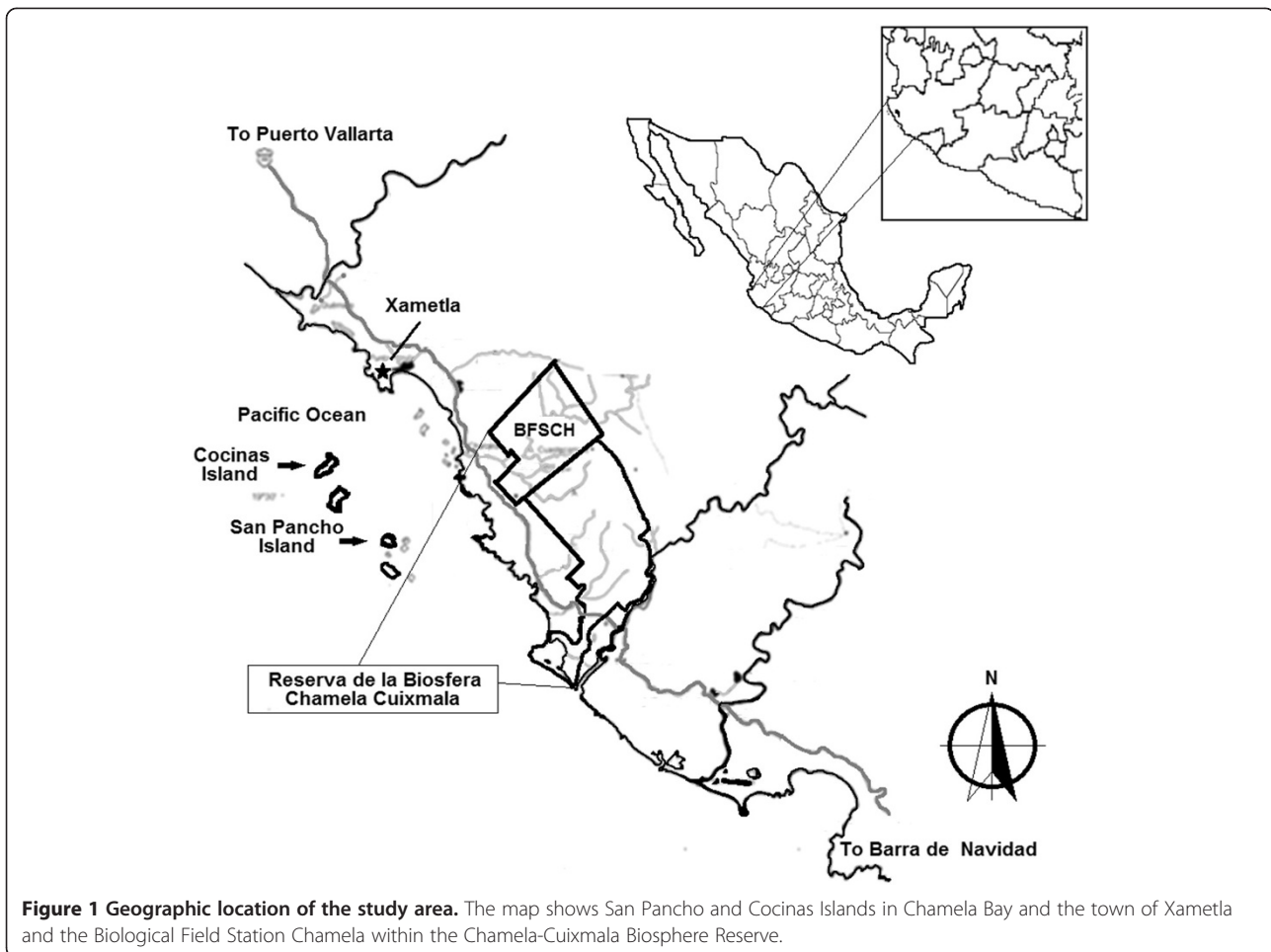
Figure 1 Geographic location of the study area. The map shows San Pancho and Cocinas Islands in Chamela Bay and the town of Xametla and the Biological Field Station Chamela within the Chamela-Cuixmala Biosphere Reserve.

population, we marked individuals by toe clipping technique, and the following linear measurements were recorded to ±1 mm on adult lizards in accordance with Ramírez-Bautista et al. (2013): snout-vent length (SVL), head length (HL), head width (HW), arm length (AL), forearm length (FOL), femur length (FL), tibia length (TL), and pelvic girdle length (PGL).

Data analysis

All morphometric comparisons between populations of each species and sex were performed only on adult lizards. Measures of body size and morphometric variables (SVL, HL, HW, AL, FOL, FL, TL, and PGL) were analyzed by sex and population (island vs. mainland); as not all morphometric variables exhibited a normal distribution (Zar 1999), we used non-parametric Mann-Whitney U tests. Furthermore, to test if sexual dimorphism exists between males and females from both populations and species, we performed a Mann-Whitney U test to compare SVL, HL, HW, AL, FOL, FL, TL, and PGL between sexes (Ramírez-Bautista and Pavón 2009).

To identify an allometric pattern in lizard form (e.g., dimensions of the head and limbs) with respect to SVL of both sexes and populations of each species, we used multivariate allometric coefficients obtained from the loadings of variance-covariance from principal component analysis (PCA). This analysis was performed as suggested by Jolicoeur (1963) and Mora et al. (2003), which is based on testing whether the variation explained by principal component 1 (PC1; SVL in this case) is greater than the other components or morphometric variables, because the analysis expresses the relationship between coefficients of each variable with respect to PC1. Depending on the value of the allometric coefficient of each combination (SVL vs. morphometric character), we determined whether there was an isometric or allometric relationship between morphometric variables and body size. Isometry was considered when the allometric coefficient represented values equal to 1, and allometry if the coefficient differed from 1, either positive (>1) or negative (<1; Huxley and Teissier 1936). According to PCA and its variance-covariance matrix, we identified those variables that explain most of the variation in the shape

(dimensions of the head and limbs) of both males and females from each species and population. We excluded the SVL of PC1 from hypothesis testing, since our goal was to isolate the overall effect of body size (SVL) and represent the components that show changes in body shape (Mora et al. 2003), factors that should be subject to natural selection. To meet criteria of normality and homogeneity of variances prior to each analysis, all data were transformed to $\log_{10}$ to fit a normal distribution (Zar 1999). Statistical analyses were performed using Past v. 1.81 (Hammer et al. 2008) and StatView IV (Abacus Concepts 1992). Means are given ±1 S.E. unless otherwise indicated and with a significance level of 0.05.

Results

We measured a total of 300 adult lizard *A. nebulosus*, 149 from SPI population (64 females and 85 males) and 151 from the mainland (42 females and 109 males). For *A. lineattissima*, we measured 134 lizards, 66 from CI (30 females and 36 males) and 68 from the mainland (29 females and 39 males).

Body size

For both males and females of *A. nebulosus*, the size of each morphological trait (SVL, HL, HW, AL, FOL, FL, TL, and PGL) was greater in lizards from the island population than that from the mainland (Table 1). In female *A. lineattissima*, all morphological characteristics were similar between populations (Table 2); however, males of this species from the island population exhibited larger morphological traits than those from the mainland for all measured morphological characteristics except FOL and TL (Table 2).

PCA confirms the pattern observed in the morphometric variation between populations of males and females of *A. nebulosus* and *A. lineattissima* (Figures 2 and 3). In males of *A. nebulosus* from both SPI and BFSCH populations, PC1 and PC2 explained 85.0% and 5.55%, respectively, of the variation. Both components indicate that HL,

AL, FOL, FL, TL, and PGL are highly correlated variables that provide the most morphometric variation (Table 3). For females, PC1 and PC2 explained 54.7% and 11.9% of the variation, respectively, and revealed that between populations, AL, FL, TL, FOL and PGL explain this variation (Table 3). These patterns are shown in Figure 2, in which males and females from SPI are distributed primarily on the right where the highest values for each component are located, and those from the mainland on the left.

For males of *A. lineattissima* from both CI and Xametla, PC1 and PC2 explain 76.0% and 7.54% of the variation, respectively; HW, AL, FL, TL, and PGL showed the greatest morphometric variation between populations. In contrast, for female *A. lineattissima*, PC1 and PC2 explained 57.5% and 17.5% of the total variation, respectively; this variation was explained only by AL, FOL, FL, TL and PGL (Table 3). Morphometric variation observed in both males and females of *A. lineattissima* from both populations is represented in Figure 3. Males from CI are clustered to the right of both components, whereas males from the mainland (Xametla) are clustered to the left, indicating that males with smaller morphometric dimensions correspond to those from the mainland population. For females from both populations, overlapping is extensive, indicating little morphometric difference.

Allometry

There are a greater number of negative allometries for *A. nebulosus* than for *A. lineattissima* (Table 4). Multivariate allometric coefficients indicate that 32% of positive allometry in AL, FOL, and PGL exists in *A. nebulosus* with respect to SVL in males and females, which equals to an increase in these morphometric variables with increasing body size (Table 4). While those greater numbers of allometric relationships are targeted in a negative way, they show a greater percentage (68%) and reveal that the variables HL, HW, FL, and TL decreased proportionally as body size increased in both males and females (Table 4).

Table 1 Comparisons of morphometric variables of females and males of *Anolis nebulosus*

Variables (mm)	Females			Males		
	San Pancho Island	BFSCH		San Pancho Island	BFSCH	
	Mean ± S.E. (range)		*P*	Mean ± S.E. (range)		*P*
SVL	43.4 ± 0.26 (39.6 to 48.7)	38.4 ± 0.36 (33.5 to 43.8)	<0.05	51.8 ± 0.28 (47.6 to 59.3)	38.3 ± 0.037 (32.0 to 48.8)	<0.05
HL	11.9 ± 0.08 (10.2 to 13.2)	10.8 ± 0.08 (10.0 to 12.1)	<0.05	14.3 ± 0.09 (12.4 to 16.5)	11.2 ± 0.09 (10.0 to 12.1)	<0.05
HW	6.5 ± 0.6 (5.7 to 7.7)	6.1 ± 0.06 (5.4 to 7.0)	<0.05	7.6 ± 0.06 (6.3 to 9.0)	6.2 ± 0.05 (5.1 to 7.8)	<0.05
AL	7.06 ± 0.10 (5.2 to 9.3)	6.08 ± 0.08 (4.9 to 7.1)	<0.05	8.4 ± 0.10 (6.5 to 10.6)	6.1 ± 0.08 (4.4 to 8.4)	<0.05
FOL	6.1 ± 0.06 (5.1 to 7.9)	5.6 ± 0.07 (4.8 to 7.0)	<0.05	7.3 ± 0.06 (5.7 to 8.5)	5.4 ± 0.06 (3.9 to 6.8)	<0.05
FL	9.6 ± 0.09 (8.0 to 11.8)	8.2 ± 0.08 (7.3 to 9.6)	<0.05	11.4 ± 0.09 (9.7 to 13.5)	8.5 ± 0.09 (6.1 to 10.6)	<0.05
TL	9.1 ± 0.09 (7.8 to 11.7)	8.1 ± 0.08 (6.8 to 9.1)	<0.05	10.9 ± 0.07 (8.9 to 12.7)	8.4 ± 0.08 (6.5 to 11.7)	<0.05
PGL	3.9 ± 0.05 (3.0 to 5.1)	3.4 ± 0.04 (3.1 to 4.2)	<0.05	4.6 ± 0.04 (3.8 to 5.7)	3.3 ± 0.04 (2.1 to 4.7)	<0.05

Samples are from San Pancho Island and a nearby mainland population, BFSCH, in Jalisco, Mexico. S.E., standard error.

Table 2 Comparisons of morphometric variables of females and males of *Aspidoscelis lineattissima*

Variables (mm)	Females			Males		
	Cocinas Island	Xametla		Cocinas Island	Xametla	
	Mean ± S.E. (range)		*P*	Mean ± S.E. (range)		*P*
SVL	73.9 ± 0.68 (68.6 to 81.8)	76.4 ± 1.34 (68.0 to 91.4)	0.43	82.9 ± 1.32 (67.9 to 101.1)	78.2 ± 1.80 (59.0 to 105.4)	<0.05
HL	17.5 ± 0.17 (15.9 to 19.6)	17.4 ± 0.28 (15.2 to 20.4)	0.4	20.2 ± 0.36 (16.5 to 24.8)	18.7 ± 0.41 (14.4 to 23.7)	<0.05
HW	9.7 ± 0.09 (8.9 to 10.8)	9.9 ± 0.18 (8.7 to 12.4)	0.82	11.8 ± 0.28 (8.6 to 16.0)	10.9 ± 0.32 (7.9 to 17.3)	<0.05
AL	8.7 ± 0.18 (6.5 to 10.9)	9.1 ± 0.23 (7.0 to 12.9)	0.32	10.4 ± 0.22 (7.4 to 13.3)	9.6 ± 0.26 (6.3 to 13.5)	<0.05
FOL	8.2 ± 0.15 (5.9 to 10.3)	8.4 ± 0.19 (6.7 to 10.6)	0.8	9.6 ± 0.19 (7.0 to 11.7)	9.2 ± 0.23 (6.7 to 13.1)	0.18
FL	14.3 ± 0.23 (11.9 to 17.2)	14.6 ± 0.33 (12.2 to 19.3)	0.74	16.7 ± 0.31 (12.3 to 20.5)	15.5 ± 0.43 (9.4 to 22.1)	<0.05
TL	13.8 ± 0.23 (11.7 to 17.5)	13.6 ± 0.33 (10.6 to 18.8)	0.37	15.9 ± 0.30 (12.1 to 19.1)	15.3 ± 0.40 (9.5 to 20.3)	0.33
PGL	6.9 ± 0.10 (5.9 to 8.1)	7.1 ± 0.16 (4.9 to 11.2)	0.67	8.1 ± 0.20 (5.6 to 10.3)	7.4 ± 0.23 (4.9 to 11.2)	<0.05

Samples from Cocinas Island and a nearby mainland population, Xametla, in Jalisco, Mexico. S.E., standard error.

In *A. lineattissima*, 39% of positive allometric relationships was observed (Table 4). The AL and FOL showed positive allometry with respect to female body size from the island population (CI), whereas FOL, TL, and PGL exhibited positive allometry with respect to SVL in females from the mainland (Xametla). For males from CI, positive allometric relationships were found for HW, FOL, and PGL with respect to SVL, whereas for males from the mainland, positive allometric relationships were found for HW, FOL and PGL; AL and TL showed a marginally significant response (Table 4). Overall, 61% of the allometric relationships in *A. lineattissima* in both sexes and populations were negative, revealing only one isometric relationship in males from the mainland, the relationship between FL and SVL (Table 4).

Sexual dimorphism

Males of both *A. nebulosus* and *A. lineattissima* from insular environments were larger than females (Table 5). Males and females of *A. nebulosus* from the mainland were similar in all measured morphometric characteristics but less in HL, whereas in *A. lineattissima* from the mainland, males were larger than females in HL, HW, FOL and TL only (Table 5).

Discussion and conclusions
Body size

Results of this study showed that both males and females of *A. nebulosus* from the island population (SPI) were larger in SVL and in other morphometric characteristics than those from the mainland population (BFSCH). A
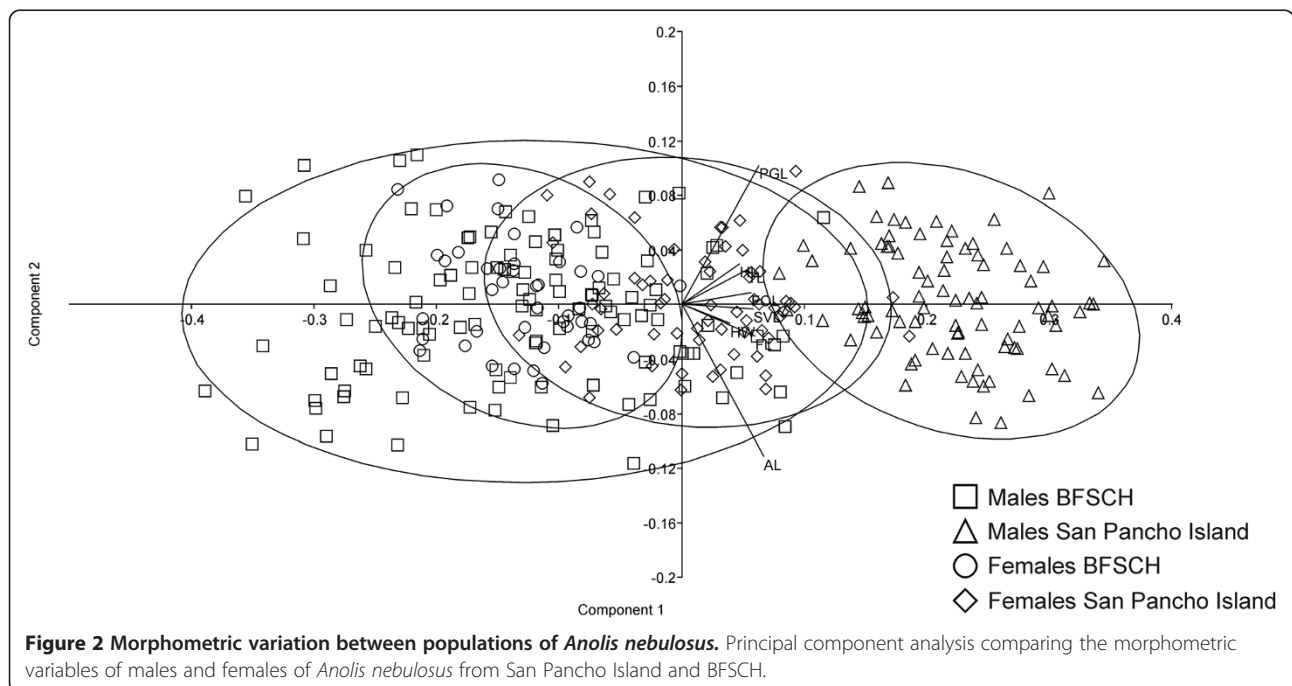

Figure 2 Morphometric variation between populations of *Anolis nebulosus*. Principal component analysis comparing the morphometric variables of males and females of *Anolis nebulosus* from San Pancho Island and BFSCH.
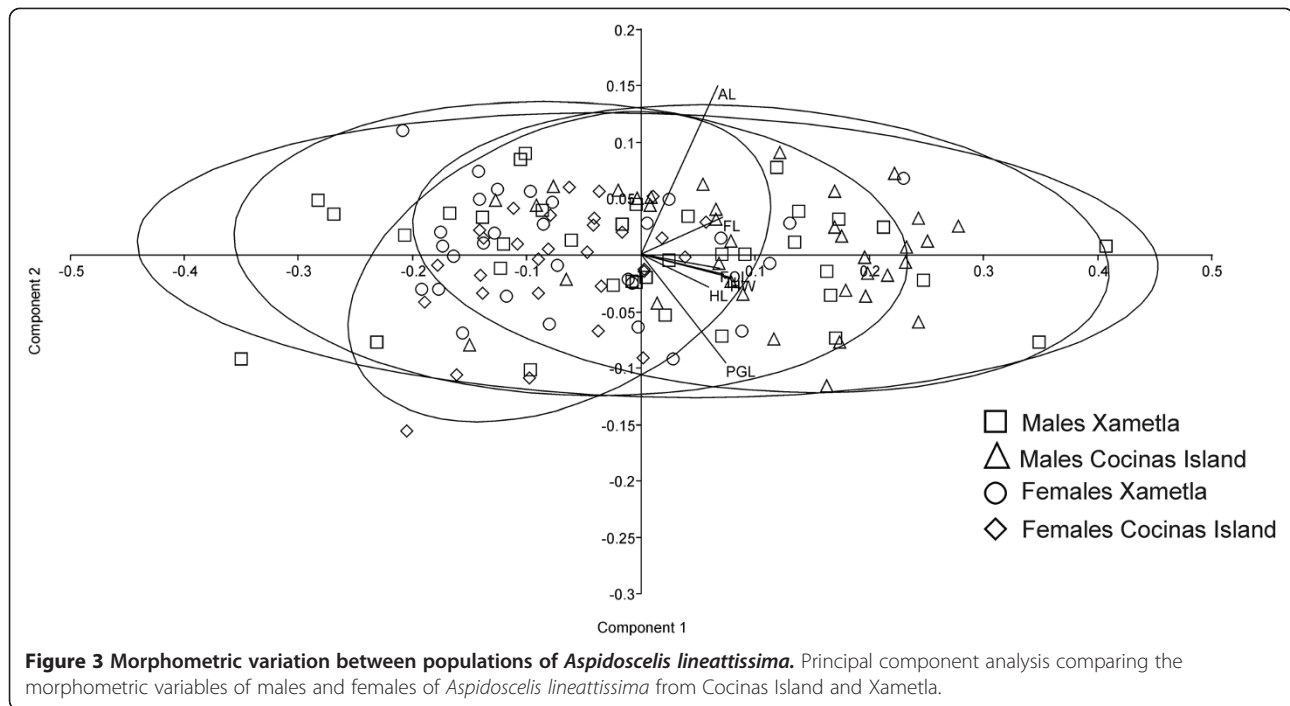
Figure 3 Morphometric variation between populations of *Aspidoscelis lineattissima*. Principal component analysis comparing the morphometric variables of males and females of *Aspidoscelis lineattissima* from Cocinas Island and Xametla.

Table 3 Loading scores for PC1 and PC2

| | *Anolis nebulosus* | | | |
| | Males | | Females | |
Variables (log)	PC1	PC2	PC1	PC2
HL	0.314	−0.289	0.266	−0.062
HW	0.261	0.037	0.254	−0.226
AL	0.444	0.682	0.533	−0.612
FOL	0.402	0.070	0.264	0.482
FL	0.397	0.176	0.438	−0.095
TL	0.355	−0.127	0.350	0.253
PGL	0.435	−0.630	0.441	0.512
Variation explained (%)	85.0	5.55	54.7	11.9

| | *Aspidoscelis lineattissima* | | | |
| | Males | | Females | |
Variables (log)	PC1	PC2	PC1	PC2
HL	0.322	−0.197	0.259	−0.139
HW	0.430	−0.158	0.296	−0.084
AL	0.340	0.692	0.411	0.833
FOL	0.334	0.120	0.480	−0.283
FL	0.399	0.252	0.376	0.149
TL	0.362	0.066	0.427	−0.155
PGL	0.438	−0.611	0.347	−0.389
Variation explained (%)	76.0	7.54	57.5	17.5

The variation for each morphometric variable for both males and females between island and mainland populations of *Anolis nebulosus* and *Aspidoscelis lineattissima* are shown.

similar pattern was found in males of *A. lineattissima*, but not in females, which exhibited similar morphological characteristics at both populations. The latter pattern in female *A. lineattissima* can be explained in that the female growth rate of *A. lineattissima* is similar at both CI and Xametla, and females reach sexual maturity at a similar body size (Table 2); a similar pattern has been observed in other lizard species with a broad distribution (Losos et al. 2003). Another explanation could be that the mortality rate in both populations of *A. lineattissima* is higher in females than in males and that females are responding to this pressure by growing quickly and reaching sexual maturity at a smaller SVL, a strategy observed in other vertebrate groups (Stearns and Koella 1986).

On the other hand, larger body sizes in both males and females of *A. nebulosus* and in males of *A. lineattissima* from island populations as compared to mainland populations could be explained in that the insular populations have evolved to attain a large size as a function of the absence of mainland predators, an hypothesis that has been tested in other lizards from island and mainland habitats (Andrews 1979; Lister and García 1992). The absence from SPI of golden-orb weaver spiders (*Nephila*), known predators of *A. nebulosus*, as well as various avian and snake predators of *A. lineattissima* from CI (Ramírez-Bautista and Vitt 1997; Ramírez-Bautista et al. 2000) could be a factor influencing the evolution of larger body sizes. By reducing the number of predators, lizards can eliminate time and energy costs associated with escape behavior and therefore direct a

Table 4 Multivariate allometric coefficients obtained by PCA for different morphometric variables

Variables (mm)		*Anolis nebulosus*			
		San Pancho Island		BFSCH	
		Females	Males	Females	Males
SVL vs.	HL	0.30	0.63	0.18	0.52
	HW	0.70	0.67	0.02	0.50
	AL	1.38	1.12	0.55	0.96
	FOL	0.90	1.12	2.01	1.18
	FL	0.70	0.86	0.03	0.75
	TL	0.60	0.79	0.40	0.72
	PGL	2.50	1.77	3.85	2.19
Variables (mm)		*Aspidoscelis lineattissima*			
		Cocinas Island		Xametla	
		Females	Males	Females	Males
SVL vs.	HL	0.33	0.73	0.65	0.65
	HW	0.47	1.2	0.96	1.09
	AL	2.07	0.86	0.81	0.95
	FOL	1.94	1.02	1.24	1.06
	FL	0.84	0.88	0.86	1
	TL	0.84	0.68	1.06	0.98
	PGL	0.50	1.6	1.39	1.4

Results were obtained with respect to SVL for males and females of *Anolis nebulosus* and *Aspidoscelis lineattissima* from both island and mainland populations. Coefficients = 1 indicates isometry, >1 indicates positive allometry, and <1 indicates negative allometry.

greater amount of energy toward growth (Tinkle and Ballinger 1972; Sinervo et al. 1991). Another explanation could be that lizards with a large body size have a higher survival rate during periodic food shortages because they are able to store more energy as fat bodies (Michaud and Echternacht 1995). This idea is also related to the hypothesis that lizards of a large body size (by energy

Table 5 Mann-Whitney *U* tests of comparisons of sexual dimorphism among populations of each species

Variables (mm)	*Anolis nebulosus*		*Aspidoscelis lineattissima*	
	San Pancho Island	BFSCH	Cocinas Island	Xametla
	Females-males	Females-males	Females-males	Females-males
	P	P	P	P
SVL	<0.05	0.49	<0.05	0.5
HL	<0.05	<0.05	<0.05	<0.05
HW	<0.05	0.19	<0.05	<0.05
AL	<0.05	0.92	<0.05	0.22
FOL	<0.05	0.13	<0.05	<0.05
FL	<0.05	0.15	<0.05	0.09
TL	<0.05	0.07	<0.05	<0.05
PGL	<0.05	0.11	<0.05	0.55

storage) can better withstand catastrophic weather events such as hurricanes and storms over longer periods, events that are generally more intense on islands than on the mainland (Whittaker and Fernández-Palacios 2007).

Allometry

Allometric analysis of males and females of both populations of *A. nebulosus* and *A. lineattissima* revealed a positive or negative trend in growth of the morphometric characters with respect to body size. In lizards, both types of allometry are considered to be adaptive responses to the selective pressures of the environment, such as predation, diet, and microhabitat (Vitt and Congdon 1978; Meiri 2010; Feldman and Meiri 2013).

In both populations of *A. nebulosus*, the allometric relationships of HL and HW, along with anatomical structures that provide agility, such as FL and TL, were negative, which could indicate that in both populations, individuals exhibit limited movement, primarily reduced to foraging, or escape from predators. This suggests that *A. nebulosus* is highly sedentary, a strategy that favors optimal energy expenditure, unlike in other groups such as whiptail lizards, which have large claws, sturdy limbs, and a long tail to escape in an agile way from their predators (Aguilar-Moreno et al. 2010). Studies of species in the genus *Anolis* have documented that microhabitat use and/ or perch types (e.g., shrubs, brush, trunk-ground, trunk-rock, branches, and large rocks) are correlated with different ectomorphs that vary in body size, length of fingers, claws, and number of digital lamellae (Butler and Losos 2002). It has also been proposed that selection of microhabitats by lizards is associated with different types of allometric growth of the locomotory morphometric structures; which could explain differences in *A. nebulosus* populations from the island and mainland (Vitt and Cooper 1985).

On the other hand, in females of some species of *Anolis*, the relationships between SVL and PGL may have a stable (stable = positive) allometric pattern (Michaud and Echternacht 1995; Butler and Losos 2002); for example, in *A. nebulosus*, this morphometric characteristic (PGL) revealed a high allometric growth rate in relation to body size. In some species of *Anolis*, the pelvic girdle is positively correlated with egg size or volume and with the quantity and quality of food resources in the environment (Michaud and Echternacht 1995). For example, in *A. carolinensis*, there is a positive allometric relationship between SVL and aperture of the pelvic girdle; in other words, at greater SVL, there is a greater amplitude of the pelvic girdle. In the northernmost populations, the environment is subject to relatively low temperatures for extended periods of time; such populations have relatively large SVL, perhaps to allow for more storage of energy as fat bodies to help survive harsh winters (see Michaud and Echternacht 1995).

In *A. lineattissima*, most coefficients of allometry were positive for HW, FOL, AL, and TL, which could indicate that the anterior and posterior limbs are physiologically and/or ecologically more functional than those of *A. nebulosus*, enabling greater speed to escape successfully from predators and also to better explore the litter layer and ground during foraging, a behavior that has been observed in most whiptail lizards (Aguilar-Moreno et al. 2010; Mata-Silva et al. 2013). On the other hand, a positive allometric relationship in HW with respect to SVL in males from both populations could be related to sexual dimorphism (Aguilar-Moreno et al. 2010). Males exhibited larger heads and jaws than females, which could be explained by male-male combat and/or divergence in prey selection (e.g., males and females may specialize on prey of different sizes).

Sexual dimorphism

According to Andrews (1979), sexual dimorphism in lizard species inhabiting islands is more common and conspicuous than in lizard species from mainland habitats. This asymmetry has been called 'ecological relaxation' and has been associated with the decreased interspecific competition and low intensity of predation characteristic of islands (Stone et al. 2003). Ecological relaxation has been observed in some lizard species of the genus *Anolis* and *Microlophus* inhabiting in some islands of the Greater Antilles and the Galapagos; in these species, males are larger than females (Butler and Losos 2002; Stone et al. 2003). In this study, we found that males of *A. nebulosus* and *A. lineattissima*, from SPI and CI, respectively, were larger than conspecific females in all morphometric variables measured (Table 5). In contrast, males of *A. lineattissima* from the mainland were larger than females only in HL, HW, FOL, and TL. We observed sexual dimorphism just in HL for *A. nebulosus* from the mainland.

Sexual dimorphism of species from the island and mainland could be explained under the assumption that if resources (e.g., space and food) are limited and male populations are locally dense, then there may be intrasexual competition; lizards of large body sizes are better competitors for these resources. The hypothesis of niche divergence (Schoener 1967; Hierlihy et al. 2013) suggests that a degree of overlap in diet between males and females results in a strong competition for food; thus, a divergence in eating habits may be indicative of sexual dimorphism (Ramírez-Bautista and Pavón 2009; Aguilar-Moreno et al. 2010; Hierlihy et al. 2013). In addition, if the sex ratio is skewed toward males, then agonistic interactions between males for access to females during reproductive season should be intense; thus, sexual dimorphism would be explained by sexual selection (Hierlihy et al. 2013). Consequently, a large body size and head are

morphometric attributes that could generate higher fitness in males, a pattern observed in gonochoristic *Aspidoscelis* species and in most species of *Anolis* from island and mainland populations (Anderson and Vitt 1990; Losos et al. 2003; Aguilar-Moreno et al. 2010). Finally, if body size at sexual maturity is larger in males than in females, then males should have a higher growth rate and are faster to defend territory and reproduce successfully, which would explain why males of *A. nebulosus* and *A. lineattissima* from islands are larger and have higher growth rates than males and females from mainland populations (Andrews 1976).

The absence of sexual dimorphism in *A. nebulosus* from mainland populations could be due to food resources are sufficiently abundant in the environment that competition is limited. This pattern has been observed in other species of *Anolis* from the Greater Antilles (Losos et al. 2003) and in species of the genus *Sceloporus* (from Central Mexico; Ramírez-Bautista and Pavón 2009; Ramírez-Bautista et al. 2013).

In general, lizards from insular environments are larger than lizards from conspecific mainland populations. However, we still need to evaluate the role of other factors in generating differences between island and mainland populations, such as distance between islands and mainland populations, variation in reproductive characteristics, and differences in feeding habits among populations.

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