

## MULTIVARIATE PHENOTYPIC EVOLUTION AMONG ISLAND AND MAINLAND POPULATIONS OF THE ORNATE DAY GECKO, *PHELSUMA ORNATA*

LUKE J. HARMON<sup>1,3</sup> AND RICHARD GIBSON<sup>2,4</sup>

<sup>1</sup>Department of Biology, Washington University, St. Louis, Missouri 63130

<sup>2</sup>Mauritian Wildlife Foundation, Grannum Road, Vacoas, Mauritius

**Abstract.**—Interpopulation variation in morphology, such as that among small island populations, plays a key role in speciation and diversification. There are two approaches to investigating evolution of morphological characters: comparing patterns of trait variances and covariances within and among populations, and testing particular adaptive scenarios. Here, we combine both approaches to infer the role of natural selection in shaping morphological variation in body size, head color pattern, and body shape among 10 populations of a day gecko, *Phelsuma ornata*, and its close relative, *P. inexpectata*, in the Mascarene Islands. We find that local populations are morphologically distinct, and that natural selection has likely influenced phenotypic diversification in the group. Lizards on small outer islands tend to be larger than lizards on the mainland of Mauritius. For body shape and head color pattern, comparisons of variation within and among populations reveal that differences among populations for some variables are too great to be explained by neutral processes alone, although we cannot identify the causal agents for this selection. These results reveal that the forces shaping different sets of organismal traits may be distinct, such that a variety of statistical approaches are needed to investigate selection in natural populations.

**Key words.**—Genetic drift, islands, morphometrics, phenotypic variance-covariance matrix, selection.

Received June 16, 2006. Accepted September 12, 2006.

Organisms on islands frequently exhibit unique features compared to their mainland relatives (see Grant 1998a and references therein). Previous research has suggested both adaptive and nonadaptive explanations for the evolution of these differences (Barton 1996). Island species may adaptively evolve different traits as a response to the unique habitats and simplified community structure of islands (Schluter 1988). For example, because island ecosystems generally contain fewer species than those on the mainland (MacArthur and Wilson 1967), island species might encounter reduced levels of interspecific competition and/or predation (Carlquist 1965; MacArthur and Wilson 1967). Alternatively, small population sizes and founder effects associated with island invasion may lead to genetic drift, such that island forms evolve new traits that are selectively neutral (Mayr 1954). Moreover, these two processes are not independent; for example, genetic drift can move a population off a local adaptive peak, allowing selection to shift the population to a different peak in the adaptive landscape (Simpson 1944). By providing circumstances that potentially accelerate adaptation and genetic drift, small island systems offer unique opportunities to investigate microevolutionary patterns.

To investigate the adaptive forces shaping phenotypic variation among populations, one must first reject the null hypothesis that traits are evolving solely by genetic drift. For morphological characters, this null hypothesis has traditionally been tested in the context of particular adaptive scenarios. For example, comparative statistical methods can be used to test for trait-environment correlations resulting from adaptive evolution (Wainwright and Reilly 1994). Additionally, adaptation can be inferred in cases where organisms repeat-

edly evolve similar responses when confronted with the same environment (Diamond 1991; Losos et al. 1998; Gillespie 2004). In cases where no adaptive hypotheses are supported, it is tempting to accept the null hypothesis of evolution by genetic drift (e.g., Bostwick and Brady 2002); however, for many sets of traits, forces affecting diversification are not known a priori. Negative results from such studies are inconclusive, as an argument can always be made for the importance of unmeasured forces influencing diversification.

This limitation can be overcome by using tests for the presence of natural selection that do not depend on any particular adaptive hypothesis. For example, for DNA sequence data, a number of tests compare patterns of variation to infer selection on particular genes (e.g., King and Jukes 1969; Hudson et al. 1987; Fu and Li 1993). A common test is to compare variation at nucleotide sites within and among populations; for a given level of within-population variance, sites under diversifying selection are expected to vary more among populations than neutral loci (Hudson et al. 1987). These tests provide a more convincing test for selection in cases where little is known about the particular ecological forces driving selection.

Ackermann and Cheverud (2002) recently outlined a test for selection on morphological traits that, like the molecular tests described above, can reject drift even in the absence of particular adaptive hypotheses for a group of traits. Under genetic drift, the genetic variances and covariances of traits among populations will be proportional to those within populations (Lande 1979). If the relative patterning of trait variance and covariance among populations differ significantly from patterns within populations, then genetic drift can be rejected (Ackermann and Cheverud 2002). Since obtaining genetic variances and covariances of traits (as expressed in the **G**-matrix) is very difficult for wild populations (but see Bégin and Roff 2003; Cano et al. 2004), Ackermann and Cheverud (2002) advocate using within- and between-population phenotypic variances and covariance (**P**) matrices (see

<sup>3</sup> Present address: Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada; E-mail: harmon@zoology.ubc.ca.

<sup>4</sup> Present address: Zoological Society of London, Regent's Park, London NW1 4RY, United Kingdom.

also Marroig and Cheverud 2004). This matrix is often very similar to the **G**-matrix (Cheverud 1988, 1996; Roff 1995, 1997; Koots and Gibson 1996; Arnold and Phillips 1999; Stepan et al. 2002). Since the phenotypic variance-covariance matrix (**P**-matrix) is a combination of both genetic and environmental effects, this method assumes that the shape of the **P**-matrix is not differentially influenced within and among populations by environmental effects, such as phenotypic plasticity, maternal effects, and other nongenetic factors (Stepan 1997; Ackermann and Cheverud 2002; Marroig and Cheverud 2004). We explore the implications of using **P**-matrices as surrogates for **G**-matrices in the discussion.

Additionally, even under selection, differences among populations can be strongly influenced by genetic covariances, such that populations evolving along “genetic lines of least resistance” will show the same patterns as expected under drift (Schluter 1996). This means that a lack of significance in this test is not necessarily evidence that characters are evolving neutrally. Still, this test provides a potentially powerful method for rejecting the null hypothesis of genetic drift in situations where the potential forces driving adaptation cannot be identified.

Thus, there are two ways to statistically reject genetic drift: comparing patterns of trait variance to those expected under drift and testing particular adaptive scenarios. In this study, we use both approaches to investigate the patterns of trait variation among populations of the ornate day gecko (*Phelsuma ornata*) and its close relative, the Manapany day gecko (*P. inexpectata*), in the Mascarene Islands. Day geckos are small, brightly colored, mainly arboreal lizards that survive on a diet of insects along with pollen and nectar (Vinson and Vinson 1969; NyHagen et al. 2001; Hansen et al. 2006). *Phelsuma ornata* lives only on mainland Mauritius and surrounding satellite islands. It is most common in coastal regions and is particularly abundant in more xeric habitats (Vinson 1976). A closely related species, *P. inexpectata*, occupies a very small area along the southwest coast of the nearby island of Réunion (Mertens 1970) and resembles *P. ornata* in both morphology and habitat use. Austin et al. (2004) showed that *P. ornata* and *P. inexpectata* are genetically distinct sister taxa.

Previous studies of *Phelsuma* have shown substantial morphological variation among island populations (Gardner 1986; Radtkey 1996). In this study, we test hypotheses about the processes generating such variation. We first attempt to reject the influence of genetic drift by comparing patterns of phenotypic variances and covariances within and among populations (Ackermann and Cheverud 2002). We also test two particular adaptive hypotheses: (1) variation in morphological traits will be correlated with measured aspects of lizard habitat use, and (2) geographic variation in morphology will be due to local adaptation to different community types. By combining the results of these analyses, we hope to maximize power to identify traits under selection in these lizards.

## MATERIALS AND METHODS

### Study Area

We collected data on morphology and habitat use of *P. ornata* at nine sites on Mauritius and nearby islands (Fig. 1).

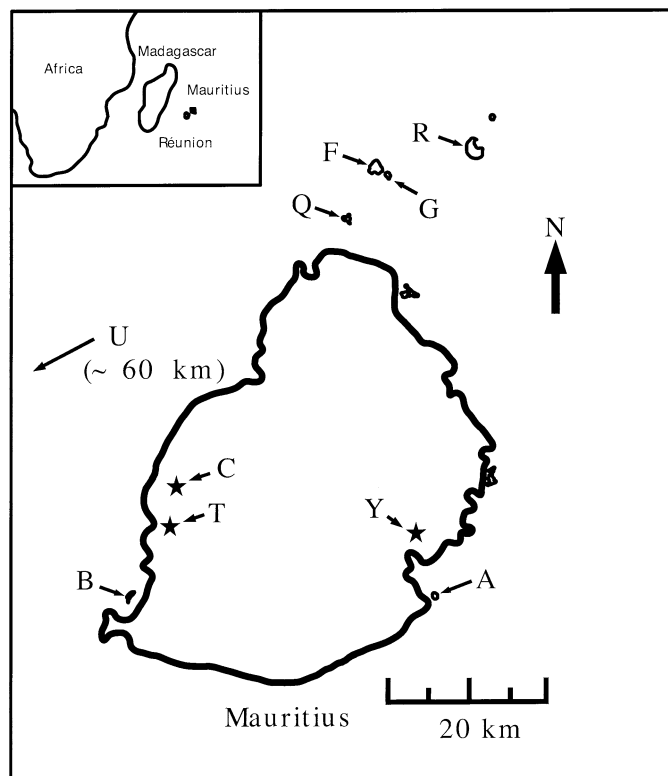


FIG. 1. Map of sampling localities for *Phelsuma ornata* and *P. inexpectata* included in this study. Abbreviations: R, Round Island; F, Flat Island; G, Ilôt Gabrielle; Q, Gunner's Quoin; B, Ile Aux Bénitiers; A, Ile Aux Aigrettes; C, Casela Bird Park; T, Tamarin Mountain; Y, Ylang-Ylang Estate; U, Réunion.

Six of these sites were small islands off the coast of Mauritius: Round Island (R), Flat Island (F), Ilôt Gabrielle (G), Gunner's Quoin (Q), Ile aux Bénitiers (B), and Ile aux Aigrettes (A). We also included three sites on mainland Mauritius: Tamarin Mountain (T) and Casela Bird Park (C) on the west coast, and Ylang-Ylang Estate (Y) in the east. We collected data on the closely related species *P. inexpectata* at Grand Anse, Réunion, France (U), an island about the same size as Mauritius located 60 km to the southwest. This species, formerly considered a subspecies, shares a recent common ancestor with Mauritian *P. ornata* and is very similar genetically, ecologically, and morphologically (Austin et al. 2004). Sample sizes for all localities, listed in the Appendix (available online only at <http://dx.doi.org/10.1554/06-37.1.s1>), averaged 17 for morphological measurements (range: 5–24) and 42 for habitat use (range: 18–66).

Habitat differed somewhat among localities included in the study. The small outer island habitats (F, G, Q, A, B, R) were generally more open than the mainland habitats. Also, the small island populations tend to have fewer total lizard species than the mainland populations (Arnold 2000). Sites also differed in *Phelsuma* community composition, with *P. ornata* and *P. inexpectata* the only species of day gecko at five outer island localities (F, G, Q, T, A) and Réunion, occurring in sympatry with *P. cepediana* at two localities (B, Y), with *P. cepediana* and *P. guimbeaui* at one locality (C), and with *P. guentheri* at one locality (R). Introduced agamid

(*Calotes versicolor*) are present in every locality except the northern islands (Q, F, G, and R), and introduced house geckos (*Hemidactylus frenatus*) are present at every locality except for two (R and Q).

#### Data Collection

At each site, we walked through suitable habitat searching for adult *P. ornata* or *P. inexpectata*. When an individual was located, we collected the following microhabitat data: perch height (measured or estimated to the nearest 0.5 m), perch diameter (to the nearest 1 cm), percent canopy cover (visual estimate), perch type (ground, rock, shrub, or tree), and, if the lizard was on a plant, whether it was a palm or a nonpalm species. There are several nonpalm plants in Mauritius that have palmlike features relevant to gecko survival, mainly the presence of smooth fronds with narrow, water-containing crevices; these plants (*Ravenala*, *Pandanus*, and *Lomatophyllum*) were included in the “palm” category for the purposes of this study. When lizards were on a tree, the DBH (diameter at breast height) of the tree was measured with a measuring tape, and trees were placed into one of four categories based on their DBH (<10 cm, 10–20 cm, 20–30 cm, >30 cm). The substrate that the lizard was perched on was also noted (bark, palm frond, leaf, rock, fruit, or burlaplike coconut husk) and categorized as “smooth” or “rough” (rough: significant visible texture present, otherwise smooth; all categorizations made by L. J. Harmon). To avoid pseudoreplication of individual lizards, each area in a particular site was only searched for lizards in this way once. Data were only collected when the weather was sunny or partly cloudy (i.e., the sun was out at least 50% of the time).

We opportunistically caught adult lizards in each population using a dental floss noose. We measured only adult males, as determined by the presence of distinct femoral pores and hemipenial bulges. Using a ruler, we took the following morphological measurements to the nearest 0.5 mm: snout-vent length (SVL), head length (HL: distance from ear hole to tip of snout), head width at eyes (Heyes), head width at ears (Hears), head height at eyes (HH), interlimb distance (IL: distance from the posterior of the insertion of the front limb to the anterior of the insertion of the hind limb), pelvis width (PW), humerus length (F1: distance from shoulder to apex of elbow), antibrachium length (F2: distance from elbow apex to center of wrist), forefoot length (F3: distance from center of wrist to tip of longest toe [IV]), femur length (H1: distance from insertion of hind leg at pelvis to apex of knee), crus length (H2: distance from apex of knee to heel), and hind foot length (H3: distance from heel to tip of longest toe [IV]).

To quantify variation in head color pattern and shape, we took photographs of each of these measured lizards’ heads from above using a Nikon CoolPix 995 digital camera (Nikon USA, Melville, NY). A ruler was included in each photo to provide scale. We attempted to take all photographs with the same alignment from directly above the lizard’s head. We then used tpsDig version 1.40 (Rohlf 2004) to obtain two-dimensional coordinates for seven landmarks on the head of each lizard. Four of these landmarks were repeated on the right and left side of each head, and three were along the

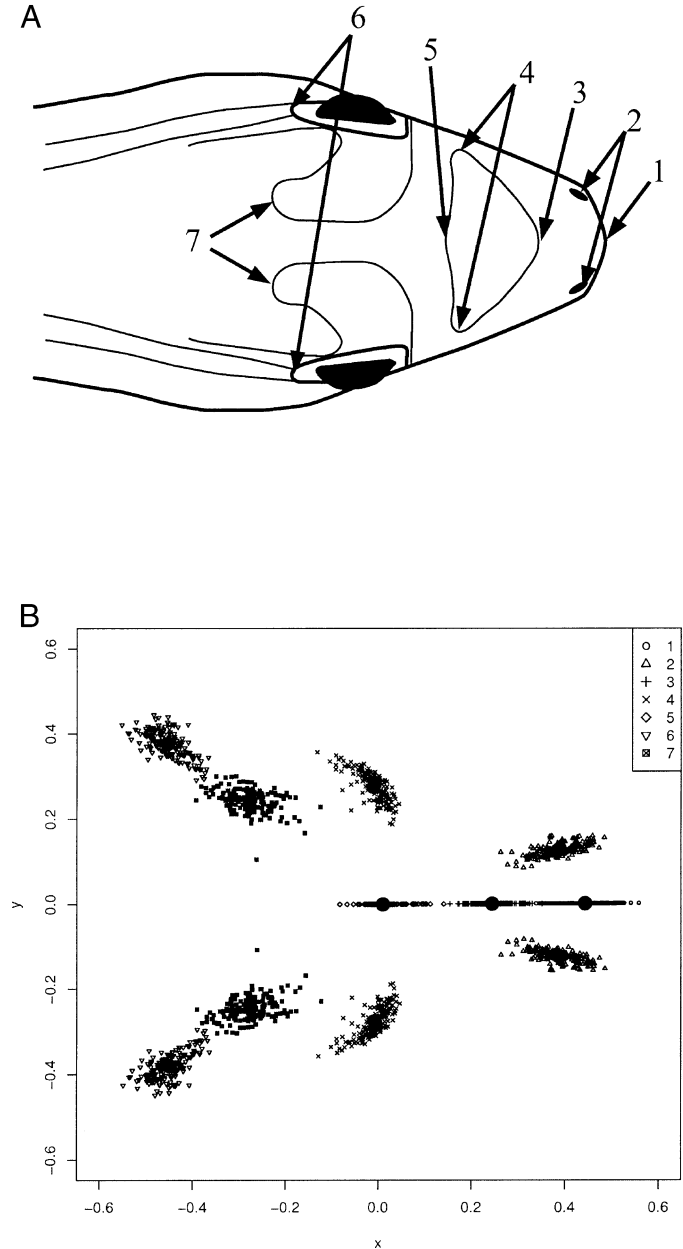


FIG. 2. (A) Landmarks on the head of *Phelsuma ornata*. Locations of landmark points are described in the text. (B) Aligned coordinates for all lizards included in this study. Individual landmark points are denoted by distinct symbols and the overall mean head color pattern is indicated with large filled black circles.

midline, for a total of 11 landmarks per photo. Landmarks were defined at the following points (Fig. 2): (1) anterior tip of snout; (2) point along outline of head corresponding to center of nostril; (3) anteriormost, (4) distal, and (5) posteriormost points of green pigment patch on front of snout; (6) point where dorsal edge of white/gray supraciliary stripe meets eye; and (7) center of posterior end of red supraorbital stripe. Scale information was used to obtain coordinates in mm, identical to the units of all other morphological measurements we used. We removed asymmetry by averaging landmarks from the right and left sides of each specimen

(Klingenberg et al. 2002). We did this by superimposing each specimen with its reflection across the x-y plane using generalized Procrustes analysis (Gower 1975) with no rescaling, and finding the mean of these two shapes. For this procedure, the four landmarks on each side of the head (2, 4, 6, and 7) were matched with the corresponding reflected landmark from the other side of the head, and the three landmarks along the midline (1, 3, and 5) were matched with themselves. We then superimposed the resulting coordinates for all individuals using generalized Procrustes analysis (Gower 1975), again with no rescaling, and rotated all resulting coordinates so that the three midline points were along the x-axis. We then deleted all redundant coordinates (2, 4, 6, and 7 on the right side of the head, and the y-coordinate of landmarks 1, 3, and 5). We treated the remaining 11 coordinates as variables in all analyses.

To investigate the error involved in these geometric morphometric measurements, we took two photos of the heads of each of 14 lizards, repositioning the lizard independently each time. We then generated the 11 two-dimensional coordinates, as above, twice independently for each photo, for a total of four sets of coordinates per individual lizard. We used these data to calculate the repeatability of each coordinate for the two different photos with a nested analysis of variance (ANOVA), with lizard ID and photograph nested within ID as effects. Repeatability was calculated as the sum of squares for the lizard ID effect divided by the total sum of squares. Because measurement error was small (see Results), we used one set of coordinates from a single photograph for each lizard in all further head color pattern analyses.

#### Analyses

Since populations within a species share both historical and demographic connections, they may not be statistically independent. Previous genetic data (Austin et al. 2004) showed substantial genetic variation among populations of *P. ornata* in Mauritius, with distinct phylogeographic structure among both island and mainland localities. A reanalysis of these data shows that the population structure among localities for this species fits an isolation-by-distance model; average genetic dissimilarity between sites is highly correlated with geographic distance ( $r = 0.97$ ; see online Appendix) but not related to island versus mainland comparisons (see online Appendix). This may reflect the fact that small offshore islands in Mauritius were likely connected to the main part of the island during the Pleistocene (Vinson and Vinson 1969). Since populations that are closer together geographically tend to be more genetically similar, we conducted all analyses controlling for geographic distance wherever possible.

We compared all pairs of within-population phenotypic correlation matrices using Mantel tests with 9999 permutations (Manly 1991). We then generated principal component (PC) axes from the pooled within-locality variance-covariance matrix and projected all the data into this new PC space.

We tested for differences among localities in morphology and habitat use using multivariate analysis of variance (MANOVA). For morphology, we used the PC axes described above. Since we included lizards of varying sizes, we re-

peated the above axis excluding PC1, an index of body size (see below). Perch height and percent canopy were  $\ln(x + 1)$  transformed, whereas perch diameter was log-transformed. For the MANOVA, we visualized any differences among populations by plotting locality means for the first two canonical variates. We used post-hoc analyses of variance (ANOVAs) for each variable to identify all variables that differed between localities.

To test for differences in each of the categorical habitat use variables among localities we used a chi-squared test with significance determined by permutations. We permuted the data so that individuals were randomly assigned to localities and used these permuted datasets to construct a null distribution of the chi-squared statistic. We generated this distribution from 9999 permutations. We also carried out a multiple correspondence analysis of all discrete ecological variables to create a four-dimensional continuous ecological data space. We assessed differences among localities in this space using MANOVA, and visualized differences by plotting means of the first two canonical variates for each locality. All of the above analyses were repeated excluding *P. inexpectata* to investigate variation among Mauritian populations of *P. ornata*.

We attempted to reject the null hypothesis of genetic drift by comparing variance and correlation of principal axes of morphological variation within and among populations (Ackermann and Cheverud 2002). We calculated the variance within and among populations along each PC axis described above, and then regressed these log-transformed variances against the log-transformed eigenvalues of the pooled within-population variance covariance matrix. Under genetic drift, the slope of the regression of these variances will be one; slopes greater than one indicate that the first few PC axes are more variable among populations than would be expected under drift (Ackermann and Cheverud 2002; Marroig and Cheverud 2004). We also calculated the population means for these PC axes. We then tested for significant correlations among population means for only the first nine of these PC axes (one less than the number of localities; Marroig and Cheverud 2004) using Bartlett's test of sphericity and tested for correlations among all possible pairs of these nine axes after correcting for multiple comparisons. Because these axes are, by definition, independent within populations, correlations among populations reflect the influence of correlational selection.

We then tested adaptive hypotheses for morphological evolution in these geckos using Mantel tests with 9999 permutations of pairwise difference matrices among all localities (Manly 1991). To create these difference matrices for both morphology and habitat use, we found the centroid for each locality in the PC space. Each entry in these matrices represents the Euclidean distance between a pair of localities in each data space. For morphology, since we retained all PC axes extracted from the pooled within-locality variance-covariance matrix, distances between locality means were identical whether these PC axes or the original variables were used. We created a Mauritian island-mainland matrix by assigning each locality to either of these two categories (small island: GQ, FI, GAB, RI, IAA, IAB; mainland: CAS, TAM, YY; RUN was excluded because it has a large potential area



but is separated from the population of *P. ornata* in Mauritius). For this variable, the difference matrix contained a “0” if both localities were in the same category, and a “1” otherwise. Finally, we created a community difference matrix by calculating the difference in the number of sympatric *Phelsuma* species between each pair of localities (as noted above). For all of these tests, we controlled for genetic similarity among geographically proximate populations using three-way Mantel tests controlling for geographic distances among localities (Thorpe 2002) calculated using a map of Mauritius (IGN 2001).

First, we tested for a relationship between morphology and habitat use by comparing the morphological difference matrix with the habitat use difference matrix using Mantel tests. We also carried out pairwise regressions to test for correlations between individual pairs of morphological and habitat use variables. Secondly, we tested for convergent or parallel evolution in similar habitats by correlating each morphological data difference matrix with the island-mainland matrix described above, as well as with a community matrix describing the difference in the number of sympatric *Phelsuma* species present. All statistical tests were carried out using R statistical software (R Development Core Team 2005); code is available from L. J. Harmon.

## RESULTS

### *Differences among Localities*

Repeatabilities for head color pattern coordinates taken from individual lizards photographed twice were generally higher than 0.9 (range: 0.84–0.99, average 0.94). Furthermore, partial warp axes with the lowest repeatabilities also tended to have smaller total sums of squares, that is, smaller variance among individuals (results not presented). Error associated with different photos of the same individual was generally small compared to differences among individuals (average: 4.6% of total variance). Thus, we used coordinates taken from a single photo of each individual for all remaining analyses. These coordinates revealed substantial variation in head size, shape, and color pattern arrangement among individuals (Fig. 2B).

All pairs of within-population correlation matrices were significantly correlated (all  $P < 0.05$ , mean  $r = 0.70$ ; see online Appendix). Thus, we extracted 24 principal component (PC) axes from the pooled within-locality variance-covariance matrix (first two axes depicted for body measurements in Table 1 and for head coordinates in Fig. 3; see online Appendix for full details). These axes were, for the most part, statistically independent within each individual population as well; of the  $(24 \times 23 \times 10)/2 = 2760$  possible within-population comparisons of pairs of PC axes, only 128 (4.6%) were significantly correlated at  $\alpha = 0.05$ .

Male lizards differed significantly in morphology among sites (Wilks'  $\lambda = 0.001$ ,  $df = 216$ , 1195.7,  $P < 0.0001$ ; Fig. 4A). The first two canonical axes derived from the MANOVA, which together explain 80% of the total variance in body shape, mainly describe changes in relative limb length (Table 1) and head color pattern (Fig. 3; other canonical axes described in the online Appendix). Univariate ANOVAs showed significant differences among localities in all 24 PC

TABLE 1. Correlations of first two principal component (PC) and canonical axes with body shape axes, along with the percentage of original variance explained (PC axes) and the proportion of the trace of the covariance matrix (canonical axes). See text for variable abbreviations.

Variable	PC1	PC2	Canonical 1	Canonical 2
SVL	-0.99	0.20	0.19	0.36
HL	-0.91	0.20	0.22	0.56
Heyes	-0.74	0.14	0.35	0.22
Hears	-0.84	0.10	0.13	0.47
HH	-0.70	0.07	0.05	0.62
IL	-0.84	-0.50	0.05	0.43
PW	-0.77	0.13	0.18	0.36
F1	-0.61	-0.03	0.29	0.47
F2	-0.59	0.22	0.20	0.26
F3	-0.64	-0.13	0.17	0.43
H1	-0.72	0.24	0.33	0.32
H2	-0.81	0.08	0.30	0.51
H3	-0.79	0.10	0.11	0.39
% variance	99.0	0.9	34.7	22.4

axes (Table 2). Many of these comparisons involved *P. inexpectata*, which is quite different from every population of *P. ornata* (Fig. 4). However, qualitatively similar results were obtained when *P. inexpectata* from Réunion were excluded from the analysis (Table 2). When PC1 (body size) was excluded from the analysis, lizard morphology still differed among populations (Wilks'  $\lambda = 0.002$ ,  $df = 207$ , 1197.7,  $P < 0.0001$ ; Fig. 4B).

Lizards differed in habitat use among localities (Wilks'  $\lambda = 0.35$ ,  $df = 27$ , 1151.3,  $P < 0.0001$ ; Fig. 4C). The first canonical axis, which described 87.5% of the variation, contrasts lizards living on low, open perches versus those on high perches with substantial canopy cover (correlations with original axes: perch height  $r = -0.76$ , perch diameter  $r = 0.63$ , percent canopy  $r = -0.85$ ; for details of other canonical axes, see online Appendix). The most divergent site in terms of habitat use was Gunner's Quoin, where the lizards perched on the ground a large proportion of the time. Correspondence analyses of categorical habitat use variables resulted in four axes that explained 52.6% of the total variance and differed significantly among localities (Wilks'  $\lambda = 0.23$ ,  $df = 36$ , 1527,  $P < 0.0001$ ). Individual ANOVAs and chi-squared tests showed significant differences in all habitat use categories among sites (perch height:  $F_{9,396} = 23.9$ ,  $P < 0.001$ ; perch diameter:  $F_{9,396} = 19.7$ ,  $P < 0.001$ ; percent canopy:  $F_{9,396} = 34.9$ ,  $P < 0.001$ ; vegetation type  $\chi^2 = 331.0$ ,  $P < 0.001$ ; palm vs. nonpalm  $\chi^2 = 196.4$ ,  $P < 0.001$ ; DBH category  $\chi^2_{30} = 70.3$ ,  $P < 0.001$ ; substrate  $\chi^2_{60} = 456.8$ ,  $P < 0.001$ ; substrate texture  $\chi^2_{10} = 66.2$ ,  $P < 0.001$ ; tree location  $\chi^2_{50} = 555.6$ ,  $P < 0.001$ ).

### *Hypothesis Tests*

The regression slope of log-transformed PC variances within and among populations was significantly greater than one (slope  $\pm$  SE:  $1.09 \pm 0.05$ ;  $p_{\text{slope} \neq 1} = 0.07$ ; PC1 excluded, slope  $\pm$  SE:  $1.10 \pm 0.05$ ;  $p_{\text{slope} \neq 1} = 0.05$ ; Fig. 5), with several axes occurring outside the confidence limits for the regression (high among-population variance: PC axes 6, 7, 15, 17, 19; low among-population variance: PC axes 2, 8, 9, 11, 12, 13, 22; Fig. 5). Bartlett's test rejected the null hypothesis of no cor-

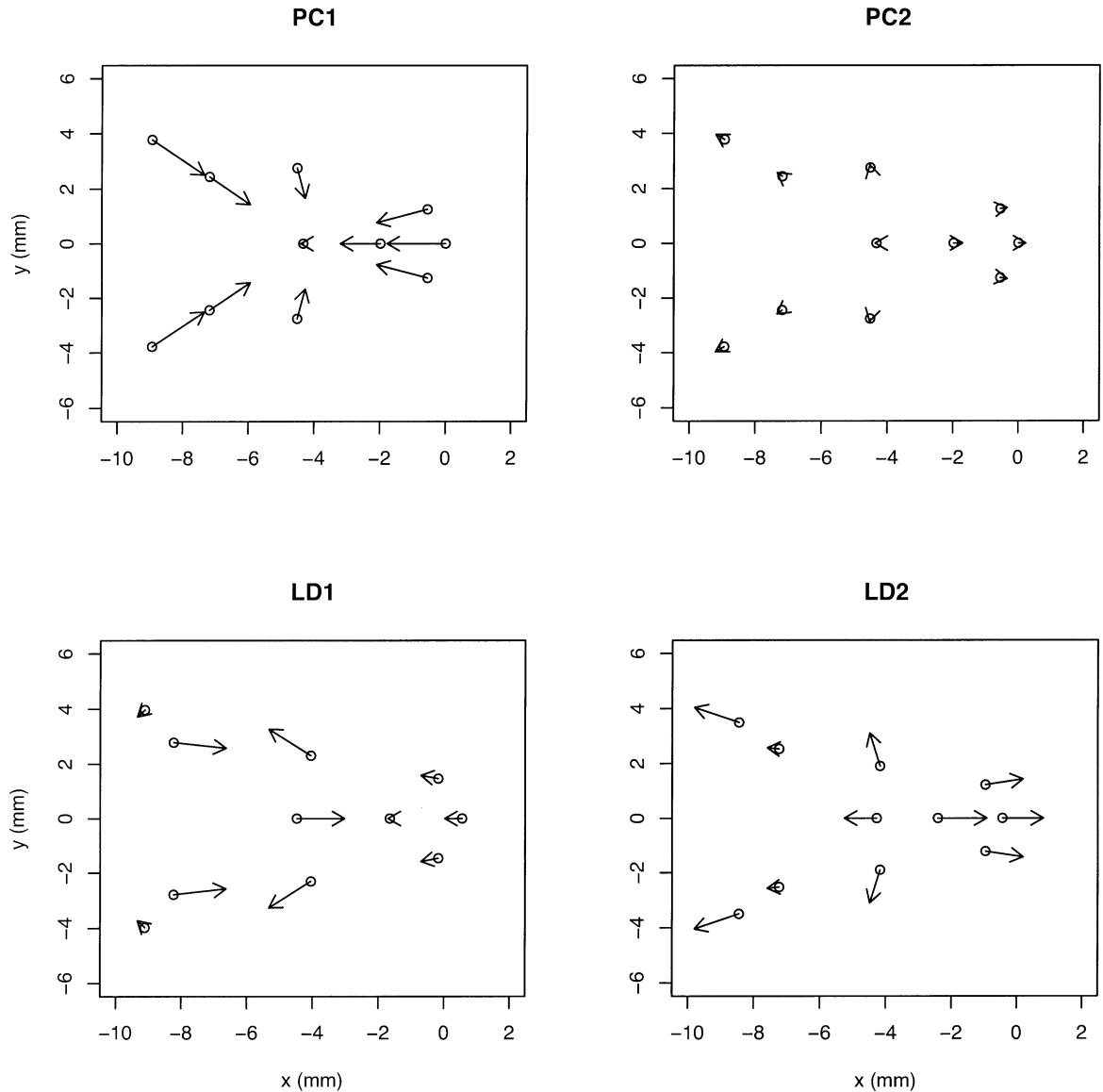


FIG. 3. Head color pattern deformations represented by the first two principal component (PC) axes and the first two canonical axes. For the PC axes, deformations represent an increase of six standard deviations in the positive direction along each PC axis from the mean head color pattern. For the canonical axes, deformations represent change from the head with the smallest value on that canonical axis to that with the largest.

relations among the first nine PC axes ( $\chi^2 = 55.4$ ,  $df = 36$ ,  $P = 0.02$ ). Two pairs of within-population PC axes were significantly correlated among population means, but neither of these correlations was significant after Bonferroni correction (see online Appendix). These results were qualitatively similar when each original measurement variable was rescaled to unit variance before all analyses (slope  $\pm$  SE:  $1.13 \pm 0.05$ ;  $p_{\text{slope} \neq 1} = 0.03$ ; PC1 excluded, slope  $\pm$  SE:  $1.13 \pm 0.06$ ;  $p_{\text{slope} \neq 1} = 0.04$ ; Bartlett  $\chi^2 = 57.9$ ,  $df = 36$ ,  $p = 0.01$ ; two pairs of axes correlated among populations, one pair significant after Bonferroni correction; see online Appendix, Fig. 5).

We found a strong correlation between differences in continuous and categorical habitat use variables among sites (Mantel test,  $r_M = 0.82$ ,  $p = 0.02$ ), indicating that these two datasets varied similarly among sites. Thus, only the distance matrix

based on continuous habitat variables was used in the remainder of analyses; results of analyses using the habitat distance matrix based on categorical variables were similar (results not presented). When the population in Réunion was excluded, morphological differences among pairs of sites were correlated with the geographic distance separating them (Réunion included  $r_M = -0.01$ ,  $P = 0.4$ ; excluded  $r_M = 0.50$ ,  $P = 0.02$ ). These correlations were qualitatively unchanged when PC1 (body size) was excluded (Réunion included  $r_M = 0.3$ ,  $P = 0.2$ ; excluded  $r_M = 0.2$ ,  $P = 0.05$ ). Habitat use differences were not correlated with geographic distance (Réunion included  $r_M = -0.2$ ,  $P = 0.9$ ; excluded  $r_M = -0.1$ ,  $P = 0.9$ ).

Differences in morphological traits among sites were not correlated with measured aspects of habitat use ( $r_M = -0.09$ ,  $P = 0.2$ ; size removed  $r_M = -0.15$ ,  $P = 0.6$ ). These results

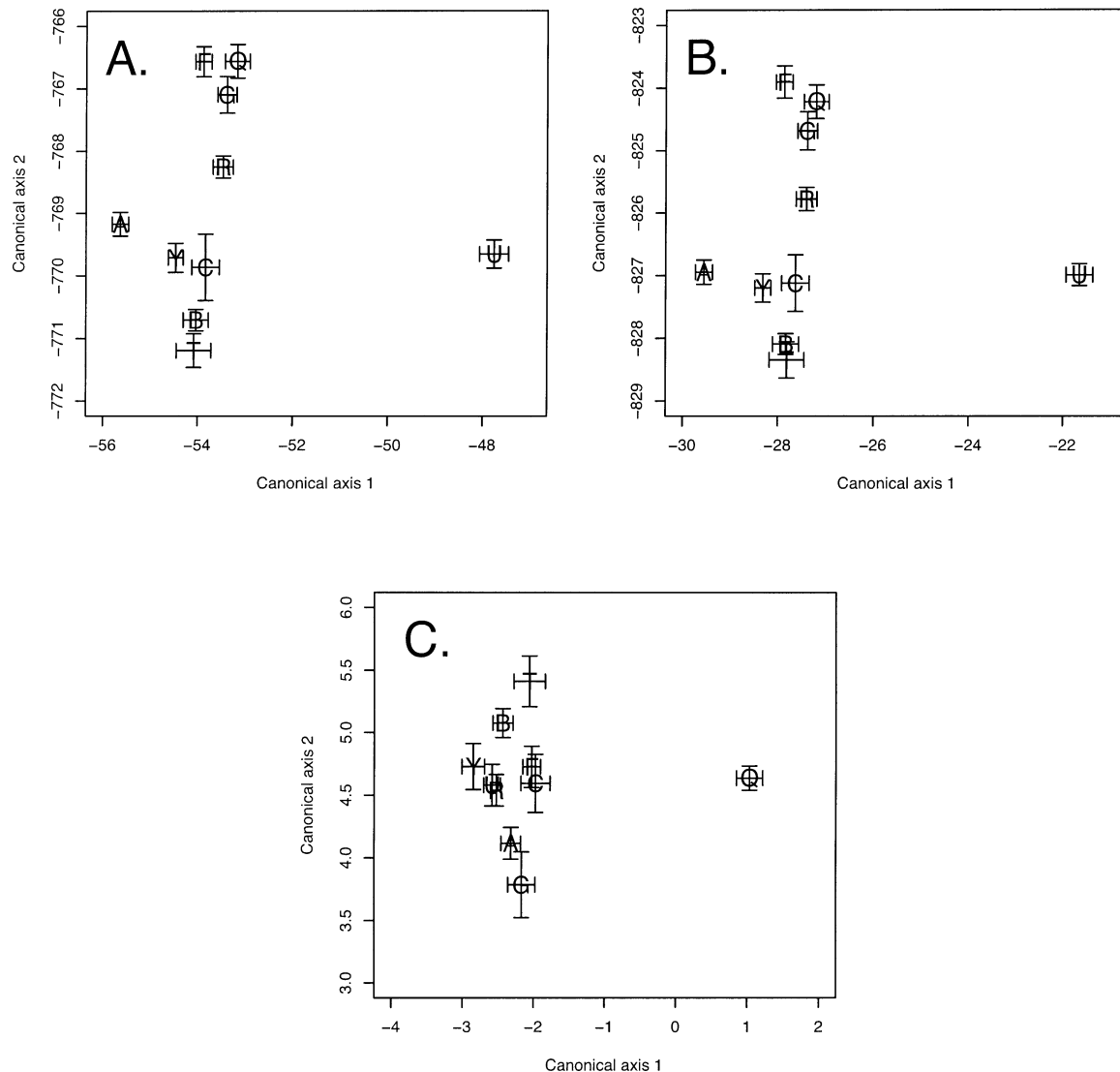


FIG. 4. Canonical axes 1 and 2 from MANOVA on locality. Locality means are indicated by the placement of letters (see text for locality abbreviations), and error bars represent  $\pm 1$  SE. (A) Morphology with body size (PC1) included; (B) morphology with body size excluded; (C) microhabitat use.

were qualitatively unchanged when controlling for geographic distance among sites ( $r_M = 0.09$ ,  $P = 0.2$ ; size removed  $r_M = -0.1$ ,  $P = 0.5$ ) or excluding the population from Réunion (all Mantel tests nonsignificant; results not presented). Only four of 192 possible pairs of morphological PC axes and habitat use were significantly correlated (PC2 vs. % palm trees, PC17 vs. % trunk, and PC19 vs. perch height and % canopy); none were significant after correcting for multiple comparisons (see online Appendix).

There were significant differences among mainland and small island localities in morphology, but not body shape or habitat use (Table 3). Lizards on small outer islands were, on average, larger than lizards on mainland Mauritius (SVL, mean  $\pm$  SD: mainland  $50.7 \pm 4.3$  mm, island  $54.3 \pm 3.2$  mm). Furthermore, lizard morphology was weakly, but not significantly, related to the number of other *Phelsuma* species present in the community; body shape and habitat use were not related to community composition (Table 3).

## DISCUSSION

### *Genetic and Morphological Differences among Populations*

Significant variation among small-island populations may be a general feature of isolated or semi-isolated island populations (e.g., Scott et al. 2003; Wilder and Hollocher 2003). These small peripheral populations likely play a role in speciation (Grant 1998b). Investigating the causal factors influencing interisland variation within a species or a group of closely related species can be informative about the processes driving differentiation and speciation (Thorpe and Malhotra 1998; Gübitz et al. 2000). In the case presented here, lizards vary substantially among populations in morphology and habitat use. However, likely explanations for these differences vary. In the case of body size evolution, a priori adaptive explanations were useful. For nonallometric changes in body shape and head color pattern, patterns of trait covariance revealed evidence for the action of natural selection even

TABLE 2. Results from univariate ANOVAs of differences among sites along all PC axes.

Axis	Full dataset		Réunion excluded	
	$F_{10,162}$	$P$	$F_{9,147}$	$P$
PC1	5.9	<0.001	16.0	<0.001
PC2	4.7	<0.001	9.5	<0.001
PC3	12.1	<0.001	13.3	<0.001
PC4	9.2	<0.001	7.4	<0.001
PC5	10.4	<0.001	9.3	<0.001
PC6	13.4	<0.001	9.6	<0.001
PC7	12.2	<0.001	5.7	<0.001
PC8	5.5	<0.001	4.0	<0.001
PC9	3.5	<0.001	3.6	<0.001
PC10	11.0	<0.001	2.5	<0.001
PC11	3.3	<0.001	4.8	<0.001
PC12	3.1	0.001	1.1	0.001
PC13	4.6	<0.001	11.7	<0.001
PC14	6.4	<0.001	9.4	<0.001
PC15	36.8	<0.001	7.2	<0.001
PC16	7.2	<0.001	9.1	<0.001
PC17	11.0	<0.001	6.1	<0.001
PC18	6.1	<0.001	4.5	<0.001
PC19	22.4	<0.001	21.2	<0.001
PC20	7.6	<0.001	3.5	0.002
PC21	8.2	<0.001	2.9	<0.001
PC22	1.9	0.04	2.0	0.09
PC23	6.4	<0.001	6.7	<0.001
PC24	1.9	0.04	2.1	0.03

while a priori tests for adaptation failed. These traits show the imprint of selection associated with unmeasured factors in the system.

*Gigantism on Small Offshore Islands*

Lizards tend to be larger on small offshore islands compared to those on the mainland; this difference is not correlated with any measured habitat use variable. In studies of other reptile species, both insular dwarfism and gigantism

have been encountered (e.g., Case 1978; Petren and Case 1997; Arnold 2000; Boback 2003; Keogh et al. 2005). In snakes, several studies have provided evidence that changes in body size on islands are due to differences in the size of available prey (Boback 2003; Keogh et al. 2005). This is also a possible explanation in *Phelsuma*; Gardner (1984) suggested a relationship between size and diet in *Phelsuma* in the Seychelles, with larger species selecting larger prey.

Another explanation relies on the idea that consistent environmental differences between mainland and island habitats, such as reduced species diversity, alter the balance between competitive abilities and energetics (Schoener 1969; Case 1978; Lomolino 1985). This could potentially lead to convergent or parallel body size changes among island populations. In the case of *Phelsuma*, this explanation is supported by the observation that offshore Mauritian Islands tend to have fewer species than mainland populations. Intraspecific aggressive behavior is frequently observed in *Phelsuma* (L. J. Harmon, pers. obs.; Evans and Evans 1980; Gardner 1984). Large body size may give individuals an advantage in intraspecific dominance, and would provide a greater advantage in island populations if lizard densities were higher and aggressive intraspecific interactions more frequent compared to mainland populations (Lomolino 1985). This seems to be the case for several groups of lizards, including *P. ornata* (Rodda et al. 2001; Rodda and Dean-Bradley 2002). In our data, the relationship between lizard morphology and the number of sympatric *Phelsuma* species was marginally nonsignificant, but this could be an artifact of the low number of localities used in this test. Size differences among populations also may be influenced by nongenetic factors, such as phenotypic plasticity or predation (Barahona et al. 2000). Common garden experiments (Thorpe et al. 2005) would be necessary to evaluate the relative roles of genetic and environmental factors in determining these body size differences.

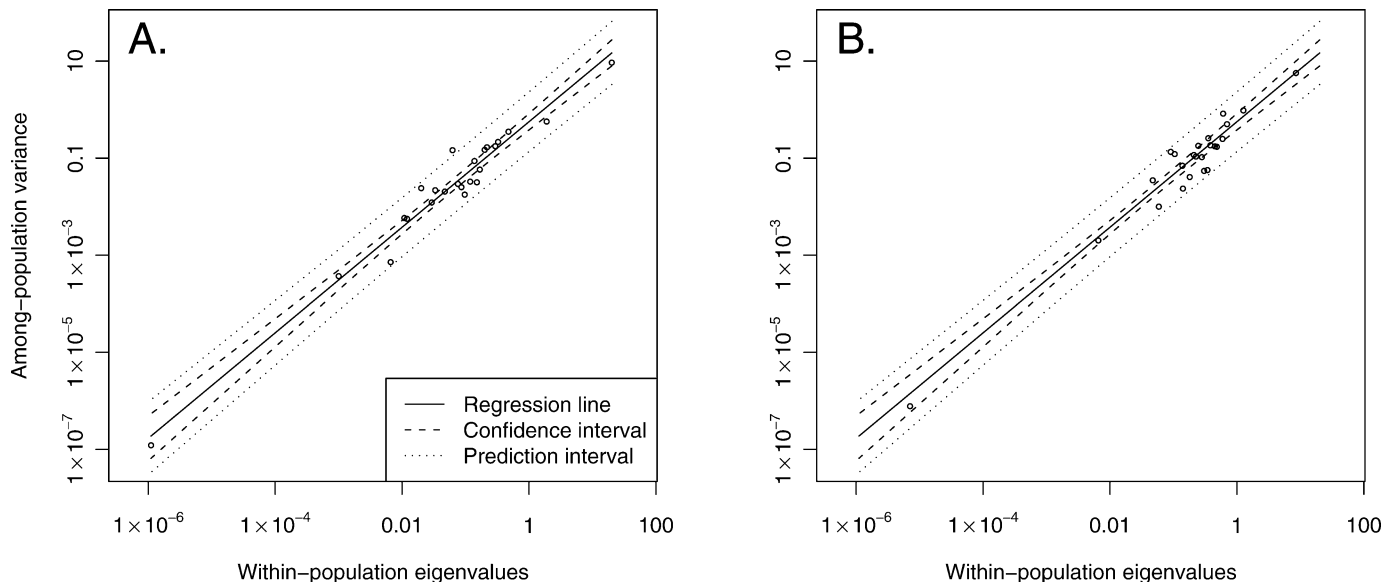


FIG. 5. Relationships between variance of PC axes within and among populations, with best-fit line, confidence limits, and prediction limits. (A) Raw data; (B) standardized data (all measurements standardized to unit variance).



TABLE 3. Mantel tests.

Matrix 1	Matrix 2	Control matrix	P
Microhabitat	island vs. mainland	none	0.7
		geography	0.6
	community composition	none	0.9
		geography	0.9
Morphology	island vs. mainland	none	0.02
		geography	0.004
	community composition	none	0.08
		geography	0.08
Morphology (size removed)	island vs. mainland	none	0.8
		geography	0.9
	community composition	none	0.4
		geography	0.3

Although we find evidence for evolution of large body size on offshore islands, the patterns of variation in PC1 among and within populations (Fig. 5) do not reveal the imprint of that selection. Instead, variation among populations in body size is approximately equal to that expected given the level of body size variation within populations. However, we suspect that this result may be partially due to the fact that these data include lizards of varying ages within each population. These lizards continue to grow after reaching sexual maturity; thus, some of the lizards that we measured were likely newly mature males who had not yet reached their full adult size. This has the effect of inflating body size variation within populations while leaving variation among population means unchanged, and likely greatly reduced our power to detect selection on body size. If it were possible to measure only fully-grown males in each population, we suspect that variance within populations along PC1 would be greatly reduced.

#### *Selection on Body Shape and Head Color Pattern*

Differences in body shape among localities are more enigmatic. Regression of within- and among-population variance of PC axes suggests that along the most variable axes, more variation exists among populations than would be expected by drift (Fig. 5). This could be due to diversifying selection along these main axes, or stabilizing selection along the minor PC axes (Ackermann and Cheverud 2002; Marroig and Cheverud 2004). The axes that are above the regression line and thus possibly under the influence of diversifying selection involve aspects of the front limbs (PC axes 6 and 7) and landmarks associated with the location of white stripes on the back of the head (PC axes 15, 17, and 19), while axes below the regression line and likely influenced by stabilizing selection involve torso (interlimb) length (PC axis 2) and overall head dimensions (PC axes 8, 9, 11, 12, 13, and 22).

However, body shape differences are neither correlated with geographic distance nor with any measured ecological habitat use variable. One possibility is that the pattern seen is due to stabilizing selection along minor PC axes, in which case no ecomorphological correlations would be observed, despite the fact that selection is occurring, because all populations are on the same adaptive peak. Alternatively, our lack of significant results may be due to low statistical power from this comparison of only 10 populations.

Finally, we tested only a few a priori hypotheses; it is possible that the measured morphological variables are related to other, unmeasured ecological variables. For example, rainfall, temperature, and other environmental variables may play an important role in the ecology of these lizards. For example, lizards from more xeric habitats in Mauritius seemed to be duller in coloration than those from more mesic habitats (L. J. Harmon, pers. obs.), a pattern also documented for *Anolis* lizards (e.g., Thorpe and Stenson 2003). A future study investigating correlations between variation in body shape and such environmental variables would be informative. Another possibility is that bright coloration might play a role in sexual selection, similar to the role played by coloration in other lizards with conspicuous markings (e.g., Calsbeek and Sinervo 2002; Stuart-Fox et al. 2003, 2004; Stuart-Fox and Ord 2004). In that case, it might be expected that the particular arrangement of colors on a lizard's head would be important in terms of attractiveness to mates. Mate choice experiments using lizards from different localities would be interesting in this context. If sexual selection plays a role in the evolution of these traits, lizards should show a strong preference for traits from their own population.

**P** matrices are a useful surrogate for **G** matrices for species that are highly threatened, cannot be bred easily in the lab, or are otherwise not readily amenable to genetic studies (Arnold and Phillips 1999). However, making inferences based on comparisons of phenotypic variance-covariance matrices can be problematic if they do not accurately reflect underlying patterns of genetic variance and covariance (Willis et al. 1991). The extent to which **G** and **P** are expected to differ is mainly an empirical question (Cheverud 1982, 1988); most reviews have concluded that **G** and **P** are proportional, at least for morphological traits (Cheverud 1988, 1996; Koots and Gibson 1996; Roff 1995, 1997). To interpret our **P**-matrix comparisons in terms of selection with genetic variances and covariances, one must assume that environmental variances and covariances among traits (**E** matrices) among populations are similar to those within populations. This assumption has yet to be tested in these lizards.

We have shown that populations of *P. ornata* and *P. inexpectata* are morphologically distinct. Body size tends to be larger on small offshore islands, suggesting a role for adaptation. Both head color patterns and body shape variation show some evidence of past selection, although the particular

selective force is unknown. Phenotypic patterns among populations of these island lizards have likely been shaped by the interplay of natural selection and genetic drift. This substantial among-population variation in island forms likely plays a key role in the process of diversification during adaptive radiations. Given that the Mascarenes are home to an endemic radiation of these lizards (Austin et al. 2004), the patterns seen here may give insight into how speciation proceeds in a limited geographic area.

## ACKNOWLEDGMENTS

We thank C. Jones, L. Harmon, V. Tatayah, A. Khadun, C. Gibson, T. Wolff, M. Barry, N. Cole, L. Cole, T. Ross, J.-M. Probst, A. Cheke, K. Freeman, Mauritius National Parks and Conservation, and the Mauritian Wildlife Foundation for assistance and advice. J. Kolbe, D. Hansen, J. Melville, N. Cole, M. Whitlock, S. Otto, J. Weir, D. Schluter, and three anonymous reviewers provided helpful comments on this manuscript. A National Science Foundation Dissertation Improvement Grant, DEB 0309361, supported this work.

## LITERATURE CITED

- Ackermann, R. R., and J. M. Cheverud. 2002. Discerning evolutionary processes in patterns of tamarin (genus *Saguinus*) craniofacial variation. *Am. J. Phys. Anthropol.* 117:260–271.
- Arnold, E. N. 2000. Using fossils and phylogenies to understand evolution of reptile communities on islands. Pp. 309–323 in G. Rheinwald, ed. *Isolated vertebrate communities in the tropics: Bonner Zoologische Monographien* 46. Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn, Germany.
- Arnold, S. J., and P. C. Phillips. 1999. Hierarchical comparison of genetic variance-covariance matrices. II. Coastal-inland divergence in the garter snake, *Thamnophis elegans*. *Evolution* 53:1516–1527.
- Austin, J. J., E. N. Arnold, and C. G. Jones. 2004. Reconstructing an island radiation using ancient and recent DNA: the extinct and living day geckos (*Phelsuma*) of the Mascarene islands. *Mol. Phylogenet. Evol.* 31:109–122.
- Barahona, F., S. E. Evans, J. A. Mateo, M. Garcia-Marquez, and L. F. Lopez-Jurado. 2000. Endemism, gigantism and extinction in island lizards: the genus *Gallotia* on the Canary Islands. *J. Zool. Lond.* 250:373–388.
- Barton, N. H. 1996. Natural selection and random genetic drift as causes of evolution on islands. *Philos. Trans. R. Soc. Lond. B* 351:785–794.
- Bégin, M., and D. A. Roff. 2003. The constancy of the **G** matrix through species divergence and the effects of quantitative genetic constraints on phenotypic evolution: a case study in crickets. *Evolution* 57:1107–1120.
- Boback, S. 2003. Body size evolution in snakes: evidence from island populations. *Copeia* 2003:81–94.
- Bostwick, K. S., and M. J. Brady. 2002. Phylogenetic analysis of wing feather taxis in birds: macroevolutionary patterns of genetic drift? *Auk* 119:943–954.
- Calsbeek, R., and B. Sinervo. 2002. Uncoupling direct and indirect components of female choice in the wild. *Proc. Natl. Acad. Sci. USA* 99:14897–14902.
- Cano, J. M., A. Laurila, J. Palo, and J. Merilä. 2004. Population differentiation in **G** matrix structure due to natural selection in *Rana temporaria*. *Evolution* 58:2013–2020.
- Carlquist, S. 1965. *Island life*. Natural History Press, New York.
- Case, T. J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59:1–18.
- Cheverud, J. M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution* 36:499–516.
- . 1988. A comparison of genetic and phenotypic correlations. *Evolution* 42:958–968.
- . 1996. Quantitative genetic analysis of cranial morphology in the cotton-top (*Saguinus oedipus*) and saddle-back (*S. fuscicollis*) tamarins. *J. Evol. Biol.* 9:5–42.
- Diamond, J. 1991. A new species of rail from the Solomon Islands and convergent evolution of insular flightlessness. *Auk* 108:461–470.
- Evans, P. G. H., and J. B. Evans. 1980. The ecology of lizards on Praslin Island, Seychelles. *J. Zool. Lond.* 191:171–192.
- Fu, Y. X., and W. H. Li. 1993. Statistical tests of neutrality of mutations. *Genetics* 133:693–709.
- Gardner, A. S. 1984. The evolutionary ecology and population systematics of day geckos (*Phelsuma*) in the Seychelles. Ph.D. diss. University of Aberdeen, U.K.
- . 1986. Morphological evolution in the day gecko *Phelsuma sundbergi* in the Seychelles: a multivariate study. *Biol. J. Linn. Soc.* 29:223–244.
- Gillespie, R. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303:356–359.
- Gower, J. C. 1975. Generalized Procrustes analysis. *Psychometrika* 40:33–51.
- Grant, P. R. 1998a. *Evolution on islands*. Oxford Univ. Press, New York.
- . 1998b. Speciation. Pp. 83–101 in P. R. Grant, ed. *Evolution on islands*. Oxford Univ. Press, Oxford, U.K.
- Gübitz, T., R. S. Thorpe, and A. Malhotra. 2000. Phylogeography and natural selection in the Tenerife gecko *Tarentola delalandii*: testing historical and adaptive hypotheses. *Mol. Ecol.* 9:1213–1221.
- Hansen, D. M., K. Beer, and C. B. Muller. 2006. Mauritian colored nectar no longer a mystery: a visual signal for lizard pollinators. *Biol. Lett.* 2:165–168.
- Hudson, R. R., M. Kreitman, and M. Aguade. 1987. A test of neutral molecular evolution based on nucleotide data. *Genetics* 116:153–159.
- IGN. 2001. *Île Maurice: Carte Touristique et Routière*. Institut Géographique National, Paris.
- Keogh, J. S., I. A. W. Scott, and C. Hayes. 2005. Rapid and repeated origin of insular gigantism and dwarfism in Australian tiger snakes. *Evolution* 59:226–233.
- King, J. L., and T. H. Jukes. 1969. Non-Darwinian evolution. *Science* 164:788–798.
- Klingenberg, C. P., M. Barluenga, and A. Meyer. 2002. Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. *Evolution* 56:1909–1920.
- Koots, K. R., and J. P. Gibson. 1996. Realized sampling variances of estimates of genetic parameters and the difference between genetic and phenotypic correlations. *Genetics* 143:1409–1416.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* 33:402–416.
- Lomolino, M. V. 1985. Body size of mammals on islands: the island rule reexamined. *Am. Nat.* 125:310–316.
- Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodriguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279:2115–2118.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton Univ. Press, Princeton, NJ.
- Manly, B. F. J. 1991. *Randomization and Monte Carlo methods in biology*. Chapman and Hall, New York.
- Marroig, G., and J. M. Cheverud. 2004. Did natural selection or genetic drift produce the cranial diversification of Neotropical monkeys? *Am. Nat.* 163:417–428.
- Mayr, E. 1954. Change of genetic environment and evolution. Pp. 157–180 in J. Huxley, A. C. Hardy and E. B. Ford, eds. *Evolution as a process*. Allen and Unwin, London.
- Mertens, R. 1970. Neues über einige taxa der geckonengattung *Phelsuma*. *Senck. Biol.* 51:1–13.
- NyHagen, D. F., C. Kragelund, J. M. Olesen, and C. G. Jones. 2001. Insular interactions between lizards and flowers: flower visitation by an endemic Mauritian gecko. *J. Trop. Ecol.* 17:755–761.

- Petren, K., and T. J. Case. 1997. A phylogenetic analysis of body size evolution and biogeography in chuckwallas (*Sauromalus*) and other iguanines. *Evolution* 51:206–219.
- R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Radtkey, R. R. 1996. Adaptive radiation of day-geckos (*Phelsuma*) in the Seychelles archipelago: a phylogenetic analysis. *Evolution* 50:604–623.
- Rodda, G. H., and K. Dean-Bradley. 2002. Excess density compensation of island herpetofaunal assemblages. *J. Biogeogr.* 29: 623–632.
- Rodda, G. H., G. Perry, R. J. Rondeau, and J. Lazell. 2001. The densest terrestrial vertebrate. *J. Trop. Ecol.* 17:331–338.
- Roff, D. A. 1995. The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. *Heredity* 74:481–490.
- . 1997. *Evolutionary quantitative genetics*. Chapman and Hall, New York.
- Rohlf, F. J. 2004. tpsDig. Ver. 1.40. State University of New York, Stony Brook, New York.
- Schluter, D. 1988. The evolution of finch communities on islands and continents: Kenya vs. Galapagos. *Ecol. Monogr.* 58: 229–249.
- . 1996. Adaptive radiation along genetic lines of least resistance. *Evolution* 50:1766–1774.
- Schoener, T. W. 1969. Models of optimal size for solitary predators. *Am. Nat.* 103:277–313.
- Scott, S. N., S. M. Clegg, S. P. Blomberg, J. Kikkawa, and I. P. F. Owens. 2003. Morphological shifts in island-dwelling birds: the roles of generalist foraging and niche expansion. *Evolution* 57: 2147–2156.
- Simpson, G. G. 1944. *Tempo and mode in evolution*. Columbia Univ. Press, New York.
- Steppan, S. J. 1997. Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and common principal component analyses. *Evolution* 51:571–586.
- Steppan, S. J., P. C. Phillips, and D. Houle. 2002. Comparative quantitative genetics: evolution of the **G** matrix. *Trends Ecol. Evol.* 17:320–327.
- Stuart-Fox, D. M., and T. J. Ord. 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proc. R. Soc. Lond. B* 271: 2249–2255.
- Stuart-Fox, D. M., A. Moussalli, N. J. Marshall, and I. P. F. Owens. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Anim. Behav.* 66:541–550.
- Stuart-Fox, D. M., A. Moussalli, G. R. Johnston, and I. P. F. Owens. 2004. Evolution of color variation in dragon lizards: quantitative tests of the role of crypsis and local adaptation. *Evolution* 58: 1549–1559.
- Thorpe, R. S. 2002. Analysis of color spectra in comparative evolutionary studies: molecular phylogeny and habitat adaptation in the St. Vincent anole (*Anolis trinitatis*). *Syst. Biol.* 51: 554–569.
- Thorpe, R. S., and A. Malhotra. 1998. Molecular and morphological evolution within small islands. Pp. 67–82 in P. R. Grant, ed. *Evolution on islands*. Oxford Univ. Press, Oxford, U.K.
- Thorpe, R. S., and A. G. Stenson. 2003. Phylogeny, paraphyly and ecological adaptation of the colour and pattern in the *Anolis roquet* complex on Martinique. *Mol. Ecol.* 12:117–132.
- Thorpe, R. S., J. T. Reardon, and A. Malhotra. 2005. Common garden and natural selection experiments support ecotypic differentiation in the Dominican anole (*Anolis oculatus*). *Am. Nat.* 165:495–504.
- Vinson, J.-M. 1976. The saurian fauna of the Mascarene Islands II: the distribution of *Phelsuma* species in Mauritius. *Mauritius Inst. Bull.* 8:177–195.
- Vinson, J., and J.-M. Vinson. 1969. The saurian fauna of the Mascarene Islands. *Mauritius Inst. Bull.* 6:203–320.
- Wainwright, P. C., and S. M. Reilly. 1994. *Ecomorphology: integrative organismal biology*. Univ. of Chicago Press, Chicago.
- Wilder, J. A., and H. Hollocher. 2003. Recent radiation of endemic Caribbean *Drosophila* of the *dunni* subgroup inferred from multilocus DNA sequence variation. *Evolution* 57:2566–2579.
- Willis, J. H., J. A. Coyne, and M. Kirkpatrick. 1991. Can one predict the evolution of quantitative characters without genetics? *Evolution* 45:441–444.

Corresponding Editor: K. Schwenk