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Rapid Ecomorphological Divergence between Island and Mainland Populations of the Peruvian Lava Lizard (*Microlophus peruvianus*) in Northern Peru

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Abstract—Island-mainland systems provide ideal scenarios in which to study the influence that contrasting ecological pressures have on closely related taxa. In exceptional cases, recent colonization events or anthropogenic introduction of continental individuals to islands can facilitate the study of rapid phenotypic divergence experienced by newly formed insular populations. The Peruvian Lava Lizard (*Microlophus peruvianus*) is an abundant and conspicuous species found along the Peruvian coastal desert. This species was introduced to several offshore Peruvian islands in the 1940s as a potential biological control of guano-bird ectoparasites. Less than a century later, some populations of *M. peruvianus* still thrive in some of these islands. Relative to continental environments, the islands have barren, sparsely vegetated landscapes, and terrestrial vertebrates are generally scarce. Thus, potential differences in the availability of microhabitats and prey and the presence of predators might have imposed distinct selective pressures on island and mainland populations, consequently resulting in the evolution of diverging phenotypes. In this study we compared the morphology of an insular and a continental population of *M. peruvianus* and found significant differences possibly driven by the contrasting ecological pressures they experience. For example, the larger heads of mainland lizards might allow them to take advantage of the higher diversity of prey found in the continent, which apparently includes items of relatively greater hardness that require stronger bite forces to subdue and consume. Similarly, the relatively longer hindlimb traits found in mainland individuals might allow them to navigate their habitat with higher speed, a beneficial trait in open terrains. In contrast, high speeds might not be as necessary for island individuals due to high population density and lack of predators that often characterize insular habitats. Despite strong morphological divergence, further studies on the ecological and population dynamics at both localities are necessary to clarify these potential ecomorphological relationships. Besides highlighting the importance of insular environments in driving phenotypic diversity, this study represents the first morphological comparison between populations found in the Peruvian desert and its offshore islands, a virtually unexplored island-mainland system.

Islands represent exceptional opportunities to study the evolution of biodiversity. Reduced area, isolation, and the relative simplicity of their biotas present particular scenarios that allow us to learn more about the evolutionary processes that have shaped life on Earth (MacArthur and Wilson 1967; Grant 1998; Losos and Ricklefs 2009a, 2009b; Whittaker et al. 2017). Island species have undergone divergent processes of adaptive evolution in response to unique habitats and community dynamics usually not found in continental areas (Adler and Levins 1994; Lomolino et al. 2006). Consequently, island taxa often exhibit ecological, behavioral, and morphological adaptations to cope with the selection pressures exerted by island life (Schluter 1988; Raia et al. 2010; Lomolino et al. 2012).

Adaptations to unique environments are known to drive the evolution of morphological diversity (Wainwright and Reilly 1994). In fact, many links between form and function have previously been identified in nature, and likely are consequences of diverging ecological needs (e.g., Wainwright et al. 2002; Nogueira et al. 2009; Blom et al. 2016). Comparisons of island and mainland systems provide opportunities to investigate morphological adaptations and how they can

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occur over relatively short periods of time due to the recent colonization of islands by populations of continental origin. Indeed, previous studies have shown that differences between insular and continental habitats can lead to significant morphological variation between related populations and/or species over the span of only a few generations (e.g., Losos et al. 1997; Clegg et al. 2002; Lomolino et al. 2006; Herrel et al. 2008; de Amorim et al. 2017).

Among the least explored insular systems in the world are the dozens of islands and islets off the Pacific Coast of Peru. They originated as parts of the geological evolution of the continent at the end of the Tertiary and beginning of the Quaternary Periods as a result of the collapse of the Cordillera de la Costa, an ancient mountain formation (Schweigger 1964). Some of these islands are composed of weathered sedimentary, metamorphic, and phosphoric rocks mixed with seabird guano (Schweigger 1964). These islands are barren, most of them support little vegetation, and mimic to some extent the arid landscapes found on the coast. Consequently, although the subaquatic, intertidal, and ornithological faunas related to these islands are relatively diverse (Hooker et al. 2005, 2012; Figueroa and Stucchi 2008; Ramírez et al. 2019), only a few terrestrial vertebrates are known to inhabit them (Schweigger 1947; Pérez and Jahncke 1998; Pérez and Lleellish 2015).

Peruvian Lava Lizards, *Microlophus peruvianus* (Lesson 1830), the most conspicuous diurnal lizards in the Peruvian desert, occupy the entire coastal extension of Peru and southern Ecuador (Carrillo and Icochea 1995; Toyama and Boccia 2022). In continental localities *M. peruvianus* is a highly territorial species that exhibits sexual size dimorphism, with males reaching 140 mm SVL and females 97 mm SVL (Toyama and Boccia 2021). These lizards are microhabitat and dietary generalists (Péfaur and López-Tejeda 1983; Pérez and Balta 2007; Quispitúpac and Pérez 2009). In addition to the mainland coast, *M. peruvianus* occurs on several offshore Peruvian islands ranging from Foca Island in the north to Santa Rosa Island off southern Peru (Dixon and Wright 1975; Pérez and Lleellish 2015), onto which it was deliberately introduced as a potential biological control of guano-bird ectoparasites in the 1940s (Vogt 1939; Pérez and Jahncke 1998; Pérez and Lleellish 2015). In some ways, these introduced populations appear to be preadapted to insular environments (e.g., Pérez and Lleellish 2015); however, whether island and mainland populations differ morphologically due to different ecological pressures has remained unexplored.

In this study, we tested whether insular populations of *M. peruvianus* have diverged morphologically from their continental relatives after less than a century of isolation, seeking to identify the individual traits that contributed the most to hypothetical differences between populations. Additionally, we explored whether the morphological differences between island and mainland populations and the differences among all individuals occur along the same morphological axis using a multivariate dataset consisting of ecologically relevant morphological traits from insular and continental specimens from localities at comparable latitudes. This comparison provides insight into the alignment between interpopulational divergence and overall morphological diversification. We discuss our results within an ecomorphological framework, considering the contrasting ecological contexts likely represented by this previously unexplored island-mainland system.

Methods

Data collection.—We examined 61 preserved adult *Microlophus peruvianus* from mainland and island localities; 39 were collected in the mangroves near San Pedro de Vice, Piura, Peru (-5.49052, -80.90994) and 22 on Lobos de Tierra Island (-6.42778, -80.85806) (Fig. 1). Sex can sometimes be inferred from coloration in this species; however, colors had faded in many of the examined specimens, making accurate determination unreliable. Despite this limitation, we expected both sexes to be similarly affected by most ecological differences between island and mainland systems (e.g., differences in prey and microhabitat availability), so we pooled males and females in our analyses.

Figure 1. Map showing the localities where specimens were collected at San Pedro de Vice, Peru, and on Lobos de Tierra Island, off the Pacific Coast of Peru.

The individuals from San Pedro de Vice were collected in February and September 2001 near grassy areas where the dominant vegetation consisted of Sea Purslane (*Sesuvium portulacastrum*) and Desert Saltgrass (*Distyclis spicata*) (Figs. 2A & C). This area supported a high diversity of insects and was the habitat of other lizard species, including Central Leaf-toed Geckos (*Phyllodactylus microphyllus*), Tschudi's Lava Lizards (*Microlophus thoracicus*), and Knobbed Lava Lizards (*M. occipitalis*), the latter being the most abundant. The individuals from Lobos de Tierra were collected in October 1997 and appeared to be experiencing a very different ecological scenario than the mainland lizards. They were found near nesting sites in marine bird colonies without nearby vegetation (Fig. 2B), were the only diurnal lizards on the island, and had access to a less diverse variety of trophic resources, evidenced by the dominance of a soft tick (*Ornithodoros amblus*) in their diet (Pérez and Jahncke 1998).

We measured morphological traits using digital calipers (0.01 mm), focusing on the following morphological traits because of their recognized ecomorphological relevance in lizards (e.g., Losos 1990; Herrel et al. 2001a): Snout-vent length (SVL), head length, head width, head height, body width, interlimb distance, humerus length, radius length, metacarpus length, length of the longest finger, femur length, tibia length, metatarsus length, and length of the longest toe. All morphological data were log-transformed prior to analyses.

Data analysis.—To account for the influence of body size, we performed linear regressions between each trait and SVL. The residuals for each individual were considered a set of size-corrected morphological traits. Then, to test whether island and mainland individuals exhibited different multivariate morphological phenotypes, we performed a multivariate analysis of variance (MANOVA) using the entire set of size-corrected morphological traits as dependent variables and the island/mainland category as a predictor variable. Next, to identify which traits were more strongly associated with the potential phenotypic difference between island and mainland individuals, we performed a discriminant function analysis (DFA, function "lda," R-package *MASS*; Venables and Ripley 2002), again considering the entire set of size-corrected morphological traits as dependent variables and island/mainland categories as the discriminating groups. We subsequently performed a principal component analysis (PCA) on the entire set of size-corrected traits and retained the first principal components (PC) that together explained more than 70% of the morphological variation among individuals. We then tested whether the axis of maximum morphological discrimination between island and mainland groups (as captured by the DFA) aligned with the main axes of morphological variation among individuals (i.e., the PCs). Both DFA and PCA are similar techniques used to reduce the dimensionality of the data through linear transformations; however, a DFA does so through the construction of axes that maximize the differences between categories defined *a priori*, whereas a PCA defines the axes that maximize the differences among all datapoints. Thus, an association between the axes defined by a DFA and a PCA would suggest that the overall morphological variability within our sample is related to the differences driven by the island-mainland dichotomy.

We also tested for differences in the allometric trajectories of each trait between island and mainland individuals through analyses of covariance (ANCOVA) with the island/mainland category as a moderator (i.e., log(trait) ~ log(SVL) * island/mainland). Significant interaction terms indicated that differences between groups in the relative dimensions of a given trait are due to the evolution of different allometric slopes. In the absence of a significant interaction term, the interaction was removed and the analysis was repeated with only additive terms. In this case, a significant locality term (i.e., island/mainland) indicated that differences between island and mainland individuals were due to the evolution of different allometric intercepts. We used the function "lm.rrpp" from the R package *RRPP* (Collyer and Adams 2018) to test these linear models. One thousand iterations were performed in each model. Finally, we tested for differences in body size (SVL) of island and mainland individuals using a t-test. All statistical analyses were conducted in R (version 4.2.1; R Development Core Team 2022).

Figure 2. A sandy beach in San Pedro de Vice, Peru, with scattered patches of vegetation (A). Typical landscape on Lobos de Tierra Island occupied by populations of various species of marine birds (B). A male Peruvian Lava Lizard (*Microlophus peruvianus*) basking in a patch of Sea Purslane (*Sesuvium portulacastrum*) at San Pedro de Vice (C). Photographs by Eliana Quispitúpac (A–B) and Aquiles García-Godos (C).

Results

The MANOVA indicated that insular and continental individuals of *M. peruvianus* were morphologically different (F = 10.05; $p < 0.001$). A subsequent discriminant function analysis (DFA) showed that this difference was strongly driven by island individuals having a relatively longer tibia, a wider body, and relatively longer interlimb distances (negative DF values in Table 1). On the other hand, mainland individuals tended to have relatively longer and taller heads and relatively longer fingers, toes, and femora (positive DF values in Table 1).

The first four principal components (PCs) from a PCA represented 72.12% of the total variance (Fig. 3A, Table 1). PC1 alone explained 32.69% of the variation among individuals and was strongly related to the discriminant function (DF) described above (Fig. 3B; t = 24.34, $p < 0.001$). PC2 explained 19.64% of the total variation among species and was positively associated with the relative compaction of body shape (i.e., individuals with positive PC2 scores had shorter appendices relative to body size). We did not find a significant relationship between PC2 and DF (t = 1.56, p = 0.124). PC3 and PC4 explained 12.30% and 7.48% of the total morphological variation, respectively, and were not significantly related to DF (DF ~ PC3: t = -0.20, p = 0.844; DF ~ PC4: t = -0.58, p = 0.565).

We found no differences between the allometric slopes of island and mainland individuals for any trait (all $p > 0.05$). However, the allometric intercepts of all considered traits differed significantly between island and mainland individuals (Fig. 4), except for body width (for which we only found weak evidence supporting a difference between populations, Fig. 4D), metacarpus length (Z = 0.74, p = 0.251), and metatarsus length (Z = 0.83, p = 0.226). On average, island individuals had relatively longer humeri, radii, tibiae, and interlimb segments. Mainland individuals showed relatively longer, wider, and taller heads; longer fingers, femora, and toes (Fig. 4). Finally, a t-test indicated that island individuals were larger in overall size than mainland individuals (t = 3.13, p = 0.003; Fig. 4L).

Table 1. Coefficients representing the association of each size-corrected morphological variable with the discriminant function (DF) and the first four principal components (PC).

Variable	DF	PC1	PC2	PC3	PC4
Head length	1.47	0.17	-0.06	0.11	0.05
Head width	-0.32	0.12	-0.13	0.02	0.03
Head height	1.59	0.24	-0.20	0.16	0.43
Body width	-1.90	-0.12	0.17	0.06	0.50
Interlimb length	-3.98	-0.51	-0.13	-0.12	0.16
Humerus length	0.13	-0.17	-0.15	0.16	0.41
Radius length	0.65	-0.23	-0.25	0.64	-0.38
Metacarpus length	0.28	-0.04	-0.59	-0.63	-0.19
Finger length	1.55	0.30	-0.23	0.12	-0.20
Femur length	0.93	0.21	-0.25	0.16	0.01
Tibia length	-8.53	-0.42	-0.38	0.23	-0.04
Metatarsus length	-0.29	0.19	-0.45	0.02	0.40
Toe length	1.93	0.45	-0.07	0.13	-0.05

Discussion

Islands present unmatched opportunities to understand how ecomorphological evolution can occur over short timescales, especially when mainland colonizers are suddenly exposed to ecological contexts not experienced on the continent (Baeckens and Van Damme 2020). In this study, we showed how insular populations of *Microlophus peruvianus* have diverged morphologically from their mainland counterparts after only decades of isolation. Moreover, this morphological differentiation between faunas seems to represent an important axis of morphological variation within this species, as we identified clear differences between groups in most individual morphological traits (Figs. 3 & 4). In general, these strong patterns of divergence add to our knowledge of how evolution can occur rapidly in populations recently introduced to islands, but also represent the first effort in describing ecomorphological differences in this largely unexplored island-mainland system.

We found strong differences in the morphological proportions of island and mainland populations, which represent an additional example of how insularity promotes phenotypic diversity both within and between species (e.g., Harmon and Gibson 2006; Pinto et al. 2008; Yamada et al. 2014; Andrade et al. 2015). Moreover, the direction of these differences suggests that morphological evolution might have responded to specific ecological needs in both populations. For example, mainland individuals tended to have relatively shorter forelimb traits, shorter interlimb distances, and longer femora and toes than island individuals (Table 1, Fig. 4). Relatively long hindlimbs and toes, and shorter interlimb distances are often associated with high sprint speeds in lizards, which could be beneficial in open habitats (Bonine and Garland 1999; Melville and Swain 2000; Kohlsdorf et al. 2001). In contrast, relatively long forelimbs and fingers have been previously associated with lifestyles that rely heavily on climbing (Teixeira-Filho et al. 2001; Herrel et al. 2002; Losos 2009). These results would thus suggest that *M. peruvianus* in the insular population might rely less on performance traits like sprint speed and acceleration than mainland individuals in our samples, for which such performance measures might be more relevant. Although continental *M. peruvianus* frequently live in rocky formations near the ocean (Dixon and Wright

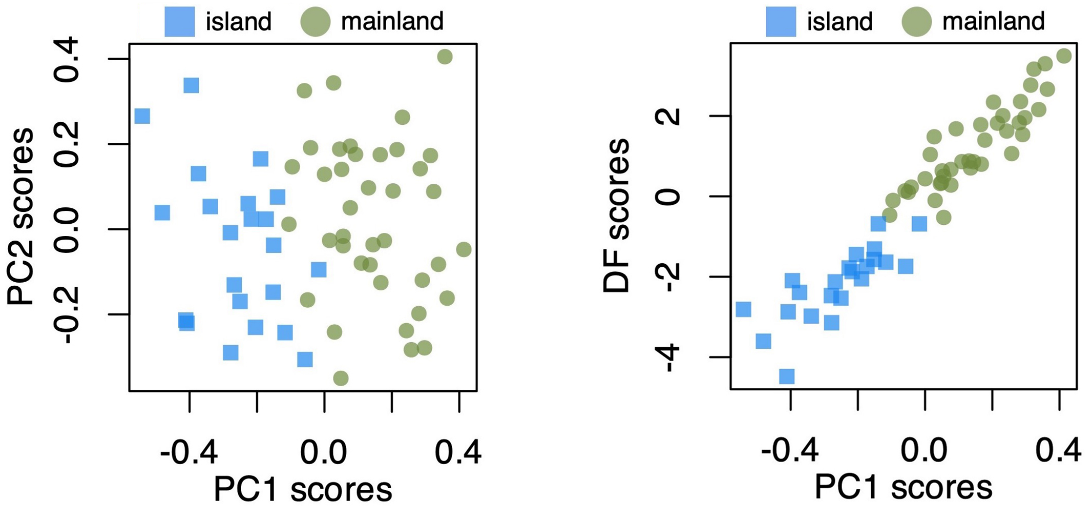

Figure 3. Scatterplot showing scores of principal components 1 and 2 (PC1 and PC2) corresponding to island (blue squares) and mainland (green circles) Peruvian Lava Lizards (*Microlophus peruvianus*) (left). Scatterplot showing the relationship between the scores of the discriminant function (DF), which separates island and mainland individuals, and PC1 (right). Notice the strong relationship between both variables, which is consistent with the observed separation between groups along PC1 in scatterplot on the left.

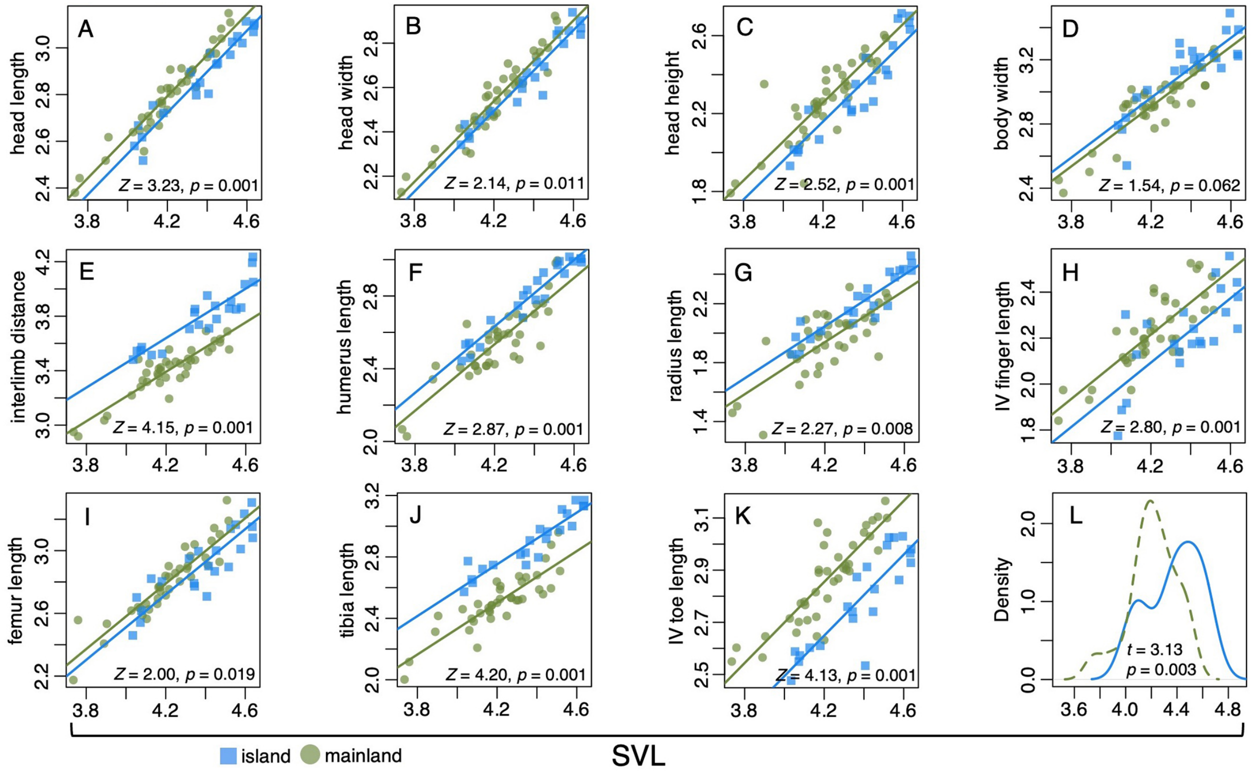

Figure 4. Allometric differences between island (blue squares) and mainland (green circles) Peruvian Lava Lizards (*Microlophus peruvianus*). Blue and green solid lines represent fitted linear models for island and mainland lizards, respectively. (A–K) No interaction between size (SVL) and the island/mainland category was significant for any trait, but the intercept differences between island and mainland lizards were significant for all traits (see results from linear models within each panel) except body width (D), metatarsal, and metacarpus lengths (the latter two not shown in the figure). (L) Island lizards had significantly larger body sizes than mainland lizards (result from a t-test shown in the panel).

1975; KST, personal observations), other populations, like that from San Pedro de Vice in our samples, occupy open habitats (Fig. 2A). This could favor the evolution of increased sprint speeds to move faster between refuges, avoid predators, or to defend territories more efficiently. In contrast, the increased population densities often experienced by insular populations (Andrews 1979; Baeckens and Van Damme 2020) plus the limited available space might force island individuals to exploit alternative microhabitats (e.g., inclined surfaces), thus favoring the evolution of divergent morphological proportions that favor alternative locomotion modes. Further studies describing the specific microhabitats used by these particular insular and continental populations, as well as measures of population density and predator pressure, will be useful in elucidating the drivers of these ecomorphological differences.

Regarding head traits, continental lizards had relatively longer, wider, and higher heads compared to those on the island. Differences in head proportions can be a result of direct selection for bite-force performance, as stronger bites should be produced by more robust skulls that allow the attachment of larger muscles (e.g., Herrel et al. 2001b; Lappin and Husak 2005; Lappin et al. 2006; Wittorski et al. 2016). Head shape has been found to respond to selective forces on islands (Sagonas et al. 2014; Donihue et al. 2016), suggesting that the intensity of selection on bite-force performance differs between insular and continental contexts. Differences in head proportions between insular and continental populations can be related to differences in food availability. Diet is an important axis of lizard ecology (Pianka 1973; Pianka et al. 2017) and likely imposes strong selection pressures on biting performance, as certain dietary items require stronger bite forces (Herrel et al. 2001a, 2001b; McBrayer 2004). Associations between relative head robustness and hardness of prey have been previously reported among species and age groups of *Microlophus* (Toyama 2016; Toyama et al. 2018), suggesting that differences in food availability could have driven the divergence in head shape between island and mainland populations of *M. peruvianus*. If true, our results suggest that mainland individuals would include hard items in their diet more frequently than island individuals. This is expected given the wider range of available resources in continental areas, including tough items like plant material and crustaceans, known to be consumed by some coastal populations of *M. peruvianus* (Pérez and Balta 2007; Quispitúpac and Pérez 2009). On the other hand, the diets of some insular populations in Lobos de Tierra and other islands are known to consist mainly of soft ticks, which are ectoparasites of guano birds (Pérez and Jahncke 1998; Pérez and Lleellish 2015). These likely require less mandibular strength to process compared to the tougher food items found more frequently on the mainland. However, we have no data on the diets of continental populations of *M. peruvianus* in northern Peru, which limits our understanding of potential differences in feeding ecology between island and mainland populations.

Differences in the intensity of sexual selection between insular and continental populations can also drive differences in head proportions. Male lizards of territorial species bite each other when fighting for access to mates, thus larger heads, which produce stronger bites, are often sexually selected (Lappin et al. 2006; Vanhooydonck et al. 2010). Such ecological contexts can produce cascading effects that ultimately define the strength of sexual selection on males (Andrews 1979; Sacchi et al. 2015). For example, low levels of predation on islands should increase population densities, which would in turn increase the frequency of encounters between individuals. This likely would emphasize the evolution of male-male aggression and traits associated with those interactions (Knell 2009). On the other hand, islands tend to be resource limited, reducing the available energy that could be allocated to the development of traits that would favor the competitive performance of individuals (e.g., body size or secondary sexual characters) (Case 1978; Palkovacs 2003). Our results do not show a clear pattern supporting any theoretical expectation involving sexual selection. Head proportions are relatively larger in mainland individuals, but body sizes tend to be larger on the island. Measuring competitive performance and the observation of territorial behavior in both populations could increase our understanding of these differences in the light of sexual selection.

Insular individuals in our sample were significantly larger than mainland lizards. Although an insular lifestyle is traditionally thought to promote the evolution of dwarfism or gigantism (Lomolino 2005), previous studies indicate that, in general, no clear trend links body size and insularity in lizards (Meiri 2007; Meiri et al. 2011). Instead, the evolution of body size seems to be related to the ecological contexts experienced by some populations, like the availability of resources, degree of intra- and interspecific competition, and the life-history strategies favored in a given habitat (Palkovacs 2003; Novosolov et al. 2013). For instance, long-term competition strategies (i.e., K strategies) (Pianka 1970; Stearns 1989) usually evolve in predator-limited environments like islands and can result in the evolution of large body sizes (Palkovacs 2003), as observed in our samples of insular *M. peruvianus*. On the other hand, despite the apparent higher resource availability in the mainland habitat, increased mortality due to predators and the presence of competitor species could limit body sizes attainable by continental *M. peruvianus*. Further studies addressing the evolution of life histories in island and mainland populations should shed light on the processes driving body-size evolution in this species.

The results of this study represent the first step in future avenues of research involving this island-mainland system.

First, the hypothetical ecomorphological links we described based on morphological proportions will need to be complemented by additional ecological and performance studies. These include descriptions of habitat use, diet, territoriality, life-history strategies, locomotion, and male fighting performance. Next, a comprehensive ecomorphological comparison between males and females could shed light on sexual dimorphism in this species, especially if males and females use available resources in different ways — and this is reflected in their morphology (Slatkin 1984; Shine 1989). These intersexual comparisons could also shed light on the potential differences in the intensity of sexual selection on island and mainland populations. In general, the morphological differences we found will need further natural-history and ecological data to provide support for ecomorphological hypotheses. Nonetheless, our results highlight this virtually unexplored island-mainland system as a promising model for further ecomorphological studies.

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