Short Note

Sexual size dimorphism and life history traits in an island-mainland system: an overview of the lizard genus *Microlophus*

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Abstract. Opposing life history strategies are a common result of the different ecological settings experienced by insular and continental species. Here we present a comprehensive compilation of data on sexual size dimorphism (SSD) and life history traits of *Microlophus*, a genus of lizards distributed in western South America and the Galápagos Islands, and test for differences between insular and continental species under life history theory expectations. Contrary to our predictions, we found no differences in SSD between localities or evidence that *Microlophus* follows Rensch's rule. However, as expected, head dimensions and maturity sizes were significantly larger in insular species while continental species had larger clutches. Our results show that *Microlophus* exhibits some of the patterns expected from an island-mainland system, but unexplained patterns will only be resolved through future ecological, morphological and behavioural studies integrating both faunas.

Keywords: clutch size, Galápagos, insularity, island syndrome, Rensch's rule, size at maturity, tropidurid.

Islands have perennially attracted the attention of biologists as they represent exceptional opportunities to observe evolutionary patterns and processes and have motivated some of the most important theoretical postulates of evolutionary biology. Their isolation, reduced area and idiosyncratic ecological characteristics subject their inhabitants to conditions that differ greatly from those of the continental 'mainland' and yield unusual evolutionary outcomes (Losos and Ricklefs, 2009).

Opposing life history strategies are a common result of the island-mainland dichotomy, resulting in what has been termed "the island syndrome" (Adler and Levins, 1994; Novosolov, Raia and Meiri, 2013). The r-K selection continuum theory (Pianka, 1970) predicts that the lower predation pressure of insular localities should lead to higher population densities, increased longevity and, consequently, to higher investment in maintenance and intraspecific competition through the evolution of slower life histories (Stearns, 1989; Montiglio et al., 2018). Lower predation risk and high population density could also lead to the evolution of increased body sizes (Palkovacs, 2003), and an evolutionary cascade where sexual selection triggers the evolution of sexual size dimorphism (SSD) and the exaggeration of sexually selected traits (e.g., intrasexually selected weapons, Rico-Guevara and Hurme, 2019; although these changes could also be a product of character displacement, e.g., Dayan and Simberloff, 1994; Jones, 1997). Conversely, predation pressure is thought to be higher in mainland localities (Carlquist, 1974) which should promote the development of faster life histories. A greater investment in reproduction rather than maintenance, higher offspring numbers, and earlier maturation are some

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of the reproductive strategies that are expected to evolve under high predation conditions, as short-term reproduction becomes more important than intrasexual competition and longevity (e.g., larger clutch sizes are found in mainland lizards, Meiri et al., 2020; shorter incubation times are shown by mainland birds, Covas, 2012). Despite this well-established theoretical framework, studies aiming to elucidate the influence of insularity on the evolution of body size and life histories have demonstrated how theoretical expectations can be influenced by geographical- and taxa-specific factors (e.g., Meiri, Cooper and Purvis, 2008; Schwarz and Meiri, 2017).

Microlophus is a genus of diurnal and omnivorous iguanian lizards that includes 13 continental species ("Pacific iguanas") distributed along the western coast of South America and 10 insular species ("lava lizards") that have radiated in the Galápagos Islands after two independent colonization events (Benavides et al., 2009). Although this genus represents an exceptional opportunity to explore the patterns of life history evolution in an island-mainland system, previous studies on the ecology, morphology and behaviour of *Microlophus* have assessed either the islands or the mainland in isolation. In this study, we provide a comprehensive overview of the *Microlophus* system. Specifically, we aimed to (1) compile and summarize the available data on body size, SSD and life history characteristics (size at maturity and clutch size) for island and mainland *Microlophus*, and (2) to compare both groups of species regarding the summarized data under life history theory expectations. We hypothesized that *Microlophus* would exemplify the island syndrome and we therefore predicted that island species would show higher levels of SSD, larger sizes at maturity and smaller clutch sizes than mainland species.

We collected data on body size for males and females of *Microlophus* species from the literature and from our own field and museum measurements (see supplementary table S1). The maximum snout-vent lengths (SVL) found

for males and females of each species were retained as representative body sizes for each sex and species (table 1). We chose to use maximum rather than average SVLs because different studies usually focus on different age classes (e.g., only adults vs. all individuals including juveniles), which could strongly affect average values. Moreover, the use of maximum sizes has been previously shown to be a good indicator of asymptotic size, even with small sample sizes (Stamps and Andrews, 1992). Using these maximum sizes, we calculated a sexual dimorphism index (SDI = size of larger sex/size of smaller sex − 1) for each species based on Lovich and Gibbons (1992). Additionally, to test for differences in the effect of sexual selection on head dimensions between localities, we examined SVL, head length, head width, and head height data from 204 preserved specimens representing 16 *Microlophus* species (see supplementary text about supplementary table S1) using digital callipers (0.01 mm precision). Of these 16 species, nine were continental and seven were insular. We also surveyed the literature for female size at maturity and clutch size data. We did not consider size at maturity in males for this study because records based on histological evidence were rare and records based on coloration might not represent sexual maturity accurately. Coloration would also be particularly difficult to use as a maturity indication in species with little dimorphism in colour, which would in turn bias the availability of the data. To generate estimates of female size at maturity, we gleaned records from studies with applicable data, taking the smallest size at which a female of any of our focal species was observed to have eggs detectable by abdominal palpitations. The smallest female size at maturity recorded for each species was retained for analysis (but is presented as a proportion of maximum female SVL in fig. 1C and table 1). Clutch sizes were taken from studies that reported average observed clutch sizes; one value was taken per species for each study surveyed. A species average was then calculated based on the mean of all literature records for that species (table 1). Detailed records for these variables can be found in the supplemental material (supplementary table S1).

Prior to island-mainland comparisons we examined the allometry of SSD in *Microlophus*. As suggested for empirical tests of allometry (Fairbairn, 1997) we calculated the slope of the reduced major axis (RMA) regression of log_{10}(maximum female size) on log_{10}(maximum male size) for all species, where the null hypothesis states that the allometric slope is isometric ($b = 1$); i.e., as female size increases, there is a commensurate increase in male size. In this case, a slope significantly lower than 1 (male size increases outpace female size increases allometrically) would support the presence of Rensch's rule (Rensch, 1950), indicating that stronger selection on male body size, potentially through sexual selection, could be driving SSD patterns. We expected a male-divergent pattern of allometry given the apparent influence of sexual selection on male *Microlophus* (Watkins, 1996; Miles, Snell and Snell, 2001), which would be particularly strong in insular species. We also performed a phylogenetic RMA regression (Revell, 2012) to account for phylogenetic relatedness. To this end, a phylogenetic hypothesis for *Microlophus* was

Table 1. Body size and life history traits in *Microlophus* lizards. The sexual dimorphism index (SDI), maximum male and female SVL (in mm), average clutch size and the proportional female maturity size (proportional to maximum female SVL) per species are shown. ND = no data available.

	Species	SDI	Max. SVL males	Max. SVL females	Avg. clutch size	Proportional maturity size (females)
Island	*M. albemarlensis*	0.471	125	85	2.1	0.85
	M. barringtonensis	0.353	115	85	3	0.84
	M. bivittatus	0.400	105	75	ND	0.63
	M. delanonis	0.393	155	111.3	3.6	0.75
	M. duncanensis	0.235	105	85	ND	ND
	M. grayii	0.294	110	85	ND	ND
	M. habelii	0.278	115	90	2.5	0.84
	M. indefatigabilis	0.307	98	75	2.3	0.76
	M. jacobii	0.250	100	80	2	0.74
	M. pacificus	0.167	105	90	3	0.84
Mainland	*M. atacamensis*	0.259	129.3	102.7	4.5	ND
	M. heterolepis	0.540	130	84.4	4	ND
	M. koepckeorum	0.191	81	72.8	3.1	0.69
	M. occipitalis	0.231	80	65	4	0.68
	M. peruvianus	0.443	140	97	3.7	0.52
	M. quadrivittatus	0.253	146	116.5	3.4	0.58
	M. stolzmanni	0.380	138	100	2.9	0.48
	M. tarapacensis	0.308	110.4	84.4	4.5	ND
	M. theresiae	0.338	107	80	3.2	0.69
	M. theresioides	0.090	120	110.1	2.8	0.53
	M. thoracicus	0.237	94	76	2.8	0.61
	M. tigris	0.458	105	72	3.4	0.68
	M. yanezi	0.207	109	90.3	ND	ND

trimmed from the squamate phylogeny of Pyron, Burbrink and Wiens (2013). The trimmed phylogeny included 19 of the 23 *Microlophus* species (*M. barringtonensis*, *M. indefatigabilis*, *M. jacobii* and *M. tarapacensis* were not present in the original phylogeny).

To test for differences in proportional head traits between insular and continental species, we performed analyses of variance (ANOVA) with each of the $\log_{10}$-transformed traits and locality (island vs. mainland) as factors and $\log_{10}$-transformed SVL as a covariate. Since the hypothetical differences in head proportions might be relevant only for adult males, we repeated these analyses using only specimens whose SVLs were larger than the maximum reported female SVL of their species (table 1) to reduce the potential for error due to sex misclassifications. To account for phylogenetic relatedness, we calculated the average SVL and head dimensions from the three largest males per species. Then, we performed phylogenetic generalized least squares (PGLS) regressions (function "gls" from *nlme*, Pinheiro et al., 2018) between each head trait and SVL, with locality as a factor (e.g., head length ∼ body size + insularity). Finally, we compared $\log_{10}$-transformed female size at maturity and clutch size between island and mainland species accounting for the effect of body size using PGLS regressions (e.g., clutch size ∼ female body size + insularity) and performing ANOVAs on the obtained models. We used the option corPagel to estimate Pagel's λ in all PGLS regressions of

this study (Paradis and Schlieb, 2019). All analyses were performed in R (R Core Team, 2019).

Our results indicated that all *Microlophus* species exhibit male-biased SSD, with males being on average 31% larger than females (mean SDI = 0.31, range = 0.09–0.54, table 1). The average SDI values were 0.31 and 0.30 for insular and continental species respectively, and were not significantly different (phylogenetic ANOVA, $F_{1,17} = 0.153$, $p = 0.70$). Body size was not different between island and mainland species when comparing males ($F_{1,17} = 0.10$, $p = 0.75$) or females ($F_{1,17} = 0.01$, $p = 0.92$), indicating no evidence for the island rule (i.e., smaller and larger taxa exhibiting trends towards gigantism and dwarfism on islands, respectively; Meiri, 2007). The linear RMA relationship between female and male size was not significantly different from isometry ($b = 0.88$, 95% confidence interval = 0.66–1.16). Similarly, the phylogenetic RMA
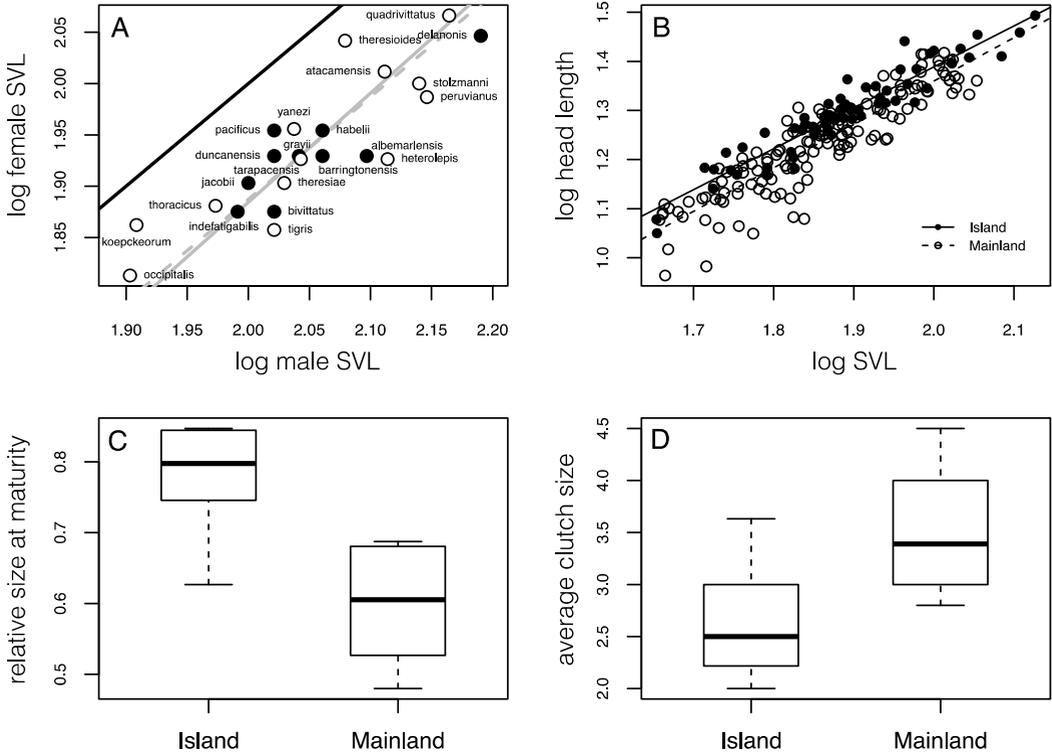
Figure 1. The allometry of SSD and island-mainland comparisons in *Microlophus*. (A) Phylogenetic RMA regression of $\log_{10}$(female size) on $\log_{10}$(male size). Model and isometric relationship are represented by solid and dashed grey lines, respectively. Solid black line represents a 1:1 relationship. Closed circles = island species, open circles = mainland species. Species names are shown. (B) Linear relationship between SVL and head length. Closed circles and solid line = island individuals, open circles and dashed line = mainland individuals. (C–D) Comparison between island and mainland *Microlophus* for (C) relative size at maturity in females and (D) average clutch size.

did not show a significant departure from isometry (H0: $b = 1$, $p = 0.69$; estimated $b = 1.06$; fig. 1A). Regarding head traits, insular individuals exhibited proportionally longer heads than continental ones (ANCOVA, $F_{1,201} = 34.64$, $p < 0.001$, fig. 1B). However, no differences between island and mainland were found for head height ($F_{1,201} = 0.125$, $p = 0.724$) and head width ($F_{1,201} = 2.127$, $p = 0.146$). Analyses considering only males led to the same conclusions (island lizards have longer heads; $F_{1,43} = 4.883$, $p < 0.05$). No significant interactions were found between SVL and localization (island vs. mainland) for any of the traits, suggesting that species from both localities have similar head allometric trajectories. Similarly, the results from the PGLS regressions

indicated that insular species have proportionally longer heads than continental ones (PGLS, $F_{1,14} = 6.0$, $p < 0.05$, $\lambda = 1.03$), but no significant differences were found for head height ($F_{1,13} = 0.0$, $p = 0.94$, $\lambda = -0.21$) or width ($F_{1,13} = 1.0$, $p = 0.43$, $\lambda = -0.34$).

The average proportional size at maturity of females (female size at maturity/maximum female SVL) was 0.78 (± 0.08) for island species and 0.60 (± 0.08) for continental ones (fig. 1C, table 1). Female size at maturity increased with maximum female body size (PGLS, $F = 29.0$, $p < 0.01$). After accounting for this effect, females of island species showed proportionally larger sizes at maturity than females from mainland species ($F_{1,11} = 23.32$, $p < 0.001$, $\lambda = 0.81$). Average

clutch size was 2.65 (±0.58) for island species and 3.52 (±0.61) for mainland ones (fig. 1D, table 1). Average clutch size was not related to maximum female body size ($F = 0.20$, $p = 0.66$), but was significantly larger in continental species when compared to insular species ($F_{1,12} = 10.88$, $p < 0.01$, $\lambda = -0.25$).

Our results represent the first effort to compile and summarize the available information on body size, SSD and life history traits in *Microlophus*, a genus of iguanian lizards distributed in Western South America and the Galápagos Islands. Contrary to our expectations, we found no differences between the SDI of mainland and island species and the RMA analyses showed an isometric relationship between female and male body sizes. This latter result is compatible with previous analyses that showed similar patterns of isometry in other Tropidurid lizards (Brandt and Navas, 2013), suggesting that selection on male body size is not the only factor driving patterns of SSD in this family. When compared to the mainland, insular habitats often represent unusual ecological settings (e.g., lower predation pressure) that could promote the evolution of male-biased SSD through the evolution of K-selected reproductive strategies (Andrews, 1979). The fact that SSD is similar between island and mainland species suggests that both localities might not differ in characteristics such as predation or resource availability, which in turn could result in them exhibiting similar population densities and sex ratios (Emlen and Oring, 1977). Such ecological similarities could be a result of contemporary anthropogenic activities: Galápagos *Microlophus* are known to be heavily predated by recently introduced fauna (e.g., cats, Carrión and Valle, 2018) which could be equalizing the predation pressure difference usually noted between mainland and islands environments.

Insular species had relatively longer heads than continental ones (fig. 1B). Head length has been previously associated with bite force and reproductive success in other lizard taxa

(Herrel et al., 2001), supporting the hypothesis that insular *Microlophus* lizards invest more resources in intrasexual competition. However, even though larger head widths and heights have also been linked to stronger bite force, no differences in these traits were found between localities. A potential alternate explanation for our results could be diet. Skull shape in lizards is also known to influence what food items may be consumed efficiently; e.g., it has been shown that harder food items require stronger bite forces to be consumed (Herrel et al., 2001; Metzger and Herrel, 2005). Habitat use is also known for constraining head shape. For example, lizards with a saxicolous lifestyle require flatter heads and bodies, potentially interfering with the influence of sexual selection (e.g., Kaliontzopoulou, Carretero and Adams, 2015). Relationships between diet type, habitat use, and head morphology have already been reported for continental *Microlophus* species (Toyama et al., 2018) and tropidurid lizards in general (Kohlsdorf et al., 2008; Toyama, 2017), suggesting that natural and sexual selection may act simultaneously in shaping head morphology in these lizards. Further research involving measurements of bite force performance and additional head traits not considered in this study should help uncover the role of head shape in male-male antagonistic interactions in *Microlophus*.

As expected, mainland species showed, on average, smaller relative female sizes at maturity and larger clutch sizes than island species (fig. 1C, D). These patterns were expected based on the theoretical differences between insular and continental habitats and are consistent with the contrasting life history strategies seen in other island-mainland lizard systems (e.g., Schwarz and Meiri, 2017). Additionally, these results support the potential importance of fecundity selection acting on female body size in driving SSD patterns in *Microlophus*. The isometric scaling between male and female sizes might be caused by selection for larger female sizes, not only to increase clutch size

on the mainland, but potentially to increase egg size in island species. Published data on egg dimensions are, however, scarce for *Microlophus* and future studies that include female body shape and egg size measurements from island and mainland species are needed to test this hypothesis.

These findings illustrate the potential of *Microlophus* as an island-mainland system for testing evolutionary hypotheses. Future morphological, behavioural, ecological and life history studies are necessary to fill the gaps indicated by this compilation; only an integrative view of this system will fully elucidate the different evolutionary processes experienced by island and mainland *Microlophus* lineages.

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