

## SIMILAR FEEDING ECOLOGIES, DIFFERENT MORPHOLOGIES IN *LIOLAEMUS PICTUS* (DUMÉRIL & BIBRON, 1837) (LIOLAEMIDAE) FROM CHILOÉ ARCHIPELAGO, CHILE

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### ABSTRACT

Insularity promotes dietary divergence in vertebrates due to changes in biotic parameters as intra-specific competition, predation and resource availability. *Liolaemus pictus* is a lizard species from Southern Chile that has populations in mainland and insular territories. The aim of this paper was to test the correlation between dietary preferences and morphological differences between mainland and insular populations. We did not find differences in the dietary composition, but the proportion of the consumption of Coleoptera and Hymenoptera is higher in the mainland. Herbivory is present in both populations and there is no relation between the diet and the morphology. The presence of herbivory could be related with reduced prey availability, conditions that could be present in islands and high elevation environments.

**Keywords:** Diet; Herbivory; Insularity; Morphology; Populations

### RESUMEN

La insularidad promueve divergencia dietaria en vertebrados debido a cambios en los parámetros bióticos así como la competencia intraespecífica, depredación y la disponibilidad de recursos. *Liolaemus pictus* es una especie de lagartija del sur de Chile con poblaciones en territorio continental e insular. El objetivo de este trabajo es probar la correlación entre las preferencias dietarias y las diferencias morfológicas entre las poblaciones continentales e insulares en esta especie. Los resultados no mostraron diferencias en la composición de la dieta, pero la proporción del consumo de Coleoptera e Hymenoptera es más alta en continente. La herbivoría está presente en ambas poblaciones y no hay relación entre la dieta y la morfología. La presencia de herbivoría podría estar relacionada con la reducida disponibilidad de presas, condición que podría estar presente en islas y en ambientes de altura.

**Palabras clave:** Dieta; Herbivoría; Insularidad; Morfología; Poblaciones

### INTRODUCTION

Dietary differentiation can be a key mechanism for the adaptation to an heterogeneous habitat, which promotes a morphological change in ecological time (Adams and Rohlf 2000). The most studied morphological differentiation associate to diet is the island-mainland isolation (Olsen and Valido 2003). This is explained by the absence or reduction in predators on island in comparison to the mainland, which increases intraspecific competition and could produce dietary changes (Rocha *et al.* 2004; Godínez-Álvarez 2004). Specifically in reptiles, it has been shown that in conditions of isolation they can reach high population densities (density compensation) because of the absence of predators. In parallel, the diversity and abundance of insects on islands tend to be lower than in the mainland, favoring dietary expansion, particularly, towards herbivory (Olsen and Valido 2003). In this way, both factors favor a dietary expansion towards herbivory (Olsen and Valido 2003; Godínez-Álvarez 2004).

The genus *Liolaemus* has been considered an evolutionary dynamic group from South America by high species richness, endemism, and an extensive intraspecific morphological variation (Victoriano *et al.* 2008; Avila *et al.* 2010). It has more than 230 described species found mainly in Argentina and Chile

(Etheridge and Espinoza 2000; Schulte *et al.* 2000; Avila *et al.* 2010; Lobo *et al.* 2010). In Chile, there are species that live in the continent and insular territories (*i.e.* *L. cyanogaster*, *L. nigromaculatus* and *L. pictus*; Donoso-Barros 1966, Pincheira and Nuñez 2005). *Liolaemus pictus* has one of the most austral distributions in Chile, which extends from Concepción to the islands of the Chiloé Archipelago [37°S-44°S] (Velloso and Navarro 1988). Six subspecies of *L. pictus* have been described on the basis of morphological traits and geographic distribution (Donoso-Barros 1966, 1970; Urbina and Zúñiga 1977; Pincheira and Nuñez 2005), four of them restricted to the south central Chile (36°-43°S). In this study we will focus on two of them, one from the mainland (*L. p. pictus*) and the other from an island (*L. p. chiloensis*).

Anecdotal evidence indicates that mainland populations feed primarily on invertebrates, whereas island populations feed on fruit (Ortiz 1974; Wilson *et al.* 1996). Vidal *et al.* (2006) hypothesized that morphometric differences among *L. pictus* from the mainland and Chiloé Island are evidence of insular divergence resulting from diet differences (see also Ortiz 1974; Wilson *et al.* 1996). Moreover, Vidal *et al.* (2006) demonstrated that the specimens from the Chiloé have morphological differences in head structures (the terminal portion of the mouth is more posterior) with respect to the mainland counterparts. These authors suggested that dietary differences could be related with this morphological divergence.

The goal of this study is to compare the dietary composition of two populations of *L. pictus*, one from an insular territory (*L. p. chiloensis*) and another from the mainland (*L. p. pictus*). According to previous antecedents, our prediction is that the insular population will present a low consumption of insects, but a high degree of fruit consumption in comparison to the mainland population. We expect to find bigger preys (fruit mainly) in lizards with bigger mouth aperture (island population).

#### MATERIALS AND METHODS

The sampling was done during January of 2004 on the austral summer from Isla Grande de Chiloé (south of Ancud, 41°55'46"S, 73°53'36"O; 141 m) and the mainland (Antillanca volcano, 40°46'67"S, 72°12'86"O; 1011 m). Animals (n=30 Isla Grande de Chiloé, n=22 Antillanca) were weighted ( $\pm 0.01$  g), euthanized with T61© and stored in liquid nitrogen for posterior analysis of stable isotopes (results published on Vidal and Sabat 2010). Samples were transported to the laboratory in Santiago de Chile where all analyses were performed. In the laboratory, specimens were thawed and the entire digestive tract was removed and deposited in ethanol 70°. Gut contents were thawed and prey items were separated, counted and identified to the lowest possible taxonomic level, based on the keys of Peña (1986) and Lazo (2002). The plant items were classified at the species level based in the comparison with dry samples, where the plant content is quantified in terms of the number of seeds of the plants consumed. For each sample, the frequency of occurrence and the percent composition of prey taxa by number (percent number) were calculated. Frequency of occurrence is the percentage of all non-empty stomachs containing food in which prey taxon *i* was found and percent number is the percentage that prey taxon *i* contributes to the total number of food items in all stomachs (Bowen 1996). The relative importance index, RI (George and Hadley 1979) was calculated as:  $RI_i = 100AI = \Sigma AI$  where  $AI = (\% \text{ frequency of occurrence of animal or plants content} + \% \text{ total number of animal or plants content})$  is the absolute importance of prey taxon *i*. This index reduces the amount of bias that may occur if measures are used separately (Wallace 1981). The heads were photographed in a lateral view with a Sony Mavica camera. Based on the photograph was calculated the proportion Mouth Length (ML)/Head Length (HL) using the system of measurement in mm. The ML was measured from the peak of the rostral scale to the fold of the commissure of the mouth, while the HL was measured considering the maximum height (mm) of the head. Finally, the specimens were deposited in the herpetological collection of the Museo de Zoología Universidad de Concepción (MZUC).

Prior to statistical analyses, the variables were examined for assumptions of normality and homogeneity of variance, using Kolmogorov–Smirnov and Levene tests, respectively. Differences of diet composition among localities (Chiloé Island) (n = 30) and Antillanca (n = 22) were tested by one-way ANOVA in the software Statistica\* 1998, Version 5.1 (Statsoft, Inc. USA.) using locality as a factor. The dependent variables were the different prey items. The height, length and width for each complete prey were estimated

using an ocular micrometer with  $\pm 0.005$  cm sensitivity. The volume was estimated considering the prey as a parallelepiped following Díaz-Páez and Ortiz (2003) and then it was related with the proportion ML/HL (Sokal and Rohlf, 1995; Berrios *et al.*, 2002). The correlation was quantified using the Pearson correlation coefficient because is used when the data follow a normal distribution to check whether two quantitative variables have a linear relationship to each other.

## RESULTS

The diet composition of *L. pictus* included 18 taxonomic groups (Table 1). On average, 92% corresponds to invertebrate preys, while the remainder corresponds to vegetation (fruits and seeds). Of these, mainland lizards consume on average 91% invertebrates and 9% vegetation, and island lizards consume 93% invertebrates and 7% of vegetation. We found no significant differences between mainland and island populations for both invertebrate (ANOVA,  $F_{1,95}=1.27$ ;  $p=0.1$ ) and fruit (ANOVA,  $F_{1,95}=0.07$ ;  $p=0.1$ ) consumption. For each locality, the RI varied in the taxonomic origin of prey. In both, mainland and island localities, Diptera, Coleoptera and Hymenoptera were the more represented items, whereas seeds of *Nertera granadensis* were those of high importance in vegetation prey. However, other prey were relevant in the diet from mainland as Dermaptera, and Thysanoptera, while the diet from island Odonata, Quilopoda and *Gaultheria* sp. were the more consumed prey (Table 1). On the other hand, there is no relationship between the volume of the prey and the proportion ML/HL of the lizards (Figure 1) neither in the mainland ( $r = 0.17$ ,  $p = 0.297$ ) or in the island ( $r = 0.42$ ,  $p = 0.054$ ). By using ML/HL we remove any allometric effect where specimens could eat bigger preys, just because they have a larger body size. The ML/HL ratio allows detecting when the ML is proportionally larger independently of the actual size of the lizard.

TABLE 1. Frequency of occurrence (%FO), percentage by number (%Number) and Index of relative importance (RI) of prey taxa in the diets of *Liolaemus pictus* from island and mainland localities. Chiloé Island (CHI, n = 30); Antillanca (ANT, n = 22). Samples sizes (n) refer to the total number of lizard stomachs examined.  
Data based on Vidal *et al.*, 2010

Prey item	%FO		%NUMBER		RI	
	CHI	ANT	CHI	ANT	CHI	ANT
Homoptera	23.3	22.7	6.3	3.9	7.7	5.7
Dermaptera	0	4.5	0.0	0.5	0.0	1.1
Lepidoptera	10.0	18.2	3.6	1.9	3.5	4.3
Odonata	3.3	0	0.3	0.0	0.9	0.0
Orthoptera	10.0	31.8	1.2	6.7	2.9	8.2
Diptera	36.6	54.5	14.2	19.3	13.2	15.8
Thysanoptera	0	9.1	0.0	0.4	0.0	2.0
Hemiptera	26.7	31.8	3.8	5.6	7.9	8.0
Coleoptera	83.3	86.4	49.0	38.4	34.2	26.7
Hymenoptera	53.3	40.9	7.7	10.0	15.8	10.9
Aracnidae	16.7	4.5	7.2	0.3	6.2	1.0
Quilopoda	3.3	0	1.1	0.0	1.1	0.0
Gastropoda	0	13.6	0.0	1.0	0.0	3.1
Insecta larvae	0	18.2	0.0	1.9	0.0	4.3
<i>Galium hypocarpium</i>	0	4.5	0.0	3.0	0.0	1.6
<i>Nertera granadensis</i>	10.0	18.2	2.6	3.8	3.3	4.7
<i>Gaultheria</i> sp	3.3	0	1.7	0.0	1.3	0.0
Vegetal rests	6.6	9.1	1.3	3.5	2.0	2.7
Total Invertebrates	100	100	94.4	89.7	93.4	91.0
Total Vegetation	13.3	18.2	5.6	10.3	6.6	9.0

## DISCUSSION

The diet of both localities is integrated by Coleoptera, Diptera, Homoptera and Hymenoptera. These results are very similar to the once described by Vidal and Sabat (2010) and previously Ortiz (1974) in a mainland population. The same lack of divergence in the dietary composition has also been described for another species of lizard present in Ilha Grande, Brazil (Rocha *et al.* 2004). The relative importance values are higher in Antillanca than Chiloé, suggesting a potential higher abundance of insects in the mainland. The consumed proportion of Coleoptera in Chiloé is similar to *L. p. talcanensis* on the island of Talcán (Urbina and Zúñiga 1977). In other words, the data from this study shows that in the continent the relative importance of many items is similar, while in the island only a small proportion of them are relevant (Ortiz 1974; Urbina and Zúñiga 1977; Vidal and Sabat 2010; Cotoras and Vidal this study). It is important to point out that the prey items are very similar in both subspecies, but the total amounts are different.

In the insular populations of *L. pictus* there are records of plants as sources of food (*N. granadensis*, *G. hypocarpium*, *G. magellanica*, seeds of grasses, among others; Urbina and Zúñiga 1977; Wilson *et al.* 1996). According to Sih and Christensen (2001), the optimal diet theory's includes fruits as non-mobile prey that contributes in a lower energetic expenditure for the predator. In this way, the classic prediction is that for the same species of lizard, the insular population would expand the diet incorporating other prey items as fruits, flowers or nectar. This is explained for changes in the biotic variables of the environment as intraspecific competence, predation pressure, availability of prey, etc. (Olsen and Valido 2003). The data from this study shows that on the island there is a high frequency of seed (40%) in relation with the other items. Nevertheless, in the mainland they are also present. Indeed, the continent has a higher percentage by number. This scenario has been previously hypothesized by Godínez-Álvarez (2004).

The explanation for herbivory in the mountain environment (Antillanca) could be related with two factors: (1) a potential reduced availability of insects due to montane conditions and (2) a phylogenetic element (Espinoza *et al.* 2004). The herbivory in Squamata has an origin previous to a diversification event that happened between the upper Triassic and the early Jurassic (Vitt 2004). In this divergence event the Iguania separated from the Scleroglossa; the first group retained the ancestral condition of herbivory while the second turned into carnivory. This is congruent with the findings of a literature review in lizard omnivory that indicates "evolution towards herbivory is only mildly constrained by functional tradeoffs" (Herrel *et al.* 2004). However, only 2% of the more than 7,800 species of Squamata are herbivores (Espinoza *et al.* 2004). They are mostly big sized lizards with high body temperature that live in tropical areas (Sokol 1967; Vitt 2004). Nevertheless, in the group Liolaemidae (small lizards from cold environments, Schulte *et al.* 2000) the herbivory presents nearly nine independent origins (Espinoza *et al.* 2004). Espinoza *et al.* (2004) indicate that these multiple origins are related with the life in high elevation environments in the Andes, where there are similar conditions than the one on continental islands. These similar conditions are specifically related with scarcity of insects, absence of many predators and geographic isolation. Indeed the aridity has been suggested as another factor that could induce herbivory (Cooper and Vitt 2002), but this is not be an important factor in the Antillanca locality.

On morphology, the differences between both populations are not related with the size of the consumed preys (Fig. 1). The lack of relation on these variables has been reported also in frogs (Díaz-Páez and Ortiz 2003), salamanders (Parker 1994) and other insular lizards (Valido and Nogaes 2003).

These findings are congruent with stable isotopes studies and gut morphology on the same populations, which also have shown an absence of significant differences (Vidal and Sabat 2010). In terms of genetic differentiation, the insular and mainland populations do not share haplotypes and their divergence time is older than the last glaciación (Vidal *et al.* 2012). Then, interestingly, even if at the genetic level there is a clear divergence it does not have a correlation with other phenotypic variables. This situation could be explained by a precondition to herbivory present on the species, idea that has been previously suggested (Herrel *et al.* 2004). However, this tendency differs from what has been reported for the insular population of the lizard *Mabuya agilis* in the island of Ilha Grande, Brazil, where the prey size is affected by lizard body and head size (Rocha *et al.* 2004). In terms of behavioral ecology, there are studies that show big be-

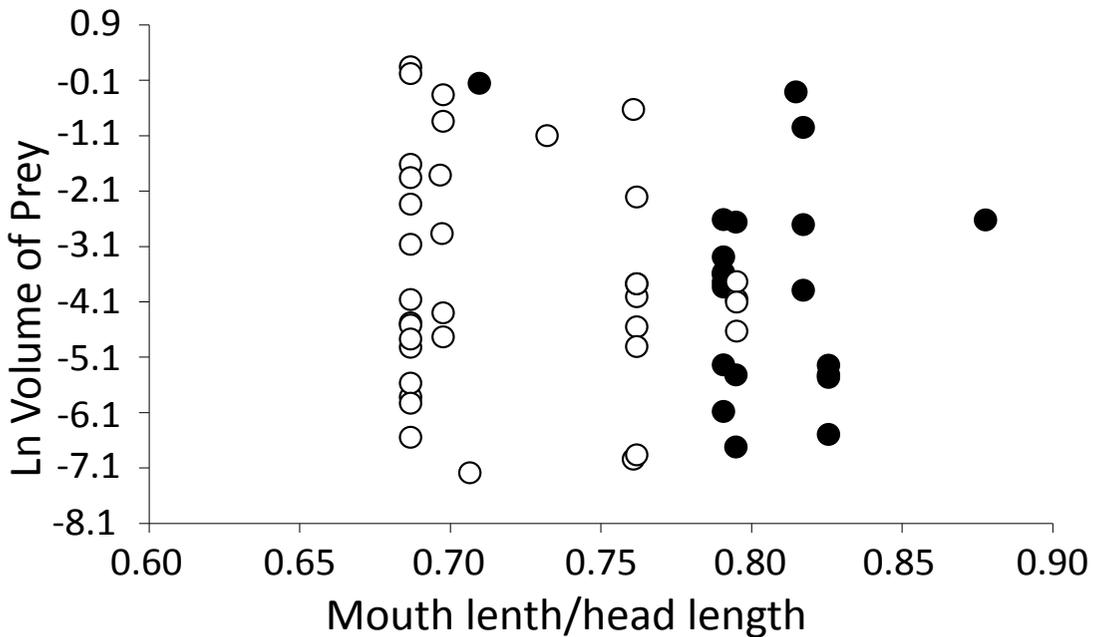


FIGURE 1. Relation between the proportion Mouth length/head length and the prey volume on *Liolaemus pictus* from mainland (open circles) and island (close circles)

havioral differences between insular and mainland populations of lizards. That is the case of the *Podarcis* lizards on continental Spain and the island Columbrete Grande, the island population tend to prey on scorpions, but not the one on the mainland (Castilla *et al.* 2008). Another dramatic change has been described for another species in the same genus, *P. sicula*. In 1971 a small population was introduced in the islet of Pod Mrčaru from the islet of Pod Kopašće (Croatia). The new population evolved rapidly changes in population density, social structure, external and internal morphology. Associated with the morphological changes there was an increase in the herbivory (Herrell *et al.* 2008). However, more detailed studies are required on *L. pictus* to explain why even if there is a strong genetic break between island and mainland populations (Vidal *et al.* 2012), there are no big differences in morphology and feeding ecology.

In conclusion, there is not a direct correlation between the size of the prey and the facial morphology of *L. pictus*. The most important prey items for both populations of *L. pictus* are Coleoptera and Hymenoptera. There are differences in the total numbers, been higher in the mainland. Finally, the presence of herbivory on both sites can be explained by similar factors present on both environments and a phylogenetic propensity to herbivory on the group.

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