Herbivory in *Liolaemus poecilochromus*, a Small, Cold-Climate Lizard from the Andes of Argentina

María Soledad Valdecantos[1], Federico Arias[1], and Robert E. Espinoza[2]

Herbivory is generally thought to be restricted to reptiles with large body sizes that live in warm climates. We show that *Liolaemus poecilochromus* is primarily herbivorous (>80% plants in diet) even as juveniles, making them the smallest herbivorous reptile known. We detected relatively few differences in diet between the sexes, despite male-biased sexual dimorphism in head and body size. Adults consumed more mites and flowers than juveniles, and we detected a weak ontogenetic shift from omnivory to herbivory that is attributable to the lower volumetric consumption of plants by juvenile males. We discuss the abiotic and biotic conditions that likely selected for herbivory in this and other small-bodied, high-elevation *Liolaemus*.

Herbivoría en general se cree que se limita a los reptiles con cuerpos grandes que viven en climas cálidos. Mostramos que *Liolaemus poecilochromus* es principalmente herbívora (>80% de plantas en la dieta) incluso los juveniles, convirtiéndolo por esto en el reptil herbívoro más pequeño conocido. Asimismo, detectamos pocas diferencias en la dieta entre los sexos, a pesar del dimorfismo sexual a favor de los machos en el tamaño de la cabeza y el cuerpo. Los adultos consumen más ácaros y flores que los juveniles, por otro lado se detectó un cambio ontogenético débil de omnivoria a herbivoría en los machos juveniles, debido a su bajo consumo de plantas. Discutimos las condiciones abióticas y bióticas que probablemente favorecieron la herbivoría en este y otros *Liolaemus* de cuerpo pequeño y alta elevación.

AN animal's diet can be a fundamental determinant of other aspects of its biology including morphology, physiology, ecology, and behavior. Most herbivorous reptiles, for example, share a suite of characteristics that are considered to facilitate the procurement, digestion, and assimilation of plants. Among these characteristics, conventional wisdom once held that herbivory was restricted to reptiles with large body sizes that lived in warm climates (Pough, 1973; Wilson and Lee, 1974; Iverson, 1980, 1982; Van Devender, 1982; Zimmerman and Tracy, 1989; Cooper and Vitt, 2002; Vitt, 2004). From an ecophysiological perspective, these ''rules'' of herbivory (*sensu* Espinoza et al., 2004) make good sense. First, plant tissues have relatively less assimilable energy and nutrients than animal tissues (Zimmerman and Tracy, 1989; Van Soest, 1994), requiring herbivores to be more metabolically conservative or efficient than nonherbivores. Larger bodies partially afford herbivores this energetic efficiency, because large bodies have lower mass-specific energy demands (Pough, 1973; Wilson and Lee, 1974). Additionally, foraging for plants is considered to be less energetically demanding than chasing small arthropods (Pough, 1973). Large body cavities can also accommodate the long and voluminous guts needed to digest plant tissues (Iverson, 1980, 1982). Second, warm climates provide opportunities to achieve the high body temperatures that are apparently needed to digest plants (Zimmerman and Tracy, 1989; Schall and Dearing, 1994; Espinoza et al., 2004; Vitt et al., 2005).

Recently, these rules of herbivory were challenged by the finding that small-bodied, cold-climate liolaemid lizards (*Liolaemus* and *Phymaturus*) have repeatedly and independently evolved herbivory—apparently more times than for all other squamates combined, and at a much faster rate (Espinoza et al., 2004). All but one of these origins of herbivory was found in *Liolaemus*, the largest clade of liolaemid lizards, which currently has >220 species (Lobo et al., 2010a). Species of *Liolaemus* are distributed over most of arid and semiarid southern South America from sea level to >5000 m and range in body size (snout–vent length; SVL) from approximately 50–115 mm (Espinoza et al., 2004). Although herbivorous species of *Liolaemus* are, on average, larger than their nonherbivorous congenerics, they are nonetheless the smallest herbivorous lizards known (Espinoza et al., 2004; O'Grady et al., 2005). Yet for most herbivorous *Liolaemus*, detailed diet analyses are lacking. For example, it is not known whether intraspecific variation in morphology (i.e., sexual dimorphism in body and head size) is reflected in the diet. Such differences might be expected for lizard species that exhibit sexual dimorphism in head size because plants and hard-bodied prey (e.g., beetles) require greater bite force for oral processing, which is afforded by relatively short snouts and tall, wide heads (Stayton, 2005, 2006; Herrel, 2007; Vanhooydonck et al., 2007; Herrel et al., 2008). Likewise, it is not known whether herbivorous liolaemids undergo ontogenetic diet shifts (insectivory to omnivory to herbivory), as has been reported for other small omnivorous and herbivorous lizards (Pough, 1973; Ballinger et al., 1977; Schluter, 1984; Greer, 1989; Duffield and Bull, 1998; Rocha, 1998; Durtsche, 2000; Fialho et al., 2000).

Here we describe the diet composition of *Liolaemus poecilochromus*, a small-bodied (<70 mm SVL), high-elevation (3500–4130 m) lizard from the Andes of northwestern Argentina. This species was previously classified as omnivorous (Espinoza et al., 2004) based on specimens collected over what was considered the range of the species at that time. Ongoing studies of the species limits among and within taxa belonging to the *L. andinus* group (including *L. poecilochromus*) indicate that the ''*L. poecilochromus*'' sampled by Espinoza et al. (2004) represents more than one species (Lobo et al., 2010b). Thus, a reanalysis of the diet of individuals collected from the vicinity of the type locality (Catamarca, Argentina) is warranted.

[1] Cátedras de Anatomía Comparada e Histología Animal, Facultad de Ciencias Naturales, Universidad Nacional de Salta, Avenida Bolivia 5150, Salta 4400, Argentina.

[2] Department of Biology, California State University, Northridge, Northridge, California 91330-8303; E-mail: Robert.e.espinoza@csun.edu. Send reprint requests to this address.

Our study addresses three principal questions. First, is the diet of *L. poecilochromus* consistent with the former ''rules'' of herbivory for lizards—specifically, is the proportion of plant matter eaten by this species unusual relative to similarly sized lizards? Second, is male-biased size dimorphism in body and head size reflected in the proportion of plants or other items in the diet (e.g., hard-bodied prey)? And third, does *L. poecilochromus* exhibit an ontogenetic shift in diet (i.e., increasing the proportion of plants in the diet with increasing body size)? We tested these hypotheses on a population of *L. poecilochromus* occurring approximately 55 km (straight line) from the type locality, which is Los Nacimientos, Departamento Antofagasta de la Sierra, Catamarca (Laurent, 1986).

MATERIALS AND METHODS

Field site and specimen data.—*Liolaemus poecilochromus* is distributed in the high-elevation Puna regions of Catamarca and Salta provinces of northwestern Argentina (Laurent, 1986; Cei, 1993). The Puna is high-desert phytogeographic province characterized by its extreme climatic conditions: high daily and seasonal variation in air temperature (-20 to $30°$C), low annual precipitation (100–200 mm), low partial pressure of oxygen, and among the most intense measures of solar radiation recorded on the planet (Cabrera, 1994; Piacentini et al., 2003; Lobo et al., 2009). We studied a population of *L. poecilochromus* along the margins of the Salar del Hombre Muerto, Departamento de Antofagasta de la Sierra, Provincia de Catamarca (25°29′31.79″S, 67°06′46.63″W, 3986 m). The region surrounding this massive saltpan is generally rocky with extensive volcanic extrusions and the vegetation, where present, is dominated (albeit patchily so) by ''tola'' or small spiny shrubs (primarily *Ademsia* spp., Fabaceae) and *Festuca* bunch grass (Cabrera, 1994; Martínez Carretero, 1995; Lobo et al., 2009). Both arthropod species richness and abundance are relatively low in Puna habitats (Mann, 1968; de Morales, 1994). The only other lizard species known from the region of our study site is *L. dorbignyi* (Lobo et al., 2009). Although the diet of *L. dorbignyi* has not been studied, a closely related species, *L. scrocchii* (recently recognized as distinct from *L. dorbignyi*; Quinteros et al., 2008), is principally herbivorous (Espinoza et al., 2004; O'Grady et al., 2005; Abdala et al., 2008).

In 2006, we collected 60 *L. poecilochromus* by hand or noose during two sampling periods: 22 January ($n = 18$) and 10 March ($n = 42$), which correspond to mid and late summer, respectively and are the peak activity period of this species (Lobo et al., 2009). Lizards were killed via an injection of sodium pentothal immediately after capture, fixed in 10% formalin, preserved in 70% ethanol, and deposited in the herpetological collection of the Museo de Ciencias Naturales (MCN) at the Universidad Nacional de Salta, Argentina (January: MCN 1987–89, 1991–92, 1994–2006; March: MCN 2053–77, 2079–95). Age classes (juvenile and adult) and sexes were determined via examination of gonads following Valdecantos et al. (2007). The combined samples included 28 juveniles (13 females, 15 males) and 32 adults (20 females, 12 males). We measured the SVL, trunk length (axilla–groin distance), and head dimensions (length, width, and height) of each preserved specimen with digital calipers ($\pm$ 0.05 mm) following Lobo et al. (2010b).

Stomach-content analysis.—A longitudinal incision was made in the belly region of each lizard to expose the gut, and the stomach was opened with a transverse incision to reveal the contents. We used forceps and gently flushed stomachs with 70% ethanol from a 1 ml syringe to recover all stomach contents. Contents were placed into prelabeled 1.5 ml plastic vials and covered with 70% ethanol for subsequent microscopic examination (10–200×). Arthropod prey were determined to taxonomic order, except Coleoptera and Hymenoptera, which were identified to family. We determined the frequency (number of individuals with a particular prey type in their stomach) and counted the number (number of a particular prey type in each stomach) of prey for each lizard. Prey volume (V) was estimated from the length (L) and width (W) of each prey item using the formula for a prolate spheroid: $V = 4/3 \pi (L)(W)^2$, where L is ½ prey length and W is ½ prey width (Vitt, 1991). For plant items, we counted the number of flowers and combined fruits + seeds in each lizard stomach, but we were unable to determine the number of leaves because some were leaflets of compound leaves and most were fragmented (bitten off in pieces). We estimated the volume of plants consumed by each lizard for each of the three categories of plant tissues (leaves, flowers, and fruits + seeds) by placing the moisture-blotted tissues into scaled syringes: 1 ml tuberculin syringe (when $V < 1$ ml) or a 10 ml syringe ($V > 1$ ml).

To test whether *L. poecilochromus* exhibit differences between juveniles vs. adults or between adult females vs. males in the frequency of each diet type, we compared means for each age or sex class with a proportion k comparison test using XLSTAT v. 7.5 (Addinsoft USA, New York, NY). This test uses Monte Carlo simulations that are constrained by the sample sizes of the k groups to compute the distribution of the χ^2 distances. Thus, the simulations (5000 in this study) provide an empirical distribution with critical values that are more reliable than those obtained from the theoretical χ^2 distribution, which is asymptotic (Levine et al., 2008). If a statistical difference was detected in the overall model, we used the Marascuilo procedure in XLSTAT to identify which pair(s) of proportions was/were statistically different from each other. The Marascuilo procedure calculates the observed (M_{obs}) differences $p_j - p_{j'}$ among all $c(c-1)/2$ pairs then computes the corresponding critical range (M_{crit}) for each pairwise comparison of sample proportions:

$$M_{crit} = \sqrt{\chi_U^2} \sqrt{\frac{p_j(1-p_j)}{n_j} + \frac{p_{j'}(1-p_{j'})}{n_{j'}}},$$

where c is number of proportions compared, χ_U^2 is from the chi-square distribution with $c-1$ degrees of freedom, and p_j, $p_{j'}$ and n_j, $n_{j'}$ are the proportions and sample sizes of pair 1 and 2, respectively. Each of the $c(c-1)/2$ pairs of sample proportions is then compared to its corresponding critical range. Pairs are considered significantly different if the absolute difference in the sample proportions $|p_j - p_{j'}|$ is greater than the critical range (Levine et al., 2008).

Sexual differences between adults in body size and proportions (SVL, trunk length, and head size) were analyzed with either *t*-tests (when assumptions of normality and homogeneity of variance were met) or Kruskal-Wallis tests (when these assumptions were not met). ANCOVA (SVL as covariate) was used to test for relative differences in body proportions between the sexes.

To determine whether *L. poecilochromus* exhibit numerical or volumetric differences in diet composition as a function

of body or head size, we calculated the relative number of each animal prey type and relative volume of each prey type or plant tissues in each stomach. As some prey categories had zero values, we added 0.5 to all proportions then square-root transformed these data prior to analyses. Statistical comparisons were made with either ANOVA or a Kruskal-Wallis test, depending on whether the data met assumptions of normality and homogeneity of variance.

To determine whether *L. poecilochromus* exhibit sexual differences or ontogenetic shifts in diet (i.e., insectivory → herbivory or prey hardness), we tested for correlations between lizard body size (SVL) and head dimensions, which are proxies for bite force (Stayton, 2005, 2006; Herrel et al., 2006), with the relative volume of plant tissues or hard prey (Coleoptera with hard elytra) in stomachs. For plants, we arcsine*square-root transformed the relative volume prior to analysis. For beetles, we added 1 to the estimated beetle prey volumes then $\log_{10}$ transformed these data prior to analysis. Likewise, lizard SVL and head dimensions were $\log_{10}$ transformed prior to analysis. We used regression analysis or two-factor ANCOVA (sex and age class as factors; SVL as covariate) implemented in SuperANOVA v. 1.11 or XLSTAT v. 7.5 to test for statistical trends in these data.

To compare niche breadths (*B*) among age classes and sexes of *L. poecilochromus*, we calculated the inverse of Simpson's (1949) index:

$$B = \left[\sum_{i=1}^{n} p_i \right]^{-1},$$

where p_i is the proportion of the total diet made up of prey *i*. Finally, to estimate the overlap in food-resource use among age classes and sexes of *L. poecilochromus*, we calculated Pianka's (1973) symmetric niche overlap index (*Q*):

$$Q_{jk} = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^{2} \sum_{i=1}^{n} p_{ik}^{2}}},$$

where p_{ij} is the proportion of the total diet made up of prey *i* for age class or sex *j*, and p_{ik} is the proportion of the total diet made up of prey *i* for age class or sex *k*.

RESULTS

Arthropod prey.—The frequency, number, and volume of each prey type recovered from the stomachs of *L. poecilochromus* are summarized in Table 1. Two major clades of arthropod prey were recovered from the stomachs: (1) Hexapoda, represented by Collembola and Insecta: Diptera, Hymenoptera (principally Formicidae), Coleoptera (Curculionidae and Tenebrionidae), Homoptera, Hemiptera, Lepidoptera, Isoptera, Orthoptera, Diplura, and Thysanoptera; and (2) Arachnida, represented by Araneae, Solifugae, and Acarina (both mites and ticks). We also found larvae of Coleoptera and Lepidoptera and nymphs of Homoptera. Two scorpion pedipalps were recovered (one each from the stomachs of an adult and a juvenile), but were not included in the analyses. Although these may represent unsuccessful predation attempts, we suspect that they were the outcomes of fights. In support of this assertion, scorpions were recently reported to prey upon another high-elevation *Liolaemus* (Pérez et al., 2010), and *L. poecilochromus* and

scorpions were found in similar retreats (shallow burrows) at our study site. The most common prey (i.e., found in at least half of the stomachs of both age classes and sexes) were ants (Formicidae) and springtails (Collembola), with true bugs (Hemiptera), beetles (Coleoptera), and mites (Acarina) also commonly eaten by adults.

Herbivory.—All specimens examined had eaten plants (leaves, flowers, fruit, and/or seeds; Table 1, Fig. 1). Plant tissues accounted for ≥90% of the total diet volume for 57% (34) of the lizards sampled, and only 12% (7) had <50% plants by volume in their stomachs (Fig. 1). The mean volume of plants consumed was 82.9% for adults (females: 84.1%; males: 81.1%) and 80.1% for juveniles (females: 94.8%; males: 69.0%; Fig. 2), indicating that this species is primarily herbivorous, even as juveniles. The relative volume of leaves (45.3–54.3%) and flowers (25.0–28.5%) in stomachs varied less among age and sex classes than seeds, which were eaten in lower proportions by adult females (2.8%) than by adult males (7.2%) or juveniles (4.5%; Table 1). The plant parts recovered from lizard stomachs that could be identified to species were common Puna shrubs or forbs: *Adesmia horrida* and *Hoffmannseggia minor* (Fabaceae) and *Glandularia microphylla* (Verbenaceae). However, it was not possible to quantify the number or relative proportion of each plant species eaten because most plant parts recovered from the stomachs were in small pieces (bites) that could not be identified.

Age, sex, and size dependence of diet selection.—Differences in prey selection were detected in the frequency of springtails between age classes and sexes ($\chi^2 = 10.057$, $P = 0.007$). Nineteen of 20 (95%) adult females had eaten springtails, whereas these prey items occurred in only 50% of the stomachs of both adult males (females vs. males: $M_{obs} = 0.450 > M_{crit} = 0.373$) and juveniles (females vs. juveniles: $M_{obs} = 0.370 > M_{crit} = 0.258$). A similar trend was detected for mites, which occurred in 15 of 20 (75%) of the stomachs of adult females, but just 36% of the stomachs of juveniles (females vs. juveniles: $\chi^2 = 7.385$, $P = 0.020$; $M_{obs} = 0.393 > M_{crit} = 0.324$), and 58% of the stomachs of adult males (not significantly different from females). Thirty of 32 (94%) adults had eaten flowers (95% females and 92% males; Table 1), whereas flowers were recovered in only 57% of the stomachs of juveniles ($\chi^2 = 11.233$, $P = 0.004$; juveniles vs. females: $M_{obs} = 0.379 > M_{crit} = 0.258$; juveniles vs. and males: $M_{obs} = 0.345 > M_{crit} = 0.301$). There was a significant interaction between age and sex classes in the relative volume of plants in stomachs (ANCOVA of transformed data, $F_{1,55} = 3.537$, $P = 0.020$), with juvenile males eating 18.8–21.8% less plant matter than the other age and sex classes (Fig. 2).

Adult female *L. poecilochromus* ate numerically more mites ($H = 5.71$, $P = 0.042$) and flowers ($H = 12.19$, $P = 0.002$) than either juveniles or adult males. No other differences in prey item abundance were detected among the age classes or sexes. Although all three plant-tissue categories were represented in the stomachs of both age classes and sexes, adults ate proportionately more flowers than juveniles (Mann–Whitney $U = 691.0$, $P = 0.015$), yet juveniles consumed higher proportions of formicids ($U = 985.0$, $P = 0.047$).

We did not detect an ontogenetic shift in the relative volume of plants in the diet as a function of body size (SVL)
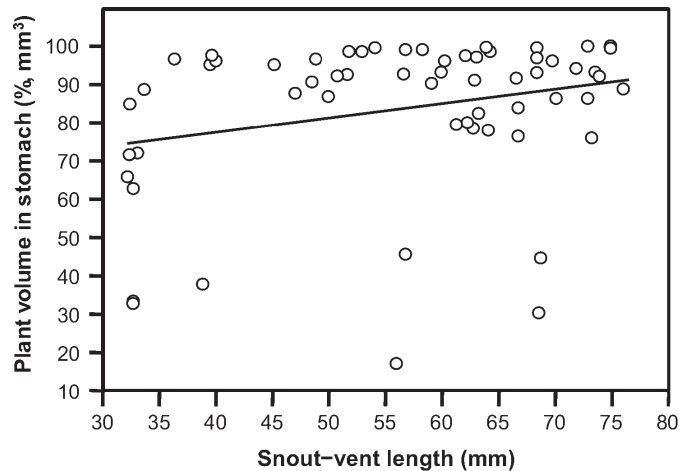
Fig. 1. Percent of plant volume in the stomachs of *Liolaemus poecilochromus* ($n = 60$) from Salar del Hombre Muerto, Catamarca, Argentina as a function of their body size (snout–vent length). The positive statistical trend based on transformed data ($r^2 = 0.098$, $P = 0.015$; see text) suggests that *L. poecilochromus* exhibit an ontogenetic shift in diet, as shown for other species of small herbivorous lizards. However, the weakness of this correlation indicates poor explanatory power and uncertainty regarding its biological significance (see text).

with the Kruskal-Wallis test ($H = 2.61$, $P = 0.272$); however, the regression analysis of transformed data revealed a statistically significant ($n = 60$, $P = 0.015$), albeit weak positive trend ($r^2 = 0.098$) between SVL and the relative volume of plants in lizard stomachs (Fig. 1). The apparent discrepancy between these analyses is attributable to the dramatically lower consumption of plants by juvenile males, as described above.

Body proportions and diet.—Adult males ($n = 12$) were 12.4% larger than adult females ($n = 20$) in SVL ($t = -6.97$, $P < 0.0001$) and 14.3% larger than adult females in trunk length ($t = -8.74$, $P < 0.0001$). Accordingly, males had larger head dimensions than females (length: 16.6%, $t = -8.10$, $P < 0.0001$; width: 18.2%, $t = -9.03$, $P < 0.0001$; height: 18.6%, $t = -7.91$, $P < 0.0001$; Table 2). Analysis of covariance (SVL as covariate) revealed that males also have relatively larger heads than females: length ($F_{1,28} = 7.221$, $P = 0.012$), width ($F_{1,28} = 14.687$, $P = 0.001$), height ($F_{1,28} = 6.755$, $P = 0.015$).

We did not detect relationships between SVL ($n = 32$, $r^2 = 0.003$, $P = 0.668$) or head dimensions (length: $r^2 = 0.003$, $P = 0.661$; width: $r^2 = 0.003$, $P = 0.683$; height: $r^2 = 0.003$, $P = 0.667$) and the relative volume of beetles in stomachs. However, as described for SVL (Fig. 1), similarly weak trends were detected relating the volumetric consumption of plants to head dimensions: length ($r^2 = 0.090$, $P = 0.020$), width ($r^2 = 0.094$, $P = 0.017$), and height ($r^2 = 0.098$, $P = 0.015$).

Niche breadth and overlap.—Dietary niche breadth was highest for juveniles (5.20) and lower, yet similar for adult females (3.72) and males (3.63). Dietary niche overlap was high when comparing adult males to females (0.96) and intermediate for juveniles vs. adult females (0.66) and adult males (0.51).

Both juvenile and adult *L. poecilochromus* had larval nematodes in their stomachs. Although presumed commensal nematodes are commonly reported from the hindguts of herbivorous lizards (Nagy, 1977; Iverson, 1982; O'Grady
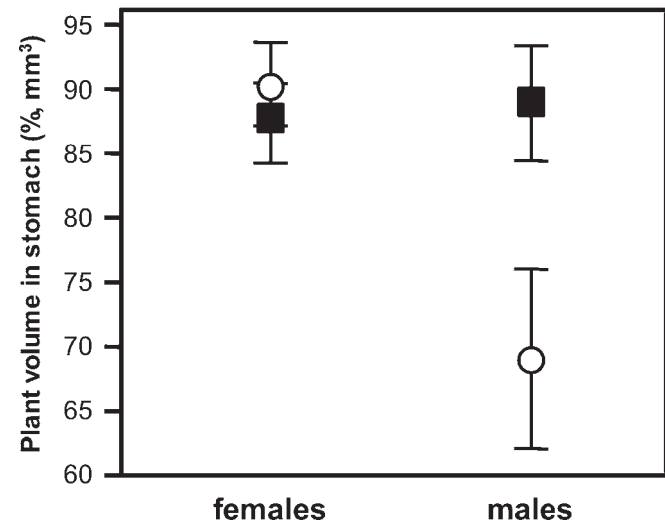
Fig. 2. Percent of plant volume in the stomachs of *Liolaemus poecilochromus* from Salar del Hombre Muerto, Catamarca, Argentina by sex and age class. Sample sizes: juvenile females ($n = 13$), juvenile males ($n = 15$), adult females ($n = 20$), and adult males ($n = 12$). An ANCOVA of the transformed data revealed a significant interaction between sex and age class ($F_{1,55} = 3.537$, $P = 0.020$), with juvenile males eating relatively less plant matter than the other sex and age classes. Adults: black squares; juveniles: white circles. Error bars are ±SE.

et al., 2005), nematodes occurring in the stomachs of reptiles (including herbivorous lizards) are generally parasitic (Greiner and Mader, 2006), so we hypothesize that these larvae represent parasitic infestations of *L. poecilochromus*.

DISCUSSION

Herbivory in small lizards.—The finding that *L. poecilochromus* is primarily herbivorous (>70% plants in diet; Cooper and Vitt, 2002; Espinoza et al., 2004) is surprising for several reasons. First, the former ''rules'' of herbivory for lizards (*sensu* Espinoza et al., 2004) stipulate that herbivores must be large bodied. For example, Pough (1973) showed that lizard species weighing <100 g are primarily insectivorous, and argued that a body mass >300 g was required for herbivorous species. Herbivorous liolaemids appear to be an exception to the body-size ''rule,'' although within liolaemids, herbivorous species are generally larger than non-herbivorous species (Espinoza et al., 2004; O'Grady et al., 2005). Yet, as shown here for *L. poecilochromus*, the mean adult body size of 68 mm (and corresponding body mass of approximately 10 g) is more than an order of magnitude below Pough's (1973) predicted size threshold for an herbivorous lizard. This species is also approximately 25 mm (27%) smaller than the mean body size (94 mm SVL) of species of *Liolaemus* classified as herbivores by O'Grady and coworkers (2005). In fact, the body size of *L. poecilochromus* falls within the ranges of *Liolaemus* classified as either omnivores (71 mm) or insectivores (70 mm) by O'Grady et al. (2005).

Second, even more exceptional was our finding that juvenile (approximately 45 mm SVL, 3–4 g) *L. poecilochromus* are also primarily herbivorous (Table 1). In contrast to *L. poecilochromus*, other small-bodied lizards that are omnivorous or primarily herbivorous as adults start life as insectivores and gradually increase the proportion of plant

Table 1.   Food Type, Frequency, Number, and Volume for Juvenile (*n* = 28) and Adult Female (*n* = 20) and Male (*n* = 12) *Liolaemus poecilochromus* from Salar del Hombre Muerto, Catamarca, Argentina. Percentages of total sample in parentheses. Larvae include Coleoptera and Lepidoptera and nymphs are Homoptera.

Food type	Frequency of occurrence			Number of prey in stomachs			Total prey volume (mm3)		
	Juveniles	Females	Males	Juveniles	Females	Males	Juveniles	Females	Males
Plants	28 (100)	20 (100)	12 (100)	—	—	—	2500 (80.1)	5480 (84.1)	3580 (81.1)
leaves	28 (100)	20 (100)	12 (100)	—	—	—	1580 (50.6)	3540 (54.3)	2000 (45.3)
flowers	16 (57.1)	19 (95.0)	11 (91.7)	96 (16.2)	307 (47.8)	130 (49.1)	780 (25.0)	1760 (27.0)	1260 (28.5)
fruits and seeds	5 (17.9)	10 (50.0)	6 (50.0)	13 (2.2)	30 (4.7)	33 (12.5)	140 (4.5)	180 (2.8)	320 (7.2)
Hexapoda									
Collembola	16 (57.1)	19 (95.0)	6 (50.0)	188 (31.7)	86 (13.4)	11 (4.2)	17.7 (0.6)	7.5 (0.1)	0.8 (<0.1)
Diptera	7 (25.0)	8 (40.0)	3 (25.0)	12 (2.0)	15 (2.3)	6 (2.3)	10.3 (0.3)	100.7 (1.6)	6.9 (0.2)
Hymenoptera: Formicidae	18 (64.3)	15 (75.0)	6 (50.0)	139 (23.4)	51 (7.9)	15 (5.7)	60.8 (2.0)	41.4 (0.6)	14.1 (0.3)
Hymenoptera: other families	5 (17.9)	4 (20.0)	3 (25.0)	7 (1.2)	5 (0.8)	14 (5.3)	10.3 (0.3)	10.4 (0.2)	13.8 (0.3)
Coleoptera: Curculionidae	2 (7.1)	4 (20.0)	2 (16.7)	2 (0.3)	5 (0.8)	2 (0.8)	25.3 (0.8)	21.8 (0.3)	36.2 (0.8)
Coleoptera: Tenebrionidae	4 (14.3)	7 (35.0)	4 (33.3)	8 (1.4)	14 (2.2)	8 (3.0)	415.2 (13.3)	716.5 (11.0)	662.2 (15.0)
Homoptera	5 (17.9)	8 (40.0)	2 (16.7)	37 (6.2)	31 (4.8)	5 (1.9)	16.7 (0.5)	62.0 (1.0)	22.1 (0.5)
Hemiptera	12 (42.9)	10 (50.0)	7 (58.3)	24 (4.0)	18 (2.8)	17 (6.4)	35.3 (1.1)	18.5 (0.3)	17.7 (0.4)
Lepidoptera	0	1 (5.0)	0	0	1 (0.2)	0	0	11.7 (0.2)	0
Isoptera	1 (3.6)	0	0	1 (0.17)	0	0	0.1 (<0.1)	0	0
Orthoptera	0	0	1 (8.3)	0	0	1 (0.4)	0	0	37.7 (0.9)
Diplura	0	1 (5.0)	0	0	3 (0.5)	0	0	0.4 (<0.1)	0
Thysanoptera	5 (17.9)	1 (5.0)	0	6 (1.0)	1 (0.2)	0	0.3 (<0.1)	<0.1 (<0.1)	0
Larvae	6 (21.4)	4 (20.0)	1 (8.3)	10 (1.7)	7 (1.1)	1 (0.4)	18.2 (0.6)	17.1 (0.3)	0.6 (<0.1)
Nymphs	3 (10.7)	4 (20.0)	0	6 (1.0)	5 (0.8)	0	1.1 (<0.1)	12.6 (0.2)	0
Arachnida									
Araneae	1 (3.6)	2 (10.0)	1 (8.3)	1 (0.2)	2 (0.3)	1 (0.4)	2.0 (<0.1)	9.8 (0.2)	7.9 (0.2)
Solifugae	0	1 (5.0)	1 (8.3)	0	1 (0.2)	1 (0.4)	0	1.7 (<0.1)	14.5 (0.3)
Acarina: Mites	10 (35.7)	15 (75.0)	7 (58.3)	41 (6.9)	58 (9.0)	18 (6.8)	5.7 (0.2)	5.3 (<0.1)	1.8 (<0.1)
Acarina: Ticks	3 (10.7)	2 (10.0)	2 (16.7)	4 (0.7)	2 (0.3)	2 (0.8)	0.6 (<0.1)	0.4 (<0.1)	0.9 (<0.1)
Totals	—	—	—	594	642	265	3119.5	6517.7	4417.1

matter in the diet as they grow (Pough, 1973; Ballinger et al., 1977; Schluter, 1984; Greer, 1989; Duffield and Bull, 1998; Rocha, 1998; Durtsche, 2000; Fialho et al., 2000). Consequently, juvenile *L. poecilochromus* are the smallest known herbivorous reptiles—likely even the smallest herbivorous amniotes.

Age and sex differences in diet.—For sexually dimorphic lizard species like *L. poecilochromus*, the proportion of plants or prey eaten can vary by sex (Rocha, 1998; Halloy et al., 2006). In *L. lutzae*, for example, the proportion of plants in the diet increases with body size at the same rate for both sexes, but males, which have larger heads, have a higher proportion of

Table 2.   Summary of Morphometric Measures for Juvenile and Adult Female and Male *Liolaemus poecilochromus* from Salar del Hombre Muerto, Catamarca, Argentina. Data are presented as means (± SD) ranges (second row). All measures are in mm.

Morphometric character	Juveniles (*n* = 28)	Females (*n* = 20)	Males (*n* = 12)
Snout–vent length	44.9 (10.5)	63.4 (4.0)	72.5 (2.6)
	32.1–66.7	56.6–70.1	68.3–76.1
Axilla–groin distance	5.9 (1.5)	8.2 (0.5)	10.1 (0.8)
	4.1–8.8	7.2–8.8	8.9–11.4
Head length	9.9 (1.9)	12.5 (0.6)	15.0 (1.0)
	7.6–14.0	11.4–13.3	13.4–16.6
Head width	8.9 (1.9)	11.5 (0.5)	14.1 (0.9)
	6.4–12.6	10.6–12.3	12.6–15.9
Head height	5.9 (1.5)	8.2 (0.5)	10.1 (0.8)
	4.1–8.8	7.2–8.8	8.9–11.4

plants in their diets than females (Rocha, 1998). This is not surprising because head size is positively correlated with bite force, which influences the ability to crop plant tissues (Stayton, 2005, 2006; Herrel et al., 2006, 2008; Herrel, 2007; Vanhooydonck et al., 2007). Yet despite sexual dimorphism in head size (Table 2), we detected no differences in the frequency or volume of plants in the diets of adult female and male *L. poecilochromus*. Small differences between the sexes were detected in the proportion of fruits eaten, but not in the leaves (Table 1). From a functional perspective, if the differences in body and head size evolved for trophic reasons, we would have expected adult males to eat relatively more leaves, which are the toughest of the three categories of plant tissues eaten. Likewise, neither the frequency nor the proportion of hard-bodied prey items (beetles) differed between adult males and females (Table 1). Thus, differences in body and head size between the sexes are likely driven by selective factors other than diet (e.g., sexual selection; Teixeira-Filho et al., 2003). Although no significant differences were detected in the consumption of beetles between juveniles and adults, no beetles were found in the stomachs of juveniles <50 mm SVL. This suggests a minimum body-size threshold for eating these insects, which may be attributable to the challenge of orally processing these hard-bodied prey. Curiously, juvenile males consumed a lower proportion of plants than the other sex and age-class groups, despite the lack of apparent differences in microhabitat selection among sex and age classes at our study site (unpubl. obs.). Juveniles do emerge earlier in the day than adults (unpubl. obs.), which may increase their encounter rate of prey items at this time. However, this does not explain why juvenile females eat, on average, >20% more plants than juvenile males (Fig. 2). Perhaps juvenile males eat more arthropods relative to plants because of selective pressures for faster rates of growth relative to juvenile females. Additional studies are needed to address this puzzling finding.

There was substantial overlap in the trophic niche breadths of adult female and male *L. poecilochromus* (0.96), but the overlap between adults and juveniles was considerably lower: adult females vs. juveniles (0.66); adult males vs. juveniles (0.51). The differences in niche breadth between juveniles and adults are explained primarily by their differential consumption of springtails and ants. Interestingly, some juveniles consumed many ants whereas others ate none. Omitting either of these diet items from the analyses substantially elevates niche breadth overlap across all age class and sex contrasts (0.89–0.98). Additionally, a few rare diet items were recorded in the stomachs of a small number of lizards. These include the single orthopteran found in the stomach of an adult male and the two solifuges found in the stomachs of an adult of each sex.

Evolution of herbivory and other unanswered questions.— Herbivorous *Liolaemus* tend to live in cool environments, with an elevational range of 3500–4130 m (Espinoza et al., 2004). One force likely selecting for plant eating in *Liolaemus* is the paucity of arthropod prey (in both abundance and species richness) in cold environments (Mann, 1968; de Morales, 1994). This should select for a generalist diet (Schoener et al., 1982; Espinoza et al., 2004). We propose an adaptive scenario for the evolution of herbivory in these and similar lizards. Initially, plant parts are eaten incidentally as lizards capture arthropod prey that are foraging on leaves,

flowers, or fruits. Lizards that can digest the plant tissues more efficiently have a fitness advantage, and over time, selection favors individuals that can sustain themselves principally on plants.

Many questions related to diet remain unanswered for *L. poecilochromus* and other small, cold-climate liolaemids. First, although volumetrically a small diet component, why would adult female *L. poecilochromus* eat more mites and springtails (or, why would adult males and juveniles avoid these prey items)? At first glance it seems unlikely that mites and springtails are eaten incidentally with the plant tissues that they occur on, as no concomitant differences were detected in plant-tissue selection by adult females relative to adult males or juveniles (Table 1). However, we were unable to identify the species of plants eaten, so it is possible that mites and springtails occur disproportionately on plant species that females happen to eat at higher frequencies. Alternatively, females may forage for mites and springtails to satisfy specific micronutrient requirements provided by these arthropods. Second, do the diets of *L. poecilochromus* change seasonally, and does this vary by population or age or size class as it does in other omnivorous and herbivorous lizards (van Marken Lichtenbelt, 1993; Fialho et al., 2000; Dutra et al., 2011; Siqueira et al., 2011)? More generally, how do small-bodied lizards, with their small guts, assimilate sufficient energy and nutrients from plant tissues? For example, aside from having short guts on an absolute scale, herbivorous liolaemids lack the semilunar valves or colic septae that have been reported for larger herbivorous lizards (Iverson, 1980, 1982; O'Grady et al., 2005). Also, it is not known whether herbivorous liolaemids, like other herbivorous lizards (Nagy, 1977; McBee and McBee, 1982; Troyer, 1991; Foley et al., 1992; Bjorndal, 1997), harbor the hindgut microsymbionts (primarily bacteria and protozoa) that are responsible for fermenting plant tissues (e.g., hemicellulose, cellulose) into volatile fatty acids that are absorbed by their host's gut. Until more studies are conducted, the largely secret lives of these small-bodied, cold-climate herbivores will remain enigmatic.

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