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Diet and Reproductive States in a High Altitude Neotropical Lizard Species, *Liolaemus ramirezae* (Iguania: Liolaemidae)

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Abstract.—The diet of an animal may be influenced by both its reproductive biology and seasonal changes. Here we investigate these factors in the lizard species, *Liolaemus ramirezae*, from the prepuna of northwestern Argentina, during spring, summer, and autumn. We found that *L. ramirezae* eats mainly Hemiptera, Coleoptera, and Formicidae. Considering total plant volume with respect to prey volume, this species was mostly insectivorous. Food intake varied among the different seasons and between the sexes. We recorded males with the greatest increase in testicular volume in spring, most females being gravid at that time. In summer, females were in a previtellogenic state, and in autumn most were previtellogenic with one being vitellogenic. When females were gravid they ate significantly less. In contrast, the relationship between male reproductive state and amount of prey consumed was not as distinct. Therefore, in *L. ramirezae*, the amount of food consumed by males would not be affected by their reproductive state; however, in females reproductive state could be regulating the amount and type of food ingested, particularly when they are in a gravid state.

Resumen.—La biología trófica y reproductiva de los animales pueden influenciarse entre sí y a su vez estar relacionadas con las estaciones. Aquí investigamos estos parámetros en la lagartija, *Liolaemus ramirezae*, de la prepuna del noroeste de Argentina, durante la primavera, verano y otoño. Encontramos que *Liolaemus ramirezae* consume principalmente Hemiptera, Coleoptera y Formicidae. En base al volumen porcentual de plantas consumidas, determinamos que esta especie es principalmente insectívora. El consumo de alimentos cambió entre estaciones y entre los sexos. Registramos machos con el mayor incremento de volumen testicular en primavera, siendo la mayoría de las hembras grávidas en ese momento. En el verano, las hembras estaban previtelogénicas y en otoño la mayoría se encontró previtelogénica y sólo una hembra vitelogénica. Cuando las hembras estaban grávidas comieron significativamente menos. En cuanto a machos la relación entre su estado reproductivo y la cantidad de alimento consumido no fue tan marcado. Por lo tanto, en *L. ramirezae*, el volumen de alimento que consumen los machos no estaría afectado por el ciclo reproductivo. En las hembras en cambio, el ciclo reproductivo podría regular la cantidad y tipo de alimento que ingieren, principalmente cuando éstas se encuentran grávidas.

Diet and reproductive biology are two important life history traits of an animal that may interact in a complex manner (Huey and Pianka, 1981; Barden and Shine, 1994). Studying the diet of an animal can give insight into its physiology, ecology, and behavior (King, 1996). It also may provide information on the vulnerability of a species (Christie, 1984) and on strategies to improve the conservation status of poorly known species (Reca et al., 1994; Giraudo et al., 2012). Furthermore, what an animal eats may depend on factors such as reproductive state (Martori, 2005), season (Rocha, 1996), and variations in climate conditions (Brown and Pérez-Mellado, 1994). Hence, investigating the diet of a species during different seasons and its relation to its reproductive biology may provide important information on how they may affect diet.

Ramírez Pinilla (1992) reported that oviparous lizards living at high altitudes may start their reproductive activity in the fall, starting the vitellogenic process at this time, and completing the cycle in the spring with courtship and mating. We found little information on how the reproductive cycle may affect diet, if at all, particularly in females.

Liolaemus is a genus of lizards found mainly throughout the arid west of South America (Avila et al., 2010) that includes 260 species (Lobo et al., 2010; Abdala and Quinteros, 2014). Various studies describe their diet (e.g., Aún et al., 1999; Halloy et al., 2006; Kozykariski et al., 2011; Valdecantos, 2011) or reproductive biology (e.g., Martori and Aún, 1997; Vega and Bellagamba, 2005; Martori and Aún, 2010), but few consider both traits simultaneously (e.g., Martori, 2005, in the oviparous *Liolaemus koslowskyi*; Semhan et al., 2013, in the viviparous *Liolaemus crepuscularis*).

Liolaemus ramirezae (subgenus *Liolaemus sensu* stricto, Schulte et al., 2000) is an oviparous lizard which belongs to the *Liolaemus alticolor–bibroni* group (Lobo, 2005; Quinteros, 2012). It inhabits shrubby slopes above 2,600 m in prepuna areas of northwestern Argentina (Lobo and Espinoza, 1999; Quinteros, 2012).

Here we: 1) study and describe the diet of a population of *Liolaemus ramirezae*; 2) evaluate diet differences between seasons and between sexes; and 3) determine whether diet may be related to different reproductive states of males and females.

Materials and Methods

The study site was located in Mina Capillitas (27°40′53.8′′S, 66°22′43.5′′W, 3,048 m), Andalgalá Department, Catamarca Province, Argentina. Precipitation was typical of an arid mountain climate, characterized by marked variations in temperatures. Annual precipitation was $\leq$300 mm, usually as snow. Vegetation consisted mainly of small scattered shrubs and grasses (*Festuca* sp.; *Pappophorum* sp.; *Satureja parvifolia*) (Abdala and Díaz Gómez, 2006).

Lizards were captured by hand or noose during the austral spring (October 2009 and November 2010), summer (February 2012), and beginning of autumn (March 2010). We collected a total of 53 specimens of *Liolaemus ramirezae*, all adults, 24 males (average snout–vent length, SVL = 49.7 $\pm$ 0.4 SD mm) and 29 females (average SVL = 52.1 $\pm$ 3.4 mm). The lizards were immediately sacrificed with a 1% sodium pentothal injection,

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TABLE 1. General diet of *Liolaemus ramirezae*. F = the number of lizards that ate a particular prey item; F% = percentage of frequency of occurrence of a particular prey item; N = Number of particular prey items; N% = percentage of prey items; V = volume of each prey item in mm^3; V% = volume percentage; AN = average number of animal prey items; AV = average volume of prey items consumed for all individuals.

Prey	F	F%	N	N%	V	V%
Formicidae	44	83.02	228	21.73	205.83	3.54
Coleoptera	39	73.58	91	8.67	1,907.1	32.76
Larvae (ui)	9	16.98	15	1.43	17.76	0.31
Hemiptera	49	92.45	667	63.58	1,367.0	23.48
Hymenoptera (nf)	4	7.55	5	0.48	315.39	5.42
Orthoptera	7	7.55	10	0.95	440.18	7.56
Lepidoptera	10	5.66	11	1.05	496.89	8.53
Araneae	17	32.08	22	2.10	69.92	1.20
Vegetation	15	28.30	-	-	1,001.7	17.21
n	53					
Prey items	9					
AN	20.32					
AV	91.75					

fixed with 10% formaldehyde, and finally preserved in 70% alcohol. The specimens will be deposited in the Herpetological Collection of the Fundación Miguel Lillo (FML), Tucumán, Argentina.

To analyze diet, we dissected the animals and extracted the digestive tract completely. We then analyzed its contents with a Boeco microscope (×0.7–4.5; Boeco, Inc., Hamburg, Germany). We measured prey items with a Mitutoyo (Aurora, Illinois, USA) digital caliper, 0.01-mm precision, and we identified to Order or Family taxonomic levels whenever possible. For the quantitative analysis, we determined relative numerosity (N, the number of particular prey items per lizard), absolute frequency of different categories (F, the number of lizards that ate a particular prey item), volume of each prey (V), and average volume (AV). We calculated prey volume measuring its length (L) and width (W) using the spheroid formula of Dunham (1981): $V = 4/3\ \pi\ (L/2) * (W/2)^2$ in mm^3. For plant material, we made a small spheroid package and we measured its volume as we did for insects.

In addition, we calculated percentages of N (N%), F (F%), and V (V%). For animal prey, these three measurements were used to calculate the index of relative importance (IRI) proposed by Pinkas et al. (1971), equal to $100\ AL / \sum AL$; where AL = F% + N% + V%. Furthermore, to calculate diet hierarchy (only in animal prey), the hierarchy index (dynamic jasper [DJ]) was applied. This index considers the following ranges: if the percentage of prey consumption is between 100% and 75%, it is considered fundamental; if it occurs between 75% and 50%, it is categorized as secondary; if included between 50% and 25%, it is accessory; and less than 25% is considered accidental (Montori, 1991). Diet was compared among seasons and between males and females with a Kruskal-Wallis analysis of variance and a Mann-Whitney test, respectively.

Considering reproductive states for males, we measured the length and width of the right testicle with a digital caliper and then calculated its volume using the spheroid formula; we used variation in testicular size as an indicator of reproductive activity. We correlated testicular volume with total volume of all prey items using Spearman's correlation coefficient (Zar, 1999).

As for females, we recorded the presence of nonvitellogenic follicles, yolked follicles (yellow colored and greater than 2 mm), or eggs, defining thus three reproductive states in females: previtellogenic, vitellogenic, and gravid (Ramírez Pinilla, 1992). Follicle and egg volumes were obtained using the spheroid formula. We compared reproductive states and total volume of all prey items using a Kruskal-Wallis analysis of variance. All summary statistics are expressed as mean ± SD and $\alpha = 0.05$ for all statistical tests.

RESULTS

Diet Analysis.—We identified nine alimentary items: Formicidae, Coleoptera, unidentified (ui) larvae, Hemiptera, Hymenoptera (non-Formicidae, nF), Orthoptera, Lepidoptera, Araneae, and plants (Table 1). The most numerous and frequent prey were Hemiptera followed by Formicidae and Coleoptera. The highest percentages of volumes were represented by Coleoptera followed by Hemiptera. Other items showed considerably lower values (Table 1).

We found no significant seasonal differences in food volume (Kruskal-Wallis analysis of variance, $H = 6.21$, $P = 0.05$). The total average volume of plants was 17.2% and consisted mainly of leaves. Overall, males included a significantly higher proportion of plants in their diet than did females (Mann-Whitney, $T = -3.24$, $P = 0.006$). During spring, plant volumes were similar in both males and females, although during summer and autumn they were greater in males (Table 2).

Prey Hierarchy.—Considering the IRI and the prey DJ, *L. ramirezae* fed mainly on Hemiptera (IRI = 34.3, DJ = 100%, fundamental prey) followed by Coleoptera (IRI = 22.7; DJ = 66.1%) and Formicidae (IRI = 20.3; DJ = 59.1%), both as secondary prey, with the rest of prey items being accidental (less than 25%). Incorporating seasons, Hemiptera was fundamental in both sexes during spring and autumn whereas Formicidae was secondary in both sexes during autumn; in spring, Formicidae was accessory in males and fundamental in females. Coleoptera, on the other hand, was secondary in males and fundamental in females during spring; in autumn, it was accessory in males and secondary in females. Because summer sample sizes were small, we did not consider them here ($n = 7$, Table 2).

Analysis of Gonadal Volume.—In spring, 88.2% of *L. ramirezae* females were gravid, with a clutch size of 3–9 eggs (mean egg volume = 157.7 ± 47.2 mm^3, $n = 15$), the rest being vitellogenic (11.8%, $n = 2$). In summer, all the females were previtellogenic, with follicles between 1.4 and 1.7 mm^3 and ovaries with an average volume of 5 ± 1.3 mm^3 ($n = 4$). In autumn, most females (87.5%) still had previtellogenic follicles of 2.6–2.8 mm^3 (9.4 ± 4.9 mm^3, $n = 7$), the remaining 12.5% being vitellogenic, with follicles between 1.4 and 2 mm^3. With respect to males, we observed an increase in testicular volume in spring (37 ± 18.6 mm^3, $n = 8$) and a decrease in summer (5.2 ± 5.2 mm^3, $n = 4$), whereas during the fall it increased slightly (11.5 ± 11 mm^3, $n = 13$).

Relation between Diet and Reproductive State.—Overall, we observed a significantly lower volume of food consumption ($H = 8.48$, $P = 0.01$) in gravid females (67.32 ± 63.25 mm^3), than in previtellogenic females (164.13 ± 110.28 mm^3). Diets of vitellogenic females (97.84 ± 119.12 mm^3) were not significantly different from the other two reproductive states (Fig. 1). Considering female reproductive state and principal prey items, however, we did not find a significant difference between a gravid female and the other two reproductive states with respect to volume of Hemiptera ($H = 5.23$, $P = 0.15$), Coleoptera ($H = 2.61$, $P = 0.45$), and Formicidae ($H = 5.83$, $P = 0.12$). As for males,

TABLE 2. Diet of *Liolaemus ramirezae* considering seasons and sexes. F% = percentage of frequency of occurrence of a particular prey item; N% = percentage of prey items; V% = volume percentage; AN = average number of animal prey items; AV = average volume of prey items consumed for all individuals.

	Spring						Summer						Autumn					
	Males			Females			Males			Females			Males			Females		
Prey	F%	N%	V%	F%	N%	V%	F%	N%	V%	F%	N%	V%	F%	N%	V%	F%	N%	V%
Formicidae	50	20	0.81	100	32.96	4.71	100	16.67	0.53	50	17.39	23.97	84.62	14.43	2.03	87.05	18.55	2.72
Coleoptera	62.50	12.19	27.92	76.47	0.63	38.77	100	12.50	55.65	75	15.22	46.99	69.23	0.58	19.60	75	6.72	29.19
Larvae (ui)	0	0	0	11.76	1.48	1.38	0	0	0	0	0	0	0	0	0	12.50	0.27	0.28
Hemiptera	100	62.20	17.21	76.47	50.74	15.18	100	58.33	11.91	100	63.04	28.02	100	71.82	26.98	100	71.24	31.33
Hymenoptera (nF)	12.50	1.20	37.57	0	0	0	33.3	8.33	3.66	0	0	0	7.69	0.34	1.72	0	0	0
Orthoptera	0	0	0	0	0	0	0	0	0	0	0	0	15.38	1.72	3.56	37.5	1.34	10.49
Lepidoptera	0	0	0	11.76	1.11	21.46	0	0	0	0	0	0	23.08	0.34	12.45	50	1.08	18.00
Araneae	37.50	6.10	1.18	47.06	4.07	3.90	33.3	4.17	2.96	0	0	0	23.08	0.69	0.51	37.5	0.27	0.58
Vegetation	25	-	15.30	25.53	-	15.98	33.3	-	25.29	0	-	0	46.15	-	33.16	25	-	7.42
n	8			17			3			4			13			8		
Prey items	5			7			6			3			8			8		
AN	10.25			16.12			2			5			7			11		
AV	98.77			53.45			85.06			78.99			131.20			197.60		

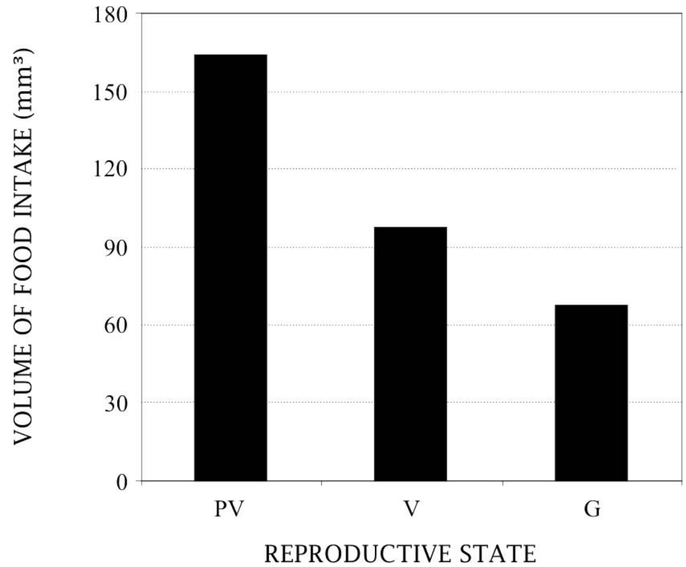

FIG. 1. Average volume of food intake with respect to different reproductive states in female *Liolaemus ramirezae*. PV = previtellogenic, V = vitellogenic, G = gravid.

there was no correlation between testicular volume and that of prey volume ($r = 0.04$, $P = 0.84$).

DISCUSSION

Based on our results, this population of *L. ramirezae* is primarily insectivorous, consuming mainly Hemiptera followed by Coleoptera and Formicidae. In another population of *L. ramirezae* from Los Cardones, province of Tucumán (Halloy et al., 2006), lizards showed the same preferences. In a closely related species, *Liolaemus bibroni*, from southern Argentina (Lobo, 2005), Belver and Avila (2001) reported the diet as strictly insectivorous, Hemiptera being the main prey item. In contrast, other species belonging to the same subgenus (*Liolaemus* sensu stricto, Schulte et al., 2000) were omnivorous, such as *Liolaemus umbrifer* (O'Grady et al., 2005) which lives in high altitude environments, and *L. elongatus* (Quatrini et al., 2001) which lives in southern Argentina. Other high altitude *Liolaemus* species from northern Argentina and that belong to the other subgenus *Eulaemus* (Schulte et al., 2000), such as *Liolaemus irregularis*, *Liolaemus albiceps*, *Liolaemus multicolor*, *Liolaemus yanalcu* (Valdecantos, 2011), and *Liolaemus pacha* (Halloy et al., 2006), all ate Formicidae as their main prey.

Although arthropods were the main prey items, *L. ramirezae* also included plant material in their diet. Espinoza et al. (2004) reported that in cold climates, consumption of plants will be favored because insects may not be as abundant or diverse as in warmer climates. *Liolaemus crepuscularis*, a viviparous species that lives in sympatry with *L. ramirezae* at our study site, presented an omnivorous diet that varied between seasons and between sexes (Semhan et al., 2013). Although competition could be a factor, it does not necessarily explain the differences found in the diet of these two species (Huey, 1979; Valdecantos, 2011). Phylogenetic constraints may be more important (Pérez-Barberia and Gordon, 2001; Espinoza et al., 2004; Valdecantos, 2011; Semhan, 2015), especially when considering that these two species belong to different subgenera (Abdala, 2007; Quinteros, 2012).

We found differences in diet between males and females, mainly with respect to average volume consumed. Differences may be partly because of lesser mobility of females when gravid (Martori and Aun, 1997) but also, and possibly more importantly, because of a lack of space in their body (Semhan et al., 2013). Because of this, consuming small insects may be the best strategy during pregnancy because plant tissues contain less energy and nutrients per gram than do insects (Iverson, 1982; Troyer, 1991). Diet differences between the sexes have been reported for several species of *Liolaemus* such as in *L. scapularis* (García et al., 1989), *L. wiegmannii* (Aún et al., 1999), *L. multimaculatus* (Vega, 1999), *L. quilmes* (Halloy et al., 2006), and *L. pseudoanomalus* (Kozykariski et al., 2011), but in other species sex differences were small or absent (Aún and Martori, 1998; Moreno Azócar and Acosta, 2011; Valdecantos, 2011).

Liolaemus ramirezae showed variation in plant consumption and arthropod types among seasons and between the sexes. This may be common in high altitude environments such as in Mina Capillitas (Abdala and Díaz Gómez, 2006). The scarcity of food resources during some periods of the year may force lizards to select what is available, i.e., plants (Hodar et al., 1996). We found little information on seasonal changes in diet for this genus of lizards except for studies in *L. wiegmannii* (Aún et al., 1999), *L. poecilochromus* (Valdecantos et al., 2012), and *L. crepuscularis* (Semhan et al., 2013), whose diets differed among seasons.

Males showed the greatest increase in testicular volume in spring, indicating readiness to be reproductively active; however, most females were gravid at that time with only two females being vitellogenic. Females were previtellogenic in summer, and in autumn most were also previtellogenic except for one that was vitellogenic. This coincides with reports for many high altitude or intermediate latitude (or both) oviparous lizards of *Liolaemus* species belonging to the same taxonomic group, such as in the populations of *L. ramirezae* from Los Cardones, Tucumán (Ramírez Pinilla, 1989), *L. bibroni* and *L. austromendocinus* from southwestern Mendoza (Ramírez Pinilla, 1992), and *L. bitaeniatus* (Ramírez Pinilla, 1995) and *L. gracilis* from the phytogeographic Monte regions (Vega and Bellagamba, 2005), where vitellogenesis starts in autumn and, in general, culminates with ovulation in spring.

Food intake in *L. ramirezae* females was negatively affected when they were gravid. Martori (2005) and Semhan et al. (2013) obtained similar results in *L. koslowskyi*, also an oviparous species, and in the viviparous species *L. crepuscularis*, respectively. This effect may be related to reproductive costs for females.

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