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

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Abstract. Diet and reproduction are two important characteristics in animals that can be related to environmental conditions and time of year. In this study, we investigated these two parameters in a viviparous lizard, *Liolaemus crepuscularis,* from the arid Prepuna of northwestern Argentina, for two months of the austral spring (October 2009 and November 2010) and one month at the beginning of the fall (March 2010). Formicidae was the main prey item, similar to what was found in other *Liolaemus* species; but plant material was also very important, especially in the latter month when lizards consumed the greatest amounts of food. In October 2009 and November 2010, testicular volume in males was low whereas females were gravid. In March 2010, males showed a great increase in testicular volume and females showed vitellogenic follicles, indicating reproductive activity. A negative correlation was found in females between amount of food consumed and advancement of pregnancy. Females ate very little while gravid, possibly in part due to the space occupied by embryos and increased difficulty in foraging, as well as predation vulnerability. No association was found in males between food consumption and testicular volume.

Keywords. Sauria; Feeding; Reproduction; Prepuna; Argentina.

Resumen. La dieta y la reproducción de los animales son dos características importantes que pueden estar relacionadas con las condiciones ambientales y la época del año. Aquí se investigaron estos parámetros en una lagartija vivípara, *Liolaemus crepuscularis,* de la Prepuna del noroeste de Argentina, durante dos meses del verano austral (octubre de 2009 y noviembre de 2010), y un mes al inicio del otoño (marzo de 2010). Formicidae fue la presa principal, similar a lo hallado en otras especies de *Liolaemus,* pero el material vegetal fue también muy importante, especialmente en este último mes, cuando las lagartijas consumieron la mayor cantidad de alimentos. En octubre de 2009 y noviembre de 2010, el volumen testicular en los machos fue bajo, mientras que las hembras se encontraron grávidas. En marzo de 2010, los machos presentaron un gran incremento en el volumen testicular y en las hembras se observaron folículos vitelogénicos, lo que indica la existencia de actividad reproductiva. En las hembras, se observó una correlación negativa entre la cantidad de alimento consumido y el volumen de las crías. Estas hembras comieron muy poco durante el preñez, posiblemente en parte debido al espacio ocupado por los embriones, así como una mayor dificultad para forrajear y una mayor vulnerabilidad ante los depredadores. En machos, no se encontró una relación entre alimento consumido y volumen testicular.

INTRODUCTION

The study of what an animal feeds on, as well as when it feeds, may provide important clues regarding its natural history and adaptive strategies within its environment (Duvall *et al.,* 1982). Considering food habits, many species can be found along a continuum that ranges between carnivory, omnivory, or herbivory; some of them fluctuating between one or another, depending on different factors (Roca, 1999). Seasonal changes in environmental conditions may promote changes in diet composition. This may lead, for example, to consumption of plant material when animal prey is lacking or not as abundant (Brown and Pérez-Mellado, 1994). Seasonal changes in diet are common in many lizard species (Pianka, 1970; Búrquez *et al.,* 1986; Maya and Malone, 1989; Rocha, 1996). Some species considered herbivores might actually be facultative herbivores, or simply omnivores (Roca, 1999).

Climatic conditions may also influence the reproductive activity of lizards (Vitt and Carvalho, 1992; Smith *et al.,* 1995). Seasonal changes in lizard reproductive patterns might be coupled with seasonal changes in diet because energetic requirements for these animals should change depending on their reproductive state.

Within Iguania, few families are known to include viviparous species. One of these is Liolaemidae, which includes two genera, *Phymaturus* and *Liolaemus*. Viviparity in *Liolaemus* is related to high altitude and latitude environments (Ramírez Pinilla, 1991; Espinoza *et al.,* 2004; Abdala, 2007). Temperatures in those environments do not favor the development of eggs nor food availability (Blackburn, 1982; Ramírez Pinilla, 1991). Hence we can expect differences in reproductive strategies and food intake with respect to lizard species found in habitats of lower altitude and latitude.

Our objectives were: a) to describe the diet of *Liolaemus crepuscularis* during three different months in the austral spring and beginning of fall, and compare the dietary habits of males and females; b) to describe the reproductive biology of males and females during those same months; and c) to explore whether an association between diet and reproductive state existed. This is the

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first paper to describe important aspects of the biology of this recently described species.

MATERIALS AND METHODS

Liolaemus is a South American genus of lizards, which comprises more than 240 species (Avila *et al.,* 2010; Lobo *et al.,* 2010; Abdala *et al.,* 2012). It is found mainly across the arid west of South America, from Peru in the North to Tierra del Fuego, Argentina, in the South.

Several studies exist on the trophic biology and reproduction of *Liolaemus:* seasonal variation in diet of *L. wiegmannii* (Aun *et al.,* 1999); evolution of herbivory in small lizards of cold climates (Espinoza *et al.,* 2004); diet in two syntopic *Liolaemus* species (Halloy *et al.,* 2006); reproductive activity in *L. quilmes* (Ramírez Pinilla, 1992); reproductive cycle and fat bodies in *L. scapularis* (Ramírez Pinilla, 1994) and in *L. wiegmannii* (Martori and Aun, 1997); reproduction and diet in *L. koslowskyi* (Aun and Martori, 1998); reproductive cycle in *L. gracilis* (Vega and Bellagamba, 2005); and reproduction and group size variation in *L. koslowskyi* (Martori and Aun, 2010), among others.

Liolaemus crepuscularis belongs to the *L. darwinii* group (Etheridge, 1993; Avila *et al.,* 2006; Abdala, 2007; Lobo *et al.,* 2010), which includes 18 species, in turn nested within the *laurenti* group (Abdala, 2007). Within the *darwinii* group, it belongs to the *L. ornatus* clade (Abdala, 2007), which includes species that inhabit high altitude environments, mainly in the Puna of Argentina (Cabrera and Willink, 1980). Several species in this clade have been identified as viviparous, with a tendency towards herbivory (Espinoza *et al.,* 2004; Abdala, 2007; Valdecantos, 2011).

Liolaemus crepuscularis is a recently described by Abdala and Díaz Gómez (2006). Its biology and natural history are unknown, except for its viviparity. It is endemic, as are other species of this group, such as *L. albiceps, L. irregularis, L. lavillai* and *L. calchaqui.* The species of this study is restricted to the southwestern slopes of the Nevados, Aconquija Mountains, in the province of Catamarca, Argentina; it is always found above 2800 m. This region presents an arid climate with annual precipitations of less than 300 mm, which generally occur as winter snow.

The study area was located at approximately 1 km from Puesto Flores, Minas Capillitas (27°40'53.8"S, 66°22'43.5"W), at 3048 m, department of Andalgalá, province of Catamarca, Argentina. Data were collected for three different months, corresponding to the southern hemisphere spring (October 2009 and November 2010) and beginning of fall (March 2010). A total of 44 specimens of *L. crepuscularis* were captured, 23 males (average snout-vent lengths ± 1 standard deviation: 54.8 ± 4.4 mm) and 21 females (SVL = 56.3 ± 5.2 mm). The lizards were sacrificed shortly after capture with an injection of sodium pentothal 1%, preserved in formaldehyde 10% for 24 hours, after which they were kept in alcohol 70%. The specimens were deposited in the Colección Herpetológica, Fundación Miguel Lillo (FML), Tucumán, Argentina.

In order to determine their diet, the animals were dissected and digestive tracts were extracted. Contents were studied using a binocular microscope (Boeco, Germany, NTB-3A, 10-40x). Prey items were measured using a digital caliper (0.01 mm precision) and identified to the level of order or family when possible. For quantitative analyses, absolute frequency of different categories (F, number of lizards who ate a particular food item), relative abundance of items (N, number of prey consumed for each food item), and the volume of each prey (V, volume or amount of space occupied by a specific food item) were considered. To measure the volume, length (L) and width (W) were estimated, and the spheroid formula (Dunham, 1981) was applied: $V = 4/3\ \pi\ (L/2)*(W/2)^2$ (in mm^3), where L is prey length and W is prey width. When plant matter was present, a small spheroid package was formed and its volume was estimated in the same manner as for insect prey.

In order to establish a hierarchy of food items and categorize the diet of *Liolaemus crepuscularis,* two methods were used. The first consisted of calculating an index of relative importance (Pinkas *et al.,* 1971) RI = 100 AL / ∑ AL, where AL = frequency of occurrence % (F%) + % of total number (N%) + % of total volume (V%) (George and Hadley, 1979). In order to estimate a hierarchy for the diet, the RI index percentage was considered. If this value fell between 75% and 100%, it was considered fundamental; between 50% and 75%, secondary; between 25% and 50%, accessory; and finally, if less than 25%, it was considered accidental (Montori, 1991).

The second method of diet categorization used consisted of calculating the volumetric proportion of plant and animal matter. Depending on the percentage of plants consumed, the following definitions were applied: insectivorous, 0–10%; omnivorous, 11–50%; and herbivorous, 51–100% (Espinoza *et al.,* 2004).

For analyses of the reproductive condition of males and females during the three different months of study, we considered those specimens that had a snout-vent length of 50 mm or more. This criterion was based on other studies on reproduction of similar-sized *Liolaemus* species of the *darwinii* group. According to these studies, this is the approximate minimum size for reproduction, *e.g., L. koslowskyi* (Martori and Aún, 2010). In males, the testicular length and width were measured with a digital caliper (0.01 mm precision); the spheroid formula was used to measure volume (Dunham, 1981). In females, volume of the left ovary or of embryos (in the case of a gravid female) was calculated. In addition, volume of the embryos, together with the vitelline mass, was measured in order to determine the total space occupied in a female body. Increase in testicle size in males and the presence of yolked follicles in females were used as indicators of reproductive maturity (Licht and Gorman, 1970).

Table 1. Diet composition in females (n = 21) and males (n = 23) of *Liolaemus crepuscularis*, during the months of October 2009, March 2010, and November 2010. Percentage of frequency of occurrence (%F, percentage of lizards that contained a certain food item), numerosity (%N, percentage of prey items per category), and volume (%V, percentage of the volume or amount consumed of a certain food item) are given. The highest values for %F, %N and %V for each month are shown in bold.

	***L. crepuscularis* males**								
	October 2009			**March 2010**			**November 2010**		
Food types	%F	%N	%V	%F	%N	%V	%F	%N	%V
Hymenoptera	100	76.36	66.39	100	37.93	4.85	100	82.26	19.29
Formicidae	**100**	**76.36**	**66.39**	**100**	**37.93**	4.85	**100**	**81.72**	14.40
Hymenoptera (non Formicidae)	-	-	-	-	-	-	12.50	0.54	4.89
Coleoptera	20	5.45	15.59	45.45	17.24	6.38	50	7.53	25.13
Hemiptera	40	18.18	23.24	81.82	31.03	4.28	50	2.15	1.01
Orthoptera	-	-	-	18.18	6.89	8.20	-	-	-
Lepidoptera	-	-	-	9.09	3.44	3.11	-	-	-
Thysanoptera	-	-	-	-	-	-	12.50	1.08	7.50
Araneae-	-	-		9.09	3.44	0.92	4	4.84	2.53
Acarina	-	-	-	-	-	-	2	2.15	0.01
Plant material	40	0.46	**100**	-	**72.26**	6	-	**52.01**	
n	5			10			8		
Food items	4			7			8		
N total average	22			2.63			23.25		
V total average (mm^3)	43.38			192.13			135.87		
	***L. crepuscularis* females**								
	October 2009			**March 2010**			**November 2010**		
Food types	%F	%N	%V	%F	%N	%V	%F	%N	%V
Hymenoptera	60	92.59	42.32	100	65	10.67	100	95.74	28.08
Formicidae	**60**	**92.59**	42.32	**100**	**65**	10.67	**100**	**95.74**	28.08
Coleoptera	-	-	-	25	11.76	18.04	12.50	2.13	12.85
Hemiptera	40	7.41	15.20	37.50	5.88	0.95	12.50	1.06	1.73
Orthoptera	-	-	-	-	-	-	12.50	1.06	**51.63**
Thysanoptera	-	-	-	12.50	2.94	0.01	-	-	-
Araneae	-	-	-	12.50	2.94	0.11	-	-	-
Plant material	**60**	-	**42.49**	75	-	**70.22**	87.5	-	5.72
n	5			8			8		
Food items	3			6			5		
N total average	5.4			7			11.75		
V total average (mm^3)	7.01			435.63			23.59		

Results of analyses on diet and reproduction in males and females were compared in order to explore possible associations between reproductive state and food intake in both sexes. A Spearman correlation test was performed using the statistical program Info Stat, Di Rienzo *et al.*, 2011 to determine whether there was an association between volume of food consumed by females and volume of embryos with their respective vitelline mass, or ovaries when not gravid. The same procedure was followed with males, whereby food volume was correlated to testicular volume.

RESULTS

Description of diet

A total of 10 food items were identified. Formicidae was the most common during the three periods of study (95.45% of all 44 lizards), followed by plant material (72.1%), Hemiptera (46.5%), and Coleoptera (30.2%). Although Formicidae was greater in numerosity and frequency than other food items, in March 2010 plants were the most important in volume.

Considering males, the mean volume of food consumption was rather low in October 2009 (43.4 ± 41.6 mm^3), with almost no plant consumption (0.5%). It was high in March 2010 (192.1 ± 159.9 mm^3), with 72.3% consisting of plant material. In November 2010, the mean food volume was 135.9 ± 90.7 mm^3; 52% being plant material (Table 1).

As for females, in October 2009 they ate very little (7.0 ± 9.5 mm^3); 42.5% being plant material. In March 2010, the beginning of fall, the total volume was very high (435.6 ± 285.5 mm^3), most of it consisting of plant material (70.2%). In November 2010, food intake was 23.6 ± 53.9 mm^3, with only a little less than 6% of plants (Table 1).

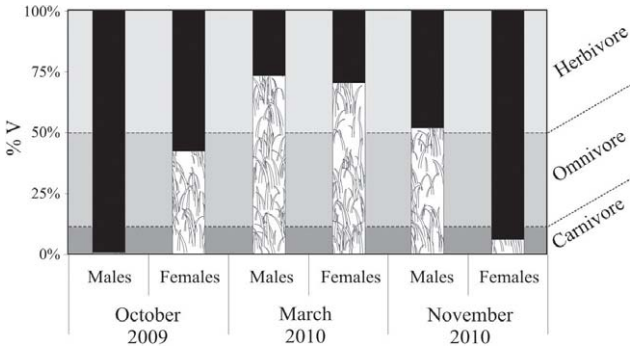

Figure 1. Proportion of plant matter consumed relative to animal prey, and classified as carnivores, omnivores, or herbivores, depending on the volume percentage (V%) of plants in males and females of *Liolaemus crepuscularis,* in October 2009, March 2010, and November 2010. Bars with grass: plant matter. Black bars: animal prey.

Animal prey

Considering the hierarchical index of Relative Importance (RI), Formicidae (RI: 100%) was the fundamental prey item in the three periods of the study. In October 2009, only three prey items were found, the second most important being Hemiptera with a low RI value (RI: 20.8%), followed by Coleoptera (RI: 9.6%), both values falling into the accidental category. In March 2010, seven prey items were identified. After Formicidae, the most important item was Coleoptera (RI: 43.0%), followed by Hemiptera (RI: 42.7%); both having RI values corresponding to the accessory category. In November 2010, eight prey items were identified, of which Coleoptera (RI: 35.4%) was the second in importance. The other arthropod orders found during the three months of the study — Araneae, Thysanoptera, Orthoptera, Acarina, Lepidoptera and Hymenoptera (non-Formicidae) — fell into the accidental category.

Plant material

Plant remains found in the digestive tracts consisted mainly of leaves, flowers, and some fruits. The total volume of plant material for the 44 lizards was 62.5%, the remainder being prey items. However, differences in volume were found among the three months and between males and females. In October 2009, only about 0.5% of males ate plants, a value that placed them, following the methodology of Espinoza *et al.* (2004), among carnivores (Fig. 1). Females, on the other hand, in the same month ate about 42.5% plant material, corresponding to the category of omnivores, although food consumption in general was low. In March 2010, both males and females consumed approximately 70% plant material, in which case both would be considered herbivores (Fig. 1). In November 2010, important differences between the sexes were observed, as males consumed more plant material than females (52%), placing them among herbivores (Fig. 1); whereas in females, plant content was only 5.7%, corresponding to carnivores.

Reproduction

In October 2009 and November 2010 (austral spring months), all females of *Liolaemus crepuscularis* contained embryos with a high degree of development, particularly in November 2010. The size of the clutch ranged between 3 and 6 ($\bar{X}$ = 4.5 ± 0.9, n = 11). The average volume of the clutch was 88.3 ± 40.4 mm³ in October, with large reserves of vitellus, which together reached an mean volume of 353.9 ± 87.8 mm³ per pregnant female (Fig. 2). In November 2010, volume of the embryos measured 240.6 ± 122.1 mm³, which together with the vitellus reached a mean volume of 277.6 ± 73.9 mm³. In March 2010 (late summer), 66% of females were vitellogenic, presenting yolked follicles; the rest were still at an early stage of vitellogenesis. The mean volume of the ovaries was 54.1 ± 50.5 mm³ (Fig. 2).

In October 2009 and November 2010, average testicular volume was 19.7 and 63.2 mm³, respectively, whereas in March 2010 it was 307.7 mm³. This great increase in size coincided with the presence of yolked follicles in females.

Relation between diet and reproduction

Results of a Spearman correlation test for females indicated that the gonadal or embryo volume was negatively correlated to the volume of food intake (r_s = -0.66, P = 0.004, n = 17, Fig. 2). In males, results showed no evidence of a correlation between testicular and food volume (r_s = 0.15, P = 0.55, n = 16).

DISCUSSION

Formicidae constituted a fundamental part of the diet of *Liolaemus crepuscularis,* as has been reported in several other *Liolaemus* species (*e.g., L. koslowskyi,* Aun and Martori, 1998; *L. wiegmannii,* Aun *et al.,* 1999; *L. elongatus,* Quatrini *et al.,* 2001; *L. pseudoanomalus,* Kozykariski *et al.,* 2011; *L. cuyanus,* Moreno Azócar and Acosta, 2011; *L. irregularis, L. albiceps, L. multicolor, L. yanalcu,* Valdecantos, 2011). In Minas Capillitas, several species of ants were observed and they were generally abundant. The foraging of ants possibly does not present a high cost (Stephens and Krebs, 1986). Some of the studies cited above explore differences in diet among seasons and between sexes, *e.g., L. wiegmannii* (Aun *et al.,* 1999) and *L. quilmes* (Halloy *et al.,* 2006). In the former species, the authors

did not find significant differences between months, as was found in *L. crepuscularis;* and in the latter, it was reported that females significantly selected more ants characterized by soft bodies and lack of functional stings than males. This was not investigated in *L. crepuscularis*.

Male and female *Liolaemus crepuscularis* fluctuated between herbivory and insectivory; in March 2010 they were both herbivores. Males remained herbivores in November 2010, whereas in October 2009 they were strictly insectivores. Females, on the other hand, were omnivores in October 2009 and insectivores in November 2010. Plant consumption in Liolaemidae may be explained, among other factors, by a combination of environmental conditions, such as cool climates and isolated regions (Espinoza *et al.,* 2004). These are very common in high altitude habitats, which make it possible for *L. crepuscularis* to present some degree of herbivory. One of the advantages of facultative herbivory is that plants are abundant and require less energy to obtain (Pough, 1973). Different degrees of herbivory have been reported in high altitude species such as *L. alticolor* (57.6%), *L. aymararum* (87.2%), *L. jamesi* (67.8%), and *L. signifer* (68.9%) (Valencia *et al.,* 1982). In March 2010, the high consumption of plant material in both sexes could be due to a greater variety of plants being more accessible than insects at this time of year, although this was not evaluated here. Due to plants providing fewer nutrients (King, 1996), lizards must eat considerably more of them.

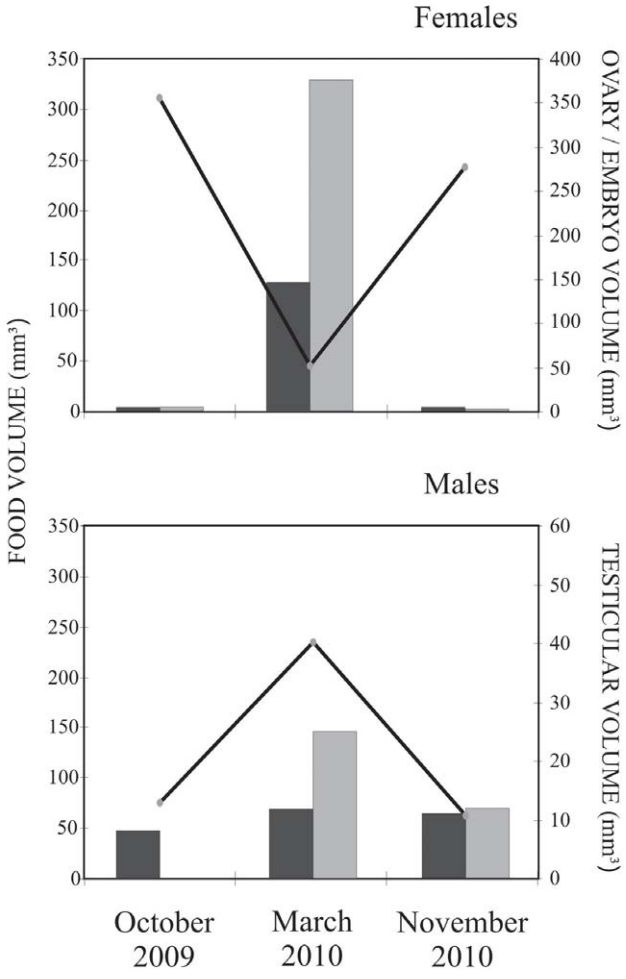

Figure 2. Relationship between food volume and volume of embryos (with vitellus), or female ovaries, depending on the period of the study (October 2009, March 2010, and November 2010); and on food volume and testicular volume in males of *Liolaemus crepuscularis* (all in mm³). Black bars: volume of insects consumed. Grey bars: volume of plants consumed. Black line: volume of gonads.

Liolaemus crepuscularis therefore, did not present a strict diet but rather varied between seasons, showing some important contrasts between sexes. Considering only animal prey, seasonal and sex differences were found, although Formicidae was the prey most eaten in every case. *Liolaemus crepuscularis* alternated feeding on insects with greater or lesser incorporation of plant material in its diet, depending on season and sex. According to the classification criterion of Espinoza *et al.* (2004), and as observed by Roca (1999) for other reptiles, the diet of *L. crepuscularis* fluctuated through a continuum between "carnivory-omnivory-herbivory".

Considering reproductive condition, this has often been observed to vary in high altitude species (Donoso-Barros and Cei, 1971; Guillette *et al.,* 1980; Leyton *et al.,* 1982). *Liolaemus crepuscularis* exhibits a seasonal reproductive pattern. In March 2010, two thirds of adult females presented vitellogenic follicles, indicating reproductive maturity (Licht and Gorman, 1970). In species of the *L. laurenti* group (Abdala, 2007) found at lower altitudes, such as *L. wiegmannii* (Martori and Aun, 1997), *L. multimaculatus* (Vega, 1997), and *L. koslowskyi* (Martori and Aun, 2010), this condition is found between August and September. In October 2009 and November 2010, all female *L. crepuscularis* were gravid.

In October 2009, the embryos remained surrounded by a large mass of vitellus, whereas in November 2010 their development was more advanced and the amount of vitellus decreased considerably. It has been reported for some high altitude and high latitude species that females are pregnant throughout the winter and give birth in the spring (Leyton *et al.,* 1982; Guillette and Casas-Andreu, 1987; Ramírez Pinilla, 1991; Halloy and Halloy, 1997; Schulte *et al.,* 2000). This may be the case for this species, although samples need to be obtained during the winter months to confirm this.

Males showed an increase in testicular size in March 2010, as has been observed in other high altitude species (Ramírez Pinilla, 1991). These results suggest that *Liolaemus crepuscularis* is reproductively active at this time of year, a common trait in high altitude viviparous species of this genus, such as *L. gravenhorsti* (Leyton *et al.,* 1982), *L. huacahuasicus* (Halloy and Halloy, 1997), and *L. pagaburoi* (Schulte *et al.,* 2000).

The reproductive cycle may be important in determining food consumption in *Liolaemus crepuscularis,* since, depending on the reproductive state in which a lizard was found, its diet varied in type and quantity of food consumed. The large decrease of food consumption in females in October 2009 and November 2010 significantly coincided with their gravid condition. In March 2010, females greatly increased food consumption — particularly plants — at the same time that vitellogenesis began. We found a negative relationship between volume of the embryos and the amount of food consumed. Pregnancy produces a great distension in the female body, which could affect the ability to find food, in turn influencing dietary composition (Barden and Shine, 1994). This could be one of the reasons why, when vitellogenesis occurred, food intake in female *L. crepuscularis* increased, with a significant proportion of plant material greater than that of insects. Food intake decreased greatly when females were pregnant, during which time they ate only insects and practically no plants. After observing the space that the developing embryos occupied, particularly in October 2009 when the vitellus tripled the size of the embryos, it was clear that there was no room left for food. A similar phenomenon was reported for the oviparous *L. koslowskyi,* as female gonadal volume was negatively related to the volume of food consumed (Martori, 2005). Thus the lack of space inside the mother's body may constitute one of the major causes for a lesser intake of food. For this reason, small insects might be the best food option during pregnancy, since plant tissue (especially leaves) contains less energy and nutrients per gram than insects (Iverson, 1982; Troyer, 1991; King, 1996).

In males, the relationship between testicular volume and amount of food intake was not statistically significant. This may be due to variability of data and a samples size of 16 not being large enough to pick up any significant difference. Nevertheless, a positive difference was observed in males of *Liolaemus koslowskyi* (Martori, 2005), a species that also belongs to the same *darwinii* group (Etheridge, 1993; Abdala, 2007), although it is oviparous and occurs at lower altitudes. More studies are needed with more months of sampling to better understand diet and reproduction patterns in male and female *L. crepuscularis*.

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