Diet of the lizard *Liolaemus occipitalis* in the coastal sand dunes of southern Brazil (Squamata-Liolaemidae)

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(With 1 figure)

Abstract

Knowledge of a species' diet provides important information on adaptation and the relationship between the organism and its environment. The genus *Liolaemus* occurs in the southern region of South America and is an excellent model to investigate the adaptive processes of vertebrate ecology in ecosystems of this region of the world. *Liolaemus occipitalis* is an endangered species that inhabits the coastal sand dunes of southern Brazil. This species is the most abundant vertebrate in this environment, and it presents unique adaptation characteristics to the *restinga* environment. The present study analyzed this lizard's diet to verify similarities or differences between this species and other species of the same genus. Specimens were collected monthly from January 1996 to December 1997. The number of items, frequency of occurrence and volume of each prey taxon were determined. Arthropods were identified to the order level, and plant material was identified as flower, fruit, seed and leaves. Variations in the diet of males and females, adults and juveniles and seasons were also analyzed. The data indicate that *Liolaemus occipitalis* is a generalist, "sit-and-wait" or ambush predator as well as omnivorous, feeding on both arthropods and plant material. Significant ontogenetic differences were verified. Juveniles are more carnivorous, and the intake of plant material increases with size and age. Seasonal differences in diet composition were also observed. In the spring, arthropod and plant materials were more diversified and, therefore, consumed more often.

Keywords: Liolaemus, southern Brazil, *restinga*, foraging, seasonal variation.

Dieta do lagarto *Liolaemus occipitalis* nas dunas costerias do sul do Brasil (Squamata-Liolaemidae)

Resumo

O conhecimento sobre a dieta de uma espécie traz informações importantes sobre a adaptação e relações entre o organismo e seu ambiente. O gênero *Liolaemus*, que ocorre na região austral da América do Sul, tem-se mostrado como excelente modelo em ecologia de vetebrados para entender os processos adaptativos nos ecossistemas desta região do mundo. *Liolaemus occipitalis* é uma espécie ameaçada de extinção que habita as dunas costeiras do extremo sul do Brasil. É o vertebrado mais abundante neste ambiente e apresenta características peculiares de adaptação aos ambientes de restingas. No presente estudo analisou-se a dieta deste lagarto com o intuito de verificar se há diferenças com as espécies do gênero ou segue o mesmo padrão. Foram realizadas coletas mensais entre janeiro/96 e dezembro/97. Determinou-se o número de itens, a frequência de ocorrência e o volume de cada táxon de presa, identificados até o nível de ordem, no caso dos artrópodes, e como flor, fruto, semente e folhas o material vegetal. Foram analisadas as variações da dieta entre machos e fêmeas, entre adultos e jovens, e também entre as estações. Os dados indicam que *Liolaemus occipitalis* possui uma dieta onívora consumindo tanto artrópodes como material vegetal. Caracteriza-se por ser um predador generalista, forrageando de modo "senta-e-espera". Determinaram-se diferenças significativas entre a dieta de jovens e adultos. Entre as variações ontogenéticas, constatou-se que lagartos jovens apresentam um hábito mais carnívoro, e a inclusão do material vegetal na dieta aumenta sucessivamente com o tamanho/idade do animal. Verificaram-se diferenças na composição da dieta ao longo das estações, sendo mais diversa na primavera em relação ao consumo de artrópodes, e com maior consumo de material vegetal.

Palavras-chave: Liolaemus, sul do Brasil, restinga, forrageio, sazonalidade.

1. Introduction

The trophic relationship between lizards and their environment and the foraging strategies for obtaining food resources are important aspects of the ecology of these organisms (Pianka, 1982; Silva and Araújo, 2008). Foraging is related to different aspects of a lizard's life history, such as reproductive cycle, seasonal patterns, population dynamics, growth patterns (Vitt, 1990) and predator escape mechanisms (Huey and Pianka, 1981; Magnusson et al., 1985; Vitt, 1990).

Lizards may have two basic foraging strategies: "sit-and-wait" or sedentary ambush foraging and active or wide-ranging foraging. Lizard species are found along a continuum between these two extremes (Huey and Pianka, 1981; Cooper, 1995; Stephen et al., 2007). One of the primary outcomes of the different foraging patterns of diurnal lizards is the diversity and abundance of the consumed prey, which results from the range of the foraging territory.

The diet composition of a lizard species may vary between sexes, seasonally or ontogenetically. The diet of males and females of some species differs quantitatively and qualitatively to reduce intersexual competition (Schoener, 1967) or because of morphological differences, especially head and jaw size (Fitch, 1978). Seasonal variations in diet are usually associated with the availability of prey in the environment. This variation was verified in *Cnemidophorus tigris* BAIRD and GIRARD, 1852 (Pianka, 1970), *Polychrus acustirostris* SPIX, 1825 (Vitt and Lacher, 1981), *Iguana iguana* (LINNAEUS, 1758) (Schoener et al., 1982), *Plica plica* (LINNAEUS, 1758) (Vitt, 1991), *Tropidurus itambere* (RODRIGUES, 1987) (Van Sluys, 1995), *Mabuya macrorhyncha* (HOGE, 1946) (Vrcibradic and Rocha, 1995), *Liolaemus lutzae* (MERTENS, 1938) (Rocha, 1996), *Tropiduru torquatus* (WIED-NEUWIED, 1820) (Fialho et al., 2000) and *C. littoralis* (ROCHA, ARAÚJO, VRCIBRADIC and COSTA, 2000) (Teixeira-Filho et al., 2003). Ontogenetic variations may appear in the size or type of prey. Juveniles of many species are essentially carnivorous and feed on larger quantities of smaller prey, whereas adults are omnivorous or herbivorous and feed on smaller quantities of larger prey (Schoener and Gorman, 1968; Ortiz, 1974; Ortiz and Riveros, 1976; Stamps et al., 1981; Rocha, 1989; Magnusson and Silva, 1993; Fialho et al., 2000).

The austral herpetofauna of South America exhibits significant diversity and richness of lizard species of the Liolaemini clade, which includes the genus *Liolaemus* WIEGMANN, 1834 (approx. 225 species according to Ávila et al., 2010). Lizards of this genus exhibit ecological variability that is independent of their phylogenetic relationships, which makes these lizards excellent models for vertebrate ecological studies (Espinoza et al., 2004; Tulli et al., 2011). Several studies on the diet of this genus have been published (Ortiz and Riveros, 1976; Fuentes and Ipinza, 1979; Jaksic and Fuentes, 1980; Rocha, 1989; Ávila and Acosta, 1993; Vega, 1999; Belver and Avila, 2001; Halloy et al., 2006; Azócar and Acosta, 2011). *Liolaemus* ssp. are excellent representatives of the pattern observed in species of the Iguana group within the foraging models of lizards (Huey and Pianka, 1981). The genus *Liolaemus* encompasses insectivorous, omnivorous and herbivorous species (Etheridge and Espinoza, 2000; Espinoza et al., 2004). Carnivorous and omnivorous *Liolaemus* lizards are ambush foragers and present features of the sit-and-wait model for Squamata, such as the prevalence of mobile prey and relatively diverse diets. Most lizards of this genus present ontogenetic variation throughout their lifespan. Omnivorous *Liolaemus* species increase their intake of plant material in the adult stage. Several smaller species than those considered by Pough (1973) show an evident tendency to herbivory (Jaksic, 1978; Greene, 1982; Rocha, 1992; Van Sluys, 1993; Espinoza et al., 2004). The genus *Liolaemus* also shows the same tendency, including *L. pictus pictus* (DUMÉRIL and BIBRON, 1837) (Ortiz, 1974), *L. nigromaculatus kulhmani* MÜLLER and HELLMICH, 1933 (Jaksic, 1978) and *L. lutzae* (Rocha, 1989; 1992). However, Espinoza et al. (2004) stated that different herbivory levels in the genus *Liolaemus* have appeared during evolution as adaptations to cold environments. Therefore, the *Liolaemus* species are part of a group of small omnivorous and/or herbivorous tropidurid lizards that occur in the southern extreme of South America (Vitt and Caldwell, 2009).

Brazil contains three species of the genus *Liolaemus*: *Liolaemus lutzae* MERTENS, 1938; *L. occipitalis* BOULENGER, 1885 and *L. arambarensis* VERRASTRO *et al*., 2003. *L. occipitalis* is a small sand lizard that is found in the coastal sand dune environment in the southern extreme of Brazil (sandbank vegetation, or *restinga*, habitat) in the states of Rio Grande do Sul (RS) and Santa Catarina (SC) (Peters et al., 1986; Lema, 1994; Verrastro, 2004). These lizards are also found on the east coast of Uruguay (Verrastro et al., 2006). This lizard, which reaches a maximum size of 60 mm, is oviparous and active during the day between 10 a.m. and 4 p.m., and its reproductive period lasts from September to March (Verrastro and Bujes, 1998; Verrastro and Krause, 1999). The lizards are associated with clumps of herbaceous vegetation spread throughout the mobile sand dunes where the lizards find food resources, shelter from predators and thermoregulation sites (Verrastro and Bujes, 1998; Bujes and Verrastro, 2006). These lizards bury themselves in the soft sand and may build burrows in the harder sand to seek refuge during the hottest hours of the day or during winter (Bujes and Verrastro, 2006; Bujes and Verrastro, 2008).

Liolaemus occipitalis was included in the *Lista Nacional das Espécies Ameaçadas de Extinção* (Brazilian's list of endangered species) by the official document entitled *Instrução Normativa n° 003, de 26 de maio de 2003*, and it remains on this list (ICMBio-MMA, 2013). The state of RS reviewed its list of endangered species in 2013 and categorized *L. occipitalis* as Vulnerable (VU) due to threats to its habitat and a severe reduction in its home range (http://www.liv.fzb.rs.gov.br/livcpl/?id_modulo=1&id_uf=23).

Knowledge of natural history is important to better establish conservation criteria for this species and its environment.

We sought to describe the diet of a population of *Liolaemus occipitalis* in the sand dunes of the municipality of Cidreira, state of RS, to verify whether this species follows the patterns within the genus.

This study investigated the composition of this species' diet, foraging behavior, ontogenetic and intersexual variations in the diet composition and seasonal variations in diet.

2. Material and Methods

This study was performed in the municipality of Cidreira (30°17'07" S and 50°11'05" W) on the RS 786 highway, which connects the municipalities of Tramandaí and Cidreira in the State of RS, Brazil. The study was performed between January 1996 and December 1997, except for a period between June and August 1996, when the access to the area was prevented by rainfall. The area is characterized by the presence of mobile sand dunes and mostly sandy soil, and herbaceous vegetation covers 10 to 15% of the terrain (Waechter, 1990; Dillenburg et al., 1992). The climate is subtemperate according to Maluf's classification (Maluf, 2000). The mean annual rainfall is 1323 mm with no typical dry season and a mean annual temperature of 20 °C (Hasenack and Ferraro, 1989).

Individuals were collected manually once a month between 10:30 a.m. and 2:30 p.m. Specimens were weighed in the field on a set of 0.1 g precision scales and sacrificed with Citanest (3%) immediately afterwards. The specimens were fixed in 10% formalin for 72 h, preserved in 70% ethanol and vouchered in the Collection of Amphibians and Reptiles of the Department of Zoology of the Universidade Federal do Rio Grande do Sul (UFRGS). The biometric measurements of snout-vent length (SVL) and jaw width (JW) were taken in the laboratory using a caliper with 0.1 mm precision. Sex was identified by the presence or absence of cloacal pores and color according to Verrastro (2004). Males were considered adults if the SVL was at least 50.0 mm, and females were considered adults if the SVL was at least 45.0 mm (Verrastro and Krause, 1994).

The lizards were dissected, and their stomach contents were analyzed under a stereomicroscope to identify, quantify and measure the food items. Arthropods were identified to the Order level with the additional separation of Hymenoptera into two categories, "Formicidae" and "Others". Coleoptera and Lepidoptera were also classified into two categories, "Adults" and "Larvae". All plant material was grouped together and subdivided into flowers, fruits, seeds, fibers and leaves.

The diet of *L. occipitalis* was analyzed quantitatively and qualitatively. The diet was compared using the Kolmogorov-Smirnov test to determine whether the data from the two years should be analyzed together or separately (Siegel, 1975). The qualitative analysis considered only the presence of each food item in the diet composition. Non-parametric tests were used because the data were not normally distributed.

The presence of each food item (prey) determined the diet composition in the qualitative analysis. The diet composition of males and females and of adults and juveniles was analyzed separately. The number of stomachs (individuals) that contained each prey was recorded, and the data were compared using the Kolmogorov-Smirnov test (Siegel, 1975).

The quantitative analysis considered the number of consumed items in each prey taxon that was present in the stomachs. The frequency of occurrence was estimated as the number of stomachs in which a given prey item was found with respect to the total number of stomachs (individuals). Volume was estimated by measuring each item present in the stomach and applying the ellipsoid (spheroid) formula proposed by Mayhew (1963): $V = 4/3\ \pi\ ab^2$, where "a" is 1/2 of the larger length of the prey and "b" is 1/2 of the smaller larger. The volume percentages of each prey and the number of items consumed by each individual were also calculated. Plant material was analyzed only in terms of volume and frequency of occurrence. The volume of sand was ignored in these calculations.

Ontogenetic variations were based on the two classes of body size between adults and juveniles and compared with respect to the number and volume of the consumed items using the Mann-Whitney test. The mean volume of the five larger items and the number of items consumed with respect to the SVL of a given lizard were tested using linear regression to compare differences in prey consumption between adults and juveniles and its relationship with the SVL of each individual. The size of the largest prey consumed and the lizard's JW were similarly compared. A linear regression analyzed the consumption of plant material and the SVL to assess differences in the consumption of plant material between age classes. The effect of the lizard's size on the proportion of plant material in the stomach was calculated using a regression analysis. The proportion of plant material was transformed in an arcsine square root prior to this analysis (Zar, 1984; Van Sluys, 1993; Rocha, 1996; Fialho et al., 2000).

Seasonal variations in the diet were analyzed in groups (autumn = March, April and May; winter = June, July and August; spring = September, October and November; summer = December, January and February). Simpson's Diversity Index compared the diversity of arthropods that were consumed by the population during the four seasons. Bootstrapping tested the differences in diversity among the seasons (Krebs, 1999; Magurran and McGill, 2011).

3. Results

A total of 285 individuals were collected in the *restingas* in Cidreira. A total of 114 individuals were collected in 1996, and 171 were collected in 1997. The sample included 135 males, 108 females and 42 juveniles. Only one empty stomach was recorded.

Because the diet composition between 1996 and 1997 was not significantly different, the data from both years were analyzed together (D = 0.2857; p = 0.541).

A total of 16 food items were identified in the diet of *L. occipitalis* (Table 1), which consisted of both plant and animal items. The most frequent items were Formicidae (79.65%), Coleoptera adults (69.12%), Thysanoptera (28.07%) and Araneae (25.26%). Plant material was found in 28.07% of the stomachs (Table 1). The following categories of plant material were found: flowers (19.3%), fibers (7.02%), seeds (1.75%), fruits (1.05%) and leaves (0.35%) (Table 1). The food items with the largest total volume were Coleoptera adults (15.76%), followed by Formicidae (9.52%) and Coleoptera larvae (5.54%). Plant material corresponded to 7.32% of the ingested items (Table 1). Sand was found in 100% of the stomachs.

The diet composition changed throughout life, and significant differences were observed between the food items consumed by adults and juveniles (D = 0.4667; $p < 0.05$). Juvenile stomachs contained more Diptera, Coleoptera and Hemiptera adults and larvae; in contrast, plant material, Orthoptera and Lepidoptera were more frequently observed in the adult stomachs (Table 2; Figure 1). No significant differences in the number of items consumed by adults and juveniles were observed (U = 6969; p = 0.2178), but a marginally significant correlation between the number of consumed items and lizard size was noted ($r^2 = 0.1211$; p = 0.068). However, it was evident that adults consumed larger prey (U = 5093; $p < 0.0001$). This difference was also observed in the relationship between the mean of the five largest items and SVL ($r^2 = 0.3706$, $p < 0.0001$; N = 164) and the size of the largest prey and JW ($r^2 = 0.3589$; $p < 0.0001$; N = 113). Plant material was found in approximately 35% of the adult stomachs, and plant material was the most important item in the juvenile stomachs. However, only one item was

Table 1. Number of items (No.), frequency per taxon (%), frequency of occurrence in the stomach contents (Freq), volume (mm^3) and volume percentage (Vol%) consumed per taxon by *L. occipitalis* in the sandbank vegetation at Cidreira (Brazil, RS) in 1996 (N = 114) and 1997 (N = 171).

Item	No	%	Freq	Vol	Vol %
1. Hymenoptera - Formicidae	2661	68.80	79.65	4,217.58	9.52
2. Hymenoptera - others	3	0.08	4.21	22.41	0.05
3. Coleoptera - Adultus	604	15.62	69.12	6,979.18	15.76
4. Coleoptera - Larvae	138	3.57	10.18	2,452.77	5.54
5. Diptera	36	0.93	9.12	445.89	1.01
6. Isoptera	1	0.03	0.35	5.64	0.01
7. Homoptera	6	0.16	1.40	308.20	0.70
8. Hemiptera	145	3.75	20.35	1,617.73	3.65
9. Orthoptera	110	2.84	16.49	2,280.87	5.15
10. Neuroptera	5	0.13	1.75	85.61	0.19
11. Ephemeroptera	6	0.16	2.11	277.02	0.63
12. Araneae	100	2.59	25.26	1,183.29	2.67
13. Thysanoptera	7	0.18	28.07	11.22	0.03
14. Lepidoptera - Adults	36	0.93	10.18	1,499.24	3.38
15. Lepidoptera - Larvae	10	0.26	3.51	938.50	2.12
16. Vegetal matter	-	-	28.07	3,241.50	7.32
Flower	-	-	19.30	-	-
Fruit	-	-	1.05	-	-
Fiber	-	-	7.02	-	-
Seed	-	-	1.75	-	-
Leaves	-	-	0.35	-	-
Sand				18,608.76	42.01
Overall	3,868			44,175.41	
Nº stomachs			285		

Table 2. Number of items (No.), frequency of occurrence in the stomach contents (Freq) and volume percentage (Vol%) consumed by adults and juveniles (D = 0.4667, p = 0.05, N = 285) and by males and females (D = 0.2; p = 0.889; N = 242) of *L. occipitalis* in the sandbank vegetation at Cidreira (RS, Brazil).

Item	Adult			Juvenile			Male			Female		
	Nº	Freq	Vol %	Nº	Freq	Vol %	Nº	Freq	Vol %	Nº	Freq	Vol %
1. Araneae	90	27.1	5.04	10	22	3.33	46	26.1	5.09	48	28.7	4.07
2. Coleoptera	580	74.6	30.45	28	80.5	6.37	312	69.4	25.46	260	51.9	31.24
3. Larvas de Coleoptera	130	13.1	9.19	9	17.1	23.42	50	17.2	10.06	82	8.33	7.58
4. Diptera	24	8.61	1.8	13	17.1	4.46	11	6.72	1.01	17	6.48	2.82
5. Ephemeroptera	5	2.05	1.04	1	2.44	2.6	4	2.99	1.49	1	0.93	0.26
6. Hemiptera	135	21.3	6.98	12	24.4	2.58	47	23.1	8.69	64	18.5	3.59
7. Homoptera	4	1.64	1.34	2	4.88	0.36	4	1.49	2.17	2	9.26	0.06
8. Hymenoptera – Formicidae	2,528.00	83.6	18.07	160	75.6	17.18	1,214	79.9	15.44	1,219	84.3	18.95
9. Hymenoptera - other	0.00	0.00	0.00	3	7.32	0.00	1	0.75	0.13	2	1.85	0.04
10. Isoptera	1	0.41	0.02	0	0	0	1	0.75	0.04	0	0	0
11. Lepidoptera	33	11.9	6.26	3	2.44	5.26	20	11.9	7.38	13	12	3.6
12. Larvas de Lepidoptera	10	4.1	4.16	0	0	0	7	5.22	3.54	3	2.78	4.16
13. Neuroptera	4	2.46	0.36	1	2.44	0.32	2	1.49	0.38	4	3.7	0.32
14. Orthoptera	106	17.2	10	8	7.32	1.36	65	19.4	6.87	66	10.2	12.18
15. Thysanoptera	7	2.46	0.05	0.00	0.00	0.00	5	2.99	0.06	2	1.85	0.02
16. Vegetal	-	33.6	11.88	-	17.1	34.79	-	33.6	12.32	-	34.3	10.83
Flower		68.8			42.9							
Fruit		4.68			0							
Fiber		17.2			42.9							
Seed		7.81			14.3							
Leaves		1.56			0							
Nº stomachs		244			41			134			108	
Overall	3,602			247			1,788.00			1,781.00		

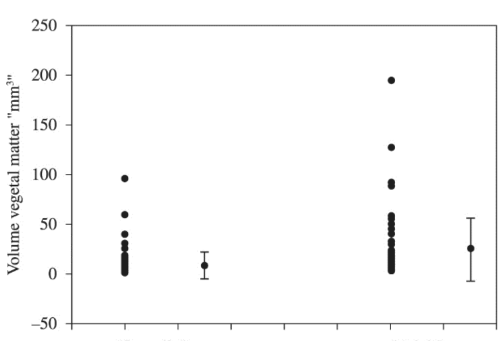

Figure 1. Percentage of plant material consumed by juveniles and adults of *L. occipitalis* in 1996 and 1997. The horizontal point and the vertical lines to the right represent the mean and standard deviation, respectively, for each group according to the scatter plot shown on the right (N = 96 juveniles and N = 69 adults, values expressed after arcsine square root transformation). Significant differences in the consumption of plant material were observed between juveniles and adults (Mann-Whitney Test = U' = 5093.0; p < 0.0001).

found in the stomach of a single juvenile. Adults consumed larger portions of flowers, leaves and fruits (Table 2), and juveniles consumed larger portions of seeds and fibers (Table 2). The consumption of plant material was observed in lizards with a minimum SVL of 30 mm and a minimum mass of approximately 0.8 g. The proportion of total plant material volume in the lizard stomachs exhibited a highly significant and positive correlation with size ($r^2 = 0.9987$; $p < 0.00001$; N = 74).

No significant differences were observed between the diets of males and females ($D_{max} = 0.2$, $p = 0.889$), but some subtle differences were observed. Males more frequently consumed Coleoptera larvae and Hemiptera (Table 2).

Nematode parasites (Nematoda) were found in 49 stomachs (17.19%) of *L. occipitalis* (34 adults and 15 juveniles). The infected individuals had an average of 3.6 worms per stomach.

The diet of *L. occipitalis* was composed of basically the same categories of food items in all study periods, but some items were not found in all seasons. Homoptera

Table 3. Number of items (No.), frequency per taxon (%), frequency of occurrence in the stomach contents (Freq), volume (mm^3) and volume percentage (Vol%) of each taxon consumed by *L. occipitalis* in 1996 and 1997 in the sandbank vegetation at Cidreira (RS, Brazil) (N = 114 and N = 171, respectively).

ITEM	AUTUMN					WINTER					SPRING					SUMMER				
	No.	%	Freq	Volume	Vol %	No.	%	Freq	Volume	Vol %	No.	%	Freq	Volume	Vol %	No.	%	Freq	Volume	Vol %
Araneae	33	3.06	30.34	302.43	4.03	15	3.30	23.50	144.70	6.30	36	2.59	26.37	512.75	4.69	16	1.66	13.46	231.29	4.63
Coleoptera - adults	112	10.37	62.92	1348.90	17.97	108	24.00	70.60	648.60	28.00	262	18.85	71.43	2901.19	26.52	124	12.84	71.15	2080.49	41.65
Coleoptera - larvae	11	1.02	12.36	157.40	2.10	4	0.80	7.80	707.90	30.70	100	7.19	12.09	1403.33	12.83	2	0.21	25.00	150.24	3.01
Diptera	13	1.20	10.11	73.85	0.98	8	1.70	11.70	84.60	3.60	24	1.73	12.09	287.44	2.63	0	0.00	0.00	0.00	0.00
Ephemeroptera	6	0.56	6.74	277.02	3.69	0	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00	0.00
Hemiptera	52	4.81	29.21	1040.92	13.87	7	1.50	11.70	5.70	0.20	50	3.60	19.78	319.48	2.92	34	3.52	17.31	251.63	5.04
Homoptera	5	0.46	3.37	306.64	4.08	0	0.00	0.00	0.00	0.00	0	0.00	0.00	1.56	0.01	0	0.00	0.00	0.00	0.00
Hymenoptera - Formicidae	777	71.94	83.15	1057.75	14.09	296	65.60	78.40	472.50	20.50	821	59.06	82.42	1657.41	15.15	774	80.12	73.08	1169.90	23.42
Hymenoptera - other	1	0.09	1.12	17.7	0.24	0	0.00	0.00	0.00	0.00	2	0.14	2.20	4.71	0.04	0	0.00	0.00	0.00	0.00
Isoptera	0	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00	0.00	1	0.07	1.10	5.60	0.05	0	0.00	0.00	0.00	0.00
Lepidoptera	19	1.76	16.85	650.34	8.66	7	1.50	13.70	189.30	8.20	6	0.43	6.59	303.44	2.77	2	0.21	1.92	24.80	0.50
Lepidoptera - larvae	5	0.46	5.62	823.90	10.98	2	0.40	3.90	3.40	0.14	1	0.07	1.10	31.30	0.29	4	0.41	3.85	79.90	1.60
Neuroptera	2	0.19	2.25	53.22	0.71	0	0.00	0.00	0.00	0.00	3	0.22	3.30	32.39	0.30	0	0.00	0.00	0.00	0.00
Orthoptera	36	3.33	22.47	623.36	8.30	3	0.60	5.80	49.20	2.10	86	6.19	17.58	716.81	6.55	10	1.04	19.23	891.50	17.85
Thysanoptera	6	0.56	5.62	9.72	0.13	1	0.20	1.90	1.50	0.06	0	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00	0.00
Vegetal	-	-	24.72	449.75	5.99	-	-	7.80	29.30	1.30	-	-	49.45	1010.10	9.23	-	-	15.38	115.34	2.31
Overall	1080			7506.56		451			2336.70		1390			10938.61		966			4995.19	
Nº. stomachs			89					51					93					52		

Table 4. Simpson's Diversity Index of the diet of *L. occipitalis* in the different seasons in the population of Cidreira/RS. The "p" values reflect significant differences between the seasons.

	autumn	winter	spring	summer
autumn	0.4636			
winter	p=0.153	0.5099		
spring	p=0.001	p=0.001	0.6041	
summer	p=0.003	p=0.001	p=0.001	0.3779

were found only in autumn, Neuroptera were not found in summer and winter, and Thysanoptera were not found in the spring and summer. Plant material was more frequently consumed in the spring, and Lepidoptera were more frequently consumed in the autumn and winter. Diptera were consumed more frequently in the summer (Table 3). The diversity of consumed items was greatest in the spring and lowest in the summer (Table 4). Significant differences in the diversity of the consumed items were observed among all seasons except winter and autumn (Table 4).

4. Discussion

L. occipitalis is an omnivorous species that feeds on at least 16 food items, including arthropods and plant material. This lizard's diet is similar to many species of the same genus, which encompasses carnivorous, omnivorous and exclusively herbivorous species (Espinoza et al., 2004; Acosta et al., 1996; Rocha, 1996). *L. occipitalis* exhibits a foraging behavior that is closer to the sit-and-wait or ambush predator mode in the foraging continuum model proposed MacArthur and Pianka (1966), Schoener (1971) and Huey and Pianka (1981). The predominance of winged and mobile prey in the diet suggests that this species, similar to most Iguanid lizards, moves infrequently while searching for food, usually consumes more active prey and has a relatively diversified diet (Huey and Pianka, 1981; Vitt and Carvalho, 1995). This categorization is corroborated by the territoriality of this species, which means that individuals tend to move very little during the day and throughout their life (Verrastro, 2001). The ambush predator strategy is associated with generalist species, which likely include *L. occipitalis*. The great diversity of prey confirms this association (Schoener, 1971; Vitt and Carvalho, 1995). A high frequency of ants was also observed in the stomach, and ants were the most frequently identified food item. Ants are associated with the diet of sit-and-wait foragers, but termites are associated with widely active foragers (Huey and Pianka, 1981; Magnusson et al., 1985; Vitt et al., 2003; Silva and Araújo, 2008). The high mobility and local abundance of ants favors encounters between these insects and ambush predator lizards, which facilitates the capture of this type of prey. Species of the genus *Liolaemus*, such as *L. cuyanus* CEI and SCOLARO, (1980), (Azócar and Acosta, 2011), *L. pseudoanomalus* BURMEISTER, (1981), (Kozykariski et al., 2011), *L. bibronii* (BELL, 1843) (Belver and Avila, 2001), *L. wiegmannii* (DUMÉRIL & BIBRON, 1837) (Aun et al., 1999), *L. koslowskyi* ETHERIDGE, 1993, (Aun and Martori, 1998), *L. boulengeri* KOSLOWSKY, 1898, (Acosta et al., 1996), *L. darwini* (BELL, 1843), (Avila and Acosta, 1993; Videla, 1983) and *L. lutzae* (Rocha, 1989), and lizards of the genus *Tropidurus* also exhibit a preference for ants (Van Sluys, 1993, 1995; Vitt and Carvalho, 1995). According to Vitt et al. (2003), Iguanid lizards consume larger proportions of ants and other Hymenoptera because these lizards occupy a different microhabitat than the Scleroglossa lizards, which consume larger proportions of termites and spiders and avoid the consumption of prey with toxic chemical defenses.

Differences between the volume of food items consumed by juveniles and adults were recorded. A positive and significant correlation between the mean size of the five largest volumes and the body size of *L. occipitalis* was observed. This species tended to consume larger prey as its body size increased. Additionally, the size of the food items was significantly correlated with the lizards' JW. This variation may be the result of morphological limitations (head size vs. jaw size) because smaller lizards can only capture smaller prey (DeMarco et al., 1985; Rocha, 1989; Van Sluys, 1993). Both body size and head size facilitate the competition for resources (Schoener, 1967, 1971) based on the decrease in intraspecific competition.

Significant differences were also observed in the quality of the items consumed by juvenile and adult lizards. Juveniles tended to consume prey with smaller amounts of chitin. Therefore, they consumed larger volumes of flies and Coleoptera larvae, whereas beetles predominated the adult diet. The ontogenetic differences in diet may be a consequence of different nutritional needs because juveniles have higher metabolic demands due to their greater growth rate compared with adults (Andrews, 1976; Stamps et al., 1981; Verrastro and Krause, 1994). Differences in the quality, size and number of consumed items in juveniles and adults were also observed in other *Liolaemus* species, including *L. nigromaculatus*, *L. pictus pictus*, *L. lutzae* and *L. cuyanus* (Ortiz, 1974; Ortiz and Riveros, 1976; Rocha, 1989; Azócar and Acosta, 2011).

The consumption of plant material by *L. occipitalis* increased positively and significantly with the individual's SVL, indicating ontogenetic variations in herbivory. This variation has been shown in several lizard species. The diet of juveniles is mostly carnivorous, but it passes through different omnivorous stages during maturation into adult life (Schoener and Gorman, 1968; Pough, 1973; Schoener et al., 1982). Several species of the genus *Liolaemus* (Fuentes and Di Castri, 1975; Rocha, 1989, 1996; Acosta et al., 1996) show the same pattern. Pough (1973) attributes this observation to the larger amount of protein in a carnivorous diet. According to Szarski (1962), digesting plant material is more difficult than digesting animal material. Fuentes and Di Castri (1975) showed experimentally that three out of five *Liolaemus* species from Chile tend towards herbivory and that these species are present in environments with low insect abundance and marked fluctuations in the availability of these prey. Jaksic (1978) grouped the theories of Pough (1973) and Fuentes and Di Castri (1975) and proposed that the determining factor of carnivorous, omnivorous or herbivorous characteristics is the body mass – energetic cost and prey availability in the environment. *Liolaemus occipitalis* is another example of omnivory in small-sized lizards.

Many recent studies have demonstrated that the presence of Nematoda in the stomachs and intestines of lizards is associated with the consumption of plant material (Schad et al., 1964; Nagy et al., 1984; Iverson, 1982; Vrcibradic et al., 2000; O'Grady et al., 2005). According to O'Grady et al. (2005), the nematode parasite type and location in the digestive tract of *Liolaemus* lizards are highly correlated with the species' diet. Herbivorous species of this genus have a greater quantity of these parasites, which are usually found in the posterior intestine. The incidence of nematodes in omnivorous species was two times lower, and the parasites were spread throughout the intestines. Insectivorous species had four times fewer nematodes, which were usually found in the stomach (O'Grady et al., 2005). These results agree with our observation of a nematode occurrence frequency of 17% in the intestines of *L. occipitalis*. The presence of these parasites in this lizard could be associated with the consumption of plant material. This statement is supported by our observation that nematodes were more frequently found in adult *L. occipitalis*, which also consume a greater volume of plant material.

Seasonal differences in the diversity of food items consumed by *L. occipitalis* were observed. The diet of many lizard species varies according to the food availability in the environment (Pianka, 1970; Schoener et al., 1982; Rocha, 1996; Van Sluys, 1993, 1995), but this association should be confirmed experimentally for *L. occipitalis*. The same strategy was observed in other species of this genus, such as *L. pictus pictus* (DUMÉRIL & BIBRON, 1837), (Ortiz, 1974), *L. nigromaculatus* WIEGMANN, 1834, (Ortiz and Riveros, 1976), *L. lutzae* (Rocha, 1989), *L. wiegmannii* (Aun et al., 1999), *L. bibronii* (Belver and Avila, 2001) and *L. ruibali* DONOSO-BARROS, 1961, (Villavicencio et al., 2005). According to Schoener (1971), Pyke et al. (1977) and Pianka and Vitt (2003), the generalist diets of most lizards are the result of environmental resource fluctuations, which is the case in the sand dunes of Cidreira (RS) because it is a region with seasonal climatic changes (Nordstrom, 2008; Würding and Freitas, 2009).

In conclusion, *L. occipitalis* is an omnivorous lizard that feeds on both arthropods and plant material. This species is a "sit-and-wait" forager and a generalist lizard. The diet varied between adults and juveniles, mostly due to morphological differences, which indicates a reduction of intraspecific competition. The consumption of plant material increased with lizard size and age. Seasonal variations were observed in the diet of *L. occipitalis*, which is similar to the diet of other species of the same genus.

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