Seasonal variation of prey consumption by *Liolaemus barbarae*, a highland lizard endemic to Northern Chile

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Abstract
Liolaemus barbarae is a small liolaemid lizard (SVL: 56 mm) endemic to the high Andes of northern Chile. Diet and prey availability were assessed during three seasons of activity (spring 2003, summer 2004, autumn 2004) in order to determine patterns of prey consumption and eventual selection. *Liolaemus barbarae* was strictly insectivorous preying on flying and epigeous insects, mainly chinch bugs (Lygaeidae) and ants. Prey types were consumed in different proportions than available in the environment. The selection for Lygaeidae, the most frequent prey consumed, was inversely correlated with their availability suggesting a nutrient-optimization strategy. Ants acted as complementary prey but they were less consumed than available. Despite the harsh environmental conditions, this Andean lizard seems able to fulfil its trophic requirements, its annual diet being less variable than the seasonal fluctuations of insects in the environment.
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Introduction

Ectotherms inhabiting areas with extremely low productivities display morphological, physiological, ecological and behavioural adaptations to minimize both energetic and hydric costs (Cloudsley-Thomson, 1991). In such environments, reptiles are physiologically more efficient than endothermal vertebrates. Due to their low energetic requirements, high assimilation rate and ability to remain inactive during shortage

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periods (Fuentes and Jaksic, 1978; Pough, 1980; Espinoza et al., 2004), they prevail in areas where water and food suffer strong fluctuations (Ayal, 2007). From this point of view, Andean deserts are extremely restrictive not only in terms of water and food but also due to their extreme environmental temperatures (Ramirez and Pincheira-Donoso, 2005). Nevertheless, some lizards, mainly belonging to the family Liolaemidae, have successfully colonised such environments (Marquet et al., 1989). Because of these extreme conditions and the simplicity of Andean ecosystems, liolaemid lizards can become extremely useful models in trophic ecology. By monitoring the seasonal changes in both diet and available food, trophic strategies can be analysed within the framework of the Optimal Foraging Theory (OFT) (Emlen, 1966; Pianka, 1966). Working with *Anolis aeneus*, Stamps et al. (1981) defined three optimisation models to be tested according with different predictions. 1) Prey switching: lizards select prey items to minimise time devoted to predation; the selection of a prey type is expected to be positively correlated with its abundance in the environment. 2) Energy optimisation: lizards select the most valuable items in terms of energetic content; prey selection and abundance should be at least not negatively correlated, that is, when increasing the potential prey its contribution to the total diet increases or remain constant if saturated. 3) Nutrient optimisation: lizards select items to fulfil their requirement of certain nutrients; selection and availability of a certain prey type should be negatively correlated, assuming that prey traits (i.e. profitability, noxiousness) differ between types. Such strategies may coexist changing with prey type within the same predator (Stamps et al., 1981). Unfortunately, the predictions of the three models have seldom been tested and comparative studies are urgently needed (Carretero, 2004).

Liolaemus barbarae is a small (SVL: 56 mm) and not sexually dimorphic Andean lizard endemic to northern Chile (Pincheira-Donoso and Núñez, 2005). It was previously ascribed to *L. walkeri*, but recent evidence justify a separate specific status (Ramirez and Pincheira-Donoso, 2005; Pincheira-Donoso and Núñez, 2005). Due to its restricted range, it has been catalogued as rare by the Chilean law (SAG, 2006). It inhabits the high plateau steppes associated with stocky scrub vegetation typical from highlands of San Pedro of Atacama with populations in the border with Argentina (Ramírez and Pincheira-Donoso, 2005). Its ecology is poorly known since available literature vaguely reports a viviparous reproduction and an omnivorous diet (Valencia et al., 1982; Pincheira-Donoso and Núñez, 2005). As in other Andean *Liolaemus* (Marquet et al. 1989), it displays restricted activity both daily and seasonally due to the constraints imposed by the harsh thermal environment.

Here, we analysed the prey types consumed by *L. barbarae* and those potentially available in the environment through the three active seasons aiming 1) to describe the general diet and their seasonal variation, 2) to assess prey selection, and 3) if true, to test for diet optimisation.

Material and methods

Adult specimens were collected from "Quebrada Agua de Llareta" (a ravine located in II Region, Antofagasta, Chile, 21° 53' 54"S and 68° 49' 53"W, 4.150 masl.).

The region is characterised by a high desert climate (Novoa and Villaseca, 1989), with an annual precipitation of 12 mm with 89% occurring between the months of May and July. Average annual temperatures were Tmean = 6.49°C, Tmax = 11.9 °C and Tmin = 2.2°C (data from Mina Meteorological Station). Seasonal temperature values [Tmean (Tmax-Tmin)] were 7.2°C (13.3-2.2) in spring, 8.6°C (14.0-4.5) in summer, 6.0°C (11.1-2.1) in autumn and 4.2°C (9.4-0.0) in winter. Vegetation was dominated by bushes of the genera *Baccharis, Artemisia, Azorella,* and *Parastrephia.*

Sampling was carried out during three seasons of activity: spring 2003 (October-November), summer 2004 (January), and autumn 2004 (April). Due to its conservation status no lizards were sacrificed. For each season, active adults were collected with a slipknot within three consecutive days. Specimens were kept in single cages in order to collect their faeces, which were individually preserved in 75% ethanol and then taken at the Laboratory of Animal Physiology of the Universidad de La Serena for diet analysis and then released in the capture site. Lizards were photographed and individually identified on the basis of scalation and natural marks then preventing recapture and pseudoreplication of samples. A total of 35 faecal pellets from different individuals were analysed (autumn 10, spring 16, summer 9). Prey items were separated and identified under a stereoscopic microscope (WILD - M3 magnification 64X, 160X and 400X). Item counting was based on cephalic capsules, and, in some cases, wings and legs, following the minimum numbers criterion by sample. Separation of prey items was made following the criterion of the Operational Taxonomy Unit (OTU) that in this work is approximated to family level.

Foraging behaviour of *L. barbarae* has never been investigated with only few incidental observations available; whereas literature indicates that, in contrast with other Iguania, *Liolaemus* sp. use both visual and chemical cues to recognise their prey (Labra, 2008). Because of that, a non aprioristic approach was used to estimate prey availability. Arthropods were captured using a combination of: 1) 36 pitfall traps that were set at random for 48 hours to capture epigeous insects, and 2) 36 aerial traps that were installed parallel to pitfall traps. The later consisted on yellow plastic plates fixed by elastics to a platform placed approximately 40 cm high from the floor. The pitfall traps were filled with a mixture of ethanol 75%, liquid glycerine, and detergent. The collected material was identified at specific level when possible and then classified using the same OTUs that for the consumed prey.

The percentage of pellets containing an item (% P), the percentage of numerical abundance of each item (% N), and the use index (UI) (Jover, 1989) were used as diet descriptors. UI emphasises homogeneity as a criterion for evaluating the importance of different OTUs and it is calculated multiplying the numerical abundance by the diversity of each OTU throughout all the individual contents (extensively reviewed in Carretero, 2004; for recent applications see Santos and Llorente, 1998 and Montori *et al.* 2006). Brillouin's diversity index was used to estimate the diet richness and diversity according to Magurran (2004). The average individual diversity (Hi) was obtained by the average of the values calculated individually and population diversity was estimated through a deleted-one jack-knife resampling (Jover, 1989; Magurran, 2004). This method involves recalculating the total diversity missing out each sample in turn

and generating pseudovalues, which are normally distributed. In this way, not only individual diversity but also population diversity allows statistical inference. The total accumulated diversity of all the contents is a fixed value only provided for comparing with the literature (Ruiz and Jover, 1981). Similarity between seasonal diets was evaluated by means of Horn's index of trophic overlap (Horn, 1966) after Krebs (1999). Normality (Lilliefors test) and homoscedasticity (Fisher test) was assured prior to the application of parametric tests. Individual diversity and number of prey per pellet were compared between seasons using one-way ANOVA. Population diversity estimations coming obtained through jack-knife could not be compared using ANOVAS since the software provide only mean±SE and diversity is non-additive (Carretero and Llorente, 1993). Instead, t-tests corrected for multiple tests (using False Discovery Rate, FDR, Benjamini and Hochberg, 1995) were applied. Trap contents were analysed in the same way as the faecal pellets. Prey selection was calculated using Ivlev's (1961) index as modified by Jacobs (1974). Confidence intervals of the Ivlev's index were calculated following Strauss (1979). For the most consumed OTUs, availability and selection were correlated by seasons according to Stamps et al. (1981).

Results

The mean number of insects by pellet varied from 7.06 in spring to 7.78 in summer and to 11.80 in autumn (table 1), although such differences were not statistically significant ($F_{2,34} = 1.61$; $p < 0.22$). The number of available insect taxa varied from 39 in summer to 50 in spring. The order Hemiptera was the most consumed prey in all three seasons followed by Hymenoptera in spring and autumn. In contrast, Diptera were the second most consumed prey in summer (23.95%) followed by the Hymenoptera (11.10%) (table 1).

   The overall diet spectrum of *L. barbarae* was dominated by the Hemiptera of the family Lygaeidae (chinch bugs) and by Formicidae (ants) and did not include plant matter (table 1). In more detail, during spring, eight different OTUs were consumed, three of them (Piralydae, Diptera indet. and Phoridae) in a proportion less than 1.00%. The Hemiptera of the family Lygaeidae (chinch bugs) represented more than half of the diet (UI = 59.62%) and were positively selected in terms of the Ivlev index. In contrast, ants, the second prey in importance (UI = 22.71%), were negatively selected. Coleoptera were absent from the diet in this season. During summer, nine OTUs were consumed but five of them contributed to the diet less than 1.00%. The most consumed prey types were Lygaeidae and Sciaridae, both positively selected from the environment whereas Formicidae were negatively selected. Bombillidae were consumed only in summer, but in a low proportion. In autumn, *L. barbarae* consumed four prey types, one of them (Anthocoridae) being only anecdotal whereas the others had a relative importance higher than 20.00% (table 1). The most consumed prey were Lygaeidae and Formicidae in more and less proportion than available, respectively. The consumption of Coleoptera and Formicidae was higher that in the other seasons. Very interestingly, seasonal availability and electivity of Lygaeidae (the main prey) were inversely

Table 1.
Diet descriptors of *Liolaemus barbarae*. OTU: Operational taxonomical unit, %P: Percentage of presence; %N: percentage of numerical abundance; IU: Resource use index: - not consumed; 0.00: consumed but index value next to zero. %A: Availability; IV: electivity (Ivlev index) ± 95 confidence index.

OTUs	Spring					Summer					Autumn					Total		
	%P	%N	IU	%A	IV±95%	%P	%N	IU	%A	IV±95%	%P	%N	IU	%A	IV±95%	%P	%N	IU
Hemiptera	93.75	59.29	65.23	24.68	0.57±0.43	88.89	62.86	64.96	27.87	0.60±0.49	60.00	50.00	46.19	9.92	0.09±0.48	82.86	60.61	62.86
Lygaeidae	93.75	53.98	59.62	11.39	0.65±0.42	88.89	57.14	64.96	19.67	0.49±0.49	60.00	45.83	46.19	3.82	0.85±0.44	82.86	53.25	58.67
Anthocoridae	18.75	5.31	3.16	1.90	0.47±0.33	11.11	2.86	0.00	0.82	0.55±0.27	10.00	4.17	0.00	0.76	0.69±0.47	14.29	4.33	2.66
Calophyidae	18.75	4.43	2.45	11.39	-0.44±0.42	11.11	2.86	0.00	7.38	-0.44±0.47	-	-	-	5.34	-1.00	11.43	3.03	1.53
Diptera	50.00	15.05	11.39	17.72	0.29±0.22	88.89	24.29	23.95	38.53	0.04±0.49	-	-	-	17.55	0.01±0.47	45.71	14.73	11.97
Diptera indet.	12.50	2.66	0.84	0.63	0.61±0.41	22.22	2.86	1.27	0.82	0.55±0.27	-	-	-	0.76	-1.00	11.43	2.17	1.05
Phoridae	6.25	0.89	0.00	4.43	-0.67±0.39	11.11	1.43	0.00	34.43	-0.92±0.49	-	-	-	11.45	-1.00	5.71	0.87	0.23
Sciaridae	37.50	11.50	10.55	10.13	0.06±0.42	88.89	18.57	22.68	2.46	0.77±0.42	-	-	-	4.58	-1.00	40.00	11.26	10.69
Bombyliidae	-	-	-	2.53	-1.00	11.11	1.43	0.00	0.82	0.27±0.13	-	-	-	0.76	-1.00	2.86	0.43	0.00
Coleoptera																		
Carabidae	-	-	-	1.27	-1.00	11.11	1.43	0.00	0.82	0.27±0.13	70.00	20.83	22.57	1.53	0.86±0.44	22.86	4.76	3.56
Hymenoptera																		
Formicidae	75.00	19.47	22.71	54.43	-0.47±0.44	55.56	11.43	11.10	29.51	-0.44±0.49	70.00	29.17	31.25	70.23	-0.41±0.48	68.57	19.05	21.38
Lepidoptera																		
Piralydae	12.50	1.77	0.66	1.90	-0.04±0.31	-	-	-	3.28	-1.00	-	-	-	0.76	-1.00	5.71	0.87	0.23
Total	16 pellets, 113 prey items, 158 trap it.					9 pellets, 70 prey items, 122 trap it.					10 pellets, 118 prey items, 131 trap it.					35p., 301p.i., 411t.i.		

Table 2.
Diet diversity and prey abundance in the pellets of *Liolaemus barbarae*. Hi: Individual diversity; Hp: population diversity; Hz: total accumulated diversity. All using Brillouin's index.

Group	N	Hi (mean±SE)	Hp (mean±SE)	Hz	Abundance (mean±SE)
L. barbarae spring	16	0.81±0.02	2.04±0.14	1.87	7.06±1.24
L. barbarae summer	9	0.89±0.06	1.98±0.20	1.75	7.78±1.39
L. barbarae autumn	10	0.58±0.04	1.72±0.17	1.54	4.80±0.68
L. barbarae total	35	0.76±0.02	2.13±0.11	2.02	-

correlated (Pearson r = -0.9971, n = 3, *P* = 0.0481). For the remaining OTUs seasonal availability and electivity were not significantly correlated.

Regarding diet diversity (table 2), neither individual diversity (Hi) nor population diversity (Hp) differed statistically among seasons ($F_{2, 31}$ = 0.96, p = 0.3944; T tests p > 0.21 p_{FDR} > 0.62, respectively). Diet similarity (estimated by trophic overlap) was higher between autumn-summer (R_o = 0.760) and spring-summer (R_o = 0.737) than between autumn-spring (R_o = 0.502).

Discussion

Liolaemus barbarae belongs to the members of its genus with a strictly insectivore diet (Espinoza et al., 2004). Hemiptera and Formicidae, the most consumed prey, are also important for other small *Liolaemus* (Rocha, 1989; Belver and Avila, 2002; Villavicencio et al., 2005; Halloy et al., 2006). The high seasonal variation in the insect availability in the study site probably derives from the strong seasonality of these highland environments. Nevertheless, the insect taxa consumed by *L. barbarae* were extremely restricted (4-9) when compared to those available in the study area (39-50), which suggests prey selection (see below).

During the three studied seasons *L. barbarae* mainly fed on flying and epigeous insects, probably as a consequence of its ability of starting activity early in the morning and forage widely in search of prey (Marquet et al., 1989; pers, obs.). The most consumed prey were flying Hemiptera, especially family Lygaeidae, associated with shrubby vegetation where *L. barbarae* also basks and find shelter. Although hemipterans of other prey categories were also abundant in thicket areas (pers. obs.), they were consumed in low proportions. Ants, highly consumed during autumn and spring, belong to *Solierella* aff. *fritzi*, a flying middle size Formicidae (3.03 mm). Bigger ant species (e.g., *Camponotus hellmichi*) were also abundant but not consumed by *L. barbarae*, although they are reported in the diet of *Liolaemus monticola* (SVL 57.2 mm) from the central Chile (Fuentes and Ipinza, 1979). The low consumption of phorid flies (Diptera) could be also interpreted in terms of prey size.

Seasonal variations in the diet of *L. barbarae* are evident (see also Rocha, 1996). The diet similarity (estimated by means of the trophic overlap) indicated strong shifts which were higher between the non-consecutive seasons (spring and autumn). Whereas thermal load is decisive abiotic factor in lizards and insects activity, at a behavioural and

physiological level (Tracy and Christian, 1986; Angilletta, 2001), the higher diet differences between these two thermally similar seasons suggest that changes in prey availability/selection are clearly involved. When comparing their frequencies in pellets and traps, the two main prey types showed evidence for prey selection, positive in Lygaeidae and negative in Formicidae. Moreover, even with only three sampling periods, Lygaeidae were demonstrated to be less selected when abundant in the environment and vice-versa. Even if digestion may have slightly overrepresented both OTUs in the pellets (see Carretero and Llorente, 2001), such bias should remain similar between seasons (see also Luiselli, 2008). In the only *Liolaemus* species specifically investigated, the omnivorous *L. lutzae* (Rocha, 1996, 2000), prey selection based on their water content has been reported. Because of that, results for this prey type are univocally explained by nutrient optimization (Stamps et al., 1981). In fact, the other two optimisation models are discarded since, under prey switching and energy optimisation, positive or non-negative correlations between consumption and availability would be expected, respectively (Stamps et al., 1981). Among the few similar studies available, Pérez-Mellado et al. (1991) and Carretero (2004) report similar strategies in two mountain lacertid lizards. Alternatively, toxin avoidance (Lygaeidae and ants are noxious) could also produce similar results (Dearing and Schall, 1992; Carretero, 2004). These aspects would deserve experimentation and further comparative analysis with other species and environments. One factor that may have facilitated the high consumption of Lyageidae in periods with low arthropod availability is the gregarious behaviour of this family (Tullberg et al., 2000) which decreases the searching costs by prey item. The role of ants, also gregarious but always negatively selected, seems to be only complementary. Some studies indicate that ants are less profitable than hemipterans for the same size in terms of manipulation time and biomass (Díaz and Carrascal, 1993).

In conclusion, although this Andean lizard inhabits an extremely restrictive environment in terms of temperature and trophic availability, it seems able to select for its prey to fulfil its requirements keeping an annual diet less variable than the seasonal fluctuations of insects in the environment.

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Addendum

During the reviewing process of this paper, a taxonomical note (Quinteros & Lobo, 2009) appeared suggesting that *L. barbarae* may be a junior synonym of *L. puna* Lobo & Spinoza, 1999. Because the target of the study was ecological, the genetic support for such arrangement is still lacking and our study site was clearly located, we prefer to regard the name of species as it states and wait for a taxonomic clarification of this group.

Quinteros, A.S. & Lobo, F. (2009) The Iguanian Lizard *Liolaemus barbarae* Pincheira-Donoso and Nunez Is a Junior Synonym of *Liolaemus puna* Lobo and Espinoza. *J. Herpet.*, 43, 336-339.