

Article

Prey availability, prey selection, and trophic niche width in the lizard *Psammodromus algirus* along an elevational gradient

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Abstract

Mountains imply enormous environmental variation, with alpine habitats entailing harsh environments, especially for ectotherms such as lizards. This environmental variability also may imply variation in prey availability. However, little is known about how lizard trophic ecology varies with elevation. In this study, we analyze diet, prey availability, prey selection, and trophic niche width in the lacertid lizard *Psammodromus algirus* along a 2,200-m elevational gradient in the Sierra Nevada (SE Spain). The analysis of fecal samples has shown that Orthoptera, Formicidae, Hemiptera, Coleoptera, and Araneae are the main prey, although, according to their abundance in pitfall traps, Formicidae and Coleoptera are rejected by the lizard whereas Orthoptera, Hemiptera, and Araneae are preferred. Prey abundance and diversity increase with elevation and diet subtly varies along with the elevational gradient. The consumption of Coleoptera increases with elevation probably as a consequence of the lizard foraging more in open areas while basking. The electivity for Araneae increases with elevation. Araneae are rejected in the lowlands—where they are relatively abundant—whereas, at high elevation, this lizard positively selects them, despite they being less abundant. The lizard trophic niche width expands with elevation due to concomitant greater prey diversity and hence this lizard feeds on more prey types in highlands. Although no sex difference in diet has been found, the trophic niche is broader in females than males. As a whole, alpine lizards show a trophic niche similar to that found at lower elevations, suggesting that *P. algirus* is well adapted to the harsh environment found in alpine areas.

Key words: alpine habitats, arthropods, mountain ecology, niche variation hypothesis, trophic ecology

High mountains present harsh environmental conditions for life, such as low temperatures, high solar radiation, and low oxygen pressure (Körner 2007). Consequently, diversity is usually lower in alpine zones in comparison with mid- and lowlands (Nogués-Bravo et al. 2008). However, widespread species may occur along the elevational gradient in mountains, embracing different environmental conditions. In such cases, species broadly distributed over an elevational gradient typically show phenotypic divergence, with populations locally

adapted to the conditions of each elevation (Keller et al. 2013). If local adaptation is insufficient, as these species move away from their optimal habitat, their fitness drops, being minimal in marginal habitats such as alpine environments (Kawecki 2008).

Trophic ecology is fundamental to understand ecosystem functioning and relationships among species (Thébault and Fontaine 2010), as well as the evolution of several life-history traits (Edwards et al. 2013). An optimal diet (in quality as well as in quantity) is

fundamental to maximize fitness (Franzke and Reinhold 2012; Lefcheck et al. 2013; Nel et al. 2015). It also affects aspects as relevant as the immune system or sexually selected traits (Schlotz et al. 2013; Brunner et al. 2014; Kopena et al. 2014). In this sense, little information is available on how the diet of widespread species varies with elevation. If animals are locally adapted along the elevational gradient, their diet is expected to be optimal along it. However, if some habitat—particularly the alpine area—is suboptimal for the species, diet may be impoverished. A narrower trophic niche may imply fewer nutrients, which may translate as lower consumer fitness (Pulliam 1975; Raubenheimer and Simpson 1997; Lefcheck et al. 2013).

Diet may change with elevation as a consequence of different factors, such as variation in microhabitat use or in prey availability. For example, with elevation, ectotherms should spend more time basking in open areas (Díaz 1997), where available prey may differ from those found near their shelters (Belliure et al. 1996). As a consequence of a reduced activity period with elevation, animals may vary their foraging mode, being more selective and preying on more profitable species (Perry 2007). Moreover, if morphological or physiological changes are associated with elevation, we can expect associated changes in their diet. For example, if animals vary in speed or other ability to catch, subdue, or handle prey, concomitant changes in the percentage of highly evasive prey are expected (Miles et al. 2007). For instance, populations with larger specimens may show a diet richer in larger and more chitinous species.

Moreover, ecosystem conditions could influence dietary variation with elevation. On the one hand, lower diversity with higher elevation may imply fewer competitors, allowing a niche release (Pianka 1994), and hence an increase of the niche width with elevation (Comas et al. 2014; also see Costa et al. 2008a). On the other hand, if the decreased diversity also applies to prey, then niche width may narrow with elevation. Whatever the pattern with elevation, greater total niche width at the population level may result from 2 different mechanisms: more variety of trophic specialist individuals (the niche variation hypothesis, Van Valen 1965; Bolnick et al. 2007), or every individual being more generalist (Bearhop and Adams 2004). At the same time, if body size varies along the gradient, populations with larger animals might show a greater diet width as a result of the higher diversity of the prey being consumed (Díaz 1994b).

In this regard, lizards can be used as model organisms, because they play an important role in ecosystems as generalist predators (Huey and Pianka 1981; Huey et al. 1983; Reilly et al. 2007). In particular, lacertids, the dominant group of lizards in Mediterranean ecosystems, perform an essential role as a vehicle of matter and energy from invertebrates to birds and mammals (Valverde 1967). Accordingly, in the present study, we analyze the variation in diet, prey availability, prey selection, and trophic niche width of the lizard *Psammotromus algirus* along an elevational gradient of 2,200 m in the Sierra Nevada (SE Spain). With the aim of characterizing the diet of this lizard, we undertake the following:

1. We examine the elevational variation in diet and analyze how prey availability and prey selection vary with elevation. We predict that diet will change with elevation according to several factors such as variation in prey availability, the lizard's use of microhabitat, and body size of the lizards. For this species, considering how its basking behavior varies with elevation (Belliure et al. 1996; Díaz 1997; Zamora-Camacho et al. 2016), we predict the diet to be richer in species found in open areas at high

elevations, and in prey found under shrubs at lowlands. Moreover, we predict a greater proportion of highly chitinous species in the diet with elevation, since lizards are larger at high altitudes (Zamora-Camacho et al. 2014a), and hence they may subdue harder prey.

2. We determine how the trophic niche width of this lizard varies with elevation, with special emphasis in the alpine zone. We predict that diet may diversify with elevation as a consequence of different factors such as reduced interspecific competition (Comas et al. 2014), increased body size with elevation (Zamora-Camacho et al. 2014a), or increased prey diversity. We test the niche variation hypothesis by comparing the elevational variation in population diet width with the mean of individual diet width of lizards. If population diet diversifies as a result of greater individual diet diversity for each lizard, a positive correlation between population diet width and individual diet width is predicted. However, if population diet width augments due to a greater diversity of specialized individuals, no correlation between population diet width and that of the individual is expected.
3. We test for sex differences in diet and diet width. Males are more mobile while defending their territories and searching for mates (Díaz 1993), implying a higher rate of encounters with different prey types. Males are also quicker (Zamora-Camacho et al. 2014b), which would favor the capture of a more diverse array of prey (sedentary as well as evasive). They also have larger heads (Mellado and Martínez 1974), favoring the capture of more diverse prey in hardness and size. Accordingly, we predict that males will show a wider diet and will consume more evasive and harder species than do females.

Materials and Methods

Study species

Psammotromus algirus is a medium-sized lizard (60–90 mm adult snout–vent length, SVL) distributed in south-western Europe and north-western Africa, where it inhabits shrubby habitats (Díaz and Carrascal 1991). In SE Spain, it occurs along an elevational gradient from sea level to more than 2,600 m.a.s.l. (Fernández-Cardenete et al. 2000). This lizard typically searches actively for its prey (Belliure et al. 1996). Its diet is very broad, composed mainly of arthropods such as Araneae, Formicidae, Coleoptera, Hemiptera, Orthoptera, and Diptera (review in Salvador 2015).

Study area

The study area was located in the Sierra Nevada mountain (SE Spain, 2°56'1"2–3°38'02"2 W and 36°56'10"0–37°12'58"9 N). Six sampling plots were established along the elevational gradient, separated by roughly 500 m of elevation: 300, 700, 1,200, 1,700, 2,200, and 2,500 masl (Figure 1). Sampling was carried out consistently within the typical habitat of *P. algirus*: areas with abundant herbs and shrubs ranging from 40 to 100 cm high and relatively high vegetation cover (Díaz and Carrascal 1991). Care was taken selecting locations with similar habitat structure despite the variation in plant communities along the elevational gradient. For more details on the study area, see Zamora-Camacho et al. (2013, 2016).

Diet analysis

Fecal samples (pellets) were used for diet analysis, this information on lizards' diet being as reliable as stomach contents (Garrido et al. 2011) and allowing us to keep individuals alive. As a part of a

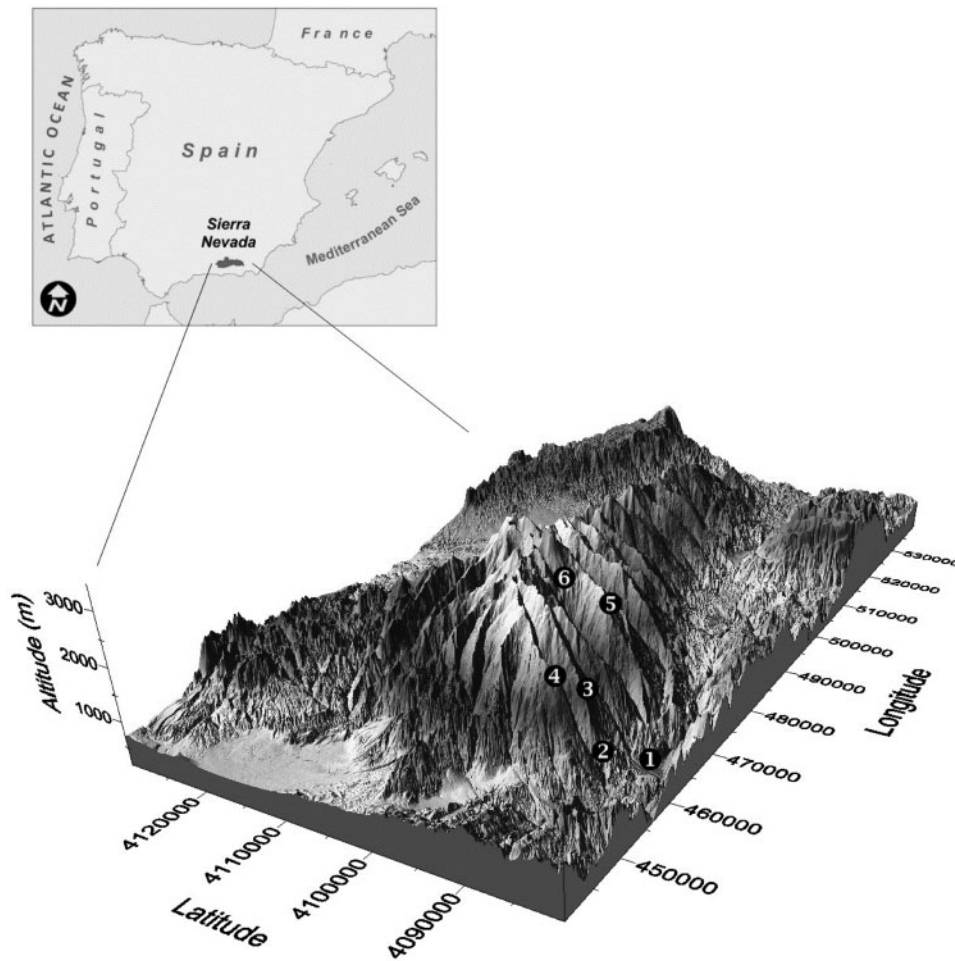


Figure 1. Location of the Sierra Nevada mountain in Spain, and location of the 6 sampling points, where the study was performed, in a 3-dimensional map. Numbers indicate the location of sampling points at 300 masl (1), 700 masl (2), 1,200 masl (3), 1,700 masl (4), 2,200 masl (5), and 2,500 masl (6).

long-term study between 2010 and 2012, we regularly captured lizards along the elevational gradient. When lizards deposited feces just after being captured (hence, being ensured that fecal content was from the diet of the animal in the field), we kept feces in labeled vials with ethanol (96%). Only pellets from adult individuals were considered. Adults were recognized as those reaching a minimum SVL (measured with a ruler, 0.1 mm of accuracy) for each sex and each elevation (according to Reguera et al. 2014). Sex was determined by secondary sex characters, mainly femoral pores, which are more developed in males (Iraeta et al. 2011). Pellets were examined in the laboratory through a 10–40× binocular dissecting microscope, and items were identified to the lowest taxonomical level possible. Identification was based on non-digestible remaining fragments such as cephalic capsulae, jaws, thoraxes, etc. Then, we assigned the items to operational taxonomic units (OTUs, Sneath and Sokal 1962), usually at the level of Order, except for the Formicidae family, which was separated from other Hymenoptera because of their particular morphological and ecological characteristics, and for larvae, usually included in the same OTU. Moreover, OTUs were assigned to categories of easiness and hardness (in both cases: low, medium, and high) according to criterion in Table 14.1 in Vanhooydonck et al. (2007).

For each prey type, we calculated relative occurrence as the percentage of individuals consuming that prey type (% of presence),

and relative abundance as the percentage of a prey item in relation to the total number of prey items (% of frequency). We also determined the number of prey per pellet. Trophic niche width was estimated using the B Levins' index (Simpson 1949; Levins 1968), in its standardized version B_s (Hurlbert 1978):

$$B = \frac{1}{\sum p_i^2},$$

$$B_s = \frac{B - 1}{n - 1},$$

where p_j is the fraction of items in the diet that are of food category j , and n is the number of possible food categories (Krebs 1999). B_s ranges from 0 (100% utilization of a single food category) to 1 (equal use of all categories). Levins' index was estimated as a whole and for each sex and elevation. Moreover, we estimated the individual trophic niche width (B_i) for each lizard, considering the prey found in individualized pellets. It should be noted that, while B_s indicates the trophic width niche at the population level, B_i indicates the trophic width niche at the individual level. The trophic niche overlaps between sexes (m and f corresponding to males and females) with resource utilization p_{mi} and p_{fi} , was calculated by Pianka's index (O_{mf}) (Pianka 1974):

$$O_{mf} = O_{fm} = \frac{\sum_{i=1}^n p_{mi} p_{fi}}{\sqrt{\sum_{i=1}^n (p_{mi})^2 (p_{fi})^2}}$$

To make an elevational comparison, we had to use similar sample sizes along the elevational gradient. If some sampling points had larger sample sizes than others, prey species rarely consumed would be easier to detect, the number of OTUs could be larger, and trophic niche width would appear greater. To avoid this bias, we used only 12 fecal samples per elevation, 6 from males and 6 from females. A rarefaction curve showed that 12 samples were sufficient to attain 75% of the whole diversity of OTUs, and increasing the number of OTUs recorded to up 90% would require twice this sample size (Figure 2). However, we had collected a large quantity of feces ($n=65$; 35 from males and 30 from females) for the alpine zone (2,200 and 2,500 masl). Given that this was the elevational limit for this species (Fernández-Cardenete et al. 2000), we considered that more detailed knowledge of the diet in the alpine zone would be useful, and hence added a separate analysis restricted to this area.

Prey availability

To estimate the availability of potential prey for *P. algirus*, during 2010, we installed 30 pitfall traps in each location along the elevational gradient (Woodcock 2005). Given that this species is an opportunistic active forager, we tried to cover the whole range of foraging places, dividing sampling areas into 2 micro-habitats: open areas (basking sites) and under shrubs (shelter sites), with 15 traps in each, a minimum of 5 m apart to safeguard the independence of the data (Ward et al. 2001). Traps remained open from early morning until dusk, once every 2 weeks, entirely coinciding with the activity period of the lizards for each elevation (Zamora-Camacho et al. 2013). At sundown, trap content was individually collected in labeled vials and preserved with ethanol (96%). In this way, we captured only arthropods that could have been potentially consumed by this diurnal lizard. Pitfall traps may underestimate some groups such as sedentary prey, flying insects, or Orthoptera, and therefore, the findings must be interpreted taking into account that the availability of these groups may be underestimated. Each prey was identified in the laboratory under a 10–40× binocular microscope and assigned to an OTU, using the same criteria applied in the diet analysis.

To measure the use of a resource (p_i) compared with its availability (q_i), we calculated the Ivlev's electivity index, E_i (Ivlev 1961):

$$E_i = \frac{p_i - q_i}{p_i + q_i}$$

This index ranges from -1 to 1 , with zero indicating random selection, negative values indicating avoidance or inaccessibility of the prey item and positive values showing active selection.

Statistical Analysis

To compare the frequency of consumption of each OTU between sexes or among elevations, or differences in availability between microhabitats, we used the Chi-squared test. For variables with a continuous distribution, such as number of prey per pellet or individual trophic niche width, we compared the 2 sexes and the various elevations (i.e., sampling points) with a 2-way factorial ANOVA, considering the interaction elevation * sex. For comparisons between sexes restricted to the alpine zone, the t -test was used. To test for the average number of potential prey available per elevation, we performed an ANOVA, considering as the statistical unit each day the set of pitfall traps at a given elevation was activated at every elevation ($n=98$). When we were interested in elevational patterns,

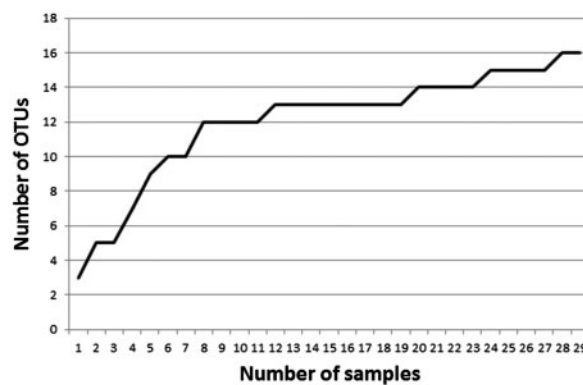


Figure 2. Curve of rarefaction showing the rate at which new OTUs are incorporated as sample size increases, from a randomly selected sample.

we used the Spearman rank binary correlation (ρ) in order to test a relationship between the elevation (considered here as a continuous variable) and the dependent variable to test. The data were transformed when necessary in order to fulfil the criterion for normality and homoscedasticity. All the analyses were performed with Statistica 8.0 (StatSoft 2007) following Quinn and Keough (2002).

Results

Diet of *P. algirus* along the elevational gradient

In the analysis comparing the points along the elevational gradient, overall, we found 456 prey of 15 different OTUs ($n=72$ individuals; Table 1). The main preys (those with frequencies over 10%) were Orthoptera, Formicidae, Coleoptera, and Hemiptera (Table 1). Moreover, Orthoptera was notable for being present in 79% of the feces samples, and Araneae were found in more than a half of the samples (54%; Table 1), hence these prey types were widely consumed. Considering only the 5 most frequent OTUs in the diet of *P. algirus* (Orthoptera, Formicidae, Coleoptera, Hemiptera, and Araneae), there were no significant differences in the consumption frequency between males and females (Table 2). The overlap between sexes for each elevation was tight, that is, between 0.60 and 0.71, with the exception of the location at 1,200 m, where it was very low (0.39), and at 2,500 m, where it was very high (0.90). The frequency of each prey appearing in the diet did not significantly differ with elevation, except Formicidae (Table 3). Nonetheless, the consumption of Coleoptera increased with elevation ($\rho=0.94$, $P=0.005$, $n=6$ locations). According to hardness, most of the prey consumed had a high degree of hardness (37.6%; medium hardness: 31.2%; low hardness: 31.2%). Regarding evasiveness, *P. algirus* consumed mainly prey with intermediate evasiveness (43.3%), followed by prey with high evasiveness (32.5%), prey with low evasiveness being minor in the diet (24.2%). We discerned no significant elevational pattern for consumption of prey according to their hardness or evasiveness (data not shown for simplicity).

Prey availability for *P. algirus* along the elevational gradient

A total of 14,793 individuals, from 19 different OTUs, were captured in 1,534 pitfalls-day (Table 4). All OTUs found in the lizard diet were recorded in pitfalls, except Pseudoscorpionida. By contrast, 4 taxa recorded in pitfalls were not consumed by lizards: Isopoda, Diplopoda, Collembola, and Zygentoma. Formicidae stand out as the most abundant potential prey, 74% of the total, being

Table 1. Frequency (and percentage) of the different OTUs in the diet of *P. algirus* in the Sierra Nevada, as well as the number (and percentage) of feces in which they were present

	Frequency	% Frequency	Presence	% Presence
Orthoptera	90	19.78	57	79.17
Formicidae	87	19.12	13	18.06
Coleoptera	58	12.75	33	45.83
Hemiptera	52	11.43	30	41.67
Araneae	42	9.23	39	54.17
Larvae	28	6.15	17	23.61
Hymenoptera	26	5.71	17	23.61
Embioptera	26	5.71	7	9.72
Lepidoptera	18	3.96	18	25.00
Other taxa	28	6.15	15	20.83

Notes: "Other taxa" includes OTUs that appeared <10 times: Acarina (9), Blattodea (7), Diptera (7), Pseudoscorpionida (2), Neuroptera larvae (2), and Mantodea (1). Larvae include those of unidentified taxa. Hymenoptera does not include formicidae. $N=72$ individual lizards.

Table 2. Frequency in males and females ($n=36$ in each cases) of the 5 most frequent OTUs in the diet of *Psammodromus algirus*

	Females	Males	χ^2
Orthoptera	41	49	0.36 ^{ns}
Formicidae	49	38	0.70 ^{ns}
Coleoptera	31	27	0.14 ^{ns}
Hemiptera	24	28	0.15 ^{ns}
Araneae	25	17	0.77 ^{ns}

Note: Sexual differences in the frequency were checked with a Chi-squared test for each OTU; in no case were differences significant (^{ns} $P>0.05$).

Table 3. The frequency of the 5 most common OTUs in the diet of *P. algirus* according to elevation ($n=12$ individual lizards at each elevation)

	300	700	1200	1700	2200	2500	χ^2_5
Orthoptera	7	18	15	13	18	19	6.80 ^{ns}
Formicidae	31	8	32	7	8	1	17.73 ^{**}
Coleoptera	4	10	5	11	13	15	9.60 ^{ns}
Hemiptera	10	9	6	6	13	8	4.00 ^{ns}
Araneae	7	5	7	4	9	10	3.71 ^{ns}

Notes: Variation with elevation was tested with a Chi-squared test, whose values are shown in the table; ^{ns} indicates non-significant ($P>0.05$); ^{**} $P<0.01$.

present in 71% of the pitfalls (Table 4). Excluding Formicidae, the most abundant potential prey for *P. algirus* were Coleoptera, Orthoptera, Acarina, and Araneae (Table 4). These OTUs were, together with Hemiptera and Hymenoptera, the most widely distributed (collected in >10% of the pitfalls; Table 4). Hemiptera was more abundant under shrubs whereas Coleoptera and Formicidae were more abundant in open areas (Table 5).

To analyze how prey abundance varies with elevation, we considered only the OTUs most consumed by *P. algirus* (Orthoptera, Coleoptera, Hemiptera, and Araneae). Formicidae was not considered, despite their high frequency in the *P. algirus* diet, because they were excessively abundant in pitfall traps, precluding analyses (Greenslade 1973), and, moreover, given their small size and high degree of chitinization, they presumably provide low biomass to

Table 4. Frequency (and percentage) of each OTU collected in the pitfall traps ($n=1,534$ traps-day), as well as number (and percentage) of pitfalls in which each OTU was caught

	Frequency	% Frequency	Presence	% Presence
Formicidae	10,970	74.16	1,062	71.04
Coleoptera	1,173	7.93	442	29.57
Acarina	519	3.51	249	16.66
Orthoptera	506	3.42	235	15.72
Araneae	406	2.74	304	20.33
Hemiptera	276	1.87	213	14.25
Hymenoptera	267	1.80	210	14.05
Diptera	162	1.10	109	7.29
Collembola	119	0.80	74	4.95
Diplopoda	100	0.68	36	2.41
Zygentoma	88	0.59	37	2.47
Lepidoptera	65	0.44	45	3.01
Isopoda	31	0.21	20	1.34
Larvae	30	0.20	27	1.81
Embioptera	28	0.19	23	1.54
Blattodea	24	0.16	24	1.61
Neuroptera	17	0.11	17	1.14
Opilionida	9	0.06	9	0.60
Mantodea	3	0.02	3	0.20

Notes: In the case of neuroptera, only larvae were captured. Hymenoptera does not include formicidae. Larvae refer to those of unidentified taxa.

Table 5. Number of individuals of each OTU found in pitfall traps under shrubs ($n=768$) and in open habitat ($n=766$)

	Open	Shrub	χ^2
Formicidae	5,668	5,302	6.11*
Coleoptera	686	487	17.01 ^{***}
Araneae	229	177	3.34 [§]
Orthoptera	262	244	0.32 ^{ns}
Hemiptera	113	163	4.57*
Hymenoptera	126	141	0.42 ^{ns}
Lepidoptera	32	33	0.01 ^{ns}
Larvae	16	14	0.07 ^{ns}
Embioptera	15	13	0.07 ^{ns}

Notes: The value of the Chi-squared testing for statistical differences between microhabitats is shown; ^{ns} indicates non-significant differences ($P>0.5$); [§] $P=0.07$; * $P<0.05$; ^{***} $P<0.001$. Only OTUs that formed part of the diet of *P. algirus* were considered (see Table 1).

lizards. Our analysis showed that the overall prey abundance significantly varied with elevation ($F_{5,92}=6.92$, $P<0.001$; Figure 3), showing a linear increase ($\rho=0.94$, $P=0.005$). However, the relative frequency of Araneae significantly decreased with elevation ($\rho=-0.89$, $P=0.019$); the remaining OTUs showed no significant trend with elevation (Figure 4).

Trophic niche width of *P. algirus* along the elevational gradient

For *P. algirus* in the Sierra Nevada, trophic niche width (standardized Levins' index, B_s) was 0.497, suggesting an intermediate amplitude. Trophic niche width increased with elevation ($\rho=0.89$, $P=0.019$; Figure 5), and with prey abundance in the locations ($\rho=0.94$, $P=0.005$). The diversity of available prey also increased with elevation ($\rho=0.83$, $P=0.042$; Figure 5). Analyzing sexes separately, we found that females showed greater diet width (i.e., they

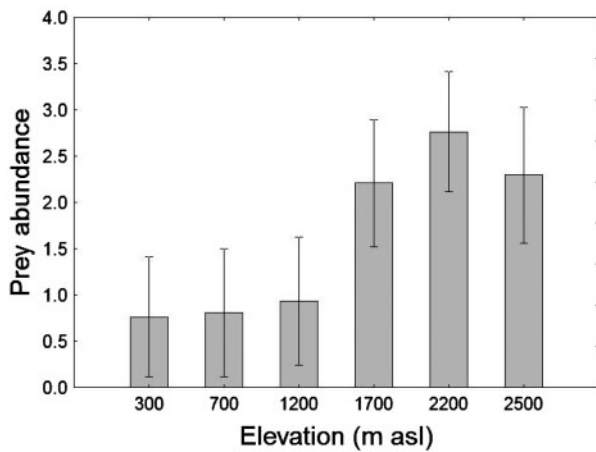


Figure 3. Average number of overall items of the most consumed prey (Orthoptera, Hemiptera, Coleoptera, and Araneae), except Formicidae, collected daily in pitfalls according to elevation (masl). Bars indicate the 95% confidence intervals.

were more generalist) in the high- and lowlands, whereas males were more generalist in the midlands (Figure 5). In fact, the trophic niche width of the 2 sexes showed an inverse pattern across the locations studied ($\rho = -0.83$, $P = 0.042$; Figure 5).

Considering the individual diet width (Bi), we found significant differences between sexes ($F_{1,60} = 5.97$, $P = 0.017$) and among elevations ($F_{5,60} = 2.51$, $P = 0.039$), which explained 15% of variation in Bi (whole model: $F_{1,60} = 2.15$, $P = 0.03$, adjusted $R^2 = 0.15$). The interaction was not significant ($F_{5,60} = 1.15$, $P = 0.35$). Females showed a wider diet than did males (0.14 ± 0.013 vs. 0.10 ± 0.014 ; mean \pm SE), suggesting that females are more generalist. Regarding elevation, individual diet width was fairly stable up to 1,700 m, and then showed a lineal increase (Figure 6). Individual diet niche width correlated positively with elevation ($\rho = 0.83$, $P = 0.042$) and with total niche width ($\rho = 0.89$, $P = 0.019$). The average prey per pellet was 6.32 ± 0.71 (mean \pm SE) and did not vary with elevation ($F_{5,60} = 0.77$, $P = 0.58$; data not shown for simplicity) or sex (males: 6.03 ± 0.84 ; females: 6.59 ± 1.15 prey per pellet; $F_{1,60} = 0.20$, $P = 0.66$; sex * elevation: $F_{5,60} = 1.82$, $P = 0.12$).

Prey selection along the elevational gradient

We restricted the analysis of prey selection to the main prey of *P. algirus*: Orthoptera, Coleoptera, Hemiptera, and Araneae. We excluded Formicidae since, given their elevated abundance in pitfall traps, its inclusion in the analysis would provoke spurious results (i.e., in comparison, the remaining prey will give positive selection; Greenslade 1973). We did not consider less representative prey, either. Our findings showed that electivity for Araneae increased with elevation ($\rho = 0.89$, $P = 0.019$), being negatively selected at low elevations, and positively so at high elevations (Figure 7). Orthoptera was in all cases positively selected, except at 2,200 m, which was the location with the highest abundance of Orthoptera (here we collected more Orthoptera than at all the other locations together). Indeed, selection for Orthoptera was negatively correlated with its absolute abundance in the locations ($\rho = -0.89$, $P = 0.019$). Hemiptera was also positively selected in every elevation, except at 1,200 m, where they were the dominant taxon (see Figure 4). Lastly, Coleoptera was negatively selected across the overall elevational gradient (Figure 7).

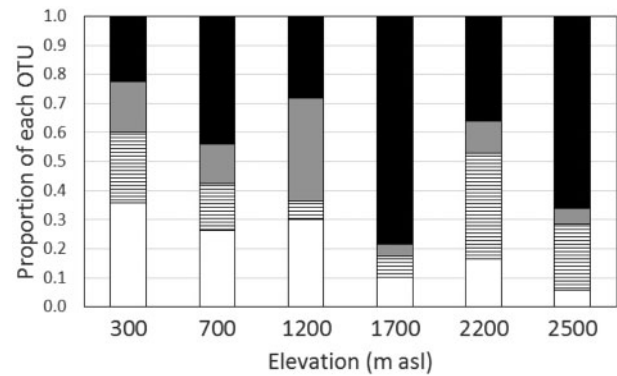


Figure 4. Relative abundance, according to elevation, of the main OTUs consumed by *Psammodomus algirus* (except Formicidae): Araneae (white), Orthoptera (hatched), Hemiptera (gray), and Coleoptera (black).

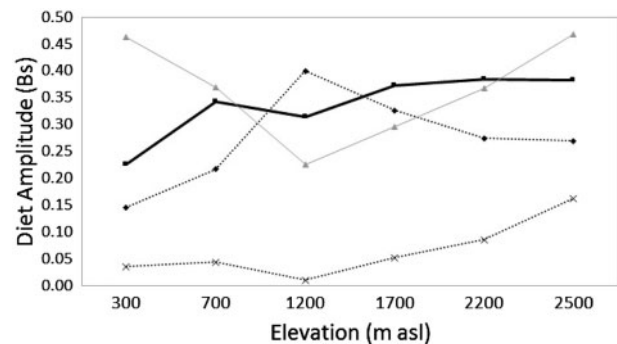


Figure 5. Trophic niche width (Bs) according to elevation (masl), as a whole (squares and heavy black line), males (rhombus and dotted line) and females (triangles and gray line). The diversity of available prey is indicated with crosses joined by a dotted line.

Diet of *P. algirus* in the alpine zone

In a more detailed analysis at the alpine zone (2,200 and 2,500 m), we recorded 14 OTUs in lizard feces ($n = 65$ individuals), including 2 OTUs not recorded in the sample previously analyzed for the complete elevational gradient: Diplopoda and Odonata (Table 6). The diet of alpine lizards was composed mainly of Orthoptera and Coleoptera, which comprised almost 50% out of the prey (Table 6). In comparison with the diet for the overall mountain, it was remarkable the low frequency of Formicidae in the alpine zone (only 6%), the absence of Embioptera, and the higher importance of Blattodea (almost 6%) (see Tables 1 and 6 to compare). There were no sex differences in number of prey per pellet (females: 7.33 ± 0.71 , males: 6.29 ± 0.42 ; $t_{63} = 0.84$, $P = 0.40$, test carried out with data log-transformed), or in the individual diet width (females: 0.19 ± 0.018 , males: 0.16 ± 0.016 ; $t_{63} = 1.34$, $P = 0.18$). The Chi-squared test revealed no differences in the diet between males and females (for every OTUs, $P > 0.10$).

Discussion

The diet of *P. algirus* along the elevational gradient

Psammodomus algirus consumed 17 different OTUs in the Sierra Nevada mountain (including Diplopoda and Odonata, reported in the alpine subsample). The main components of the diet of this lizard were Orthoptera, Formicidae, Coleoptera, Hemiptera, and

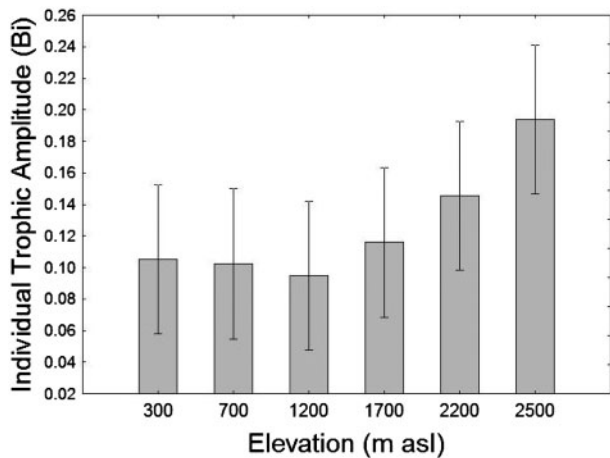


Figure 6. Elevational variation in the individual trophic niche width (B_i) in the lizard *Psammodromus algirus*. Bars indicate the 95% confidence intervals.

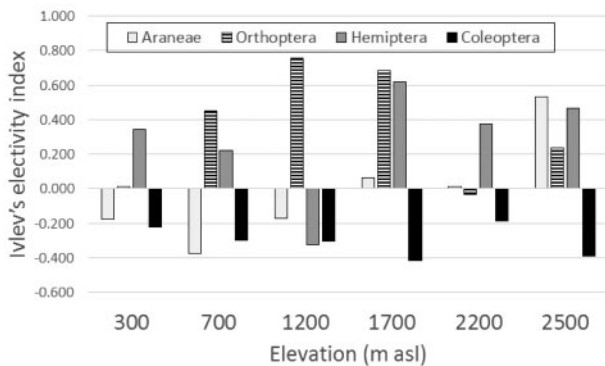


Figure 7. Values of the Ivlev's selectivity index for every elevation and for every of the main OTUs consumed by *P. algirus* (except Formicidae): Araneae (white), Orthoptera (hatched), Hemiptera (gray), and Coleoptera (black). Positive values indicate positive selection (i.e., prey were consumed more than expected by chance according to their availability in pitfalls) whereas negative values indicate negative selection. Values of the index oscillate between -1 and $+1$.

Araneae, embracing 72.3% of prey types. These OTUs correspond to the main prey described in other studies throughout the distribution range of the species (Table 7). The main prey were terrestrial arthropods, according to the foraging mode of *P. algirus*, actively searching for prey at the ground level. We detected subtle variation in the diet along the elevational gradient, which is, however, small in comparison with the wide variation in diet over the entire distribution range (see Table 7). For example, Diptera (minority prey in the Sierra Nevada) was an important part of the diet in several studies (Pérez-Quintero and Rubio-García 1997; Roug et al. 2007; Bouam et al. 2016), and Orthoptera proved to be the most important prey in the Sierra Nevada but was not relevant in several other studies (Table 7). In general, the reason for these geographic differences is poorly known. Our study, in fact, compares 6 locations along a wide elevational gradient (2,200 m), allowing us to test some of the reasons for geographic variation in diet.

Orthoptera was the main prey of *P. algirus* along the elevational gradient in the Sierra Nevada. It is an evasive prey, difficult to capture, and probably to subdue and swallow (considering its hind limbs and wings), hence providing low profitability to *P. algirus*

Table 6. Frequency and percentage, separated by females ($n=30$) and males ($n=35$), of each OTU found in the feces of the lizard *Psammodromus algirus* in the alpine zone (2,200 and 2,500 masl)

	Females		Males	
	Frequency	% Frequency	Frequency	% Frequency
Orthoptera	44	20.09	63	28.64
Coleoptera	48	21.92	52	23.64
Hemiptera	22	10.05	24	10.91
Larvae	20	9.13	19	8.64
Araneae	19	8.68	19	8.64
Formicidae	20	9.13	8	3.64
Hymenoptera	16	7.31	10	4.55
Blattodea	13	5.94	13	5.91
Lepidoptera	8	3.65	9	4.09
Other taxa	9	4.11	3	1.36

Notes: Other taxa included 7 Acarina, 2 Diptera, 1 Diplopoda, 1 Odonata, and 1 Mantodea. Hymenoptera does not include Formicidae. Larvae refer to those of unidentified taxa.

(Díaz and Carrascal 1993). Nonetheless, it probably is an attractive prey for this lizard given its size (Díaz and Carrascal 1990). It is positively selected by this lizard, but its abundance is probably underestimated in pitfall traps (Woodcock 2005), and therefore its electivity is probably lower than estimated. However, Orthoptera are not consumed simply according to its abundance in the environment; contrarily, along the elevational gradient, its electivity is negatively correlated with total abundance.

Hemiptera was other prey positively selected by this lizard at every elevation, except where it was the most abundant prey (at 1,200 m). Given that this is the most profitable prey for *P. algirus* (Díaz and Carrascal 1993), it remains intriguing why it is not more frequently consumed. Several Hemiptera are toxic (Blum 1981), and thus lizards perhaps limit their consumption (Vitt and Pianka 2007).

Coleoptera, despite being widely consumed (both in the Sierra Nevada and throughout the complete distribution range of *P. algirus*, Table 7), was negatively selected considering its high availability. Although with large size, they are very chitinous (Herrel et al. 2001), and thus energy intake is constrained by the costs associated with handling time and digestion (Díaz and Carrascal 1993). Moreover, some of them are toxic, rich in alkaloids (Blum 1981), and lizards show aversion to alkaloids (Cooper et al. 2002), or even the scent of beetles (Cooper and Pérez-Mellado 2002). The consumption of Coleoptera increased with elevation, a pattern that was unrelated to their abundance. Instead, it might be a consequence of the use of microhabitat by lizards, which employ more time basking in open areas, the contrary occurring at low elevations (Díaz 1997; also see Zamora-Camacho et al. 2016). Given that Coleoptera are more abundant in open areas than under shrubs, this elevational change in microhabitat use could boost the encounter rate with elevation. Alternatively, given that *P. algirus* lizards are larger with elevation (Zamora-Camacho et al. 2014a), they could easily consume hard prey. However, as a whole, the consumption of hard prey did not covary with elevation.

Araneae are present with relevant frequency ($>5\%$) in all studies carried out along the distribution range of *P. algirus* (Table 7; with the exception of Valverde [1967]). Araneae are softly chitinous (Herrel et al. 2001) and may be very profitable for lizards (Díaz and Carrascal 1993), although some of them can be dangerous (and even may prey on lizards, Hódar and Sánchez-Piñero 2002) and cursory species may be difficult to capture. Its electivity increased with the

Table 7. Literature review of the percentage of consumption of the most common prey (>5% frequency) in the diet of *Psammodromus algirus* according to different studies

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
Coleoptera	13	52	38	17	14	31	5		16	28	17	25	34	7	14	24	26
Araneae	9		7	12	9	6*	7	20	8	7	13	10	18	16	12	14	10
Hemiptera	11			15	11	19	61	20		29	22	32	19	10	16		7
Formicidae	19	15	13	10	26	8		17		6				9	9	13	6
Orthoptera	20	7	9	13		19	6	17	6							13	
Hymenoptera	6		10			6		6	6	6		9		12	9		17
Diptera		10		8					14		30	7	9	32	31	28	17
Larvae	6		13	13					38	11	8						
Plecoptera										8							
Phasmidae										7							
Diplopoda								7									
Embiodoptera	6																
Collembola														5			
Vegetal					23												

Notes: A, this study; B, Valverde (1967); C, Mellado et al. (1975); D, Pérez-Mellado (1982); E, Di Palma (1984); F, Seva (1984); G, Pollo and Pérez-Mellado (1988); H, Díaz and Carrascal (1990); I, Ortega-Rubio (1991); J, Gil (1992); K, Carretero (1993, Aiguemolls); L, Carretero (1993, Torredembarra); M, Carretero and Llorente (1993); N, Pérez-Quintero and Rubio-García (1997, El Rompido); O, Pérez-Quintero and Rubio-García (1997, Asperillo); P, Rouag et al. (2007); Q, Bouam et al. (2016). Larvae include larvae of different taxa. Hymenoptera does not include formicidae. Vegetal refers to plant matter. *In this study the taxa reported is Arachnida.

elevational gradient, following a reversed pattern with its relative abundance.

Formicidae, despite being the second most frequent prey, were negatively selected when considering their enormous availability in the environment (>70% of available prey). Formicidae are small, highly chitinous, and potentially dangerous, and therefore *P. algirus* only occasionally consumed them, probably when the availability of other prey is very low. Like Formicidae, many other prey only occasionally occurred in the diet of this lizard, small prey such as Acari (very abundant in the environment, but rarely consumed) or Collembola. This result is consistent with the idea that *P. algirus* selects prey according to prey size rather than prey type (Díaz and Carrascal 1990, 1993). Other prey, highly evasive (flying prey such as Hymenoptera, Lepidoptera, and Diptera) or chitinous (Diplopoda), also seemed not to be positively selected. However, Orthoptera and Coleoptera were the main prey of this lizard, and they are highly evasive and hard, respectively. Therefore, other things should cause lizards not to consume flying prey and Diplopoda. Diplopoda is probably avoided as a consequence of its repugnatorial glands more than as a consequence of its hardness. Hymenoptera may be dangerous and is very chitinous, but Lepidoptera and Diptera probably would be adequate for *P. algirus*. However, if *P. algirus* forages mainly on the ground, its rate of encounters with these flying prey is probably very low, while encounters with Orthoptera are much more frequent. Similarly, one of the most profitable prey for *P. algirus* are larvae (Díaz and Carrascal 1993), but their abundance in the environment was low (Table 4), limiting their consumption.

As a whole, *P. algirus* feeds mainly on arthropods, behaving as a generalist species along its geographic range. Foraging behavior of *P. algirus*, however, is not simply based on encounter rate. At least for Hemiptera, Orthoptera, and Araneae, they are consumed in a frequency contrary to their abundance. A pattern of negative correlation between relative abundance and electivity is general in lizards and might be explained if lizards avoid toxic or dangerous prey above a threshold (Carretero 2004). However, this pattern may also be explained if lizards search for a balanced diet, which would be

achieved by preying on different prey types in order to cover a wide range of nutrients (Pérez-Mellado et al. 1991). This last explanation would also explain why the diet of *P. algirus* was very similar along the elevational gradient.

Other possible patterns with elevation were not supported. First, given that ability for prey capture improves with body temperature (Díaz 1994a), and environmental temperature diminishes with elevation, so that the consumption of evasive prey would be expected to decrease with elevation. This was not supported, but it should be noted that lizard body temperature shows no change with elevation in our study system (Zamora-Camacho et al. 2013, 2016). Moreover, sprint speed of *P. algirus* does not vary with elevation in the Sierra Nevada (Zamora-Camacho et al., 2014b). In addition, lizard body size increases with elevation in the Sierra Nevada (Zamora-Camacho et al. 2014a), and therefore, we predicted hardness of prey to increase with elevation, but this prediction was not supported, either.

Trophic niche width

The parameter trophic niche width was intermediate, but increased with elevation. This pattern could be due to several reasons. First, *P. algirus* body size becomes greater with elevation (Zamora-Camacho et al. 2014a), and then the range of body sizes (see Díaz 1994b) and/or the number of prey consumed could increase with elevation, augmenting niche width. Nevertheless, trophic niche width seems to decrease, rather than to increase, with body size in lizard species (Costa et al. 2008b). Moreover, the number of prey consumed per individual did not vary with elevation. Alternatively, the diversity of competitors could decline with altitude, favoring a niche release and greater trophic niche width (Comas et al. 2014). Effectively, the lizard community accompanying *P. algirus* (*Psammodromus edwardsianus*, *Podarcis hispanicus*, *Timon neva-densis*, *Tarentola mauritanica*, and *Acanthodactylus erythrurus*) shows a diminishing of diversity with elevation (Caro et al. 2010). Nevertheless, the clearest reason for the greater trophic niche width with elevation is a concomitant rise in prey diversity (Figure 5). Moreover, the greater trophic niche width was the result of every

lizard increasing the diversity of prey consumed, as shown by a correlation between both population and individual trophic niche width. Therefore, our findings do not support the niche variation hypothesis.

We found sex differences in trophic niche width, diet being more varied in females than in males, which agrees with that found in a population from NE Spain (Carretero and Llorente 1993). This sex difference was not due to differences in the quantity of prey consumed, which did not differ between sexes. The reason why females are more generalist remains unknown and is remarkable, given that, as was explained in the “Introduction,” we expected a wider trophic niche in males. One possibility is that females need a higher diversity of resources for reproduction, especially egg formation. For example, Navarro-López et al. (2014) reported that diet width improves reproductive success in the common kestrel (*Falco tinnunculus*). We also found an inverse interpopulation relationship between male and female niche width (Figure 5), which could suggest certain niche segregation, but we failed to find sex differences in diet (Table 2). Other studies found a similar absence of sex differences in diet in this species (Pollo and Pérez-Mellado 1988; Pérez-Quintero and Rubio-García 1997). Indeed, diet overlap was relatively high.

Adaptation to the alpine environment

The alpine environment is harsh for ectotherms. Moreover, it marks the elevational limit for *P. algirus*, and therefore, it is expected to be a marginal habitat for which the lizard is poorly adapted. However, the results indicate that the alpine habitat is not suboptimal for *P. algirus*, as diet in alpine environments for this species proves very similar to that at lower elevations, and, in fact, prey abundance and diversity are the highest in the alpine zone. Time available for foraging decreases with elevation (Zamora-Camacho et al. 2013). However, at highlands, there is a burst of resources that lizards seem to exploit to reach high densities, almost as high as at midlands, and much higher than in the lowlands (see Zamora-Camacho et al. 2013). Nevertheless, this burst of trophic resources occurs only for a small window of time, limiting the capacity of lizards to inhabit this extreme environment. To profit from this burst of resources, *P. algirus* starts its activity earlier in the season (Zamora-Camacho et al. 2013), requiring it to reach high body temperatures in the cold conditions of the alpine zone. To attain this, *P. algirus* employs an array of adaptations, such as larger body size (Zamora-Camacho et al. 2014a) in combination with darker coloration (Reguera et al. 2014). Therefore, *P. algirus* seems to show local adaptation in the alpine zones of the Sierra Nevada, allowing it not only survive and reproduce, but also to be highly successful. However, in this context of local adaptation, lizards adapted to profit from high prey abundance for limited time, it is unclear how the current climate warming will affect alpine populations of this species.

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