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
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 (Diaz 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 (Diaz 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 Psammodromus 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; Diaz 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, a 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 (Diaz 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 Martinez 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

Psammodromus 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 (Diaz 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°38'2"0' W and 36°56'10"0'–37°12'38"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 (Diaz 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
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 capsules, jaws, thoraxes, etc. Then, we assigned the items to operational taxonomic units (OTUs, Sneth 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 evasiveness 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):

\[
B = \frac{1}{\Sigma p_i^2},
\]

\[
B_s = \frac{B - 1}{n - 1},
\]

where $p_i$ is the fraction of items in the diet that are of food category $i$, 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 niche width, $B_i$ indicates the trophic niche width 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 (Omal) (Pianka 1974):

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).
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 day (\( n = 98 \)). When we were interested in elevational patterns, we used the Spearman rank binary correlation (\( \rho \)) 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 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 pitfall-days (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
prevalent 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 lizards. Our analysis showed that the overall prey abundance significantly varied with elevation (*F* = 6.92, *P* < 0.001; Figure 3), showing a linear increase (*p* = 0.94, *P* = 0.005). However, the relative frequency of Araneae significantly decreased with elevation (*p* = 0.005). The diversity of available prey also increased with elevation (*p* = 0.83, *P* = 0.042; Figure 4).

**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.

| 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 |
| Embiopodia | 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: Aracina (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 case) of the 5 most frequent OTUs in the diet of *Psammodromus algirus*.

| Orthoptera | 41 | 49 | 0.36* |
| Formicidae | 49 | 38 | 0.70* |
| Coleoptera | 31 | 27 | 0.14* |
| Hemiptera | 24 | 28 | 0.15* |
| Araneae | 25 | 17 | 0.77* |

Notes: Sexual differences in the frequency were checked with a Chi-squared test for each OTU; in no case were differences significant (*p* > 0.05).

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

| 300 | 700 | 1200 | 1700 | 2200 | 2500 | χ² |
|---|---|---|---|---|---|---|
| Orthoptera | 7 | 18 | 15 | 13 | 18 | 19 | 6.80* |
| Formicidae | 31 | 8 | 32 | 7 | 8 | 1 | 17.73** |
| Coleoptera | 4 | 10 | 5 | 11 | 13 | 15 | 9.60** |
| Hemiptera | 10 | 9 | 6 | 6 | 13 | 8 | 4.00** |
| Araneae | 7 | 5 | 7 | 4 | 9 | 10 | 3.71** |

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

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

| Orthoptera | 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 |
| 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 |
| Zygotesma | 88 | 0.59 | 37 | 2.47 |
| Lepidoptera | 65 | 0.44 | 45 | 3.01 |
| Embioptera | 31 | 0.21 | 20 | 1.34 |
| Larvae | 30 | 0.20 | 27 | 1.81 |
| Embiopodia | 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 | 39 | 0.26 | 39 | 2.60 |

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 | 5,668 | 5,302 | 6.11* |
| Shrub | 686 | 487 | 17.01*** |
| Araneae | 229 | 177 | 3.34* |
| Orthoptera | 262 | 244 | 0.32* |
| Hymenoptera | 113 | 163 | 4.57* |
| Hymenoptera | 126 | 141 | 0.42* |
| Lepidoptera | 32 | 33 | 0.01* |
| Larvae | 16 | 14 | 0.07* |
| Embiopodia | 15 | 13 | 0.07* |

Notes: The value of the Chi-squared testing for statistical differences between microhabitats is shown; * indicates non-significant (*p* > 0.5); **P < 0.05; ***P < 0.001. Only OTUs that formed part of the diet of *P. algirus* were considered (see Table 1).
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 ($F_{3,60} = 2.51, P = 0.039$), which explained 15% of variation in $Bi$ (whole model: $F_{4,60} = 2.15, P = 0.03$, adjusted $R^2 = 0.15$). The interaction was not significant ($F_{3,60} = 1.15, P = 0.35$). Females showed a wider diet than did males ($0.14 \pm 0.013$ vs. $0.10 \pm 0.014$; 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 linear 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 $6.32 \pm 0.71$ (mean $\pm$ SE) and did not vary with elevation ($F_{3,60} = 0.77, P = 0.58$; data not shown for simplicity) or sex (males: $6.03 \pm 0.84$; females: $6.59 \pm 1.15$ prey per pellet; $F_{1,60} = 0.20, P = 0.66$; sex $\times$ elevation: $F_{1,60} = 1.82, P = 0.12$).

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 election; Greenslade 1973). We did not consider less representative prey, either. Our findings showed that selectivity 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).

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 Embioptri, 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: $7.33 \pm 0.71$, males: $6.29 \pm 0.42$; $t_{63} = 0.84$, $P = 0.40$, test carried out with data logarithm-transformed), or in the individual diet width (females: $0.19 \pm 0.018$, males: $0.16 \pm 0.016$; $t_{63} = 1.34$, $P = 0.18$). 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

$Psammodromus algirus$ 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
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; Rouag 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* (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 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)

| OTU       | Females | Males |
|-----------|---------|-------|
| Orthoptera| 44      | 63    |
| Coleoptera| 48      | 52    |
| Hemiptera | 22      | 24    |
| Larvae    | 20      | 19    |
| Araneae   | 19      | 19    |
| Formicidae| 20      | 8     |
| Hymenoptera| 16  | 10    |
| Blattodea | 13      | 13    |
| Lepidoptera| 8    | 9     |
| Other taxa| 9       | 3     |

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.
Effectively, the lizard community accompanying 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).

The parameter trophic niche width was intermediate, but increased with elevation. This pattern could be due to several reasons. First, the diversity of competitors could decline with altitude, favoring a niche release and greater trophic niche width (Comas et al. 2014). 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, Podarctis hispanicus, Timon nevadensis, Tarentola mauritanica, and Acanthodactylus erythraeus) 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

### 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 | 7 | 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 | 13 | 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 |
| Phasmatidae | 7 |
| Diplopora | 7 |
| Embiophora | 6 |
| Collombola | 23 |
| Vegetal | 5 |

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, Aiguesmolls); 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, Aspilillo); 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.*
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 what 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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References

Bearhop S, Adams C, 2004. Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012.

Bellure J, Carrascal LM, Díaz JA, 1996. Covariation of thermal biology and foraging mode in two Mediterranean lacertid lizards. Ecology 77:1163–1173.

Blum MS, 1981. Chemical Defenses of Arthropods. New York: Academic Press.

Bolnick DL, Svanback R, Araújo MS, Persson I, 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proc Nat Acad Sci USA 104:10075–10079.

Bouam I, Necer A, Saoudi M, Tahar-Chaouch L, Khelfaoui F, 2016. Diet and daily activity patterns of the lacertid lizard Psammodromus algirus (Sauria: Lacertidae) in a semi-arid Mediterranean region. Zool Écol 26:244–252.

Brunner FS, Schmid-Hempel P, Barrabé SM, 2014. Protein-poor diet reduces host-specific immune gene expression in Bombus terrestris. Proc R Soc B 281:20140128.

Caro J, Fernández Cardenete JR, Benítez M, Chirosa M, Zamora-Camacho FJ et al., 2010. Estudio de Anfibios y Reptiles en el Espacio Natural de Sierra Nevada, en el Marco del Cambio Global. Unpublished Report. Universidad de Granada.

Carretero MA, 1993. Ecología de los lacértidos en arenas costeras del nor- este ibérico [Phd thesis]. Universitat de Barcelona.

Carretero MA, 2004. From set menu to a la carte. Linking issues in trophic ecology of Mediterranean lacertids. Ital J Zool 71:S121–S133.

Carretero MA, Llorente GA, 1993. Feeding of two sympatric lacertids in a sandy coastal area Ebro Delta (Spain). In: Valakos ED, editor. Lacertids of the Mediterranean Region. A Biological Approach. Athens: Hellenic Zoological Society, 155–172.

Comas M, Escoriza D, Moreno-Rueda G, 2014. Stable isotope analysis reveals variation in trophic niche depending on altitude in an endemic alpine gecko. Basic Appl Ecol 15:362–369.

Cooper WE, Pérez-Mellado V, 2002. Responses by a generalist predator, the Balearic lizard Podarcis lilfordi, to chemical cues from taxonomically diverse prey. Acta Ethol 4:119–124.

Cooper WE, Pérez-Mellado V, Vitt LJ, Budzinsky B, 2002. Behavioral responses to plant toxins by two omnivorous lizard species. Physiol Behav 76:297–303.

Costa GC, Mesquita DO, Colli GR, Vitt LJ, 2008a. Niche expansion and the niche variation hypothesis: does the degree of individual variation increase in deapauperate assemblages? Am Nat 172:868–877.

Costa GC, Vitt LJ, Pianka ER, Mesquita DO, Colli GR, 2008b. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. Global Ecol Biogeogr 17:670–677.

Di Palma G, 1984. Regime alimentaire de Psammodromus algirus (Reptilia, Lacertidae) dans une population insulaire du Canal de Sicile. Rev d’Écol 41:225–230.

Díaz JA, 1993. Breeding coloration, mating opportunities, activity, and survival in the lacertid lizard Psammodromus algirus. Can J Zool 71:1104–1110.

Díaz JA, 1994a. Effects of body temperature on the predatory behaviour of the lizard Psammodromus algirus hunting winged and wingless prey. Herpetol J 4:145–150.

Díaz JA, 1997. Ecological correlates of the thermal quality of an ectotherm’s habitat: a comparison between two temperate lizard populations. Funct Ecol 11:79–89.

Díaz JA, Carrascal LM, 1990. Prey size and food selection of Psammodromus algirus (Lacertidae) in central Spain. J Herpetol 24:342–347.
Díaz JA, Carrascal LM, 1991. Regional distribution of a Mediterranean lizard: influence of habitat cues and prey abundance. *J Biogeogr* 18:291–297.

Díaz JA, Carrascal LM, 1993. Variation in the effect of profitability on prey size selection by the lacertid lizard *Psammodromus algirus*. *Oecologia* 94: 23–29.

Díaz M, 1994b. Variability in seed size selection by granivorous passerines: effects of bird size, bird size variability, and ecological plasticity. *Oecologia* 99:1–6.

Edwards S, Tolley KA, Vanhooydonck B, Measey GJ, Herrel A, 2013. Is dietary niche breadth linked to morphology and performance in Sandveld lizards *Nacras* (Sauria: Lacertidae)? *J Linn Soc* 110:674–688.

Fernández-Cardenete JR, Luzón-Ortega JM, Pérez-Contreras J, Tierno de la Sierra de Gredos [PhD thesis]. Universidad de Salamanca.

Figueroa JM, 2000. Revisión de la distribución y conservación de los anfibios y reptiles en la provincia de Granada (España). *Zool Baetica* 11: 77–104.

Franzke A, Reinhold K, 2012. Transgenerational effects of diet environment on life-history and acoustic signals of a grasshopper. *Behav Ecol* 24: 734–739.

Garrido M, Pérez-Cembranos A, Corti C, Luiselli L, Pérez-Mellado V, 2011. Using focal samples in lizard dietary studies. *Amphibia–Reptilia* 32:1–7.

Gil CM, 1992. *Greenslade PJM, 1973. Sampling ants with pitfall traps: digging-in effects. Insect Soc* 20:343–353.

Herrel A, Van Damme R, Vanhooydonck B, De Vree F, 2001. The implications of bite performance for diet in two species of lacertid lizards. *Can J Zool* 79:662–670.

Hódar JA, Sánchez-Piñero F, 2002. Feeding habits of the black widow spider *Latrodectus bilaliane* (Araneae: Theridiidae) in an arid zone of south-east Spain. *J Zool* 257:101–109.

Huey RB, Pianka ER, 1983. Ecological consequences of foraging mode. *Ecology* 62:991–999.

Huey RB, Pianka ER, Schoener TW, 1983. *Lizard Ecology: Studies of a Model Organism*. Cambridge: Cambridge University Press.

Hurlbert SH, 1978. The measurement of niche overlap and some relatives. *Ecology* 59:67–77.

Iraeta P, Monasterio C, Salvador A, Díaz JA, 2011. Sexual dimorphism and interpopulation differences in lizard hind limb length: locomotor performance or chemical signalling? *Biol J Linn Soc* 104:318–329.

Ivlev VS, 1961. *Experimental Ecology of the Feeding of Fishes*. Boston: Yale University Press.

Kawecki TJ, 2008. Adaptation to marginal habitats. *Annu Rev Ecol Evol Syst* 39:321–342.

Keller I, Alexander J, Holderegger R, Edwards P, 2013. Widespread pheno typic and genetic divergence along altitudinal gradients in animals. *J Evol Biol* 26:2527–2543.

Kopena R, López P, Martin J, 2014. Relative contribution of dietary carotenoids and vitamin E to visual and chemical sexual signals of male Iberian green lizards: an experimental test. *Behav Ecol Sociobiol* 68:571–581.

Körner C, 2007. The use of ‘altitude’ in ecological research. *Trends Ecol Evol* 22:569–574.

Krebs CJ, 1999. Niche measures and resource preferences. In: Krebs CJ, editor. *Ecological Methodology. New York: Addison-Wesley Publishers*. 455–496.

Lefcheck JS, Whalen MA, Davenport TM, Stone JP, Duffy JE, 2013. Physiological effects of diet mixing on consumer fitness: a meta-analysis. *Ecology* 94:565–572.

Levins R, 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton: Princeton University Press.

Lloyd JD, Martínez F, 1974. Dimorfismo sexual en *Psammodromus algirus* (Reptilia, Lacertidae). *Doñana Acta Vert* 1:33–41.

Mellado J, Amores F, Parreño FF, Hiraldo F, 1975. The structure of a Mediterranean lizard community. *Doñana Acta Vert* 2:145–160.

Miles DB, Losos JB, Irsichk DJ, 2007. Morphology, performance, and foraging mode. In: Reilly SM, McBrayer LB, Miles DB, editors. *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*. Cambridge: Cambridge University Press. 49–93.

Navarro-López J, Vergara P, Fargallo JA, 2014. Trophic niche width, offspring condition and immunity in a raptor species. *Oecologia* 174: 1215–1224.

Nel K, Rimbach R, Pillay N, 2015. Dietary protein influences the life-history characteristics across generations in the African striped mouse *Rhabdomys*. *J Exp Zool* 323A:97–108.

Noguez-Bravo D, Arazo M, Romdal T, Rahbek C, 2008. Scale effects and human impact on the elevational species richness gradients. *Nature* 453: 216–219.

Ortega-Rubio A, 1991. Trophic partitioning and community organization in a guild of lizards in La Sierra de Guadarrama, Spain. *Ekologia* 10:19–29.

Pérez-Mellado V, 1982. Estructura en una taxocenosis de Lacertidae (Sauria, Reptilia) del Sistema Central. *Mediterranea* 6:39–64.

Pérez-Mellado V, Bauwens D, Gil M, Guerrero F, Lizana M et al., 1991. Diet composition and prey selection in the lizard *Lacerta monticola*. *Can J Zool* 69:1728–1735.

Pérez-Quintero JC, Rubio-García JC, 1997. Alimentación de la lagartija colilarga, *Psammodromus algirus* (L.) Sauria, (Lacertidae), en el litoral de Huelva (SO España). *Doñana Acta Vert* 24:3–26.

Perry G, 2007. Movement patterns in lizards: measurements, mobility, and behavioral correlates. In: Reilly SM, McBrayer LB, Miles DB, editors. *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*. Cambridge: Cambridge University Press. 13–48.

Pinta ER, 1974. Niche overlap and diffuse competition. *Proc Nat Acad Sci USA* 71:2141–2145.

Pinta ER, 1994. *Evolutionary Ecology*. New York: Harper Collins.

Pollo CJ, Pérez-Mellado V, 1988. Trophic ecology of a taxocenosis of Mediterranean Lacertidae. *Ecol Mediterr* XIV:131–148.

Pulliam HR, 1975. Diet optimization with nutrient constraints. *Am Nat* 109: 765–768.

Quinn GP, Krough MJ, 2002. *Experimental Design and Data Analysis for Biologists*. New York: Cambridge University Press.

Raubenheimer D, Simpson SJ, 1997. Integrative models of nutrient balancing: application to insects and vertebrates. *Nutr Res Rev* 10:151–179.

Reguera S, Zamora-Camacho FJ, Moreno-Rueda G, 2014. The lizard *Psammodromus algirus* (Squamata: Lacertidae) is darker at high altitudes. *Biol J Linn Soc* 112:132–141.

Reilly SM, McBrayer LB, Miles DB, 2007. *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*. Cambridge: Cambridge University Press.

Rouag R, Djilali H, Guercasie H, Luiselli L, 2007. Resource partitioning patterns between two sympatric lizard species from Algeria. *J Arid Environ* 69: 158–168.

Salvador A, 2015. Lagartija colla larga—*Psammodromus algirus*. In: Salvador A, Marco A, editors. *Enciclopedia Virtual de los Vertebrados Españoles*. Madrid: Museo Nacional de Ciencias Naturales, MNCN-CSIC.

Schloot N, Ebert D, Martin-Creuzburg D, 2013. Dietary supply with polysaturated fatty acids and resulting maternal effects influence host–parasite interactions. * BMC Ecol* 13:41.

Seva E, 1984. *Reparto de recursos en dos especies psamfríolos de saurios: Acantodactilus eritrurus y Psammodromus algirus. Mediterranea* 7:5–25.

Simpson EH, 1949. *Measurement of diversity*. Nature 163:688.

Sneath P, Sokal R, 1962. *Numerical taxonomy*. Nature 193:855–860.

StatSoft, Inc., 2007. *STATISTICA (data analysis software system), version 8.0*. Tulsa: StatSoft, Inc.

Thibault E, Fontaine C, 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Trends Ecol Evol* 8.0. Tulsa: StatSof, Inc.
McBrayer LB, Miles DB, editors. *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*. Cambridge: Cambridge University Press, 427–449.

Vitt LJ, Pianka ER, 2007. Feeding ecology in the natural world. In: Reilly SM, McBrayer LB, Miles DB, editors. *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*. Cambridge: Cambridge University Press, 141–172.

Ward DF, New TR, Yen AL, 2001. Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. *J Insect Conserv* 5: 47–53.

Woodcock B, 2005. Pitfall trapping in ecological studies. In: SR Leather, editor. *Insect Sampling in Forest Ecosystems*. Oxford: Blackwell Publishing, 37–57.

Zamora-Camacho FJ, Reguera S, Moreno-Rueda G, Pleguezuelos JM, 2013. Patterns of seasonal activity in a Mediterranean lizard along a 2200 m altitudinal gradient. *J Therm Biol* 38:64–69.

Zamora-Camacho FJ, Reguera S, Moreno-Rueda G, 2014a. Bergmann's rule rules body size in an ectotherm: heat conservation in a lizard along a 2200-meter elevational gradient. *J Exp Biol* 27:2820–2828.

Zamora-Camacho FJ, Reguera S, Rubiño-Ascánsio MV, Moreno-Rueda G, 2014b. Effects of limb length, body mass, gender, gravidity, and elevation on escape speed in the lizard *Psammodromus algirus*. *Evol Biol* 41:509–517.

Zamora-Camacho FJ, Reguera S, Moreno-Rueda G, 2016. Thermoregulation in the lizard *Psammodromus algirus* along a 2200-m elevational gradient in Sierra Nevada (Spain). *Int J Biometeorol* 60:687–697.