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Trophic ecology of two sympatric lizard species: the Algerian sand lizard and the wall lizard in Djurdjura, northern Algeria

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ABSTRACT

In this study, we present the first data on the diet of two sympatric lizard species *Psammodromus algirus* and *Podarcis vaucheri* of the Djurdjura Mountains. The analysis of 100 feces (43 *Ps. algirus* and 57 *P. vaucheri*) allowed us to identify 560 prey items (254 for *Ps. algirus* and 312 for *P. vaucheri*) distributed across 17 operational taxonomic units. Insects were most commonly consumed by both species, but spiders were also preferred by *P. vaucheri*. The five most commonly ingested categories of prey among insects were: Coleoptera, Hymenoptera, Homoptera, Heteroptera and Orthoptera. During the study period, the interspecific diet overlap was very high ($C_H = 0.86$). But the diet of *P. vaucheri* ($B_A = 0.50$) was slightly more diversified than that of *Ps. algirus* ($B_A = 0.41$). The diets of both species were, however, not strongly different. A significant influence of seasonal variation on diet was detected.

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Diet; *Psammodromus algirus*;
Podarcis vaucheri; Djurdjura;
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Introduction

Understanding the ecology of species is a necessary condition for the proper management and preservation of natural sites. In this context, food resources are a critical parameter to consider in conservation biology (Tatin et al. 2013). Among the three classic dimensions of the niche (diet, space, and time), diet is without a doubt the most studied in lizards (Carretero et al. 2006, 2010; Luiselli 2008). In general, lacertid lizards are generalist opportunist predators (Arnold 1987; Lo Cascio and Capula 2011; Mou 1987; Pérez-Mellado and Corti 1993). Consequently, terrestrial invertebrates, especially insects, occupy a predominant part of their diet (Arnold 1987; Carretero 2004). However, the feeding ecology of the family shows an impressive variability and numerous factors appear to affect prey choice (Carretero 2004).

An animal's niche is often studied in the context of interspecific competition and the patterns of resource use (Pianka 1981). Several studies have examined the diet of sympatric species and have suggested that the partitioning of trophic resources may be important for regulating coexistence in lizard communities (Luiselli 2008). However, differences in resource use by two sympatric species of lizards may not necessarily indicate the existence of competition (Znari et al. 2000). In his review Luiselli (2008) concludes that the trophic niche is not a resource generally partitioned by sympatric lizards.

In the Mediterranean basin lacertids are the dominant group of lizards. Their role in the transfer of matter and energy from arthropods and other small invertebrates to birds and mammals constitutes a major function within Mediterranean ecosystems (Carretero 2004). Among, the phylogenetic and phylogeographic studies conducted on North African and Mediterranean lizards over the last decade, many have been devoted to the systematic of Algerian species (see Carranza et al. 2006; Carretero 2008; Fonseca et al. 2008, 2009; Kaliontzopoulou et al. 2008, 2011; Kaliontzopoulou, Carretero, and Llorente 2012; Larbes, Carretero, and Brito 2007; Lima et al. 2009; Verdú-Ricoy et al. 2010). However, information on the biology and ecology of these lizards in Algeria is scarce (but see Arab and Doumandji 2003; Carretero et al. 2011; Rouag, Berrahma, and Luiselli 2006; Rouag et al. 2007). The aim of the present study is to fill this gap and provide qualitative and quantitative data about the trophic spectrum of two lacertid lizards: the Algerian sand lizard *Psammodromus algirus* (Linnaeus, 1758) and the wall lizard *Podarcis vaucheri* (Boulanger, 1905) living in sympatry in the Djurdjura National Park, Algeria.

Materials and methods

Study site

Tala Guilef is located in the western part of the northern slope of the Djurdjura Mountain (Djurdjura National Park),

Kabylie, Algeria. It is located approximately 140 km south-east of Algiers and 45 km southwest of Tizi Ouzou (36°39' N, 4°01' E). The region is characterized by a mountain climate influenced by the Mediterranean Sea and belongs to the humid climate scene (Hamdine et al. 1993).

The samples were collected in two types of habitats that seem attractive for the two lizard species. The first habitat is characterized by the presence of stones and rocks from the Haizer massif and bushy vegetation including: hawthorn (*Crataegus monogyna* and *Crataegus laciniata*), elmleaf blackberry (*Rubus ulmifolius*), dog rose (*Rosa canina*), Mediterranean rose (*Rosa sicula*), mountain cherry (*Prunus prostrata*) and Spanish barberry (*Berberis hispanica*). In grass stratum, we essentially find: camomile (*Anthemis kabilica*), absinthe (*Artemisia absintium*), astragalus (*Astragalus armatus*), sea holly (*Eryngium tricuspdatum*), spurges (*Euphorbia luteola*) and giant fennel (*Ferula communis*). The second habitat is a river situated between the first rocky habitat and a cedar forest and often frequented by the lizards during warm hours and/or days. It is characterized by very dense vegetation including: Montpellier maple (*Acer monspesulanum*), common alder (*Alnus glutinosa*), elmleaf blackberry (*Rubus ulmifolius*), white willow (*Salix alba*), black poplar (*Populus nigra*), hawthorn (*Crataegus laciniata*), southern polypody (*Polypodium cambricum*), wild mint (*Mentha arvensis*), pennyroyal (*Mentha pulegium*), false yellowhead (*Inula viscosa*) and maidenhair spleenwort (*Asplenium trichomanes*).

Methods

The study was conducted in spring (May–April) and summer (June–July) of 2013–2014. The lizards were caught by hand or by noose and taken to the laboratory. Feces were obtained by keeping individuals in a terrarium 44 cm × 55 cm × 77 cm, heated with a lamp (160 W) placed above one end. Water was provided *ad libitum*. After a day of observation, lizards were taken back to their site of capture.

The analysis of the feces was done by placing them in an aqueous ethanol solution to dissolve them. Preys were identified using a binocular microscope with 10–40×. Sclerotized parts of invertebrates such as mandibles, heads, thorax, wings and legs were counted. The items were classified in groups called operational taxonomic units (OTUs; Carretero 2004; Sneath and Sokal 1973) and their determination was performed down to the lowest possible taxonomic level. The following abbreviations were used to indicate the OTUs in the text and figures: Aca, Acari; Ara, Aranea; Dict, Dictyoptera; Dip, Diptera; Col, Coleoptera; For, Formicidae; Gas, Gasteropoda; Hem, Hemiptera; Het, Heteroptera; Hym: Hymenoptera (other than Formicidae); Hom, Homoptera; Iso, Isoptera; Lep, Lepidoptera larvae; Odo, Odonatoptera; Opil, Opilionida; Orth, Orthoptera; Vegt, Vegetal matter.

Data analysis

In order to characterize the diet of the two species, we calculated relative abundance (%N), relative occurrence (%P), and the standardized index of Levin (B_A) to estimate the taxonomic diversity as follows:

$\%N = (p_i/p) \times 100$, where (p_i) is the number of prey of categories (i) and (p) is the total number of prey (Zaime and Gautier 1989).

$\%P = (n_i/N) \times 100$, where (n) is the number of feces containing the prey category (i) and (N) is the total number of feces. Prey were further grouped according to the classification used by Bigot and Bodot (1973):

- Constant prey of which the occurrence is equal to or higher than 50%;
- Common prey of which the occurrence varies between 25 and 50%;
- Accidental prey of which the occurrence varies between 10 and 25%;
- Very accidental prey of which the occurrence is less than 10%.

$B_A = (B - 1)/(n - 1)$, where (n) is the number of prey categories and (B) is the Levin's index of niche breadth: $B = 1/\sum p_i^2$, (p_i) is the proportion of each category (i). This index describes the breadth of the trophic niche where a value of '1' indicates a generalized diet and a value of '0' indicates a specialized tendency (Krebs 1999).

The food niche overlap (or similarity) was evaluated using the Morisita-Horn index (Horn 1966): $C_H = \frac{2 \sum p_{ij} p_{ik}}{\sum p_{ij}^2 + \sum p_{ik}^2}$, where (p_{ij}) is the proportion of categories (i) in the diet (j) and (p_{ik}) the proportion of categories (i) in the diet (k). This parameter varies from '0' for no similarity to '1' for a complete similarity (Krebs 1999).

To examine the relation between occurrence of the ingested prey and their abundance, we used a Spearman rank correlation between relative abundance (%N) and relative occurrence (%P) of prey categories. We also used the chi-squared test (χ^2) to study seasonal and interspecific variations in the diet and the Mann-Whitney test for the comparison of the number of items per feces.

Results

Diet composition

A total of 566 preys were identified in the overall sample (100 feces). The 43 feces of *Ps. algirus* revealed the presence of 254 items grouped in 15 OTUs. The diet of *P. vaucheri* was composed of 16 OTUs and contained 312 prey from 57 feces. The mean number of prey consumed per feces did not differ between the two species (*Ps. algirus*: 5.91 ± 0.66 ; *P. vaucheri*: 5.47 ± 0.51 ; Mann-Whitney U test: $Z = -0.278$, $p = 0.781$).

Levin's index showed that the food spectrum of *P. vaucheri* ($B_A = 0.50$) was more diversified than that of *Ps. algirus* ($B_A = 0.41$), but the statistical analysis on the

Table 1. Descriptive parameters of the diet in the two species.

OTUs	<i>Ps. algirus</i>			<i>P. vaucheri</i>		
	<i>n</i>	% <i>N</i>	% <i>P</i>	<i>n</i>	% <i>N</i>	% <i>P</i>
Opilionida	0	0.00	0.00	1	0.32	1.75
Araneae	16	6.3	37.21	39	12.5	56.14
Acari	1	0.39	2.33	2	0.64	1.75
Dictyoptera	4	1.57	9.30	5	1.6	8.77
Orthoptera	23	9.06	39.53	29	9.29	43.86
Formicidae	16	6.3	25.58	28	8.97	31.58
Hymenoptera	39	15.35	41.86	31	9.94	29.82
Coleoptera	76	29.92	58.14	61	19.55	45.61
Hemiptera	1	0.39	2.33	11	3.53	15.79
Heteroptera	35	13.78	51.14	13	4.17	21.05
Homoptera	23	9.06	18.60	60	19.23	29.82
Isoptera	3	1.18	2.33	0	0.00	0.00
Lepidoptera larvae	7	2.76	16.28	8	2.56	14.04
Diptera	7	2.76	13.95	20	6.41	29.82
Odonatoptera	0	0.00	0.00	1	0.32	1.75
Gasteropoda	2	0.79	4.65	1	0.32	1.75
Vegetal matter	1	0.39	2.33	2	0.64	3.51
Sum	254			312		
B_A	0.41			0.50		

Notes: %*P*: occurrence; %*N*: abundance; *n*: number of identified items; and B_A : standardized index of Levin.

proportion of consumed prey showed that the two diets were not different ($\chi^2 = 20.763$, $p = 0.188$, $df = 16$). The index of Morisita-Horn showed a high similarity in the two trophic spectra ($C_H = 0.86$).

The diets of both species were clearly dominated by insects (Table 1). In contrast, the proportion of spiders in the diet of *P. vaucheri* seemed important (%*N* = 12.3%). Among the insects, five categories (OTUs) were commonly consumed: Col, Hym (other than Formicidae), Hom, Het and Orth. In *Ps. algirus*, Coleoptera were the most commonly consumed prey followed by Hym, Het, Hom and Orth, Ara and For. The proportions of the other categories did not exceed 5%. Among beetles, the family of Scarabaeidae dominated with 55%. The genera we could identify were: *Onthophagus* sp., *Aphodius* sp. and *Rhizotrogus* sp. Two families of Hymenoptera were most commonly consumed: Formicidae 29.09%, in which we determined *Camponotus* sp., *Tapinoma* sp., *Messor* sp., *Crematogaster* sp., *Aphenogaster depilis*, and Ichneumonidae (21.82%). For Heteroptera, the most important family was Pentatomidae with 51.52%: *Sciocoris* sp., *Sehirus* sp. and *Aelia* sp. were identified. For Homoptera, the Cicadellidae (73.91%) family was the most often consumed and the genera identified were: *Eupelix* sp. and *Cicadella* sp. Regarding Orthoptera, Acrididae were highly consumed (86.96%), and the genera and species identified were: *Calliptamus* sp., *Omocestus* sp., *Pezottetix giornae*, *Dociostaurus jagoi jagoi* and *Thysiocetrus littoralis*.

In *P. vaucheri* the two most abundant categories (OTUs) had similar proportions: Col and Hom, and were followed by Ara, Hym, Orth, For and Dip. The proportions of the other categories did not exceed 5%. For Coleoptera, most prey belonged to two families: Staphylinidae (32.79%) with two identified genera: *Quedius* sp. and *Philonthus* sp., and Scarabaeidae (19.67%) with only one determined genus: *Aphodius* sp. Among Homoptera, Cicadellidae (98.33%) were most commonly consumed

(only one prey belonged to Aphidiidae family), and recognized genera and species were: *Agallia* sp., *Eupelix* sp. and *Macrosteles septemnotatus*. The dominant families of Hymenoptera were: Formicidae (47.45%) with several genera and species that could be identified (*Pheidole pallidula*, *Tapinoma* sp., *Messor* sp., *Messor barbarus*, *Monomorium* sp. and *Camponotus* sp.) and Ichneumonidae (35.59%). Concerning Orthoptera, two families were ingested: Acrididae (58.62%) with several genera identified (*Calliptamus* sp., *Omocestus* sp., *Pezottetix giornae*, *Dociostaurus jagoi jagoi*, *Oedipoda* sp. and *Acrotylus* sp.) and Gryllidae (48.28%) for which we could identify two genera: *Gryllus* sp. and *Gryllulus* sp.

The occurrence of the different prey categories in both lizard species were in accordance with their relative abundance (Figure 1). However, Araneae formed an exception in their occurrence in both species (*P. vaucheri*: %*P* = 56.14%; *Ps. algirus*: %*P* = 37.21%) despite their low values of relative abundance.

Using the classification of Bigot and Bodot (1973) we see that Col and Het were constant preys in the diet of *Ps. algirus*. The common preys were Hym, Orth, Ara and For. Three categories were accidental, Hom, Lep and Dip. The other categories can be considered very accidental prey.

In the diet of *P. vaucheri*, only Aranea were constant. Six categories of prey were common: Col, Orth, For, Hym, Hom and Dip. Three categories were accidental: Het, Hem and Lep. The others can be considered very accidental. A significant positive correlation between relative abundance (%*N*) and the occurrence (%*P*) of prey groups was observed in both species (*Ps. algirus*: $r_s = 0.965$, $p < 0.0001$; *P. vaucheri*: $r_s = 0.942$, $p < 0.0001$).

Seasonal variation

No significant difference in the mean number of items per feces was observed between the two seasons (*Ps. algirus*: in spring: 5.40 ± 1.10 , in summer: 6.18 ± 0.84 ;

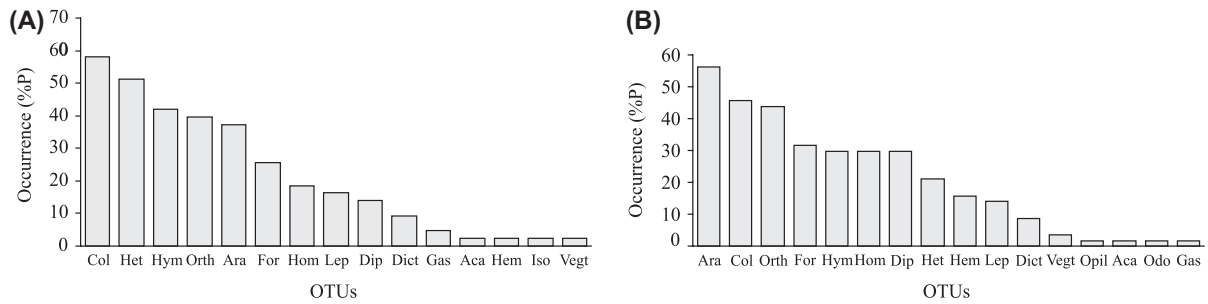


Figure 1. Occurrence of the different prey categories in the diet of the two species: (A) *Ps. algirus*, (B) *P. vaucheri*.

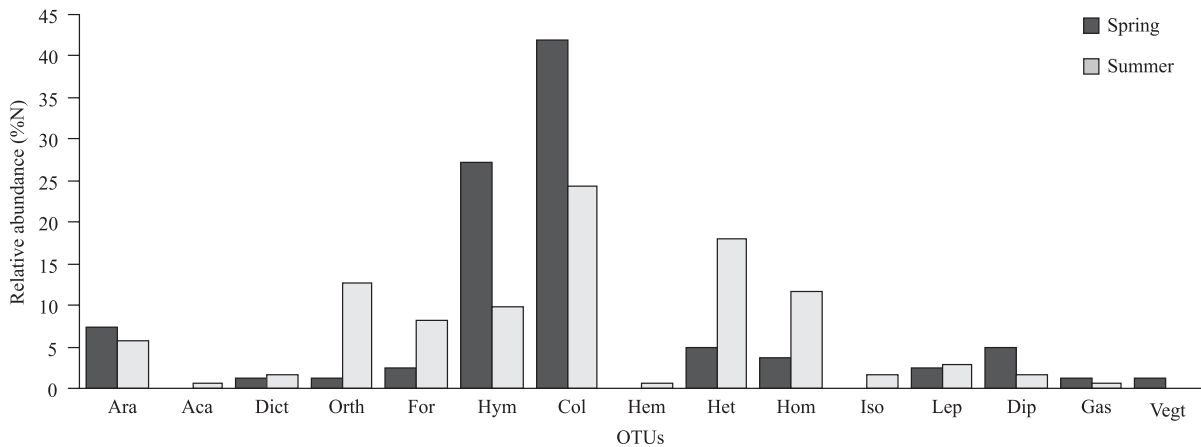


Figure 2. Seasonal variation among the different food categories in the diet of *Ps. algirus*.

Mann–Whitney U test: $Z = -1.04$, $p = 0.30$; *P. vaucheri*: in spring: 6.00 ± 0.72 , in summer: 5.12 ± 0.71 ; Mann–Whitney U test: $Z = 1.34$, $p = 0.18$). Within the categories of prey (OTUs), we observed a significant influence of seasonal variation on diet in both species in the Tala Guilef sector (*Ps. algirus* $\chi^2 = 42.94$, $p < 0.0001$, $df = 14$ and *P. vaucheri* $\chi^2 = 60.68$, $p < 0.0001$, $df = 15$).

Figure 2 illustrates the seasonal variation for *Ps. algirus*. In spring, this species showed a specialized diet ($B_A = 0.25$), and among the 12 OTUs ingested, two categories were strongly consumed: Col and Hym. However, in summer this species became an opportunist and the consumed prey among the 14 OTUs listed were: Col, Het, Orth, Hom, Hym, For. The other proportions were lower than 5%.

For *P. vaucheri*, the seasonal variation in different prey categories is illustrated in Figure 3. In spring, $B_A = 0.42$ and 12 OTUs were identified. The most consumed were: Col, Hym, Ara and Dip. In summer, we observed an important difference in the diet and a light reduction in trophic niche breadth ($B_A = 0.37$). Among the 15 OTUs consumed, the most common were: Hom, Orth, For, Ara and Col.

Discussion

Our results indicate that (1) the diet of both species is composed of arthropods and principally of insects and (2) both species express an opportunistic feeding behavior which is translated by a great number of prey

categories ingested and an important seasonal variation. Several authors have reported a dominance of arthropods in other populations of *Ps. algirus* (Arab and Doumandji 2003; Carretero and Llorente 1993; Castilla, Bauwens, and Llorente 1991; Diaz and Carrascal 1990; Mellado et al. 1975; Ortega-Rubio 1991; Pérez-Mellado 1982; Pérez-Quintero and Rubio-García 1997; Pollo and Perez-Mellado 1988; Rouag et al. 2007; Seva 1984; Valverde 1967) and in other species of the genus *Podarcis* (Adamopoulou, Valakos, and Pafilis 1998; Capula and Luiselli 1994; Capula, Luiselli, and Rugiero 1993; Carretero et al. 2006, 2010; Lo Cascio and Capula 2011; Maragou et al. 1996; Mou 1987; Rugiero 1994; Vincente, Araujo, and Barbault 1995). The only previous study on *P. vaucheri* (Carretero et al. 2006) revealed that the population of the Oukaïmeden Plateau in Morocco has a similar diet compared to what we describe here for Djurdjura, with a slight difference manifested by a high consumption of Diptera in the Moroccan population.

However, particular adaptations to periods of food scarcity can be observed in some populations, mainly in insular ecosystems. For example, Di Palma (1984) reported that vegetal matter and ants are the most commonly consumed prey by *Ps. algirus* on an island in the Sicily Channel. The same holds for lacertids of the genus *Podarcis* for which several populations in the Mediterranean region were studied and where herbivory and myrmecophagy are commonly observed on islands (Adamopoulou and Legakis 2002; Bombi

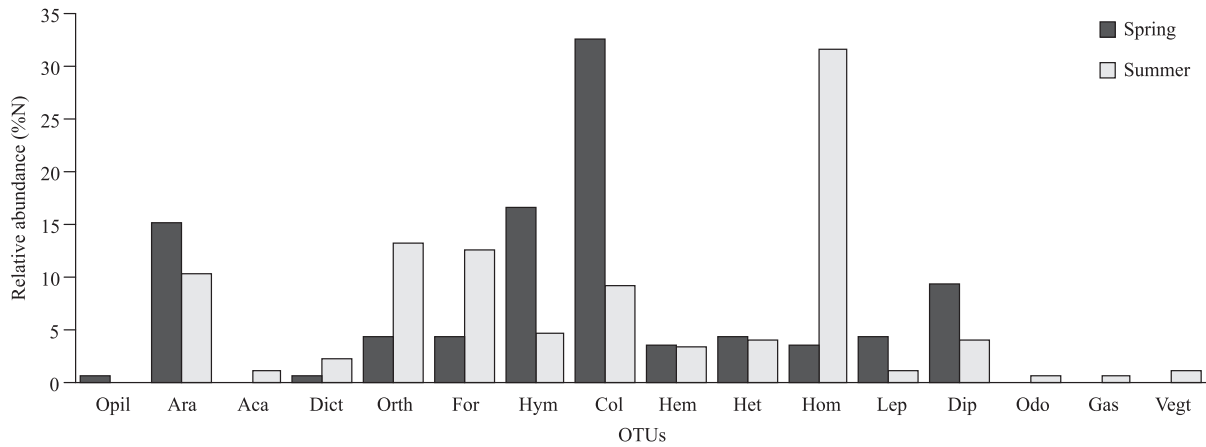


Figure 3. Seasonal variation among the different food categories in the diet of *P. vaucheri*.

et al. 2005; Carretero 2004; Carretero et al. 2010; Herrel et al. 2008; Ouboter 1981; Pérez-Mellado and Corti 1993; Van Damme 1999). Extreme diets, including cannibalism (Adamopoulou and Legakis 2002; Bombi et al. 2005; Burke and Mercurio 2002; Capula and Aloise 2011; Carretero et al. 2010; Pérez-Mellado and Corti 1993; Simović and Marković 2013; Žagar and Carretero 2012), oophagy (Brock, Donihue, and Pafilis 2014; Dappen 2011), and the consumption of marine prey (Castilla, Herrel, and Gosa 2009; Castilla, Vanhooydonck, and Catenazzi 2008; Lo Cascio and Pasta 2006), as well as small mammals and reptiles (Capula and Aloise 2011) are sometimes observed.

Many lacertids prefer Coleoptera (Adamopoulou, Valakos, and Pafilis 1998; Amat et al. 2008; Angelici, Luiselli, and Rugiero 1997; Carretero and Llorente 1993; Carretero et al. 2006; Castilla, Bauwens, and Llorente 1991; Hódar, Campos, and Rosales 1996; Lo Cascio and Capula 2011; Maragou et al. 1996; Perera et al. 2006; Pollo and Perez-Mellado 1988; Rouag, Berrahma, and Luiselli 2006; Rouag et al. 2007; Sagonas et al. 2015; Tatin et al. 2013; Thirion, Grillet, and Cheylan 2009; Vincente, Araujo, and Barbault 1995). This dominance is also seen in the species included in our study. It is, however, important to note that we included only adults in this study, which may explain the dominance of Coleoptera. According to Carretero et al. (2006), hard preys are more common in adults than in immature animals. Indeed, experimental studies have highlighted ontogenetic and sexual differences in bite force linked to jaw muscles mass (Herrel et al. 1999, 2001). This may provide a proximate explanation for the dominance of hard prey in adults.

Despite their difference in size, the comparison of consumed prey types revealed a high dietary overlap between the two species. However, this does not mean necessarily strong competition for dietary resources (Barbault 1981; Luiselli 2008; Znari et al. 2000), and this is for three reasons. First, we lack quantitative data on food availability. If food abundance is high, then animals may not compete for food resources despite strong similarities in diet. Second, we lack data on the use of the

other ecological niche dimensions (time and space). Shifts in daily activity cycles and difference in the use of microhabitats can allow coexistence even if dietary overlap is high. Finally, the difficulty to identify the ingested preys (especially insects and other arthropods) at the specific level. If the lizards consume different species (e.g. Coleoptera) and the identification is done only at the level of order, then the two species may show high dietary similarity at the level of Coleoptera (Luiselli 2008; Ortega-Rubio, González-Romero, and Barbault 1995) despite eating different species of Coleoptera.

Food opportunism constitutes an adaptation to the variation in environmental conditions. Seasonal variations in the prey consumed by the two lizards were prominent during the period of study. This is probably a response to seasonal changes in prey availability. Alternatively, this may reflect a reduction in activity during the hot months. The seasonal variation is driven by the strong consumption of Homoptera, Heteroptera and Orthoptera in summer when they are most common. Homoptera and Heteroptera are likely the easiest prey to catch, relatively soft, and become really abundant in summer (Mou 1987). Therefore, temperature can be considered an important abiotic factor that may impact diet in lizards (Tracy and Christian 1986).

The analysis of seasonal variation also shows an important difference in the feeding strategies of the two lizards. *Podarcis vaucheri* presents an eclectic diet, variable over time and consuming principally the available prey. This may allow this species to reduce the energy used in its search for food. This is reminiscent of an 'optimal foraging' approach, defined as the difference between energetic contribution of prey and expended energy by predator to catch and ingest it, relative to the time needed to capture a prey (Schoener 1971). This strategy was also met in the ocellated lizard *Timon pater* in Oléron Island (France) (Thirion, Grillet, and Cheylan 2009). But Lo Cascio and Capula (2011) describe a selective predation in *Podarcis raffonei*, endemic to the Aeolian island (Aeolian Archipelago, Sicily).

In contrast, *Ps. algirus* presents a more specialist diet in spring, concentrated essentially on Coleoptera and Hymenoptera, despite the abundance of prey typical of Mediterranean ecosystems during this period (Perera et al. 2006). This corresponds to a model in which certain predators tend to specialize when trophic resources become abundant in environment by searching profitable and common prey (Amat et al. 2008; Mou 1987). In summer, this species maintains Coleoptera as the most consumed prey, but responds to changes in invertebrate populations and secondarily consumes Heteroptera, Orthoptera and Homoptera. In several species of lacertidae, Coleoptera are selected in spite of the seasonal variations in food availabilities (Maragou et al. 1996; Mou 1987; Vincente, Araujo, and Barbault 1995). But other food strategies were observed in other populations of *Ps. algirus*. It is the case in Huelva (Spain), where this species shows an eclectic mode which coincides with the changes of the trophic availabilities (Pérez-Quintero and Rubio-García 1997). Also, to compensate the lack of water in summer, this species consumed great amounts of Homoptera and Heteroptera in the province of Salamanca in Spain (Pollo and Perez-Mellado 1988) and insect's larvae in Madrid (Ortega-Rubio 1991).

In spite of a clear difference in their diet, the comparison of the mean number of items by feces indicates that the difference between the two seasons in the number of prey eaten is not significant. This suggests that despite the seasonal change in the prey availability, this site does not present food restrictions. The greater consumption of terrestrial prey like Coleoptera, spiders, Hymenoptera, Homoptera, Heteroptera, ants, and Orthoptera by these two lizards suggests an active hunting strategy typical of most Mediterranean lacertids.

Our results also indicate a low consumption of ants, and their role is only secondary. It seems that myrmecophagy is associated to poor environments with few trophic resources (Carretero 2004; Maragou et al. 1996), as in arid and desert areas (Znari and El Mouden 1997; Znari et al. 2000), or in insular populations where this was interpreted as the result of a long-term evolution (Carretero 2004; Pérez-Mellado and Corti 1993). This strategy can reduce the foraging cost thanks to the gregarious behavior of ants, and thus may compensate for their weak profitability and noxiousness (Carretero 2004; Mella et al. 2010; Pérez-Mellado and Corti 1993; Pollo and Perez-Mellado 1988, 1991).

The consumption of the plants is also negligible at our study site. This may be explained by an important availability of invertebrate prey in this area. Vegetable matter typically provides less energy compared to animal prey and is difficult to assimilate (Bombi et al. 2005; Cooper and Vitt 2002). Herbivory is most commonly observed in insular Mediterranean lacertids or in species in isolated areas characterized by low food availability at least during some seasons (Ouboter

1981; Pérez-Mellado and Corti 1993; Van Damme 1999).

This study enabled us to elucidate a part of the ecology of two lacertid lizards living in sympatry. However, our results do not allow us test the hypothesis of a trophic competition between these species due to a lack of data on prey availability. Nevertheless, our data do suggest that the feeding strategy and trophic niche of these two lizards are determined by the environmental conditions and ecological needs rather than by interactions of competition as is suggested by the seasonal changes in diet. Future studies examining food availability and temporal and spatial aspects of the niche are needed to better understand how these species are able to coexist despite their close phylogenetic and morphological proximity.

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References

- Adamopoulou, C., and A. Legakis. 2002. "Diet of a Lacertid Lizard (*Podarcis milensis*) in an Insular Dune Ecosystem." *Israel Journal of Zoology* 48: 207–219.
- Adamopoulou, C., E. D. Valakos, and P. Pafilis. 1998. "Summer Diet of *Podarcis milensis*, *P. gageae* and *P. erhardii* (Sauria: Lacertidae)." *Bonner Zoologische Beiträge* 48: 275–282.
- Amat, F., V. Pérez-Mellado, J. Á. Hernández-Estévez, and T. G. Díez. 2008. "Dietary Strategy of a Pyrenean Lizard, *Iberolacerta aurelioi*, Living in a Poor Resources Alpine Environment." *Amphibia-Reptilia* 29: 329–336.
- Angelici, F. M., L. Luiselli, and L. Rugiero. 1997. "Food Habits of the Green Lizard, *Lacerta bilineata*, in Central Italy and a Reliability Test of Faecal Pellet Analysis." *Italian Journal of Zoology* 64: 267–272.
- Arab, K., and S. E. Doumandji. 2003. "Etude du regime alimentaire de la Tarente de Mauritanie *Tarentola mauritanica* (Linné. 1758) (Gekkonidae) et le psammodrome algire *Psammodromus algirus* (Linné. 1758) (Lacertidae) dans un milieu sub-urbain pres d'Alger [Diet of the Common Wall Gecko *Tarentola mauritanica* (Linné, 1758) (Gekkonidae) and the Algerian sand lizard *Psammodromus algirus* (Linné, 1758) (Lacertidae) in a Suburban Area Near Algiers]." *Bulletin de la Société Herpétologique de France* 106: 10–16.
- Arnold, E. N. 1987. "Resource Partition among Lacertid Lizards in Southern Europe." *Journal of Zoology* 1: 739–782.
- Barbault, R. 1981. *Ecologie des populations et des peuplements: des théories aux faits* [Ecology of Populations and Communities: Theories to the Facts]. Paris: Masson.
- Bigot, L., and P. Bodot. 1973. "Contribution à l'étude biocenotique de la garrigue à *Quercus coccifera* – Composition biotique du peuplement des invertébrés [Contribution to the Biocenotic Study of *Quercus Coccifera* Garrigue - biotic Composition of Invertebrate Community]." *Vie et Milieu* 23: 229–249.

- Bombi, P., L. Vignoli, R. Scalera, and M. A. Bologna. 2005. "Food Habits of *Podarcis filfolensis* (Reptilia, Lacertidae) on a Small Mediterranean Island during the Dry Season." *Amphibia-Reptilia* 26: 412–417.
- Brock, M. K., M. C. Donihue, and P. Pafilis. 2014. "New Records of Frugivory and Ovophagy in *Podarcis* (Lacertidae) Lizards from East Mediterranean Islands." *Northwestern Journal of Zoology* 10: 223–225.
- Burke, R. L., and R. J. Mercurio. 2002. "Food Habits of a New York Population of Italian Wall Lizards, *Podarcis sicula* (Reptilia, Lacertidae)." *The American Midland Naturalist* 147: 368–375.
- Capula, M., and G. Aloise. 2011. "Extreme Feeding Behaviours in the Italian Wall Lizard, *Podarcis siculus*." *Acta Herpetologica* 6: 11–14.
- Capula, M., and L. Luiselli. 1994. "Resource Partitioning in a Mediterranean Lizard Community." *Bolletino di Zoologia* 61: 173–177.
- Capula, M., L. Luiselli, and L. Rugiero. 1993. "Comparative Ecology in Sympatric *Podarcis muralis* and *P. sicula* (Reptilia: Lacertidae) from the Historical Centre of Rome: What about Competition and Niche Segregation in an Urban Habitat?" *Bolletino di Zoologia* 60: 287–291.
- Carranza, S., D. J. Harris, E. N. Arnold, V. Batista, and J. P. Gonzalez de la Vega. 2006. "Phylogeography of the Lacertid Lizard, *Psammmodromus algirus*, in Iberia and across the Strait of Gibraltar." *Journal of Biogeography* 33: 1279–1288.
- Carretero, M. A. 2004. "From set menu to a la carte. Linking Issues in Trophic Ecology of Mediterranean Lacertids." *Italian Journal of Zoology* 71: 121–133.
- Carretero, M. A. 2008. "An Integrated Assessment of a Group with Complex Systematics: The Iberomaghrebian Lizard Genus *Podarcis* (Squamata, Lacertidae)." *Integrative Zoology* 3: 247–266.
- Carretero, M. A., and G. A. Llorente. 1993. "Feeding of Two Sympatric Lacertids in a Sandy Coastal Area (Ebro Delta, Spain)." In *Lacertids of the Mediterranean Region. A Biological Approach*, edited by W. Böhme, V. Pérez-Mellado, E. Valakos, and P. Maragou, 155–172. Athens: Hellenic Zoological Society.
- Carretero, M. A., P. Lo Cascio, C. Corti, and S. Pasta. 2010. "Sharing Resources in a Tiny Mediterranean Island? Comparative Diets of *Chalcides ocellatus* and *Podarcis filfolensis* in Lampione." *Bonn Zoological Bulletin* 57: 111–118.
- Carretero, M. A., A. Perera, D. J. Harris, V. Batista, and C. Pinho. 2006. "Spring Diet and Trophic Partitioning in an Alpine Lizard Community from Morocco." *African Zoology* 41: 113–122.
- Carretero, M. A., V. Roca, S. Larbes, A. Ferrero, and F. Jorge. 2011. "Intestinal Helminth Parasites of Wall Lizards, *Podarcis vaucheri* Complex (Sauria: Lacertidae) from Algeria." *Journal of Herpetology* 45: 385–388.
- Castilla, A. M., D. Bauwens, and G. A. Llorente. 1991. "Diet Composition of the Lizard *Lacerta lepida* in Central Spain." *Journal of Herpetology* 25: 30–36.
- Castilla, A. M., A. Herrel, and A. Gosa. 2009. "Marine Prey in the Diet of *Podarcis atrata* from the Columbretes Islands." *Munibe* 57: 187–190.
- Castilla, A. M., B. Vanhooydonck, and A. Catenazzi. 2008. "Feeding Behaviour of the Columbretes Lizard *Podarcis atrata*, in Relation to Isopoda (Crustaceae) Species: *Ligia italica* and *Armadillo officinalis*." *Belgian Journal of Zoology* 138: 146–148.
- Cooper Jr., W. E., and L. J. Vitt. 2002. "Distribution, Extent, and Evolution of Plant Consumption by Lizards." *Journal of Zoology* 257: 487–517.
- Dappen, N. 2011. "Cold-blooded Cannibals. Observations on Cannibalistic Egg Eating and Predation on Juveniles within *Podarcis pityusensis*." www.lacerta.de art. 113.
- Di Palma, M. G. D. 1984. "Régime alimentaire de *Psammmodromus algirus* (Reptilia, Lacertidae) dans une population insulaire du canal de Sicile [The Diet of *Psammmodromus Algirus* (Reptilia, Lacertidae) in an Insular Population of the Sicily Channel]." *Revue d'Ecologie (Terre et Vie)* 39: 225–230.
- Diaz, J. A., and L. M. Carrascal. 1990. "Prey Size and Food Selection of *Psammmodromus algirus* (Lacertidae) in Central Spain." *Journal of Herpetology* 24: 342–347.
- Fonseca, M. M., J. C. Brito, O. S. Paulo, M. A. Carretero, and D. J. Harris. 2009. "Systematic and Phylogeographical Assessment of the *Acanthodactylus erythrurus* Group (Reptilia: Lacertidae) Based on Phylogenetic Analyses of Mitochondrial and Nuclear DNA." *Molecular Phylogenetics and Evolution* 51: 131–142.
- Fonseca, M. M., J. C. Brito, H. Rebelo, M. Kalboussi, S. Larbes, M. A. Carretero, and D. J. Harris. 2008. "Genetic Variation among Spiny-Footed Lizards in the *Acanthodactylus pardalis* Group from North Africa." *African Zoology* 43: 8–15.
- Hamdine, W. H., M. Thévenot, M. Sellami, and K. De Smet. 1993. "Régime alimentaire de la Genette (*Genetta genetta* Linné, 1758) dans le Parc national du Djurdjura, Algérie [Feeding Ecology of the Genet (*Genetta genetta* Linné, 1758) in Djurdjura National Park, Algeria]." *Mammalia* 57: 9–18.
- Herrel, A., K. Huyghe, B. Vanhooydonck, T. Backeljau, K. Breugelmans, I. Grbac, R. Van Damme, and D. J. Irschick. 2008. "Rapid Large-scale Evolutionary Divergence in Morphology and Performance Associated with Exploitation of a Different Dietary Resource." *Proceedings of the National Academy of Sciences* 105: 4792–4795.
- Herrel, A., L. Spithoven, R. Van Damme, and F. De Vree. 1999. "Sexual Dimorphism of Head Size in *Gallotia galloti*: Testing the Niche Divergence Hypothesis by Functional Analyses." *Functional Ecology* 13: 289–297.
- Herrel, A., R. Van Damme, B. Vanhooydonck, and F. D. Vree. 2001. "The Implications of Bite Performance for Diet in Two Species of Lacertid Lizards." *Canadian Journal of Zoology* 79: 662–670.
- Hódar, J. A., F. Campos, and B. A. Rosales. 1996. "Trophic Ecology of the Ocellated Lizard *Lacerta lepida* in an Arid Zone of Southern Spain: Relationships with Availability and Daily Activity of Prey." *Journal of Arid Environments* 33: 95–107.
- Horn, H. S. 1966. "Measurement of "Overlap" in Comparative Ecological Studies." *The American Naturalist* 100: 419–424.
- Kalioztopoulou, A., J. C. Brito, M. A. Carretero, S. Larbes, and D. J. Harris. 2008. "Modelling the Partially Unknown Distribution of Wall Lizards *Podarcis* in North Africa: Ecological Affinities, Potential Areas of Occurrence and Methodological Constraints." *Canadian Journal of Zoology* 86: 992–1001.
- Kalioztopoulou, A., M. A. Carretero, and G. A. Llorente. 2012. "Morphology of the *Podarcis* Wall Lizards (Squamata: Lacertidae) from the Iberian Peninsula and North Africa: Patterns of Variation in a Putative Cryptic Species Complex: Morphology of Iberian *Podarcis*." *Zoological Journal of the Linnean Society* 164: 173–193.
- Kalioztopoulou, A., C. Pinho, D. J. Harris, and M. A. Carretero. 2011. "When Cryptic Diversity Blurs the Picture: A Cautionary Tale from Iberian and North African *Podarcis* Wall Lizards." *Biological Journal of the Linnean Society* 103: 779–800.
- Krebs, C. 1999. *Ecological Methodology*. New York: Addison Wesley Longman.
- Larbes, S., M. A. Carretero, and J. C. Brito. 2007. "Contribution à l'étude de la variabilité phénotypique du lézard des murailles *Podarcis* Sp. dans deux régions d'Algérie du nord (Kabylie et Belezma) [Contribution to the Study of the Phenotypic Variability of the Wall Lizard *Podarcis* Sp. in two Regions of Northern Algeria (Kabylie and Belezma)]." In *Abstract Book 'First Mediterranean Herpetological Congress' 16–20 Avril 2007*, edited by T. Slimani, 91. Marrakech.

- Lima, A., C. Pinho, S. Larbes, M. A. Carretero, J. C. Brito, and D. J. Harris. 2009. "Relationships of *Podarcis* Wall Lizards from Algeria Based on MtDNA Data." *Amphibia-Reptilia* 30: 483–492.
- Lo Cascio, P., and M. Capula. 2011. "Does Diet in Lacertid Lizards Reflect Prey Availability? Evidence for Selective Predation in the Aeolian Wall Lizard, *Podarcis raffonei* (Mertens, 1952) (Reptilia, Lacertidae)." *Biodiversity Journal* 2: 89–96.
- Lo Cascio, P., and S. Pasta. 2006. "Preliminary Data on the Biometry and the Diet of a Microinsular Population of *Podarcis wagleriana* (Reptilia: Lacertidae)." *Acta Herpetologica* 1: 147–152.
- Luiselli, L. 2008. "Do Lizard Communities Partition the Trophic Niche? A Worldwide Meta-analysis Using Null Models." *Oikos* 117: 321–330.
- Maragou, P., E. D. Valakos, Z. Giannopoulos, A. Stauropoulou, and B. P. Chondropoulos. 1996. "Feeding Ecology of *Podarcis peloponnesiaca* (Sauria: Lacertidae) in Spring." *Herpetozoa* 9: 105–110.
- Mella, J., C. Tirado, A. Cortés, and M. A. Carretero. 2010. "Seasonal Variation of Prey Consumption by *Liolaemus barbarae*, a Highland Lizard Endemic to Northern Chile." *Animal Biology* 60: 413–421.
- Mellado, J., F. Amores, F. Parreño, and F. Hiraldo. 1975. "The Structure of a Mediterranean Lizard Community." *Doñana, Acta Vertebrata* 2: 145–160.
- Mou, Y. 1987. "Ecologie trophique d'une population de lézards des murailles *Podarcis muralis* dans l'ouest de la France [Trophic Ecology of Population of Wall Lizards *Podarcis Muralis* in the West of France]." *Revue d'Ecologie (Terre et Vie)* 42: 81–100.
- Ortega-Rubio, A. 1991. "Trophic Partitioning and Community Organization in a Guild of Lizards in La Sierra De Guadarrama, Spain." *Ekologia* 10: 19–29.
- Ortega-Rubio, A., A. González-Romero, and R. Barbault. 1995. "Food Analysis and Resource Partitioning in a Lizard Guild of the Sonoran Desert, Mexico." *Journal of Arid Environments* 29: 367–382.
- Ouboter, P. E. 1981. "The Ecology of the Island-Lizard *Podarcis siculasalfii*." *Amphibia-Reptilia* 2: 243–257.
- Perera, A., V. Pérez-Mellado, M. A. Carretero, and D. J. Harris. 2006. "Variation between Populations in the Diet of the Mediterranean Lizard *Lacerta perspicillata*." *Herpetological Journal* 16: 107–113.
- Pérez-Mellado, V. 1982. "Estructura en una taxocenosis de Lacertidae (Sauria, Reptilia) del Sistema Central [Structure of a Lacertidae Taxocenosis (Sauria, Reptilia) of the Sistema Central]." *Mediterránea. Serie De Estudios Biológicos* 6: 39–64.
- Pérez-Mellado, V., and C. Corti. 1993. "Dietary Adaptations and Herbivory in Lacertid Lizards of the Genus *Podarcis* from Western Mediterranean Islands (Reptilia: Sauria)." *Bonner Zoologische Beiträge* 44: 193–220.
- Pérez-Quintero, J. C., and J. C. Rubio-García. 1997. "Feeding of *Psammmodromus algirus* (L.) (Sauria, Lacertidae) in Coastal Areas of Huelva (SW Spain)." *Doñana, Acta Vertebrata* 24: 3–26.
- Pianka, E. R. 1981. "Competition and Niche Theory." In *Theoretical Ecology: Principles and Applications*, edited by R. M. May, 167–196. London: Blackwell.
- Pollo, C. J., and V. Perez-Mellado. 1988. "Trophic Ecology of a Taxocenosis of Mediterranean Lacertidae." *Ecologia Mediterranea* 14: 131–147.
- Pollo, C. M., and V. Pérez-Mellado. 1991. "An Analysis of a Mediterranean Assemblage of Three Small Lacertid Lizards in Central Spain." *Acta Oecologica* 12: 655–671.
- Rouag, R., I. Berrahma, and L. Luiselli. 2006. "Food Habits and Daily Activity Patterns of the North African Ocellated Lizard *Timon pater* from Northeastern Algeria." *Journal of Natural History* 40: 1369–1379.
- Rouag, R., H. Djilali, H. Gueaiche, and L. Luiselli. 2007. "Resource Partitioning Patterns between Two Sympatric Lizard Species from Algeria." *Journal of Arid Environments* 69: 158–168.
- Rugiero, L. 1994. "Food Habits of the Ruin Lizard, *Podarcis sicula* (Rafinesque-Schmaltz, 1810), from a Coastal Dune in Central Italy." *Herpetozoa* 7: 71–73.
- Sagonas, K., P. Pafilis, P. Lymberakis, and E. D. Valakos. 2015. "Trends and Patterns in the Feeding Ecology of the Widespread Balkan Green Lizard *Lacerta trilineata* (Squamata: Lacertidae) in Insular and Continental Greece." *North-Western Journal of Zoology* 11: 117–126.
- Schoener, T. W. 1971. "Theory of Feeding Strategies." *Annual Review of Ecology and Systematics* 2: 369–404.
- Seva, E. 1984. "Reparto de recursos en dos especies psammofilas de saurios: *Acanthodactylus erythrurus* y *Psammmodromus algirus*. Arenal costero de Alicante [Resource Sharing Between Two Psammophile Species of Lizards: *Acanthodactylus Erythrurus* and *Psammmodromus Algirus*. Arenal Coast of Alicante]." *Mediterránea. Serie De Estudios Biológicos* 7: 5–25.
- Simović, A., and A. Marković. 2013. "A Case of Cannibalism in the Common Wall Lizard, *Podarcis muralis*, in Serbia." *Hyla* 2013: 40–41.
- Sneath, P. H. A., and R. R. Sokal. 1973. *Numerical Taxonomy*. San Francisco, CA: Freeman.
- Tatin, L., J.-D. Chapelin-Viscardi, J. Renet, E. Becker, and P. Ponel. 2013. "Patron et variations du regime alimentaire du lézard ocelle *Timon lepidus* en milieu steppique mediterraneen semi-aride (plaine de Crau, France) [Diet Pattern and Variations of Ocellated Lizard *Timon Lepidus* in a Mediterranean Steppe Area (Crau Plain, France)]." *Revue d'Ecologie (Terre et Vie)* 68: 47–58.
- Thirion, J.-M., P. Grillet, and M. Cheylan. 2009. "Composition et variation saisonniere du regime alimentaire du lézard ocelle *Timon lepidus* sur l'île d'Oléron (France) à partir des feces [Composition and Seasonal Variation of the Diet of the Ocellated Lizard *Timon Lepidus* on Oleron Island (France) Through Scat Analysis]." *Revue d'Ecologie (Terre et Vie)* 64: 239–250.
- Tracy, C. R., and K. A. Christian. 1986. "Ecological Relations among Space, Time, and Thermal Niche Axes." *Ecology* 67: 609–615.
- Valverde, J. A. 1967. *Estructura de una comunidad mediterránea de vertebrados terrestres* [Structure of a Mediterranean Community of Terrestrial Vertebrates]. Monografías de Ciencias Moderna, 76. Madrid: CSIC. Estación Biológica de Doñana, 1.
- Van Damme, R. 1999. "Evolution of Herbivory in Lacertid Lizards: Effects of Insularity and Body Size." *Journal of Herpetology* 33: 663–674.
- Verdú-Ricoy, J., S. Carranza, A. Salvador, S. D. Busack, and J. A. Díaz. 2010. "Phylogeography of *Psammmodromus algirus* (Lacertidae) Revisited: Systematic Implications." *Amphibia-Reptilia* 31: 576–582.
- Vincente, L. A., P. R. Araujo, and R. Barbault. 1995. "Écologie trophique de *Podarcis bocagei berlengensis* et de *Lacerta lepida* (Sauria, Lacertidae) sur l'île de Berlenga (Portugal) [Trophic Ecology of *Podarcis Bocagei Berlengensis* and *Lacerta lepida* (Sauria, Lacertidae) on the Island of Berlenga (Portugal)]." *Revue d'Ecologie (Terre et Vie)* 50: 317–351.

- Žagar, A., and M. A. Carretero. 2012. "A Record of Cannibalism in *Podarcis muralis* (Laurenti, 1768) (Reptilia, Lacertidae) from Slovenia." *Herpetology Notes* 5: 211–213.
- Zaime, A., and J.-Y. Gautier. 1989. "Comparaison des regimes alimentaires de trois especes sympatriques de Gerbillidae en milieu saharien, au Maroc [The Diet of Three Sympatric Gerbillid Species in a Saharan Environment, Morocco]." *Revue d'Ecologie (Terre et Vie)* 44: 153–163.
- Znari, M., and E. El Mouden. 1997. "Seasonal Changes in the Diet of Adult and Juvenile *Agama impalearis* (Lacertilia: Agamidae) in the Central Jbilet Mountains, Morocco." *Journal of Arid Environments* 37: 403–412.
- Znari, M., E. H. El Mouden, H. Benfaida, and A. Boumezzough. 2000. "Partage des ressources spatiales et trophiques au sein d'un peuplement de lézards insectivores des Jbilet centrales (Maroc occidental) [Sharing Space and Food Resources in an Insectivorous Lizards Community of Central Jbilet (Western Morocco)]." *Revue d'Ecologie (Terre et Vie)* 55: 141–160.