

VARIATION BETWEEN POPULATIONS IN THE DIET OF THE MEDITERRANEAN LIZARD *LACERTA PERSPICILLATA*

A. PERERA¹, V. PÉREZ-MELLADO¹, M. A. CARRETERO² AND D. J. HARRIS²

¹*Departamento de Biología Animal, Facultad de Biología, Universidad de Salamanca, Campus Unamuno s/n. 37071 Salamanca, Spain*

²*CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, 4485-661 Vairão, Portugal*

We examined the diet of *Lacerta perspicillata* in populations from different localities, thus providing the first quantitative data on the diet of this species. Five continental populations in Morocco located at different altitudes and an introduced insular population were analysed during April. Our results confirm that *L. perspicillata* is an insectivorous species and those found at medium altitudes with comparable ecological conditions in Morocco have a similar diet. In Taza, however, both sympatric *L. perspicillata* forms have different diets. The most varied diets were observed at high altitude and in insular populations. Local diet variability is probably more related to different ecological conditions and, consequently, changing trophic availability than to lizard body size or other morphological or behavioural constraints. Further studies, including studies on trophic availability and seasonal variation, could confirm our preliminary results on local differences in the dietary habits of this species and the potential role of insularity.

Key words: altitude, feeding ecology, insularity, Lacertidae

INTRODUCTION

L. perspicillata (Duméril & Bibron, 1839) is a small North African lacertid lizard endemic to the Western Maghreb (Bons & Geniez, 1996) presently distributed across Morocco (Medium and High Atlas, Oulmés Plateau, Debdou Mountains and some introduced populations in the Atlantic Coast) and the north-west of Algeria (Oran and Western area of the Tellian Atlas; Mateo, 1997). At an indeterminate time, it was introduced in Menorca (Balearic Islands, Spain) constituting the only non-African stable population and one of the only two insular localities of its distribution (Perera, 2002). In Morocco, this species lives in subhumid, humid, semiarid and arid Mediterranean areas from sea level up to 2800 m altitude while in Menorca it is not present above 100 m (Bons & Geniez, 1996; Perera, 2003). *L. perspicillata* is a small, very agile, climbing species that prefers rocky areas like walls, cliffs and big stones with small crevices. Despite being a relatively common species, studies concerning its biology and, in particular its feeding ecology, are very scarce (see Richter, 1986 and Perera, 2003 for review). A recent study on an introduced insular population in Menorca (Perera & Pérez-Mellado, unpublished) shows that *L. perspicillata* is insectivorous feeding mainly on terrestrial prey like beetles, spiders, ants, and less frequently flying prey like bees. Moreover, they eat fleshy fruits when available. However, we lack quantitative data about diet from natural African populations and information is reduced to field observations describing the consumption of small insects, ants, grubs, spiders, snails (Richter, 1986; Schleich *et al.*, 1996), and fruits (Doumergue, 1901).

The aim of our study is to provide the first quantitative data about the feeding ecology of the Moroccan lizard in its native area of distribution and to compare it with the diet of an introduced insular population. To do this, we analysed lizards from five populations occupying distinct localities within its natural range in Morocco at different altitudes (Oukaïmeden, in the upper limit of its altitudinal range, and four localities at medium altitude: Debdou, Balcon d'Ito, Taza and Caves of Chiker) and one insular introduced population in Menorca, all studied during the spring period.

MATERIAL AND METHODS

Lizards from Morocco were collected during April 2003 and 2004 in five localities (Fig. 1): Oukaïmeden is a high mountain lake in the upper limit of the altitudinal distribution of the species (2650 m. a.s.l.) with typical subalpine vegetation; Gaada of Debdou is a subhumid medium high area (1500 m. a.s.l.) with low shrub vegetation; and Balcon d'Ito (1640 m. a.s.l.), Taza (1265 m. a.s.l.) and the Caves of Chiker (1480 m. a.s.l.) - the latter 15 km away from Taza - have denser vegetation dominated by *Quercus* sp. and shrublands (Fig. 1). Insular samples were also collected during April 2003 near Ciutadella (Menorca Island, Balearic Islands, Spain; Fig. 1) in an old disused quarry with typical Mediterranean shrub vegetation located at 50 m. a.s.l.

It should be noted that this taxon is undergoing a systematic revision. Bons (1968) described three different subspecies based on body size, coloration and body pattern: *L. p. perspicillata*, *L. p. chabanaudi* and *L. p. pellegrini*. However, recent phylogeographic analyses of the species, including some of the populations comprised in this study (Taza, Debdou and Menorca), show that subspecific groupings do not match with genetically identified clades (Harris *et al.*, 2003). Moreover, two different subspecies (*L. p. chabanaudi* and *L. p.*

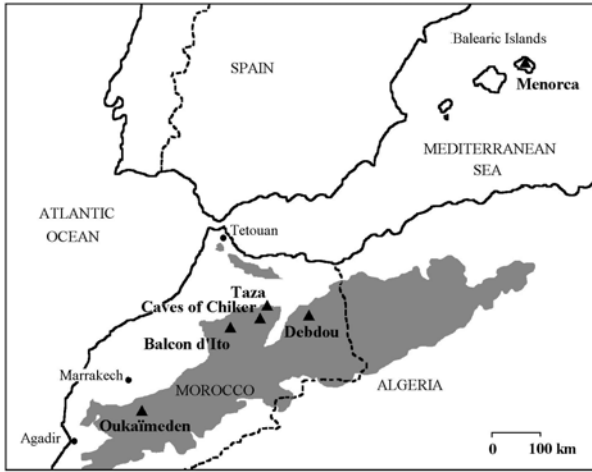


FIG. 1. Study area. Localities included in this study are indicated by triangles.

pellegrini) found syntopically in one of those localities (Taza) belong to two genetically different clades (Harris *et al.*, 2003). For this reason, we have analysed separately those two forms named hereafter as “Taza *chabanaudi*” and “Taza *pellegrini*”.

Lizards were caught with a noose, sexed and the snout-vent length (SVL) and head width (HW) measured. Faecal pellets were obtained during handling, so they could be individually assigned. There are no published data about minimal body size at sexual maturity in this species. In Menorca, sexual maturity is attained during the first year at 38.5 mm and 40.0 mm of SVL in females and males respectively. Hence we used this measurement as the minimum body size for sexual maturity. We considered three different classes: 1=adult males, 2=adult females, 3=juveniles. Faeces were analysed in the laboratory through a binocular dissecting microscope. Remains were identified to the Order level, except Formicidae, which we separated from other Hymenoptera based on their non-flying aggregated behaviour. Animal prey were typologically grouped as flying (i.e. Diptera, Lepidoptera, Hymenoptera and Odonata) and terrestrial prey (all others). Intact body parts (Coleoptera elytra, Hymenoptera and Diptera wings and Homoptera and Heteroptera hemielytra) from faecal pellets were measured to the nearest 0.5 mm. Plant consumption was estimated as the percentage of vegetal matter with respect to the total amount of the pellet content.

We calculated occurrence, relative occurrence (frequency and percentage of individuals consuming a given item respectively), abundance and relative abundance (frequency and percentage of a prey item in relation to the total number of prey items respectively) for each prey type and population considered. Diet diversity was computed using the standardised version of *B* Levins's index of niche breadth (Levins, 1968), namely B_s (Hurlbert, 1978):

$$B_s = (B-1) / (n-1) = [(\sum p_j^2) - 1] / (n-1)$$

where p_j^2 is the fraction of items in the diet that are of food category j , and n 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).

As B_s cannot be compared across groups because of the lack of associated confidence intervals, we used a delete-one Jack-knife resampling procedure (Magurran, 1988). This method entails recalculating B_s missing out each sample in turn and generating pseudovalues (VP_i), which are normally distributed. Hence, VP_i were calculated for each group and then compared using an ANOVA. Duncan or Games-Howell *post-hoc* tests for homogeneous or heterogeneous variances respectively were computed to compare differences among pairs of means (Sokal & Rohlf, 1995).

Differences between localities in diet composition and frequencies of terrestrial and flying prey were analysed with a *G*-test. We grouped low frequency items with similar attributes or behaviour to get frequencies equal or higher than 1. However, in some cases expected frequencies were lower than 5, so we performed a Monte Carlo simulation with 1000 replications and 95% confidence interval. This randomisation method allows estimation of exact significance without relying on the assumptions of the asymptotic method, like expected frequencies higher than five (Sokal & Rohlf, 1995). Multiple comparisons were corrected using sequential Bonferroni adjustment (Holm, 1979) with the program MacBonferroni (©2002 by Marley W. Watkins). We calculated Morisita's index of similarity (Krebs, 1999) to compare diet between pairwise localities. We then used the similarities matrix to perform a multidimensional scaling (MDS) to show the relationships between localities (Manly, 1986).

Lizard body measurements (SVL and HW) and mean prey sizes were log-transformed to fit the normality and homoscedasticity assumptions. Differences between localities were analysed with an ANOVA or an ANCOVA when the dependent variable covaried with another one.

The degree of association between pairs of variables was analysed with a Pearson correlation. The significance level for all tests was $\alpha = 0.05$.

RESULTS

We analysed a total of 192 pellets, all of them individually identified. We found 878 arthropod prey grouped in 21 taxa (Table 1). We detected a low occurrence of other prey items, like plant (10 pellets) or reptile remains (1 pellet).

DIET COMPOSITION

The most common prey of the Moroccan lizard were Diptera, Coleoptera, Hymenoptera, Homoptera, Araneae and larvae (all of them >5% occurrence; Table 1). However, diet composition differed between populations ($G_{42,878} = 234.7$, $P < 0.001$). The plot of the

first two dimensions of the multidimensional scaling (MDS) clearly shows these differences (Fig. 2).

The diet composition of continental samples differed ($G_{35,687}=129.5, P<0.001$). Hence, the MDS plot defines a group formed by Balcon d'Ito, the Caves of Chiker and Debdou with a similar diet based on Diptera, Coleoptera and Hymenoptera ($G_{14,284}=16.7, P=0.357$) separated from Oukaïmeden, Taza and Menorca, the former being the most distinct mainland locality. Diet composition in Oukaïmeden includes a higher consumption of Coleoptera and lower Hymenoptera consumption (Table 1). Both forms from Taza have a clearly different composition ($G_{7,249}=15.5, P=0.038$; Fig. 2) with *Taza pellegrini* having a diet more similar to the populations of Balcon d'Ito and Caves of Chiker ($G_{14,284}=16.7, P=0.357$). Thus, *Taza chabanaudi* had a higher consumption of Isoptera, Hymenoptera and larvae, whereas *Taza pellegrini* ate more Diptera and other minor items (Table 1). Finally, lizards from Menorca displayed a different diet composition than lizards from the continental populations, (G -test, $G_{7,878}=105.2, P<0.001$), with Coleoptera as the most important prey, followed by Araneae and Homoptera (Table 1).

We detected sporadic consumption of plant matter in three mainland localities: Oukaïmeden (two pellets; <10% in both cases) Debdou (one pellet, <10%) and Taza (Table 1). The latter had higher plant consumption: six *pellegrini* form lizards (mean=33.3%; min-max=10-80% of the total pellet matter) and one *chabanaudi* form lizard (30% of the total pellet matter). Remains included small stems, fragments of gramineae or seed plums, but not fruits, often occurring in a very low proportion.

FLYING VS. TERRESTRIAL PREY

The Menorcan population had a more varied diet (18 taxa) with 87% of identified items corresponding to terrestrial prey. Continental populations fed, in general, on

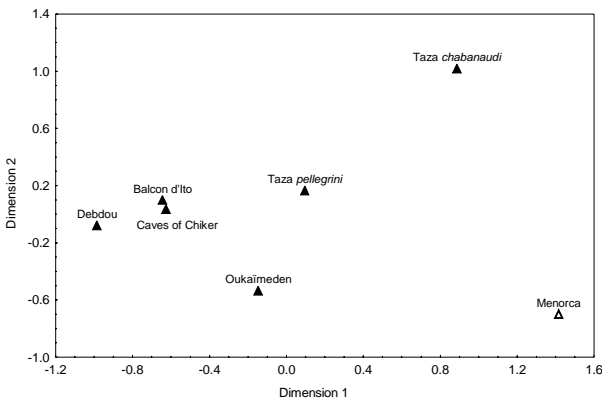


FIG. 2. Plot of *L. perspicillata* localities under study against the first two dimensions of the configuration produced by three-dimensional non-metric multidimensional scaling of a similarity matrix. Similarity matrix was performed using Morisita's index of similarity between two populations (Stress=0.001). The open symbol represents the insular population and solid symbols continental populations.

fewer prey types (10, except for *Taza chabanaudi* that fed on 14 prey types), but prey tended to be of the flying variety (Table 1). Proportions varied, however, between 69% in Debdou to 29% for the *Taza chabanaudi* form. The latter percentage was due mainly to the consumption of Isoptera by only one lizard.

DIET DIVERSITY

Adults and juveniles (One-way ANOVA: interaction - locality \times age: $F_{8,143}=1.4, P=0.198$), and males and females (interaction - locality \times sex: $F_{6,144}=2.1, P=0.057$) had similar diet diversity in the localities studied. Thus, we pooled them for further analyses. We found significant differences in niche breadth between localities (ANOVA: $F_{6,184}=5.3, P<0.001$; Table 1), the Debdou population being the most specialised and *Taza chabanaudi* the most generalist. A *post-hoc* Duncan test showed three homogeneous groups: (1) Oukaïmeden, Debdou, Menorca, *Taza pellegrini* and the Caves of Chiker; (2) Oukaïmeden, Menorca, *Taza pellegrini*, Caves of Chiker and Balcon d'Ito; and (3) *Taza pellegrini*, the Caves of Chiker, Balcon d'Ito and *Taza chabanaudi*. Hence, Oukaïmeden had similar B_s to other continental and insular localities, but *Taza chabanaudi* and Balcon d'Ito, *Taza pellegrini* and the Caves of Chiker populations had similar B_s but differed from other medium altitude localities, i.e., Balcon d'Ito and *Taza chabanaudi*. Insular B_s was similar to all continental populations except *Taza chabanaudi*.

PREY SIZE

We lack data from juveniles for some populations, and sample sizes did not allow comparisons between age or sex classes. Hence only adult lizards were considered in this analysis. Lizard snout-vent length (SVL) and head width (HW) varied between forms (SVL: $F_{2,151}=10.2, P<0.001$; HW: ANCOVA, $F_{2,150}=9.8, P<0.001$; in both analyses Games-Howell *post-hoc* test: *chabanaudi* with other groups $P<0.01$, other pairwise comparisons: $P>0.05$) and populations (SVL: $F_{6,147}=6.2, P<0.001$; HW: ANCOVA, $F_{6,147}=4.6, P<0.001$; Table 2). Considering all populations together, mean prey size was positively correlated with SVL ($r=0.238, P<0.01, n=118$) and HW ($r=0.276, P<0.01, n=118$) but considering each locality separately correlation between mean prey size and lizard measurements (SVL and HW) was not significant (correlation values in all cases $P>0.05$). However, we used them as covariates in subsequent prey size analyses. As results did not vary using SVL or HW, only results using HW are presented. After correcting for size, individuals from Menorca fed on smaller prey than those from continental populations, except those from Debdou and *Taza pellegrini* (ANCOVA, $F_{6,110}=2.4, P=0.032$; after a Duncan *post-hoc* test, two homogeneous groups: Menorca-Debdou-*Taza pellegrini*; Debdou-*Taza chabanaudi* - Oukaïmeden-Balcon d'Ito-Caves of Chiker; Table 2). Both forms from Taza fed on similar

TABLE 1. Diet analysis of faecal samples from *L. perspicillata* from Morocco [six populations, five localities: Oukaïmeden, Debdou, Balcon d'Ito, Taza (2 distinct populations) and Caves of Chiker in April 2003 and 2004], and Menorca (one population, April 2003). %P = relative incidence, %A = relative abundance, B_s = standardized diversity of Levins.

	Oukaïmeden		Balcon d'Ito		Taza <i>chabanaudi</i>		Taza <i>pellegrini</i>		Caves of Chiker		Debdou		Menorca	
	%P	%A	%P	%A	%P	%A	%P	%A	%P	%A	%P	%A	%P	%A
Gastropoda	-	-	5.9	1.4	-	-	4	1.8	16.7	5.6	-	-	-	-
Pseudoescorpionidae	-	-	-	-	-	-	4	0.9	-	-	-	-	1.9	0.5
Aranea	9.7	1.9	11.8	2.7	31.8	5.2	32	7	16.7	5.6	9.7	1.7	44.4	13.1
Acarina	-	-	-	-	-	-	-	-	-	-	-	-	1.9	1.6
Isopoda	-	-	-	-	-	-	-	-	-	-	-	-	11.1	3.1
Chilopoda	3.2	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Diplura	-	-	-	-	-	-	-	-	-	-	-	-	1.9	0.5
Orthoptera	-	-	-	-	-	-	-	-	-	-	-	-	20.4	6.3
Dictyoptera	3.2	0.6	-	-	-	-	4	0.9	-	-	-	-	7.4	2.1
Isoptera	-	-	-	-	4.5	14.1	-	-	-	-	9.7	4.6	1.9	0.5
Dermoptera	-	-	-	-	4.5	0.7	4	0.9	-	-	-	-	1.9	1.6
Homoptera	51.6	11	29.4	10.8	18.2	4.4	28	7	25	11.1	16.1	4	35.2	10.5
Heteroptera	32.3	8.4	11.8	2.7	-	-	16	3.5	16.7	5.6	-	-	3.7	1
Diptera	64.5	33.1	70.6	35.1	59.1	14.1	68	27.2	41.7	30.6	87.1	53.4	16.7	4.7
Trychoptera	-	-	-	-	-	-	-	-	-	-	3.2	0.6	-	-
Lepidoptera	-	-	-	-	-	-	4	0.9	8.3	2.8	-	-	3.7	1
Coleoptera	74.2	33.8	29.4	16.2	50	22.2	68	22.8	33.3	13.9	48.4	15.5	63	35.1
Hymenoptera	29	6.5	47.1	13.5	50	14.1	36	9.6	50	16.7	41.9	10.9	22.2	7.3
Formicidae	6.5	1.9	17.6	5.4	27.3	5.2	20	4.4	8.3	2.8	6.5	1.7	5.6	2.1
Indt. Arthrop.	9.7	1.9	29.4	6.8	13.6	2.2	12	2.6	16.7	5.6	32.3	6.3	16.7	5.2
Indt. Larvae	-	-	11.8	5.4	31.8	17.8	44	10.5	-	-	6.5	1.1	13	3.7
Indt. matter	12.9	-	11.8	-	-	-	4	-	-	-	29	-	5.6	-
Reptiles	-	-	5.9	-	-	-	-	-	-	-	-	-	-	-
Plant matter	6.5	-	-	-	4.5	-	24	-	-	-	3.2	-	-	-
%terrestrial	59.6	-	47.83	-	71.21	-	61.82	-	48.48	-	31.29	-	87.15	-
%flying	40.4	-	52.17	-	28.79	-	38.18	-	51.52	-	68.71	-	12.85	-
<i>n</i> items	10	-	10	-	10	-	14	-	10	-	10	-	18	-
<i>n</i> pellets	31	-	17	-	22	-	25	-	12	-	31	-	54	-
<i>B</i>	4.025	-	5.215	-	6.743	-	6.224	-	6	-	3.029	-	5.902	-
B_s	0.336	-	0.468	-	0.638	-	0.402	-	0.556	-	0.225	-	0.288	-

TABLE 2. Lizard body measurements (SVL and HW) and mean prey size consumed in localities under study.

	SVL(mm)		HW (mm)		Mean prey size (mm)	
	mean±SE	n	mean±SE	n	mean±SE	n
Oukaïmeden	58.115±1.243	26	9.502±0.291	26	3.915±0.263	23
Balcon d'Ito	58.767±3.222	15	9.703±0.546	15	3.839±0.358	12
Taza <i>chabanaudi</i>	53.050±2.749	20	8.740±0.480	20	3.686±0.351	14
Taza <i>pellegrini</i>	50.976±0.883	21	7.860±0.233	21	3.953±0.619	17
Caves of Chiker	51.375±1.920	12	7.579±0.311	12	3.826±0.868	6
Debdou	53.476±1.541	21	8.395±0.307	21	3.132±0.347	17
Menorca	47.692±0.787	39	7.813±0.183	39	2.602±0.257	29

mean size prey ($P>0.05$). We did not find a significant correlation between consumption of hard prey, such as Coleoptera and HW ($r=0.084$, $P=0.300$, $n=154$).

DISCUSSION

Previous observations on the diet of *L. perspicillata* in its native North African populations documented the consumption of snails, spiders, larvae and ants (Richter, 1986; Schleich *et al.*, 1996) suggesting that this species is insectivorous. However, Doumergue (1901) reported a lizard consuming fleshy fruits of *Rhamnus* sp. in Oran during August. On the other hand, a recent extensive study (Perera & Pérez-Mellado, unpublished) on diet composition in Menorca throughout the year confirms the insectivorous trend of this lizard in an introduced insular population and the tendency to consume fleshy fruits in the summer, as some authors previously noted (Mayol, 1985). In fact, our analysis on diet composition in continental and insular populations during the spring shows that in all cases *L. perspicillata* feeds mainly on insects such as Homoptera, Diptera, Coleoptera, Hymenoptera, larvae and other invertebrates like Araneae. However, we found differences between localities at different altitudes. Altitude variation involves important ecological changes as a consequence of differences in temperature, rainfall and other precipitations, windspeed and radiation input (Barry, 1992). Those factors may potentially influence the phenology and composition of insect communities as well as species richness (Whittaker, 1952; Gaston & Williams, 1996). For lizards located at 2800 m in the high mountainous area of Oukaïmeden, this could determine a different trophic availability and, consequently, a different diet composition to lizards found in medium altitude localities. In fact, Caves of Chiker, Taza, Balcon d'Ito and Debdou are located at 1600 m and have similar Mediterranean vegetation including *Quercus* sp. and shrublands, but with different cover density and stages of cattle exploitation. All lizards in those localities, except Taza, have a similar diet composition as a result of comparable ecological conditions, and it is likely that they share similar trophic availability. However, both syntopic *L. perspicillata* forms from Taza show some interesting differences in the abundance of consumed prey. *Chabanaudi* lizards ate a wider variety of prey, a higher proportion of which were

terrestrial, whereas the diet of the *pellegrini* form varied less but had a similar proportion of both terrestrial and flying prey and, interestingly, a high consumption of plant matter. Nevertheless, mean prey size was the same in both forms. Resource partitioning between lizards can be a strategy to minimize resource competition, leading to differences in habitat use or prey utilization (Schoener, 1977; Losos, 1994). In our case, in Taza both *L. perspicillata* forms live in strict syntopy (Harris *et al.*, 2003) and recent phylogenetic analyses show that those two forms are genetically distinct (Harris *et al.*, 2003). Thus, differences in the diet could then be the result of a competitive interaction between them. Seasonal and trophic availability studies would be interesting to evaluate the real importance of this competition on food resource partitioning and its effect on diet.

The insular population from Menorca has the most distinct diet. This population consumes the highest variety of prey types, most of them terrestrial, in contrast with the Moroccan populations where flying prey are, in general, more common. Prey types consumed depend, among other factors, on the predator foraging strategy (Schoener, 1971; Pianka, 1973; Stephens & Krebs, 1986). The comparatively higher consumption of terrestrial groups, like Araneae, Coleoptera, Isopoda and Orthoptera by the insular population may suggest an active foraging strategy, while continental lizards may be closer to 'sit and wait' foragers. However, these results could be due to different trophic availability rather than a different strategy (Arnold, 1987) or just a consequence of different sample sizes among populations (sample size in Menorca was almost twice that found among some mainland populations). Current results do not allow the determination of which factors are the most influential in this species. Thus, more studies including trophic availability analyses have to be undertaken to evaluate this hypothesis.

Our results show a low consumption of plant matter among the Moroccan populations, except those in Taza where plant material is, in some cases, high. However, this does not support in any case a consistent pattern of herbivory. Plant consumption and mirmecophagy are frequent in Mediterranean lacertids and commonly related to resource scarcity due to drought periods or arid environments (Eisentraut, 1950; Pianka, 1986; Pérez-

Mellado & Corti, 1993; Van Damme, 1999). Our study was carried out in April, one of the months with higher trophic availability in Mediterranean ecosystems. A recent study (Perera & Pérez-Mellado, unpublished) on *L. perspicillata* diet variation in Menorca later in the year shows consumption of fruits and ants during the summer. Recent studies suggest that frugivory can typically be considered an insular phenomenon (Van Damme, 1999; Cooper & Vitt, 2002; Olesen & Valido, 2003; Herrel *et al.*, 2004). Interestingly, Doumergue (1901) documented consumption of fleshy fruits of *Rhamnus oleoides* by the Moroccan lizard in Oran during August indicating a potentially similar plant consumption pattern in mainland populations. Unfortunately, we lack quantitative data on summer diet confirming this field observation. Hence, further seasonal studies on the diet of the mainland populations of *L. perspicillata* could be useful to determine the existence of differences in insular and continental trophic availability as well as evaluate the possible insular effect on the diet of this species.

Diet variability of *L. perspicillata* in localities under study is probably more related to changes in ecological conditions and habitat and, consequently changing trophic availability rather than lizard body size or other morphological differences. In this way, Moroccan populations with comparable ecological conditions, except in Taza, have a similar diet, which differed from the high mountain population. Moreover, insular lizards show some peculiarities when compared to continental lizards such as different diet composition and a high proportion of terrestrial items. However, we do not know when the introduction of the Moroccan lizard in Menorca occurred (Perera, 2003), a key factor to explain potential adaptation to its new insular environment. Further studies on diet including trophic availability throughout the different seasons are needed to fully evaluate our preliminary results with regards to the potential role of insularity in this species.

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