Trophic ecology of the Ocellated Lizard *Lacerta lepida* in an arid zone of southern Spain: relationships with availability and daily activity of prey

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The diet of the Ocellated Lizard *Lacerta lepida* was studied by means of faecal analysis, during two consecutive summers, in an arid zone of south-east Spain. The analysis of 181 faecal samples revealed 1929 prey items. Coleoptera was consistently the main group in the diet; two beetle species, *Ditomus capito* and *Morica hybrida*, maintained a frequency of around 40% in the diet. Vertebrates and gastropods were scarce, whereas plant food, comprised of fleshy fruits of Caper *Capparis spinosa* and Ephedra *Ephedra distachya*, varied in importance throughout the study period. The lizard diet was also compared with prey availability, estimated by pitfall traps. Selectivity analysis showed strong selection of the lizard upon some groups and systematic rejection of others. Daily activity of the Ocellated Lizard, as well as its diet composition, was studied in relation to daily activity of prey. The lizard diet proved to be based on nocturnal prey, implying active searching for these groups during the day, or a partially crepuscular-nocturnal activity in the lizard, overlapping with prey activity. The lack of diurnal sightings of the lizard throughout the summer favours the second option. The ecological implications of this feeding strategy in arid systems are discussed.

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Keywords: Carabidae; faecal analysis; frugivory; nocturnal activity; selectivity; Tenebrionidae

Introduction

Living in arid habitats usually requires a series of adaptations to water and food scarcity and extreme temperatures that are not sustainable by some animals. Many, however, have mechanisms to avoid the most hostile conditions of these habitats. One of the most usual avoidance mechanisms is to reduce the activity to periods of time, either annual or daily, in which climatic conditions are less extreme (Louw & Seely, 1982; Polis, 1991*a*). Another common feature is opportunism in the diet. The animals

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inhabiting arid zones display low selectivity (Wiens & Rotenberry, 1979; Rotenberry, 1980; but see Kaspari & Joern, 1993) because the scarcity of resources forces them to eat whatever they can find. Desert trophic webs therefore show a high degree of complexity, related to the unpredictability of the diet of desert animals (Polis, 1991*b, c*).

For animals which are not typical desert inhabitants, behavioural adaptations of this type constitute the only way of colonizing arid habitats. The Ocellated Lizard *Lacerta lepida* Daudin, inhabiting arid lands of south-eastern Spain, is a good example. Some steparic zones around Almería, in south-east Spain, receive as little as 200 mm annual rainfall, with warm temperatures and high solar radiation (Castillo-Requena, 1989), but the Ocellated Lizard inhabits this zone as well as the rainy and cold regions of north-western Spain, with over 1500 mm rainfall (Bas, 1982; Mateo & Castanet, 1994). The constraints that the severe setting imposes on ectotherm animals such as lizards provides an opportunity for the study of these adaptations. However, no data have been available until now regarding this particular feature, despite the widespread studies of this species in the last few years (e.g. Mateo, 1988; Busack & Visnaw, 1989; Castilla & Bauwens, 1989, 1990; Castilla *et al.*, 1991; Hernández *et al.*, 1991). Only recently, Mateo & Castanet (1994) analysed the effect of strong climatic variations on the reproductive strategies of the Ocellated Lizard, by comparing three different Spanish populations distributed along a climatic gradient.

In this work, we analyse diet composition and diet relationships with availability in the Ocellated Lizard inhabiting the arid inland basins of south-eastern Spain. The diet of this lizard in the Iberian Peninsula is well known, providing a direct comparison of our results with those from wetter and colder zones. Furthermore, knowledge of diet and its relationship to availability can suggest some of the resources that enable the lizard to inhabit this harsh environment.

Study area and methods

Study area

The general study area, the Guadix-Baza basin, is a Neogene basin with an altitude 700–1100 m a.s.l. surrounded by high mountains (1700–3000 m a.s.l.). The climate is continental Mediterranean, with warm, dry summers and cold winters (average temperatures 25·0°C in July, 5·3°C in January, Castillo-Requena, 1989). Annual rainfall averages around 300 mm, irregularly distributed in spring and autumn.

Field work was carried out between 1991 and 1993 in the Barranco del Espartal (30sWG2754, TM Baza, Granada, 750 m a.s.l.), a seasonal watercourse (hereafter 'rambla') in a 'badlands' landscape with a substrate of silt with gypsum sediments. The work zone was about 40 ha in the lower part of the rambla, where the vegetation is sparse, 46% bare ground, 21% grassland and 33% shrub coverage (230 sample points following the procedure of Wiens & Rotenberry, 1981). A more detailed description of the zone can be found in Sánchez-Piñero & Gómez (1995).

Diet analysis

Faecal samples were the only source of diet data, collected between May and September in 1991 and 1992. Faecal analyses gave results similar to those from stomach analyses (Seva, 1982; Hernández *et al.*, 1991), the most common method used in this species (e.g. Valverde, 1967; Mellado *et al.*, 1975; Pérez-Mellado, 1981; Busack & Visnaw, 1989; Castilla *et al.*, 1991), and avoids the necessity of killing the animal. We searched the rambla for faeces monthly throughout the activity period of

the lizards in the zone, using two–three observers with 4–10 field days per month each. Faeces collected were stored without mixture until laboratory analysis. Because other lizards, mainly *Acanthodactylus erythrurus* and *Psammodromus algirus*, are also abundant in the rambla, we used only those faeces whose size indicated that they were definitely from *L. lepida*. Both *A. erythrurus* and *P. algirus* measured about 80 mm maximum snout-vent length (SVL) (Barbadillo, 1987), and their largest faeces do not exceed 20 mm length, whereas adult Ocellated Lizards are usually up to 150 mm SVL (Busack & Visnaw, 1989; Mateo & Castanet, 1994) and their faeces measure 35–50 mm. Therefore, we used only faeces of 25 mm or larger (see also Hernández *et al.*, 1991). That is, the diet analysed here corresponds only to that of adult lizards.

In the laboratory, dry faeces were broken apart, and their components were sorted, identified and measured under a binocular microscope $10–40 \times$ equipped with a micrometer. Prey determination was usually to the species level. Measuring characteristic body parts enabled us to estimate length and biomass of the prey, using a series of regression equations prepared from arthropods caught in the zone (J.A. Hódar, unpublished manuscript; see Díaz & Díaz, 1990, for a similar procedure). When prey was identified to the species level but measurements were not possible, we assigned the average length and weight recorded in the faeces for that prey species. We categorized the diet data into 19 food types (15 arthropod types, two vertebrate and two plant; see Table 1), and calculated numeric frequency and monthly biomass for each animal food type (Rosenberg & Cooper, 1990). For plant material, we visually estimated the percent volume in each faecal sample, and we recorded the frequency of occurrence (that is, number of times that plant matter appeared in the faeces) and the average volume.

Selectivity analysis

Diet availability was estimated by means of 36 pitfall traps set every 2 weeks throughout the study period, collecting all specimens caught after 48 h (see Sánchez-Piñero & Gómez, 1995, for greater detail). A total of 648 traps yielded 8613 arthropods, which were identified and measured. To assess the lizard's choice of the prey types recorded in pitfalls, we used Jacobs' (1974) selectivity index S.

Pitfall traps are usually considered biased estimators of availability, because they show a strong dependence of the mobility pattern of a given arthropod. Several studies discuss these biases (e.g. Parmenter *et al.*, 1989; Cooper & Whitmore, 1990), and caution is needed in interpreting the results, because of evident limitations (Southwood, 1978). Pitfalls are considered useful for estimating ground-dwelling arthropods (see e.g. Cooper & Whitmore, 1990). In any case, since no method of trapping arthropods can give an accurate idea of how the lizard perceives prey availability, we modified the pitfall data for a better comparison with diet data (Cooper & Whitmore, 1990; Wolda, 1990). Firstly, we removed Acarina, Collembola and all arthropods with less than 2 mm body length from pitfalls, because these groups of very small size were not eaten by the lizard. Secondly, we arbitrarily assigned a frequency of 0·01% to prey types that appeared in the diet but not in pitfalls. This was required for calculation of selectivity, given that the lizards cannot prey upon groups that are not actually present. This adjustment was applied in 13 out of 129 cases.

Daily activity of lizard and arthropods

For an objective assessment of the activity rhythms of the Ocellated Lizard in the Barranco del Espartal, a 975 m transect was marked, crossing all the different microhabitats present in the rambla, and lizard censuses were carried out biweekly

between May and September of 1993. Six censuses were performed each day, every 2 h between sunrise and sunset.

Due to the summertime nocturnal activity of Carabidae and Tenebrionidae, the main prey of the Ocellated Lizard in the zone, in July 1992 we implemented a more accurate method for measuring availability (in this zone, July is the hottest and driest month, Castillo-Requena, 1989). We placed traps as usual, and during a 48-h sampling period we collected specimens every sunrise and sunset, in order to separate diurnal and nocturnal captures. We compared these data with the diet recorded for the lizard in the same month.

Statistical analysis

Nonparametric statistics were used because of the non-normality and hetero-scedasticity of variables (Zar, 1984). We compared taxonomic composition between years and between months with the *G* test. Comparisons in prey length and biomass between years and between the corresponding months in the 2 years were performed with the Mann–Whitney test. In each summer, prey length and biomasss were compared with the Kruskal–Wallis test. The relationship between availability and diet was compared with the Spearman rank correlation. All statistics were performed with JMP statistical package (JMP, 1989).

Results

A total of 181 faecal samples (98 in 1991, 83 in 1992) were analysed, providing a total of 1929 prey (1101 in 1991, 828 in 1992). Faeces were not found in May 1992, because a snowstorm in late April variously affected arthropod (Sánchez-Piñero, 1994) and lizard activity in the following weeks.

Animal food

Diet analysis (Table 1) showed that Carabidae and Tenebrionidae were the most abundant prey throughout the study period. Two species, *Ditomus capito* (Serv.) (Carabidae) and *Morica hybrida* Charp. (Tenebrionidae) together accounted for more than 40% of the recorded prey (14·7% and 27·6%, respectively). Scarabeidae, Curculionidae, and other Coleoptera and Orthoptera filled out the diet spectrum; other groups had only scant frequency and biomass. Vertebrate prey included only two small lizards (*Psammodromus* sp.) and a Thekla Lark (*Galerida theklae*) nestling. Apart from arthropods and vertebrates, the only other animal prey identified were three small snails, *Helicella* sp. Unusual elements found in faeces included a piece of sheep fleece, and a fragment of a PVC cork.

Plant food

Plant food was restricted to the fleshy fruits of the Caper *Capparis spinosa* and Ephedra *Ephedra distachya*, in sharply different quantities in each year. Summer 1991 showed a high Caper consumption in August and September, but not Ephedra; on the contrary, summer 1992 showed a few Ephedra fruits but only one Caper fruit. In fact, the Caper had a good crop in 1991, between 100–300 ripe fruits ha^{-1} in August–September (Hódar, 1993) but nearly zero in 1992. These two plants are the only fleshy-fruit producers in the zone; but the Caper is usually common (2·3% cover in

Table 1. Taxonomic composition of the diet of Lacerta lepida* in the Barranco del Espartal

Year	1991										1992							
Month	May		June		July		August		September		June		July		August		September	
Group	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B
Arachnida (not including Araneae and Acarina)	0·8	0·3	3·1	2·9	1·7	1·0	1·3	0·6	1·5	1·6	2·0	2·3	0	0	0	0	0	0
Araneae	0	0	0·3	0·2	0	0	0	0	0	0	2·0	2·4	0·7	0·4	0	0	0·5	0·2
Isopoda	0	0	0·8	0·7	0·3	0·2	0	0	0	0	0	0	0·3	0·1	4·5	1·5	0·5	0·3
Myriapoda	0·8	0·3	1·8	1·2	0·3	0·1	1·9	0·6	3·0	1·6	0·7	0·6	0·3	0·3	5·2	11·4	6·7	12·3
Orthoptera	2·3	2·5	3·4	18·8	3·3	10·6	5·2	7·4	6·8	9·1	6·7	21·9	7·4	23·5	2·6	0·4	1·9	0·5
Heteroptera	3·1	0·9	2·6	1·1	1·7	0·4	1·9	0·5	1·5	0·6	6·7	2·9	7·1	1·8	0	0	0	0
Lepidoptera larvae	3·9	3·4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carabidae	11·6	3·5	24·4	13·4	27·0	9·5	9·1	2·7	28·8	10·0	7·4	3·3	23·3	10·7	8·4	2·6	2·9	0·8
Tenebrionidae	38·0	48·5	10·8	19·2	47·7	71·4	63·6	82·5	23·5	57·2	32·9	50·5	24·3	44·6	57·4	75·9	66·2	81·2
Scarabaeidae	2·3	0·9	12·1	16·8	0·7	0·6	0	0	0	0	3·4	1·6	3·2	1·3	0	0	0	0
Curculionidae	10·9	4·3	4·2	2·4	6·7	3	8·4	2·8	22·0	14·8	7·4	3·2	5·2	2·5	9·0	3·8	12·9	3·1
Coleoptera others	18·6	33·9	11·8	11·5	6·7	2·5	3·2	2·2	4·5	2·7	24·2	11·0	20·1	12·7	7·1	3·3	3·3	1·0
Hymenoptera	6·2	1·5	2·6	0·9	2·3	0·5	3·9	0·5	4·5	1·5	0	0	1·0	0·5	5·8	1·1	2·4	0·4
Formicidae	0	0	15·5	0·4	0·3	0·1	0	0	2·3	0·1	4·0	0·1	5·8	0·1	0	0	1·0	0·1
Insecta others	1·6	0·2	6·0	1·0	1·3	0·2	1·3	0·2	1·5	1·1	2·7	0·2	1·0	0·1	0	0	1·9	0·3
Reptiles	0	0	0·3	2·9	0	0	0	0	0	0	0	0	0·3	1·5	0	0	0	0
Aves	0	0	0·3	6·6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capparis fruit	0	–	0	–	0	–	4·8	–	52·6	–	0	–	4·0	–	0	–	0	–
Other plants	0	–	0	–	0	–	0	–	0	–	8·3	–	4·0	–	9·5	–	4·0	–
% vol. animal	100·0		100·0		100·0		95·2		81·3		99·6		97·5		95·0		96·0	
% vol. plant	0		0		0		4·8		18·7		0·4		2·5		5·0		4·0	
No samples	13		21		24		21		19		12		25		21		25	
Prey identified	129		381		300		154		132		149		311		156		212	
Prey measured	119		363		292		144		118		137		293		149		197	
Mean prey length	18·4±9·1		13·6±5·9		17·0±4·7		18·6±4·6		14·6±4·8		14·4±6·1		14·5±6·3		17·4±5·2		17·4±5·5	

*Data are presented as percentage of numerical frequency (%F) and biomass (%B) except in plant fragments, in which %F means frequency of occurrence. Prey length, as mean ± S.D. is given in mm.

August–September, Hódar, 1993), whereas Ephedra is very scarce. Apart from Caper and Ephedra, only traces of *Helianthemum* sp. flowers and leaves were found in two faecal samples.
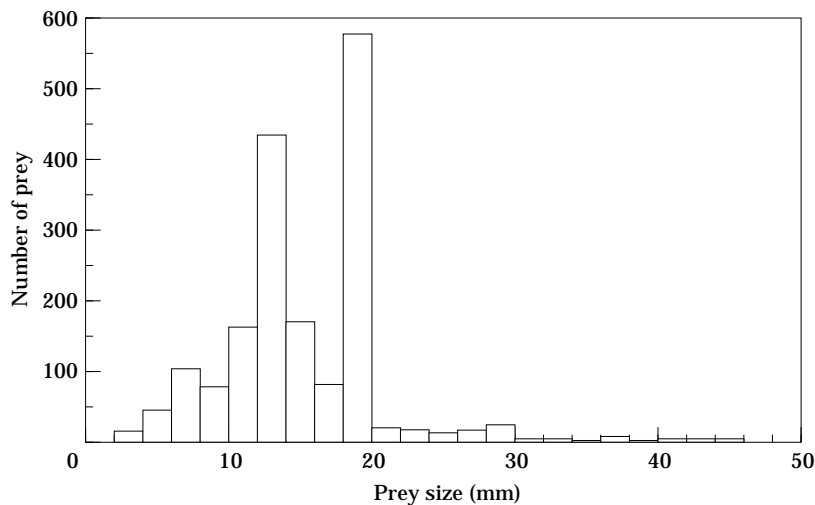
Prey size and biomass

The average prey size ranged from 14 to 18 mm (Table 1). Only in May 1991 was mean prey size below 14 mm, due to the high frequency of ants. Worker ants appeared in a faecal sample together with Dermestidae larvae and Staphylinidae, raising the possibility that the lizard fed on a carcass. Prey size distribution (Fig. 1) clearly showed peaks for *Ditomus* and *Morica* lengths.

The biomass values reflected the importance of Tenebrionidae even more than did frequency. Only in June 1991 did this family account for less than 40% of biomass (Fig. 2). Carabidae, other Coleoptera and Orthoptera were the other main groups in terms of biomass. Vertebrates were not common in the diet. On the contrary, the plant fraction was highly important with respect to volume. In September 1991 the Caper accounted for 18·7% of faeces volume, but in other months it remained below 5%.

Prey size and biomass showed significant differences between summers ($Z = -3·55$, $p < 0·0004$ and $Z = -2·86$, $p < 0·0043$, respectively, Mann–Whitney test) and were significantly heterogeneous in each summer (prey size, 1991: $H = 163·09$, 1992: $H = 82·29$; biomass, 1991: $H = 180·59$, 1992: $H = 108·54$, $p = 0·0001$ in all, Kruskal–Wallis test). Differences between the same month in different summers were also significant ($p < 0·0003$ always), both in prey size as well as in biomass, except in June (prey size $Z = 0·53$, $p < 0·60$; biomasss $Z = 1·76$, p $< 0·08$, Mann–Whitney test).

Diet composition vs. *prey availability*

Overall, the lizard diet and availability did not show a significant correlation ($r_S = 0·01–0·47$, $n = 13–15$, $p > 0·10$ always). Accordingly, selectivity values had clear patterns (Table 2). All Coleoptera had positive values except, incidentally, Scarabeidae. Myriapoda and Orthoptera also showed positive values, while Hyme-

Figure 1. Prey-size distribution of *Lacerta lepida* diet in the Barranco del Espartal.
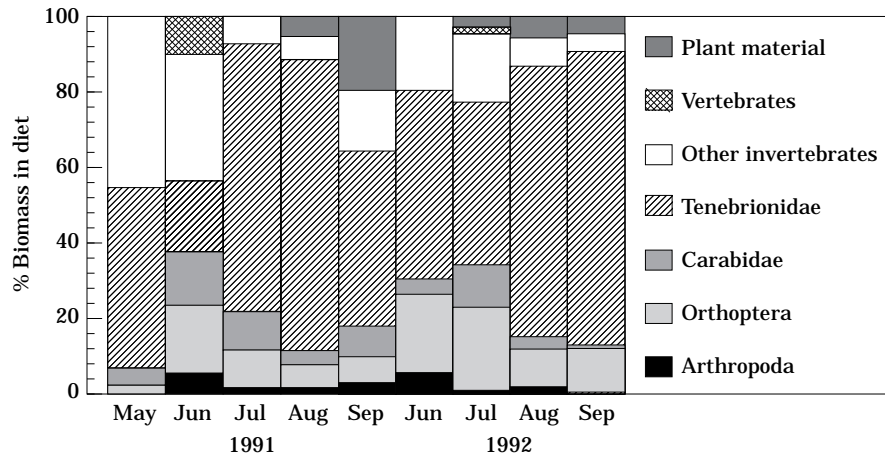
Figure 2. Monthly variations in the relative importance by biomass for the main prey types found in the diet of *Lacerta lepida* in the Barranco del Espartal. Arthropoda includes Arachnida, Myriapoda and Isopoda; Other invertebrates includes Insecta (except Orthoptera, Carabidae and Tenebrionidae) and Gastropoda. The plant fraction was estimated as volume (see Methods), and does not correspond exactly with biomass calculations.

noptera was quite variable. The case of Arachnida was remarkable in being positive throughout 1991 and negative (except June) in 1992. Isopoda, Formicidae and Others showed consistently negative values. The plotted distribution of S values (Fig. 3) showed pronounced peaks for the extreme values; that is, taxonomic groups were selected or rejected, and only rarely fed upon according to availability.

Table 2. *Selectivity values* for the different prey types found in the diet of* Lacerta lepida *in the Barranco del Espartal*

Group	1991					1992			
	May	Jun	Jul	Aug	Sept	Jun	Jul	Aug	Sept
Arachnida (not including Araneae and Acarina)	0.43	0.77	0.77	0.67	0.99	0.99	−1.00	−1.00	−1.00
Araneae	−1.00	−0.89	−1.00	−1.00	−1.00	0.24	−0.72	−1.00	−1.00
Isopoda	−1.00	−0.41	−0.63	−1.00	−1.00	−1.00	−0.79	0.36	−0.61
Myriapoda	0.97	0.76	0.94	0.99	0.99	0.97	0.94	−1.00	0.96
Orthoptera	0.01	0.52	0.47	0.83	0.78	0.78	0.60	0.39	0.34
Heteroptera	0.68	0.68	0.77	0.94	0.54	0.97	0.91	0.84	0.60
Lepidoptera larvae	0.58	−1.00	–	–	–	−1.00	−1.00	–	−1.00
Carabidae	0.93	0.99	0.98	1.00	0.99	0.78	0.98	0.86	0.71
Tenebrionidae	0.78	0.64	0.89	0.99	0.72	0.46	0.40	0.88	0.86
Scarabaeidae	0.67	0.87	0.97	−1.00	−1.00	0.99	0.99	–	–
Curculionidae	0.88	0.96	1.00	0.97	0.88	0.80	0.91	0.77	0.22
Coleoptera others	0.45	0.73	0.59	0.73	−0.12	0.87	0.81	0.49	0.06
Hymenoptera	0.40	0.22	0.11	0.70	0.61	−1.00	−0.30	0.33	−0.19
Formicidae	−1.00	−0.90	−1.00	−1.00	−0.99	−0.97	−0.94	−1.00	−0.98
Others	−0.88	0.04	−0.45	0.26	−0.42	0.10	−0.70	−1.00	−0.68

*S, Jacob's index.
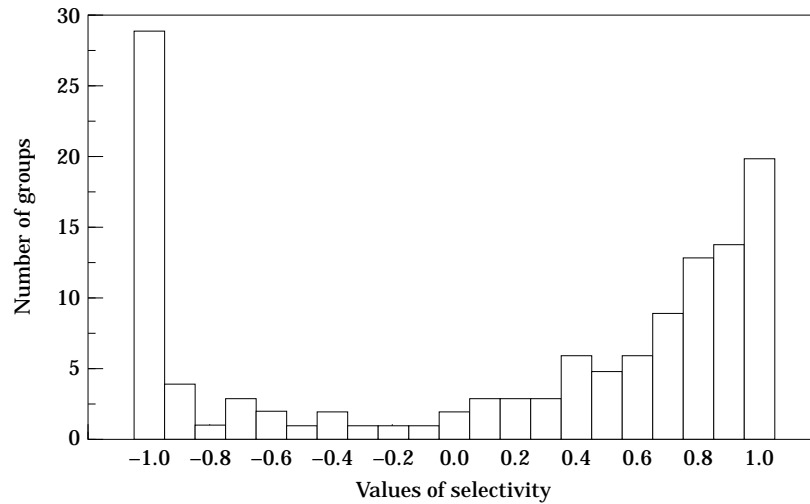
Figure 3. Distribution of selectivity values (*S*, Jacobs' index) of *Lacerta lepida* in the Barranco del Espartal. All months and prey types pooled.

Activity of the lizard

During 1991 and 1992, direct sightings of Ocellated Lizards were recorded only in late May and early June; during the rest of the sampling period the only evidence of the lizards' activity was the presence of faeces. The results of the censuses during 1993 were consistent with these records. In a total of 58·5 km of censuses, only five sightings of Ocellated Lizards were made (Table 3) at the beginning of the work period, despite the consistent occurrence of fresh faeces throughout the summer.

Diet composition vs. *prey activity*

Diet in July 1992 showed a closer relationship with nocturnal availability ($r_S = 0.34$) than with diurnal ($r_S = 0.19$), although neither proved significant (n = 15 both, $p < 0.21$ and $p < 0.48$, respectively). Tenebrionidae showed marked nocturnal activity (Table 4), although some pitfall catches were made during the day; Carabidae was exclusively nocturnal. Partially diurnal Tenebrionidae species like *Pimelia integra* Sol. and *Tentyria incerta* Sol. were rarely or never eaten, despite their abundance, whereas *Ditomus*, strictly nocturnal, and *Morica*, mainly nocturnal (and both very rarely caught in pitfall traps), were commonly eaten.

Table 3. *Number of lizards seen during the censuses* carried out in the Barranco del Espartal*

Species	May	Jun	Jul	Aug	Sept
Lacerta lepida	3	2	0	0	0
Psammodromus algirus	21	13	7	6	0
Psammodromus hispanicus	58	17	15	28	14
Acanthodactylus erythrurus	56	48	52	23	20

*Figures indicate sightings per 11·7 km (12 censuses = 2 days, six censuses daily, of 975 m each). See Methods for details.

Discussion

General traits of the diet

The diet observed for the Ocellated Lizard in our study is broadly similar to that reported for other zones of the Iberian Peninsula (Pérez-Mellado, 1981; Mateo, 1988; Busack & Visnaw, 1989; Castilla *et al.*, 1991; Hernández *et al.*, 1991) and southern France (Bischoff *et al.*, 1984). Coleoptera were almost always the basis of the diet, although the contribution of different types of beetle shows considerable variation. In dry zones such as the coastal dunes in Almería (Valverde, 1967) or Alicante (Seva, 1982) the most predated beetles are Tenebrionidae, but in central Spain Scarabeidae (Castilla *et al.*, 1991). Other groups like Hymenoptera, Orthoptera and Hemiptera are also common.

Gastropoda, a common prey in wetter climates (Peters, 1962; Bas, 1982; Mateo, 1988), are also eaten in arid zones in which certain snails are adapted to dry conditions, such as *Sphincterochilla* sp. in Almería (Valverde, 1967). In Barranco del Espartal, however, cold winters and silt soils seem to discourage snails, which are only rarely found.

Vertebrates, another important food group, are also very scarce. Vertebrates usually found in the diet of the Ocellated Lizard are small mammals, small lizards and ground birds, mainly nestlings (Mellado *et al.*, 1975; Mateo, 1988; Castilla *et al.*, 1991). However, in dry zones of south-eastern Spain, small mammals are nearly absent, and

Table 4. *The diet of* Lacerta lepida *compared to diurnal and nocturnal availability of prey (recorded by means of pitfall traps) in the Barranco del Espartal in July 1992*

Taxa	Diet	Day	Night
Arachnida (not including Araneae and Acarina)	0	2	0
Araneae	2	17	22
Isopoda	1	4	23
Myriapoda	1	0	0
Orthoptera	23	8	11
Heteroptera	22	3	1
Lepidoptera larvae	0	1	3
Carabidae	72	0	4
Ditomus capito	70	0	2
Carabidae others	2	0	2
Tenebrionidae	75	14	60
Pimelia integra	1	5	45
Morica hybrida	66	1	3
Scaurus sp.	5	0	7
Tentyria incerta	0	8	2
Tenebrionidae others	3	0	3
Scarabaeidae	10	0	0
Curculionidae	16	1	1
Coleoptera others	62	14	14
Hymenoptera	3	13	6
Formicidae	18	508	219
Others	3	19	30
Acarina+Collembola	–	41	226

ground-nesting birds showed low densities in the study area (Hódar, 1993). On the contrary, small lizards are abundant in the Barranco del Espartal, and the records found in this zone agree with other studies in Spain (Castilla *et al.*, 1991; Hernández *et al.*, 1991).

Plant food and seed dispersion

The high consumption of plant food, mainly the Caper, has special dietary importance. The Caper, a vine inhabiting slopes of the ramblas in dry habitats of south-east Spain, produces large fruit which open when ripe, offering a red pulp with numerous seeds. In middle and late summer, when arthropod availability is reduced by drought, and arthropods shift to nocturnal activity (see below), the Caper is an important food source for the Ocellated Lizard. Only when the Caper crop is very low, as in 1992 (Hódar, 1993), is it obliged to search for other fleshy fruits, such as Ephedra, which was not eaten in 1991.

The high incidence of plant material, as well as the high occurrence but low volume in stomachs, has been already reported (Mateo, 1988; Castilla *et al.*, 1991). Certainly, the lizard is at the limit of the body mass associated with a shift to herbivory in lizards (Pough, 1973; Schoener *et al.*, 1982), but it seems that this drift is effective only under special conditions, such as insularity (Schoener *et al.*, 1982; Mateo, 1988; Pérez-Mellado & Corti, 1993; Valido & Nogales, 1994) or, in our case, a combination of animal prey scarcity and high availability and quality of vegetal food, at least in the Caper. In fact, when fruit is abundant, the Caper is eaten by many different animals in the rambla, including several ant species, birds and Fox *Vulpes vulpes* (Hódar, 1993, 1994). Seeds, both for Caper and Ephedra, appeared undamaged and viable in faeces, implying that the lizard can play an important role in seed dispersion (see also Hernández, 1990; Valido & Nogales, 1994).

Availability and daily activity

The Ocellated Lizard has been considered an opportunistic predator (Busack & Visnaw, 1989; Hernández *et al.*, 1991), although some preferences in diet selection have also been reported (Castilla *et al.*, 1991; Hernández *et al.*, 1991). Certainly, other lizards seem to discriminate and select prey according to particular parameters, mainly prey size (see e.g. Díaz & Carrascal, 1990, 1993). The high values for selectivity in our study, and especially the contrast between rejected and selected prey (Fig. 3), suggest a clear prey selection. Pitfall traps, though having some biases in sampling the actual arthropod availability, are usually considered good estimators of the abundance of ground-dwelling arthropods (e.g. Southwood, 1978; Cooper & Whitmore, 1990). In our case, the only group that seems to be biased in sampling is Orthoptera, because its locomotion systems makes it difficult to catch. Consequently, selectivity values for this group may be overestimated. However, the other important groups in the diet seem to be adequately estimated. Prey size seems to be a main selection factor, since although adult lizards sometimes feed on small prey, prey size significantly increases with lizard size (Castilla *et al.*, 1991, but see Busack & Visnaw, 1989). Accordingly to our data, selected groups (Tenebrionidae, Myriapoda, Orthoptera) had larger sizes than non-selected groups (Formicidae, most of Araneae; Table 2). An unexpected case was Isopoda, rejected in Baza but commonly eaten in Almería (Valverde, 1967) and Cádiz (Busack & Visnaw, 1989).

Nevertheless, a more specific question arises regarding the importance of *Ditomus* and *Morica* in the diet of the lizard in the Barranco del Espartal. Both prey are mainly nocturnal, and conspicuously scarce in traps (Table 4, see also Appendix in Sánchez-

Piñero & Gómez, 1995). The activity of these animals is apparently restricted to very specific microhabitats. *Ditomus*, in fact, belongs to the subfamily Ditominii, which differs from other Carabidae in its granivorous habits, parental care, and activity linked to the immediate proximity of breeding burrows (Schremmer, 1960; Brandmayr & Brandmayr-Zetto, 1974). *Morica*, on the other hand, is strongly linked to ant-nest debris (Sánchez-Piñero & Gómez, 1995), in which it finds shelter during day and food at night.

This means that the Ocellated Lizard must be active during sunset or even later, when the two beetles are active and visible, and/or actively search for these animals during day, looking for them in ant-nest debris and *Ditomus* burrows. The first possibility has some arguments in its favour: large lizards have higher thermic inertia; black prey are easily located walking on white gypsum soil even in poor light conditions; and average minimum nocturnal temperature in July and August is around 16·5°C (a figure included in the Ocellated Lizard activity interval, Busack & Visnaw, 1989). The Ocellated Lizard shows two pronounced activity peaks in summer (Busack & Visnaw, 1989); perhaps it prolongs the afternoon peak into the evening, overlapping its activity as much as possible with that of the prey. This could also explain why no direct lizard sightings were made after mid-June, despite search intensity (Table 3). Although noctural activity in the lizard is highly unlikely given its usual life habits (strictly diurnal, Busack & Visnaw, 1989), and the general limitations of nocturnal activity in an ectotherm, nocturnal activity has been previously reported for other typically diurnal reptiles in Mediterranean habitats during summer (Valverde, 1967; Franco *et al.*, 1980; Cheylan, 1986; Bea *et al.*, in press). The second possibility seems plausible for *Morica*, because ant-nest debris can be dug easily by the lizard, but it is difficult to imagine how *Ditomus* are caught in their deep nests (Schremmer, 1960; Brandmayr & Brandmayr-Zetto, 1974). Furthermore, active searching for prey in selected micro-habitats is different from the usual foraging behaviour reported for lizards, based on pause-travel walking and prey detection by direct sighting of prey movements (Avery *et al.*, 1987; Cowlishaw & Avery, 1991; Avery, 1993). *Morica* is rarely active before sunset or after sunrise, and thus lizards must start searching for ant nests without sighting prey. The same could be said about *Ditomus*.

In conclusion, three main features provide the framework in which the Ocellated Lizard constructs its diet in Barranco del Espartal: a shift towards frugivory in scarcity periods, a marked prey selectivity, and a partial nocturnal activity. The last is surprising in view of what is known about the species in other Mediterranean areas, whereas the two former have been sometimes reported in other situations (Mateo, 1988; Castilla *et al.*, 1991; but also the opposite, e.g. Busack & Visnaw, 1989; Hernández *et al.*, 1991). The versatility shown in their feeding habits agrees with the geographical variations in their reproductive characteristics (Mateo & Castanet, 1994) and shows the Ocellated Lizard to be an adaptable species (*sensu* Endler, 1986), able to profit from different resources in different ways in order to survive in harsh and extreme habitats.

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