Spring diet and trophic partitioning in an alpine lizard community from Morocco

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Oukaïmeden Plateau is a herpetologically rich locality in the High Atlas (Morocco) where four lizard species coexist in strict sympatry: three lacertids (*Lacerta perspicillata chabanaudi*, *L. andreanszkyi* and *Podarcis vaucheri* – formerly *P. hispanica vaucheri*) and one gekkonid (*Quedenfeldtia trachyblepharus*). The diet composition of this lizard community during the early spring was analysed based on 132 faecal pellets which could be individually assigned to a species and a size and sex class. *Quedenfeldtia trachyblepharus* had the highest prey number and the most specialized prey composition based mainly on small Coleoptera (62.5%) which were consumed in aggregates. All three lacertids displayed higher but similar levels of populational prey diversity. *Lacerta p. chabanaudi* mainly fed on flying insects, whereas *L. andreanszkyi* and *P. vaucheri* had diets based on terrestrial prey. Larger lizards ate larger prey at both inter- and intraspecific levels. Species overlap was medium-high (48–84%). Within species, *P. vaucheri* showed moderate segregation between males and females (74% overlap) whereas the other species did not (>94%). Pseudocommunity analyses revealed community structure based on segregation due to prey not consumed (species) and to the restriction of niche breadth (classes). The influences of species interactions on habitat use, restrictions in trophic availability and evolutionary history as determinant factors are discussed.

Key words: trophic ecology, communities, pseudocommunity analysis, *Lacerta perspicillata, Lacerta andreanszkyi, Podarcis vaucheri, Quedenfeldtia trachyblepharus,* Morocco.

INTRODUCTION

Lizard communities have become an especially developed field of study in ecology due to the methodological resources available for this vertebrate group. Of the three classical niche dimensions (diet, place and time), diet is surely the most studied. In fact, a substantial fraction of pioneering theoretical developments in this field were based on lizard studies (Pianka 1966, 1973; Schoener 1968; Winemiller & Pianka 1990), particularly in deserts and tropical areas where species richness is higher (Pianka 1986; Vitt & Caldwell 1994; Vitt & Carvalho1995; Vitt & Zani 1998; Vitt *et al.* 2000; Akani *et al.* 2002). However, less attention has been devoted to the simpler communities in temperate regions, most corresponding to assemblages of Mediterranean lacertids in Europe (Pérez-Mellado 1982; Strijbosch *et al.*1989; Carretero 1993; Capula & Luiselli 1994a). In such areas, abiotic restrictions could play an equally important role besides species interactions on

the community organization (Barbault 1991). Alpine lizard communities are rare since harsh and extremely seasonal climatic conditions in high mountain environments often restrict the number of sympatric species present to one or two (Pérez-Mellado *et al.* 1991; Richard & Lapini 1993; Roig *et al.* 1998). Although Morocco has most of the known Alpine stages in North Africa, virtually no similar studies have been conducted except on lowland areas of arid climate (Pérez-Mellado 1992; Znari *et al.* 2000).

Oukaïmeden Plateau is a herpetologically rich locality in the High Atlas (Morocco) situated at 2600 m.a.s.l. (7°52′52″W, 31°12′32″N, Fig. 1). The habitat consists of a mountain stream with marshes and an artificial dam surrounded by alpine meadows, rock outcrops with small cliffs and several stone walls (Schleich *et al.* 1996). The climate corresponds to high mountains, with cold winters (Jabiri *et al.* 2000). Of the species constituting the local herpetological community, four lizards are abundant and live in strict sympatry:

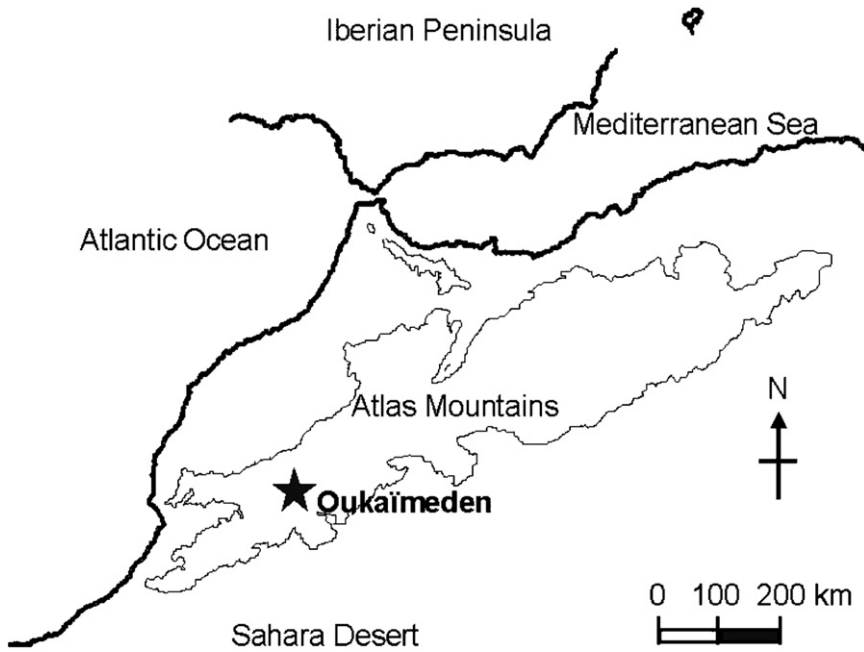*Author for correspondence: E-mail: carretero@mail.icav.up.pt

Fig. 1. Location of study site.

three lacertids, *Lacerta perspicillata chabanaudi,
L. andreanszkyi* and *Podarcis vaucheri* (formerly
P. hispanica vaucheri) and one gekkonid, *Queden-
feldtia trachyblepharus*; although some qualitative
information indicates differential habitat use by
them (Schleich *et al.* 1996; Fig. 2).

Here, the diet composition of this lizard commu-
nity is analysed during the early spring considering
both inter- and intraspecific variation. Moreover,
the hypothesis of community structure at the
trophic level is tested against the null hypothesis
of random trophic overlap.

MATERIALS & METHODS

Study species

Lacerta perspicillata is a strictly saxicolous lizard
found in the rocky, mountainous areas of Morocco
and western Algeria (Bons & Geniez 1996;
Schleich *et al.* 1996) from the sea level to 2800 m
altitude and it has also been introduced in
Menorca in the Balearic Islands (Perera 2002). The
systematics of this species is far from being
resolved since current studies identify several
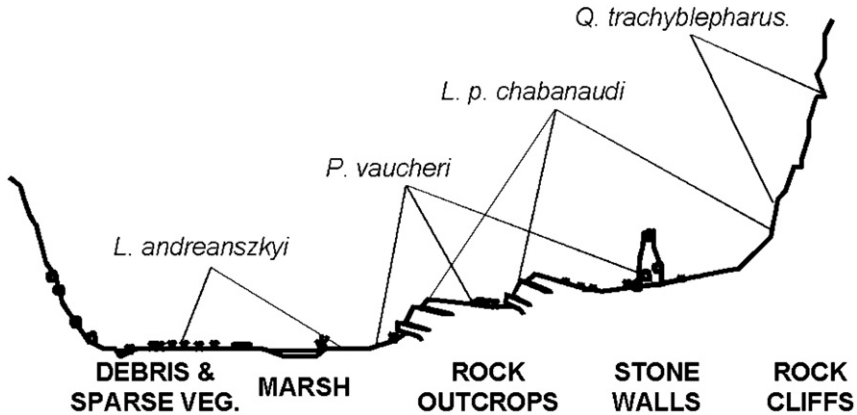colour morphs and distinct genetic lineages, not

Fig. 2. Schematic diagram of habitat use (modified from Schleich *et al.* 1996). All four species can be found in a transect of 200 m.

Table 1. Body size (SVL, mean ± SE, *n*) of the lizards and number of faecal pellets collected by species and class.

	Males	Females	Immatures	Total
L. p. chabanaudi	59.56 ± 1.42	59.75 ± 1.08	38.58 ± 1.48	
	15	10	7	32
L. andreanszkyi	43.73 ± 0.59	46.00 ± 0.90	27.31 ± 1.82	
	13	12	8	33
P. vaucheri	50.00 ± 1.21	49.74 ± 1.34	38.00 ± 1.00	
	15	10	2	27
*Q. trachyblepharu*s	46.28 ± 0.58	42.71 ± 1.02	25.33 ± 1.33	
	23	14	3	40
All species	66	46	20	132

mutually correspondent (Bons & Geniez 1996; Harris *et al.* 2003; A. Perera *et al.,* unpubl. data). Thus, we provisionally refer the spotted form found in this locality as *L. p. chabanaudi* (Bons & Geniez 1996). *Lacerta andreanszkyi,* a Moroccan endemic, is a ground-dwelling species inhabiting alpine meadows over 2000 m in the High Atlas (Bons & Geniez 1996).

Podarcis hispanica sensu lato, distributed throughout the Iberian Peninsula, southern France and northern Morocco, Algeria and Tunisia, constitutes a highly diverse species complex (Harris & Sa-Sousa 2001, 2002; Pinho *et al.* 2003, 2004, 2006). The form *vaucheri,* henceforth *P. vaucheri,* occupies the extreme south of Iberia, north and central Morocco (Rif and Medium and High Atlas) and an undetermined area in northern Algeria (Bons & Geniez 1996; Schleich *et al.* 1996; Pinho *et al.,* in press). This generalist can be found in rocky, bushy or even forest areas from the sea level to 3100 m (Schleich *et al.* 1996). Finally, *Quedenfeldtia trachyblepharus,* one of the two members of an endemic genus of diurnal geckoes (Arnold 1990), is restricted to the High Atlas and occupies mountain cliffs reaching up to 4000 m (Bons & Geniez 1996).

Sampling and laboratory methods

In April 2003, 132 lizards (Table 1) belonging to all four species were collected in the study area. Faecal pellets were obtained by handling, so they could be individually assigned to a species and sex and size class. The snout–vent length (SVL) of every specimen was measured using callipers to the nearest 0.5 mm. Size and sex (adult males, adult females and immatures) was assigned using sexual secondary characters and the SVL values given in the literature for adults (Schleich *et al.* 1996 and references therein). According to Carretero & Llorente (1993b), the term immatures is preferred instead of juveniles to designate those lizards smaller than the size at sexual maturity if the year when it is attained is not known. Lizards were released at the capture site at the end of the sampling, preventing repeated captures of the same individual.

Pellets were analysed under a binocular dissecting microscope. The minimum numbers criterion was used for prey counting (Escarré & Vericad 1981). Prey items were identified to order level (except Formicidae) and intact prey were measured with an ocular eyepiece to the nearest 0.05 mm.

Statistical analysis

Following Carretero (2004), Jover's method (Jover 1989) was used for statistical analysis of diet description and trophic diversity. Three descriptors were calculated: the abundance (%P), the occurrence (%N) and the resource use index (IU). The last one emphasizes homogeneity as a criterion for evaluating the importance of the different prey operative taxonomic units (OTUs) consumed (Jover 1989). Abundance (number of prey items), richness (number of OTUs), diversity and evenness were calculated for every individual and compared by species and class. Such variables were log-transformed in order to achieve normality (assessed by Kolmogorov-Smirnov tests) prior to comparisons at individual level. Brillouin's indices were used for calculating diversity and evenness (Magurran 1988). Populational diversity (Hp) was estimated by Jack-knife pseudosampling (Jover 1989) and compared by multiple *t*-tests due to the non additive nature of diversity (Carretero & Llorente 1991) applying the sequential Bonferroni correction (Rice 1989).

Trophic overlap was estimated through the Pianka index applied on IU values for every species and class (Carretero & Llorente 1991, 1993a; Carretero *et al.* 2001) and represented by means of a MDS (multidimensional scaling, Kruskal & Wish 1989) plot. Hypothesis of non-

Table 2. Descriptors and diversity parameters of the taxonomic diet of the four species. %P: occurrence; %N: abundance; IU: resource use index; Hi: individual diversity; Hp: populational diversity; Hk: total accumulated diversity; Ei: evenness (Brillouin indices).

	L. p. chabanaudi			L. andreanszkyi			P. vaucheri			Q. trachyblepharus			Community		
	%P	%N	IU	%P	%N	IU	%P	%N	IU	%P	%N	IU	%P	%N	IU
Araneae	15.63	3.09	2.11	37.50	10.91	12.02	51.85	12.40	15.38	7.69	0.99	0.39	26.15	5.11	5.02
Opilioni	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.56	0.33	0.00	0.77	0.14	0.00
Acarina	0.00	0.00	0.00	6.25	1.82	0.56	3.70	2.33	0.00	0.00	0.00	0.00	2.31	0.71	0.17
Chilopoda	3.13	0.62	0.00	3.13	0.91	0.00	3.70	0.78	0.00	0.00	0.00	0.00	2.31	0.43	0.13
Orthoptera	0.00	0.00	0.00	0.00	0.00	0.00	3.70	0.78	0.00	0.00	0.00	0.00	0.77	0.14	0.00
Dictyoptera	3.13	0.62	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.77	0.14	0.00
Homoptera	50.00	10.49	12.13	71.88	38.18	48.27	62.96	28.68	26.43	41.03	8.88	8.45	55.38	17.45	18.23
Heteroptera	31.25	8.03	7.11	9.38	2.73	1.33	3.70	0.78	0.00	33.33	4.93	4.42	20.77	4.54	4.09
Diptera	65.63	32.10	37.09	21.88	10.00	6.04	33.33	16.28	15.75	30.77	5.92	4.60	37.69	14.47	14.54
Lepidoptera	0.00	0.00	0.00	3.13	0.91	0.00	3.70	0.78	0.00	7.69	0.99	0.39	3.85	0.71	0.33
Coleoptera	75.00	32.72	33.23	43.75	18.18	19.42	62.96	27.13	36.91	89.74	62.50	69.91	69.23	42.27	45.78
Hymenoptera	28.13	6.17	5.56	18.75	5.46	4.33	11.11	2.33	1.29	38.46	5.26	5.07	25.38	4.97	4.91
Formicidae	6.25	1.85	0.46	0.00	0.00	0.00	3.70	0.78	0.00	12.82	2.96	1.45	6.15	1.84	0.97
Other arthrop.	9.38	1.85	0.86	25.00	7.27	6.71	18.52	3.88	3.15	25.64	3.62	2.93	20.00	3.83	3.54
Larvae	0.00	0.00	0.00	9.38	2.73	1.33	7.41	1.55	0.54	20.51	2.63	1.99	10.00	1.84	1.36
Undetermined	12.50	2.47	1.45	3.13	0.91	0.00	7.41	1.55	0.54	7.69	0.99	0.39	7.69	1.42	0.94

	n	Mean ± S.E.	n	Mean ± S.E.	n	Mean ± S.E.	n	Mean ± SE	n	Mean ± S.E.
Abundance	32	4.94 ± 0.56	33	3.30 ± 0.29	27	4.70 ± 0.67	40	7.53 ± 0.84	132	5.27 ± 0.35
Richness	32	3.00 ± 0.22	32	2.53 ± 0.15	27	2.78 ± 0.20	39	3.18 ± 0.21	130	2.89 ± 0.10
Hi	32	0.81 ± 0.12	32	0.67 ± 0.09	27	0.78 ± 0.11	39	0.81 ± 0.11	130	0.77 ± 0.05
Hp	–	2.53 ± 0.14	–	2.74 ± 0.14	–	2.75 ± 0.16	–	2.10 ± 0.12	–	2.66 ± 0.08
Hk	–	2.37	–	2.50	–	2.50	–	2.00	–	2.59
Ei	32	0.46 ± 0.04	32	0.46 ± 0.04	27	0.50 ± 0.04	39	0.46 ± 0.03	130	0.47 ± 0.02

random overlap distribution in the lizard community (Gotelli & Graves 1996) was tested at both class and species level using Ecosym software (Gotelli & Entsminger 2001). We used the RA2 (niche breadth relaxed/zero states retained) and RA3 (niche breadth retained/zero states reshuffled) Monte Carlo randomization algorithms (Winemiller & Pianka 1990). Two assumptions concerning resource states were considered: equiprobability of OUTs and probabilities according to their availability. Owing to the lack of a direct estimate of the trophic availability, we used the diet of the whole lizard community (IU) as a reliable indirect measure of prey potentially eaten by the lizards (Winemiller & Pianka 1990; Vitt & Carvalho 1995). A total of 1000 pseudocommunities were generated in each case. Significant deviation ($\alpha < 0.05$) of mean real overlap from simulations indicates structure in the data set.

RESULTS

Body size is relatively small for all four lizard species (Table 1). However, based on the adult specimens collected, *L. p. chabanaudi* was bigger than the other three (males, ANOVA, $F_{3,62} = 47.33$, $P = 4.94 \times 10^{-16}$, Scheffé tests $P < 0.001$; females, $F_{3,42} = 45.18$, $P = 3.30 \times 10^{-13}$, Scheffé tests $P < 0.0005$). No sexual differences in body size were detected either for *L. p. chabanaudi* or for *Podarcis vaucheri* ($t_{23} = 0.09$, $P = 0.92$ and $t_{23} = 0.14$, $P = 0.89$, respectively) whereas female *L. andreanszkyi* were bigger than males ($t_{23} = -2.14$, $P = 0.04$) and male *Q. trachyblepharus* were bigger than females ($t_{23} = 46.28$, $P = 0.002$).

Two of the pellets (one from a male *L. andreanszkyi* and another from a male *Q. trachyblepharus*) were excluded from the sample because they were only composed of indistinguishable matter and uric acid, hence preventing prey identification. The highest number of prey items by pellet was found in *Q. trachyblepharus* (ANOVA, $F_{3,127} = 4.84$, $P = 0.003$, Scheffé tests $P < 0.003$).

All four species showed relatively distinct diets (Table 2, Fig. 3). The diet of *L. p. chabanaudi* comprised mainly Diptera (IU = 37.1%) and Coleoptera (33.2%). Whereas adult males and females
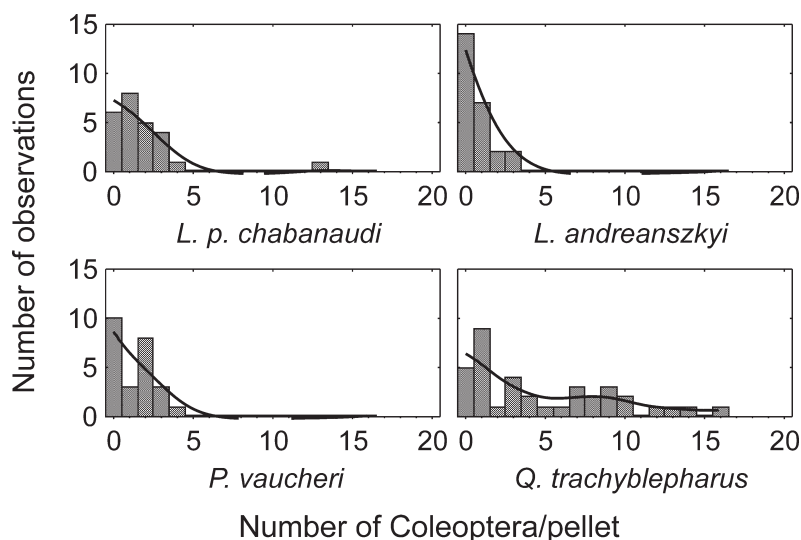
Fig. 3. Size distribution of Coleoptera consumed by every species. Lines were adjusted by least squares.

consumed both prey taxa in similar proportions, the diet of immatures was biased on Diptera (54.1%) and Coleoptera just represented a secondary prey (22.5%). *Lacerta andreanszkyi* mainly consumed Homoptera (48.3%), and lower proportion of Coleoptera (19.4%) and Araneae (12.0%). No relevant differences at the intraspecific level were found in this species, except that immatures consumed less beetles than adults. *Podarcis vaucheri* showed a very eclectic diet based on Coleoptera (36.9%), Homoptera (26.3%), Diptera (15.8%) and Araneae (15.4%). Adult males were the only class eating an appreciable proportion of beetles. Finally, *Q. trachyblepharus* displayed the most distinct prey composition (Fig. 4) based mainly on Coleoptera (69.9%) of small size but found in great numbers by pellet; such specialization did not show intraspecific variation (two-way ANOVA, species $F_{3,119} = 12.81$, $P = 3.15 \times 10^{-7}$, Scheffé tests $P < 0.002$; class $F_{2,119} = 0.11$, $P = 0.89$; species × class $F_{6,118} = 0.80$, $P = 0.72$).

No significant differences, either interspecific or intraspecific, were detected in diet richness (two-way ANOVA, species $F_{3,118} = 2.04$, $P = 0.11$; class $F_{2,118} = 1.87$, $P = 0.16$; species × class $F_{6,118} = 0.30$, $P = 0.93$), individual diversity (two-way ANOVA, species $F_{3,118} = 1.34$, $P = 0.28$; class $F_{2,118} = 1.98$, $P = 0.14$; species × class $F_{6,118} = 0.36$, $P = 0.90$) and evenness (two-way ANOVA, species $F_{3,118} = 0.42$, $P = 0.73$; class $F_{2,118} = 1.53$, $P = 0.22$; species × class $F_{6,118} = 0.29$, $P = 0.94$). However, diet diversity at the population level was lower in *Q. trachyblepharus* than in the three lacertid species, which

displayed high but similar values (*t*-tests, $P < 0.01$ after sequential Bonferroni correction, Table 2). Population diversity was higher than individual diversity in all cases (*t*-tests, $P < 0.01$).

At the interspecific level, lizards consumed median prey sizes according to their SVL; essentially, *L. p. chabanaudi* ate bigger prey than the other species. However, no evidence of immatures consuming smaller median prey than adults was detected (two-way ANOVA, species $F_{3,120} = 6.07$, $P = 0.0007$; class $F_{2,120} = 0.76$, $P = 0.47$; species × class $F_{6,120} = 0.99$, $P = 0.44$). All differences disappeared when corrected for lizard size using SVL as a covariate (two-way ANCOVA, species $F_{3,118} = 0.42$, $P = 0.73$; class $F_{2,118} = 1.06$, $P = 0.35$; species × class $F_{6,118} = 0.99$, $P = 0.44$).

Taxonomic overlap of prey of the four species fell within medium-high values (48–84%), *P. vaucheri* being the only species overlapping similarly with the others (Table 3). At the intraspecific level (Fig. 5), this species was the only one showing moderate taxonomic segregation between males and females (74%) whereas the others did not (>94%). In all cases, immature lizards did not differ extensively from adults regarding the taxa eaten.

Pseudocommunity analysis at the species level considering each OTU equiprobable indicated that real overlap was higher than simulated in the RA3 matrix (niche breadth retained) but similar to the RA2 matrix (zero states retained). By contrast, when considering the prey electivities, values were lower than in the RA3 matrix (niche breadth
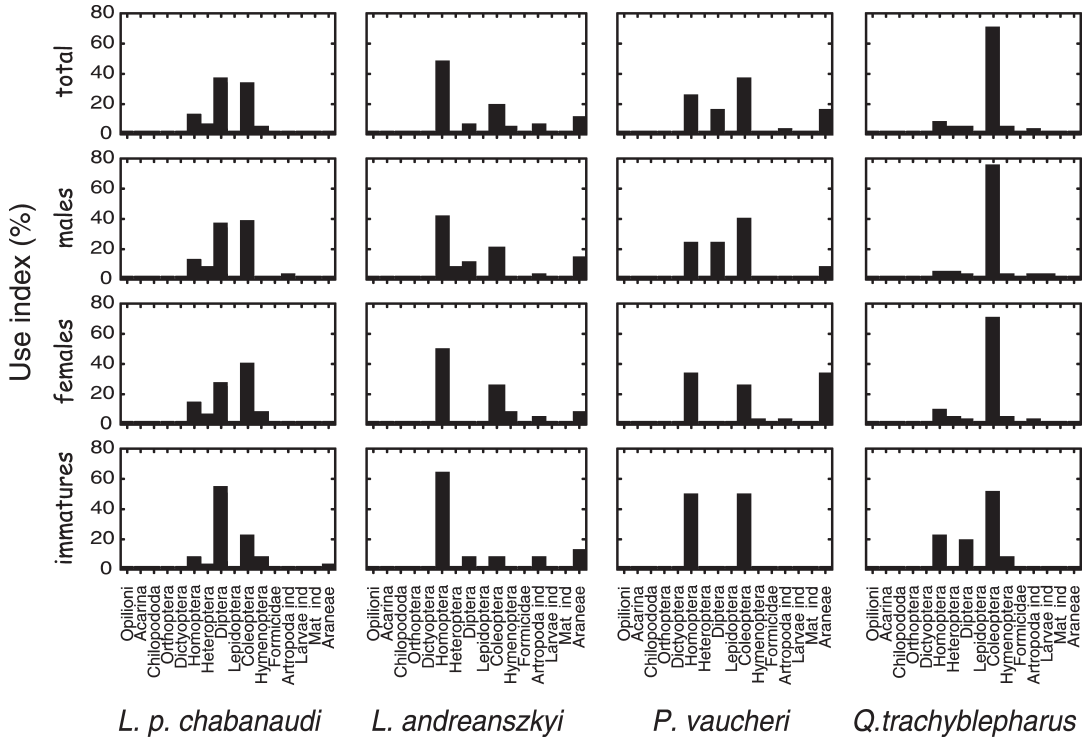
Fig. 4. Taxonomic composition of the diet by species and classes.

Table 3. Matrix of taxonomic overlaps (Pianka's index) between species.

|	L. p. chabanaudi	L. andreanszkyi	P. vaucheri	Q. trachyblepharus
L. p. chabanaudi	–			
L. andreanszkyi	53.6	–		
P. vaucheri	82.5	83.7	–	
Q. trachyblepharus	71.9	47.9	80.7	–

retained) but again not different from the RA2 matrix (zero states retained). The same analyses at the class level revealed higher overlap with equiprobability than expected in both RA3 (niche breadth retained) and RA2 (zero states retained) matrices ($P < 10^{-5}$) and overlap based on availability lower than expected in the RA3 matrix (niche breadth retained) ($P < 10^{-5}$) but similar to the RA2 matrix (zero states retained). Overlap variances were significantly ($P < 0.005$) higher only when compared with the RA2 matrices.

DISCUSSION

Diet composition in lizard communities depends on many factors including anatomical constraints, sex, body condition, reproductive state, experience, habitat, prey distribution and abundance, predation pressure, competition and phylogeny (Schoener 1968, 1974; Dunham 1980; Pianka 1986; Losos 1992, 1994; Ricklefs & Schluter 1993; Vitt & Zani 1996; Vitt *et al.* 1999; Perry & Pianka 1999; Pitt & Ritchie 2002; Desfilis & Font 2002; Carretero 2004). In the present case, body size clearly limited the size of the prey consumed by lizards at both the interspecific and intraspecific level. Prey sizes usually follow a logarithmic distribution within each lizard species, immatures showing a narrower spectrum of prey sizes than adults (Pianka 1986) and just change from one species to another independently of size if drastic divergence in anatomy or foraging tactics take place (Carretero 2004). Nevertheless, this was not the only evidence
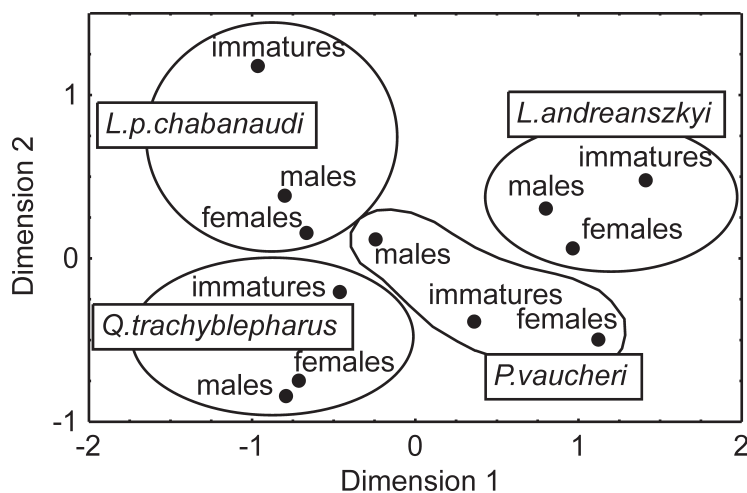
Fig. 5. MDS plot of class overlaps (Pianka index). Stress = 0.0448. Stress is a measure of degree of distortion of distances when forced to plot (in two dimensions in this case). The value can be considered low (Kruskal & Wish 1989).

for anatomical constraints. In fact, hard prey (i.e. Coleoptera) was more frequent in adults (mainly males) than in immatures in the four species. The same finding has been observed in other members of the family Lacertidae (Araujo 1990; Carretero & Llorente 1991) and there is experimental evidence of ontogenic and sexual differences in bite force for prey crashing associated with the jaw muscle mass (Herrel *et al.* 1999, 2001).

Whereas prey size accounted for most of intraspecific variation found, taxonomic composition varied markedly at the interspecific level independently of the class. All four species show distinctive habitat use (Schleich *et al.* 1996) which could determine some of the differences observed (Arnold 1987) but an assessment of trophic availability may distinguish between environmental and phylogenetic trends in prey consumption.

Nevertheless, present evidence strongly suggests that prey selection is responsible for most intraspecific variation in diet. The diet of *Q. trachyblepharus* not only indicates some specialization but also suggests consumption of aggregated prey (small beetles). This is unexpected for Mediterranean gekkonids, which are usually sit-and-wait foragers feeding on mobile, individual prey (Capula & Luiselli 1994b; Schleich *et al.* 1996; Arnold & Ovenden 2002) and adds another distinctive trait to the ecology of this genus (Arnold 1990; Schleich *et al.* 1996). Almost all the observations of this gecko during the field work were of active animals moving on steep or vertical surfaces of large rocks and not to passive animals

close to a shelter (pers. obs.).

Of the three lacertids, *P. vaucheri* and *L. andreanszkyi* mainly fed on terrestrial prey (see also Busack 1987; Schleich *et al.* 1996) whereas almost 50% of the diet of *L. p. chabanaudi* was composed of flying insects (see also Perera *et al.* in press, for comparison with other localities). Although *P. vaucheri* and *L. p. chabanaudi* were observed in close syntopy in rock outcrops, the former was also observed moving in search of prey on ground and isolated stonewalls far from them (Schleich *et al.* 1996). By contrast, *L. p. chabanaudi* never abandoned the vicinity of rock crevices and spent long periods of time immobile suggesting ambush foraging. *Lacerta andreanszkyi* was usually found moving actively on open ground or under small stones in the meadows (Busack 1987; Schleich *et al.* 1996).

The analysis of trophic diversity reinforces such statements since the lowest values at the population level were found in the most specialized species, *Q. trachyblepharus.* Remarkably, diversity was much higher (three times) in populations than in individuals for all four species, which indicates strong interindividual variation typical of generalistic predators (Carretero & Llorente 1991, 1993a).

Finally, taxonomic overlap was also concordant with the trophic traits of the community previously indicated. Thus, overlap between species was low whereas intraspecific overlap was high. Species sharing microhabitats more frequently displayed higher overlap (*L. p. chabanaudi* and *Q. trachyblepharus, P. vaucheri* and the other three species)

that those segregating spatially (*L. andreanszkyi* with *L. p. chabanaudi* and *Q. trachyblepharus*). Pseudocommunity analysis with resource equiprobability does not support community structure at the species level and even indicates higher overlap that expected at the class level. However, data from experimental sampling on invertebrate availability of similar ecosystems (Roig *et al.* 1998) show that such an assumption is untenable and even an indirect estimation of availability is preferable (Winemiller & Pianka 1990; Vitt & Carvalho 1995). Under these conditions, Monte Carlo simulations reveal trophic segregation between species based on the prey taxa not consumed (zero states) and segregation between classes based on both niche breath changes and taxa not consumed. Therefore, it must be concluded that there is trophic segregation at both inter- and intraspecific levels. Whereas the latter is clearly related to anatomical constraints of immature lizards (hence, not found in studies at species level, Winemiller & Pianka 1990), the former may result from either historical constraints or species interactions. It is obvious that the most distinctive trophic strategy corresponds to the most divergent species in the phylogeny. Nevertheless, as already mentioned, *Q. trachyblepharus* is an ecologically atypical member of its family. However, feeding on aggregated prey neither makes this species segregate from the three lacertids in prey composition nor groups them according to the phylogeny (see Harris *et al.* 1998). By contrast, species were 'packed' according to the habitat they used. Manipulative experiments or comparison with other communities would be required to determine whether trophic niche is subordinated to spatial one (Arnold 1987) eventually mediated by species interference, or an independent consequence of restriction of trophic resources (Pianka 1986; Vitt & Carvalho 1995), or even that both niche axes depend on species constraints on morphology and behaviour (Vitt 1995; Vitt & Zani 1996, 1998; Vitt *et al.* 1999, 2000).

In conclusion, regardless of the extreme seasonality and habitat simplicity of mountain ecosystems, the Oukaïmeden community appears complex and well structured from the trophic point of view in comparison with other mountain assemblages in the Mediterranean Basin (Pérez-Mellado 1991; Richard & Lapini 1993; Roig *et al.* 1998). Furthermore, it must be noted that the present study only constitutes an instantaneous picture of a dynamic system and present conclusions may not be generalizable to the whole year. For instance,

trophic availability in Alpine ecosystems is restricted only at the beginning and at the end of the active season and usually peaks in summer (Roig *et al.* 1998). Moreover, new-borns of all four species gradually appear throughout this season (Schleich *et al.* 1996). Previous studies on communities of Mediterranean lizards indicate seasonal variation of niche overlap (Carretero & Llorente 1998) which strongly increases in autumn. In fact, this may constitute a critical period in mountain environments because of the accumulation of immatures and adult lizards when thermal conditions and food availability become more constraining (Pérez-Mellado *et al.* 1991; Roig *et al.* 1998).

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REFERENCES

AKANI, G.C., CAPIZZI, D. & LUISELLI, L. 2002. Community ecology of scincid lizards in a swamp rainforest of south-eastern Nigeria. *Russian Journal of Herpetology* **9**: 125–134.

ARAUJO, A.P.R. 1990. Sobreposiçao de nicho alimentar de *Podarcis berlengensis* (Vicente, 1989) e *Lacerta lepida* (Daudin, 1802) (Sauria Lacertidae) na Ilha da Berlenga, Portugal. Graduate thesis, University of Lisbon. Portugal.

ARNOLD, E.N. 1987. Resource partition among lacertid lizards in southern Europe. *Journal of Zoology London* (B) **1**: 739–782.

ARNOLD, E.N. 1990. The two species of the Morocco day-geckoes, *Quedenfeldtia* (Reptilia: Gekkonidae). *Journal of Natural History* **23**: 757–762.

ARNOLD, E.N. & OVENDEN, D. 2002. *A Field Guide to the Reptiles and Amphibians of Britain and Europe.* Collins, London.

BONS, J. & GENIEZ, P. 1996. *Amphibians and Reptiles of Morocco.* AHE, Barcelona.

BARBAULT, R. 1991. Ecological constrains and community dynamics: linking community patterns to organismal ecology. The case of tropical herpetofaunas. *Acta Oecologica* **12**: 139–163.

BUSACK, S.D. 1987. Notes on the biology of *Lacerta andreanszkyi* (Reptilia: lacertidae). *Amphibia-Reptilia* **8**: 231–236.

CAPULA, M. & LUISELLI, L. 1994a. Resource partitioning in a Mediterranean lizard community. *Bollettino*

di Zoologia, **61**: 173–177.

CAPULA, M. & LUISELLI, L. 1994b. Trophic niche overlap in sympatric *Tarentola mauritanica* and *Hemidactylus turcicus:* a preliminary study. *Herpetological Journal* **4**: 24–25.

CARRETERO, M.A. 2004. From set menu to *à la carte.* Linking issues in trophic ecology of Mediterranean lacertids. *Italian Journal of Zoology* Suppl. **2**: 121–133.

CARRETERO, M.A. & LLORENTE, G.A. 1991. Alimentación de *Psammodromus hispanicus* en un arenal costero del nordeste ibérico. *Revista Española de Herpetología* **6**: 31–44.

CARRETERO, M.A. & LLORENTE, G.A. 1993a. Feeding of two sympatric lacertids in a sandy coastal area (Ebro Delta, Spain). In: *Lacertids of the Mediterranean Region. A Biological Approach,* (eds) W. Böhme, V. Pérez-Mellado, E. Valakos & P. Maragou, pp. 155–172. Hellenic Zoological Society, Athens.

CARRETERO, M.A. & LLORENTE, G.A. 1993b. Morfometría en una comunidad de lacértidos mediterráneos, y su relación con la ecología. *Historia Animalium* **2**: 77–79.

CARRETERO, M.A., LLORENTE, G.A., SANTOS, X. & MONTORI, A. 2001 The diet of an introduced population of *Podarcis pityusensis.* Is herbivory fixed? In: *Mediterranean Basin Lacertid Lizards. A Biological Approach,* (eds.) L. Vicente & E.G. Crespo, pp. 113–124. ICN, Lisbon.

CARRETERO, M.A. & LLORENTE, G.A. 1998. Seasonal variation of niche overlap in a lacertid community. Abstract book. *Third International Symposium on the Lacertids of the Mediterranean Basin,* Cres, Croatia.

DESFILIS, E. & FONT, E. 2002. Efectos de la experiencia sobre el comportamiento depredador de los reptiles. *Revista Española de Herpetología* special volume: 79–94.

DUNHAM, A.E. 1980. An experimental study on interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus. Ecological Monographs* **50**: 309–330.

ESCARRÉ, A. & VERICAD, J.R. 1981. *Cuadernos de Fauna Alicantina I. Saurios y Ofidios.* Diputación de Alicante, Alicante, Spain.

GOTELLI, N.J. & ENTSMINGER, G.L. 2001. *EcoSim: Null models software for ecology.* Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepages. together.net/~gentsmin/ecosim.htm

GOTELLI, N.J. & GRAVES, G.R. 1996. *Null Models in Ecology.* Smithsonian Institution Press, Washington, D.C.

HARRIS D.J., ARNOLD E.N. & THOMAS R.H. 1998. Relationships of the lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proceedings of the Royal Society of London Series B* **265**: 1939–1948.

HARRIS, D.J., CARRETERO, M.A., PERERA, A., PÉREZ-MELLADO, V. & FERRAND, N. 2003. Complex patterns of genetic diversity within *Lacerta (Teira) perspicillata*: preliminary evidence from 12S rRNA sequence data. *Amphibia-Reptilia* **24**: 386–390.

HARRIS, D.J. & SÁ-SOUSA, P. 2001. Species distinction and relationships of the Western Iberian *Podarcis* lizards (Reptilia, Lacertidae) based on morphology and mitochondrial DNA sequences. *Herpetological Journal* **11**: 129–136.

HARRIS, D.J. & SÁ-SOUSA, P. 2002. Molecular phylogenetics of Iberian wall lizards (*Podarcis*): is *Podarcis hispanica* a species complex*? Molecular Phylogenetics and Evolution* **23**: 75–81.

HERREL, A., SPITHOVEN, R., VAN DAMME, R. & DE VREE, F. 1999 Sexual dimorphism of head size in *Gallotia galloti:* testing the niche divergence hypothesis by functional analyses. *Functional Ecology* **13**: 289–297.

HERREL, A., VAN DAMME, R., VANHOOYDONCK, B. & DE VREE, F. 2001. The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology* **79**: 662–670.

JABIRI, A., BENKHALDOUM, Z., VERNIN, J. & MUÑOZ-TUÑÓN, C. 2000. A meteorological and photometric study of the Oukaimeden site. *Astronomy and Astrophysics Supplementary Series* **146**: 271–284.

JOVER, L. 1989. Nuevas aportaciones a la tipificación trófica poblacional: el caso de *Rana perezi* en el Delta del Ebro. Ph.D. thesis, University of Barcelona, Barcelona.

KRUSKAL, J.B. & WISH, M. 1989. *Multidimensional Scaling.* Sage University Paper series on Quantitative Applications in Social Sciences 11. Sage Publications, Beverly Hills and London.

LOSOS, J.B. 1992. The evolution of convergent structure in Caribbean *Anolis* lizards. *Systematic Biology* **41**: 403–420.

LOSOS, J.B. 1994. Historical contingency and lizard community ecology. In: Lizard Ecology: Historical and Experimental Perspectives, (eds.) L.J. Vitt & E.R. Pianka. Princeton University Press. Princeton.

MAGURRAN, A.E. 1988. *Ecological Diversity and its Measurement.* Crom. Helm., London.

PERERA, A. 2002. *Lacerta perspicillata* Duméril y Bibron, 1839. Lagartija de Marruecos. In: *Atlas y libro Rojo de los Anfibios y Reptiles de España* (2nd impression), (eds.) J.M. Pleguezuelos, R. Márquez & M. Lizana, pp. 231–232. DGCN-AHE, Madrid.

PERERA, A., PÉREZ-MELLADO, V. CARRETERO, M.A. & HARRIS, D.J. In press. Site variation in the diet of the Mediterranean lizard *Lacerta perspicillata. Herpetological Journal.*

PÉREZ-MELLADO, V. 1982. Estructura de una taxocenosis de Lacertidae (Sauria, Reptilia) del Sistema Central. *Mediterránea Ser. Biol.* **6**: 39–64.

PÉREZ-MELLADO, V., BAUWENS, D., GIL, M., GUERRERO, F., LIZANA, M. & CIUDAD, M.J. 1991. Diet composition and prey selection in the lizard *Lacerta monticola. Canadian Journal of Zoology* **69**: 1728–1735.

PEREZ-MELLADO, V. 1992. Ecology of lacertid lizards in a desert area of eastern Morocco. *Journal of Zoology London (B)* **226**: 369–386.

PERRY G. & PIANKA E. 1999. Animal foraging: past, present and future. *Tree* **12**: 360–364.

PIANKA, E.R. 1966. Convexity, desert lizards and spatial heterogeneity. *Ecology* **47**: 1055–1059.

PIANKA, E.R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* **4**: 53–74.

PIANKA, E.R. 1986. *Ecology and Natural History of Desert Lizards.* Princeton University Press, Princeton, NJ.

PINHO, C., HARRIS, D.J. & FERRAND, N. 2003. Genetic

polymorphism of 11 allozyme loci in populations of wall lizards (*Podarcis* sp.) from the Iberian Peninsula and North Africa. *Biochemical Genetics* **41**: 343–359.

PINHO, C., FERRAND, N. & HARRIS, D.J. 2004. Genetic variation within the *Podarcis hispanica* species complex – new evidence from protein electrophoretic data. In: *The Biology of Lacertid Lizards. Evolutionary and Ecological Perspectives,* (eds) V. Pérez-Mellado, N. Riera & A. Perera, pp. 269–277. Recerca 8. Institut Menorquí d' Estudis, Recerca, Maó, Spain.

PINHO, C., FERRAND, N. & HARRIS, D.J. 2006. Reexamination of the Iberian and North African *Podarcis* (Squamata: Lacertidae) phylogeny based on increased mitochondrial sequencing. *Molecular Phylogenetics and Evolution* **38**: 266–273.

PITT, W.C. & RITCHIE, M.E. 2000. Influence of prey distribution on the functional response of lizards. *Oikos* **96**: 157–153.

RICE, W.C. 1989. Analyzing tables of statistical tests. *Evolution* **43**: 223–225.

RICHARD, J. & LAPINI, L., 1993. Trophic niche overlap in syntopic populations of *Lacerta horvathi* and *Podarcis muralis* (Reptilia, Lacertidae). *Atti del Museo civico di Storia naturale di Trieste* **45** : 151–157.

RICKLEFS, R.E. & SCHLUTER, D. (eds) 1993. *Species Diversity in Ecological Communities.* University of Chicago Press. Chicago.

ROIG, J.M., CARRETERO, M.A. & LLORENTE, G.A. 1998. Trophic selection in a Pyrenean population of *Zootoca vivipara*. In: *Abstract book. Third International Symposium on the Lacertids of the Mediterranean Basin,* Cres, Croatia.

SCHLEICH, H.H., KÄSTLE, W. & KABISCH, K. 1996. *Amphibians and Reptiles of North Africa.* Koeltz. Koenigstein.

SCHOENER, T.W. 1968. The *Anolis* lizard of Bimini: resource partitioning in a complex fauna. *Ecology* **51**: 408–418.

SCHOENER, T.W. 1974. Resource partitioning in ecological communities. *Science* **185**: 27–39.

STRIJBOSCH, H., HELMER, W. & SCHOLTE, P.T. 1989. Distribution and ecology of lizards in the Greek province of Evros. *Amphibia-Reptilia* **10**: 151–174.

VITT, L.J. 1995. The ecology of tropical lizards in the Caatinga of Northeastern Brazil. *Occasional Papers of the Oklahoma Museum of Natural History* **1**: 1–29.

VITT, L.J. & CALDWELL, J. 1994. Resource partitioning and guild structure of small vertebrates in the Amazon forest leaf litter. *Journal of Zoology London (B)* **234**: 463–476.

VITT, L.J. & CARVALHO, C.M. 1995. Niche partitioning in a tropical wet season: lizards in the Lavrado area of Brazil. *Copeia* **1995**: 305–329.

VITT, L.J. & ZANI, P.A. 1996. Organization in a taxonomically diverse lizard assemblage in Amazonian Ecuador. *Canadian Journal of Zoology* **74**: 1313–1335.

VITT, L.J. & ZANI, P.A. 1998. Ecological relationships among sympatric lizards in a transitional forest in the northern Amazon of Brazil. *Journal of Tropical Ecology* **14**: 63–86.

VITT, L.J., ZANI, P.A. & ESPØSITO, M.C. 1999. Historial ecology of Amazonian lizards: implications for community ecology. *Oikos* **87**: 286–294.

VITT, L.J., SARTORIUS, S.S., AVILA-PIRES, M.T., ESPØSITO, M.C. & MILES, D.B. 2000. Niche segregation among sympatric Amazonian teiid lizards. *Oecologia* **122**: 410–420.

WINEMILLER, K.O. & PIANKA, E.R. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* **60**: 27–55.

ZNARI, M., EL MOUDEN, E.H., BENFAIDA, J. & BOUMEZZOUGH, A. 2000. Partage des ressources spatiales et trophiques au sein d'un pouplements de lezards insectivores dels Jbilets centrales (Maroc occidental). *Revue d'Ecologie (La Terre et la Vie)* **55**: 141–160.