A preliminary study on thermal ecology, activity times and microhabitat use of *Lacerta agilis* (Squamata: Lacertidae) in the Pyrenees

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Received 28 September 2002; Accepted 21 February 2003

A b s t r a c t . The thermal relations, diel, and annual activity and microhabitat use of *Lacerta agilis* were studied in the Pyrenean isolated range of this species. Although, this heliothermic lizard demonstrated thermoregulatory capability, thermal constraints attributable to the mountain climate were observed. The activity pattern was that typical of cold temperate lizards but the beginning of activity was delayed in comparison with lowland populations. The reproductive cycle determined different activity patterns for males and females. The ontogenetic and seasonal changes in microhabitat use detected suggest influence of body size, reproductive condition in adults, and interference with other individuals in juveniles.

Key words: thermoregulation, diel activity, annual activity, habitat, Sand lizard, Pyrenees

Introduction

The sand lizard (*Lacerta agilis* Linnaeus, 1758) is, after *Lacerta (Zootoca) vivipara*, the second lacertid with the largest geographical range, from Lake Baikal to the Pyrenees and from S Sweden to N Greece (B i s c h o f f 1988). In addition, this species is distributed across a wide altitudinal range (0–2200 m) and occupies a great diversity of biotopes such as dunes, steppes, forest margins, rocky slopes or meadows (B i s c h o f f 1984, K o r s ó s & B i s c h o f f 1997) offering a remarkable example of ecological plasticity in lizards. Obviously, the next question that arises is how the same species is able to live under such different biotic and abiotic conditions. A plausible biogeographic scenario (Y a b l o k o v et al. 1980), now supported by phylogeographic analyses (K a l y a b i n a et al. 2001), postulates recent European dispersal from the Caucasus, attributing a pleistocenic origin to the isolated Pyrenean populations. If true, analysing the use of ecological resources by these populations living in this southwestern boundary would be especially interesting because results could reveal eventual species constraints. Some aspects of Sand lizard biology such as sexual selection, clutch parameters or population genetics have already been intensively investigated (O l s s o n 1993, O l s s o n et al. 1996, 1997, O l s s o n & S h i n e 1996, 1997, G u l l b e r g et al. 1998, 1999). However, more general studies on the thermal and spatial ecology have been restricted to lowland populations (G l a n d t 1979, 1991, 1995, H o u s e et al. 1980, V a n N u l a n d & S t r i j c h b o s c h 1981, H o u s e & S p e l l e r b e r g 1983, O l s s o n 1986, S t r i j c h b o s c h 1986, N i c h o l s o n & S p e l l e r b e r g 1989) and little is know about them in the high altitude populations of this species.

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In a previous paper (A m a t et al. 2000), the reproductive biology of Pyrenean populations was analysed in search of changes with regard to the northern European populations, since subalpine Pyrenean environments may have the most limited resources, due to climatic restrictions. Following the same line of reasoning, the present study aims to analyse the thermal, temporal, and spatial characteristics of the Sand lizard in the Pyrenees and compare the results with available studies carried out in the rest of the range.

Material and Methods

A survey carried out in 1993 of the NW slope of Tossa d'Alp (Serra del Cadí, Western Pyrenees, UTM 31T DG18) discovered an extensive population of *Lacerta agilis* in a subalpine meadow at 1600 m (for an extensive description see A m a t et al. 2000). This population was selected for the present study. The sampling was carried out during 1994–96 from May to October and from 6:00 to 20:00 (GMT) since all visits carried before and after that period did not report lizard observations. An itinerary in search of lizards with a uniform effort crossed all microhabitat categories and covered an area of approximately 150 ha. This transect was designed for avoiding repeating observations of one individual during the same sampling and was carried out only in sunny days without strong wind.

Population class was determined for each lizard observed (N=565) or captured (N = 229), according to the dimorphic colour pattern and minimum snout-vent lengths (SVL) for adult males and females (60 and 70 mm respectively, A m a t et al. 2000). Separation of subadults and juveniles followed the criteria of C a r r e t e r o & L l o r e n t e (1993). SVL of captured lizards was measured with a calliper (0.05 mm accuracy), and pregnancy in females was assessed by palpation during the reproductive period (from the beginning of May to the end of June, A m a t et al. 2000). In all cases, the behaviour of the lizards when sighted was classified as to movement and immobility.

Temporal variation in the number of individuals detected was categorised in two-hour (diel), 15-day (seasonal) and reproductive/non-reproductive season intervals. Since sampling effort by time could not be kept constant for logistic reasons, it was standardised *a posteriori* in each case by dividing the number of individuals observed in each time interval by the percentage of sampling time in that interval in comparison with the total time.

Microhabitat in the exact location of the lizard was typified according to 7 categories: low meadow (only *Festuca* grass), high meadow (grass, annual plants and bushes since 40 cm high), *Juniperus communis*, *Buxus sempervirens*, *Rosa canina*, *Cirsium eriophorum* and others. For lizards captured, cloacal (= body, Tb), air (Ta) and substrate temperatures (Ts) were measured using a digital thermometer with a k-thermocouple probe (Digitron 3208K, accuracy 0.01 °C, for more details see C a r r e t e r o & L l o r e n t e 1995). The relationships between the ecological categorical variables were analysed using logistic ANOVA models (C h r i s t e n s e n 1990). Thermal relations were analysed by means of partial correlations, least-squares regression and ANCOVA (S o k a l & R o h l f 1995) using the environmental temperature most correlated with Tb as a covariate. Temperatures were not transformed prior to analyses since they were normally distributed (all but Tb: Kolmogorov-Smirnov tests, $p > 0.05$), homosedastic and means and variances were uncorrelated. Although Tb was skewed to higher values, robustness of ANOVA was assumed (Z a r 1999) since the pattern was the same in all groups compared. Nevertheless, a subanalysis restricted to moving animals revealed normality for this variable and produced identical results.

Diversity in microhabitat use was calculated by means of Brillouin's index according to Magurran (1988). Population diversity (Hp) was estimated by the Jack-knife technique (Jover 1989) and compared by t-tests Bonferroni corrected (Carretero & Llorente 1991).

Results

Thermal ecology

Table 1 shows the descriptive values of temperatures for each class. Values of Tb (overall mean ± SE.: 30.3 ± 0.22 °C, range: 35.9–15.2) were correlated only with air temperature ($r_{partial}$ = 0.40, P < 0.001, 19.6 ± 0.26 °C, 35.8–9.7) for the 229 individuals collected. Tb showed lower variation than Ts, which was less variable than Ta (Levene test $F_{1,436}$ = 5.093, P = 0.024). Intraspecific differences between Tb, adjusted for Ta, were detected (Fig. 1, ANCOVA $F_{2,213}$ = 5.50, P = 0.047). Although *post hoc* tests did not reveal which pairs of comparisons were different, adult males showed the highest mean value of adjusted Tb. In fact, males were captured with lower Ta than the rest of the population (ANOVA $F_{2,216}$ = 8.423, P < 0.01, Sheffé's test P = 0.007 and P = 0.001 for comparisons with females and immatures, respectively).

Table 1. Descriptive statistics of the body (Tb) air (Ta) and substrate (Ts) temperatures of Pyrenean *Lacerta agilis*.

Class		n	mean	SE	min.	max.
Adult males	Tb	56	30.18	0.49	15.20	35.20
	Ta	56	17.90	0.49	9.70	25.50
	Ts	56	20.00	0.64	7.80	32.00
Adult females	Tb	87	29.34	0.41	18.40	35.80
	Ta	87	19.93	0.38	13.50	27.40
	Ts	87	21.26	0.46	11.80	33.10
Immatures	Tb	76	30.29	0.41	16.50	35.90
	Ta	74	20.32	0.46	11.20	29.00
	Ts	76	21.27	0.54	10.20	38.20

The slopes of the Tb/Ta regression lines of all classes (Fig. 1) were significantly different from each other and from 0 and 1 (t tests, P < 0.01). No temperature variation was found either between reproductive and non-reproductive periods or depending on pregnancy. No differences in Tb (adjusted to Ta) were detected between months considering the population class.

Activity

Sand lizards were observed between the first week of May and the end of September (Fig. 2). Adult males started activity one week before the rest of the population but the number of observations declined progressively, reaching a minimum by the end of the reproductive season (second half of June). Afterwards, a slight recovery was observed and, finally, it decreased again. In contrast, the observations of females increased gradually throughout the reproductive period and reached a maximum in June, this class remaining very active in

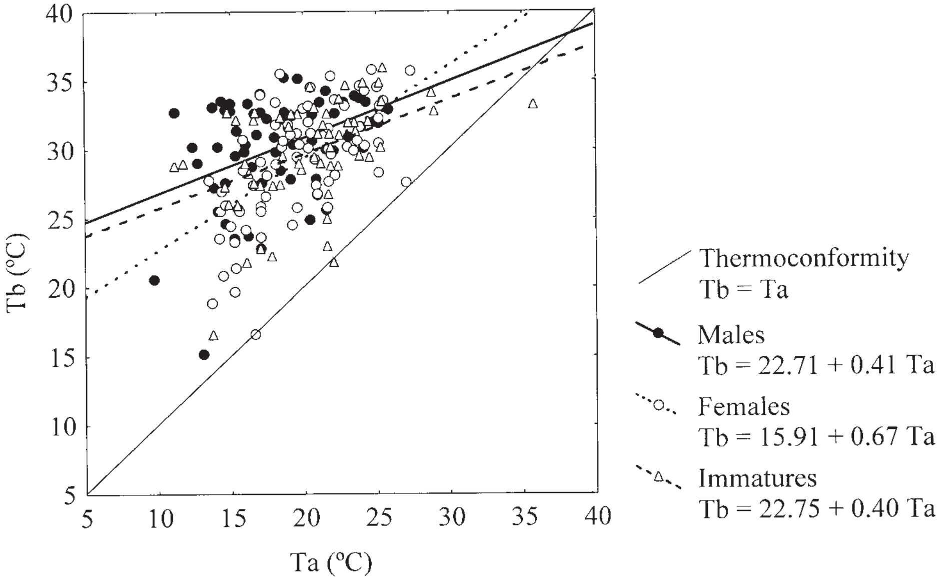

Fig. 1. Regression lines between body (Tb) and air (Ta) temperatures for adult male, adult female, and immature *Lacerta agilis* from the Pyrenees.

summer and showing strong variations in autumn. Subadults showed a delay in beginning activity and were more frequently observed in summer. Observations of juveniles remained constant activity in spring, disappearing due to their incorporation into the subadult class in summer. Hatchlings coming from the first clutches produced a second peak of observations for this class.

A logistic model was performed for assessing relations between movement (M), population class (PC), diel activity (D, two-hour intervals) and reproductive or non-reproductive period (RP) of the lizards observed. The population class was not directly associated with either daily interval or movement (marginal association test: PC/M $\chi^2 = 2.89$, df = 4, P = 0.576; PC/D $\chi^2 = 34.65$, df = 24, P = 0.073). The reproductive period was related with population class, diel activity and movement, independently from the influence between the last two factors (marginal association test: RP/PC $\chi^2 = 17.74$, df = 4, P = 0.001; RP/D $\chi^2 = 21.82$, df = 6, P = 0.001; RP/M $\chi^2 = 9.31$, df = 1, P = 0.002; M/D $\chi^2 = 14.53$, df = 6, P = 0.02).

Males were more frequently observed during the reproductive period (61.87 % of total male observations) than during the rest of the year. In contrast, adult and subadult females, and subadult males were more frequently detected in the non-reproductive period (55.07%, 53.95%, and 65.98% of the observations of each class, respectively). Moreover, during the reproductive period, more sand lizards were observed at midday or in the afternoon. Although the lizards were most commonly observed immobile (81.46 % for the complete period of activity) at midday the percentage of individuals in movement increased. Moreover, after the reproductive period, more individuals in movement were detected (44.67% compared with 36.79%). The graphic analysis of diel activity in the different classes (Fig. 3) revealed a unimodal pattern in adult and subadult females (midday) and

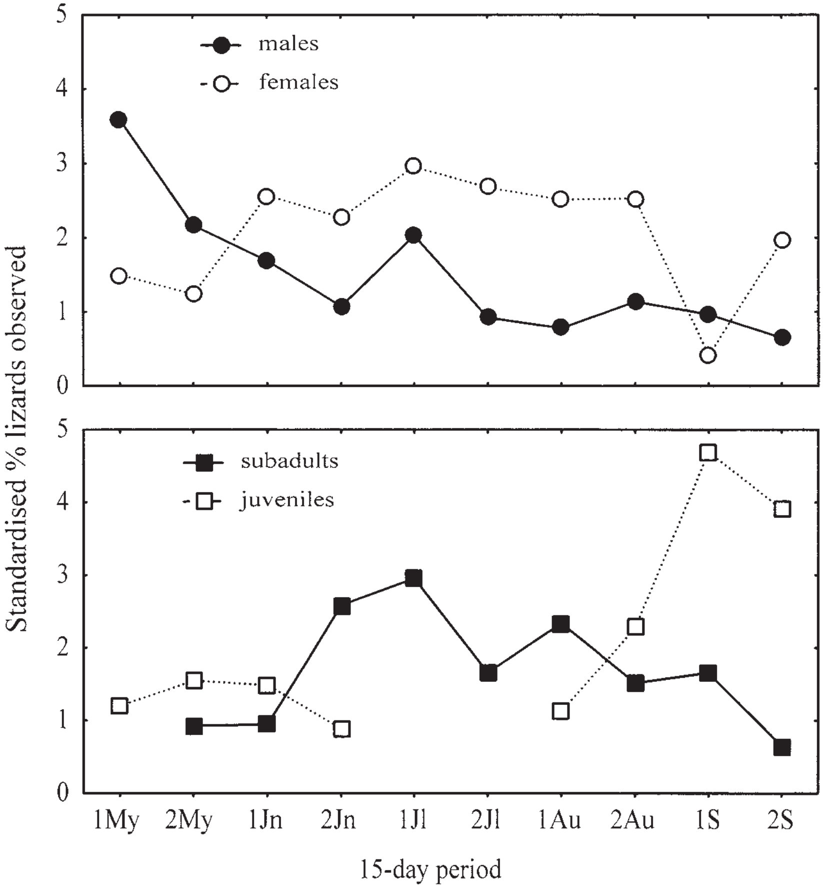

Fig. 2. Annual activity plots of adult male, adult female, subadult, and juvenile *Lacerta agilis* in the Pyrenees.

juveniles (morning). Conversely, adult and subadult males showed a tendency to bimodality, with two peaks, in the morning and in the afternoon.

M i c r o h a b i t a t

Intraspecific differences were found in microhabitat use (MH). Although Fig. 4 shows results pooled by class for simplification, some seasonal variation was detected. The reproductive period (RP) modified microhabitat use independently in each population class (PC) (marginal association tests: PC/RP $\chi^2 = 16.33$, df = 4, P = 0.003; MH/PC $\chi^2 = 37.059$, df = 24, P = 0.04; MH/RP $\chi^2 = 22.27$, df = 6, P = 0.001). Both kinds of meadow were the most commonly used microhabitats. Males were more frequently seen in *Rosa canina* bushes than in *Juniperus communis*, whereas females (both pregnant and non-pregnant) used both microhabitats equally. The pattern of subadult males was similar to that shown by adult males, whereas subadult females were intermediate between adult females and juveniles (Fig. 4), which were rarely found in bushes (mainly *Rosa canina* and *Cirsium eriophorum*). Microhabitat of adult

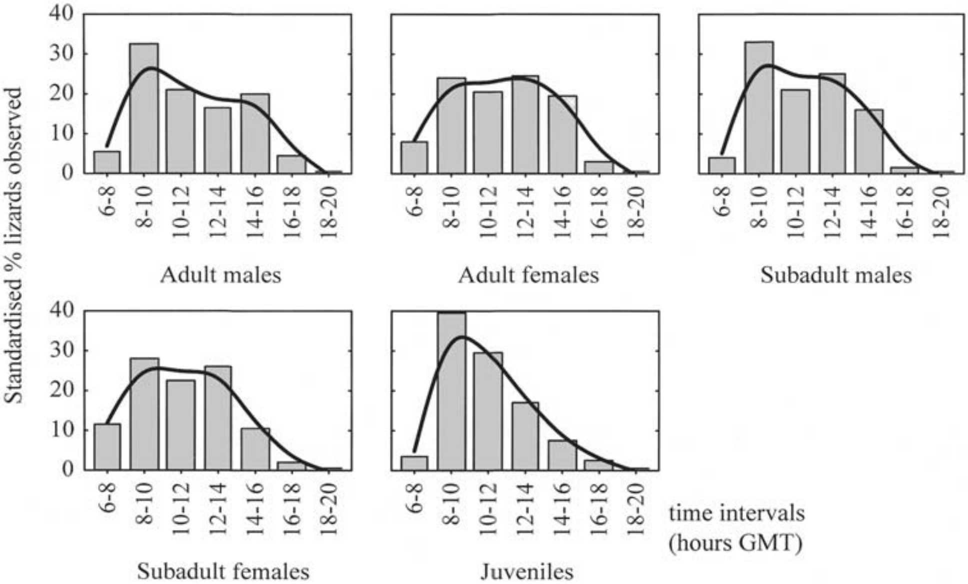

Fig. 3. Diel activity histograms for adult male, adult female, subadult male, subadult female, and juvenile *Lacerta agilis* in the Pyrenees. Lines have been adjusted by minimum squares.

males was affected by breeding season. After this period, the use of the low meadow and *Rosa canina* bushes underwent an important decrease (t-tests for proportions: 93.7 to 6.25% $t_{72} = 4.57$, $P < 0.00001$; low meadow, 70.5 to 29.4% *Rosa canina* $t_{72} = 4.57$, $P < 0.00001$). Females increased the use of high meadow and the *Buxus sempervirens* and *Rosa canina* bushes during the post-breeding period (25.3 to 74.6% high meadow $t_{181} = 4.38$, $P < 0.00001$; 33.3 to 66.6% *Buxus sempervirens* $t_{181} = 4.38$ $p < 0.00001$; and 36.0 to 64.0% *Rosa canina* $t_{181} = 4.38$ $p < 0.00001$). Subadult males and females showed a similar pattern, characterised by a more frequent use of both types of meadows after the reproductive period and an increase of *Buxus sempervirens* and *Rosa canina* bushes (subadult males: 33.3 to 66.6% low meadow $t_{60} = 2.49$, $p = 0.008$; 35.4 to 64.5% high meadow $t_{60} = 2.19$, $P = 0.016$; 20 to 80% *Buxus sempervirens* $t_{60} = 4.63$, $P < 0.00001$; and 33.3 to 66.6% *Rosa canina* $t_{60} = 2.49$, $P = 0.008$; subadult females: 38.4 to 61.5% low meadow $t_{85} = 2.01$ $P = 0.024$; 33.3 to 66.6% high meadow $t_{85} = 2.90$, $P = 0.0024$; 0 to 100% *Buxus sempervirens* and 33.6–66.6% *Rosa canina* $t_{85} = 2.90$. $P = 0.0024$). In contrast, juveniles were more frequently observed in low meadow, *Juniperus communis* and *Cirsium eriophorum* inside the reproductive period than outside (32.3 vs. 67.6% low meadow $t_{127} = 3.16$, $P = 0.001$; 25.0 vs. 75% *Juniperus commu nis* $t_{127} = 3.83$, $P < 0.00001$; and 16.6 vs. 83.3% *Cirsium eriophorum communis* $t_{127} = 3.83$, $P < 0.00001$).

Microhabitats used were more diverse in adults (males Hp = 2.31 ± 0.11, females 2.38 ± 0.08) and subadults (males 2.11 ± 0.15, females 2.21 ± 0.13) than in juveniles (1.68. ± 0.12); these differences were statistically significant (t-tests, $P < 0.02$ in all cases). When considering seasonal variation, diversities tended to decrease after the reproductive period in females (2.51 ± 0.10 vs. 2.12 ± 0.11, $t = 2.60$, df = 182, $P = 0.01$) but they were similar in the rest of the classes (males 2.16 ± 0.12 vs. 2.09 ± 0.17, n.s.; subadult males 2.08 ± 0.25 vs.

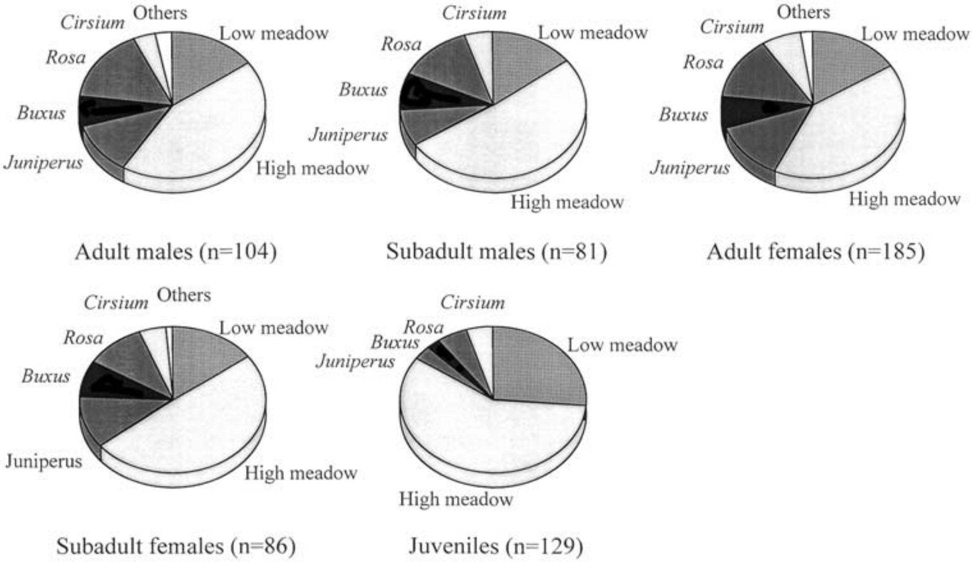

Fig. 4. Standardised percentage of microhabitat use by adult male, adult female, subadult male, subadult female, and juvenile *Lacerta agilis* in the Pyrenees.

2.09 ± 0.19, n.s.; subadult females 2.03 ± 0.22 vs. 2.18 ± 0.14, n.s.; juveniles: 1.49 ± 0.19 vs. 1.79 ± 0.15, n.s.).

Discussion

Mean body temperature values of *L. agilis* measured in the Pyrenees were lower than those observed in British populations (Langton 1988) and also lower than the temperatures selected in a thermal gradient (Bauwens et al. 1995). If the conservative nature of this trait within the species limits for lacertids is assumed (Gvoždík & Castilla 2001), only 58.07% of the temperatures recorded in the field fell into the interval selected in the laboratory. This finding reveals thermal constraints attributable to the environmental conditions of the high mountain climate of the Pyrenees.

According to the thermal relations observed (Huey & Slatkin 1976), *Lacerta agilis* is a heliothermic lizard with thermoregulatory capability. Males are very active in the morning (see Activity) when environmental temperatures are low, but maintain a body temperature similar to the other classes. This suggests that males may have longer basking periods or occupy more exposed sites in microhabitats than the rest of the population (pers. obs.). The analysis did not detect either diel or seasonal variation of the body temperatures. Although environmental temperatures remain very similar during the activity of the lizards, the limitations of the sample size should also be taken into account. Measures of thermal environment for each class and season could be sensibly improved by analysing operative temperatures using copper models randomly located in the habitat (see Castilla et al. 1999, Gvoždík 2002, and references therein).

The general activity pattern of *L. agilis* is the typical one displayed by the lizards inhabiting cold temperate regions (Paulissen 1988, Adolph & Porter 1993). The beginning of the annual activity of the Pyrenean population was delayed in comparison with other European populations living in lowlands: 45 days later than in Britain (Langton 1988); 40–30 days later than in a population in seminatural conditions in NW France (Saint-Girons 1976) and Germany (Glandt 1995), respectively; 21 days later than in the Netherlands (Van Nuland & Strijbosch 1981) and 15 days later than in Sweden (Olsson et al. 1996). However, these comparisons should be interpreted with caution since different authors could have estimated the beginning of the activity in different ways. Nevertheless, the general pattern was very similar (see Van Nuland & Strijbosch 1981, Korsós & Gyovai 1988, Glandt 1995). The decrease in male activity in June is attributed to the stress associated with the breeding activities of the preceding period (Glandt 1995, see Ortega & Barbault 1986, for an extreme example). Female activity continues to increase throughout the reproductive season but decreases in the beginning of June when the first clutches are laid (Amat et al. 2000). The high ecological and physiological costs of egg production (Partridge & Harvey 1985) together with the predation risk have been the factors invoked for explaining similar patterns (Rose 1981, Etheridge & Wit 1993). The low activity of immature animals in early spring coincides with a period of low prey availability in Pyrenean habitats (Roig et al. 1999) and with high risk of interference with adult males in the beginning of the breeding season (Fig. 2, Olsson & Madsen 1996). However, the increase of subadults observed in summer is mostly due to the demographic effect of gradual incorporation of the last cohort of juveniles in this class (Glandt 1988).

Regarding microhabitats used, it must be remarked that the Pyrenean habitat clearly differed from those of other populations studied where sand or bare ground was available (Glandt 1986, Strijbosch 1986). Regarding the Pyrenees, it is noteworthy that although meadows are structurally poorer than bushes and provide less shelter, they were the most frequently used microhabitats. Thermal and food availability (especially in high meadow) have been previously used to explain this pattern (House & Spellerberg 1983, Stumpel 1988, Korsós & Gyovai 1988). Meadows provided enough cover against predators for the juveniles but not for the adults. However, juveniles did not used bushes which could be suitable shelters but were usually occupied by adults. This suggest behavioural interactions between juveniles and adults as reported for other lacertids (Carretero & Llorente 1997, Carretero & Bartralot 2000). Moreover, the increase of juveniles observed in *Cirsium* bushes parallels the growth of this annual plant throughout the activity period (see Martín & López 1998, Carretero & Bartralot 2000, for a similar pattern in the lacertid *Psammodromus algirus*). In adults, both sexes shared similar habitats in the reproductive season but not during rest of the year. Nicholson & Spellerberg (1989) report larger home range size in males and higher overlap with females during this period. Thus, not only ontogenetic and but also reproductive changes in microhabitat use were detected. Body size constraints via predatory pressures (Gramentz 1996) and capability to respond to behavioural interactions could explain the increase in microhabitat diversity along lizard growth.

Acknowledgements

Study permits numbers 002908 and 0011494 were provided by the former Subdirecció General de Conservació de la Natura, Departament d'Agricultura, Ramaderia i Pesca of the Generalitat de Catalunya (Spain).

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