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Habitat selection at the sand lizard (*Lacerta agilis*): ontogenetic shifts

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Abstract. Ontogenetic shifts at lizards' microhabitat selection were studied using sand lizard (*Lacerta agilis*) as model organism. Field observations evidenced that sightings of hatchling lizards followed the distribution of microhabitat categories while yearlings and adults showed a more active perch selection. However, multivariate analysis evidenced active selection at all age categories. Genuine ontogenetic shifts in habitat selection were recorded with most outstanding differences between hatchlings and yearlings. Lizards' perching sites were significantly more homogenous than randomly selected control spots. Microhabitat characteristics measured at adults and yearlings were similar and differed significantly from those measured in the case of hatchlings. Multivariate analyses offered more detailed picture about lizards habitat use and proved to be more sensitive than the traditional goodness-of-fit tests.

Key words: microhabitat selection, ontogenetic shift, sand lizard, *Lacerta agilis*

Introduction

The distribution of animals in their natural environment is not random. Habitat selection can be regarded as an interaction between choices made by individuals and the action of agents that remove individuals from specific places (Orians 2000). On mesoscal level reptiles, including lizards', distribution is mostly explained by climate and topography (Gusian & Hofer 2003), highest variance in distribution being explained by ambient energy (Rodríguez et al. 2005). On a narrow level a complexity of factors influences habitat use and aggregation of lizards within a given habitat, such as: morphological features and locomotor performance (Vanhooydonck et al. 2000, Irschich & Losos 1999), possibilities of achieving the optimal body temperature (Melville & Schulte 2001, Grover 1996), competitive interactions (Vanhooydonck et al. 2000, Downes & Bauwens 2002), predator avoidance (Downes & Shine 1998). On the other side, the lizards' natural history (Smith 1998) and morphological characteristics (Herrel et al. 2002) are strongly linked to populated habitat and shifts in habitat characteristics leads to evolution in lizards' morphology (Vitt et al. 1997).

The purpose of this study was to characterise microhabitat selection in a population of sand lizards (*Lacerta agilis*). The sand lizard, *Lacerta agilis*, is one of the most widespread paleartic species, the distribution range extending from the British islands the Northwest China across a wide altitudinal range of 0-2200 m, occupying a vast variety of habitat types such as dunes, steps, meadows, forest margins and woodland (Korsós & Bischoff 1997).

The sand lizard is a strictly protected species in Romania (Law 462/2001, Order 1.198/2005).

The present study combines two traditional approaches (e.g Castillia & Bauwens 1992) for the analysis of lizard habitat use. First, we explore lizards' sighting frequency in relation to microhabitat availability. Second, we try to identify factors that influence lizards' microhabitat selection. Since habitat selection may involve different ontogenetic responses to the environmental factors (Heatwole 1977), we also investigated whether age category influences microhabitat selection by testing the null hypothesis of ontogenetic differences in lizards' microhabitat selection and factors that influence it. A previous assumption (Nemes unpublished data) suggests that hatchlings are generalists, adult's specialist while yearlings constitute transition between them regarding microhabitat selection. Ontogenetic shifts are expected as growing involves not only growth regarding body size and weight but gain in experience as well. Both factors have a strong influence on the behavioural profile of a lizard. An increased body size invokes different physiological needs subsequently different behaviour (e.g. Stevenson 1985, Martín & López 2003). Experience, helps lizards to choose the best possible behavioural response to an environmental factor (Goldberg et al. 1999).

Materials and Methods

Fieldwork was carried out in 2001 on the nearby meadows of Sf. Gheorghe town, Romania (45°52'0''N, 25°46'60''E). The area contains wooded hills and plain meadows. The climate is characterised by 7.6°C annual average temperature with relatively warm summers and cold winters. Annual rainfall averages about 550 mm per year. The studied lizards' population occupies a habitat with 10-20° slope with southern exposure, covered by grass, herbaceous vegetation and small bushes (up to 1.5 m). The study site is bordered by *Fagus sylvatica* forest, a brook and two small artificial lakes at the base of the slope. Observations were conducted between 0900-1130 local time on sunny days with similar meteorological conditions.

1. Sighting frequency and microhabitat availability

The lizards were located visually while the observer walked slowly through the study site. Upon spotting a lizard, the observer moved slowly to a position ca. 3 m from the lizard. After that, the lizards' age category (adult, yearling and hatchling) and the exact perching spot were noted. Each site was sampled only once to avoid replication of double check.

A total of 161 observations were made, 51 at adults, 46 at yearlings and 64 at hatchlings. Perching sites were characterized as: "open patches" in the vegetation; "bushes" with dense undergrowth vegetation and their proximate; dense "herbs and grasses" without open patches. The availability of distinct microhabitat categories was estimated by recording their presence in ten 10x10 m quadrates. The location of the quadrates was chosen at random by overlaying a grid within the site map and then picking random *x* and *y* using random number table. To test whether individuals are distributed according to the distribution pattern of distinct microhabitat categories Chi-square goodness of fit were used.

2. Microhabitat selection

The structural features of the lizards' microhabitat were quantified at 57 lizards (20 adults, 20 yearlings and 17 hatchlings). We intended to use a balanced sample design but due to the changed weather conditions only 17 hatchlings could be sampled. Another 20 random samples were collected to have comparative information using the same methodology. Lizards' microhabitat structural features were quantified at four spots (Vanhooydonck et al. 2000): at the sight where the lizard was observed initially, and the end-points of three lines at an angle of 120º and 200 cm from the first one. The direction of the lines was determined haphazardly. The lizards' sighting spot served as the centre of a circle with a radius of 50 cm, the other 3 points were each the centre of a 100 cm radius circle. Six factors were quantified: perch site height; distance to the nearest bush (both in cm); proportional cover at ground level of bushes, herbaceous vegetation and open patches; and average vegetation height. To identify differences in lizard habitat pattern the data matrix (77 samples and 6 variables) was examined by Discriminant Analysis (DA) and was subject of a Reclassification Analyse with a priori defined groups. Principal Component Analysis (PCA) analysis was used to test which factor mostly affects the three groups of lizards. The factors obtained were tested for means by one way ANOVA and post hoc Tukey test. Differences in means were tested by Kruskal–Wallis test. The homogeneity or heterogeneity of samples was compared by Hartley's F_{max}-test on homoscedasticity (Sokal & Rohlf 1995).

Results

1. Sighting frequency and microhabitat availability

Only a small proportion of the lizards habitat is made up by open patches (19%) while grasses-herbs and bushes covers the ground in a 47% respectively 34%, as was evidenced by the randomly selected quadrates. Hatchlings sighting frequency followed the general distribution pattern of microhabitat categories (χ^2=0.7 df=2, P=0.7), 12 of them perched in open places, 25 at base of bushes and 27 among the dense vegetation. Yearlings occupied in open patches in a higher amount, 18 out of 46, while 15 among them perched in vegetation and 13 at the base of bushes. The sighting frequency of yearlings differs significantly of the habitat pattern (χ^2=26.28 df=2, P<0.0001) and from the hatchlings perching pattern (χ^2=14.9.28 df=2, P<0.0008). Twenty-one adult sand lizards choose open patches to perch while 14 stopped between the dense vegetation and 16 of them retreated at the base of bushes. The sighting frequency of adult lizards were not directly proportional to availability of distinct microhabitat categories (χ^2=34.21, df=2, P<0.0001) and were similar to yearlings distribution pattern (χ^2=1.25 df=2, P=0.53) and differed significantly form the one observed at hatchlings (χ^2=16.24 df=2, P<0.0002). Ontogenetic shifts from hatchlings to adulthood involve decrease in the use of thick vegetation as perching site in favour of partly open patches and partly the proximity of bushes.

2. Microhabitat selection

A slightly different microhabitat pattern was obtained by the second sampling methodology, although the differences are not significant (Table 1). Based on the habitat structural characteristics, spots randomly selected can easily separated from the lizards' perch sites (λ=0.297, $F_{[18,\ 192]}$=5.72, P<0.0001) (Fig 1). The squared distances evidence small differences between adults and yearlings with increasing differences of both age groups toward hatchlings and random spots (Table 3). Reclassification of habitat spots had a relatively low precision as only 57% were correctly assigned. Reclassification was precise enough at hatchlings with 14 out of 17 correct classifications. Yearlings were assigned in equal proportions correctly at yearlings and falsely at adults and in a smaller extent falsely at hatchlings and random spots. Adults were 55% correctly regrouped, untrue reclassifications were mostly assigned at group of yearlings. It is important to note that from 22 false reclassifications at the three groups of lizards only 2 have been assigned to random spots. The factors measured at random spots were significantly more heterogeneous than at lizards' spots excepting bush coverage. Mean values of the recorded factors differed among not only between lizards and random spots but differences among the age groups were recorded as well (Table 2). No differences regarding scedasticity were recoded among the three groups of lizards (all P>0.05). PCA on the six-microhabitat variables yielded two new variables that together explain 60% of the total variation (Table 4). The first component axis is negatively correlated with bush coverage and positively correlated with the vegetation coverage. Mean factor scores on this axis differ significantly among the three age groups ($F_{[2,\ 54]} = 4.38$, P=0.01). Adults and yearlings had negative values with no genuine difference between them (P=0.711), while hatchlings had positive on this axis with significant differences from both adults (P<0.01) and yearlings (P=0.01). The second component axis is positively correlated with the coverage of open patches and negatively correlated with average vegetation. Mean factor scores differ significantly among the three age groups ($F_{[2,\ 54]} = 12.9$, P<0.0001) on this axis. Adults and yearlings had positive while hatchlings negative values on the second component axis. Again, there was no significant difference between adults and yearlings (P=0.86) while hatchlings differed significantly from both adults (P<0.0001) and yearlings (p<0.0001).

Table 1. Summary statistics of the microhabitat characteristics,
results of the two sampling methods.
Notice the highly overlapping 95% Confidence Intervals

Variable	Sampling Method	Mean	SD	U & L 95% CI
Open coverage	1	0.19	0.11	0.10 – 0.27
	2	0.13	0.16	0.05 – 0.20
Bush coverage	1	0.34	0,26	0.15 – 0.52
	2	0.48	0,25	0.37 – 0.60
Vegetation coverage	1	0.47	0.18	0.33 – 0.60
	2	0.37	0.32	0.22 –0.53

Table 2. Summary [mean ± SD (CV)] of structural habitat characteristics at lizard observation sites and random sites and probability of differences between their means Kruskal-Wallis-test) and variances (Hartley's F_{max}-test).

	Perch height	Bush	Average Vegetation	Open Coverage	Vegetation Coverage	Bush Coverage
Adults	7.9 ±7.2 (90.2)	62.3 ±20.2 (32.5)	52.4 ± 8.1 (15.3)	0.29 ± 0.10 (35.1)	0.56 ± 0.10 (19.2)	0.14 ± 0.13 (91.5)
Yearling	4.8 ± 4.7 (98.3)	63.7 ± 24.0 (37.7)	53.2 ± 10.6 (19.9)	0.26 ± 0.08 (32.2)	0.58 ± 0.15 (26.8)	0.15 ± 0.14 (93.5)
Hatchling	12.9 ± 8.8 (68.3)	84.2 ±16.9 (20.1)	56.4 ± 7.7 (13.7)	0.16 ± 0.09 (60.5)	0.69 ± 0.14 (21.1)	0.14 ± 0.12 (90.2)
Random	5.7 ± 5.4 (95.2)	63.2 ±51.4 (81.4)	37.3 ± 13.5 (36.3)	0.13 ± 0.16 (123.81)	0.48 ± 0.25 (51.6)	0.37 ± 0.32 (86.6)
Means	H=16.2; *P*=0.001	H=7.71; *P*=0.05	H=24.4 ; *P*<0.0001	H=16.2; *P*=0.001	H=9.73; *P*=0.001	H=6.72; *P*=0.08
Variances	F=3.51; *P*=0.04	F=9.21; *P*<0.0001	F=3.03; *P*=0.06	F=3.81; *P*=0.01	F=5.46; *P*=0.002	F=6.48; *P*=0.0001

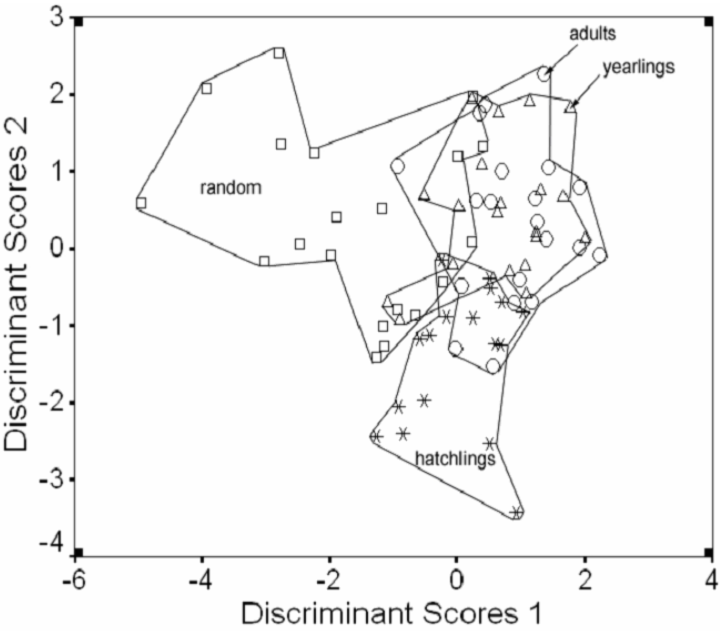

Fig 1. Discriminant analysis on microhabitat characteristics at lizards' perching sites and randomly selected control sites. Scatterplot with convex polygons of first two discriminant functions that together explain 97.7 % of total variance.

Table 3. Squared distances and the reclassification matrix of the three groups of lizards and random spots based on the environmental factors.

	Squared Distances			
	Adults	Yearlings	Hatchlings	Random spots
Adults	0.00	0.33	3.87	6.16
Yearlings	–	0.00	4.02	5.18
Hatchlings	–	–	0.00	5.80
Random spots	–	–	–	0.00

	Reclassification Matrix			
	Adults	Yearlings	Hatchlings	Random spots
Adults	11	9	2	2
Yearlings	5	9	1	2
Hatchlings	3	1	14	6
Random spots	1	1	2	10
N correct	11	9	14	10
Proportion	0.55	0.45	0.82	0.50

Table 4. Factor loadings for the first two principal components in PCA on habitat variables for adult, yearling and hatchling sand lizard. Mean and standard deviation for each factor is given.

Variable	PC 1	PC 2
Perch height	-0.113	-0.441
Distance to Bush	0.326	-0.189
Average Vegetation	-0.174	-0.503
Open Coverage	-0.303	0.574
Vegetation Coverage	0.692	-0.044
Bush Coverage	-0.529	-0.431
Eigenvalue	1.91	1.65
% Variation	31.9	27.6
Cumulated %	31.9	59.5
Age group	Mean ± SD	Mean ± SD
Adults	-0.45 ± 0.99	0.47 ± 1.30
Yearlings	-0.28 ± 1.49	0.36 ± 0.94
Hatchlings	0.83 ± 1.31	-0.98 ± 1.02

Discussion

The results of the present study confirm the null hypothesis tested but the two sampling procedures and subsequent statistical analysis bring up somewhat contradictory results regarding hatchlings. Just recording the presence of lizards in different microhabitat categories did not gave us positive result for hatchlings just for adults and yearlings. Measuring environmental factors evidenced active microhabitat chooses at all age groups. Although this contradiction have been recorded a thoughtful analysis of the results evidences that the contradiction is only apparent. Fitting the hatching lizards' distribution pattern to the environmental model evidence no genuine differences while the multivariate analysis show active perch site selection. Old and widely used as it are Chi- square tests they are among the least powerful test.

With all that the results of goodness of fit testing at hatchlings cannot be considered irrelevant because of low power. The contradiction may not have statistical nature more likely results in the poor a priori categorization of lizards' habitat. Perhaps delimitating only three mutually exclusive habitat types confers less sensibility as required. True a more detailed delimitation is not practically feasible partly because more microhabitat categories are considered less accurately becomes the delimitation (Nemes pers. obs.), and the increased number of considered categories if are not followed by a substantial increase of sample size could lead to a considerable loss of statistical power. Perhaps this approach should be replaced with logistic regression models (e.g. Mysterud & Ims 1998), especially if there are just two mutually exclusively microhabitat categories considered. The second sampling methodology endow with variance data as well. Ecological studies succeed to explain only low amounts of variance (Møller & Jennions 2002) and statisticians often regard variance as unwanted noise resulted from inexact measurements. Variance in biological systems, that are not prefect and each is different from the other, enlightens the degree of heterogeneity. All environmental factors, but average vegetation height and bush coverage, measured at the lizards' spots were significantly more homogenous that factors measured at random spots. This suggests a propulsive habitat selection regardless of age group. Bush coverage was more homogenous at random spots, but this might result from the high average coverage, lizards actively avoiding highly shadowed areas. Increasing tree, bush canopy and decreasing sunshine index is a serious threat to sand lizards' populations (Jackson 1979, Dent & Spellerberg 1987, Berglind 1988, 1995), sand lizards preferring low dense cover of grass and bushes interspersed with patches of bare ground (Glandt 1979). Regardless of age group sand lizards of the studied population tend to occupy those microhabitats that have a higher amount of open spots and smaller bush coverage. Patches with dense vegetation has practical importance to *Laceridae* in general (Vanhooydonck & Van Damme 2003) and to specifically to *L. agilis* (Török 2002) as safe refuge places in case of impending predators. Only adult and yearling sand lizards of the present population tend to use the compact vegetation at the base of bushes as shelter (Nemes 2001) the proximity of dense vegetated patches as potential shelter influences mostly hatchlings perch site chose. Bush coverage had a negative influence on hatchlings' choice, but might be the effect of adults' presence in the vicinity of bushes, as hatchlings often avoid adults with possible cannibalistic proprieties (Castillia & Van Damme 1996), interference with other individuals having a genuine influence on habitat chose at the sand lizard (Amat et al 2003). Török (1998) concluded that sand lizards prefers habitats with 60-80% of surface covered by vegetation, areas with scarcer vegetation layer not offering enough shelter places, more vegetation might reduce their movement capacity and basking opportunities. Vegetation height also influences the sand lizards distribution, vegetation structure and height being one of the most important key factors (Märtens et al. 1996, Märtens et al. 1997). Glandt (1991) find that the preferred vegetation height is up to 30 cm and there is a negative relationship between vegetation height and lizards abundance. This pattern can not be generalized, for example in Slovenia at the southern border of it's distribution area the most common habitat for the sand lizards are secondary habitats e.g. gravel pits with basic vegetation (Vogrin personal obs.). The sampling methodology used in the present does not allows estimating the relationship between vegetation height sand lizards abundance generally lizards of all age groups preferred a vegetation over half meter while the average height of the vegetation is about 35 cm (see results, Table 2). The preferred vegetation height might be influenced by many factors like: exposure through influence on sunshine index, presence of predators and type of predators (terrestrial vs. aerial) and humidity. Although the habitat use of sand lizard is well studied (Anonymus 2005, and references herein) many aspects of the habitat use in this species are not properly known. An interesting study involving habitat selection at sand lizards would be one that compares gender related differences with emphasis on pregnancy induced variations at females.

Knowing factors which influence lizards' habitat and microhabitat choose has not only theoretical importance but they are important in conservation actions and habitat managements (Martín & Salvador 1995, Martín & López 2002, James & M'Closkey 2003). Even if age dependent microhabitat selection is not a general feature of lizards (Martín et al. 1991, Reaney & Whiting 2003) the results of the present study suggest that any habitat management and conservation actions should take into consideration the behavioural and ecological variations induced by ontogenetic shifts. It is not enough to preserve habitat structures that assure the adults' continued existence but attention should be paid to those factors that guarantee the survival of the younger generations. Further studies should be conducted to find in what extent the habitat use, distribution and local abundances of sand lizard are influenced by changes in the vegetation structure (succession), food availability and predation/competition regimes at a landscape level. These studies will improve the management actions to preserve sand lizard populations and their habitats.

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