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Niche segregation of sand lizard (*Lacerta agilis*) and green lizard (*Lacerta viridis*) in an urban semi-natural habitat

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Abstract. Different types of semi natural habitats has important role in long-term survival and maintenance of reptile species in urban environments. Heterogeneous urban green islands can provide conditions that enable competing species to live together in relatively small areas. However, the key mechanism of coexistence could vary from types of habitats and taxa. We investigated the population structure, the fine scale habitat segregation and diel activity pattern of two lizard species (*Lacerta viridis* and *L. agilis*) coexisting populations in a town cemetery. We hypothesized, that fine scale habitat segregation is a more important factor in coexistence than differences in diel activity pattern, because of the environmental dependent thermoregulation constrain. During the study, 178 *L. agilis* and 79 *L. viridis* occurrences were recorded. The daily activity patterns of both species were very similar, with peaks found in the forenoon and afternoon. Lizards were found to be the most active at 31–32°C. The probability of occurrence of the species was influenced more by the differences in the random selection of parcels rather than the random differences in the survey days. Around the proximate observation point the bush covered areas was significantly higher than average in the parcels. Our results showed that niche segregation based on fine scale habitat patches had a fundamental role in the coexistence of the two lizard species. *L. agilis* preferred the more open spaces, whereas *L. viridis* preferred areas with more bushes, but there was no difference in the daily activity pattern of the two species.

Keywords: habitat selection, activity pattern, urban ecology, public cemetery

Introduction

Long-term maintenance of lizard populations depends fundamentally on the quality and accessibility of suitable habitats. Expansions of the build-up areas, increasing gardening (e.g. mowing) often lead to fragmentation, degradation and loss of habitats in suburban and urban areas (Martens and Jelden, 1992). Due to habitat fragmentation the population size of lizards decreases, which could lead to local extinctions. Hence, green areas, enclosed in urban or inhabited areas or adjacent agricultural green areas, can provide suitable habitats for reptile species (Ilosvay, 1977; Bender, 1997; Schmidt-Loske, 1997; Rugiero, 2004; Mollov, 2005; Strugariu et al., 2007). Vignoli et al. (2009) found that the richness and the diversity of the herpetofauna are strongly influenced by the occurrence of large remnant woods, water and extended ecotonal habitats presence. Heterogeneous habitat patches within the towns can highly promote the accommodation success (Faeth et al., 2005). Because of their sizes and their undisturbed conditions cemeteries contribute significantly to habitats of lizard species in urban areas (Barbault and Mou, 1988; Schwartze, 2010). However, species can response in different ways to urban effects (McKinney, 2008). Beside the less tolerant ones, some species are able to accommodate to the altered conditions.

Urban habitats can also have negative effects. The genetic isolation of urban lizard populations could be prevented by establishing green corridors (Strijbosch and Van Gelder, 1997; Altherr, 2007). The continuous anthropogenic effects of varying intensity, the drastic changes and disappearance of habitat patches and the increased number of potential predators are all intensified stresses for urban animals (Corbett, 1988, 2001; Koenig, Shine and Shea, 2002; Woods, Mcdonald and Harris, 2003; Ihász et al., 2006, Shochat, Lerman and Fernández-Juricic, 2010). The selection pressure could alter the behaviour, morphology, genetic traits, of plant and animal species in urban conditions (Shochat et al., 2006). A small lizard population of an island could be similar to an urban lizard population structure. Cats seem to be the biggest threat to the lizards in a small island (van Bree, Plantaz and Zuiderwijk, 2006). Elbing (1997) found that the social behaviour and the distribution patterns of lizards can be different on islands, than habitats with optimal condition. Arntzen and Sá-Sousa (2007) found that insular lizard populations have some morphological differences, and a lower nuclear genetic heterozygosity than on the mainland, but no correspondence was observed between morphological and molecular patterns of intra-specific differentiation. Light pollution in cities or towns also affects reptiles (Perry et al., 2008), Carretero et al. (2012) recorded nocturnal activity in *Podarcis muralis*. The invasion of alien plant species has an adverse effect on the species richness of lizard species (Jellinek, Driscoll and Kirkpatrick, 2004). Capula, Luiselli and Rugiero (1993) investigated the competition and niche segregation between lizard species living together in urban conditions, while the habitat choice of reptile species was studied by Mollov (2011); Rugiero and Luiselli (2007). Structural features of habitats can sometimes override the effect of habitat fragmentation (Santos et al., 2008). Jellinek, Driscoll and Kirkpatrick (2004) found that the structure of lizard communities is primarily determined by the vegetation composition. In contrast, Garden et al. (2007) stated that the habitat structure is more important for the reptiles and small mammals than the vegetation composition. Generally, the increasing edge zones do not affect the species richness of a region or the abundance of lizards. Some species prefer habitats with heterogeneous structures, which can only be found in larger patches (Jellinek, Driscoll and Kirkpatrick, 2004). Some lizard species show a high degree of site fidelity, so they conquer other habitat types only with difficulty, while others adapt well to changes and to the higher productivity of urban green areas (Koenig, Shine and Shea, 2001).

Our study focuses on two lizard species: *Lacerta agilis* and *L. viridis.* The sand lizard (*L. agilis*) is one of the most common lizard species in Hungary. It can be found in fields, forest edges, grassy or bushy edges of trenches, pastures, meadows, along railway embankments, marshes, peat-bogs, reedy habitats and urban gardens (Dely, 1983). The European surveys show a very diverse habitat use of the species (House and Spellerberg, 1983; Glandt, 1986; Strijbosch, 1986; Dent and Spellerberg, 1987; Amat, Llorente and Carretero, 2003; Edgar and Bird, 2006; Ceirâns, 2007; Èeirâns, 2007). Edge zones with heterogeneous vegetation and higher rates of shrub cover are also preferred by *L. agilis*. Shrubs are used both as hideouts and basking place (Stamps, 1977; Nemes, 2002; Nemes et al., 2006) while the over shaded woody habitats are avoided by the species (House and Spellerberg, 1983).

The green lizard (*Lacerta viridis*) is also a common species in Hungary, but its distribution is influenced especially by the presence of bushy edge zones. Hence, vineyards, orchards and cemeteries with tree groups and bushy patches could provide suitable habitats for the green lizard (Dely, 1983). *L. viridis* can occur in heavily disturbed areas (Iftime and Iftime, 2006). This species often climbs up trees (Mikátová, 2001; Iftime, 2005). According to some authors (Vasváry, 1926; Arnold, Burton and Ovenden, 1978; Arnold, 1987; Mollov, 2005; Covaciu-Marcov et al., 2008; Strugariu and Gherghel, 2008), the green lizard prefers the woody, bushy habitats.

The seasonal activity patterns of the two species are slightly different and there are differences between males and females in this respect, too (Glandt, 1995; Mikátová, 2001; Amat, Llorente and Carretero, 2003). The two lizard species usually have two daily activity peaks in the summer (House and Spellerberg, 1983; Korsós, 1984, 1986; Korsós and Gyovai, 1988; Sound and Veith, 2000; Amat, Llorente and Carretero, 2003; Kuranova et al., 2005). However, if the temperature at noon does not rise too high, there can be only one activity peak for sand lizard (House, Taylor and Spellerberg, 1979; Korsós, 1984, 1986).

In urban areas there could be higher competition between species, than in natural open areas so the aim of our study was to examine how the niche segregation of the two species living together in an urban green area in a cemetery takes place. Our specific questions were: 1) Does the spatial distribution of the lizard population relate to the habitat diversity of the parcels? 2) Can habitat preferences be established? 3) Are there any differences in the daily activity patterns of the two species and what factors can influence them?

Materials and methods

Study area

The total area of Public Cemetery of Dunaújváros (70 km from Budapest) is 21 ha. It is surrounded by houses and roads, but it is attached to the forest belt and a streambed, which provide corridor for lizards (Dent and Spellerberg, 1988; Scali and Zuffi, 1994; Iftime, 2005; Sos, 2007; Covaciu-Marcov et al., 2009; Mollov, 2011). In the cemetery the original indigenous vegetation with Tartar maple on loess could not be found, most of the plants having been planted (Simon, 1967; Zólyomi, 1967).

Eight parcels with the same area (2500 m^2) were selected for the investigation. In the parcels we assessed the stone covered area and the perimeter of all gravestones, the surface of grass and shrub covered areas, and the area shaded by shrubs and trees. The opening year of the parcels was given by the year of the earliest grave.

Field work

The study was carried out during the period of 1–7 July 2012. Walking of the parcels took place over the same period of time and at an even pace to spot the highest number of individuals. On the first day the parcels were walked through four times, henceforth three times a day while two walks were completed on the last day. To discover the daily activity pattern of lizards we walked each parcel during different parts of the day (early morning, at noon, in the afternoon) in random distribution and several repeats.

Always the same observer made the surveys. We walked through every other row without disturbing the lizards and always following the same route to make the surveys comparable. Usually the lizards were not frightened, they were staying at the same small plot. We recorded the species, gender, age of each individual lizard. We estimated the percentage of grass covered, grave covered and shrub covered areas around the observed individuals in a range of 1 m (4 m^2). While the eight parcels were walked, the air temperature was measured four times in the grass (twice in the sunlight and twice in the shade) and four times on the gravestone (twice in the sunlight and twice in the shade). The mean of these eight measurements was used in the analysis. The thermometer was set 5 cm above the ground. At the beginning of surveys we recorded the number of people present in the given parcel to specify the disturbing effects.

Data analyses

We used generalized linear mixed models (Zuur et al., 2009) with binomial error distribution and logit link function to reveal the relationship between the probability of occurrence of the lizards and the studied explanatory factors. We used nlme, lme4, MASS R packages for analysis. The time of observation, the mean temperature during observation and the number of humans staying within the parcel during the observation period were the fix explanatory variables in the models. In the reduced model, which describes the probability of occurrence, time, temperature and the interaction of the two had effect, whereas the number of humans staying within the parcel during the observation period was no significant effect. The parcel and the date of observation nested within the parcel were used as random factors in the models. Our models assumed that the effects of the explanatory variables on the probability of occurrence would be the same in all parcels and on each day of the observation period and differences between the parcels and days would only contribute to the occurrence probability with random fluctuations. We fitted three models, one on the general occurrence of the lizards (i.e. irrespectively of the species identity), and two others on the sand lizard and green lizard data, respectively. In order to control the autocorrelative nature of the subsequent observations within a certain parcel on a certain day, a first-order autocorrelation structure was built in the models (Zuur et al., 2009).

Principal component analysis was performed to determine which are the most important environmental factors classifying the parcels.

Pearson's Chi-squared test with Yates' continuity correction was used to compare the apparent sex-ratio and the age structure between species and within species against the hypothetical 0.5:0.5.

Two-sample Kolmogorov-Smirnov test was used to find differences between the two species' daily activity patterns and the same test was used to find differences between the two species' relative occurrence depending on the temperature.

All the tests were conducted in R statistical environment (version number 3.2) (R Core Team, 2012).

Polynomial regression model was used in two cases: 1st to indicate the daily activity patterns of the two species and 2nd to show the relationship between the observed number of individuals and the vegetation covering the parcels. The tests were conducted in Microsoft Office Excel (Winston, 2007).

Analysis of Variance (ANOVA) was used to find differences between the two species' habitat patch preference followed by the Fisher's Least Significant Difference post hoc test (LSD test). Namely we test whether the surface vegetation cover percentages measured near the observation points of the two species were different between species; or rather they were different from the mean cover of the parcels. All percentage variables were arcsine square-root transformed in order to normalize data distribution before the statistical analysis. The mean of percentage grass cover, shrub cover and gravestone cover were compared with the mean surface cover data of the eight parcels. To carry out the statistical analysis the IBM SPSS software was used (IBM Corp. Released, 2011).

Results

Differences between parcels

The traits of chosen parcels proved to be different, mainly with regard to the vegetation cover and the percentage of the shade. The results of a principal components analysis based on the covariance matrix showed that there are two main principal components. The first principal component (PC1) explained 58.8 % of total variance (eigenvalue: 2.9414) and the second principal component (PC2) explained 21.6 % of the variance (eigenvalue: 1.078). The last three PC's have little apparent significance. The percentage of grass covered areas and the absence or the very short cumulated perimeters of gravestones and absence of shrubs were the most dominant traits in the first PC. The percentage of grass covered area was higher in the E2 and XXXIV parcels. The absence of the area shaded by shrubs and trees and the absence of shrub covered area were dominant traits in the second PC (Fig. 1.).

Observation data of lizard species

178 observations were made for *Lacerta agilis* in 7 days. In parcel E2 no lizards were found. There were fewer observations made for *L. viridis*, only 79 during the study period.

In both lizard species the proportion of females among the observed individuals was higher, but the differences were not significant (Chi-squared test; $\chi^2_{L.a.} = 0$, $P = 1$, $\chi^2_{L.v.} = 0.3369$, $P = 0.5616$), and the differences in the apparent sex-ratio between the two species were also not significant ($\chi^2 = 0.4087$, $P = 0.5226$). Ratio of number of adults and subadults was 3.91 in *L. agilis*, and 7.77 in *L. viridis*. No juveniles were observed during the study period. The ratios of adults were significantly higher than the hypothetical 0.5 in both species ($\chi^2_{L.a.} = 32.8599$, $P < 0.001$, $\chi^2_{L.v.} = 25.8908$, $P < 0.001$), but the apparent age groups between the two species did not differ significantly ($\chi^2 = 2.3622$, $P = 0.1243$).

Occurrence and daily activity pattern of lizard species

The probability of occurrence described in the reduced model was mainly dependent on the time, temperature and interaction between the two (Table 1.). The variance of the probability of occurrence calculated on the basis of the differences among the parcels was 34.79 (logit scale), which was 4.28-fold higher than the variance calculated based on the days, which was 8.13 (logit scale). During a short, approx. one-week-long summer observation period the traits of the parcels were found to influence the daily activity patterns of the lizards more than the differences between the days. With regard to the variance of the probability of occurrence of *L. agilis* based on the differences of parcels was 1.63 (logit scale), while the variance based on the differences of the days was 0.10 (logit scale) (Table 1.). The probability of occurrence of the *L. viridis* showed no correspondence with any of the studied traits (Table 1.).

The mean temperature, slightly influenced the relative occurrence of the two lizard species (Fig. 2.), and the difference between the two species was not significant (Kolmogorov-Smirnov test; $D = 0.2273$ $P = 0.6208$). Both species were found to be the most active around 31–32°C.

The sample size allowed to model only the relationship between the temperature and the probability of occurrence (Table 1.) of *L. agilis*. The sand lizard probability of occurrence was the highest around 33°C, except for two parcels (Fig. 3.). In parcel XXXIV a low number of individuals were recorded in the forenoon, while in parcels E2 no individuals were observed.

The daily activity patterns of the two species were found to be very similar (Fig. 4.) and did not differ significantly (Kolmogorov-Smirnov test; $D = 0.3077$ $P = 0.5696$). Both species had their first activity peaks in morning from 9 to10 o'clock whereas in early afternoon the observed number of lizards decreased. In late afternoon they showed a second activity peak, which was much higher than the first. For both species the fourth power polynomial trend line, which describes the changes indicated a strong correlation with the mean temperature ($R^2 = 0.8489$ for *L. agilis* and $R^2 = 0.7445$; *L. viridis*, $y_{\mathrm{L.a}} = -0.045x^4 + 2.5312x^3 - 51.695x^2 + 450.85x - 1397.8$, $y_{\mathrm{L.v.}} = -0.0324x^4 + 1.827x^3 - 37.369x^2 + 326.42x - 1010.5$).

Lizard species habitat patch choice

We found strong relationship between the vegetation covering the parcels and the number of pooled data of observed individuals. The shrub covered area and the number of individuals showed strong correlation (based on the quadratic polynomial trend line $y = -1.5833x^2 + 23.083x - 28.75$, $R^2 = 0.789$).

The highest number of individuals was observed in the parcels with 5–8% shrub cover rate. In the new parcels, where there was no undergrowth or the shrub cover percentage was 3%, similarly to the very shaded parcel where the shrub cover percentage was 1,24% *L. viridis* was not and only a few *L. agilis* individuals were observed. The number of observed individuals was higher in the more heterogeneous group of parcels containing more shrubs.

The additive effect of trees and shrubs shade on the observed number of individuals showed a strong correlation (based on the quadratic polynomial trend line $y = -4.1071x^2 + 38.321x - 32.964$, $R^2 = 0.6211$). The maximum number of individuals was found in parcel XXV with 30% shade. The parcel with little vegetation cover and the ones with too much shaded area were found to provide unsuitable habitats for the lizards.

ANOVAs scores on the land cover percentage revealed significant effect on the lizard species for grass- and shrub coverage, (ANOVA; Grass %: $F_{2,\ 261}=12.418$, $P<0.001$; Shrub%: $F_{2,\ 261}=10.601$, $P<0.001$) but no significant effect on tombstone coverage (Tombstone %: $F_{2,261}=0.052$, $P=0.949$).

When measuring habitat preferences the grass cover around the observation point of individuals differed significantly between the two species (LSDtest; $P<0.001$). While in case of *L. viridis* we found significant difference between the grass cover around the observation point of individuals and the average in the parcels ($P < 0.01$), *L. agilis* did not show the same pattern ($P = 0{,}162$) (Fig. 5/A.).

The shrub cover around the direct environment of the detected individuals of *L. viridis* was found to be significantly higher, than in the direct environment of *L. agilis* (LSDtest; $P < 0.001$). The shrub cover of the close environment of *L. viridis* proved to be significantly higher ($P < 0.05$), than the shrub cover of the parcels (Fig. 5/B.).

With regard to the gravestone cover the differences between the cover rates around the two species' individuals were not significant (LSDtest; $P = 0.88$). The gravestone cover around the observation points of *L. agilis* ($P = 0{,}79$) and *L. viridis* ($P = 0.75$) did not differ significantly from the parcels' means, but the gravestone covered areas were lower around the two species (Fig. 5/C.).

Discussion

This study investigated the coexistence of two lacertid lizard species (*Lacerta agilis* and *L. viridis*) in a town cemetery serving as semi-natural green island habitat. Although our survey provides only a snapshot on the lizard populations, it seems that cemeteries with various semi-natural microhabitat patches, such as shrubs, grassy areas, or tombs could offer suitable habitats to coexist for *L. agilis* and *L. viridis*. This corresponds to former studies (Ilosvay, 1977; Bender, 1997; Schmidt-Loske, 1997; Rugiero, 2004; Mollov, 2005) that also reported urban green areas as suitable lizard habitats.

In the chosen parcels of the cemetery lizards were found except in parcel E2, which was the consequence of the high degree of shade and the scarce undergrowth vegetation. From day 3 to 4 during the survey time the observed number of individuals showed a decreasing tendency, which could be explained by the slight drop in the daily mean temperature. The number of females was not significantly higher than males in both lizard populations.

We identified that the mean temperature consisting of the temperatures measured in the sunlight and in the shade near the ground influenced the occurrence of *L. agilis* and the *L. viridis* but the two species did not differ significantly, so the air temperature had no role in their niche segregation. The optimal air temperature was between 31–32°C, when the lizards were the most active. This is corresponded to the findings of Castilla, Van Damme and Bauwens (1999).

The daily activity patterns of both species were similar, with the activity peaks in forenoon and afternoon and their retreats in the early afternoon. As a result, their daily activity patterns did not seem to play any important role in their niche segregation. The activity patterns of the two lizard species detected in summer time were identical with the results of other studies showing two activity peaks (House and Spellerberg, 1983; Korsós, 1984, 1986; Korsós and Gyovai, 1988; Sound and Veith, 2000; Amat, Llorente and Carretero, 2003; Kuranova et al., 2005). The reason for the differences in the lizards' daily activities can be attributed to their different body size (House, Taylor and Spellerberg, 1979; Strijbosch, 1986) or differences in their thermoregulation (Rismiller and Heldmaier, 1982; Castilla, Van Damme and Bauwens, 1999; Grbac and Bauwens, 2001).

Their probability of occurrence was influenced more profoundly by the differences in the characteristics of the parcels rather than the differences between the days. During a short observation period the differences arising from the random selection of the parcels had a more substantial influence on their activity patterns than the random differences between the days.

The middle aged heterogeneous parcels were suitable for the lizards unlike the shaded or lawned ones which were seldom frequented by them. The most suitable parcels were heterogeneous with bushy parts providing a suitable percentage of shaded surface. Korsós (1984, 1986) did not find statistically significant proof to support the statement that the rate of shrubbery areas was higher in the environment of the *L. viridis*, than in the environment of the *L. agilis*. Cooke (1991) obtained similar results according to which the habitat is suitable for the *L. agilis* up to 9% shrub cover. Bushes are mainly used as hiding place by the *L. agilis* (Nemes, 2002; Nemes et al., 2006), but House and Spellerberg (1983) observed them climbing up and basking on shrubs. The *L. viridis* also uses these sites as basking place (Mikátová, 2001) and hiding place, too. We also observed this behaviour.

The fine spatial scale habitat choice of the two lizard species was slightly different, which makes their coexistence in one particular habitat possible. The *L. viridis* tends to choose areas with more shrubs, than *L. agilis*, while the sand lizard usually occurs in more open areas with higher percentage of grass cover. In the majority of the parcels we observed high rates of grass cover, which could be suitable for the sand lizard preferring more open spaces, while the *L. viridis* tends to avoid the open, grass-covered areas (House and Spellerberg, 1983; Glandt, 1986; Strijbosch, 1986; Arnold, 1987; Cooke, 1991; Amat, Llorente and Carretero, 2003; Nemes et al., 2006; Ceirâns, 2007). In their close environment the rates of open areas are low. In the shaded parcels lizards cannot find large enough sunny sites, which are therefore not suitable for them (House and Spellerberg, 1983; Dent and Spellerberg, 1987; Cooke, 1991). Most of the green lizard individuals were centred around the bushy habitats offering them hiding place. The gravestone covered areas did not contribute to the separation of their habitats. In our study the preferential use of stone (gravestone) as sunny site or shelters by the lizards was not observed, as it was detected for other green lizard species before (Díaz, Monasterio and Salvador, 2006).

Our findings show that there are no differences between lizards' habitat use, and daily activity pattern in urban area and natural area. Lizards need a structurally complex habitat with a combination of different patches. This corresponds to former study (Becker 2015) that also reported urban areas as suitable lizard refuges; urbanisation do not affected sand lizard population densities. The *L. agilis* tends to choose more open areas, than *L. viridis*. Angelici, Luiselli and Rugiero (1997) found, that microhabitat differences could explain the dietary differences between young and adult lizards. Therefore predation may play a role in their niche segregation (Korsós 1984).

To conclude, our findings highlight the role of cemeteries as less disturbed, semi-natural urban areas in conservation of lizard populations. In highly populated towns, cemeteries along with city parks should be considered as potential refuge for less mobile territorial animals such as lizards. This point of view poses a question of considering the possibility of attributing limited protection to these urban areas.

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Table 1. Results of the generalized linear mixed model (GLMM) describing the general activity of lizards. Parameter estimates and their standard errors (SE) of the fixed and interaction effects. *L.a.: Lacerta agilis, L.v.: Lacerta viridis,* D.F: Degrees of freedom, t: t-value, p: p-value

Model	Species	Parameter estimates (logit scale)	*SE*	*D.F.*	*t*	*p*
time	*L.a. & L.v.*	6.726	1.131	277	5.947	< 0.001
	L. a.	1.586	0.570	256	2.780	0.006
	L. v.	-0.374	0.669	248	-0.559	0.577
mean temperature	*L.a. & L.v.*	1.657	0.331	277	5.005	< 0.001
	L. a.	0.439	0.163	256	2.702	0.007
	L. v.	-0.102	0.197	248	-0.519	0.604
time:mean temperature	*L.a. & L.v.*	-0.195	0.0319	277	-6.111	< 0.001
	L. a.	-0.046	0.0158	256	-2.888	0.004
	L. v.	0.01	0.019	248	0.528	0.598

Figure 1. Principal component analysis of the eight parcels based on the five traits investigated.

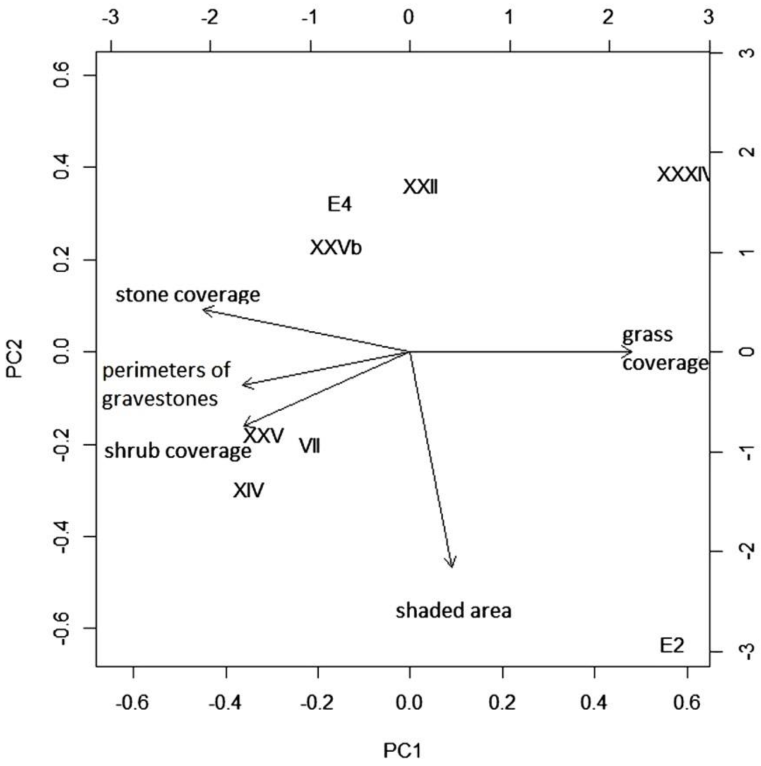

Figure 2. Relationship between mean temperature and the activity of the two species (filled circles: *Lacerta agilis,* open circles: *L. viridis*).

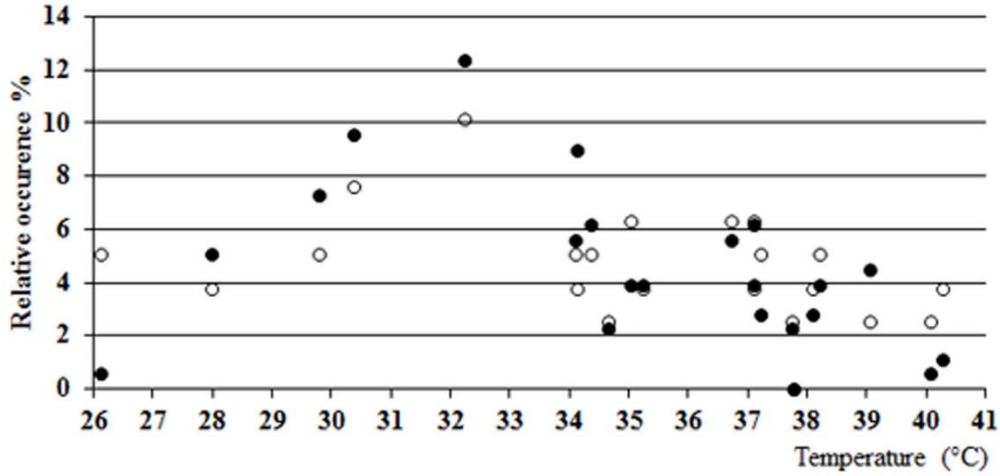

Figure 3. Probability of occurrence of *Lacerta agilis* depending on temperature.

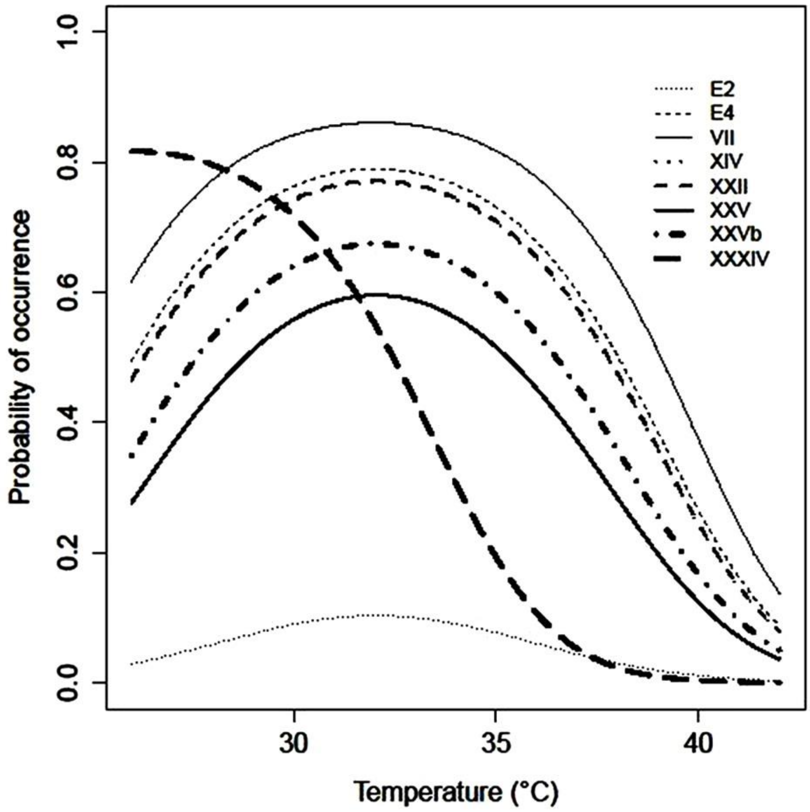

Figure 4. Relative occurrence of *Lacerta agilis* and *L. viridis* during the day (filled circles: *L. agilis,* open circles: *L. viridis,* solid line: trend line for *L. agilis,* dotted line: trend line for *L. viridis*).

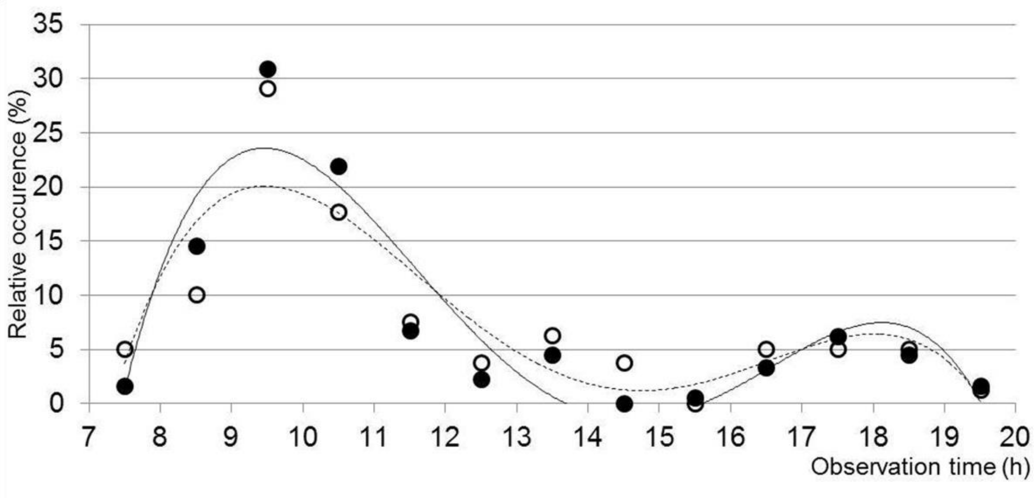

Figure 5. Percentage of areas covered with grass (A), shrub (B) or gravestone (C) on the occurrence points of the two lizard species and on the full area of parcels.