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Testing hypotheses of habitat use and temporal activity in relation to body plan in a Mediterranean lizard community

Lorenzo Rugiero[1], Massimo Capula[2], Daniele Dendi[1,3,4], Fabio Petrozzi[5], Julia E. Fa[6,7], Stephan M. Funk[8], Russell L. Burke[9], Luca Luiselli[1,3,4]

1 Institute for Development, Ecology, Conservation and Cooperation, via G. Tomasi di Lampedusa 33, I-00144 Rome, Italy; lore.rho@gmail.com; d.dendi@ideccngo.org; l.luiselli@ideccngo.org

2 Museo Civico di Zoologia, Rome, Italy; m.capula@comune.roma.it

3 Department of Applied and Environmental Biology, Rivers State University of Science and Technology, P.M.B. 5080, Port Harcourt, Nigeria

4 Department of Zoology, University of Lomé, Lomé, Togo; lucamaria.luiselli@uniroma3.it

5 Ecolobby, Rome, Italy; fapetrozzi@gmail.com

6 Department of Natural Sciences, School of Science and the Environment, Manchester Metropolitan University, Manchester, M1 5GD, UK; jfa949@gmail.com

7 Center for International Forestry Research (CIFOR), CIFOR Headquarters, Bogor, 16115, Indonesia.

8 Nature Heritage, Jersey, Channel Islands, UK; smf@natureheritage.org

9 Department of Biology, Hofstra University, New York, USA; Russell.l.burke@hofstra.edu

Abstract

A body plan (= bauplan) is a suite of morphological characters shared by phylogenetically related animals at some point during their development. Despite its value, the bauplan concept is still rarely employed to characterize functional groups in community ecology. Here, we examine habitat use and spatio-temporal activity correlates of an entire seven-species community of lizards with different bauplans. The study was carried out in three locations in central Italy, encompassing a complex landscape with a patchy mosaic of a wide variety of habitats and microclimates. We tested four hypotheses regarding niche breadth, habitat use and activity patterns. The first hypothesis, niche complementarity, in which species with similar body shapes should non-randomly partition available habitats, was not supported. By contrast, the hypotheses that larger-bodied species should have a wider niche breadth, that slower species should inhabit habitat types of higher cover, and species inhabiting open sunny habitats should exhibit more seasonally variable activity patterns, were all supported by the data. Sympatric lizard communities in our study area were clearly organized by autecological constraints and eco-physiological attributes.

Key words: Sauria; *Lacerta bilineata; Podarcis muralis; Podarcis sicula; Hemidactylus turcicus; Tarentola mauritanica; Anguis veronensis*; *Chalcides chalcides;* Mediterranean; resource partitioning; bauplan; autecological constraints; eco-physiological attributes

Introduction

In evolutionary biology, a suite of characters shared by a group of phylogenetically related animals at some point during their development is defined as body plan or "bauplan" (Woodger 1945; Rieppel 2006; Willmore 2012). The concept has represented an important element in evolutionary developmental biology, evo-devo (Tsessarsky 2020), and the evolutionary ecology of organisms (e.g., Hall 1999; Willmore 2012). However, bauplan has not been explicitly used in community ecology studies, despite this being a central concept for distinguishing the various guilds within truly “functional groups”. Most often, community ecology studies define the various guilds either in terms of phylogenetic units (for instance, varanids versus agamids, etc.) or “natural history-characterized” units (for instance, terrestrial versus arboreal, etc.). Thus, the concept of bauplan may be the ideal synthesis between phylogenetic and natural history characteristics (Stankowich and Stensrud 2019) and, therefore, particularly useful for determining assembly rules of biotic communities. To our knowledge, bauplan has not been explicitly used in community ecology studies.

Lizards are traditionally the most popular model organisms in community ecology studies (e.g., Pianka 1986; Flesch et al. 2017; Grundler et al. 2017; Jiménez-Robles and De la Riva 2019). This group of terrestrial vertebrates are particularly suited for this kind of study because they are easily observed, are found in a large range of temperate and tropical ecosystems, and often exhibiting a remarkable array of species diversity (Helmer et al. 1989; Maura et al. 2011; Zakkak et al. 2015; Simbula et al. 2019; Vacheva et al. 2020). Although sympatric lizard species often display patterns of niche partitioning along the trophic axis (Luiselli 2008; Sheu et al. 2020), the spatial dimension of the niche is instead the usual primary partitioning axis (Toft 1985; Arnold 1987; Gonçalves-Sousa et al. 2019; Sillero et al. 2020). Given this, the study of habitat use patterns by sympatric lizards can greatly contribute to ecological community theory (Arnold 1987; Gonçalves-Sousa et al. 2019; Sillero et al. 2020). For instance, previous data demonstrated remarkable discrepancies in the habitat selection patterns even within the same lizard clades , with some studies documenting a clear ontogenetic shift in habitat use (e.g., Jenssen et al. 1998) whereas others failed in finding any ontogenetic effect on structural niche use (e.g., Powell and Russell 1992).

Like Caribbean *Anolis* Daudin, 1802 lizards (Losos 2011; Pringle et al. 2019) and Australian desert lizards (Pianka 1986), European lizards offer an interesting and logistically convenient system for testing predictions of community ecology theory (e.g., Sillero et al. 2020). These animals are often abundant, conspicuous, and approachable, and therefore it is often easier to observe and record data on their spatial ecologies than for less abundant and more elusive animals.

Microhabitat features useful in studying the ecology of European lizards can be divided into structural and climatic (Arnold 1987). Structural features include whether the microhabitat is flat or elevated, whether its surfaces are more or less continuous or broken, the nature of the substrate (e.g., rock, stones, vegetation) and the types of refuges used. These are responsible for much of the apparent differences in species' spatial distribution, for instance, species that climb high have elevated scores for occurrence on rock or its functional equivalents, and for using crevices as refuges (Arnold 1987). Climatic features include humidity, temperature and shadiness of the habitats and are often inter-correlated with structural features. These are more important in large scale studies of niche ecology than in smaller scale studies (Escoriza and Amat 2021).

In the present study we examined habitat use and temporal activity correlates of an entire community of lizards in three locations in central Italy (Tolfa Mountains, province of Rome). These study sites consist of a complex landscape composed of habitat patches that include a variety of environmental typologies typical of the area. Habitats range from open dry Mediterranean maquis to habitat types with damp vegetation, tall trees with cooler climate and higher humidity. Using this wide range of habitat features potentially available to lizards, we explored the spatio-temporal patterns of lizard community structure. This community is composed of species belonging to three main types of bauplan: type (i) was a typical "lacertid bauplan" with long legs, long tail and slender body, allowing them to run quickly on the ground but also climb efficiently on vertical substrates (three species: the larger sized *Lacerta bilineata* Daudin, 1802 and the smaller-sized *Podarcis muralis* Laurenti, 1768 and *Podarcis sicula* Rafinesque, 1810); type (ii) was a typical "gecko bauplan" with adhesive toe pads allowing them to climb well even on vertical surfaces (two species: *Hemidactylus turcicus* (Linnaeus, 1758) and *Tarentola mauritanica* (Linnaeus, 1758)); type (iii) was an elongated, slender "snake-like" bauplan, allowing them to only move on ground and burrow underground (two species: *Anguis veronensis* Pollini, 1818, *Chalcides chalcides* Linnaeus, 1758).

Using this suite of sympatric species with different bauplans, we analysed four explicit hypotheses. The "niche complementarity" theory (Schoener 1974) which suggests that bauplans that use similar structural habitats tend to differ in climatic requirements and vice versa, to minimize potential interspecific competition. In lizards, species with similar bauplans tend to select structurally similar habitats (e.g., Arnold 1987) and hence potentially compete when resources are limited (Toft 1985). Therefore, we hypothesized that species with similar bauplans should non-randomly partition available habitats, showing less overlap in habitat niche overlap than for species belonging to different bauplans. For instance, the different species belonging to type (i) should differ in shadiness/vegetation cover of the habitats they occupy, with some species being linked to open sunny habitats and others to closed wet habitats. Again, the same habitat partitioning pattern should occur between geckos (type (ii)) or between the "elongated lizards" (type (iii)). For instance, in Salamanca (Spain) the lizard community was distributed in clusters, with species of the same genus (same bauplan according to our criteria presented herein) segregated almost totally by inhabiting different habitats, whereas species of different genera presented partial segregation, sharing some habitats (Sillero and Gomes 2016). In the latter study, ground-dwelling species showed partial spatial segregation whereas the saxicolous species presented a high degree of spatial segregation (Sillero and Gomes 2016). If the niche complementarity theory is supported, we predicted that (a) the habitat niche overlap between species belonging to a same bauplan group should be significantly lower than that observed between species of different bauplan groups, and (b) an evidence of a community structure compatible with non-random niche partitioning should be detected.

As a second hypothesis, we tested whether the species with largest body size exhibited a wider habitat niche breadth in the patchy mosaic landscape than smaller sized species. This hypothesis is based on the fact that, in lizards, home range sizes are generally positively correlated with individual's body size (e.g., Turner et al. 1969; Christian and Waldschmidt 1984) and therefore we predicted that the space requirements of larger bodied species exceeded the space available in habitat types within the relatively narrow mosaics of woods, maquis and pastures in the study area. Thus, in our study case, we predicted that the largest bodied species, *Lacerta bilineata*, would exhibit a wider habitat niche breadth than the other, smaller-sized species, as it has much larger individual home range size than the other species (Saint Girons and Bradshaw 1989).

Lizards represent important prey for a variety of predators in Mediterranean ecosystems (carnivores, birds of prey and snakes; e.g., Rugiero et al. 1995; Capizzi and Luiselli 1996), and thereby rely on running speed and/or cryptic colourations/behaviours to avoid predation (Vanhooydonck and Van Damme 2003). As a third hypothesis, we predicted that lizard species with slower movements and cryptic colouration would inhabit more closed habitats than those that are able to run more quickly for antipredator reasons. In our study case, *Anguis veronensis* is much slower in movements than any other lizard species in the assemblage, and therefore we predicted that it should inhabit habitats that are much denser in vegetation than any other species.

In Mediterranean environments, the high ambient temperatures (> 35°C) typical during summers may represent a constraint for reptile above-ground activities (Carretero and Llorente 1995; Rouag et al. 2007; Zamora-Camacho et al. 2013; Bouam et al. 2016). As a fourth hypothesis we predicted that those species inhabiting open sunny habitats would exhibit more seasonally variable activity patterns, with peaks during the early spring months, and scarce above-ground activity in the summer (Burke and Ner 2005). By contrast, species that are very linked to closed and cooler habitats would show a more constant above-ground activity pattern throughout the year.

Thus, the number of observed individuals by month should be seasonally more variable in the species from open-sunny habitats than those in more vegetated and cooler habitats.

Using a suite of statistical procedures including univariate, multivariate and null model (Monte Carlo methods) analyses, we tested each of the four hypotheses presented above to describe the main "functional" characteristics of the studied lizard community.

Materials and Methods

Study area

Field data were collected in a woodland area surrounding the villages of Manziana, Oriolo Romano and Canale Monterano (approximate coordinates: E 12° 05' N 42° 06'), about 50 km northwest of Rome and just outside west of the regional natural park Bracciano-Martignano (Latium, Central Italy). The study area was a mixed oak woodland with *Quercus cerris* Linnaeus, 1753 and *Q. frainetto* Ten, 1819 as dominant species, and with open grasslands surrounding the wooded patches. In the drier parts of the forest, the trees were mainly *Quercus ilex* Linnaeus, 1753; *Acer campestre* Linnaeus, 1753 and *Tilia* sp. were also common inside the main forest patches. *Rubus ulmifolius* Schott, 1818*, Rubus Cesius* Linnaeus, 1753*, Cytisus scoparius* Linnaeus and Link, 1822*, Smilax aspera* Linnaeus, 1753*, Pteridium aquilinum* L. (Kuhn, 1753)*, Prunus spinosa* Linnaeus, 1753*, Hedera helix* Linnaeus, 1753*, Crataegus monogyna* Jacq, 1775*, Rosa canina* Linnaeus, 1753 and *Sorbus domestica* Linnaeus, 1753 were the most common undergrowth species.

Monitoring

Details of the monitoring protocol were described by Rugiero et al. (2021) for *L. bilineata*. In the present paper, we also include the dataset presented in Rugiero et al. (2021). Monitoring was conducted during April-October 1991, 1992, 1993, 1996, and 1997. On each monitoring day, two or three researchers walked independently along haphazard transects without revisiting the same spots to avoid multiple sightings of the same individuals and, thus, statistical pseudoreplication (Hurlbert 1984). No fixed distance occurred between transects and there was no fixed time or fixed number of walked transects daily. Data collection was restricted to sunny days between 0900 to 1600 hrs to minimize the impact of inter-daily weather conditions. We observed lizards without any interference such as capture. We considered only those individuals that were observed active above-ground, i.e., not under stones, tree branches or other ground objects. We identified observed lizards by species, sex based on external features for those species that can be distinguished by them (not for the two gecko species and *C. chalcides*) and age class (adult or juvenile), based on both body size and, for some species (*L. bilineata, P. muralis*), dorsal coloration. For each sighted lizard we recorded a habitat category defined by the dominance of a specific bushy plant taxon. Six habitat types were distinguished (Figure 1):

(1) *Rubus* spp., that was the most wet habitat available to lizards at the study area and had in May a vegetation cover (established at 300 random 1 x 1 m spots by eye) = 72.3 ± 21.4%;

(2) *Cytisus scoparius,* with a vegetation cover = 42.1 ± 33.1%;

(3) *Spartium junceum* Linnaeus, 1753*,* with a vegetation cover = 38.7 ± 11.1%;

(4) open grassland with no bushy species*,* with a vegetation cover = 12.1 ± 3.3%;

(5) stony wall (locally called "muretti a secco")*,* with a vegetation cover = 52.1 ± 43.2%. This habitat was the only human-made feature available to lizards at the study areas;

(6) *Smilax aspera,* with a vegetation cover = 59.4 ± 27.1%.

The vegetation cover calculations at each site were always undertaken by the same person; cover percentages were assessed at the moment of sighting of individual lizards. The relative availability of the various habitat types at the study areas is summarized in Table 1.

Mean body mass (g) of the various species was obtained from measurements made by one of us (MC) during previous studies on the genetics of these species (e.g., Capula and Ceccarelli 2003) and from the literature (e.g., Ferrandino et al. 2001 for *Chalcides chalcides*). Also, no individual animals were killed for the genetic studies that preceded the current research.

Statistical procedures

Niche breadths of habitats used by species and, for those species in which it was possible to discriminate sexes, by sex, were assessed by Simpson's (1949) index (B_S) and by a standardized equation transformed from Levins' (1968) formula (B_L) with its values ranging from 0 (maximum specialisation) to 1 (maximum opportunism) (Luiselli 1992).

To verify whether one sex had, independently for each species, a higher habitat niche breadth than the other (hypothesis that can be anticipated because home ranges in reptiles are generally much larger in males than in females; see Rocha 1999), we pooled the various species and examined their average habitat niche breadth. We also examined the habitat breadth hypothesis by season, using spring (April, May and June), summer (July, August) and autumn (September and October) as season categories.

A non-metric multidimensional scaling (nMDS) analysis with the cosine distance, using PAST 4.3 software (https://www.nhm.uio.no/english/research/infrastructure/past/) was carried out to cluster lizard individuals by sex, age class and species in relation to habitat availability, with the centroids being reported in the output of the analyses for the various species, individual categories and habitat availability.

For the simulations study, datasets were inspected to determine the nonrandom structure in the studied lizard community by contrasting the actual data matrix as given in the original literature source (or as in the original data) with random ‘pseudo-communities’ generated by Monte Carlo simulations (Gotelli and Graves 1996). We used the EcoSim software (Aquired Intelligence Corp., Kesey-Bear, VT, USA) to calculate habitat niche overlap indices between sympatric species and to generate Monte Carlo simulations. For each lizard sighting, we parameterized resource (habitat) items data as presence versus absences. As too many zeroes in the matrices can distort error levels while too often rejecting structure, we fixed zeroes prior to any analyses (Pianka 1986). Pianka's (1986) overlap formula was calculated for all lizard's group combinations; then, the original species utilization matrices were randomized by shuffling the original values among the resource states (habitats). We used three randomization algorithms RA2, RA3 and RA4 of Lawlor (1980) as they have been shown to be particularly robust for niche overlap studies (Gotelli and Graves 1996). RA2 explores the assemblage structure in the generalist–specialist nature of the resource utilization matrix by conserving guild structure, but destroying observed niche breadth (Gotelli and Graves 1996). RA3 explores the guild structure by conserving niche breadth for each species, but destroying guild structure manifested by the zero structure of the resource utilization matrix (Gotelli and Graves 1996). RA4 retains both the niche breadth of the lizard species and the zero states in the resource utilization matrix, so among the lizards only the original non-zero electivities were randomly reassigned among the set of resource states originally used by that consumer (Lawlor 1980). For each pair of species, 30,000 random Monte Carlo permutations were generated. This number of permutations is enough to avoid biases in the results in calculations (Lehsten and Harmand 2006). Niche overlap values were calculated for each randomly generated matrices, and species-pair and community-summary statistics were computed (Friggens and Brown 2005). Actual overlap values were then compared to the distributions of the expected values, with the nonrandom structure being assumed when P(obs<exp) = 0.05 or less either with RA2, RA3 or RA4 (Gotelli and Graves 1996). In all cases, we define the resource use based on its availability (%) in the field.

For the seasonal analyses, we processed the data independently for spring (April, May and June), summer (July, August) and autumn (September and October). Contingency table analysis by χ^2 tests was carried out to analyze the frequency differences of lizard individuals observed by season and by species. Pearson's correlation coefficient was used to analyse the relationship between lizard body mass and habitat niche breadth, and between the observed sample sizes per species and the habitat niche breadth. In the text, means are presented ±1 Standard Deviation, with alpha set at 5%.

Results

General considerations

A total of 7257 lizard sightings, belonging to seven distinct species, were observed in the study area (Table 1). The commonest species was *P. muralis* (n = 4708 sightings), followed by *P. sicula* (n = 1706), *L. bilineata* (n = 397) and *C. chalcides* (n = 394). The other species were remarkably less common in the study area: *T. mauritanica* was seen only 31 times, *H. turcicus* 11 times and *A. veronensis* 10 times. Lacertidae species accounted for 93.8% of the total number of observed lizard individuals. A nMDS plot arranged the various groups of lizard individuals in clearly distinct sectors of the multidimensional space by sex, age class and species (Figure 2). The coordinate 1 explained 87.3% of the overall variance, and coordinate 2 explained 11.9%. *Chalcides chalcides, P. sicula* and *L. bilineata* juveniles were joined in the same cluster; *P. muralis* and *A. veronensis* were separate from each other; *L. bilineata* females clustered very close with the overall habitat availability; *T. mauritanica* and *H. turcicus* were separated from the other clusters but did not cluster jointly in the multidimensional space.

Hypothesis 1: the "niche complementarity" theory

Overall, there were no differences between the two groups (same bauplan, mean niche overlap = 0.57 ± 0.37; different bauplan, mean niche overlap = 0.51 ± 0.28; t = 0.433, P = 0.669). The three random reorganization algorithms indicated inconsistant patterns of variation in mean habitat overlaps from the overlaps actually observed for the seven species along the six habitat variables: in RA3 the observed overlap was significantly higher than the mean simulated value, whereas in RA4 the observed overlap was significantly lower, and in RA2 it was random (Table 2).

Thus, no evidence of a community structure compatible with overall interspecific competition was detected from our analyses. Therefore, the hypothesis that species with the same bauplan should non-randomly partition the available habitats and show less overlap in habitat niche overlap than species with different bauplans was not confirmed by our data.

In *L. bilineata*, the habitat niche overlap was very high between males and females (O = 0.929), low between males and juveniles (O = 0.343), and intermediate between females and juveniles (O = 0.554). In *P. sicula*, all the individual categories exhibited extremely high habitat niche overlaps: O = 0.998 between males and females, O = 0.981 between males and juveniles and O = 0.989 between females and juveniles. In *P. muralis*, the trend was very similar as that of *P. sicula*, with very high overlap between males and females (O = 0.994), males and juveniles (O = 0.970) or females and juveniles (O = 0.939). For the other sympatric species it was impossible to calculate these intraspecific overlap values because we were unable to sex them in the field.

Hypothesis 2: larger species have wider niche breadth

The largest species in the assemblage (*L. bilineata*) showed the widest habitat niche breadth (B_L= 0.38), followed by *P. muralis* (B_L= 0.28) and *P. sicula* (B_L= 0.22). The other four species had a considerably narrower niche breadth: *A. veronensis* (B_L= 0.16), *H. turcicus* (B_L= 0.09), *C. chalcides* (B_L= 0.08), and *T. mauritanica* (B_L= 0). These niche breadth values were not associated with respective sample sizes for each species (r = 0.462, n = 7, P = 0.297), but were significantly dependent on the relative body size of each species (r = 0.857, r^2 = 0.734, n = 7, P = 0.0018). The niche breadth values, by category of individuals within each species, are given in Table 3. Pooling the various species, males had on average niche breadth values similar to females (x = 0.31±0.08 versus 0.29±0.25), so it may concluded that species body size, and not the sex, significantly influenced the habitat niche breadth of these lizards. Overall, the null hypothesis 2 of larger species have no wider niche breath was rejected, thus, hypothesis 2 was supported by our field data. The niche breadth values did not vary by seasons (in all cases, $P > 0.05$), and are, therefore, not further presented here.

Hypothesis 3: the slower species inhabit the most covered habitat types

At our study areas, the frequency of occurrence of the various species in the two habitats with densest vegetation (*Rubus* and *Smilax*) differed significantly from equality (observed-versus-expected $\chi^2 = 136.8$, df = 6, $P < 0.0001$), with the slowest/most criptically coloured species (*A. veronensis*) being observed in these two habitats much more frequently (50% of the cases) than any other species (in descending order: *P. muralis* 38%, *L. bilineata* 28%, *P. sicula* 10.4%, *C. chalcides* 1.5%, *T. mauritanica* and *H. turcicus* 0%). Overall, our data rejected null hypothesis 3 of no impact of species' speed, thus, supporting the hypothesis 3.

Hypothesis 4: the species inhabiting open sunny habitats exhibit more seasonally variable activity patterns

The percentage of individuals observed by season, for each of the study species, are given in Figure 3. Contingency table analysis revealed that there were significant differences among species ($\chi^2 = 1262$, df = 24, $P < 0.0001$), with *L. bilineata* and *C. chalcides* being mostly observed in the springtime and the two *Podarcis* species more regularly throughout the year. If we consider the species that occurred more frequently in the most open-sunny habitat (open grasslands) versus those that occurred more frequently in the most covered habitats (i.e., *C. chalcides* versus *A. veronensis*), there were significant differences ($\chi^2 = 135.7$, df = 2, $P < 0.0001$), with the former species showing a strong seasonality (peak of activity during springtime; sequential $\chi^2 = 274.8$, df = 2, $P < 0.0001$) and the latter showing no significant seasonality in its activity patterns ($\chi^2 = 4.6$, df = 2, $P = 0.148$)

(Figure 3). Thus, the null hypothesis of no impact of sunnyness was rejected, thus supporting our hypothesis 4.

Discussion

General considerations

The studied lizard assemblages were characterized by a clear prevalence (over 90%) of Lacertidae species in terms of frequency of observed individuals: the two species of *Podarcis* were the most common, followed by *L. bilineata*, which is also the largest bodied of the seven saurians species present. Among the non-Lacertidae species, only *C. chalcides* were recorded frequently, while the remaining three species were clearly more rarely observed. These general frequency differences among lizard families mirror previous data from Mediterranean communities (e.g., Rugiero 2004; Santos and Poquet 2010), that are often inhabited by a remarkable variety of sympatric Lacertidae (Pérez Mellado 1982; Zakkak et al. 2015). The nMDS analysis showed that two clear groups of species were recognizable: one group of "open" areas, consisting of *C. chalcides, P. sicula* and *L. bilineata* juveniles, and one group of "close vegetation" consisting of *P. muralis* and *A. veronensis*, with the other species being not clearly assignable to any of these two well-defined groups of taxa. This result appears to mirror the known habitat characteristics that have been described for these species (e.g., Corti et al. 2011), however this is not sufficient per se to define whether the various species co-occurrences in the various habitats were determined essentially by ecological constraints ("bauplan" characteristics mediated by climatic and structural factors sensu Arnold 1987) or by interspecific relationships (niche partitioning, e.g., Luiselli 2008). However, the four hypotheses tested in the present paper allow us to make some inferences on the reasons behind the observed habitat use patterns by species at the study areas in Mediterranean central Italy.

Testing the four hypotheses

In our first hypothesis, we predicted that habitat niche overlap between species with the same bauplans should be significantly lower than the overlaps between species of different bauplan groups. Thus, we hypothesized that species with a same bauplan would have non-randomly partitioned the habitat types. We found no consistent support for either of these predictions, indeed, patterns of habitat use overlap were not associated with bauplan. In Anolis lizards, species that use similar habitats tend to evolve similar body plans (i.e., ecomorphological convergence, Williams 1983; Losos et al. 1998). In cases where species with similar body plans overlap in habitat use, they may partition resources in other ways, such as temporally or along other resource axes (Luiselli 2008). Thus, our observations of a central Italian lizard community are not similar to those of Anolis lizards, perhaps because many tropical communities have higher species richness and competition can be quite intense (e.g., on small islands, Calsbeek and Cox 2010).

Concerning hypothesis 2, the wider habitat niche breadth of the largest bodied species (*L. bilineata*) is interesting because in this species we detected a significant diversification of habitat use in relation to age. The strong propensity of juveniles to use open environments, which led them to be classified in the group also consisting of *P. sicula* and *C. chalcides*, changes ontogenetically, with adults being significantly more generalized (Rugiero et al. 2021). This is a further confirmation that it is the body size, and not other ecological characteristics, that is strongly associated with the wider habitat niche breadth of this species. Furthermore, habitat niche breadth was nearly identical in 1-2 years-old juvenile *L. bilineata* population cohorts in comparison to similarly-sized lizards of other species. Intraspecific competition avoidance and cannibalism appear to be the main reasons pushing juveniles to minimize habitat overlap with adults in the large-sized *L. bilineata* at these study areas (Rugiero et al. 2021). The same pattern was also recorded from *Anolis* lizards, with adult male density having significant effects on juvenile perch height, perch width, and substrate use, thus suggesting that strong age-class competition may contribute to the ontogenetic differences in habitat choice (Delaney and Warner 2017*a*, 2017*b*).

Our third hypothesis, that lizard species with slower movements and cryptic colouration would inhabit more closed habitats, was supported in that *Anguis veronensis* was observed in the two habitat types with the densest vegetations significantly more frequently than was any other species. However, the patterns of dense habitat use for other lizard species did not indicate decreasing movement speeed and crypticity. It is possible that this relationship is non-linear, and the benefits of dense vegetation are outweighed by other factors for lizards of a threshold movement speed sand/or crypticity.

Our fourth hypothesis was also related to vegetation density; we predicted that lizard species that use habitats with denser vegetation would show more temporally consistent, unseasonal activity, whereas those that use more open habitats would exhibit more seasonally variable activity. We found that lizard species that occurred primarily in open habitat had distinct seasonal activity peaks, while those that occurred primarily in densely vegetated habitats had unseasonal activity patterns. This interesting result should be examined more fully with detailed studies of energy budgets and metabolic rates because these dramatic differences in behaviour associated with adjacent habitats could have important life history implications.

Our data supported three of the four hypotheses of our study, with the niche complementarity hypothesis being clearly rejected by our study. The niche complementarity hypothesis was the only one that involved interspecific relationships as a causal factor for its acceptance, given that, under its assumptions, the habitat differences between species with a same bauplan should be due to the need to minimize interspecific competition (Schoener 1974). On the other hand, the other three hypotheses are based on size-related autecological exigencies (hypothesis 2), morphological constraints and physical performance (hypothesis 3), and eco-physiological constraints (hypothesis 4). Therefore, we think that these lizard communities are more clearly organized by autecological constraints and eco-physiological attributes, whereas the interspecific interactions produced apparent patterns of habitat niche divergences that are unlikely due to interspecific competition and the ghost-of-the-competition-past (Connell 1980; Alatalo and Lundberg 1983; Cressman and Křivan 2013; Bottin et al. 2016). This general conclusion was also confirmed by our null model analyses, that did not provide any evidence for a competitively-structured assemblage of species under any of the randomization algorithms (Lawlor 1980) that we used and that have been shown elsewhere to be powerful tools for detecting structure signs of nonrandom niche partitioning in biotic communities (e.g., Gotelli and Graves 1996; Solida et al. 2011; Vignoli and Luiselli 2012). Nonetheless, our data cannot give firm conclusions on this issue, as we would need to examine habitat use in sites with and without competitors to examine variation in habitat use in absence of potential competition.

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Table 1. Synthesis of the number of lizard species observed at the study area by habitat type and by individual category (male, female or juvenile). Data from all seasons are pooled.

Genus	Species	Category	Symbol	*Rubus*	*Cytisus*	*Spartium*	grassland	stony walls	*Smilax aspera*	TOTAL
Podarcis	*sicula*	males	PsM	51	77	13	369	114	41	665
Podarcis	*sicula*	females	PsF	39	73	22	401	133	28	696
Podarcis	*sicula*	juveniles	PsJ	7	17	8	211	91	11	345
Podarcis	*muralis*	males	PmM	598	233	189	31	916	176	2143
Podarcis	*muralis*	females	PmF	668	321	273	9	894	203	2165
Podarcis	*muralis*	juveniles	PmJ	133	16	4	5	231	11	400
Chalcides	*chalcides*		Cc	6	41	33	311	3	0	394
Anguis	*veronensis*	males	AvM	1	0	0	0	2	1	4
Anguis	*veronensis*	females	AvF	1	0	0	0	0	0	1
Anguis	*veronensis*	juveniles	AvJ	2	1	0	0	2	0	5
Tarentola	*mauritanica*		Tm	0	0	0	0	31	0	31
Hemidactylus	*turcicus*		Ht	0	0	0	3	8	0	11
Lacerta	*bilineata*	males	LbM	51	18	10	10	22	7	118

Lacerta	*bilineata*	females	LbF	34	22	14	20	16	11	117
Lacerta	*bilineata*	juveniles	LbJ	7	9	12	111	22	1	162
HABITAT TYPE AVAILABILITY (%)			Availability	20.69	16.73	15.41	16.87	17.54	12.75	

Table 2. Testing the "niche complementarity" hypothesis using habitat niche overlap simulation analysis for lizards at the study area in central Italy. The used algorithms were Lawlor's (1980) RA2, RA3 and RA4 algorithms, after 30,000 Monte Carlo simulations. These simulations were done from data of all seasons being pooled.

	RA2	RA3	RA4
Observed mean Overlap	0.53870	0.53870	0.53870
Mean simulated Overlap	0.57851	0.42382	0.76684
Variance simulated Overlap	0.00095	0.00053	0.00092
Standardized Effect Size	-1.29004	5.01184	-7.50843
Random seed	-1645502148	-1800479482	-1525427312
p(observed ≤ expected)	0.10400	0.99999	0.00001
p(observed ≥ expected)	0.89600	0.00001	0.99999
Observed variance	0.09309	0.09309	0.09309
Mean of simulated variances	0.06089	0.07930	0.01587
Variance of simulated variances	0.00006	0.00004	0.00002
p(observed ≤ expected)	1.00000	0.97000	0.99999
p(observed ≥ expected)	0.00000	0.03000	0.00001

Table 3. Testing the hypothesis that larger species should have wider niche breadth using the values of habitat niche breadth, calculated for each individual category of the various species, at the study area in central Italy. Data from all seasons are pooled. B_S = Simpson's formula; B_L = Levins' formula.

Genus	Species	Category	B_S	B_L
Podarcis	*sicula*	males	2.77	0.25
Podarcis	*sicula*	females	2.60	0.23
Podarcis	*sicula*	juveniles	2.23	0.18
Podarcis	*muralis*	males	3.48	0.35
Podarcis	*muralis*	females	3.20	0.31
Podarcis	*muralis*	juveniles	2.24	0.18
Chalcides	*chalcides*		1.56	0.08
Anguis	*veronensis*	males	2.67	0.24
Anguis	*veronensis*	females	1.00	0.00
Anguis	*veronensis*	juveniles	2.78	0.25
Tarentola	*mauritanica*		1.00	0.00
Hemidactylus	*turcicus*		1.66	0.09
Lacerta	*bilineata*	males	3.81	0.40
Lacerta	*bilineata*	females	5.24	0.61
Lacerta	*bilineata*	juveniles	2.01	0.14

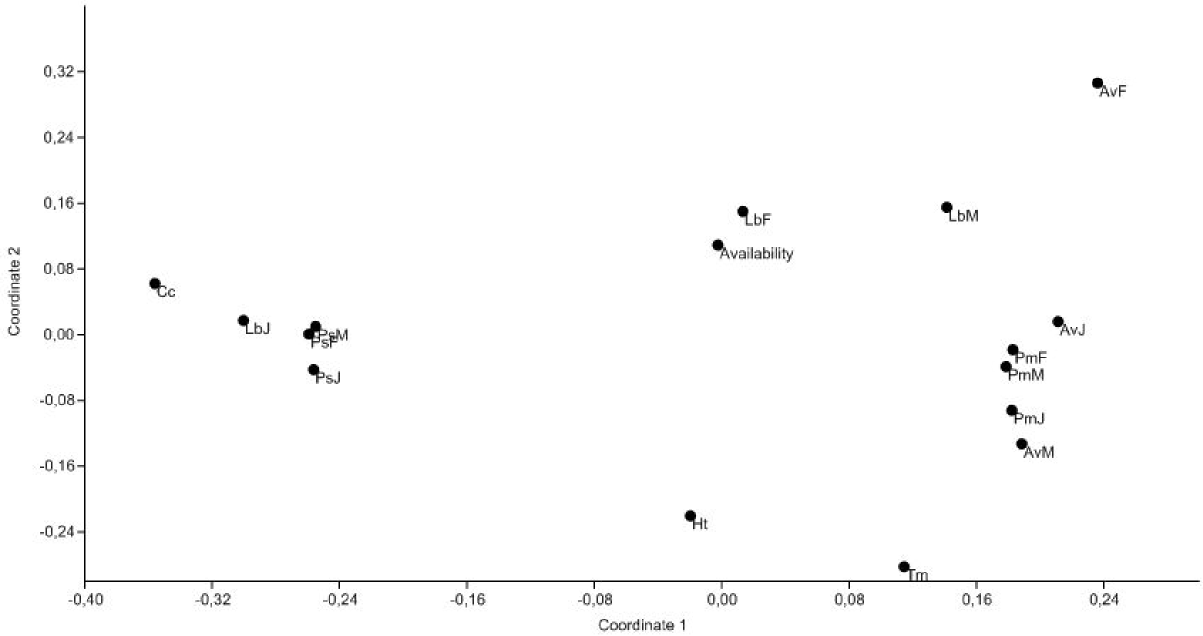
Figure 1. Some of the habitat types at the study area, during the early spring: (a) *Rubus*; (b) grassland; (c) and (d) two types of stony walls

Figure 2. Scatter plot of a non-metric multidimensional scaling (nMDS), using the cosine distance, graphically representing the resemblance matrix between lizard individuals and in relation to the habitat availability. Shown are the centroids of clusters of lizard individuals by sex, age class and species and of habitat availability. Data from all seasons are pooled. Symbols: Cc = *Chalcides chalcides*; Av = *Anguis veronensis*; Ht = *Hemidactylus turcicus*; Lb = *Lacerta bilineata*; Pm = *Podarcis muralis*; Ps = *Podarcis sicula*; Tm = *Tarentola mauritanica*; M = males; F = females; J = juveniles; Availability = habitat availability.

Figure 3. Testing the hypothesis that species inhabiting open sunny habitats should exhibit more seasonally variable activity patterns using the percent of lizard individuals observed by season at the study area in central Italy. Symbols: Cc = *Chalcides chalcides* (n = 394); Av = *Anguis veronensis* (n = 10); Ht = *Hemidactylus turcicus* (n = 11); LB = *Lacerta bilineata* (n = 397); Pm = *Podarcis muralis* (n = 4708); Ps = *Podarcis sicula* (n = 1706); Tm = *Tarentola mauritanica* (n = 28); M = males; F = females; J = juveniles

Figure 1

Figure 2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AvF
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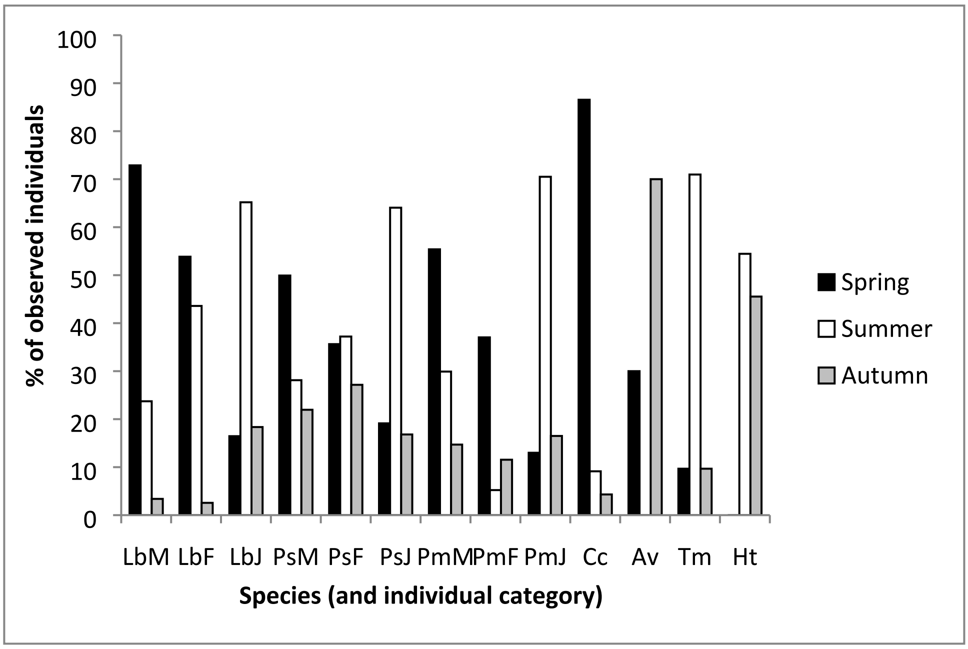
Figure 3


% of observed individuals
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90
80
70
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50
40
30
20
10
0
LbM
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PsM
PsF
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PmM
PmF
PmJ
Cc
Av
Tm
Ht
Species (and individual category)
■ Spring
□ Summer
▨ Autumn