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

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

3

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21

22

23

24 **Abstract**

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

38
39 **Key words:** Sauria; *Lacerta bilineata*; *Podarcis muralis*; *Podarcis sicula*; *Hemidactylus turcicus*;
40 *Tarentola mauritanica*; *Anguis veronensis*; *Chalcides chalcides*; Mediterranean; resource
41 partitioning; bauplan; autecological constraints; eco-physiological attributes

43 **Introduction**

44 In evolutionary biology, a suite of characters shared by a group of phylogenetically related
45 animals at some point during their development is defined as body plan or “bauplan” (Woodger
46 1945; Rieppel 2006; Willmore 2012). The concept has represented an important element in
47 evolutionary developmental biology, evo-devo (Tsessarsky 2020), and the evolutionary ecology of
48 organisms (e.g., Hall 1999; Willmore 2012). However, bauplan has not been explicitly used in
49 community ecology studies, despite this being a central concept for distinguishing the various

50 guilds within truly “functional groups”. Most often, community ecology studies define the various
51 guilds either in terms of phylogenetic units (for instance, varanids versus agamids, etc.) or “natural
52 history-characterized” units (for instance, terrestrial versus arboreal, etc.). Thus, the concept of
53 bauplan may be the ideal synthesis between phylogenetic and natural history characteristics
54 (Stankowich and Stensrud 2019) and, therefore, particularly useful for determining assembly rules
55 of biotic communities. To our knowledge, bauplan has not been explicitly used in community
56 ecology studies.

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

71
72 Like Caribbean *Anolis* Daudin, 1802 lizards (Losos 2011; Pringle et al. 2019) and Australian
73 desert lizards (Pianka 1986), European lizards offer an interesting and logistically convenient
74 system for testing predictions of community ecology theory (e.g., Sillero et al. 2020). These animals

75 are often abundant, conspicuous, and approachable, and therefore it is often easier to observe and
76 record data on their spatial ecologies than for less abundant and more elusive animals.

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

86
87 In the present study we examined habitat use and temporal activity correlates of an entire
88 community of lizards in three locations in central Italy (Tolfa Mountains, province of Rome). These
89 study sites consist of a complex landscape composed of habitat patches that include a variety of
90 environmental typologies typical of the area. Habitats range from open dry Mediterranean maquis to
91 habitat types with damp vegetation, tall trees with cooler climate and higher humidity. Using this
92 wide range of habitat features potentially available to lizards, we explored the spatio-temporal
93 patterns of lizard community structure. This community is composed of species belonging to three
94 main types of bauplan: type (i) was a typical "lacertid bauplan" with long legs, long tail and slender
95 body, allowing them to run quickly on the ground but also climb efficiently on vertical substrates
96 (three species: the larger sized *Lacerta bilineata* Daudin, 1802 and the smaller-sized *Podarcis*
97 *muralis* Laurenti, 1768 and *Podarcis sicula* Rafinesque, 1810); type (ii) was a typical "gecko
98 bauplan" with adhesive toe pads allowing them to climb well even on vertical surfaces (two species:
99 *Hemidactylus turcicus* (Linnaeus, 1758) and *Tarentola mauritanica* (Linnaeus, 1758)); type (iii)

100 was an elongated, slender “snake-like” bauplan, allowing them to only move on ground and burrow
101 underground (two species: *Anguis veronensis* Pollini, 1818, *Chalcides chalcides* Linnaeus, 1758).

102

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

124

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

134

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

143

144 In Mediterranean environments, the high ambient temperatures (> 35°C) typical during
145 summers may represent a constraint for reptile above-ground activities (Carretero and Llorente
146 1995; Rouag et al. 2007; Zamora-Camacho et al. 2013; Bouam et al. 2016). As a fourth hypothesis
147 we predicted that those species inhabiting open sunny habitats would exhibit more seasonally
148 variable activity patterns, with peaks during the early spring months, and scarce above-ground
149 activity in the summer (Burke and Ner 2005). By contrast, species that are very linked to closed and
150 cooler habitats would show a more constant above-ground activity pattern throughout the year.

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

153
154 Using a suite of statistical procedures including univariate, multivariate and null model
155 (Monte Carlo methods) analyses, we tested each of the four hypotheses presented above to describe
156 the main “functional” characteristics of the studied lizard community.

157

158 **Materials and Methods**

159 *Study area*

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

171

172 *Monitoring*

173 Details of the monitoring protocol were described by Rugiero et al. (2021) for *L. bilineata*. In
174 the present paper, we also include the dataset presented in Rugiero et al. (2021). Monitoring was
175 conducted during April-October 1991, 1992, 1993, 1996, and 1997. On each monitoring day, two or
176 three researchers walked independently along haphazard transects without revisiting the same spots

177 to avoid multiple sightings of the same individuals and, thus, statistical pseudoreplication (Hurlbert
178 1984). No fixed distance occurred between transects and there was no fixed time or fixed number of
179 walked transects daily. Data collection was restricted to sunny days between 0900 to 1600 hrs to
180 minimize the impact of inter-daily weather conditions. We observed lizards without any
181 interference such as capture. We considered only those individuals that were observed active above-
182 ground, i.e., not under stones, tree branches or other ground objects. We identified observed lizards
183 by species, sex based on external features for those species that can be distinguished by them (not
184 for the two gecko species and *C. chalcides*) and age class (adult or juvenile), based on both body
185 size and, for some species (*L. bilineata*, *P. muralis*), dorsal coloration. For each sighted lizard we
186 recorded a habitat category defined by the dominance of a specific bushy plant taxon. Six habitat
187 types were distinguished (Figure 1):

- 188 (1) *Rubus* spp., that was the most wet habitat available to lizards at the study area and had in
189 May a vegetation cover (established at 300 random 1 x 1 m spots by eye) = $72.3 \pm 21.4\%$;
- 190 (2) *Cytisus scoparius*, with a vegetation cover = $42.1 \pm 33.1\%$;
- 191 (3) *Spartium junceum* Linnaeus, 1753, with a vegetation cover = $38.7 \pm 11.1\%$;
- 192 (4) open grassland with no bushy species, with a vegetation cover = $12.1 \pm 3.3\%$;
- 193 (5) stony wall (locally called “muretti a secco”), with a vegetation cover = $52.1 \pm 43.2\%$. This
194 habitat was the only human-made feature available to lizards at the study areas;
- 195 (6) *Smilax aspera*, with a vegetation cover = $59.4 \pm 27.1\%$.

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

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

203

204

205

206 *Statistical procedures*

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

211

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

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

223 For the simulations study, datasets were inspected to determine the nonrandom structure in
224 the studied lizard community by contrasting the actual data matrix as given in the original literature
225 source (or as in the original data) with random 'pseudo-communities' generated by Monte Carlo
226 simulations (Gotelli and Graves 1996). We used the EcoSim software (Aquired Intelligence Corp.,
227 Kesey-Bear, VT, USA) to calculate habitat niche overlap indices between sympatric species and to
228 generate Monte Carlo simulations. For each lizard sighting, we parameterized resource (habitat)

229 items data as presence versus absences. As too many zeroes in the matrices can distort error levels
230 while too often rejecting structure, we fixed zeroes prior to any analyses (Pianka 1986). Pianka's
231 (1986) overlap formula was calculated for all lizard's group combinations; then, the original species
232 utilization matrices were randomized by shuffling the original values among the resource states
233 (habitats). We used three randomization algorithms RA2, RA3 and RA4 of Lawlor (1980) as they
234 have been shown to be particularly robust for niche overlap studies (Gotelli and Graves 1996). RA2
235 explores the assemblage structure in the generalist–specialist nature of the resource utilization
236 matrix by conserving guild structure, but destroying observed niche breadth (Gotelli and Graves
237 1996). RA3 explores the guild structure by conserving niche breadth for each species, but
238 destroying guild structure manifested by the zero structure of the resource utilization matrix (Gotelli
239 and Graves 1996). RA4 retains both the niche breadth of the lizard species and the zero states in the
240 resource utilization matrix, so among the lizards only the original non-zero electivities were
241 randomly reassigned among the set of resource states originally used by that consumer (Lawlor
242 1980). For each pair of species, 30,000 random Monte Carlo permutations were generated. This
243 number of permutations is enough to avoid biases in the results in calculations (Lehsten and
244 Harmand 2006). Niche overlap values were calculated for each randomly generated matrices, and
245 species-pair and community-summary statistics were computed (Friggens and Brown 2005). Actual
246 overlap values were then compared to the distributions of the expected values, with the nonrandom
247 structure being assumed when $P(\text{obs} < \text{exp}) = 0.05$ or less either with RA2, RA3 or RA4 (Gotelli and
248 Graves 1996). In all cases, we define the resource use based on its availability (%) in the field.

249

250 For the seasonal analyses, we processed the data independently for spring (April, May and
251 June), summer (July, August) and autumn (September and October). Contingency table analysis by
252 χ^2 tests was carried out to analyze the frequency differences of lizard individuals observed by season
253 and by species. Pearson's correlation coefficient was used to analyse the relationship between lizard

254 body mass and habitat niche breadth, and between the observed sample sizes per species and the
255 habitat niche breadth. In the text, means are presented ± 1 Standard Deviation, with alpha set at 5%.

256

257

258 **Results**

259 *General considerations*

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

272

273 *Hypothesis 1: the “niche complementarity” theory*

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

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

284

285 In *L. bilineata*, the habitat niche overlap was very high between males and females ($O =$
286 0.929), low between males and juveniles ($O = 0.343$), and intermediate between females and
287 juveniles ($O = 0.554$). In *P. sicula*, all the individual categories exhibited extremely high habitat
288 niche overlaps: $O = 0.998$ between males and females, $O = 0.981$ between males and juveniles and
289 $O = 0.989$ between females and juveniles. In *P. muralis*, the trend was very similar as that of *P.*
290 *sicula*, with very high overlap between males and females ($O = 0.994$), males and juveniles ($O =$
291 0.970) or females and juveniles ($O = 0.939$). For the other sympatric species it was impossible to
292 calculate these intraspecific overlap values because we were unable to sex them in the field.

293

294 *Hypothesis 2: larger species have wider niche breadth*

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

306 niche breadth values did not vary by seasons (in all cases, $P > 0.05$), and are, therefore, not further
307 presented here.

308
309
310
311 *Hypothesis 3: the slower species inhabit the most covered habitat types*

312 At our study areas, the frequency of occurrence of the various species in the two habitats
313 with densest vegetation (*Rubus* and *Smilax*) differed significantly from equality (observed-versus-
314 expected $\chi^2 = 136.8$, $df = 6$, $P < 0.0001$), with the slowest/most cryptically coloured species (*A.*
315 *veronensis*) being observed in these two habitats much more frequently (50% of the cases) than any
316 other species (in descending order: *P. muralis* 38%, *L. bilineata* 28%, *P. sicula* 10.4%, *C. chalcides*
317 1.5%, *T. mauritanica* and *H. turcicus* 0%). Overall, our data rejected null hypothesis 3 of no impact
318 of species' speed, thus, supporting the hypothesis 3.

319
320 *Hypothesis 4: the species inhabiting open sunny habitats exhibit more seasonally variable activity*
321 *patterns*

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

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

333

334 **Discussion**

335 *General considerations*

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

355

356 *Testing the four hypotheses*

357 In our first hypothesis, we predicted that habitat niche overlap between species with the
358 same bauplans should be significantly lower than the overlaps between species of different bauplan
359 groups. Thus, we hypothesized that species with a same bauplan would have non-randomly
360 partitioned the habitat types. We found no consistent support for either of these predictions, indeed,
361 patterns of habitat use overlap were not associated with bauplan. In *Anolis* lizards, species that use
362 similar habitats tend to evolve similar body plans (i.e., ecomorphological convergence, Williams
363 1983; Losos et al. 1998). In cases where species with similar body plans overlap in habitat use, they
364 may partition resources in other ways, such as temporally or along other resource axes (Luiselli
365 2008). Thus, our observations of a central Italian lizard community are not similar to those of
366 *Anolis* lizards, perhaps because many tropical communities have higher species richness and
367 competition can be quite intense (e.g., on small islands, Calsbeek and Cox 2010).

368
369 Concerning hypothesis 2, the wider habitat niche breadth of the largest bodied species (*L.*
370 *bilineata*) is interesting because in this species we detected a significant diversification of habitat
371 use in relation to age. The strong propensity of juveniles to use open environments, which led them
372 to be classified in the group also consisting of *P. sicula* and *C. chalcides*, changes ontogenetically,
373 with adults being significantly more generalized (Rugiero et al. 2021). This is a further confirmation
374 that it is the body size, and not other ecological characteristics, that is strongly associated with the
375 wider habitat niche breadth of this species. Furthermore, habitat niche breadth was nearly identical
376 in 1-2 years-old juvenile *L. bilineata* population cohorts in comparison to similarly-sized lizards of
377 other species. Intraspecific competition avoidance and cannibalism appear to be the main reasons
378 pushing juveniles to minimize habitat overlap with adults in the large-sized *L. bilineata* at these
379 study areas (Rugiero et al. 2021). The same pattern was also recorded from *Anolis* lizards, with
380 adult male density having significant effects on juvenile perch height, perch width, and substrate
381 use, thus suggesting that strong age-class competition may contribute to the ontogenetic differences
382 in habitat choice (Delaney and Warner 2017a, 2017b).

383

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

391

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

400

401 Our data supported three of the four hypotheses of our study, with the niche
402 complementarity hypothesis being clearly rejected by our study. The niche complementarity
403 hypothesis was the only one that involved interspecific relationships as a causal factor for its
404 acceptance, given that, under its assumptions, the habitat differences between species with a same
405 bauplan should be due to the need to minimize interspecific competition (Schoener 1974). On the
406 other hand, the other three hypotheses are based on size-related autecological exigencies
407 (hypothesis 2), morphological constraints and physical performance (hypothesis 3), and eco-
408 physiological constraints (hypothesis 4). Therefore, we think that these lizard communities are more

409 clearly organized by autecological constraints and eco-physiological attributes, whereas the
410 interspecific interactions produced apparent patterns of habitat niche divergences that are unlikely
411 due to interspecific competition and the ghost-of-the-competition-past (Connell 1980; Alatalo and
412 Lundberg 1983; Cressman and Krivan 2013; Bottin et al. 2016). This general conclusion was also
413 confirmed by our null model analyses, that did not provide any evidence for a competitively-
414 structured assemblage of species under any of the randomization algorithms (Lawlor 1980) that we
415 used and that have been shown elsewhere to be powerful tools for detecting structure signs of
416 nonrandom niche partitioning in biotic communities (e.g., Gotelli and Graves 1996; Solida et al.
417 2011; Vignoli and Luiselli 2012). Nonetheless, our data cannot give firm conclusions on this issue,
418 as we would need to examine habitat use in sites with and without competitors to examine variation
419 in habitat use in absence of potential competition.

420

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424

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583

584 **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).

585 Data from all seasons are pooled.

586

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

22

<i>Lacerta</i>	<i>bilineata</i>	females	LbF	34	22	14	20	16	11	117
<i>Lacerta</i>	<i>bilineata</i>	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	

Draft

588 **Table 2.** Testing the “niche complementarity” hypothesis using habitat niche overlap simulation
 589 analysis for lizards at the study area in central Italy. The used algorithms were Lawlor’s (1980)
 590 RA2, RA3 and RA4 algorithms, after 30,000 Monte Carlo simulations. These simulations were
 591 done from data of all seasons being pooled.
 592

	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 \leq expected)	0.10400	0.99999	0.00001
p(observed \geq 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 \leq expected)	1.00000	0.97000	0.99999
p(observed \geq expected)	0.00000	0.03000	0.00001

593

594

595 **Table 3.** Testing the hypothesis that larger species should have wider niche breadth using the values
 596 of habitat niche breadth, calculated for each individual category of the various species, at the study
 597 area in central Italy. Data from all seasons are pooled. B_S = Simpson's formula; B_L = Levins'
 598 formula.
 599

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

600

601

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

604

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

612

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

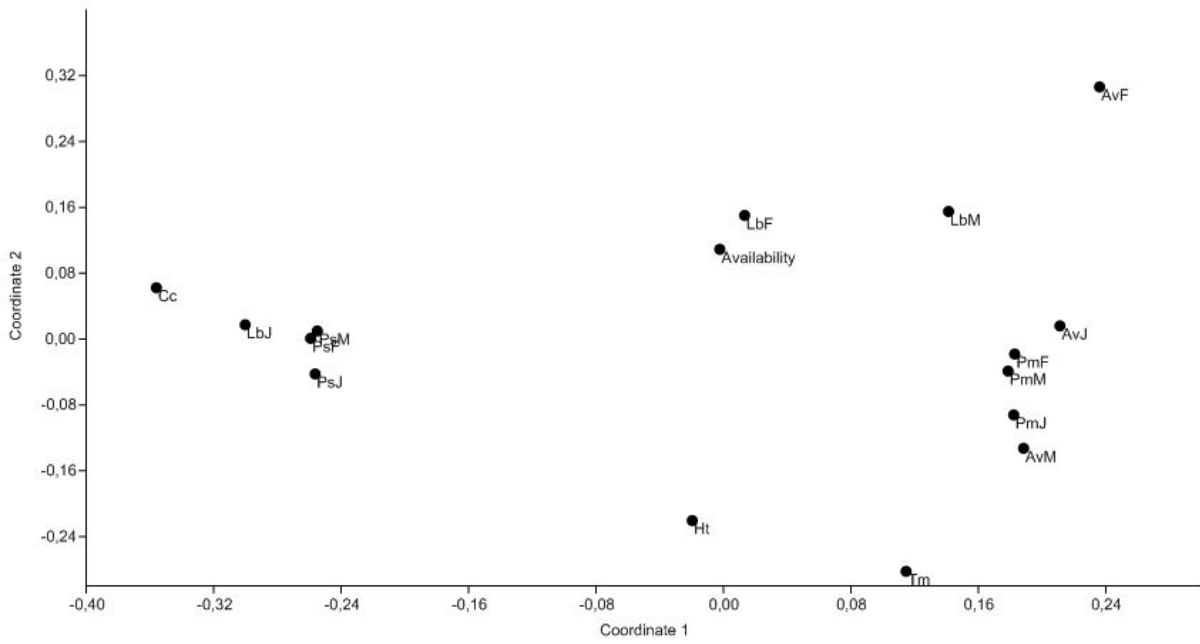
619

620 Figure 1



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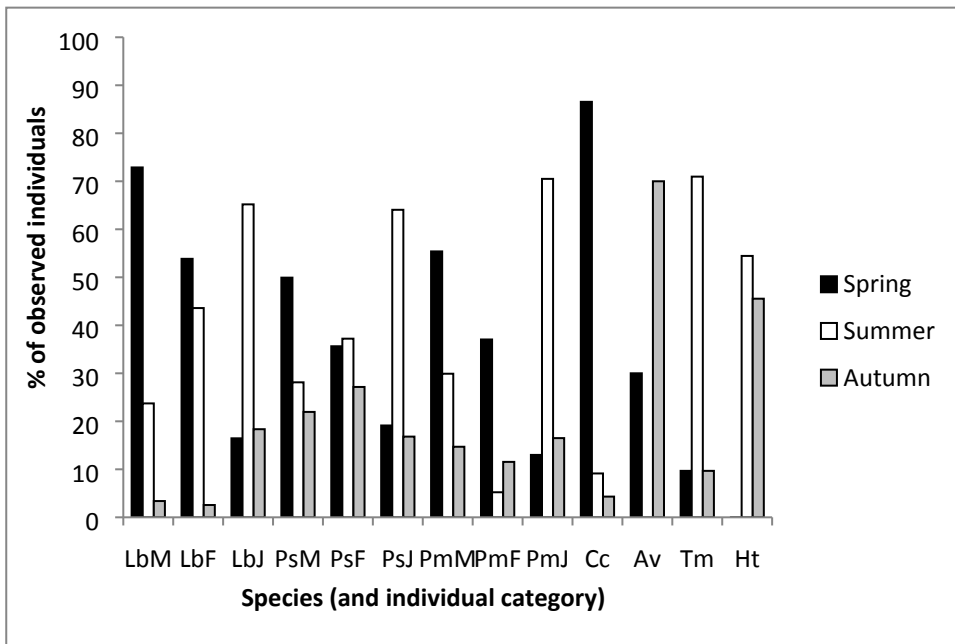
622 Figure 2



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625 Figure 3



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