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4 2 Competition with wall lizards does not explain

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6 3 the alpine confinement of Iberian rock lizards: an experimental approach

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52 22
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54 23 Keywords: agonistic behaviour, *Iberolacerta cyreni*, microhabitat selection, *Podarcis muralis*.

1 26 Abstract
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6 28 Interspecific competition can limit the distribution of species along altitudinal gradients. It has
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8 29 been suggested that west European rock lizards (genus *Iberolacerta*) are restricted to
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10 30 mountains due to the expansion of wall lizards (*Podarcis*), but there is not experimental
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12 31 evidence to corroborate this hypothesis. This study examines if interference competition with
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14 32 *Podarcis muralis* is a plausible explanation for the alpine confinement of Iberian rock lizards
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16 33 *Iberolacerta cyreni*. In a first experiment, we used an enclosure with four types of
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18 34 microhabitats to investigate whether adult rock and/or wall lizards shifted microhabitat or
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20 35 refuge preferences in the presence of the other species, and to detect aggressive interactions
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22 36 between them. In a second experiment, we staged heterospecific encounters between naïve,
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24 37 lab-born juveniles to identify behavioural differences and agonistic interactions. In the
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26 38 enclosure, neither rock nor wall lizards changed their microhabitat preferences in the presence
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28 39 of the other species. Nevertheless, rock lizards increased the diversity of microhabitats and
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30 40 nocturnal refuges used in the single species trials, which had twice the number of
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32 41 conspecifics. Aggressive interactions involved mainly large rock lizard males. Juveniles did
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34 42 not show any interspecific agonistic behaviour, but rock lizards spent more time basking and
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36 43 less time moving. Thus, we found no evidence of competition between both species in terms
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38 44 of habitat shifts or agonistic interactions, although intraspecific interactions seemed to explain
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40 45 the behaviour of adult rock lizards. We conclude that other factors are currently determining
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42 46 the alpine confinement of rock lizards.

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1 49 INTRODUCTION

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6 51 Interspecific competition, combined with other biotic and abiotic factors, can limit the
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8 52 distribution of species in potentially suitable habitats (Brown, Stevens, and Kaufmann, 1996;
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10 53 Pulliam, 2000). While dominant species exploit successfully the shared habitat, subordinate
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13 54 ones can be relegated to suboptimal areas either by their reduced exploitative ability or by
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15 55 direct behavioural interference (Schoener, 1983; Petren, Bolger and Case 1993). In
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18 56 evolutionary time, competitive exclusion can lead to phenotypic divergence of sympatric
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20 57 species, which diversify their use of resources (Schluter, 2000; Pfennig, Rice and Martín
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23 58 2007; Moen and Wiens, 2009). Also, in an effort to minimize overlapping, species can
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25 59 segregate in space by selecting different habitats, a behavioural mechanism which can
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28 60 contribute to generate allopatric distributions (Hess and Losos, 1991; Taniguchi and Nakano,
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30 61 2000).

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35 63 Lizards, for their dynamic distribution ranges and moderate dispersal ability, are good
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37 64 models to investigate the role of interspecific competition in community structure. Several
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40 65 studies have demonstrated the crucial role of interspecific competition in the evolution,
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42 66 distribution, and abundance of island lizards (see Case and Bolger, 1991 for a review). For
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45 67 example, success in island colonization by anoles is seemingly shaped by interspecific
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47 68 competition (Losos, Marks and Schoener, 1993; Losos and Spiller, 1999), and the
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50 69 evolutionary radiation and community structure of Caribbean anoles and *Phelsuma* geckos in
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52 70 the Indian Ocean were likely driven by competitive interactions (Losos, 1994; Leal,
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55 71 Rodriguez-Robies, and Losos, 1998; Harmon, Harmon and Jones, 2007).

1 73 Although much of the relevant literature concerns island species, elevation has also
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3 74 drawn the attention of biogeographers and evolutionary ecologists seeking to explore the role
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6 75 of interspecific competition in the vertical zonation of organisms (Tannerfeldt, Elmhagen and
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8 76 Angerbjorn, 2002; Cadena, 2007; Twomey, Morales and Summers, 2008). For reptiles, the
9
10 77 possible effect of competitive interactions on the distribution of species along altitudinal
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12 78 gradients is unclear. While in some cases interspecific competition appears to modify
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15 79 population responses to elevation (Buckley and Roughgarden, 2005, 2006), the altitudinal
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18 80 distribution of other communities seems unrelated to interactions among species (Hofer,
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20 81 Bersier and Borcard, 1999; Carothers, Jaksic and Marquet, 2001). Nevertheless, studies are
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23 82 still scarce, and further research is needed to improve our understanding of how biotic
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25 83 interactions shape lizard assemblages along altitudinal gradients.
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30 85 West European rock lizards within the genus *Iberolacerta* have small, widely
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32 86 separated ranges in highland areas of the western Mediterranean. They form a monophyletic
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35 87 group with four main units: *I. horvathi* of NW Croatia and neighbouring regions, the
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37 88 Pyrenean species (*I. bonnali*, *I. aranica* and *I. aurelioi*), the *I. monticola* group from Central
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40 89 Portugal and NW Spain, and *I. cyreni* of the Iberian Sistema Central, with distinctive
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42 90 populations in Béjar, Gredos and Guadarrama mountain ranges (Carranza, Arnold and Amat,
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44
45 91 2004). Molecular analyses suggest that *Iberolacerta* has produced few external branches since
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47 92 its initial fragmentation, at approximately the same time when wall lizards (*Podarcis*)
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50 93 diversified into a series of widespread lineages that have persisted until present time
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52 94 (Carranza, Arnold and Amat, 2004). Thus, *Iberolacerta* rock lizards may have been restricted
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55 95 to mountains by competition with *Podarcis* (Carranza, Arnold and Amat, 2004; Crochet et al.,
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57 96 2004).
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This study aims to clarify whether competitive exclusion by wall lizards *P. muralis* is a plausible explanation for the alpine confinement of Iberian rock lizards *I. cyreni*. To detect competition, which among lacertids is mainly manifested as direct behavioural interference rather than indirect exploitation of resources (Downes and Bauwens, 2002), we conducted two experiments. In the first one, we used adult lizards to investigate whether *I. cyreni* and/or *P. muralis* shifted microhabitat or refuge preferences in the presence of the other species, and to detect aggressive interactions. In the second one, we staged heterospecific encounters between pairs of naïve, lab-born juveniles of both species to identify behavioural differences which might lead to a competitive advantage of one species over the other.

METHODS

Study System

The lacertid lizards *I. cyreni* and *P. muralis* provide an excellent system to investigate the possible restricting role of competitive exclusion in shaping species distributions. Both are heliothermic, actively foraging, and saxicolous lizards, but they present some morphological differences, *I. cyreni* being slightly larger than *P. muralis* (adult snout vent length [SVL] of 73-80 mm and 48-70 mm, respectively). While rock lizards are endemic to the mountains of the Sistema Central in the Iberian Peninsula, wall lizards present a widespread distribution in Central Europe that reaches its southwestern limit at the Sierra de Guadarrama (Central Spain), where both species are present. In this mountain range, rock lizards are only found above 1,600 m, preferably in rocky outcrops and mixed-shrub formations (Martín and

1 121 Salvador, 1997; Monasterio, Salvador and Díaz, in press), whereas wall lizards occupy lower
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3 122 altitudes (from 1,230 m to 2,100 m a.s.l.) and a wider range of habitats, including rocky
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6 123 outcrops, oak and pine forests, forest track banks, walls, and other human constructions
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8 124 (Martín-Vallejo et al., 1995; Amo, López and Martín, 2007a). The Sierra de Guadarrama
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10 125 presents contrasting seasonal conditions, with cold wet winters and short dry summers. Its
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12 126 mountain bases (1,200-1,700 m a.s.l.) are covered with deciduous Pyrenean oak (*Quercus*
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14 127 *pyrenaica*) forests, which are progressively substituted by Scots pine (*Pinus sylvestris*) forests
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16 127 at higher altitudes. These forested areas, that can spread from 1,500 to 2,100 m a.s.l.,
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18 128 gradually become less dense until vegetation is dominated by a mosaic of dense mixed-shrub
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20 129 formations (of perennial *Juniperus communis* and *Cytisus oromediterraneus*) interspersed
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22 130 with small meadows of *Festuca* and other grasses. These alpine areas above the tree line
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24 131 (1,700-2,300 m a.s.l.) are also characterized by extensive patches of large granite rocks and
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26 132 scree interspersed among shrub formations (Costa, Morla and Sanz, 2005).
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35 135 Experimental Procedure

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40 137 Adults

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45 139 For this experiment, we captured 15 adult rock lizards (9 males and 6 females) and 15 wall
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47 140 lizards (5 males and 10 females) at the Sierra de Guadarrama and we transported them to ‘El
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49 141 Ventorrillo’ field station (1,500 m), where we weighed and measured (snout-vent length,
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51 142 SVL) them to the nearest 0.1 g and 0.5 mm, respectively. We housed lizards separately in
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53 143 outdoor terraria with a sand substrate, rocks and vegetation. Lizards were fed live crickets
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55 144 every day and they had water available ad libitum. Capture methods, housing conditions and
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1 145 release procedures were appropriate for these species, and we observed no adverse effect of
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3 146 either the experiment or the housing methods on lizards' health. All individuals were in good
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6 147 condition, both during the experiment and when released at the site of capture.
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11 149 We carried out an experiment during June and July 2007 to ascertain the microhabitat
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13 150 preferences of both species, either alone or together, when different microhabitats were
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15 151 offered. For that purpose, we used an outdoor enclosure (4x4 m²) with four types of distinct,
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18 152 representative microhabitats (Fig. 1): bare rocks (hereafter rocks), rocks with *Cytisus*
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20 153 *oromediterraneus* shrubs (hereafter rock-shrub), *Juniperus communis* shrub (hereafter shrub),
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23 154 and logs with gravel (hereafter logs). Sun was available from 09:00 h until 17:30 h (Mean
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25 155 European Time), allowing lizards to thermoregulate normally. To characterize the thermal
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28 156 environment, we placed four electronic temperature recording devices (Tidbits™, Onset
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30 157 Computer Corporation, Pocasset, MA, USA) either on the top of and inside each type of
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33 158 microhabitat. We programmed data loggers to register temperature hourly during eight days
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35 159 (for tidbits on top of microhabitats) or ten days (for tidbits inside refuges). Insect prey were
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38 160 naturally available in the enclosure, and we observed lizards feeding on several occasions.
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42 162 Our experimental design compared the behaviour of lizards when each species was
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45 163 alone in the enclosure and when both species were together. In the first treatment (each
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47 164 species alone), we introduced different combinations of 10 individuals of either rock or wall
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50 165 lizards in the enclosure. In the second treatment, we placed simultaneously different
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52 166 combinations of 5 individuals of each species in the enclosure. To decide which individuals
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55 167 were to be used in each combination, we used the following criteria: 1) we tried to keep
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57 168 constant the proportion of males and females in all cases; 2) we maintained the same
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1 169 proportion of large (72-75 mm SVL) and small (<68 mm SVL) male rock lizards; and 3)
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3 170 whenever possible, we tried to change all the individuals which were used in consecutive
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6 171 sampling sessions of 2-3 days (see below). Therefore, our design implies that most
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8 172 individuals were used more than once (only two lizards were used just once, 16 individuals
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10 173 were used twice, and 11 individuals were used three times). However, each individual yielded
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13 174 one single data for each treatment (i.e. no pseudoreplication was committed), because the
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15 175 proportion of use of each microhabitat type and the diversity of microhabitats used were
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18 176 estimated pooling together all observations for each individual in each treatment. It should be
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20 177 noted that, although 0.625 individuals/m² is obviously higher than average densities in the
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23 178 field (nevertheless, values up to 1,200 individuals/ha have been reported for the related
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25 179 species *Iberolacerta monticola*; Moreira et al., 2008), lizards can reach these and higher
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28 180 concentrations at local patches of rock and shrub habitat (authors, personal observation).
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33 182 Observations were carried out with binoculars between 8:00 and 15:00 h, from a 2 m
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35 183 high wall above the enclosure which made it possible to see the totality of the experimental
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37 184 arena without disturbing the lizards. Each individual received a unique paint code on its back
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40 185 to allow recognition. We recorded the microhabitat use by each animal every 30 minutes.
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42 186 From our experimental setup (Fig. 1), it is clear that open patches of short grass were also
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45 187 available. However, they were never used by lizards except for moving between the four
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47 188 microhabitats offering refuge. In that case, lizards that were crossing open areas at the
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50 189 moment of recording their behaviour were scored as using the microhabitat at which they
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52 190 arrived. Also, when lizards were on the grass patches but in the immediate surroundings of
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55 191 one of the four microhabitats, they were scored as using that microhabitat type. In both
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57 192 treatments, we registered all agonistic interactions observed. Lizard groups were maintained
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1 193 in the enclosure during two or three consecutive days. Before introducing a new group of
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3 194 lizards, we watered the enclosure abundantly to eliminate chemical cues. We also obtained
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6 195 data about the nocturnal refuges used by lizards. This was done in two ways. The first one
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8 196 was to find and capture all lizards while still inactive in the early morning, taking advantage
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11 197 of the fact that we had to change the group of lizards. The second one was to note the
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13 198 microhabitat from which the animals first emerged in the early morning, with the enclosure in
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16 199 full shade and no prior activity recorded during the previous hour.
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20 201 We analysed data using chi-square tests (with the null hypothesis that the four
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23 202 microhabitat types were used in equal proportions) and general linear models. We calculated
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25 203 the proportion of use of each microhabitat type for each individual in each treatment (p_i 's),
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28 204 and we estimated the diversity of microhabitats used for each individual and treatment by
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30 205 means of $\exp(H')$, the transformed Shannon diversity index (Kempton and Taylor, 1976). To
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33 206 search for differences between species and/or sexes separately for each treatment, we used
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35 207 multivariate analyses of variance (MANOVAs) where the p_i 's of the four microhabitat types
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38 208 were included as the dependent variables. To test for treatment effects (only one species vs.
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40 209 both species in the enclosure) we used a within-subjects MANOVA with the differences
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43 210 between treatments as dependent variables, calculated for each lizard and microhabitat type
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45 211 (the null hypothesis for treatment effects is that the intercept of the linear model, i.e. the mean
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48 212 difference between treatments while holding for the effects of all variables in the model, is
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50 213 equal to zero). Therefore, this repeated measures design effectively avoided
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52 214 pseudoreplication, because sample sizes were always equal to the number of lizards,
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55 215 independently of the number of observations per individual and treatment.
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1 217 We applied a similar procedure to test for differences between species and/or sexes in
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3 218 the use of nocturnal refuges, but pooling together both treatments (each species alone and
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6 219 both species together) to maintain an acceptable sample size (the nocturnal refuges procedure
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8 220 yielded only one datum per day, producing an average sample size of 4.2 observations per
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11 221 individual, vs. the much higher number of observations –one every 30 min– in the case of
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13 222 microhabitat use data). Thus, although it was not possible to compare p_i 's between treatments
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16 223 with such a small amount of data (if, for instance, one individual used rocks as a nocturnal
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18 224 refuge four of four times, thus making all the remaining p_i 's equal to zero), we could test
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21 225 overall differences between species and sexes.
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25 227 Juveniles

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30 229 To search for competitive interactions between juvenile rock and wall lizards, we staged
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33 230 short-term interspecific encounters in the laboratory. For that purpose, and as part of an
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35 231 ongoing study on the ecology of eggs and hatchlings, we reared lab-born lizards with live
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38 232 crickets and water supplied ad libitum. We formed heterospecific pairs of juveniles ($N = 17$
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40 233 pairs), matched for their body size. We used each individual only once. Since we raised
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42 234 juveniles in individual terraria, they had no social experience previous to this experiment. We
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45 235 placed heterospecific pairs of lizards in a small terrarium (265 mm length x 162 mm width x
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47 236 150 mm height) that offered rock and sand substrates in equal proportions. A 40-W focal
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50 237 lamp 25 cm above the rock acted as a heat source allowing lizards to bask. After releasing the
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52 238 lizards in the terrarium, we used a camera on a tripod to record their behaviour during 4
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55 239 minutes. We tested all pairs in the early morning and before having fed the lizards. After
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57 240 every encounter, we washed and dried the rock and we replaced the sand. In the video
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1 241 recordings, we registered all interactions detected and we measured the amount of time that
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3 242 lizards spent basking (i.e. laying flat on the rock substrate under the lamp), moving or staying
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6 243 motionless outside the basking area. We used repeated measures ANOVAs to test for
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8 244 interspecific differences in the percentage of time spent basking or moving. At the end of the
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11 245 experiment, lizards were released at their mother's site of capture.
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13 246 14 15 247 RESULTS 16 17

18 248 19 20 249 Adults 21 22

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30 253 In our sample of individuals, rock lizards had larger SVL (mean \pm 1 SE = 69.3 ± 1.5 mm) and
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32 254 body mass (mean \pm 1 SE = 7.9 ± 0.4 g) than wall lizards (SVL: 58.6 ± 1.5 mm; body mass:
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35 255 5.1 ± 0.4 g), with no sexual size dimorphism in either species (species effect in two-way
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37 256 ANOVAs: SVL: $F_{1,26} = 25.03$, $P < 0.0001$; body mass: $F_{1,26} = 22.75$, $P < 0.0001$; $P > 0.05$ for
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40 257 all sex and interaction effects). Concerning SVL-adjusted body mass, males of a given SVL
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42 258 were heavier than females, but species did not differ significantly (two-way ANCOVA: sex:
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45 259 $F_{1,25} = 7.22$, $P = 0.013$; $P > 0.25$ for the species and interaction effects).
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47 260 48 49 261 Microhabitat use 50 51

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54 263 In both treatments, the two species preferred the rocky microhabitats and avoided the shrub
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57 264 (see chi-square results in Table 1). We did not find any interspecific or sexual differences in
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1 265 the use of microhabitat types, either when the species were alone (MANOVA; species: Wilks'
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4 266 $\lambda = 0.928$, $F_{3,22} = 0.57$, $P = 0.639$; sex: Wilks' $\lambda = 0.905$, $F_{3,22} = 0.76$, $P = 0.523$; interaction:
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6 267 Wilks' $\lambda = 0.787$, $F_{3,22} = 1.98$, $P = 0.146$) or when they were together in the experimental
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9 268 enclosure (MANOVA; species: Wilks' $\lambda = 0.853$, $F_{3,24} = 1.37$, $P = 0.275$; sex: Wilks' $\lambda =$
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11 269 0.960 , $F_{3,24} = 0.33$, $P = 0.807$; interaction: Wilks' $\lambda = 0.966$, $F_{3,24} = 0.28$, $P = 0.839$).
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14 270 Similarly, a repeated measures MANOVA did not reveal differences in microhabitat use
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16 271 between treatments (one- vs two-species treatment: Wilks' $\lambda = 0.793$, $F_{3,22} = 1.91$, $P = 0.157$),
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19 272 nor did it find any significant species x treatment (Wilks' $\lambda = 0.895$, $F_{3,22} = 0.86$, $P = 0.478$)
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22 273 or sex x treatment (Wilks' $\lambda = 0.963$, $F_{3,22} = 0.28$, $P = 0.838$) interactions. Nevertheless,
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24 274 overall χ^2 values suggested lower selectivity when there was only one species than when both
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27 275 species shared the enclosure (Table 1). Estimates of effect size (results not shown) showed
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29 276 that non-significant differences in microhabitat use were due to the small size of the effects
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32 277 examined rather than to small sample sizes.
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36 279 When only one species was present in the enclosure, rock lizards showed significantly
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39 280 higher diversities of microhabitat use than did wall lizards (ANOVA; species: $F_{1,24} = 8.59$, P
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41 281 $= 0.007$; sex: $F_{1,24} = 0.68$, $P = 0.417$; interaction: $F_{1,24} = 1.52$, $P = 0.229$). However, this
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44 282 difference disappeared when both species were together (species: $F_{1,26} = 0.39$, $P = 0.539$; sex:
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46 283 $F_{1,26} = 0.19$, $P = 0.670$; interaction: $F_{1,26} = 0.04$, $P = 0.849$). This result was confirmed by a
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48
49 284 repeated measures ANOVA, which showed a significant treatment x species interaction ($F_{1,24}$
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51 285 $= 4.94$, $P = 0.036$), meaning that rock lizards, but not wall lizards, were more evenly
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54 286 distributed in the one-species treatment than in the two-species treatment (Fig. 2).
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58 288 Agonistic interactions
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3 290 Although our experiment was carried out in the post-breeding season, when aggressive
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6 291 interactions and territorial behaviour are presumably less intense, we observed twelve
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8 292 agonistic encounters (Table 2). All these chases implicated only males, and only three of them
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11 293 involved wall lizards (one chased by a conspecific and the other two by a rock lizard). In fact,
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13 294 the majority of attacks (10 of 12) came from the same rock lizard (B4), which was one of the
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15 295 three largest males (SVL = 75 mm) and was particularly aggressive (as judged from the
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18 296 number and intensity of the attacks) with a conspecific male of the same size (A3; see Table
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21 297 2). This is not unexpected, given the well-known tendency of these lizards to form clear-cut
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23 298 dominance hierarchies (Martín and Salvador 1993). To analyse these interactions, we
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25 299 considered the effects of microhabitat use by lizards using experimental groups as sampling
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28 300 units (Table 3). This was done because dominance relationships could depend not only on the
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30 301 individual traits of each lizard, but also on its social context. In each experimental group
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32 302 containing rock lizards, we signalled as dominant the individual which successfully ousted
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35 303 other males from its preferred microhabitat type (i.e. the microhabitat most frequently used),
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38 304 which was almost invariably the rock-shrub microhabitat (Table 3; for the single group in
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40 305 which no aggressions were observed [group B], the largest male [A2M, SVL = 73 mm] was
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42 306 signalled as dominant). We then noted the number of males (including the dominant one)
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45 307 which shared the same microhabitat preference, i.e. which coincided in the microhabitat type
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48 308 for which they showed the highest p_i . Despite the low sample size (only five experimental
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50 309 groups including rock lizards), the number of aggressive interactions was significantly
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52 310 correlated with the number of males sharing the preferred microhabitat type (rock-shrub or
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55 311 rocks) with the dominant one (Spearman rank's correlation: $r_s = 0.892$, $N = 5$, $P = 0.042$).

1 312 Thus, intraspecific competition among rock lizards was important for understanding their
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3 313 patterns of habitat use.
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6 314 7 8 315 Nocturnal refuges 9

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13 317 We found no significant differences between species or sexes in the use of microhabitat types
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15 318 as nocturnal refuges (MANOVA; species: Wilks' $\lambda = 0.896$, $F_{4,23} = 0.66$, $P = 0.623$; sex:
16 319 Wilks' $\lambda = 0.949$, $F_{4,23} = 0.31$, $P = 0.870$; interaction: Wilks' $\lambda = 0.964$, $F_{4,23} = 0.22$, $P =$
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18 319 0.926). Nevertheless, rock lizards used a significantly higher diversity of nocturnal refuges
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20 320 than did wall lizards (ANOVA; species: $F_{1,26} = 17.04$, $P < 0.001$; sex: $F_{1,26} = 1.06$, $P = 0.312$;
21 321 interaction: $F_{1,26} = 0.88$, $P = 0.357$). Thus, wall lizards used mainly the rocky habitats as
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23 322 nocturnal retreat sites, whereas rock lizards were found in all available types of refuge (Fig.
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25 323 3). The major difference between both species was that rock lizards also used the shrub as a
26 324 nocturnal refuge. Interestingly, most of the nocturnal use of this microhabitat type (4 of 6
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28 325 observations) corresponded to the dominant male (B4) that won most aggressive interactions
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30 326 with conspecifics (Table 3).
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60 328 61 62 329 Thermal quality of refuges 63 64 330

65 331 Average temperatures on the surface of the four microhabitat types did not differ significantly
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67 332 after controlling for the effects of time of day (ANOVA with the data in Fig. 4a; time of day:
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69 333 $F_{47,1044} = 110.1$, $P < 0.001$; microhabitat : $F_{3,1044} = 0.41$, $P = 0.745$; interaction: $F_{121,141} = 1.01$,
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71 334 $P = 0.455$), indicating that our results about microhabitat selection were largely independent
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73 335 of the thermal environment. Nevertheless, microhabitat types offered different thermal
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1 336 qualities as nocturnal refuges (Fig. 4b; time of day: $F_{47,1364} = 34.63$, $P < 0.001$; microhabitat :
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3 337 $F_{3,1364} = 10.24$, $P < 0.001$; interaction: $F_{141,1364} = 3.76$, $P < 0.001$). Although temperatures
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6 338 inside refuges were similar during most of the day, the shrub was the microhabitat type that
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8 339 offered the best thermal quality from the late afternoon to the early evening hours (Fig 4b).
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10 340 11 12 13 341 Juveniles

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18 343 Juvenile lizards did not exhibit significant differences in substrate use, although both species
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20 344 selected positively the rock surface (Table 4: $P = 0.074$ in the corresponding ANOVA with
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23 345 species as the repeated measures factor in staged encounters). Nevertheless, we found
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25 346 differences in activity patterns, because wall lizards spent more time moving around the
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28 347 terrarium than did rock lizards ($P < 0.001$), whereas rock lizards spent more time basking than
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30 348 did wall lizards ($P = 0.001$). We recorded no agonistic interactions in any of the interspecific
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33 349 encounters.
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35 350 36 37 351 DISCUSSION

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42 353 Our results show that neither rock nor wall adult lizards changed their microhabitat
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44 354 preferences in the presence of the other species, because they both selected rocky
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47 355 microhabitats independently of the treatment. Nevertheless, we found that rock lizards
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50 356 increased the diversity of microhabitats and nocturnal refuges used in the single species trials,
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52 357 which had twice the number of conspecifics. Agonistic interactions were scarce and they
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55 358 mainly involved large rock lizard males. Thus, our experimental setup allowed us to detect the
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57 359 effects of competition on microhabitat use, but such effects seemed to be acting only within
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1 360 rock lizards. Similarly, although juveniles did not show any interspecific agonistic behaviour
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3 361 in staged encounters, rock lizard hatchlings spent more time basking and less time moving
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6 362 than wall lizards. According to these results, we discuss the possible roles of inter and
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8 363 intraspecific competition in shaping the microhabitat selection of these species and the alpine
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11 364 confinement of rock lizards.

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16 366 Both species showed very similar microhabitat preferences, positively selecting rock
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18 367 and rock-shrub microhabitats and avoiding the shrub. For rock lizards, this is in agreement
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21 368 with morphological adaptations that evidence their specialization as scansorial rock-dwelling
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23 369 lizards (Arnold, 1973) and with previous field results in the study area (Martín and Salvador,
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25 370 1997; Amo, López and Martín, 2007b; Monasterio, Salvador and Díaz, 2010). Wall lizards
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28 371 seem also associated with rocks, but they occupy a wider range of habitats throughout their
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31 372 distributional range. In our experiment rocks and rock-shrub were also the microhabitats
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33 373 preferred by wall lizards. Given the small size of the experimental enclosure, the competitive
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35 374 exclusion hypothesis predicts that rock and wall lizards should compete for these preferred
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38 375 microhabitats, which would produce the displacement of the subordinate species to
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40 376 suboptimal microhabitats. Contrary to this prediction, rock and wall lizards seemed to ignore
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43 377 the presence of each other in the enclosure, and they coexisted without modifying their habitat
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45 378 preferences. Similar experiments with other species have shown that lizards shift their habitat
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48 379 preferences in the presence of a potential competitor (Vanhooydonck, Van Damme and Aerts,
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50 380 2000) or that competitive displacement increases when habitat availability is reduced (Petren
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52 381 and Case, 1998). Our experiment was successful to detect intraspecific competition by
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55 382 behavioural interference (see below), meaning that the observed absence of interspecific
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57 383 competition was not due to flaws in the experimental setup. Because we found no changes in
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1 384 the habitat preferences of any of the two species when they were together in the enclosure, we
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3 385 conclude that competitive exclusion by wall lizards is unlikely to explain the alpine
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6 386 confinement of rock lizards. In addition, body size, which has long been demonstrated to
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8 387 affect dominance relationships in lizards (Langkilde and Shine, 2004; Melville, 2002), was
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11 388 larger for rock lizards than for wall lizards, and the interspecific difference in body size found
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13 389 in our data is consistent with the general pattern already known for these species, suggesting
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16 390 that our results are representative of what it is supposed to occur in the wild. Moreover, data
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18 391 from a previous field study showed that both lizard species chose microhabitats with shorter
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21 392 distances to the nearest refuge than expected at random, that they both preferred rocks over
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23 393 shrubs as their closest retreat, and that the proportion of observations closer to rocks than to
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25 394 shrubs was higher for rock lizards than for wall lizards (Monasterio et al., 2009).

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30 396 Our experimental treatment had a significant effect on the diversity of microhabitats
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33 397 used by rock lizards. Rock lizards used all microhabitats more evenly in the one-species than
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35 398 in the two-species treatment, because their use of space was more diverse when all individuals
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38 399 in the experimental group were rock lizards. This is consistent with the hypothesis that
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40 400 intraspecific competition influences their microhabitat use. Rock lizard males defend
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42 401 territories intensely during the mating season (May-June), and they often establish dominance
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45 402 hierarchies with neighbouring males by means of aggressive interactions (Martín and
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47 403 Salvador, 1993; Martín and López, 2000; Aragón, López and Martín, 2004). Although our
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50 404 experiment was carried out in the postreproductive season, when agonistic interactions are
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52 405 much reduced (Martín and Salvador, 1993), we can explain our results in terms of territorial
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55 406 behaviour. Thus, rock lizards could avoid undesirable encounters that might lead to agonistic
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57 407 interactions by occupying different types of microhabitats. Engaging in aggressive

1 408 interactions can be costly (Marler and Moore, 1988), but such costs can be eluded by reducing
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3 409 the number and intensity of fights (Cooper and Vitt, 1987; López and Martín, 2001). In fact,
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6 410 small and subordinate male rock lizards perform less conspicuous activities to avoid fighting
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8 411 with dominant males (Aragón, López and Martín, 2004; Aragón, López and Martín, 2006). In
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11 412 our study, most chases involved *I. cyreni* individuals and were directed from the same male
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13 413 (B4). Moreover, fights were more frequent when more males shared the preferred habitat,
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16 414 suggesting that lizards could avoid aggressions by occupying other microhabitat types. On the
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18 415 other hand, fights involving wall lizards were very scarce and they were never directed from
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21 416 wall to rock lizards, supporting the idea that interspecific competition was negligible. It might
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23 417 be argued that some individuals, especially B4, could have had a disproportionately large
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25 418 effect on the patterns observed. However, dominance hierarchies have been well documented
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28 419 in this species (Martín and Salvador, 1993), which means that a dominant male which starts
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30 420 and wins a large fraction of the intraspecific aggressions is not an unexpected result.
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35 422 Refuges are valuable resources for reptiles (Huey, 1982; Huey et al., 1989; Díaz,
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38 423 Monasterio and Salvador, 2006), and in some cases it has been found that crevices are
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40 424 strongly defended by dominant lizards, which exclude subordinate species to suboptimal sites
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42 425 (Langkilde, O'Connor and Shine, 2003; Langkilde, Lance and Shine, 2005). However, there
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45 426 was no sign of negative interference in the use of nocturnal retreat-sites between the species
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47 427 studied. Again, the only noticeable pattern was the higher diversity of refuges used by rock
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50 428 lizards, indicating that individuals of this species were less prone than wall lizards to share
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52 429 their nocturnal retreats. This increased diversity was largely due to the behaviour of the
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55 430 dominant male, who avoided sharing nocturnal refuges with other lizards. Remarkably, this
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57 431 male was also the one that used the shrub microhabitat as a nocturnal refuge more frequently.
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Given the major impact that refuge selection can have on the thermal physiology of ectotherms (Huey et al., 1989; Kearney, 2002; Sabo, 2003), it should be noted that the shrub was the warmest refuge during the early evening hours, allowing lizards to attain body temperatures within the preferred thermal range (31.4-35.7°C; Bauwens et al. 1995) without moving from the shelter. Thus, a lizard could thermoregulate while minimizing its exposure to aerial predators, which could have favoured the decision to stay there during the night.

Despite the reduced area shared by heterospecific pairs of juveniles, we detected no agonistic interactions in staged encounters, which supports the results obtained with adults. Because basking opportunities increase energy intake and promote faster growth rates (Sinervo and Adolph, 1989; Niewiarowski and Roosenburg, 1993), juvenile lizards often defend basking sites (Downes and Bauwens, 2002). Although juveniles of both species did not fight over access to basking sites, rock lizards spent more time basking than did wall lizards. This might be indicative of a behavioural preference or a competitive advantage of the former, but not of their hypothesized subordinate condition. It should also be noted that juveniles were matched for their body size; since wall lizard hatchlings are smaller than rock lizard ones, this implies that wall lizard juveniles may have been older than rock lizard ones, and that the competitive ability of the later may have been underestimated relative to natural encounters.

To conclude, we found no evidence of interspecific competition between rock and wall lizards, either juveniles or adults, in terms of habitat shifts or agonistic interactions. In fact, only intraspecific interactions seemed to explain the behaviour of adult rock lizards in

1 456 the enclosure. Therefore, we suggest that other factors, different from competitive exclusion
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3 457 by wall lizards, must be currently determining the lower distribution limit of rock lizards. In
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6 458 other words, our results do not support the hypothesis that rock lizards within the genus
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8 459 *Iberolacerta* are confined to high altitude habitats due to the successful radiation and
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11 460 expansion of *Podarcis* (Arnold, 1987; Carranza, Arnold and Amat, 2004). However, it could
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13 461 be argued that rock and wall lizards have evolved different specializations in the past to
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16 462 minimize their present interactions (i.e. the ghost of competition past, sensu Connell, 1980).
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18 463 Nevertheless, other sympatric lizards whose morphological and/or ecological specializations
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21 464 are thought to have evolved by interspecific competition still respond clearly to competitive
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23 465 exclusion experiments (Leal, Rodriguez-Robies, and Losos, 1998; Harmon, Harmon and
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25 466 Jones, 2007), and our experimental setup allowed us to detect intraspecific competitive
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28 467 interactions. We can thereby conclude that, at least nowadays, interspecific competition is not
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30 468 acting as a barrier for the dispersal of rock lizards, that wall lizards colonize opportunistically
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33 469 the microhabitats they share with rock lizards, and that other factors related to local adaptation
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35 470 are preventing the range expansion of *I. cyreni*. Given the particular conditions of alpine
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38 471 environments (e.g. low temperature), rock lizards could present life history traits that allow
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40 472 them to thrive in mountains, but not at lower altitudes. Previous data suggest that the alpine
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42 473 confinement of Iberian rock lizards is caused by the compromise between environmental
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45 474 thermal quality and refuge availability (Monasterio et al., 2009). To complete these results
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47 475 and explore alternative explanations for the restricted distribution of rock lizards, we
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50 476 recommend further research on the ecophysiology of this species, including the thermal
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52 477 dependence of egg development and the availability and selection of suitable nest sites.
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57 479 Acknowledgments
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Table 1. Habitat selection based on number of observations of rock (*I. cyreni*) and wall (*P. muralis*) lizards under both experimental treatments (one vs. two species in the enclosure). Significant χ^2 values are shown in bold.

| | Only one species in the enclosure | | | | | Both species in the enclosure | | | | |
|--------------------------|-----------------------------------|----------|--------------|------|----------|-------------------------------|----------|--------------|------|----------|
| <i>I. cyreni</i> | Observed | Expected | χ^2 | d.f. | <i>P</i> | Observed | Expected | χ^2 | d.f. | <i>P</i> |
| Rocks | 84 | 69 | 3.26 | 1 | 0.071 | 80 | 55.75 | 10.55 | 1 | 0.001 |
| Rock-shrub | 87 | 69 | 4.70 | 1 | 0.030 | 77 | 55.75 | 8.10 | 1 | 0.004 |
| Shrub | 43 | 69 | 9.80 | 1 | 0.002 | 17 | 55.75 | 26.93 | 1 | < 0.001 |
| Logs | 62 | 69 | 0.71 | 1 | 0.400 | 49 | 55.75 | 0.82 | 1 | 0.366 |
| All | | | 18.46 | 4 | 0.001 | | | 46.40 | 4 | < 0.001 |
| <i>P. muralis</i> | Observed | Expected | χ^2 | d.f. | <i>P</i> | Observed | Expected | χ^2 | d.f. | <i>P</i> |
| Rocks | 53 | 41.75 | 3.03 | 1 | 0.082 | 82 | 49.25 | 21.78 | 1 | < 0.001 |
| Rock-shrub | 56 | 41.75 | 4.86 | 1 | 0.027 | 47 | 49.25 | 0.10 | 1 | 0.749 |
| Shrub | 24 | 41.75 | 7.55 | 1 | 0.006 | 14 | 49.25 | 25.23 | 1 | < 0.001 |
| Logs | 34 | 41.75 | 1.44 | 1 | 0.230 | 54 | 49.25 | 0.46 | 1 | 0.499 |
| All | | | 16.88 | 4 | 0.002 | | | 47.57 | 4 | < 0.001 |

Table 2. Agonistic interactions detected in the experiment: individuals involved (winner is the chasing individual, and loser is the individual ousted by the winner) and number of encounters of each pair.

| WINNER | | | | LOSER | | | | N° of encounters |
|--------|-------------------|---------|---------------|-------|-------------------|---------|---------------|------------------|
| Code | Species | SVL(mm) | Body mass (g) | Code | Species | SVL(mm) | Body mass (g) | |
| B4 | <i>I. cyreni</i> | 75 | 11 | A3 | <i>I. cyreni</i> | 75 | 10.5 | 4 |
| | | | | D1 | <i>I. cyreni</i> | 66 | 8 | 2 |
| | | | | A2M | <i>I. cyreni</i> | 73 | 9.5 | 1 |
| | | | | A5 | <i>I. cyreni</i> | 60 | 5.5 | 1 |
| | | | | D5 | <i>P. muralis</i> | 60 | 6 | 2 |
| A1 | <i>I. cyreni</i> | 72 | 9 | B3 | <i>I. cyreni</i> | 60 | 5.5 | 1 |
| D3 | <i>P. muralis</i> | 57 | 5.5 | DB5C1 | <i>P. muralis</i> | 60 | 6 | 1 |

Table 3. Experimental groups that included rock lizards and aggressive interactions among them. The identity of the dominant male, its preferred microhabitat, and the total number of males sharing that preference are also indicated.

| Group code | Treatment | Dominant male | Habitat(s) preferred by dominant male | N° of males in that habitat | N° of aggressive interactions |
|------------|-------------|---------------|---------------------------------------|-----------------------------|-------------------------------|
| A | One species | B4 | Rock-shrub | 1 | 1 |
| B | Two species | A2M | Rock-shrub | 1 | 0 |
| C | Two species | B4 | Rock and rock-shrub | 3 | 4 |
| D | Two species | A1 | Rock-shrub | 2 | 1 |
| E | One species | B4 | Rock-shrub | 3 | 3 |

Table 4. Behavioural variables (mean \pm SE) of rock and wall lizard juveniles in staged encounters. Results from repeated measures ANOVAs are also shown.

| | | Mean \pm SE | $F_{1,16}$ | P |
|--------------------|-------------------|------------------|------------|---------|
| Time spent on rock | <i>I. cyreni</i> | 80.93 \pm 3.59 | 3.67 | 0.074 |
| | <i>P. muralis</i> | 69.82 \pm 4.97 | | |
| Time spent moving | <i>I. cyreni</i> | 24.90 \pm 2.75 | 33.81 | < 0.001 |
| | <i>P. muralis</i> | 53.97 \pm 3.84 | | |
| Time spent basking | <i>I. cyreni</i> | 66.76 \pm 4.64 | 15.80 | 0.001 |
| | <i>P. muralis</i> | 38.58 \pm 4.52 | | |

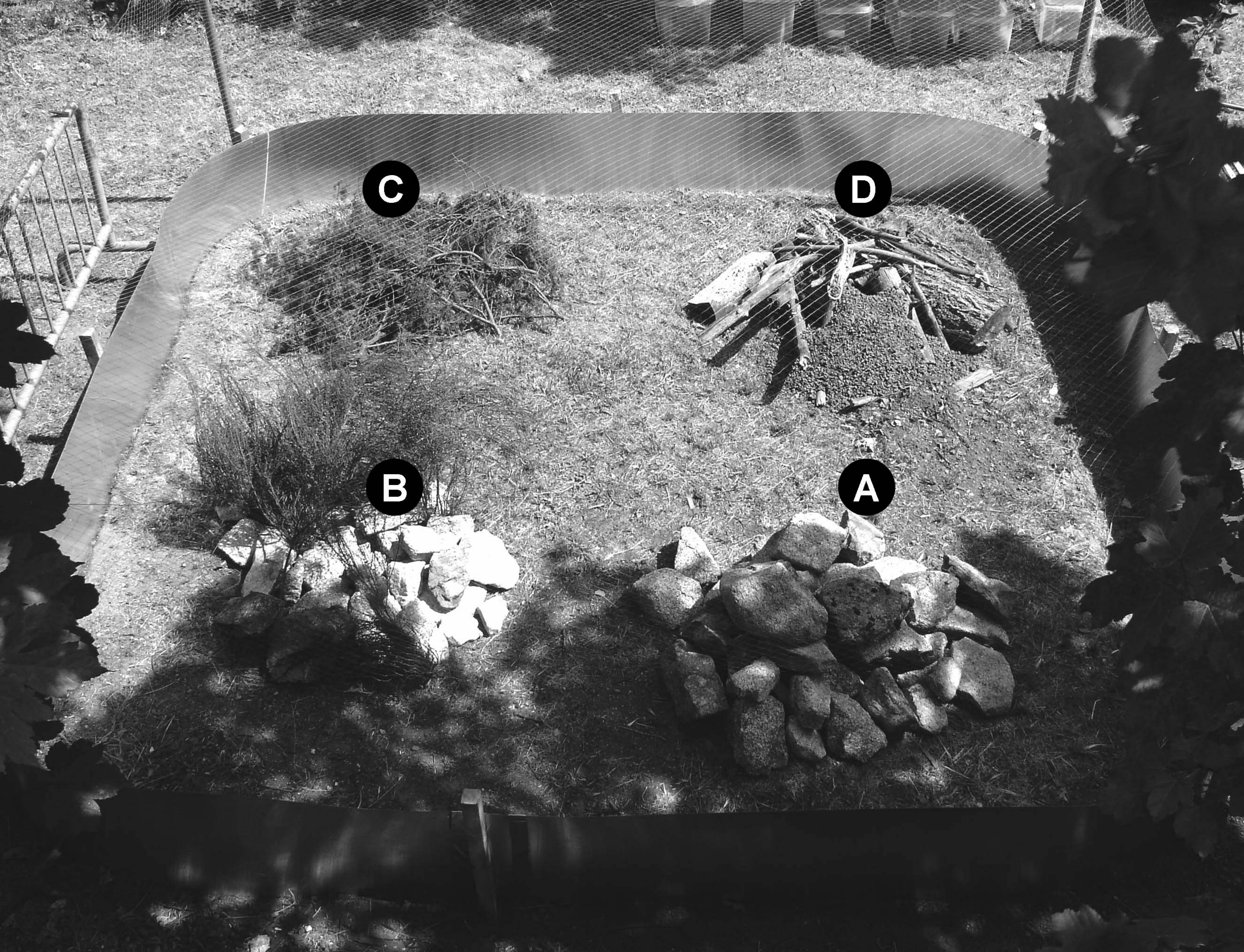
Figure legends

Figure 1. General view of the experimental enclosure used to study microhabitat preferences of adult rock and wall lizards. A = rocks, B = rock-shrub, C = shrub, and D = logs.

Figure 2. Diversity of microhabitats used (exp H') for rock and wall lizards in the one- and two-species treatments. Vertical bars denote 0.95 confidence intervals.

Figure 3. Microhabitats used as nocturnal refuges by rock and wall lizards. Data are given as percentage of observations.

Figure 4. Hourly variation of temperatures available on top and inside the refuges offered by each type of microhabitat. Data are based on the readings of four electronic temperature recording devices (Tidbits™) which were programmed to register temperature hourly during eight days (for tidbits on top of microhabitats) or ten days (for tidbits inside refuges).



C

D

B

A

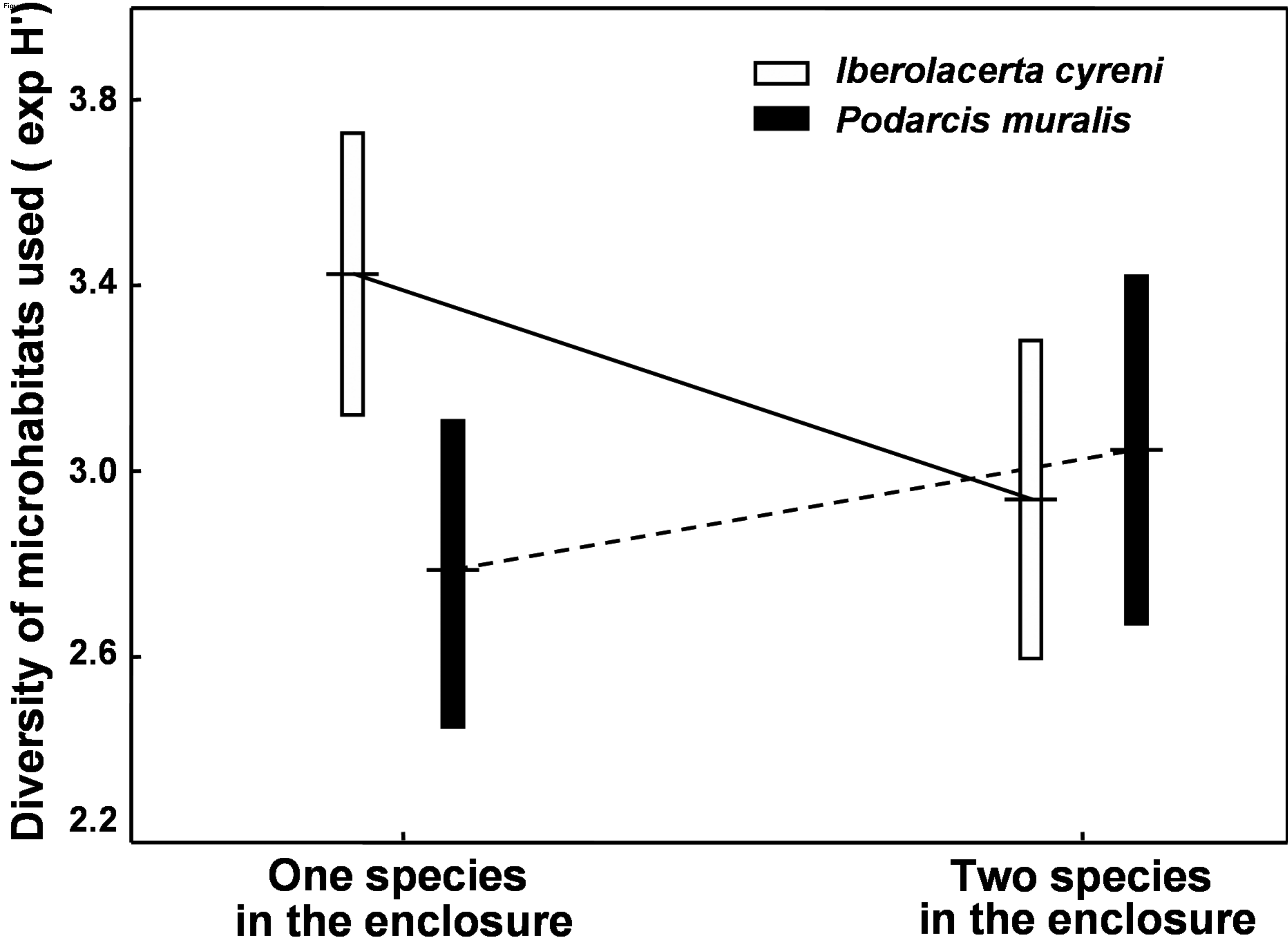
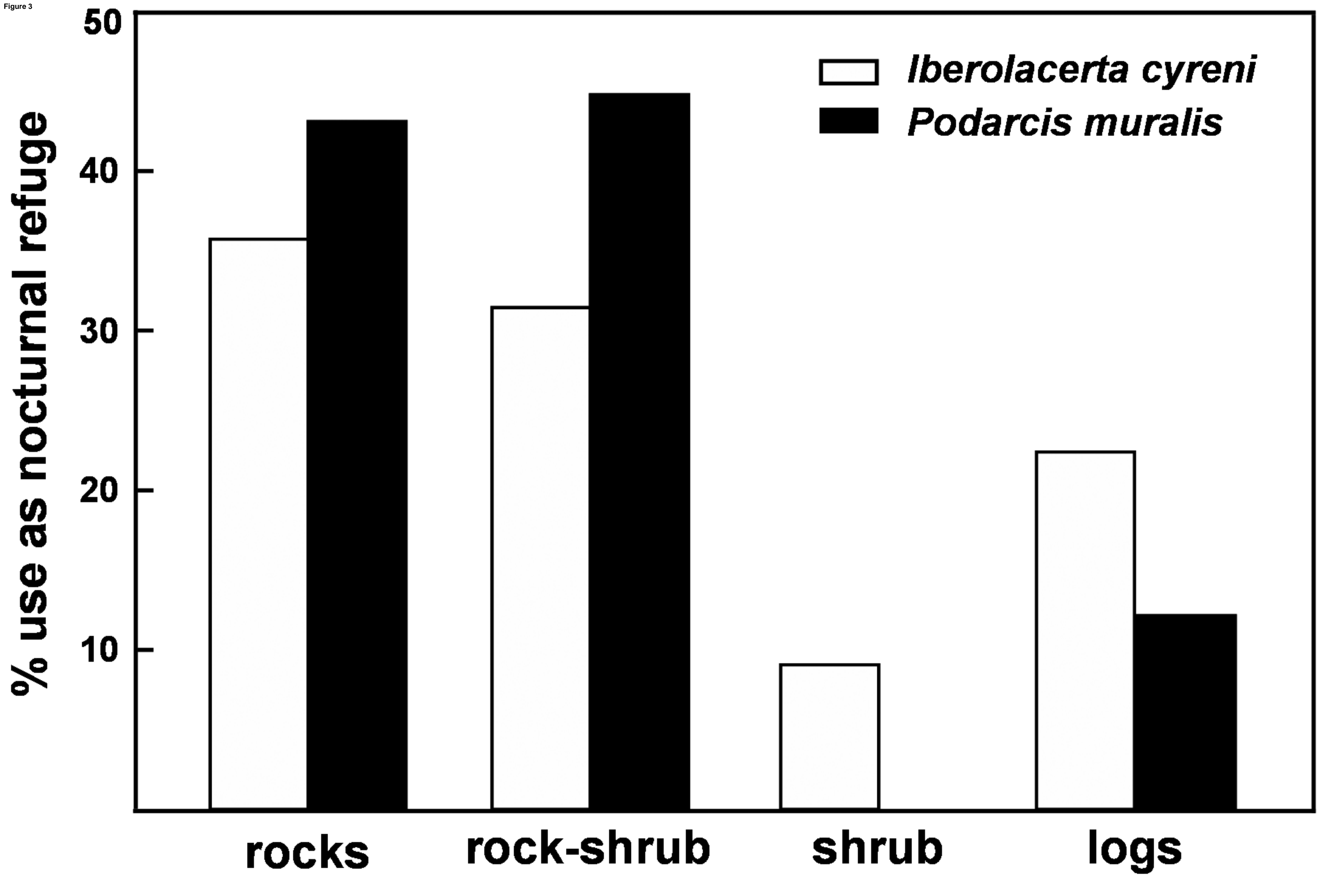


Figure 3



Above refuge**Inside refuge**