Are mountain habitats becoming more suitable for generalist than cold-adapted lizards thermoregulation?

Zaida Ortega, Abraham Mencía, Valentín Pérez-Mellado

Mountain lizards are highly vulnerable to climate change, and the continuous warming of their habitats could be seriously threatening their survival. We aim to compare the thermal ecology and microhabitat selection of a mountain lizard, *Iberolacerta galani*, and a widely distributed lizard, *Podarcis bocagei*, in a montane area. Both species are currently in close syntopy in the study area, at 1400 m above the sea level. We determined the precision, accuracy and effectiveness of thermoregulation, and the thermal quality of habitat for both species. We also compared the selection of thermal microhabitats between both species. Results show that *I. galani* is a cold-adapted thermal specialist with a preferred temperature range of 27.9-29.7 °C, while *P. bocagei* would be a thermally generalist, with a broader and higher preferred temperature range (30.1-34.5 °C). In addition, *I. galani* selects rocky substrates while *P. bocagei* selects warmer soil and leaf litter substrates. The thermal quality of the habitat is higher for *P. bocagei* than for *I. galani*. Finally, *P. bocagei* achieves a significantly higher effectiveness of thermoregulation (0.87) than *I. galani* (0.80). Therefore, mountain habitat conditions seem currently more suitable for performance of thermophilic generalist lizards than for cold-specialist lizards.

1   **Title:** Are mountain habitats becoming more suitable for generalist than cold-adapted lizards

2   thermoregulation?

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12   **Abstract**

13   Mountain lizards are highly vulnerable to climate change, and the continuous warming of

14   their habitats could be seriously threatening their survival. We aim to compare the thermal

15   ecology and microhabitat selection of a mountain lizard, *Iberolacerta galani*, and a widely

16   distributed lizard, *Podarcis bocagei*, in a montane area. Both species are currently in close

17   syntopy in the study area, at 1400 m above the sea level. We determined the precision, accuracy

18   and effectiveness of thermoregulation, and the thermal quality of habitat for both species. We

19   also compared the selection of thermal microhabitats between both species. Results show that *I.*

20   *galani* is a cold-adapted thermal specialist with a preferred temperature range of 27.9-29.7 °C,

21   while *P. bocagei* would be a thermally generalist, with a broader and higher preferred

22   temperature range (30.1-34.5 °C). In addition, *I. galani* selects rocky substrates while *P. bocagei*

23   selects warmer soil and leaf litter substrates. The thermal quality of the habitat is higher for *P.*

24   *bocagei* than for *I. galani*. Finally, *P. bocagei* achieves a significantly higher effectiveness of

25   thermoregulation (0.87) than *I. galani* (0.80). Therefore, mountain habitat conditions seem

26   currently more suitable for performance of thermophilic generalist lizards than for cold-specialist

27   lizards.

29 **Introduction**

30   Climate change has already produced several impacts in the biology and distribution of

31 many animal species worldwide (Parmesan, 2006; McCain, 2010). However, some species are

32 more vulnerable than others to the impact of global warming (Araújo, Thuiller & Pearson, 2006;

33 Sinervo et al., 2010; Huey et al., 2012). Ectotherms are particularly sensitive to climate warming

34 since they depend on external heat sources for body temperature upkeep (e.g. Hertz, Huey &

35 Stevenson, 1993; Huey et al., 2012). Knowledge on the thermal biology of ectotherms is

36 necessary to assess their vulnerability to climate change, to predict the future impacts of global

37 warming, and to adopt conservation measures to prevent their extinction (Carvalho et al., 2010;

38 Crossman, Bryan & Summers, 2012; Groves et al., 2012).

39   High elevation ectotherms would be particularly threatened by the fast increase of

40 environmental temperatures, mainly because two reasons: (1) the plasticity and evolution of

41 thermal physiology seems limited to keep pace with the fast environmental warming (e.g. Muñoz

42 et al., 2014; Gunderson & Stillman, 2015), and (2) living in mountaintops, they lack colder areas

43 to migrate (Araújo, Thuiller & Pearson, 2006; Berg et al., 2010; McCain, 2010). In addition,

44 mountain species tend to be cold-specialists (e.g. Aguado & Braña, 2014), which makes them

45 more vulnerable, because the decline of fitness when body temperatures exceed the optimum

46 temperature is greater in narrower thermal reaction norms (Martin & Huey, 2008; Huey et al.,

47 2012; Gunderson & Stillman, 2015). Mountain lizards could also be threatened by potential

48 displacement by thermally generalist species with a broader distribution at the surrounding

49 lowlands that may ascend in altitude as warming increases (Araújo, Thuiller & Pearson, 2006;

50 Huey et al., 2012; Comas, Escoriza & Moreno-Rueda, 2014). An expansion, both in altitude and

51 latitude, due to climate change has already been documented for several species (Parmesan,

52 2006; Sinervo et al., 2010; Chen et al., 2011; Moreno-Rueda et al., 2012; Bestion, Clobert &

53 Cote, 2015). These factors, altogether, would place high-mountain lizards among the most

54 vulnerable animals worldwide, especially mountain lizards of the Iberian Peninsula, due to the

55 higher warming and drought predicted for these areas (Nogués-Bravo et al., 2008; Araújo et al.,

56 2011; Maiorano et al., 2013). The study of the thermal ecology of these mountain lizards, as well

57 as the comparison with their potential competitors, would be useful to design the conservation

58 measures required to preserve the species (Urban, Tewksbury & Sheldon, 2012; Lord &

59 Whitlatch, 2015).

60 Some studies had assessed thermal ecology of other *Iberolacerta* lizards (Monasterio et

61 al., 2009; Aguado & Braña, 2014; Ortega, Mencía & Pérez-Mellado, 2016). We studied the

62 thermal ecology of the León rock lizard, *I. galani*, a mountain lizard living in its historical range,

63 and the Bocage's wall lizard, *P. bocagei*, that has expanded its altitudinal range to the study area

64 in recent years. Both are medium-size (Table 1), insectivorous and heliothermic lacertid lizards,

65 endemic from the northwestern of Spain. Their distribution ranges are considerably different

66 (Fig. 1): *I. galani* is restricted to high-mountain climate isolated areas from 1300 to 2500 m asl

67 (meters above the sea level; Arribas, Carranza & Odierna, 2006; Mencía, Ortega & Pérez-

68 Mellado, 2016, in press), whereas *P. bocagei* inhabits a variety of habitats from the sea level to

69 1900 m asl habitats (Galán, 1994; Pérez-Mellado, 1998; Galán, 2004). However, both live in

70 close syntopy in the study area nowadays, fully mixed in the same habitat. We compared the

71 thermal requirements of the two species in the laboratory and the thermal traits of their habitat in

72 order to study if mountain habitats are increasingly unsuitable for mountain lizards, and may be

73 favoring the expansion of thermal generalists instead. We first aim to assess and compare the

74 thermal preferences and behavioral thermoregulation of both species (Hertz, Huey & Stevenson,

75   1993; Angilletta, 2009). Then, we studied their selection of microhabitats and we compared the

76   thermal suitability of the habitat for both species under the current climatic conditions.

Materials & Methods

Study area

79   The study area was in the Natural Monument "Lago de La Baña" (León province, Spain;

80   42°15′N, 6° 29 W). It was an area surrounding a glacial lake, located at 1400 m asl, formed by

81   slate rocks, meadows and shrubs. The area is also circled by mountains peaks of more than 2000

82   m asl on one side and deteriorated slate quarries in the other side (Fuertes-Gutiérrez &

83   Fernández-Martínez, 2010).

Field sampling

85   Body temperatures (T_b) and operative temperatures (T_e) were recorded simultaneously in

86   the field during August 2011, 2012 and 2013, in order to avoid the effect of seasonal variations.

87   Operative temperatures (T_e) estimate the temperatures that non-thermoregulating lizards would

88   reach, if they were distributed randomly in their habitat (Hertz, Huey & Stevenson, 1993). For

89   recording T_e, we employed copper models of the same size of lizards (Bakken & Angilletta,

90   2014). One thermocouple probe was placed into each hollow model and connected to a data

91   logger HOBO H8 (® Onset Computer Corporation) programmed to take a temperature record

92   every five minutes. The data loggers with models were placed in different microhabitats: rock (in

93   different orientations), soil, log, leaf litter, and grass. For measuring T_b, we captured lizards by

94   noosing during their daily activity period, from 08.00 to 18.00 h GMT (Greenwich Mean Time).

95   On each capture, we measured cloacal body temperature (T_b) immediately after capture (< 30

96   seconds after capture) with a Testo® 925 digital thermometer (± 0.1 °C precision). We also

97   registered the time of the day, the type of substrate, the distance from the nearest potential refuge

98   and the altitude of the microhabitat from the floor.

99   For 30 individual lizards (15 *I. galani* and 15 *P. bocagei*), we also recorded these

100   variables (T_a, T_s, time of the day, type of microhabitat, altitude of the point from the floor, and

101   distance to the nearest potential refuge) at four points associated to each capture place, in order

102   to get an approach of the habitat structure. Each point was 1 m away from the capture point in

103   the direction of the four cardinal points (N, S, E, and W). Thus, the measures at random points

104   represent the availability of all variables in the habitat, in order to compare with the values in the

105   microhabitats used by both species. We refer to the values of these random points as

106   'availability' in the results section.

107   Lizards were sampled under licences of the Castilla y León Environmental Agency

108   (EP/CYL/320/2012). The study was conducted in compliance with all ethical standards and

109   procedures of the University of Salamanca.

110   **Preferred temperature range**

111   Thermal preferences of lizards in the laboratory represent the body temperatures that

112   lizards would achieve in their habitats in the absence of other ecological restrictions but

113   temperature (e.g. Hertz, Huey & Stevenson, 1993; Angilletta, 2009). The preferred temperature

114   range of *I. galani* was measured in August 2011 and the preferred temperature range of *P.*

115   *bocagei* was measured in August 2013. All conditions were replicated for both species: field area

116   of capture of lizards, laboratory conditions and materials (terraria, thermometer and lamp), as

117   well as the methodology (thermal gradient and the protocol of measurement). Lizards were

118   housed in individual terraria, fed daily with mealworms (*Tenebrio molitor*) and crickets (*Gryllus*

119   *assimilis*), and provided with water *ad libitum*. The thermal gradient was built in a glass

120   terrarium (100 x 60 x 60 cm) with a 150 W infrared lamp over one of the sides, obtaining a

121   gradient between 20 to 60 °C. A data of a preferred body temperature (T_{pref}) of a lizard was

122   recorded in the cloaca with a digital thermometer (Testo® 925) each hour in the period from

123   08.00 to 18.00 h (GMT). We used 24 adult lizards (12 males, 12 females) from each species,

124   with 6 hourly measures of T_{pref} of each individual lizard. The 50% of central values of preferred

125   body temperatures (that is, the interquartile range) was considered as the preferred temperature

126   range to assess thermoregulation, as this is a common metric used to assess thermoregulation

127   (Hertz, Huey & Stevenson, 1993; Blouin-Demers & Nadeau, 2005). After both experiments,

128   lizards were released completely unharmed at their capture sites.

129   **Indexes of thermoregulation**

130   To test the null hypothesis of thermoregulation (that is, if lizards use microhabitats

131   randomly regarding temperature) we followed the protocol developed by Hertz, Huey and

132   Stevenson (1993), and calculated three indexes of thermoregulation. The first is the index of

133   accuracy of thermoregulation ($\overline{d}_b$), that is the mean of absolute values of the deviations between

134   each T_b from the preferred temperature range. Thus, the values of the index of accuracy of

135   thermoregulation are counterintuitive: higher values of $\overline{d}_b$ indicate lower accuracy of

136   thermoregulation, and vice-versa. The second is the index of thermal quality of habitat ($\overline{d}_e$),

137   calculated as the mean of absolute values mean of the deviations of each T_e from the preferred

138   temperature range. Accordingly, the values of the index of thermal quality of the habitat are also

139   counterintuitive: higher values of $\overline{d}_e$ indicate a lower thermal quality of the habitat, and vice-

140   versa. The third is the index of effectiveness of thermoregulation (E), that is calculated as E = 1 -

141   $\overline{d}_b / \overline{d}_e$. Hence, values of E range from 0 to 1, meaning a higher effectiveness of thermoregulation

142   as higher is the value of E (see Hertz, Huey & Stevenson, 1993). Effectiveness of

143   thermoregulation was calculated with THERMO, a Minitab module written by Richard Brown.

144   THERMO has been used in previous studies of thermal ecology (e.g. Ortega et al., 2014) and

145   uses three kinds of input data: T_b, T_e and T_{pref} of the preferred temperature range, and was

146   programed to perform bootstraps of 100 iterations, building pseudo-distributions of three kinds

147   of output values: the arithmetic mean of the index of accuracy of thermoregulation ($\overline{d}_b$), the

148   arithmetic mean of the index of thermal quality of the habitat ($\overline{d}_e$), and the arithmetic mean of the

149   index of effectiveness of thermoregulation ($\overline{E}$).

150   **Data analysis**

151   All means were reported with standard deviations (sd). Parametric statistics were

152   performed when data followed the assumptions of normality and variance homogeneity. If these

153   assumptions were not fulfilled, even after log-transformation, non-parametric equivalents were

154   carried out (Crawley, 2012; Sokal & Rohlf, 1995). Analyses were conducted using R, version

155   3.1.3 (R Core Team, 2015). Post-hoc comparisons of Kruskal-Wallis tests were computed with

156   Nemenyi test with the package PMCMR (Pohlert, 2014).

157   **Results**

158   **Temperatures of the habitat**

159   There were significant differences between the T_e offered by the different microhabitats

160   (Kruskal-Wallis test, H=2669.642, df=15, P<0.0001, n=6082). According to the results of the

161   post-hoc comparisons of their T_e, the microhabitats could be classified into four groups: (1) cold

162   microhabitats that were below the PTR of both species, as would be south-facing rock in full sun,

163   and flat rock, soil and the leaf litter in shade, (2) mild microhabitats that provided T_e within the

164   PTR of both species, as would be under rock microhabitats, north-facing and the east-facing rock

165   in full sun, and flat rock, soil and the leaf litter in filtered sun, at some hours of the day, (3) warm

166   microhabitats that provided T_e that exceeded the PTR of *I. galani* but felt within the PTR of *P.*

167   *bocagei* during some hours of the day, as would be the microhabitats of flat, east-facing and

168   west-facing rock, and log in full sun, and (4) very warm microhabitats that exceeded the PTR of

169   both species during all day, as is the case of grass, log, leaf litter, and soil in full sun (see Fig. 2).

170   **Microhabitat selection**

171   Both species selected microhabitats not-randomly regarding T_a, being the mean T_a of

172   capture places of lizards higher than the mean T_a available in the habitat (Fig. 3). However, T_a

173   selected by *P. bocagei* were significantly higher than those selected by *I. galani* (Fig. 3). In

174   addition, both species selected microhabitats with similar T_s, higher than that available (Fig. 3).

175   Regarding the distance to the nearest potential refuge, both species selected microhabitats that

176   were closer to potential refuges than the mean habitat availability (*I. galani*: mean

177   distance=13.56 ± 11.52 cm, n=66; *P. bocagei*: mean distance=16.04 ± 17.24 cm, n=72;

178   availability: mean=39.76 ± 31.30 cm, n=123; Kruskal-Wallis test, H=62.198, df=2, P<0.0001,

179   post-hoc comparisons were significant only for: *I. galani*-availability, P<0.0001, and *P. bocagei*-

180   availability, P<0.0001). *I. galani* selected microhabitats higher than the mean availability, while

181   *P. bocagei* selected microhabitats of similar height of the mean available height (*I. galani*:

182   height=11.17 ± 18.24 cm, n=78; *P. bocagei*: height=7.57 ± 16.70 cm, n=72; availability =10.30

183   ± 22.17 cm, n=123; Kruskal-Wallis test, H=15.824, df=2, P<0.0001, *post-hoc* comparisons were

184   significant only for: *I. galani*- availability, P=0.009, and *I. galani-P.bocagei*, P<0.0001).

185   Both species clearly selected microhabitats with a significantly different frequency than

186   the abundance of each type of microhabitat (Fig. 4). *I. galani* selected microhabitats with a

187   smaller presence of grass than the randomly available in the habitat (Fisher exact test, P <

188   0.0001). Meanwhile, *P. bocagei* also selected soil microhabitats with a greater proportion than

189   the randomly available in the habitat (Fisher exact test, P < 0.0001; Fig. 4). Finally, there were

190   statistically significant differences between the two species in the selection of microhabitats

191   (Fisher exact test, P < 0.0001), especially regarding the higher selection of rocky areas by *I.*

192   *galani* (Fig. 4). Table 2 shows the proportion of T_e of the different types of microhabitat that felt

193   below, within and above the PTR of each species.

194   **Lizard thermoregulation**

195   There were no differences between males and females in the average preferred

196   temperatures, neither in *P. bocagei* (males: $\overline{T}_{pref} = 32.9 \pm 1.63$ °C, n=12; females: $\overline{T}_{pref} = 31.8 \pm$

197   2.44 °C, n=12; ANOVA, $F_{1, 22}=1.746$, P=0.200), nor in *I. galani* (males: $\overline{T}_{pref} = 28.9 \pm 0.48$ °C,

198   n=12; females: $\overline{T}_{pref}=28.8 \pm 0.49$ °C, n=12; ANOVA, $F_{1, 22}=0.118$, P=0.734). Thus, data of both

199   genders were combined in subsequent analyses. The average preferred temperature range was

200   lower for *I. galani* than for *P. bocagei* (*I. galani*: $\overline{T}_{pref} = 28.8 \pm 0.47$ °C, n=24; *P. bocagei*: $\overline{T}_{pref} =$

201   32.3 ± 2.11 °C, n=24; Mann–Whitney U-test, U =42.00, P<0.0001). Thus, the preferred

202   temperature range of *I. galani* was 27.9-29.7 °C and the preferred temperature range of *P.*

203   *bocagei* was 30.1-34.5 °C. Furthermore, the preferred temperature range of *I. galani* was

204   significantly narrower than the preferred temperature range of *P. bocagei* (Levene's test,

205   W=33.151, P<0.0001).

206   In the field, *I. galani* exhibited lower T_b than *P. bocagei* (*I. galani*: $\overline{T}_b$=30.9 ± 2.39 °C,

207   n=79; *P. bocagei*: $\overline{T}_b$=33.9 ± 3.03 °C, n=72; ANOVA, $F_{1,\ 149}$=45.061, P<0.0001; Fig. 5). The

208   index of thermal quality of habitat ($\overline{d}_e$) was significantly higher for *I. galani* than for *P. bocagei*

209   (Mann–Whitney U-test, U=24.0, P<0.0001; Table 3). In addition, *I. galani* showed a higher

210   value of the index of thermoregulation accuracy ($\overline{d}_b$; ANOVA, $F_{1,\ 198}$=1086.86, P<0.0001; Table

211   3). Finally, *I. galani* achieved a lower effectiveness of thermoregulation (Mann–Whitney U-test,

212   U=77.0, P<0.0001; Table 3).

213   **Discussion**

214   The preferred temperature range of a species is assumed to approximately reflect the

215   optimum range for fitness (Hertz, Huey & Stevenson, 1993; Martin & Huey, 2008). *I. galani* has

216   a low and very narrow preferred temperature range (27.9-29.7 °C), being the lowest found to

217   date in Lacertidae (Bauwens et al., 1995; Aguado & Braña, 2014; Ortega, Mencía & Pérez-

218   Mellado, 2016). By contrast, the preferred temperature range of *P. bocagei* (30.1-34.5 °C) is

219   significantly higher and wider than that of *I. galani*, and both ranges do not even overlap. Thus,

220   our data suggest that *I. galani* would be a cold-adapted thermal specialist species, like other

221   species of the genus *Iberolacerta* (Martín & Salvador, 1993; Aguado & Braña, 2014; Žagar et

222   al., 2015; Ortega, Mencía & Pérez-Mellado, 2016), while *P. bocagei* would be a thermal

223   generalist with preference for warmer temperatures, like other species of the genus *Podarcis*

224   (Bauwens et al., 1995; Bauwens, Hertz & Castilla, 1996; Capula et al., 2014; Ortega et al.,

225   2014.). Environmental temperatures are predicted to continuously rise in the mountains of the

226   Iberian Peninsula during the coming years (Araújo, Thuiller & Pearson, 2006; Nogués-Bravo et

227   al., 2008) and the difference between being a thermal specialist or a generalist will be crucial

228   when determining the vulnerability of a given species to climate change (Martin & Huey, 2008;

229   Huey et al., 2012.). Thermal reaction norms of fitness are asymmetric: fitness gradually increases

230   from the critical minimum temperature up to the physiological optimum, just to decline sharply

231   when body temperature exceeds the physiological optimal temperature (Huey & Stevenson,

232   1979; Angilletta, Huey & Frazier, 2010). Due to the asymmetry of the thermal reaction norm

233   curve, an increase in body temperatures exceeding the optimal temperature leads to a higher

234   reduction of fitness than a similar decrease in body temperatures, as predicted by the Jensen's

235   inequality (Martin & Huey, 2008; Huey et al., 2012). Moreover, this negative effect of exceeding

236   the optimal temperature is higher the more specialized the species is (Huey et al., 2012).

237   Consequently, not only *I. galani* preferred temperature range is lower than that of *P. bocagei* and

238   the increase of environmental temperatures will exceed it before, but also their narrower

239   preferred temperature range suggest that the negative effects of exceeding their optimal

240   temperatures would be more detrimental to *I. galani* (Martin & Huey, 2008; Huey et al., 2012).

241   Given a scenario of continued warming, there are three alternatives for mountain lizards:

242   to adapt, to shift their ranges, or to extinguish (Berg et al., 2010; Gunderson & Stillman, 2015).

243   The ability of *I. galani* to disperse is limited by the peaks of mountains, so that, sooner or later,

244   lizards migrating upwards to avoid overheating would run out of space to migrate (Araújo,

245   Thuiller & Pearson, 2006; Huey et al., 2012). Therefore, mountain lizards would only avoid

246   extinction by adapting to warmer environments. It was recently discovered that the plasticity of

247   the critical temperatures has little capacity for change, even lesser for the critical thermal

248   maximum, so it will probably not be enough to keep pace with the rate of environmental

249   warming (Gunderson & Stillman, 2015). However, the ability of ectotherms to behaviorally

250   buffer environmental temperature changes could probably mitigate the negative impact of global

251   warming in fitness of mountain lizards for a while (Kearney, Shine & Porter, 2009; Huey et al.,

252 2012). Their high effectiveness of thermoregulation and their ability to select the most suitable

253 microhabitats, suggest that *I. galani* may have the capacity for behavioral buffering of the impact

254 of climate warming. Furthermore, the habitat under study is heterogeneous, with a mosaic of

255 microhabitats offering different operative temperatures, some colder, some warmer, and some

256 equal to the preferred temperature range of this species. Hence, the habitat provides *I. galani*, at

257 least for some time, the possibility to use its behavioral adjustments to buffer the impact of

258 global warming (Huey et al., 2012; Sears & Angilletta, 2015). It would be also possible that the

259 acclimation of the thermal preferences would contribute to the buffering of the temperature

260 rising, at least for a while (e.g. Gvoždík, 2011).

261   *P. bocagei* select microhabitats of soil and leaf litter with higher frequency than the

262 randomly available in its habitat, which are significantly warmer than the rocky substrates

263 preferred by *I. galani*. Furthermore, the proportion of operative temperatures fitting the preferred

264 temperature range of *P. bocagei* exceeds nowadays that fitting the preferred temperature range of

265 *I. galani*. In general, air temperature diminishes as elevation rises (e.g. Körner, 2007).

266 Nonetheless, this montane habitat is, at present, more suitable for *P. bocagei* than for *I. galani*. In

267 addition, the warm habitat condition leads *I. galani* lizards to achieve a lower effectiveness of

268 thermoregulation than *P. bocagei*, which may entail less physiological performance and fitness

269 for *I. galani*. Hence, our results indicate that the thermophilic species has taken a better

270 advantage of the current thermal environment than the cold-adapted species, maybe favoured by

271 climate warming. Moreover, generalist lizard species can efficiently exploit high-elevation cold

272 habitats, by means of different adaptations (Zamora-Camacho, Reguera & Moreno-Rueda,

273 2015), which in this situation could increase *I. galani* competitive exclusion risk. Monasterio et

274 al. (2009) reported a higher effectiveness of thermoregulation of *Iberolacerta cyreni* than

275   *Podarcis muralis* in high mountain areas, a situation that should be the usual but maybe

276   reverting, as we report here, given that the mountain habitats are becoming warmer. However,

277   we do not know if *I. galani* and *P. bocagei* compete for food, refuges or any other resources.

278   Thus, the generalist could expand without the specialist being affected, unless the specialist

279   would be compromised by the new conditions, and that would not be qualified as displacement,

280   instead, the two species would be reacting independently to climate change.

281   *Iberolacerta* lizards appear to have not adapted to warm conditions in the past, after the

282   last glaciation and, consequently, they were relegated to areas of higher altitude (Carranza,

283   Arnold & Amat, 2004; Crochet et al., 2004; Mouret et al., 2011). Hence, it is unlikely that they

284   will be able to cope with the current climatic change, which entails faster warming than the

285   species have ever met before (Diffenbaugh & Field, 2013). On the contrary, *P. bocagei* lizards

286   remained in warm refugia during past cold periods, and probably colonized their current

287   distribution within last 10000 years (Pinho et al., 2011). In short, we are probably documenting,

288   with human induced climate change, a remake of past biogeographic spread of generalist lizard

289   species and the concomitant restriction of cold-adapted species to colder areas.

290   **Acknowledgements**

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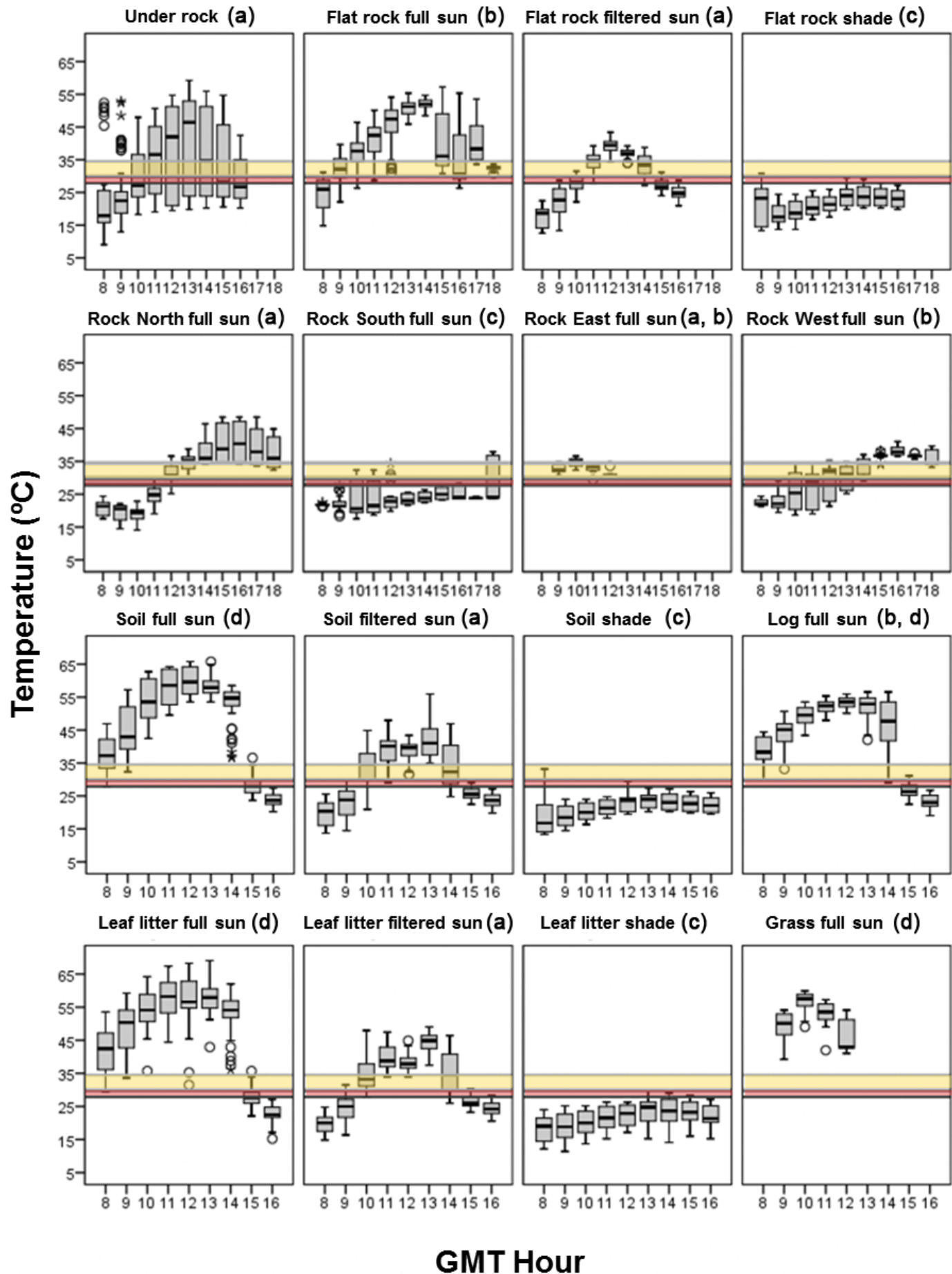
1

Distributional ranges of *Iberolacerta galani and Podarcis bocagei*
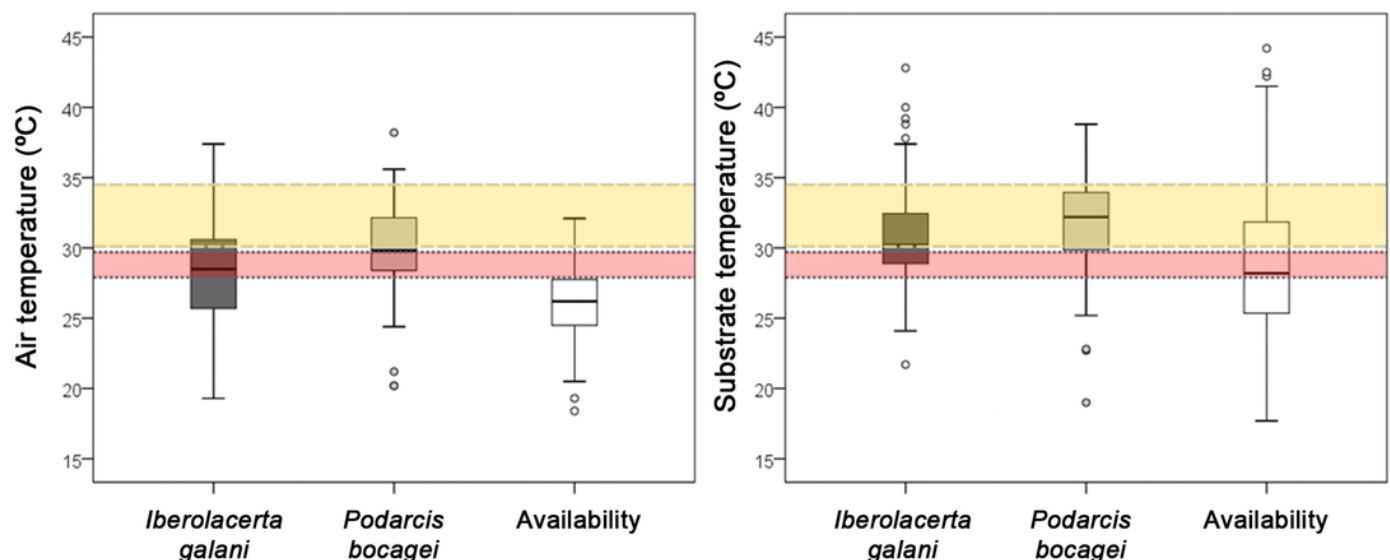
2

Operative temperatures

Boxplots of the operative temperatures of the different microhabitats of the study area during the daily activity period of lizards. Horizontal bands represent the 50 % preferred temperature range of *Iberolacerta galani* (red band) and *Podarcis bocagei* (yellow band). Non-significant post-hoc results are marked in the panels with the same letter.

Temperature (°C)

GMT Hour

3

Comparison of the environmental temperatures of the selected microhabitats of both species and the mean availability of the habitat.

Boxplots of air and substrate temperature of the capture locations of *Iberolacerta galani and Podarcis bocagei*, and the general availability of the habitat. Both species selected microhabitats with greater mean air temperature than the mean air temperature randomly available in the habitat (all post-hoc paired comparisons of Kruskal-Wallis are significant, for the paired comparison of I. galani - *P. bocagei* regarding substrate temperature). Horizontal bands represent the 50 % preferred temperature range of *Iberolacerta galani* (red band) and *Podarcis bocagei* (yellow band).
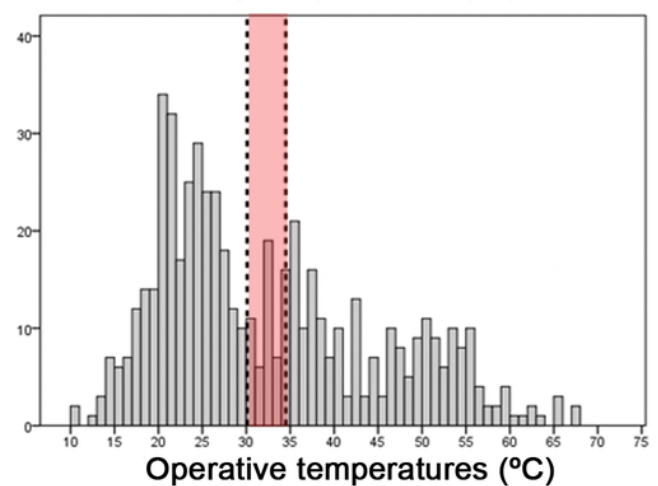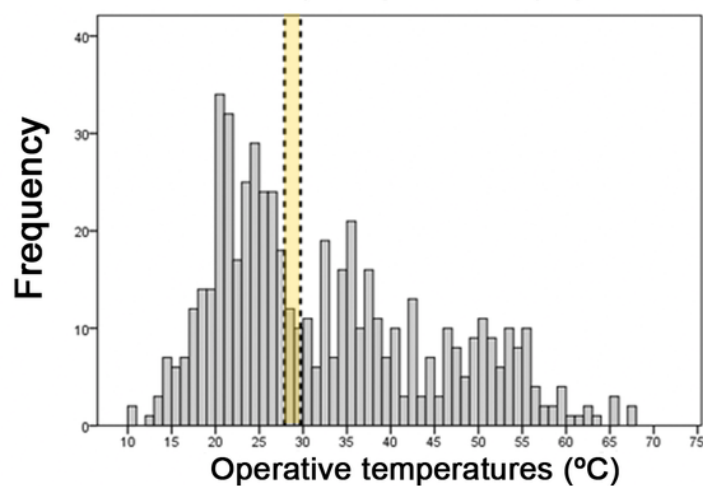
4

Microhabitat preferences of both species.

Microhabitats where *Iberolacerta galani and Podarcis bocagei* lizards occurred and availability of the different types of microhabitats measured though random points, indicated as percentage of observations for each category. The category of 'other microhabitats' includes grass and logs.

5

Themoregulation of both species

Histograms of preferred temperatures, body temperatures and operative temperatures of *Iberolacerta galani* and *Podarcis bocagei* lizards. Horizontal bands represent the 50 % preferred temperature range of *Iberolacerta galani* (red band) and *Podarcis bocagei* (yellow band).
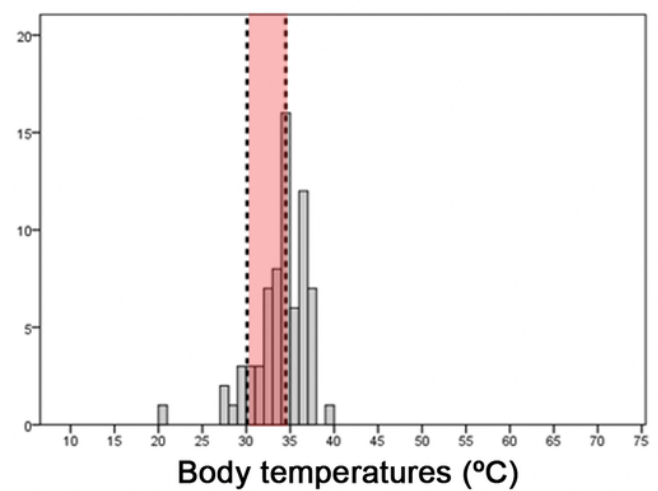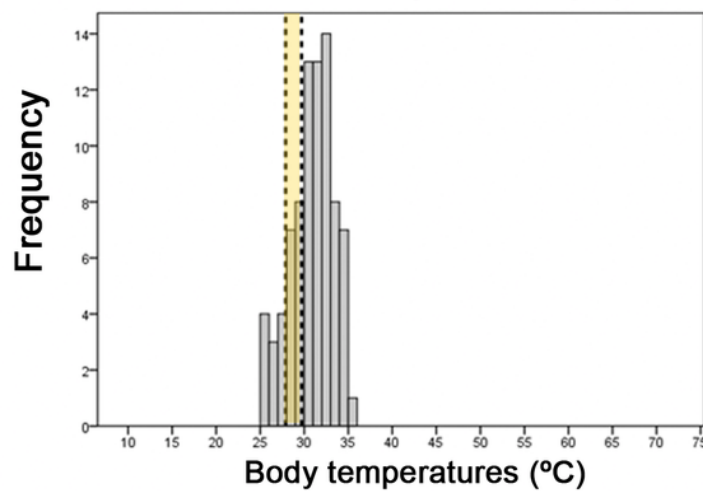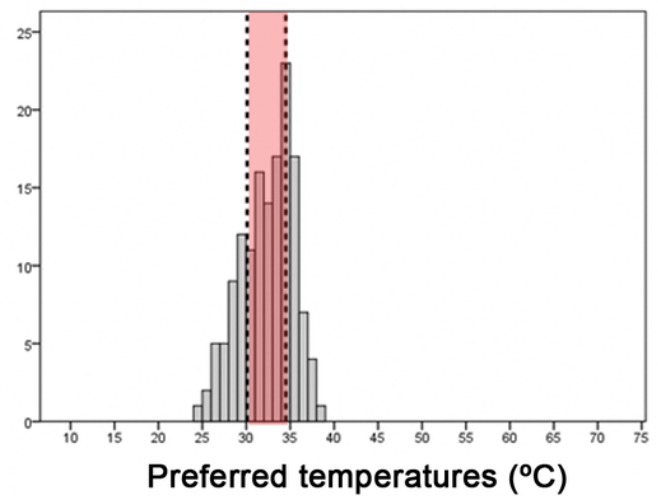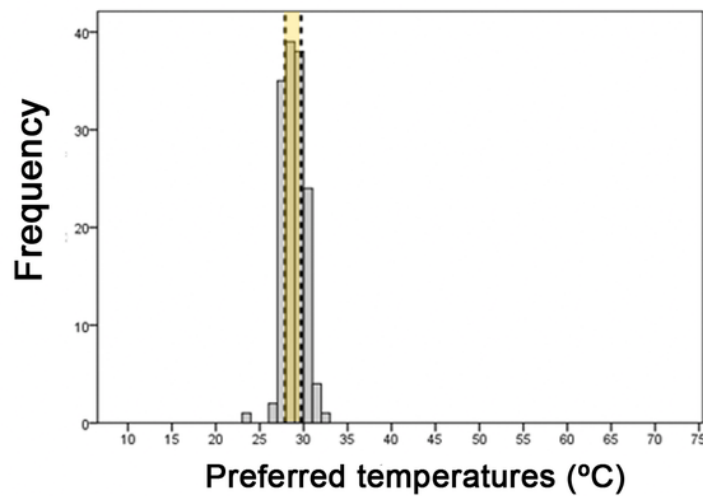
Table 1(on next page)

Size and mass of both species

Snout-vent length (SLV, in mm) and weight (in g) of adult males and females of *Iberolacerta galani* and *Podarcis bocagei* of La Baña (León, Spain) included in the study.

		SVL	weight
I. galani	Males (n=44)	65.95 ± 5.83	6.94 ± 1.87
	Females (n=53)	67.96 ± 6.07	7.02 ± 1.83
P. bocagei	Males (n=48)	58.52 ± 4.89	4.90 ± 1.27
	Females (n=25)	55.38 ± 4.66	3.86 ± 1.08

1

Table 2(on next page)

Thermal suitability of studied microhabitats for both species

Proportion (%) of the operative temperatures (T_e) of the different studied microhabitats that are lower, within, of higher than the preferred temperature range (PTR) of *Iberolacerta galani and Podarcis bocagei* during summer in the study. The microhabitat category of 'other' includes grass and logs. All microhabitats were measured under all sun situations, so it is homogeneous among them, making the proportions comparable.

		Other	Soil	Leaf litter	Rock	Total
I. galani	Lower	9.8 %	52.5 %	48.4 %	46.1 %	46.9 %
	Within	1.7 %	3.5 %	6.2 %	6.4 %	5.1 %
	Higher	88.5 %	44.0 %	45.4 %	47.5 %	48.0 %
P. bocagei	Lower	11.8 %	56.7 %	55.4 %	53.8 %	52.9 %
	Within	1.6 %	4.1 %	4.3 %	4.0 %	8.5 %
	Higher	86.6 %	39.2 %	40.3 %	38.7 %	38.6 %

1

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Table 3 (on next page)

Indexes of thermoregulation of both syntopic populations

Mean (± sd) values of the indexes of thermal quality of the habitat (d_e), accuracy of thermoregulation (d_b) and effectiveness of thermoregulation (E) for *Iberolacerta galani* and *Podarcis bocagei* living in close syntopy. Values of the 95% CI of each index are provided in brackets.

	$\overline{d}_e$ (°C)	$\overline{d}_b$ (°C)	$\overline{E}$
I. galani	9.36 ± 0.03 (9.294/9.419)	1.88 ± 0.02 (1.848/1.912)	0.80 ± 0.002 (0.795/0.802)
P. bocagei	8.30 ± 0.02 (8.249/8.347)	1.05 ± 0.02 (1.012/1.089)	0.87 ± 0.002 (0.869/0.878)

1