

Does ecophysiology mediate reptile responses to fire regimes? Evidence from Iberian lizards

Catarina C Ferreira, Xavier Santos, Miguel A. Carretero

Background. Reptiles are sensitive to habitat disturbance induced by wildfires but species frequently show opposing responses. Functional causes of such variability have been scarcely explored. In the northernmost limit of the Mediterranean bioregion, lizard species of Mediterranean affinity (*Psammodromus algirus* and *Podarcis guadarramae*) increase in abundance in burnt areas whereas Atlantic species (*Lacerta schreiberi* and *Podarcis bocagei*) decrease. *Timon lepidus*, the largest Mediterranean lizard in the region, show mixed responses depending on the locality and fire history. We tested if such interspecific differences are of functional nature, namely, if lizard ecophysiological traits may determine their response to fire. Based on the variation in habitat structure between burnt and unburnt sites, we hypothesise that Mediterranean species increasing density in open habitats promoted by frequent fire regimes should be more thermophile and suffer lower water losses than Atlantic species. **Methods.** We submitted 6-10 adult males of the five species to standard experiments for assessing preferred body temperatures (T_p) and evaporative water loss rates (EWL), and examined the variation among species and along time by means of repeated-measures AN(C)OVAs. **Results.** Results only partially supported our initial expectations, since the medium-sized *P. algirus* clearly attained higher T_p and lower EWL. The two small wall lizards (*P. bocagei* and *P. guadarramae*) displayed low T_p and high EWL while the two large green lizards (*T. lepidus* and *L. schreiberi*) displayed intermediate values for both parameters. **Discussion.** The predicted differences according to the biogeographic affinities within each pair were not fully confirmed. We conclude that ecophysiology may help to understand functional reptile responses to fire but other biological traits are also to be considered.

12 **Abstract**

13 **Background.** Reptiles are sensitive to habitat disturbance induced by wildfires but species
14 frequently show opposing responses. Functional causes of such variability have been scarcely
15 explored. In the northernmost limit of the Mediterranean bioregion, lizard species of
16 Mediterranean affinity (*Psammodromus algirus* and *Podarcis gadarramae*) increase in
17 abundance in burnt areas whereas Atlantic species (*Lacerta schreiberi* and *Podarcis bocagei*)
18 decrease. *Timon lepidus*, the largest Mediterranean lizard in the region, show mixed responses
19 depending on the locality and fire history. We tested if such interspecific differences are of
20 functional nature, namely, if lizard ecophysiological traits may determine their response to fire.
21 Based on the variation in habitat structure between burnt and unburnt sites, we hypothesise that
22 Mediterranean species increasing density in open habitats promoted by frequent fire regimes
23 should be more thermophile and suffer lower water losses than Atlantic species.

24 **Methods.** We submitted 6-10 adult males of the five species to standard experiments for
25 assessing preferred body temperatures (T_p) and evaporative water loss rates (EWL), and
26 examined the variation among species and along time by means of repeated-measures
27 AN(C)OVAs.

28 **Results.** Results only partially supported our initial expectations, since the medium-sized *P.*
29 *algirus* clearly attained higher T_p and lower EWL. The two small wall lizards (*P. bocagei* and *P.*
30 *gadarramae*) displayed low T_p and high EWL while the two large green lizards (*T. lepidus* and
31 *L. schreiberi*) displayed intermediate values for both parameters.

32 **Discussion.** The predicted differences according to the biogeographic affinities within each pair
33 were not fully confirmed. We conclude that ecophysiology may help to understand functional
34 reptile responses to fire but other biological traits are also to be considered.

35

36 **Keywords:** reptiles; habitat; functional response; preferred temperatures, water-loss rates;

37 wildfires

38 Introduction

39 Wildfire is considered among the environmental disturbances having a major impact on
40 ecosystem functioning and composition in many areas of the world (Bond et al., 2005). Global
41 climate change (Piñol et al., 1998; McKenzie et al., 2004; Kasischke & Turetsky, 2006;
42 Westerling et al., 2006) and shifts in land-use practices (i. e. agricultural abandonment and urban
43 sprawl (Moreira et al., 2001; Moreira & Russo, 2007) are considered primary causes for the
44 recent increase of fire frequency and extension. Changes in fire regimes are expected to provoke
45 profound effects on the biodiversity and composition of local communities (McKenzie et al.,
46 2004). The increase of fire risk and activity in recent decades (Pausas, 2014) has attracted
47 considerable interest mainly addressed to understand the environmental drivers and effects of
48 fire, especially in the context of global change (Bowman et al., 2009; Flannigan et al., 2009;
49 Whitlock et al., 2010). In the present context of a shift in fire regimes, a pressing question is
50 whether we are prepared to manage fire regimes and reduce impacts of fire on many ecosystem
51 components (Pausas & Keeley, 2009). An ecological-based framework to understand how
52 species respond to fire and which is the resistance and resilience of communities towards this
53 disturbance is crucial in the 21st century conservation scenario (Nimmo et al., 2015).

54 The response of species to fire is largely driven by habitat structure (Santos et al., 2015)
55 with some species selecting early or late post-fire stages following a continuum along vegetation
56 succession (Letnic et al., 2004; Santos & Poquet, 2010; Valentine et al., 2012; Santos et al.,
57 2016). The ‘habitat accommodation’ model of succession proposed by Fox (1982), applied to the
58 fire ecology, represented a fine framework to understand and predict the response of animals to
59 fire. However, field-based studies have failed to support this model (Driscoll and Henderson
60 2008; Lindenmayer et al., 2008) since the responses of species to fire vary in space and time

61 (Driscoll et al., 2012; Nimmo et al., 2012; Smith et al., 2013) due to the complexity of biotic and
62 abiotic interactions between vegetation dynamics, animal species, and climate (Nimmo et al.,
63 2014). For this reason, to improve predictive models of fire responses in animal communities,
64 detailed ecological (functional) information of species is needed (Smith et al., 2013).

65 Functional approaches have gained acceptance in community ecology due to the
66 possibility of quantification and predictive power (McGill et al., 2006). Although such analyses
67 have been rarely applied to fire ecology (i. e. traits favoured in burnt areas), some recent studies
68 highlight its importance for predict responses of reptiles to fire (see references above). Reptiles
69 are adequate organisms to examine their response to fire following habitat-based and functional
70 approaches in tandem due to their dependence on environment temperature and strait association
71 with habitat (Huey, 1982). While reptile responses to fire are often considered habitat-mediated,
72 such association is not necessarily direct. For instance, since fire opens the habitat in the short
73 term, many reptiles are expected to benefit from the thermal quality of open areas created by fire
74 (Bury, 2004). Different species, however, display opposing responses depending on their habitat
75 preferences, biogeographic affinities and life-history traits (Pastro et al., 2013; Smith et al., 2013;
76 Santos et al., 2016). For example, in a mixed reptile community composed of Mediterranean and
77 non-Mediterranean species, Santos & Cheylan (2013) detected that repeated-fire regime
78 favoured reptile assemblages composed of Mediterranean species with short lifespan and
79 insectivorous dietary habits.

80 As ectotherm and sedentary, terrestrial reptiles are directly and locally exposed to
81 environmental variation in temperature and humidity which makes them ideal subjects for
82 mechanistic ecological modelling (Kearney & Porter, 2009). Specifically, their intrinsic
83 physiological features may potentially govern the response of different species to fire. Thus,

84 body temperature is considered the most important environmental variable affecting performance
85 of ectotherms, including reptiles (Angilletta, 2010), their heat balance resulting from thermal
86 characteristics of the environment (Porter et al., 1973; Porter & Tracy, 1983). Thermoregulatory
87 reptiles respond to the heterogeneity of the thermal environment by selecting microhabitats with
88 adequate temperatures and modifying their body postures to maximize heat gain or lost.
89 However, during these processes reptiles also suffer evaporative water loss (EWL) mainly
90 through the skin but also through respiratory passages and the eyes (Shoemaker & Nagy, 1977;
91 Mautz, 1982a). Since evaporation increases with temperature, a trade-off between
92 thermoregulation and water balance in ectotherms has been suggested (Mautz, 1982a). EWL
93 could hence represent a constraint for the activity of ectotherms when water is not available. In
94 this context, reptiles exposed to unburnt and burnt habitats are expected to face opposing
95 environmental conditions. Under similar climate regimes, unburnt habitats provide more
96 abundant and complex vegetation compared to that in open burnt habitats that in turn are more
97 exposed to extreme temporal variation in environmental temperature and humidity (Ferreira
98 2015; data from NW Portugal available from the authors upon request). We hypothesize that
99 reptile species prevailing in unburnt (forested) habitats will keep lower and less variable body
100 temperatures and to experience less water loss rates as vegetation buffers daily variation of
101 humidity and temperature (Ferreira, 2015). In contrast, reptiles inhabiting burnt (open) habitats
102 will attain higher but temporally variable body temperatures and suffer higher evaporative water
103 stress.

104 To test this hypothesis we have analysed the community of lacertid lizards inhabiting
105 Northern Portugal, a transition zone between Atlantic and Mediterranean bioregions, where
106 species of different biogeographic affinities coexist. Lacertids constitute a guild of diurnal,

107 heliothermic and mainly insectivorous lizards, highly diversified in habitat use (Arnold, 1987),
108 which dominate reptile assemblages across the Mediterranean basin (Carretero, 2004). In
109 syntopy, species from both biogeographic affinities spatially segregate in a gradient from
110 forested to open microhabitats within patchy and heterogeneous landscapes (Ferriera et al.,
111 2016). Systematic monitoring during the last decade in burnt and unburnt areas in Northern
112 Portugal and other areas of the northernmost limit of the Mediterranean bioregion agrees with
113 these fieldwork evidences on the microhabitat segregation. We detected opposing responses to
114 fire by different species mostly related to their biogeographic affinity. Namely, Mediterranean
115 species *Psammodromus algirus* and *Podarcis guadarramae* increased in abundance in burnt
116 areas whereas the Atlantic species *Lacerta schreiberi* and *Podarcis bocagei* decreased (Santos &
117 Poquet, 2010; Santos & Cheylan, 2013; authors' unpublished results). The Mediterranean lizard
118 *Timon lepidus* displayed mixed responses depending on the population. Whereas in the
119 northernmost limit of its distribution, it was favoured by fire (Santos & Cheylan, 2013), in
120 Mediterranean habitats it prefers long-unburnt sites suggesting negative short-term responses to
121 fire (Santos et al., 2016). Based on this empirical evidence, we conducted a comparative
122 experimental study in order to determine whether Mediterranean and Atlantic species responses
123 to fire are correlated to their thermal and hydric physiology. Two ecophysiological traits were
124 selected to represent the general species' trends: preferred body temperature and evaporative
125 water loss. Specifically, we tested whether species favoured by repeatedly fire regimes should be
126 more thermophile and suffer lower water loss rates than those negatively affected. In this case,
127 we predict that *T. lepidus*, *P. algirus* and *P. guadarramae* species responding positively, should
128 have higher preferred temperatures and lower evaporative water loss than *L. schreiberi* and *P.*
129 *bocagei*, species that respond negatively.

130

131 **Materials and methods**132 *Study area*

133 The Iberian Peninsula features a transition region between Euro-Siberian and Mediterranean
134 biogeographic regions (Metzger et al., 2005; Soares & Brito, 2007). These biogeographic
135 crossroads are known as areas of great diversity of species and habitats (Spector, 2002). The
136 extensive contact between Mediterranean and Atlantic climates leads to a high biodiversity of
137 plants and animals, due to the co-existence of Atlantic and Mediterranean typical species in
138 sympatry (Araújo et al., 2006; Sillero et al., 2009). One of these transitional areas is found in
139 northern Portugal (Soares et al., 2005). This is one of the areas in Europe with the highest
140 amount of burnt land; wildfire is considered a fundamental agent of landscape change (Silva et
141 al., 2011). Transitional zones affected by intense fire history provide an opportunity to compare
142 the ecological trends of both types of species either in a general conservation context (Kati et al.,
143 2004) or more specifically to make predictions on the effects of fires herpetofauna biodiversity
144 (Hooper et al., 2005).

145

146 *Species sampling*

147 The five lacertid species used on physiological experiments are the reptiles most frequently
148 found in the area (Loureiro et al., 2008). These species vary in terms of body size, habitat
149 preferences, distribution, biogeographic affinities and response to fire (Table 1).

150 Lizards used in experiments were captured with a noose (García-Muñoz & Sillero, 2010)
151 in three areas: *P. algirus* were captured in Serra da Estrela (40°51' N, 7°53' W), *T. lepidus* and *L.*
152 *schreiberi* in Vairão (41°32' N, 8°67' W) and, finally, *P. bocagei* and *P. gadarramae* syntopic

153 in Moledo (41°84' N, 8°87' W). All the sites are located in Northern Portugal and selected
154 according to the availability of lizards.

155 To exclude effects of reproduction, body condition and ontogeny on T_p (Carretero et al.,
156 2005) we only captured 6-10 adult males during the peak of the reproductive season (May),
157 which were kept in individual cages before the experiments, with water and food provided *ad*
158 *libitum*. We measured body mass (BM) to the nearest 0.0001 g of each lizard with a digital
159 balance and snout–vent lengths (SVL) to the nearest 0.01 mm with a digital calliper. After a
160 short period of acclimation (1-2 days) we submitted them to temperatures and water loss
161 experiments in two consecutive days and released them at their capture sites after the
162 experiments have finished and after being fed and rehydrated.

163 The Institute for the Conservation of Nature and Forest (ICNF, Portugal) gave the
164 sampling permit (no. 459/2015/CAPT). Experiments followed the ethical guidelines of
165 University of Porto.

166

167 *Preferred temperatures*

168 Preferred body temperature (T_p , body temperature achieved in the absence of thermoregulatory
169 constraints, Huey & Bennet, 1987) provides a reliable representation of the overall thermal
170 requirements of a given species while holds some logistic advantages. Namely, 1) it correlates
171 directly with several physiological optima (Bauwens et al., 1995); 2) its temporal variation is
172 relatively narrow in good thermoregulators lacertids (Huey 1982); 3) it displays phylogenetic
173 signal (Bauwens et al., 1995) and remains conservative in conspecific populations under
174 different climate regimes in many lacertid species (i.e. Díaz et al., 2006); and 4) it can be reliably
175 recorded in the lab under standardised conditions (Osojnik et al., 2013). It is true that at the

176 individual level, T_p may change as a function of time of the day, season, feeding activity,
177 ontogeny or reproductive status (Castilla et al., 1999) but these biases can be removed by
178 restricting comparisons to a single class (i.e. adult males) and time period (i.e spring) following a
179 strict experimental protocol (Carretero et al., 2005).

180 Lizards were individually exposed to a photothermal gradient between 20 and 50°C
181 produced by a 150-W infrared bulb fixed at one end of the terrarium (1 x 0.3 x 0.4 m) (Veríssimo
182 & Carretero, 2009). The whole experiment was conducted in a room with temperature
183 maintained at 22°C to prevent wind and direct sun from affecting the temperatures in the
184 terrarium while being exposed to natural photoperiod through a window. Every day of
185 experimentation we turned on the bulb 1 h before the lizards were moved from the cages to the
186 terrariums and the first measure was at 8 h.

187 The whole experiment was conducted from local summer time 8-19 h, the period of daily
188 activity of the five species. At consecutive hourly intervals, we measured the body temperature
189 of each lizard (precision $\pm 0.1^\circ\text{C}$) using a k-thermocouple probe associated with a digital portable
190 thermometer HIBOK 14 inserted into the animals cloaca (Veríssimo & Carretero, 2009). This
191 standard procedure (García-Muñoz & Carretero, 2013; Osojnik et al., 2013) is a compromise
192 between invasiveness and accuracy since at least the two *Podarcis* sp. and *P. algirus* are too
193 small to allocate permanent cloacal probes or to implant transmitters (Clusella-Trullas et al.,
194 2007), and too slender to provide accurate infrared readings (Carretero, 2012). While these
195 methods could have been used with *T. lepidus* and probably with *L. schreiberi*, we preferred to
196 keep the same measuring procedure for all five species for comparative purposes.

197

198 *Water-loss rates*

199 Although reptilian hydric ecophysiology is less studied, evaporative water loss (EWL) rates are
200 known to differ between species from xeric and humid habitats (Mautz, 1982b; Eynan & Dmi'el,
201 1993; Carneiro et al., 2015; Rato & Carretero, 2015) and between phylogenetically distant
202 species in the same locality (García-Muñoz & Carretero, 2013; Osijnik et al., 2013). This makes
203 EWL potentially informative on the hydric constraints of a species' fundamental niche,
204 particularly under restricted water availability (Bowker et al., 1993).

205 Water-loss experiments were always performed the day after previous experiment when
206 lizards were kept rehydrated in the housing terraria. We placed the lizards in closed cylindrical
207 plastic boxes (9 cm diameter, 10 cm height) with ventilation holes in the top and the bottom.
208 Then, in groups of five boxes, lizards were placed into a bigger, opaque sealed chamber (40 x 30
209 x 20 cm) in dry conditions guaranteed by silica gel. Silica gel (~100 g) was allocated in a bag
210 made of gauze and fixed with tape on the bottom of the chamber lid. In the same way, 5 g silica
211 gel was placed at the bottom of each box containing a lizard. The amount of silica gel used
212 guaranteed a low relative humidity inside of each box (20-25%). The experiment was held from
213 8 a.m. to 8 p.m. Conditions inside the chamber were monitored with a Fluke 971 temperature
214 humidity meter (Fluke Corporation, Everett, Washington) at hourly intervals to ensure stability
215 around ~24 °C and 20-30% relative humidity. The environmental temperatures were selected
216 after lowest activity temperatures recorded for most lacertids in the field (Castilla et al., 1999) to
217 prevent lizard stress inside the chambers while still providing relevant EWL rates. Every hour,
218 the lizards were individually removed from the chamber, weighted using an analytical balance
219 (precision ± 0.0001 g; CPA model 224S, Sartorius), and immediately placed back inside their
220 respective boxes in the chamber.

221

222 *Statistical analyses*

223 Once ensured that the distribution of T_p and EWL values did not deviate from normality
224 (Shapiro–Wilk’s test, $P > 0.05$ in all cases) and the sphericity assumption was met (Mauchly’s
225 tests $P > 0.05$), analyses for dependent measures were applied since both T_p and EWL were
226 recorded for the same individual lizards along time. We first used analyses of (co)variance with
227 repeated measures (AN(C)OVA-rm) to ascertain variation in T_p as a function of species and time
228 interval (within- subject factor). In a second step, lizards’ SVL and body mass were incorporated
229 as covariates to account for the effect of lizard size and shape (Carretero et al. 2005). When
230 significant, post hoc Duncan’s tests were performed between species pairs to detect eventual
231 significant differences. For water loss experiments, we also used AN(C)OVA-rm to determine
232 differences in instantaneous water loss ($EWL_i = [(W_n - W_{n+1})/W_0]$ where W is the weight) between
233 species and hour intervals, adding lizards’ SVL and body mass as covariates. We also calculated
234 the accumulated water loss for the 11 intervals ($EWL_a = [(W_0 - W_n)/W_0]$ where W is the weight)
235 and compared it between species using AN(C)OVA, also with SVL and body mass as covariates.
236 The interaction between the mean T_p (calculated from 10 time interval measurements), BM, SVL
237 and the total amount of water lost after the 12-hour experiment ($EWL_t = [(W_0 - W_{11})/W_0]$) was
238 assessed by standard multiple regression between species (average of T_p and EWL_t by species)
239 and within species. All the analyses were performed in Statistica 12 (Dell Inc., 2015).

240

241 **Results**

242 The five lizards species (Table 2) differed in SVL (ANOVA $F_{4,36} = 176.55$; $P < 10^{-6}$) and body
243 mass (ANOVA $F_{4,36} = 151.26$; $P < 10^{-6}$). The post-hoc comparisons (Duncan tests $P < 0.05$)
244 corroborated that the two *Podarcis* species were shorter and lighter, followed by *P. algirus*, then

245 *L. schreiberi* and, finally, *Timon lepidus*, the longest and heaviest species. We also detected
246 interspecific differences in robustness (ANCOVA on mass with SVL as covariable; $F_{4,35} = 21.69$;
247 $P < 10^{-6}$), *T. lepidus* being the most robust, followed by *P. bocagei*, *P. guadarramae* and *P.*
248 *algirus*, and finally by *L. schreiberi*, which was the most slender.

249

250 Preferred temperatures

251 We recovered variation in T_p between species, time intervals and time profile by species
252 (interaction) (Tables 2 and 3; Supplemental_Table_S1). Essentially, *P. algirus* selected higher T_p
253 than all other species (Duncan tests $P < 0.05$), of which *L. schreiberi*, *T. lepidus*. *P.*
254 *gudarramae* and *P. bocagei* selected temperatures in gradually decreasing order. Such pattern
255 remained when SVL and BM were used as covariates (Table 3). While time and time*species
256 variation were also observed, patterns were complex (Fig. 1). Only *P. bocagei* displayed a clear
257 bimodal variation with higher T_p selected in the early morning and late afternoon, the other
258 species only showing irregular profiles. Finally, the significant interaction between time and the
259 covariables indicated that T_p tended to suffer stronger temporal fluctuations in small lizards
260 (Table 3).

261

262 Water-loss rates

263 Using ANOVA-rm, we also uncovered significant differences in instantaneous water loss
264 (EWLi) between species and along time, with a weak interaction between both factors (Tables 2
265 and 3). Post-hoc Duncan tests ($p < 0.05$) grouped *P. algirus* and *T. lepidus* having low rates and
266 both *Podarcis* sp. having high rates, while *L. schreiberi* occupied an intermediate position. EWLi
267 also varied along time in all species, with both *Podarcis* sp. displaying higher temporal

268 fluctuations (Fig. 2). When we added SVL and BM as covariates (ANCOVA-rm), interspecific
269 differences were smoother but still significant, while temporal differences disappeared (Table 3).

270 Accumulated water loss (EWLa) revealed even more marked differences between the five
271 species (Fig. 3). Here, two clear groups with no overlap could be distinguished; on one side the
272 larger *T. lepidus* and *L. schreiberi* plus the medium-sized *P. algirus* all losing less water by
273 evaporation and on the other side the small *P. guadarramae* and *P. bocagei* with much higher
274 water loss rates (Duncan post-hoc tests $p < 0.05$). Again, after accounting for SVL and body
275 mass, differences between species remain but differences time intervals did not while the
276 interaction between both factors was also conserved (Table 3). Either in EWLi or in EWLa, we
277 did not observe interactions between factors and covariables.

278

279 *Preferred temperatures vs. water loss rates*

280 Mean T_p and EWL_t were inversely correlated between species while SVL and BM had no
281 influence on the results ($n = 5$, $r_{\text{partial}} T_p - EWL_t = -0.99$, $T = -14.72$, $P = 0.04$; $r_{\text{partial}} SVL - EWL_t = -$
282 0.94 , $T = -2.70$, $P = 0.23$; $r_{\text{partial}} BM - EWL_t = 0.81$, $T = 1.41$, $P = 0.39$). In contrast, within species
283 EWL_t was positively correlated with SVL, negatively correlated with BM but independent from
284 T_p for *L. schreiberi* ($n = 5$, $r_{\text{partial}} T_p - EWL_t = -0.62$, $T = -1.59$, $P = 0.19$; $r_{\text{partial}} SVL - EWL_t = 0.84$,
285 $T = 3.17$, $P = 0.03$; $r_{\text{partial}} BM - EWL_t = -0.83$, $T = -2.98$, $P = 0.04$) and *P. algirus* ($n = 5$, $r_{\text{partial}} T_p -$
286 $EWL_t = -0.39$, $T = 0.84$, $P = 0.45$; $r_{\text{partial}} SVL - EWL_t = 0.90$, $T = 4.02$, $P = 0.02$; $r_{\text{partial}} BM - EWL_t$
287 $= -0.86$, $T = -3.38$, $P = 0.03$). We did not detect significant relations for the other three species.

288

289 **Discussion**

290 The environmental differences between burnt and unburnt landscapes highlight the role of
291 vegetation buffering the natural fluctuations. Specifically, burnt microhabitats often used by
292 lizards undergo larger daily variations of temperature and humidity, and also attain higher
293 temperatures, especially in summer (Ferreira, 2015). When comparing lizards within the same
294 trophic guild, this environmental contrast was expected to benefit Mediterranean lizards
295 (compared to Atlantic lizards) from the thermal quality of open habitats created by fire regimes.
296 We only have indirect support for this from several independent sources of evidence: 1) in
297 southern France, fire recurrence increased the Mediterraneanity (sensu Prodon, 1993) of the reptile
298 community (Santos & Cheylan, 2003); and 2) in multiple localities, reptile species tend to be
299 more common in burnt sites compared to unburnt ones (Santos & Poquet, 2010; Santos et al.,
300 2016). Although we hypothesised that this opposing responses would be caused by divergent
301 ecophysiological features, our results only partially met our expectations, namely, that species
302 favoured by fire should be more thermophile and economic in water loss. Certainly, the
303 Mediterranean medium-sized *P. algirus* clearly selected for higher temperatures than the
304 remaining species and loss less water than expected for its body size. However, the differences
305 among the other species seem better explained by alternative factors such as refuge use, life
306 history and body size/shape rather than by their responses to fire.

307 Thermal and hydric ecophysiology showed signs of a size/shape-independent trade-off
308 across species but this should be confirmed by a formal analysis under the comparative method
309 framework with an extended species dataset (Bauwens et al., 1995; Carneiro et al., 2016). Within
310 species, what we found was the influence of the surface/volume relationship (Schmidt-Nielsen,
311 1984) making slender and smaller lizards to show less water relative to the body mass. Thus, in
312 ecophysiological terms, species were not arranged in a Mediterranean-Atlantic axis. While the

313 demographic responses to fire of these five lizards are mostly related to their biogeographic
314 affinities and global distribution ranges (Sillero et al., 2009; Santos & Poquet, 2010; Santos &
315 Cheylan, 2013; authors unpublished data), the lack of complete concordance with their
316 physiological features suggest a more complex scenario. This supports previous claiming that the
317 functional approach to predict responses of reptiles to fire is conceptually accurate but
318 predictively weak (Smith et al. 2012, 2013).

319 *Psammodromus algirus* is considered a species with a wide ecological valence occupying
320 from the border of Sahara in North Africa to mountain oak forests and other humid environments
321 in the border of the Atlantic region in Iberia (Loureiro et al., 2008). Even if previous studies
322 reported high preferred temperatures (Bauwens et al., 1995), there is also evidence of activity
323 under suboptimal thermal conditions (Carretero & Llorente, 1995). It is also the only species of
324 the five studied with the body covered by keeled, overlapping scales (Arnold, 2002). Although
325 this scale arrangement is likely the result from an adaptation for locomotion in bushy vegetation
326 (matrix climbing, Arnold, 1987), it apparently provides protection against water loss acting as an
327 exaptation (Gould & Vrba, 1982) when humidity decreases. This may have put the species in
328 better conditions to survive in burnt areas. Although the short-term (one year after the fire)
329 response of *P. algirus* can be negative in some Mediterranean landscapes, recovery after two
330 years since fire has been reported (Santos et al., 2016). Post-fire egg mortality (Smith et al.,
331 2012) and life history of the species (Carretero & Llorente, 1997) may be subjacent for such
332 pattern.

333 Both species of large lizards undoubtedly take advantage from lower water loss rates due to
334 their lower surface/volume relationship (Schmidt-Nielsen 1984). However, despite their opposite
335 biogeographic affinities, they only differ slightly in hydric physiology which makes it difficult to

336 interpret their responses to fire (Santos & Cheylan, 2013; authors' unpublished data). Instead, the
337 variable responses of *T. lepidus* according to the population studied, and the decrease of *L.*
338 *schreiberi* in response to fire intensification should be better interpreted in terms of habitat use.
339 *T. lepidus* is more mobile and tends to occupy areas dominated by rocky substrates using big
340 rock holes as refuge (Castilla & Bauwens, 1992). In some localities, it occupies long-unburnt
341 (and structured) habitats (Santos et al., 2016) whereas in others only appears in repeated-burnt
342 ones (Santos & Cheylan, 2013). This may be due to shifts in other ecological resources (i. e.
343 habitat, prey) but also to different fire ages (Nimmo et al., 2014). In contrast, *L. schreiberi* has
344 small home ranges and use ecotonal bushy vegetation to thermoregulate, forage and hide
345 (Salvador, 1988) being its distribution mostly outside of the range of fire. We here suggest that
346 the divergent responses of both species to fire are likely habitat-mediated while shared thermal
347 (and partly hydric) ecophysiology would result from evolutionary convergence in two long-term
348 separated lacertid lineages (Arnold et al., 2007). Interestingly, competitive exclusion between
349 green (*Lacerta* sp.) and ocellated lizards (*Timon* sp.) at a geographic level is suggested to have
350 shaped the historical biogeography of both groups (Ahmadzadeh et al., 2016).

351 Particular habitat requirements may explain why the two species of wall lizards *Podarcis*
352 sp. show opposing responses to fire but similar physiological features. The geographic ranges of
353 *P. bocagei* and *P. gaudarramae* widely overlap geographically and both species are frequently
354 found in syntopy (Carretero, 2008). However, field-work experience demonstrated that *P.*
355 *guadarramae* is the only species found in repeatedly burnt spots (authors' unpublished data).
356 This lizard is more attached to bare rocky substrates than *P. bocagei*, which uses a wider variety
357 of substrates (Kaliontzopoulou et al., 2010), trend that is accentuated in syntopy (Gomes et al.,
358 2016). Since mean preferred temperatures and water loss rates did not differ, we interpret the

359 dominance of *P. guadarramae* after fire intensification as another result of different habitat and
360 refuge use. In fact, head fattening of *P. guadarramae* might confer an advantage when rock
361 crevices are used as main refuge (Kaliontzopoulou et al., 2012) as expected in burnt areas.
362 Nevertheless, the accentuated diel variation in preferred temperatures by *P. bocagei* also suggest
363 sensitiveness to midday conditions either thermal or hydric, which might provide some support
364 for an ecophysiological constraint when compared to *P. guadarramae*. This aspect should be
365 explored in the future with continuous monitoring of individual lizards (Bowker et al., 2010;
366 Bowker et al., 2013).

367 Fire is a fundamental driver of ecosystem functioning and composition in the
368 Mediterranean basin (Blondel et al., 2010). Species that mostly distributed on this bioregion
369 occupies fire-prone landscapes with biota likely resulting from a long evolutionary association
370 with fire (Pausas & Keeley, 2009). The effects of fire are observable at multiple scales from the
371 landscape (variation in land cover) to the microhabitat (variation in temperature and humidity
372 ranges). As ectotherms, reptiles have their biological and ecological processes dependent on
373 environmental temperature. However, heliothermic lizards are able to thermoregulate accurately
374 if habitat complexity provides sufficient thermal heterogeneity for shuttling and selecting
375 appropriate temperatures (Sears & Angilletta, 2015). Despite the sensitivity of reptiles to
376 modifications in habitat structure (caused by fire), factors such as life history, microhabitat
377 preferences and or thermoregulatory behaviour may have deviated results from a pure
378 ecophysiological model. Further studies should be addressed to understand interactions between
379 fire and other processes in order to more accurately predict reptile responses to fire-regimes
380 using an extended species dataset. Meanwhile current evidence advances that ecophysiology
381 plays a functional role on reptile responses to fire, which is likely habitat-mediated

382 (Lindenmayer et al., 2008; Santos & Cheylan, 2013; Nimmo et al., 2014).

383 Even if this is a first approach to a complex topic, ecophysiology already reveals relevant
384 to anticipate reptile responses to fire, even if it needs to be complemented by the analysis of
385 other biological traits. Future studies should include more species and more regions to the
386 analysis, not only to obtain better statistical support but also to allow phylogenetic correction in
387 order to exclude the effects of long-term evolutionary history. Overall, our results already
388 indicate that ecophysiology may provide mechanistic understanding on how species occurrence
389 and abundance are spatially distributed at different geographic scales, and how they may be
390 modified by human impacts (Sinervo et al., 2010; Huey et al., 2012; Lara-Reséndiz et al., 2015;
391 Valenzuela-Ceballos et al., 2015).

392

393 **Acknowledgements.** We thank D. Ferreira for sharing her environmental data from northern
394 Portugal and M. Sannolo and T. Pinto for field assistance.

395

396 **References**

- 397 Ahmadzadeh F, Flecks M, Carretero MA, Böhme W, Ihlow F, Kapli P, Miraldo A, Rödder D.
398 2016. Separate histories in both sides of the Mediterranean: Phylogeny and niche evolution
399 of ocellated lizards. *J Biogeogr.* DOI:10.1111/jbi.12703
- 400 Angilletta MJ jr. 2010. Thermal adaptation. Oxford: Oxford University Press.
- 401 Angilletta MJ jr, Cooper BS, Schuler MS, Boyles JG. 2010. The evolution of thermal physiology
402 in endotherms. *Front Biosci* E2:861-881.
- 403 Araújo MB, Thuiller W, Pearson RG. 2006. Climate warming and the decline of amphibians and
404 reptiles in Europe. *J Biogeogr* 33:1712-1728.

- 405 Arnold EN. 1987. Resource partition among lacertid lizards in southern Europe. *J Zool* 1:739-
406 782.
- 407 Arnold EN. 2002. History and Function of Scale Microornamentation in Lacertid Lizards. *J*
408 *Morphol* 252:145-169.
- 409 Arnold EN, Arribas OJ, Carranza S. 2007. Systematics of the Palaeartic and Oriental lizard tribe
410 Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera.
411 *Zootaxa* 1430:1-86.
- 412 Batllori E, Parisien MA, Krawchuk M, Moritz MA. 2013. Climate change-induced shifts in fire
413 for Mediterranean ecosystems. *Global Ecol Biogeogr* 22:1118-1129.
- 414 Bauwens D, Garland T jr, Castilla AM, Van Damme R.. 1995. Evolution of sprint speed in
415 Lacertid Lizards: Morphological, Physiological, and Behavioral Covariation. *Evolution*
416 49:848-863.
- 417 Blondel J, Aronson J, Bodiou JY, Boeuf G.. 2010). *The Mediterranean region: biological*
418 *diversity in space and time*. New York: Oxford University Press.
- 419 Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world
420 without fire. *New Phytol* 165:525-538.
- 421 Bowker RG. 1993. The thermoregulation of the lizards *Cnemidophorus exanguis* and *C. velox*:
422 some consequences of high body temperature. In: Wright JW, Vitts LJ, eds. *Biology of*
423 *Whiptail Lizards (genus Cnemidophorus)*. Norman: Oklahoma Museum Natural History,
424 117-132.
- 425 Bowker RG, Bowker GE, Wright CL. 2013. Thermoregulatory movement patterns of the lizard
426 *Podarcis carbonelli* (Lacertilia: Lacertidae). *J Therm Biol* 38:454-457.

- 427 Bowker RG, Wright CL, Bowker GE. 2010. Patterns of body temperatures: Is lizard
428 thermoregulation chaotic? *J Therm Biol* 35:1-5.
- 429 Bowman DMLS, Balch J, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, D'Antonio CM,
430 DeFries RS, Doyle JC, Harrison SP, Johnston FH, Keeley JE, Krawchuk MA, Kull CA,
431 Marston JB, Moritz MA, Prentice IC, Roos CL, Scott AC, Swetman TW, van der Werf
432 GR, Pyne SJ. 2009. Fire in the Earth System. *Science* 324:481-484.
- 433 Brotons L, Aquilué N, de Cáceres M, Fortin MJ, Fall A. 2013. How Fire History, Fire
434 Suppression Practices and Climate Change Affect Wildfire Regimes in Mediterranean
435 Landscapes. *PLoS ONE* 8: e62392.
- 436 Burnside WR. 2010. Hot research on roasted lizards: warming, evolution and extinction in
437 climate change studies. *Front Biogeogr* 2:61-63.
- 438 Bury RB. 2004. Wildfire, Fuel Reduction, and Herpetofaunas accross Diverse Landscape Mosaics
439 in Northwestern Forests. *Conserv Biol* 18: 968-975.
- 440 Carneiro D, García-Muñoz E, Kalionzopoulou A, Llorente GA, Carretero MA. 2015. Comparing
441 ecophysiological traits in two *Podarcis* Wall lizards with overlapping ranges. *Salamandra*
442 51:335-344.
- 443 Carneiro D, García-Muñoz E, Žagar A, Pafilis P, Carretero MA. 2016. Is ecophysiology
444 congruent with the present-day relictual distribution of a lizard group? Evidence from
445 preferred temperatures and water loss rates. *Herpetol J* (in press).
- 446 Carretero MA. 2004. From set menu to *a la carte*. Linking issues in trophic ecology of
447 Mediterranean lacertids. *Ital J Zool* 74:121-133.

- 448 Carretero MA. 2008. An integrated assessment of the specific status in a group with complex
449 systematics: the Iberomaghrebian lizard genus *Podarcis* (Squamata, Lacertidae). *Integr*
450 *Zool* 4:247-266.
- 451 Carretero MA. 2012. Measuring body temperatures in small lacertids: Infrared vs. contact
452 thermometers. *Basic Appl Herpetol* 26:99-105.
- 453 Carretero MA, Llorente GA. 1997. Reproduction of *Psammodromus algirus* in coastal sandy
454 areas of NE Spain. *Amphibia-Reptilia* 18:369-382.
- 455 Carretero MA, Galán P, Salvador A. 2015. Lagartija lusitana – *Podarcis guadarramae*. In:
456 Salvador A, Marco A, eds. Enciclopedia Virtual de los Vertebrados Españoles. Madrid:
457 Museo Nacional de Ciencias Naturales. Available at
458 <http://www.vertebradosibericos.org/reptiles/podgua.html> (accessed 15 December 2015).
- 459 Carretero MA, Llorente GA. 1995. Thermal and temporal patterns of two Mediterranean
460 Lacertidae. In: Llorente GA, Montori A, Santos X, Carretero MA, eds. *Scientia*
461 *Herpetologica*. Barcelona: Asociación Herpetológica Española, 213-223.
- 462 Carretero MA, Roig JM, Llorente GM. 2005. Variation in preferred body temperature in an
463 oviparous population of *Lacerta (Zootoca) vivipara*. *Herpetol J* 15:51-55.
- 464 Castilla AM, Bauwens D. 1992. Habitat selection by the lizard *Lacerta lepida* in a Mediterranean
465 oak forest. *Herpetol J* 2:27-30
- 466 Castilla AM, Van Damme R, Bauwens D. 1999. Field body temperatures, mechanisms of
467 thermoregulation and evolution of thermal characteristics in lacertid lizards. *Nat Croat*
468 8:253-274.
- 469 Christian KA, Blamires SJ. 1999. Seasonal water loss of the lizard *Lophognathus temporalis* in
470 the wet-dry tropics of northern Australia. *Amphibia-Reptilia* 20:211-215,

- 471 Clusella-Trullas S, Terblanche JS, van Wyk JH, Spotila JR. 2007. Low repeatability of preferred
472 body temperature in four species of Cordylid lizards: Temporal variation and implications
473 for adaptive significance. *Evol Ecol* 21:63-79.
- 474 Dell, Inc.. 2015. STATISTICA (data analysis software system). version 12. Available at
475 www.statsoft.com
- 476 Diaz JA, Bauwens D, Asensio B. 1996. A comparative study rates of the relation between
477 heating rates and ambient temperatures in lacertid lizards. *Physiol Zool* 69:1359-1383.
- 478 Díaz JA, Iraeta P, Monasterio C. 2006. Seasonality provokes a shift of thermal preferences in a
479 temperate lizard, but altitude does not. *J Therm Biol* 31:237-242
- 480 Driscoll DA, Henderson MK. 2008. How many common reptile species are fire specialists? A
481 replicated natural experiment highlights the predictive weakness of a fire succession
482 model. *Biol Conserv* 141:460-471.
- 483 Driscoll DA, Smith AL, Blight S, Maindonald J. 2012. Reptile responses to fire and the risk of
484 post-disturbance sampling bias. *Biodivers Conserv* 21:1607-1625.
- 485 Eynan M, Dmi'el R. 1993. Skin resistance to water loss in agamid lizards. *Oecologia*
486 95:290–294.
- 487 Ferreira D. 2015). Genetic and morphological impacts of a repeated fire regime on *Podarcis*
488 *guadarramae*. Master thesis. University of Porto.
- 489 Ferreira D, Žagar A, Santos X. 2016. Uncovering the rules of (reptile) species coexistence in
490 transition zones between bioregions. *Salamandra* (in press).
- 491 Flannigan M, Stocks B, Turetsky M, Wotton M. 2009. Impacts of climate change on fire activity
492 and fire management in the circumboreal forest. *Glob Change Biol* 15:549-560.

- 493 Fox BJ. 1982. Fire and mammalian secondary succession in an Australian coastal heath. *Ecology*
494 63:1332–1341.
- 495 Friend GR. 1993. Impact of fire on small vertebrates in mallee woodlands and heathlands of
496 temperate Australia: a review. *Biol Conserv* 65:99-114.
- 497 Galán P. 2015. Lagartija de Bocage – *Podarcis bocagei*. In: Salvador A, Marco A, eds.
498 Enciclopedia Virtual de los Vertebrados Españoles. Madrid: Museo Nacional de Ciencias
499 Naturales. Available at <http://www.vertebradosibericos.org/reptiles/podboc.html> (accessed
500 15 December 2015).
- 501 García-Muñoz E, Carretero MA. 2013. Comparative ecophysiology of two sympatric lizards.
502 Laying the groundwork for mechanistic distribution models. *Acta Herpetol* 8:123-128.
- 503 García-Muñoz E, Sillero N. 2010. Two new types of noose for capturing herps. *Acta Herpetol*
504 5:259-263.
- 505 Gomes V, Carretero MA, Kaliontzopoulou A. 2016. The relevance of morphology for habitat use
506 and locomotion in two species of wall lizards. *Acta Oecol* 70:87-95.
- 507 Gould SJ, Vrba ES. 1982. Exaptation - a missing term in the science of form. *Paleobiology* 8:4-
508 15.
- 509 Hantson S, Pueyo S, Chuvieco E. 2014. Global fire size distribution is driven by human impact
510 and climate. *Global Ecol Biogeogr* 24:1-10.
- 511 Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM,
512 Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. 2005.
513 Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol*
514 *Monogr* 75: 3-35.
- 515 Hu Y, Urlus J, Gillespie G, Letnic M, Jessop TS. 2013. Evaluating the role of fire disturbance in

- 516 structuring small reptile communities in temperate forests. *Biodivers Conserv* 22:1949-
517 1963.
- 518 Huey RB. 1982. Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH,
519 eds. *Biology of the Reptilia. Physiology C* vol. 12. New York: Academic Press, 25–91.
- 520 Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Álvarez-Pérez HJ, Garland T jr.. 2009.
521 Why tropical forest lizards are vulnerable to climate warming? *P Roy Soc B* 276:1936-
522 1948.
- 523 Huey RB, Kearney M, Krokenberger A, Holtum JAM, Jess M, Williams SE. 2012. Predicting
524 organismal vulnerability to climate warming: roles of behaviour, physiology and
525 adaptation. *Philos T Roy Soc B* 367:1165-1679.
- 526 Kaliontzopoulou A, Carretero MA, Llorente GA. 2010. Intraspecific ecomorphological variation:
527 linear and geometric morphometrics reveal habitat-related patterns within *Podarcis*
528 *bocagei* wall lizards. *J Evol Biol* 23:1234-1244.
- 529 Kaliontzopoulou A, Pinho C, Harris DJ, Carretero MA. 2011. When cryptic diversity blurs the
530 picture: a cautionary tale from Iberian and North African *Podarcis* wall lizards. *Biol J Linn*
531 *Soc* 103:779–800.
- 532 Kaliontzopoulou A, Adams DC, van der Meijden A, Perera A, Carretero MA. 2012.
533 Relationships between head morphology, bite performance and diet in two species of
534 *Podarcis* wall lizards. *Evol Ecol* 26:825-845.
- 535 Kasischke ES, Turetsky M. 2006. Recent changes in the fire regime across the North American
536 boreal region — Spatial and temporal patterns of burning across Canada and Alaska.
537 *Geophys Res Lett* 33:1-5.
- 538 Kati V, Devillers P, Dufrêne M, Legakis A, Vokou D, Lebrun P. 2004. Hotspots,

- 539 complementarity or representativeness? Designing optimal small-scale reserves for
540 biodiversity conservation. *Biol Conserv* 120:471-480.
- 541 Kearney M, Porter WP. 2009. Mechanistic niche modelling: combining physiological and spatial
542 data to predict species ranges. *Ecology Letters* 12:334-350.
- 543 Lara-Reséndiz RA, Gadsden H, Rosen PC, Sinervo B, Méndez-de-la-Cruz FR. 2015.
544 Thermoregulation of two sympatric species of horned lizards in the Chihuahuan Desert and
545 their local extinction risk. *J Therm Biol* 48:1-10.
- 546 Letnic M, Dickman CR, Tischler MK, Tamayo B, Beh CL. 2004. The responses of small
547 mammals and lizards to post-fire succession and rainfall in arid Australia. *J Arid Environ*
548 59:85-114.
- 549 Lindenmayer DB, Wood JT, MacGregor C, Michael DR, Cunningham RB, Crane M, Montague-
550 Drake R, Brown D, Muntz R, Driscoll DA. 2008. How predictable are reptile responses to
551 wildfire? *Oikos* 117:1086-1097.
- 552 Loureiro A, Ferrand N, Carretero MA, Paulo O, eds. 2008. *Atlas dos Anfíbios e Répteis de*
553 *Portugal*. 1st edn Lisboa: Instituto da Conservação da Natureza e da Biodiversidade.
- 554 Lorenzon P, Clobert J, Oppliger A, John-Alder H. 1999. Effect of water constraint on growth
555 rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*).
556 *Oecologia* 118:423-430.
- 557 Mautz WJ. 1982a. Patterns of evaporative water loss. In: Gans C, Pough FH, eds. *Biology of the*
558 *Reptilia* Vol. 12 New York. Academic Press, 443-481.
- 559 Mautz WJ. 1982b. Correlation of both respiratory and cutaneous water losses of lizards with
560 habitat aridity. *J Comp Physiol B* 149:25-30.
- 561 McGill BJ, Enquist M, Weiher E, Westoby M. 2006. Rebuilding community ecology from

- 562 functional traits. *Trends Ecol Evol* 21:178-185.
- 563 McKenzie D, Gedalof Z, Petterson DL, Mote P. 2004. Climatic Change, Wildfire, and
564 Conservation. *Conserv Biol* 18:890-902.
- 565 Metzger MJ, Bunce RGH, Jongman RHG, Múcher CA, Watkins JW. 2005. A climatic
566 stratification of the environment of Europe. *Global Ecol Biogeogr* 14:549-563.
- 567 Moreno-Rueda G, Pleguezuelos JM, Pizarro M, Montori A. 2012. Northward Shifts of the
568 Distributions of Spanish Reptiles in Association with Climate Change. *Conserv Biol*
569 26:278-283.
- 570 Moreira F, Rego F, Ferreira P. 2001. Temporal (1958-1995) pattern of change in a cultural
571 landscape of northwestern Portugal: implications for fire occurrence. *Landscape Ecol*
572 16:557-567.
- 573 Moreira F, Russo D. 2007. Modelling the impact of agricultural abandonment and wildfires on
574 vertebrate diversity in Mediterranean Europe. *Landscape Ecol* 22:1461-1476.
- 575 Moritz MA, Parisien MA, Batllori E, Krawchuk MA, Van Dorn J, Ganz DJ, Hayhoe K. 2012.
576 Climate change and disruptions to global fire activity. *Ecosphere* 3:a49.
- 577 Nimmo DG, Kelly LT, Spence-Bailey LM, Watson SJ, Haslem A, White JG. 2012. Predicting
578 the century-long post-fire responses of reptiles. *Global Ecol Biogeogr* 21:1062-1073.
- 579 Nimmo DG, Kelly LT, Farnsworth LM, Watson SJ, Bennett AF. 2014. Why do some species
580 have geographically varying responses to fire history? *Ecography* 37:805-813.
- 581 Osojnik N, Žagar A, Carretero MA, García-Muñoz E, Vrezec A. 2013. Ecophysiological
582 Dissimilarities of Two Sympatric Lizards. *Herpetologica* 69:445-454.
- 583 Pastro LA, Dickman CR, Letnic M. 2013. Effects of wildfire, rainfall and region on desert lizard
584 assemblages: The importance of multi-scale processes. *Oecologia* 173:603-614.

- 585 Pausas JG, Keeley JE. 2009. A burning story: The role of fire in the history of life. *BioScience*
586 59:593-601.
- 587 Pausas JG, Llovet J, Rodrigo A, Vallejo R. 2008. Are wildfires a disaster in the Mediterranean
588 basin? A review. *Int J Wildland Fire* 17:713-723.
- 589 Pianka ER, Vitt LJ. 2003. *Lizards: Windows to the Evolution of Diversity*. Berkeley and Los
590 Angeles: University of California Press.
- 591 Piñol J, Terradas J, Lloret F. 1998. Climate warming, wildfire hazard, and wildfire occurrence in
592 coastal eastern Spain. *Climatic Change* 38:345-357.
- 593 Porter WP, Mitchell JW, Beckman WA, Dewitt CB. 1973. Behavioral implications of
594 mechanistic ecology. Thermal and behavioral modeling of desert ectotherms and their
595 microenvironment. *Oecologia* 13:1-54.
- 596 Porter WP, Tracy CR. 1983. Biophysical analyses of energetics, time-space utilization, and
597 distributional limits. In: Huey RB, Pianka ER, Schoener TW, eds. *Lizard Ecology Studies*
598 *on a model organism*. Cambridge: Harvard University Press, 55-83.
- 599 Rato C, Carretero MA. 2015. Ecophysiology tracks phylogeny and meets ecological models in
600 an Iberian gecko. *Physiol Biochem Zool* 88:564-575.
- 601 Salvador A. 1988. Selección de microhabitat del lagarto verdinegro (*Lacerta schreiberi*) (Sauria:
602 Lacertidae). *Amphibia-Reptilia* 9:265-276.
- 603 Santos X, Badiane A, Matos C. 2016. Contrasts in short- and long-term responses of
604 Mediterranean reptile species to fire and habitat structure. *Oecologia* 180:205-216.
- 605 Santos X, Cheylan M. 2013. Taxonomic and functional response of a Mediterranean reptile
606 assemblage to a repeated fire regime. *Biological Conserv* 168:90-98.
- 607 Santos X, Poquet JM. 2010. Ecological succession and habitat attributes affect the postfire

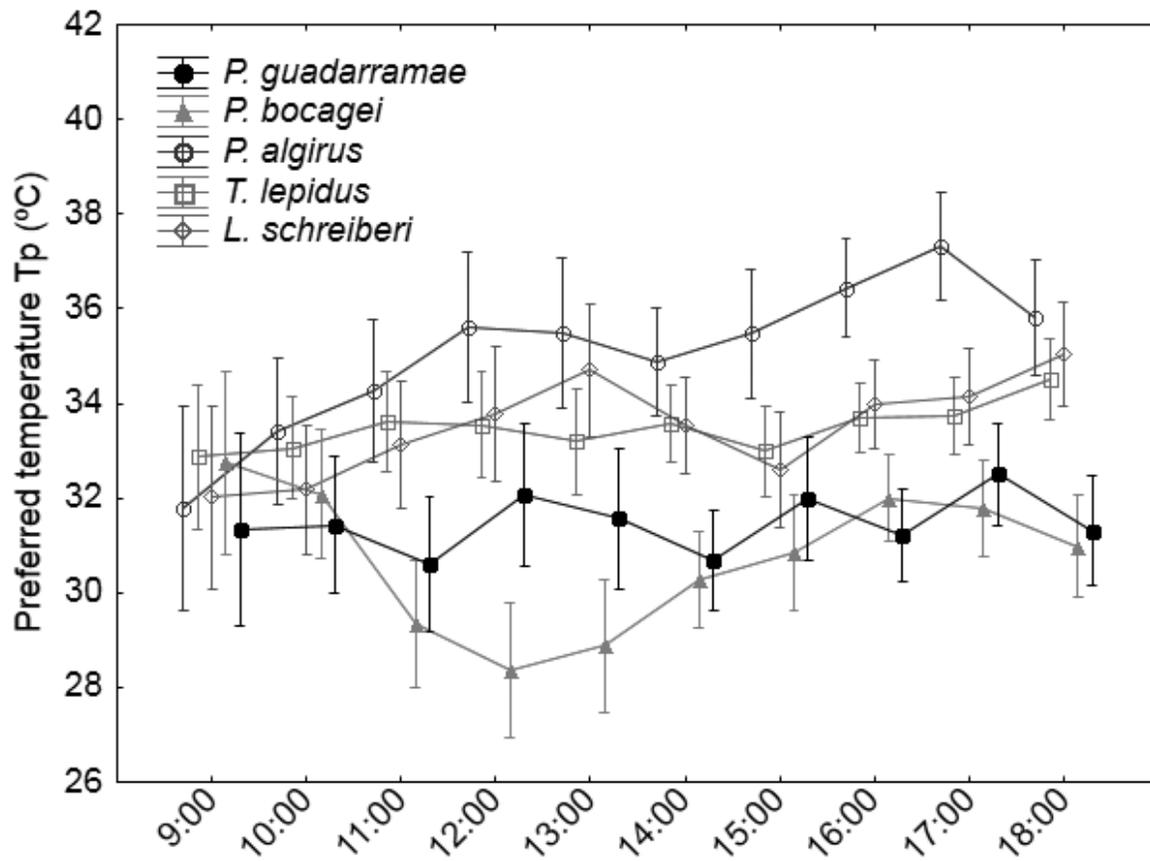
- 608 response of a Mediterranean reptile community. *Eur J Wildlife Res* 56:895-905.
- 609 Schmidt-Nielsen K. 1984. *Scaling: Why is Animal Size so Important?* New York: Cambridge
610 University Press.
- 611 Sears MW, Angilletta MJ jr. 2003. Life-history variation in the sagebrush lizard: Phenotypic
612 plasticity or local adaptation? *Ecology* 84:1624-1634.
- 613 Sears MW, Angilletta MJ jr. 2015. Costs and Benefits of Thermoregulation Revisited: Both the
614 Heterogeneity and Spatial Structure of Temperature Drive Energetic Costs. *Am Nat*
615 185:e94-102.
- 616 Shoemaker VH, Nagy KA. 1977. Osmoregulation in Amphibians and Reptiles. *Annu Rev Physiol*
617 39: 449-471.
- 618 Sillero N, Brito JC, Skidmore AK, Toxopeus B. 2009. Biogeographical patterns derived from
619 remote sensing variables: the amphibians and reptiles of the Iberian Peninsula. *Amphibia-
620 Reptilia* 30:185-206.
- 621 Silva JS, Vaz P, Moreira F, Catry F, Rego FC. 2011. Wildfires as a major driver of landscape
622 dynamics in three fire-prone areas of Portugal. *Landscape Urban Plan* 101:349-358.
- 623 Sinervo B, Méndez-de-la-Cruz FR, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz M,
624 Lara-Resendiz RA, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN,
625 Gadsden H, Avila LJ, Morando M, de la Riva I, Sepúlveda PV, Rocha CFD,
626 Ibargüengoytia NR, Aguilar Puntriano C, Massot M, Lepetz V, Oksanen TA, Chapple DG,
627 Bauer AM, Branch WR, Clobert J, Sites JW jr. 2010. Erosion of lizard diversity by climate
628 change and altered thermal niches. *Science* 328:894-899.

- 629 Smith AL, Bull CM, Driscoll DA. 2013. Successional specialization in a reptile community
630 cautions against widespread planned burning and complete fire suppression. *J Appl Ecol*
631 50:1178-1186.
- 632 Smith A, Meulders B, Bull CM, Driscoll D. 2012. Wildfire-induced mortality of Australian
633 reptiles. *Herpetology Notes* 5:233-235.
- 634 Soares C, Brito JC. 2007. Environmental correlates for species richness among amphibians and
635 reptiles in a climate transition area. *Biodivers Conserv* 16:1087-1102.
- 636 Soares C, Álvares F, Loureiro A, Sillero N, Arntzen JW, Brito JC. 2005. Atlas of the amphibians
637 and reptiles of Peneda-Gêres National Park, Portugal. *Herpetozoa* 18:155-170.
- 638 Spector S. 2002. Biogeographic Crossroads as Priority Areas for Biodiversity Conservation.
639 *Conserv Biol* 16:1480-1487.
- 640 Sillero N, Brito JC, Skidmore AK, Toxopeus B. 2009. Biogeographical patterns derived from
641 remote sensing variables: the amphibians and reptiles of the Iberian Peninsula. *Amphibia-*
642 *Reptilia* 30:185-206.
- 643 Ursino N, Rulli MC. 2011. Hydrological minimal model for fire regime assessment in a
644 Mediterranean ecosystem. *Water Resour Res* 47:1-12.
- 645 Valentine LE, Reaveley A, Johnson B, Fisher R, Wilson BA. 2012. Burning in Banksia
646 Woodlands: how does the fire-free period influence reptile communities? *PLoS ONE*
647 7:e34448.
- 648 Valenzuela-Ceballos S, Castañeda G, Rioja-Paradela T, Carrillo-Reyes A, Bastiaans E. 2015.
649 Variation in the thermal ecology of an endemic iguana from Mexico reduces its
650 vulnerability to global warming. *J Therm Biol* 48:56-64.

- 651 Veríssimo CV, Carretero MA. 2009. Preferred temperatures of *Podarcis vaucheri* from
652 Morocco: intraspecific variation and interspecific comparisons. *Amphibia-Reptilia* 30:17-
653 23.
- 654 Westerling AL, Hidalgo H, Cayan DR, Swetnam T. 2006. Warming and Earlier Spring Increases
655 Western US Forest Wildfire Activity. *Science* 313:940-943.
- 656 Whitlock C, Higuera PE, McWethy DB, Briles CE. 2010. Paleoecological perspectives on fire
657 ecology: revisiting the fire-regime concept. *Open Ecol J* 3:6-23.

658 **Figure 1.** Daily variation of the preferred body temperatures (T_p) for five lizard species.

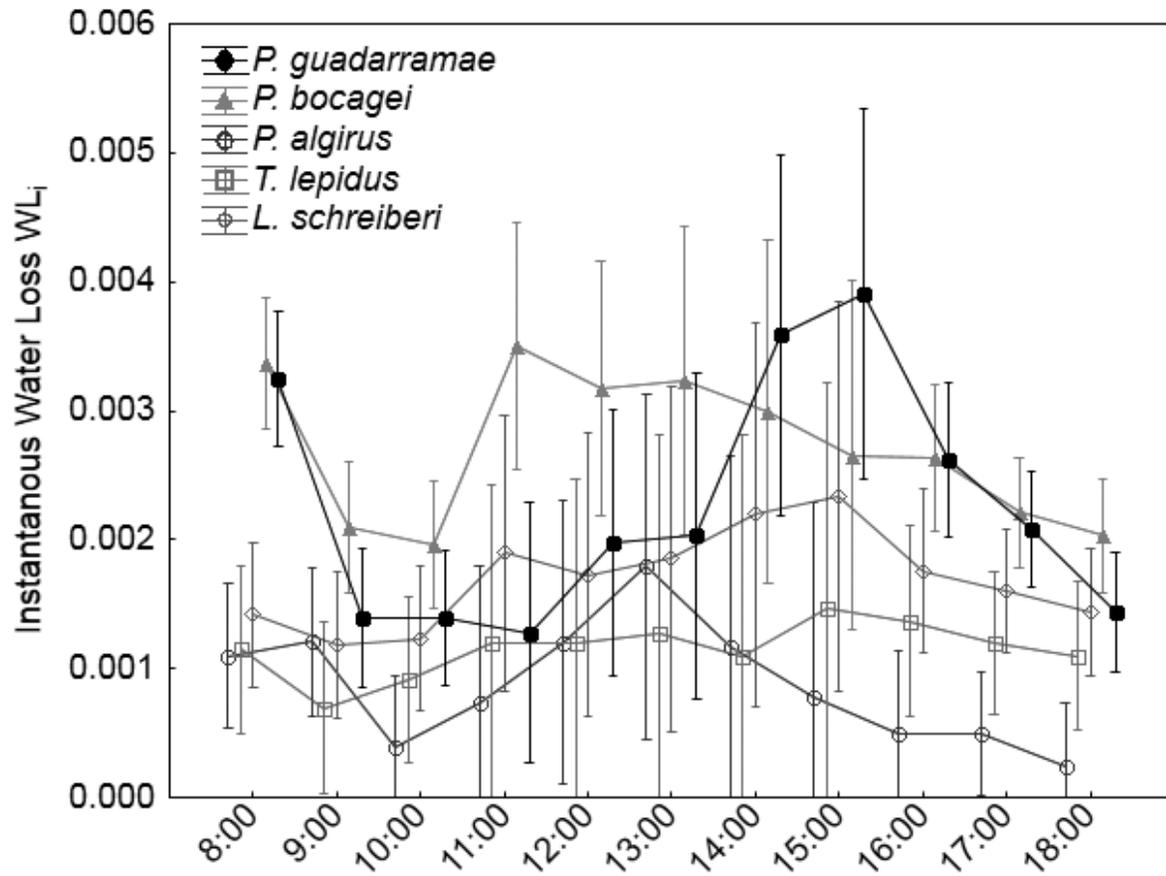
659 Displayed are median values and 0.95 confidence intervals.



660
661
662
663

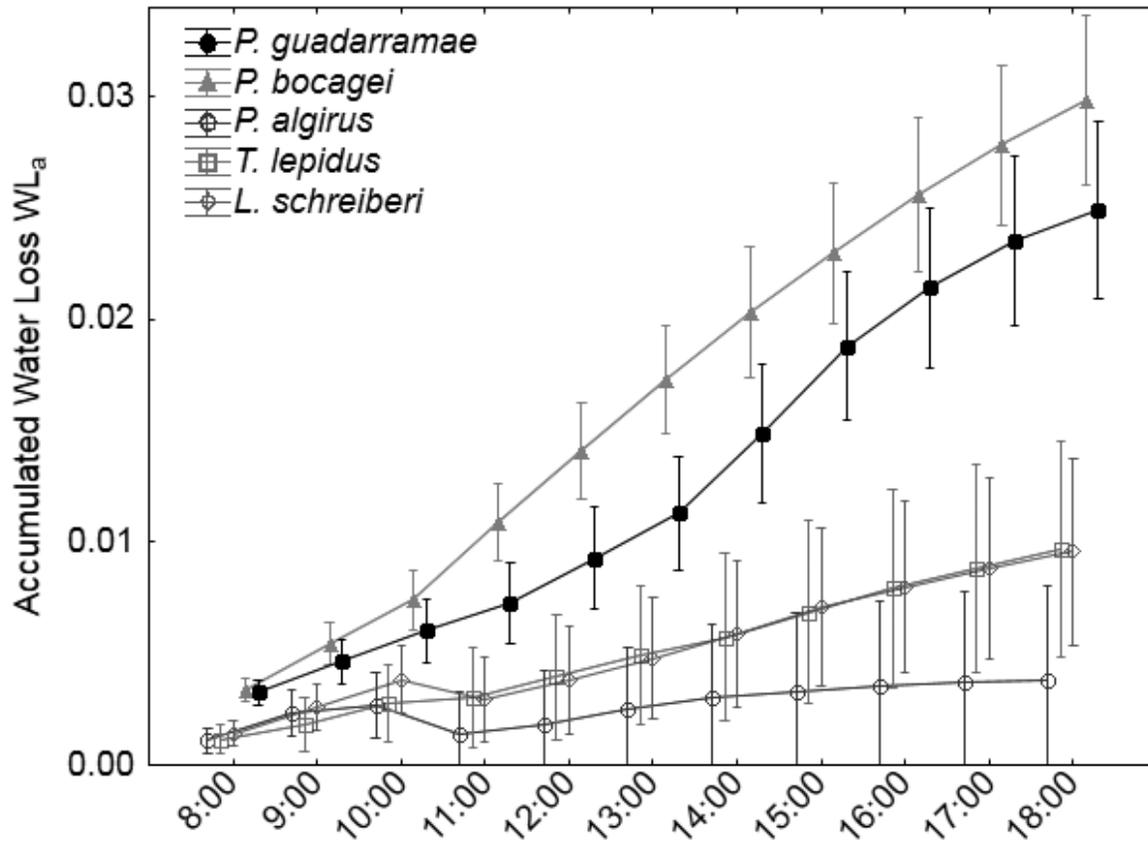
664 **Figure 2.** Patterns of instantaneous water loss (EWL_i) along a 12-hour experiment for five lizard
665 species. Displayed are median values and 0.95 confidence intervals.

666



667
668

669 **Figure 3.** Accumulated water loss (EWL_a) along a 12-hour experiment for five lizard species.
670 Displayed are median values and 0.95 confidence intervals.



671

672

673 **Table 1** General traits of the five lizard species studied. Habitat, distribution and biogeographic affinities after Carretero *et al.* (2015),
 674 Galán (2015), Kaliontzopoulou *et al.* (2011) and Loureiro *et al.* (2008). Fire responses after Santos and Cheylan, 2013; Santos and
 675 Poquet 2010; and authors' unpublished results.

Species	body size	main habitat	distribution	biogeography	fire response
<i>Timon lepidus</i>	very large	open oak forest, big rocks	Iberia, SW France	Mediterranean	increase
<i>Lacerta schreiberi</i>	large	ecotones and riverine forests	W Iberia	Atlantic	decrease
<i>Psammodromus algirus</i>	medium	shrubs	Iberia, SW France, N Africa	Mediterranean	increase
<i>Podarcis bocagei</i>	small	dunes, grasslands, walls, rocks	NW Iberia	Atlantic	decrease
<i>Podarcis gadarramae</i>	small	rocks, crevices	W and central Iberia	Mediterranean	increase

676

677

678 **Table 2** Number of adult males tested (n), snout-to-vent length (SVL), preferred body
 679 temperature (individual mean of 10 time intervals, T_p), body mass (BM) and accumulated water
 680 loss (within 12 hours, EWL_t) for the five lizard species.

Species	n	SVL (mm)	T_p (°C)	BM (g)	EWL_t
		Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE
		Min – Max	Min – Max	Min – Max	Min – Max
<i>T. lepidus</i>	6	140.72 \pm 4.09	32.7 \pm 0.3	69.7208 \pm 5.2468	0.0097 \pm 0.0012
		131.66 – 158.17	31.3 – 33.4	55.8682 – 85.7488	0.0057 – 0.0130
<i>L. schreiberi</i>	8	95.99 \pm 4.43	33.4 \pm 0.4	23.5756 \pm 2.5086	0.0096 \pm 0.0012
		71.66 – 111.45	32.3 – 35.3	10.0750 – 31.9960	0.0072 – 0.0162
<i>P. algirus</i>	8	74.38 \pm 1.39	35.0 \pm 0.1	11.5727 \pm 0.9481	0.0038 \pm 0.0006
		68.00 – 80.00	34.5 – 35.7	7.3401 – 15.1519	0.0020 – 0.0063
<i>P. bocagei</i>	10	54.04 \pm 1.21	30.7 \pm 0.3	3.5832 \pm 0.1919	0.0299 \pm 0.0024
		49.64 – 60.54	29.4 – 32.5	3.0369 – 4.8491	0.0235 – 0.0499
<i>P. guadarramae</i>	9	53.73 \pm 0.93	31.5 \pm 0.2	3.0744 \pm 0.1391	0.0249 \pm 0.0028
		49.88 – 58.57	30.7 – 32.2	2.3594 – 3.7809	0.0120 – 0.0377

681
682

683 **Table 3:** AN(C)OVA-rm of preferred temperatures (T_p) and evaporative water loss rates
 684 (instantaneous, EWL_i and accumulated, EWL_a) between the five lizard species for 10 and 11
 685 consecutive hours, respectively; in the ANCOVA-rm we used snout-vent length (SVL) and body
 686 mass (BM) as covariables.

687

	T_p			EWL_i			EWL_a		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
ANOVA-rm									
species	4, 36	37.42	<10 ⁻⁶	4, 36	13.27	10 ⁻⁶	4, 36	30.00	<10 ⁻⁶
time	9, 324	5.42	10 ⁻⁶	10, 36	3.52	0.0002	10, 360	141.50	<10 ⁻⁶
time*species	36, 324	2.73	10 ⁻⁶	40, 360	1.67	0.23	40, 360	19.07	<10 ⁻⁶
ANCOVA-rm (SVL, BM)									
SVL	1, 34	0.17	0.68	1, 34	0.23	0.64	1, 34	0.50	0.49
BM	1, 34	0.69	0.41	1, 34	0.03	0.86	1, 34	0.23	0.64
species	4, 34	21.45	<10 ⁻⁶	4, 34	6.48	0.0005	4, 34	9.73	2*10 ⁻⁵
time	9, 306	1.83	0.06	10, 340	0.57	0.84	10, 340	0.79	0.64
time*SVL	9, 306	2.23	0.02	10, 340	0.57	0.83	10, 340	0.14	0.99
time*BM	9, 306	1.96	0.04	10, 340	0.36	0.96	10, 340	0.09	0.99
time*species	36, 306	1.53	0.03	40, 340	0.97	0.52	40, 340	6.97	<10 ⁻⁶

688