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 (Tp) 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 Tp and lower EWL. The two small wall lizards (P. bocagei and P. guadarramae) displayed low Tp 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.
Does ecophysiology mediate reptile responses to fire regimes? Evidence from Iberian lizards

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Abstract

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.
Keywords: reptiles; habitat; functional response; preferred temperatures, water-loss rates; wildfires
Introduction

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

The response of species to fire is largely driven by habitat structure (Santos et al., 2015) with some species selecting early or late post-fire stages following a continuum along vegetation succession (Letnic et al., 2004; Santos & Poquet, 2010; Valentine et al., 2012; Santos et al., 2016). The ‘habitat accommodation’ model of succession proposed by Fox (1982), applied to the fire ecology, represented a fine framework to understand and predict the response of animals to fire. However, field-based studies have failed to support this model (Driscoll and Henderson 2008; Lindenmayer et al., 2008) since the responses of species to fire vary in space and time.
(Driscoll et al., 2012; Nimmo et al., 2012; Smith et al., 2013) due to the complexity of biotic and abiotic interactions between vegetation dynamics, animal species, and climate (Nimmo et al., 2014). For this reason, to improve predictive models of fire responses in animal communities, detailed ecological (functional) information of species is needed (Smith et al., 2013).

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

As ectotherm and sedentary, terrestrial reptiles are directly and locally exposed to environmental variation in temperature and humidity which makes them ideal subjects for mechanistic ecological modelling (Kearney & Porter, 2009). Specifically, their intrinsic physiological features may potentially govern the response of different species to fire. Thus,
body temperature is considered the most important environmental variable affecting performance of ectotherms, including reptiles (Angilletta, 2010), their heat balance resulting from thermal characteristics of the environment (Porter et al., 1973; Porter & Tracy, 1983). Thermoregulatory reptiles respond to the heterogeneity of the thermal environment by selecting microhabitats with adequate temperatures and modifying their body postures to maximize heat gain or lost. However, during these processes reptiles also suffer evaporative water loss (EWL) mainly through the skin but also through respiratory passages and the eyes (Shoemaker & Nagy, 1977; Mautz, 1982a). Since evaporation increases with temperature, a trade-off between thermoregulation and water balance in ectotherms has been suggested (Mautz, 1982a). EWL could hence represent a constraint for the activity of ectotherms when water is not available. In this context, reptiles exposed to unburnt and burnt habitats are expected to face opposing environmental conditions. Under similar climate regimes, unburnt habitats provide more abundant and complex vegetation compared to that in open burnt habitats that in turn are more exposed to extreme temporal variation in environmental temperature and humidity (Ferreira 2015; data from NW Portugal available from the authors upon request). We hypothesize that reptile species prevailing in unburnt (forested) habitats will keep lower and less variable body temperatures and to experience less water loss rates as vegetation buffers daily variation of humidity and temperature (Ferreira, 2015). In contrast, reptiles inhabiting burnt (open) habitats will attain higher but temporally variable body temperatures and suffer higher evaporative water stress.

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

**Study area**

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

**Species sampling**

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

Lizards used in experiments were captured with a noose (García-Muñoz & Sillero, 2010) in three areas: *P. algirus* were captured in Serra da Estrela (40°51’ N, 7°53’ W), *T. lepidus* and *L. schreiberi* in Vairão (41°32’ N, 8°67’ W) and, finally, *P. bocagei* and *P. guadarramae* syntopic
in Moledo (41°84’ N, 8°87’ W). All the sites are located in Northern Portugal and selected according to the availability of lizards.

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

The Institute for the Conservation of Nature and Forest (ICNF, Portugal) gave the sampling permit (no. 459I2015/CAPT). Experiments followed the ethical guidelines of University of Porto.

**Preferred temperatures**

Preferred body temperature ($T_p$, body temperature achieved in the absence of thermoregulatory constraints, Huey & Bennet, 1987) provides a reliable representation of the overall thermal requirements of a given species while holds some logistic advantages. Namely, 1) it correlates directly with several physiological optima (Bauwens et al., 1995); 2) its temporal variation is relatively narrow in good thermoregulators lacertids (Huey 1982); 3) it displays phylogenetic signal (Bauwens et al., 1995) and remains conservative in conspecific populations under different climate regimes in many lacertid species (i.e. Díaz et al., 2006); and 4) it can be reliably recorded in the lab under standardised conditions (Osojnik et al., 2013). It is true that at the
individual level, $T_p$ may change as a function of time of the day, season, feeding activity, ontogeny or reproductive status (Castilla et al., 1999) but these biases can be removed by restricting comparisons to a single class (i.e. adult males) and time period (i.e spring) following a strict experimental protocol (Carretero et al., 2005).

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

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

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

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

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

Results

The five lizards species (Table 2) differed in SVL (ANOVA $F_{4,36} = 176.55; P < 10^{-6}$) and body mass (ANOVA $F_{4,36} = 151.26; P < 10^{-6}$). The post-hoc comparisons (Duncan tests $P < 0.05$) corroborated that the two Podarcis species were shorter and lighter, followed by P. algirus, then...
L. schreiberi and, finally, Timon lepidus, the longest and heaviest species. We also detected interspecific differences in robustness (ANCOVA on mass with SVL as covariable; $F_{4,35} = 21.69$; $P < 10^{-6}$), T. lepidus being the most robust, followed by P. bocagei, P. guadarramae and P. algirus, and finally by L. schreiberi, which was the most slender.

Preferred temperatures

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

Water-loss rates

Using ANOVA-rm, we also uncovered significant differences in instantaneous water loss (EWLi) between species and along time, with a weak interaction between both factors (Tables 2 and 3). Post-hoc Duncan tests ($p < 0.05$) grouped P. algirus and T. lepidus having low rates and both Podarcis sp. having high rates, while L. schreberi occupied an intermediate position. EWLi also varied along time in all species, with both Podarcis sp. displaying higher temporal...
fluctuations (Fig. 2). When we added SVL and BM as covariates (ANCOVA-rm), interspecific differences were smoother but still significant, while temporal differences disappeared (Table 3). Accumulated water loss (EWLa) revealed even more marked differences between the five species (Fig. 3). Here, two clear groups with no overlap could be distinguished; on one side the larger *T. lepidus* and *L. schreiberi* plus the medium-sized *P. algerus* all losing less water by evaporation and on the other side the small *P. guadarramae* and *P. bocagei* with much higher water loss rates (Duncan post-hoc tests p < 0.05). Again, after accounting for SVL and body mass, differences between species remain but differences time intervals did not while the interaction between both factors was also conserved (Table 3). Either in EWLi or in EWLa, we did not observe interactions between factors and covariables.

**Preferred temperatures vs. water loss rates**

Mean $T_p$ and EWL$_t$ were inversely correlated between species while SVL and BM had no 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$_t$ = -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 EWL$_t$ was positively correlated with SVL, negatively correlated with BM but independent from $T_p$ 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, $T$ = 3.17, $P$ = 0.03; $r_{\text{partial}}$ BM-EWL$_t$ = -0.83, $T$ = -2.98, $P$ = 0.04) and *P. algerus* ($n = 5$, $r_{\text{partial}} T_p$-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$_t$ = -0.86, $T$ = -3.38, $P$ = 0.03). We did not detect significant relations for the other three species.

**Discussion**
The environmental differences between burnt and unburnt landscapes highlight the role of vegetation buffering the natural fluctuations. Specifically, burnt microhabitats often used by lizards undergo larger daily variations of temperature and humidity, and also attain higher temperatures, especially in summer (Ferreira, 2015). When comparing lizards within the same trophic guild, this environmental contrast was expected to beneficiate Mediterranean lizards (compared to Atlantic lizards) from the thermal quality of open habitats created by fire regimes.

We only have indirect support for this from several independent sources of evidence: 1) in southern France, fire recurrence increased the Mediterraneity (sensu Prodon, 1993) of the reptile community (Santos & Cheylan, 2003); and 2) in multiple localities, reptile species tend to be more common in burnt sites compared to unburnt ones (Santos & Poquet, 2010; Santos et al., 2016). Although we hypothesised that this opposing responses would be caused by divergent ecophysiological features, our results only partially met our expectations, namely, that species favoured by fire should be more thermophile and economic in water loss. Certainly, the Mediterranean medium-sized *P. algirus* clearly selected for higher temperatures than the remaining species and loss less water than expected for its body size. However, the differences among the other species seem better explained by alternative factors such as refuge use, life history and body size/shape rather than by their responses to fire.

Thermal and hydric ecophysiology showed signs of a size/shape-independent trade-off across species but this should be confirmed by a formal analysis under the comparative method framework with an extended species dataset (Bauwens et al., 1995; Carneiro et al., 2016). Within species, what we found was the influence of the surface/volume relationship (Schmidt-Nielsen, 1984) making slender and smaller lizards to show less water relative to the body mass. Thus, in ecophysiological terms, species were not arranged in a Mediterranean-Atlantic axis. While the
demographic responses to fire of these five lizards are mostly related to their biogeographic affinities and global distribution ranges (Sillero et al., 2009; Santos & Poquet, 2010; Santos & Cheylan, 2013; authors unpublished data), the lack of complete concordance with their physiological features suggest a more complex scenario. This supports previous claiming that the functional approach to predict responses of reptiles to fire is conceptually accurate but predictively weak (Smith et al. 2012, 2013).

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

Both species of large lizards undoubtedly take advantage from lower water loss rates due to their lower surface/volume relationship (Schmidt-Nielsen 1984). However, despite their opposite biogeographic affinities, they only differ slightly in hydric physiology which makes it difficult to
interpret their responses to fire (Santos & Cheylan, 2013; authors’ unpublished data). Instead, the
variable responses of *T. lepidus* according to the population studied, and the decrease of *L.
*schreiberi* in response to fire intensification should be better interpreted in terms of habitat use.
*T. lepidus* is more mobile and tends to occupy areas dominated by rocky substrates using big
rock holes as refuge (Castilla & Bauwens, 1992). In some localities, it occupies long-unburnt
and structured habitats (Santos et al., 2016) whereas in others only appears in repeated-burnt
ones (Santos & Cheylan, 2013). This may be due to shifts in other ecological resources (i.e.
habitat, prey) but also to different fire ages (Nimmo et al., 2014). In contrast, *L. schreberi* has
small home ranges and use ecotonal bushy vegetation to thermoregulate, forage and hide
(Salvador, 1988) being its distribution mostly outside of the range of fire. We here suggest that
the divergent responses of both species to fire are likely habitat-mediated while shared thermal
(and partly hydric) ecophysiology would result from evolutionary convergence in two long-term
separated lacertid lineages (Arnold et al., 2007). Interestingly, competitive exclusion between
green (*Lacerta* sp.) and ocellated lizards (*Timon* sp.) at a geographic level is suggested to have
shaped the historical biogeography of both groups (Ahmadzadeh et al., 2016).

Particular habitat requirements may explain why the two species of wall lizards *Podarcis*
sp. show opposing responses to fire but similar physiological features. The geographic ranges of
*P. bocagei* and *P. gaudarramae* widely overlap geographically and both species are frequently
found in syntopy (Carretero, 2008). However, field-work experience demonstrated that *P.
gaudarramae* is the only species found in repeatedly burnt spots (authors’ unpublished data).
This lizard is more attached to bare rocky substrates than *P. bocagei*, which uses a wider variety
of substrates (Kaliontzopoulou et al., 2010), trend that is accentuated in syntopy (Gomes et al.,
2016). Since mean preferred temperatures and water loss rates did not differ, we interpret the
dominance of *P. guadarramae* after fire intensification as another result of different habitat and refuge use. In fact, head fattening of *P. guadarramae* might confer an advantage when rock crevices are used as main refuge (Kaliontozopulou et al., 2012) as expected in burnt areas. Nevertheless, the accentuated diel variation in preferred temperatures by *P. bocagei* also suggest sensitiveness to midday conditions either thermal or hydric, which might provide some support for an ecophysiological constrain when compared to *P. guadarramae*. This aspect should be explored in the future with continuous monitoring of individual lizards (Bowker et al., 2010; Bowker et al., 2013).

Fire is a fundamental driver of ecosystem functioning and composition in the Mediterranean basin (Blondel et al., 2010). Species that mostly distributed on this bioregion occupies fire-prone landscapes with biota likely resulting from a long evolutionary association with fire (Pausas & Keeley, 2009). The effects of fire are observable at multiple scales from the landscape (variation in land cover) to the microhabitat (variation in temperature and humidity ranges). As ectotherms, reptiles have their biological and ecological processes dependent on environmental temperature. However, heliothermic lizards are able to thermoregulate accurately if habitat complexity provides sufficient thermal heterogeneity for shuttling and selecting appropriate temperatures (Sears & Angilletta, 2015). Despite the sensitivity of reptiles to modifications in habitat structure (caused by fire), factors such as life history, microhabitat preferences and or thermoregulatory behaviour may have deviated results from a pure ecophysiological model. Further studies should be addressed to understand interactions between fire and other processes in order to more accurately predict reptile responses to fire-regimes using an extended species dataset. Meanwhile current evidence advances that ecophysiology plays a functional role on reptile responses to fire, which is likely habitat-mediated.
(Lindenmayer et al., 2008; Santos & Cheylan, 2013; Nimmo et al., 2014).

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

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

Displayed are median values and 0.95 confidence intervals.
Figure 2. Patterns of instantaneous water loss (EWL$_i$) along a 12-hour experiment for five lizard species. Displayed are median values and 0.95 confidence intervals.
Figure 3. Accumulated water loss (EWL$_a$) along a 12-hour experiment for five lizard species.

Displayed are median values and 0.95 confidence intervals.
Table 1 General traits of the five lizard species studied. Habitat, distribution and biogeographic affinities after Carretero et al. (2015), Galán (2015), Kaliontzopoulou et al. (2011) and Loureiro et al. (2008). Fire responses after Santos and Cheylan, 2013; Santos and Poquet 2010; and authors’ unpublished results.

| Species                  | body size | main habitat                  | distribution          | biogeography | fire response |
|--------------------------|-----------|--------------------------------|-----------------------|--------------|---------------|
| Timon lepidus            | very large| open oak forest, big rocks     | Iberia, SW France     | Mediterranean| increase      |
| Lacerta schreiberi       | large     | ecotones and riverine forests  | W Iberia              | Atlantic     | decrease      |
| Psammodromus algirus     | medium    | shrubs                         | Iberia, SW France, N  | Mediterranean| increase      |
| Podarcis bocagei         | small     | dunes, grasslands, walls, rocks| NW Iberia             | Atlantic     | decrease      |
| Podarcis guadarramae     | small     | rocks, crevices                | W and central Iberia  | Mediterranean| increase      |
Table 2 Number of adult males tested \((n)\), snout-to-vent length (SVL), preferred body temperature (individual mean of 10 time intervals, \(T_p\)), body mass (BM) and accumulated water loss (within 12 hours, EWL\(_t\)) for the five lizard species.

| Species       | \(n\) | SVL (mm) Mean ± SE | SVL (mm) Min – Max | \(T_p\) (ºC) Mean ± SE | \(T_p\) (ºC) Min – Max | BM (g) Mean ± SE | BM (g) Min – Max | EWL\(_t\) (g) Mean ± SE | EWL\(_t\) (g) Min – Max |
|---------------|-------|-------------------|--------------------|------------------------|------------------------|------------------|-------------------|------------------------|------------------------|
| T. lepidus    | 6     | 140.72 ± 4.09     | 131.66 – 158.17    | 32.7 ± 0.3             | 31.3 – 33.4            | 69.7208 ± 5.2468 | 55.8682 – 85.7488 | 0.0097 ± 0.0012 | 0.0057 – 0.0130       |
| L. schreiberi | 8     | 95.99 ± 4.43      | 71.66 – 111.45     | 33.4 ± 0.4             | 32.3 – 35.3            | 23.5756 ± 2.5086 | 10.0750 – 31.9960 | 0.0096 ± 0.0012 | 0.0072 – 0.0162       |
| P. algirus    | 8     | 74.38 ± 1.39      | 68.00 – 80.00      | 35.0 ± 0.1             | 34.5 – 35.7            | 11.5727 ± 0.9481 | 7.3401 – 15.1519 | 0.0038 ± 0.0006 | 0.0020 – 0.0063       |
| P. bocagei    | 10    | 54.04 ± 1.21      | 49.64 – 60.54      | 30.7 ± 0.3             | 29.4 – 32.5            | 3.5832 ± 0.1919  | 3.0369 – 4.8491  | 0.0299 ± 0.0024 | 0.0235 – 0.0499       |
| P. guadarramae| 9     | 53.73 ± 0.93      | 49.88 – 58.57      | 31.5 ± 0.2             | 30.7 – 32.2            | 3.0744 ± 0.1391 | 2.3594 – 3.7809 | 0.0249 ± 0.0028 | 0.0120 – 0.0377       |
Table 3: AN(C)OVA-rm of preferred temperatures ($T_p$) and evaporative water loss rates (instantaneous, $EWL_i$ and accumulated, $EWL_a$) between the five lizard species for 10 and 11 consecutive hours, respectively; in the ANCOVA-rm we used snout-vent length (SVL) and body mass (BM) as covariables.

|                          | $T_p$ |   | $EWL_i$ |   | $EWL_a$ |   |
|--------------------------|-------|---|---------|---|---------|---|
|                          | d.f.  | $F$ | $P$     | d.f. | $F$     | $P$ |
| ANOVA-rm                 |       |    |         |    |         |    |
| species                  | 4, 36 | 37.42 | $<10^{-6}$ | 4, 36 | 13.27 | $10^{-6}$ |
| time                     | 9, 324 | 5.42 | $10^{-6}$ | 10, 36 | 3.52 | 0.0002 |
| time*species             | 36, 324 | 2.73 | $10^{-6}$ | 40, 360 | 1.67 | 0.23 |
| ANCOVA-rm (SVL, BM)      |       |    |         |    |         |    |
| SVL                      | 1, 34 | 0.17 | 0.68 | 1, 34 | 0.23 | 0.64 |
| BM                       | 1, 34 | 0.69 | 0.41 | 1, 34 | 0.03 | 0.86 |
| species                  | 4, 34 | 21.45 | $<10^{-6}$ | 4, 34 | 6.48 | 0.0005 |
| time                     | 9, 306 | 1.83 | 0.06 | 10, 340 | 0.57 | 0.84 |
| time*SVL                 | 9, 306 | 2.23 | 0.02 | 10, 340 | 0.57 | 0.83 |
| time*BM                  | 9, 306 | 1.96 | 0.04 | 10, 340 | 0.36 | 0.96 |
| time*species             | 36, 306 | 1.53 | 0.03 | 40, 340 | 0.97 | 0.52 |