

1 Thermal ecology or interspecific competition: what drives the warm and cold
2 distribution limits of mountain ectotherms?

3 Distribution limits in mountain ectotherms

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12

13 Abstract

14 Current climate change-forced local extinctions of ectotherms in their warmer
15 distribution limits have been linked to a reduction in their activity budgets by excess of
16 heat. However, warmer distribution limits of species may be determined by biotic
17 interactions as well. We aimed to understand the role of thermal activity budgets as
18 drivers of the warmer distribution limit of cold-adapted mountain ectotherms, and the
19 colder distribution limit of partially sympatric thermophilous species.

20 In the southern slopes of the Sierra de Guadarrama, Madrid, Spain, (1800–2200
21 m asl) we collected data from surveys of active individuals, thermal preferences,
22 thermoregulation effectiveness, and activity budgets across 12 different sites exposed to
23 different microclimates and habitats. We assessed how abundances of each species were
24 predicted by activity budgets, restriction time, temperature deviation, habitat covers and
25 date.

26 We found that *Iberolacerta cyreni* abundances are not predicted by heat-
27 restricted activity time as they were absent or rare in the areas where its activity budgets
28 are broader. Conversely, the abundances of the other lizards were positively predicted
29 by the potential activity time. Habitat preferences and date explained also part of the
30 occurrences of the four species.

31 Our results suggest that realized niches of lizards in the Sierra de Guadarrama
32 are a consequence of niche partitioning by temperature-mediated competitive exclusion.
33 The more thermophilous species were physiologically limited by the reduced chances of
34 being active due to the cold, while the cold-adapted species was abundant in those areas

1 where its potential activity is limited by cold-temperatures, but the thermophilous
2 species cannot inhabit. We provide new insights on the ecological processes affecting
3 the distribution of ectotherm mountain organisms, the assemblage of their communities
4 and how climate change could affect them.

5 Keywords: competitive exclusion, fundamental niche, *Iberolacerta*, *Podarcis*,
6 range margin, realized niche, thermoregulation, thermal ecophysiology

9 Introduction

10 The rise in greenhouse gas emissions from human activities in the last centuries
11 has increased atmospheric temperatures across the planet (Stoker et al., 2013). There is
12 mounting evidence that organisms are being affected by these changing temperatures, in
13 many cases resulting in population extinctions, range shifts, and phenological changes
14 (Pecl et al., 2017). Physiological adaptation — the evolution of temperature
15 tolerances— represents another way species may respond to increased temperatures;
16 however, warm temperature tolerances are strongly conserved across organisms (Araujo
17 et al., 2013).

18 The distribution limits, or range margins, of organisms can be delineated by
19 physiological constraints that mean the species cannot tolerate conditions beyond that
20 limit (i.e., the fundamental niche), or by biotic interactions such as competition (i.e., the
21 realized niche; Tingley, Vallinoto, Sequeira, & Kearney, 2014). It has been
22 hypothesized that cold distribution limits (those generally facing poleward or uphill) are
23 generally driven by intolerance to abiotic conditions, while warm distribution limits are
24 usually delineated by species interactions (Alexander, Diez & Levine 2015; Brown,
25 Stevens, & Kaufman, 1996; MacArthur, 1972). This would mean that under global
26 warming, cold-adapted species at their warm distribution limit would have to cope as
27 well with increased competition with other thermophilous species for which the climate
28 may become more suitable. However, a considerable number of studies have found
29 correlations of abiotic constraints with warm distribution limits (reviewed in Cahill et
30 al., 2014), although biotic factors could also play a significant role.

31 The idea of species interactions limiting species in their warm distribution limits
32 has been particularly applied to mountain biological communities, hypothesizing that
33 montane taxa are confined to high elevations due to competitive exclusion with lowland
34 species (Jankowski et al., 2010; McArthur, 1972). Mountain ranges host very different

1 climatic conditions in a reduced space (Dobrowski, Abatzoglou, Greenberg, &
2 Schladow, 2009). The main climatic variation associated with mountains is the decrease
3 of temperature with elevation (Dobrowski et al., 2009). There is evidence that
4 organisms in mountains are shifting their distribution upwards, tracking their historical
5 climatic niche (Pecl et al., 2017; Wilson, Gutiérrez, Gutiérrez, & Montserrat, 2007).
6 However, local modifications of energy flows (solar radiation, movement of air masses)
7 by complex topographies affect temperature, decoupling it from elevation (Dobrowski
8 et al., 2009). This climatic heterogeneity promotes the existence of different biological
9 communities in close proximity (Jiménez-Robles & De la Riva, 2019; Opedal,
10 Ambruster, & Graae, 2014), and is responsible for climatic refugia where some species
11 can survive during periods of unfavourable regional climate (Scherrer & Körner, 2011;
12 Morelli et al., 2016).

13 Mountains in Europe are known to have particularly high levels of endemism
14 due to their isolation along latitude (Schmitt, 2009). As a consequence of the
15 northwards and upwards movements of organisms tracking the climates after
16 glaciations, southern European mountains host many evolutionary unique lineages, and
17 relict populations of species that currently live further to the north (Hewitt, 1999). The
18 susceptibility of these montane communities to Pleistocene glacial cycles suggests
19 they are highly affected by climate change (e.g.: more than 60 % of European montane
20 flora could be extinct by 2080; Thuiller et al., 2005).

21 Ectotherms are specially affected by climate change because of their dependence
22 on environmental temperatures to be active and invest energy and resources into
23 reproduction (Adolph & Porter, 1993). This dependence is already causing worldwide
24 declines of ectotherms such as lizards, due to excess heat during the breeding season
25 restricting activity periods (Sinervo et al., 2010). Cold-adapted mountain lizards are
26 considered to have a high risk of decline, because their forced range contraction towards
27 mountaintops and the competition they may have with other lizards that may shift their
28 ranges uphill (Sinervo et al., 2010, García-Porta et al., 2019).

29 In southern Europe, the genus *Iberolacerta* is composed by several saxicolous
30 lizards, mostly endemic to mountains (Carranza, Arnold, & Amat, 2004). The restricted
31 distribution of *Iberolacerta* species has been related to their cold-adapted thermal
32 physiology (Aguado & Braña, 2014; Monasterio, Salvador, Iraeta, & Díaz, 2009;
33 Monasterio, Shoo, Salvador, Silíceo, & Díaz, 2011; Monasterio, Verdú-Ricoy,
34 Salvador, Díaz, 2016; Ortega, Mencía, & Pérez-Mellado, 2016a; Osojnik, Žagar,

1 Carretero, García-Muñoz, & Vrezec, 2013; Žagar, Carretero, Marguč, Simčič, &
2 Vrezec, 2018). However, another hypothesis for the restriction of *Iberolacerta* to
3 mountains is competitive exclusion with another more recent evolutionary lineage of
4 lizards, the genus *Podarcis* (Carranza et al., 2004). Several studies assessed how species
5 of both genera interact, most of them suggesting that competition with *Podarcis* might
6 affect the existence of *Iberolacerta* (Ortega, Mencía, & Pérez-Mellado, 2016b; Žagar,
7 Carretero, Osojnik, Sillero, & Vrezec, 2015; Žagar, Carretero, Vrezec, Drašler, &
8 Kaliontzopoulou, 2017; Žagar, Simčič, Carretero, & Vrezec, 2015; but see Monasterio,
9 Salvador, & Díaz, 2010a). Despite of this research, there is hardly any information on
10 past distributions of *Iberolacerta* species (except in northwest Iberia; Galán, Vila,
11 Remón, & Naveira, 2007), whether climate change is contracting its range, and how
12 temperatures moderate its interactions with other more thermophilous lizards.

13 We here use a species of *Iberolacerta* and sympatric Lacertidae species to test
14 whether climate or biotic interactions are the primary driver of cold and warm
15 distribution limits. We present a study case of the lizard communities that inhabit the
16 highlands of the Sierra de Guadarrama, in Central Spain. This area is a stronghold for
17 *Iberolacerta cyreni*, one of the southernmost species of its genus, endemic of the
18 Sistema Central mountain ranges (Carranza et al., 2004). Other Lacertidae occur in the
19 area, especially at lower elevations (Amo, López & Martín, 2008; Martín-Vallejo,
20 García-Fernández, Pérez-Mellado, & Vicente-Villardón, 1995; Ortega-Rubio, 1989).
21 Several organisms in the Sierra de Guadarrama are shifting their distribution upwards,
22 such as the case of butterflies (Nieto-Sánchez, Gutiérrez, & Wilson, 2015; Wilson et al.,
23 2007) or plants (García-Romero, Muñoz, Andrés, & Palacios, 2010). By combining
24 information on the abundances and activity patterns of each species across different
25 microclimates with species-specific aspects of the thermal physiology, we provide new
26 insights on the ecological processes affecting the distribution of ectotherm mountain
27 organisms, the assemblage of their communities, and how climate change could affect
28 them.

29

30 Methods

31 Study area

32 The Sierra de Guadarrama belongs to the Sistema Central mountains, which
33 latitudinally splits the central Iberian plateau in half. The Sierra de Guadarrama extends
34 over 80 km in a SE-NW direction, and reaches a maximum elevation of 2428 m asl at

1 Peñalara peak. With a continental climate of marked seasonality, the summits are
2 covered in snow during the cold winters, contrasting with the warm summers with
3 hardly any rain. Mean temperatures of the coldest and warmest months are -1.8 °C
4 (February) and 18.5 °C (July), respectively (Puerto de Navacerrada Meteorological
5 Station, 1860 m asl, 2011–2015, AEMET, tutiempo.net) (Appendix S1). Mean annual
6 precipitation is 1229 mm (Durán et al., 2013). The vegetation is approximately stratified
7 according to approximate elevational belts, which at 1200 m are composed by *Quercus*
8 *pyrenaica* forests that are replaced by *Pinus sylvestris* with increasing elevation. Above
9 the treeline (1900–2000 m), the most characteristic plants are perennial shrubs (mostly
10 *Cytisus oromediterraneus* and *Juniperus communis*), which alternate with patches of
11 alpine meadows (with *Festuca* and other grass genera) and rocky formations (rock
12 outcrops, boulders and screes; mostly granite) where vegetation becomes sparser
13 (Rivas-Martínez, Fernández-González, & Sánchez-Mata, 1987).

14

15 Field data collection

16 We selected 12 200-m transects above 1800 m asl on the southern slopes near
17 three different summits in the Sierra de Guadarrama: Alto de Guarramillas (also known
18 as Bola del Mundo), Peñalara and La Najarra (Figure 1). Apart from the high-elevation
19 specialist *Iberolacerta cyreni*, three other lizard species with lower distribution could be
20 found in the studied elevation range: *Podarcis muralis*, *P. guadarramae* and *Lacerta*
21 *schreiberi*. The former is a common species in Europe that reaches its southwestern
22 distribution limit in the Sierra de Guadarrama (Martín-Vallejo et al., 1995), while the
23 other two species are endemic from the centre and northwest of the Iberian Peninsula,
24 probably because of the Atlantic climate influence, with the southern distribution of *L.*
25 *schreiberi* confined to isolated mountain and humid riparian habitats (De la Riva, 1987;
26 Geniez, Sa-Sousa, Guillaume, Cluchier, & Crochet, 2014; Marco & Pollo, 1993).

27 In each area, four transects were distributed within two different elevation levels
28 in order to cover sites with abundant *I. cyreni* (2000–2150 m asl, cores of its
29 distribution) and sites where it is present at low abundances or even absent (1800–1900
30 m asl, *I. cyreni* lower distribution limits). Taking into account the habitat preferences of
31 *I. cyreni* (Monasterio, Salvador & Díaz 2010b), we chose the areas with more rock
32 cover within the habitat heterogeneity of every elevation level (including from open
33 pine forest and shrubs to pure rock outcrops and screes).

34 Each transect was visited at least seven times between the end of May and the

1 beginning of August of 2013 and 2014. In each visit, a previously trained observer
2 (OJR) walked along the transect recording all observed active lizards within 10 m at
3 both sides. Once a lizard was detected, its species identity and sex were determined
4 from distance using binoculars, and were later confirmed by direct approach. Whenever
5 possible, lizards were caught by noose to record their snout-vent length (SVL) and body
6 temperature (T_b ; within 10 seconds of capture). Walking speed was relatively constant
7 so that survey time across the transect was approximately 40 minutes (excluding stops
8 for catching and handling lizards).

9 We recorded operative temperatures (T_e) with two dataloggers (Onset HOBO
10 U23-003) placed near 50 and 150 m along each transect. Each datalogger was attached
11 to two thermal models that were set on rock substrate in two standard basking
12 conditions: full sun and half shade, in order to record the most extreme T_e conditions for
13 active lizards in each site every 6 minutes. Models were designed to mimic thermal
14 properties of basking lizards with polyvinylchloride tubing (8.8 cm length x 1.6 cm
15 diameter x 0.2 cm thickness), sealed with cork in one side, and with the wire of the
16 sensor penetrating the other side sealed with silicon. The whole models were painted
17 with matte grey primer spray paint. Models similar in materials and dimensions have
18 been used in other studies (e.g. Jiménez-Robles & De la Riva, 2019; Sinervo et al.,
19 2010). We verified that there were no significant differences in heat exchange between
20 the models and live lizards (Appendix S2).

21 Habitat structure was measured every 20 m along the transects, following the
22 same protocol as Monasterio, Salvador & Díaz (2010b). At each point we determined
23 the habitat features (such as stone, bare ground, shrubs, etc.) that coincided with every
24 meter radiating up to 5 m in the four cardinal directions. This allowed the calculation of
25 the cover value for each microhabitat.

26

27 Thermal preferences

28 To measure the preferred temperatures of lizards in the laboratory, we caught
29 individuals from areas more than 100 m from our transects. The laboratory was installed
30 in El Ventorrillo Biological Station at 1470 m asl, where we measured thermal
31 preferences (usually the following day or maximum two days after capture) and kept the
32 lizards until we could release them (approx. one week after capture, with water *ad*
33 *libitum* and one cricket every three days). Lizards were placed in running tracks with a
34 100-W heating lamp and aluminium foil at one end to create a thermal gradient from

1 approximately 25 °C to more than 50 °C. Body temperature of lizards was continuously
2 recorded for 2 hours at 1 minute intervals, by means of ultrathin thermocouples (0.076
3 mm of diameter; 40 AWG gauge; Omega 5SC-TT-T-40-36; with tip coated in nail-
4 polish) inserted 1 cm in the cloaca, and fastened to the cloacal lips and tail base with
5 plastic paraffin film. Lizards were visually inspected every 15 minutes, taking care to
6 avoid behavioural disturbances, in order to check that thermocouples were inside the
7 cloaca and allowed free movement of the lizards along the gradient. By visualizing the
8 recorded time series, we discarded the initial minutes in which T_b of lizards reached the
9 first maximum peak (Aguado & Braña, 2014), and obtained the values corresponding to
10 their median (preferred temperature, T_{pref}), maximum (voluntary maximum T_{Vmax}), and
11 the interquantile range bounds (set point range temperatures, T_{set} : upper and lower
12 selected temperatures, T_{upSel} and T_{lowSel})

13

14 Thermoregulation effectiveness

15 Using the values of field T_b , we calculated the individual thermoregulation
16 accuracy (d_b ; absolute deviance between T_b and T_{set}) (Hertz, Huey, & Stevenson,
17 1993). Using the local T_e recorded at the same time that every active individual, was
18 observed, we calculated the thermal quality of the environment (d_e ; absolute deviance
19 between T_e and T_{set}) (Hertz et al., 1993). Effectiveness of thermoregulation (E), was
20 calculated from the averages of d_b and d_e with the equation $E = 1 - (d_b/d_e)$ (Hertz et al.,
21 1993). When thermoregulation is the most effective, E values equal to 1, while
22 thermoconformer behaviour results in E values close to 0. The index d_e-d_b was assessed
23 as an additional measure of how much an animal departs from thermoconformity
24 (Blouin-Demers & Weatherhead, 2001).

25

26 Activity budgets

27 We defined the upper and lower thermal thresholds for activity of each species
28 as the T_{Vmax} and the 10th percentile of field T_b (emergence temperature T_{emerge}),
29 respectively. With these species-specific activity thresholds we generated three indexes
30 of the thermal quality of each sampling site from the T_e time series: a) the average
31 deviance of operative temperatures d_e (Hertz et al., 1993) for each survey; b) the daily
32 potential time for activity (summing all the time in which any of the T_e were within the
33 mean T_{Vmax} and the T_{emerge}); and c) the daily time of heat-restricted activity (cumulative
34 sum of the time in which all T_e exceeded the T_{Vmax}).

1 In each site we recorded additional operative temperatures for one day (from
2 8:00 to 20:00 approximately) from other 24 physical models placed at different
3 substrates and sun exposures, to check that the activity and restriction times that we
4 were measuring with only four T_e time series at each site were not biased by small
5 sample size (Appendix S3).

6 7 Statistical Analyses

8 Interspecific differences in thermal preferences (T_{pref} , T_{Vmax} , T_{upSel} , T_{lowSel}) and
9 thermoregulation (T_b , T_e , d_b , d_e) were assessed by means of linear models (such as
10 analysis of variance, ANOVA). The effect of source locality, sexual condition (i.e.,
11 males, non-pregnant females and pregnant females) and time of the day on thermal
12 preferences was also tested within each species. Post-hoc Tukey HSD tests were
13 performed after detecting statistically significant differences with ANOVAs. Inter-
14 species differences in thermoregulation effectiveness were assessed by comparing 1000
15 bootstrap resamplings of the indexes E and d_e-d_b for each species, generated by the *boot*
16 package (Canty & Ripley, 2008). When one species had the highest value in 95% or
17 more of the paired comparisons between its own estimates and those of another species,
18 we considered that index significantly larger (Hertz et al., 1993). Differences among
19 species in potential and heat-restricted activity times and how much of their variability
20 was explained by elevation and zones were assessed by means of linear models.

21 We selected habitat variables by exploring co-linearity through redundancy
22 analysis (RDA) using the maximum observed counts of every species of lizard in every
23 transect, including temperature variables (mean daily maximum temperature, mean
24 daily minimum temperature, and average diurnal mean temperature per transect). We
25 chose the habitat covers with strongest scores in the RDA eigenvectors. We ran Zero
26 Inflated Generalized Mixed Effects Models (ZIGLMM) for the active individuals
27 detected in the surveys, because lizards' counts included many kinds of zeros (e.g.: not
28 present, present but not active, active but not detected). ZIGLMMs were run in the R
29 package *glmmADMB* (Skaug et al., 2016), including the following fixed effects: the
30 average deviance of operative temperatures recorded during each visit, the average daily
31 activity budget and heat-restricted time in each transect, the date along the sampling
32 campaigns, and the selected habitat variables explained above (assuming they are
33 constant along the study). We verified that none of the selected habitat variables had a
34 variation inflation factor higher than 2 (Zuur, Ieno, & Elphick, 2010). Predictor values

1 were standardized, in order to get comparable standard coefficients in the ZIGLMMs
2 (Schieltzeth, 2010). Sampling sites (12 transects) nested within area (Guarramillas,
3 Peñalara or Najarra), together with the crossed factor of year (2013 or 2014), were
4 included as random effects. The logarithm of the duration of each survey was included
5 in all the models as an offset, to control the effect that survey length could have on the
6 total observed individuals for each visit.

7 Different candidate nested ZIGLMM models for individual counts of every
8 species were compared based in their AICc by means of multimodel inference
9 performed in the package *MuMIn* (Barton, 2016). All the models whose AICc was
10 below the AICc of the null models (including only random effect and offset) were
11 selected to evaluate all significantly plausible effects. Standardized coefficients β for the
12 selected models for every species were averaged accounting for their relative AICc-
13 based weights (Burnham & Anderson, 2002). Residual plots did not show deviations
14 from homocedasticity or normality.

16 Results

17 We carried out a total of 98 surveys in the sampling sites. During those visits we
18 registered 477 lizard activity events (292 *I. cyreni*, 124 *P. muralis*, 48 *P. guadarramae*,
19 and 13 *L. schreiberi*). *Iberolacerta cyreni* was the dominant species in all the high
20 elevation transects, while it appeared in smaller densities in some of the low elevation
21 transects of the three areas (Appendix S4). *Podarcis muralis* appeared in the lower sites
22 of Alto de las Guarramillas, in the lower and one of the higher sites of Peñalara, and in
23 one of the lower sites of La Najarra. *Podarcis guadarramae* appeared only in one of the
24 lower sites of Alto de las Guarramillas and all the sites of La Najarra. Finally, *Lacerta*
25 *schreiberi* was found at low densities in the lower sites of Alto de las Guarramillas, at a
26 lower and a high site in Peñalara and at a low site in La Najarra.

28 Thermal preferences and thermal thresholds of activity

29 The emergence temperature (T_{emerge}), median of preferred temperatures (T_{pref}),
30 voluntary maximum ($V_{T_{\text{max}}}$), and the upper and lower bounds of the set-point range
31 (T_{upSel} , T_{lowSel}) of the four species estimated in our laboratory are shown in Table 1.
32 ANOVA and post-hoc Tukey's test revealed significant differences among species, with
33 generally warmer thermal preferences for *P. guadarramae* (Table 1). There were
34 significant differences due to sexual condition within *I. cyreni* (Appendix S5); however

1 we assumed they did not have implications concerning our biogeographic hypotheses,
2 and therefore data were pooled at species level in subsequent analyses. Locality did not
3 have significant effects on the thermal preference parameters (Appendix S5.1). Median
4 T_{pref} and T_{upSel} increased along the day in *I. cyreni*, but not the T_{Vmax} (Appendix S5.2).

6 Activity patterns and thermoregulatory behaviour

7 In both *I. cyreni* and *P. muralis*, activity increased along the morning, peaking at
8 noon, and declining in the first hours of the afternoon, with a secondary peak at mid-
9 afternoon. An activity pattern was not detectable for *P. gadarramae* or *L. schreiberi*,
10 due to the lower number of occurrences of both species during the surveys.

11 Additionally, T_b of active individuals of all species was within or close to the T_{set} most
12 of the day, especially between 9:00 and 20:00 (Figure 2). Some animals achieved a
13 temperature near their T_{set} even at times when operative temperatures are usually lower.

14 Values and statistical significances for thermoregulation parameters are shown
15 in Table 1. *Iberolacerta cyreni* showed lower field body temperatures than *P. muralis*
16 and *P. gadarramae*, and operative temperatures simultaneous to observed active *I.*
17 *cyreni* were also lower than those for *P. gadarramae* and *L. schreiberi* (Figure 3).
18 Deviances of operative temperatures (d_e) of *I. cyreni* were lower than those of *P.*
19 *muralis* and *P. hispanica* (Figure 3). There were no differences in thermoregulation
20 accuracy (d_b) (Table 1; Figure 3). Bootstrap resampling revealed that *I. cyreni* had
21 significantly lower values than *P. muralis*, *P. gadarramae* and *L. schreiberi* for Hertz
22 et al.'s (1993) thermoregulation effectiveness index E (99.5%, 99.1% and 98.2% of
23 simulations, respectively) and for the Blouin-Demers & Weatherhead's (2001) index
24 (100%, 100% and 79.3% of simulations, respectively). The thermoregulatory efficiency
25 of *P. muralis* was higher than that one of *P. gadarramae* and *L. schreiberi*. (98.1% and
26 76.4 % of simulations with E, and 69.4% and 86.9% with d_e-d_b , respectively). With the
27 latter index, 94% of comparisons between *P. gadarramae* and *L. schreiberi* resulted in
28 higher values for *P. gadarramae* (56.8% with E).

30 Activity budgets

31 The daily potential activity times ranged from 0 to 12.1 hours, while restriction
32 times were 0–4 h. (although averages were 5.6–7.6 and 0–0.3, respectively). Controlling
33 per site and date, daily potential activity times were significantly different for each
34 species being *I. cyreni* the one with wider activity budgets, followed by *L. schreiberi* (R^2

1 = 0.91, $F_{83,3276} = 385.6$, $P < 0.001$; Appendix S6). The same predictors explained
2 significantly less variation of the restriction time ($R^2 = 0.27$, $F_{83,3276} = 14.45$, $P < 0.001$).
3 Elevation explained 0.87–0.89 of variation in the average activity budgets of all species
4 ($F_{1,10} = 66.4$ – 81.1 , $P < 0.001$ in all cases) but it was not significant for the restriction
5 time ($F_{1,10} = 0.6$ – 1.1 , $P = 0.3$ – 0.4 in all cases).

6

7 Habitat relationships

8 The exploratory RDA with habitat covers yielded four eigenvectors that
9 accounted for 77.8% of the variance (Appendix S7). Two of the most influential habitat
10 elements were stones and shrubs, which have previously been identified as important
11 for *I. cyreni* (Monasterio et al., 2010b). We discarded other habitat variables such as
12 percent cover of bare ground, grasses or leaf litter, because there was no clear
13 association with the occurrence of *I. cyreni* or any other lizard, or because they were
14 highly correlated with some of the selected variables, increasing VIFs above 2 (Zuur et
15 al., 2010).

16

17 Inference on the realized niches

18 In the ZIGLMMs we used negative binomial distribution, excepting for *L.*
19 *schreiberi*, in which we used a Poisson distribution due to its lower overdispersion
20 (variance similar to mean) as a consequence of the low densities of this species in our
21 transects. The number of plausible models (those with AICc below the one of the
22 respective null model) varied between species: 50 for *I. cyreni*, 30 for *P. muralis*, 20 for
23 *P. gadarramae* and 3 models for *L. schreiberi*. Their weighted averaged standardized
24 coefficients β and the sum of the AICc-based weights of the models containing each
25 variable ΣW_i are represented in Figure 4. Details on all the plausible nested candidate
26 models for each species are given in the Supplementary material (Appendix S8). There
27 was a significant negative effect of potential activity time on *I. cyreni* abundances, with
28 a negative effect of the deviance of operative temperatures during surveys. In *P.*
29 *muralis*, potential activity time affected positively, while restriction time and date had a
30 negative effect on their occurrences. In *P. gadarramae* the most important variable
31 was the potential activity time, with a positive significant effect, while the a priori
32 selected habitat features did not seem to have a significant effect. Counts of *L.*
33 *schreiberi* were mostly positively explained by potential activity time and stone cover.

34

1 Discussion

2 We found high correlations of temperature-defined activity budgets with the
3 abundances of different species of lizards above 1800 m of elevation in the Sierra de
4 Guadarrama. The most striking finding is that *Iberolacerta cyreni* activity was not
5 apparently restricted by warm temperatures in the lower sampling sites, where the
6 species is absent or in very low densities. In theory, this means that *I. cyreni* would be
7 able to allocate more resources and therefore potentially have more abundant
8 populations in lower sites (Adolph & Porter 1993). The same methodology applied to
9 other lizards communities (e.g., Jiménez-Robles & De la Riva 2019, Jiménez-Robles &
10 De la Riva unpub.) has never shown such a significant negative effect of the potential
11 activity hours on the occurrences of any species, so we do not believe we are
12 overestimating the potential time of activity. In fact, it is clear that potential activity
13 time was beneficial for the other three lizard species (Figure 4). Other studies have
14 shown that *I. cyreni* is able to live and even improve their physical condition when
15 captive in open enclosures at lower elevations in the summer (e.g. Megía-Palma et al.,
16 in prep.). , These results contributes to the increasing body of evidence that realized
17 niches and distribution of organisms may mismatch the thermal aspect of their
18 fundamental niche by biotic interactions (Bocsi et al., 2016; Bush et al., 2018).

19 There are several hypotheses for why *I. cyreni* does not take advantage of living
20 in warmer sites given the species' broad activity budget. One of them is that biotic
21 interactions with other species that are more abundant warmer sites, might affect the
22 existence of *Iberolacerta*. Certain levels of coexistence seems possible with all the other
23 three species but there seems to be some temperature-mediated competitive exclusion
24 that favours *Iberolacerta* in the colder sites and the other lizards in the warmer sites.
25 Other lizard communities in mountains with *Iberolacerta* species seem to have a similar
26 pattern (Carranza et al., 2004; Galán, Nieto Santín, Vázquez Graña, & Fernández Pérez,
27 2013; Ortega et al., 2016b; Osojnik et al., 2013; Žagar, Carretero et al., 2015; Žagar,
28 Simčič, et al., 2015). Distribution of species in other mountain biological communities
29 is influenced by interspecific competition (Jankowski et al., 2010). Our finding also
30 supports the hypothesis that biotic interactions drive warmer distribution limits (Brown
31 et al., 1996; McArthur, 1972). Because climate change will more severely affect
32 organisms at their warmer distribution limits, in some cases biotic interactions might be
33 more important than physiological stress when explaining range-shifts and climate-
34 forced extinctions.

1 However, there are cases in which abiotic factors may seem to set warmer
2 distribution limits (e.g., reviewed in Cahill et al., 2014). If temperature is mediating
3 competition between species along the temperature gradients in mountains, there are
4 some physiological traits that could have a role in the fitness variation of the organisms.
5 For example, another possible reason why *Iberolacerta* may not take advantage of
6 living in warmer places is because it is limited by temperatures at other crucial moments
7 of its life cycle, such as embryonic development (Monasterio et al., 2011). Underground
8 temperatures during egg incubation might explain warmer distribution limits of
9 montane lizards (Monasterio et al., 2011; 2016; Monasterio, Shoo, Salvador, Iraeta, &
10 Díaz, 2013; Telemeco, Elphick, & Shine, 2009). Embryonic development and hatchling
11 survival of *I. cyreni* and *L. schreiberi* in the Sierra de Guadarrama are impaired at
12 incubation temperatures above 24 °C (Monasterio et al., 2011; 2013). A similar pattern
13 has been documented for *P. muralis* in Asturias above 29°C (Van Damme, Bauwens,
14 Braña, & Verheyen, 1992; Braña & Ji, 2000). Although the embryonic development of
15 *P. guadarramae* has not been studied under a range of temperatures, incubation at
16 27.5°C yields quite elevated hatching rates (Ortega, Pellitteri-Rosa, López, & Martín,
17 2015). Therefore, it seems that embryos of both *Podarcis* species in the Sierra de
18 Guadarrama could develop well at temperatures that are deleterious for *I. cyreni* and *L.*
19 *schreiberi*. The costs of finding cooler conditions, excavating or finding a nest deeper in
20 the soil, under larger rocks or under shrubs (Huey, Peterson, Arnold, & Porter, 1989;
21 Telemeco et al., 2009), may prevent survival in warmer environments. *Iberolacerta*
22 *cyreni* seems to prefer open rocky habitats (Monasterio et al., 2009; 2010a), so it is
23 unlikely to benefit from the underground cooling provided by shrub cover, as *L.*
24 *schreiberi* does (Monasterio et al., 2013). However, other *Iberolacerta* species are
25 known to live in forested habitats (Arribas, 2005; Galán et al., 2007; Žagar et al., 2013),
26 so avoidance of this habitat in the Sierra de Guadarrama could be a consequence of
27 habitat partitioning by competitive exclusion. Under the same laboratory incubation
28 temperatures, hatching success and embryo survivorship was lower for clutches of *I.*
29 *cyreni* caught in low-elevations (Monasterio et al., 2016). This suggests that resource
30 allocation in marginal populations of *I. cyreni* might be reduced, affecting its
31 reproductive investment and fitness. Therefore, we conclude that the effects of
32 temperature on embryonic development by themselves, although crucial for population
33 viability, are not sufficient to explain the distribution of lizards species in the Sierra de
34 Guadarrama, and other processes such as competitive exclusion, habitat segregation,

1 and resource allocation of adults, play a role at determining species occurrences.

2 Apart from temperatures, other physiological aspects, such as water balance may
3 affect the distribution patterns of lizards (Carneiro, García-Muñoz, Žagar, Pafilis, &
4 Carretero, 2017). The general pattern in Lacertidae, is that cold-adapted species tend to
5 have higher evaporative rates than thermophilous species (García-Porta et al., 2019).
6 However, water loss rates in other *Iberolacerta* species are not clearly different to those
7 of *Podarcis* (García-Porta et al., 2019), and in some cases such as *Iberolacerta horvathi*,
8 they are even smaller than those ones of sympatric *Podarcis muralis* (Osojnik et al.,
9 2013). If *I. cyreni* has a lower water loss rate than *P. guadarramae* and *P. muralis*, that
10 could be an advantage for competing in the open habitats at high elevations in the Sierra
11 de Guadarrama, where radiation and wind can compromise water balance. Water loss of
12 *L. schreiberi* was also more reduced than in *P. guadarramae* in northern Portugal
13 (Ferreira, Santos, & Carretero, 2016). However, water loss rates might be important for
14 *Podarcis muralis* (Osojnik et al., 2013). In fact, our analysis reveals a significant
15 reduction of occurrences of *P. muralis* along the study period, as humidity decreases in
16 Mediterranean mountain ecosystems during the summer. Therefore, water balance
17 probably does not play a significant role explaining the realized niches of *I. cyreni*,
18 although it should be studied as a key component of fundamental niche, and it may
19 reveal other particularities of realized niches of the lizards in the Sierra de Guadarrama.

20 The thermoregulation efficiency we have measured for *I. cyreni* falls within the
21 values found in previous studies (Monasterio et al., 2009; Aguado & Braña 2014;
22 Ortega et al., 2016a), which identified it as an accurate and efficient thermoregulator
23 adapted to cold climates. The body temperatures we recorded in the field from active *I.*
24 *cyreni* were higher than those recorded in previous studies (Monasterio et al., 2009;
25 Aguado & Braña 2014; Ortega et al., 2016a), yielding also lower d_b values, which
26 means they thermoregulate more accurately than previously thought. In our study, *I.*
27 *cyreni* was a poorer thermoregulator than the two sympatric *Podarcis* species. This
28 result is supported by previous studies (Monasterio et al. 2009; Žagar, Carretero et al.,
29 2015; Ortega et al., 2016b), all of which identify *Iberolacerta* species as less efficient
30 thermoregulators than sympatric *Podarcis* species. This behavioural difference could
31 make their competitive interaction more asymmetric in detriment of *Iberolacerta*.

32 Other studies looked for insights about the consequences of competition between
33 *I. cyreni* and *P. muralis* in the Sierra de Guadarrama, without obtaining any strong
34 conclusion (Monasterio et al., 2009; 2010a). Both species are considered to be restricted

1 to mountain habitats in the Iberian Peninsula. *Podarcis muralis* is abundant in rocky
2 habitats in neighbour mountains, where *I. cyreni* is not present (Arribas, 1983). We
3 believe that *I. cyreni* in the Sierra de Guadarrama excludes *P. muralis* from high
4 elevation rocky habitats (O. Jiménez-Robles, obs. pers.). However, we have not
5 detected the same habitat segregation between *I. cyreni* and *P. guadarramae*, because in
6 La Najarra (and other high elevation areas of the Sierra de Guadarrama; Jiménez-
7 Robles, pers. obs), both species inhabit the same rocky habitats. Their abundances
8 change oppositely along the elevation gradient, suggesting that fitness of both species is
9 optimised at different temperature regimes. Contrarily to *P. muralis*, *P. guadarramae*
10 seems to be more specialized in open rocky habitats (Martín-Vallejo et al., 1995).
11 *Podarcis muralis* in the Sierra de Guadarrama seems to have its highest densities in
12 *Pinus sylvestris* forests and *Cytisus* formations (Amo et al., 2008; Monasterio et al.,
13 2009), probably by competition release with *P. guadarramae* and *I. cyreni*. Therefore,
14 we would expect that as the Sierra de Guadarrama summits get warmer, and *P. muralis*
15 and *P. guadarramae* disperse uphill, their interaction with *I. cyreni* could determine
16 different success establishing populations at higher elevations.

17 Another species that could increase its occurrences uphill with contemporary
18 climate change is *Lacerta schreiberi*. Within the sites we sampled, it showed preference
19 for habitats with higher rock cover, including scree slopes, probably because they
20 benefit from the possibility of receiving more solar radiation. In spite of predated
21 occasionally smaller lizards (Marco & Pérez-Mellado, 1988), due to its current low
22 densities *L. schreiberi* probably does not have a significant effect on the abundances of
23 the other three Lacertidae at high elevations in the Sierra de Guadarrama. Although the
24 ideal nest temperatures for *L. schreiberi* have been associated to forest cover at lower
25 elevations (Monasterio et al., 2013), the finding of a nest in open montane habitat
26 suggests that at least some females are already laying eggs above the treeline
27 (Monasterio & Beukema, 2014). Therefore, the alpine habitats in the Sierra de
28 Guadarrama could be considered a potential refuge for climate warming for the
29 threatened southern populations of *L. schreiberi*.

30 The exact mechanisms determining distribution ranges of lizards in the Sierra de
31 Guadarrama are still not fully understood, but undoubtedly species interactions and
32 environmental temperatures play a key role. Although our study does not take into
33 account temperature regimes and activity patterns the rest of the year, our sampling
34 effort was centred in the most critical season for the life cycle of these mountain

1 Lacertidae. Late spring, summer, and early autumn, are the main temporal window that
2 these ectotherms have to allocate resources into reproduction. The number of operative
3 temperature time series in our study was a limitation, but the design covering both core
4 and marginal populations of *I. cyreni* in southern slopes along its range in the Sierra de
5 Guadarrama, probably gathered a fair representation of the ecological limitations that
6 this species and its sympatric competitors confront. Considering this, our results are
7 relevant for inferring the suitability of local microclimates and habitats for mountain
8 ectotherm communities, and for evaluating the role of biotic and abiotic mechanisms
9 delimiting species distribution ranges.

10 Many studies regarding distribution of organisms use correlations of
11 environmental variables with the realized niche (Peterson et al., 2011). Mechanistic
12 approaches start with the establishment of the limitations that come from the
13 fundamental niche (Kearney & Porter 2004) and allow understanding the constraints in
14 the realized niche and the actual drivers of distribution ranges. For example, the
15 abundance pattern of *I. cyreni* in our study area would show a high positive correlation
16 with environmental temperatures, while in our approach, we could see it is actually not
17 limited by excess of heat. Therefore, predictions including species physiology (e.g.
18 Kearney, Shine & Porter, 2009; Sinervo et al., 2010) and the community context (such
19 as this study) are key to understand the effects of the anthropogenic global warming,
20 while correlative predictions, although useful and easy to perform, should be interpreted
21 with caution as they could be producing misleading conclusions. These insights allow
22 understanding global change threats on biological communities in mountains and other
23 environmental gradients, and together with monitoring of species landscape
24 distributions could be useful for conservation.

25
26

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8

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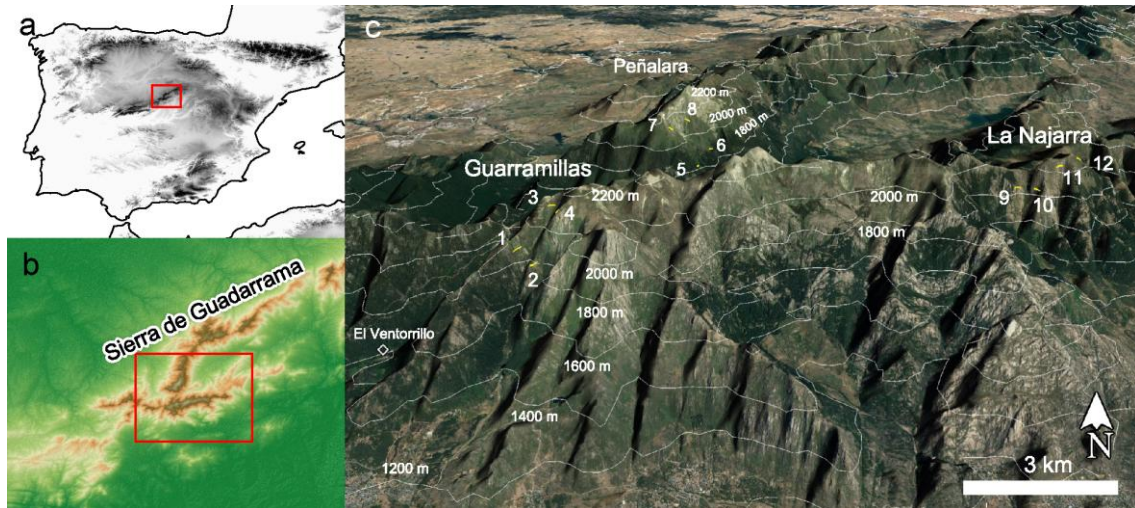
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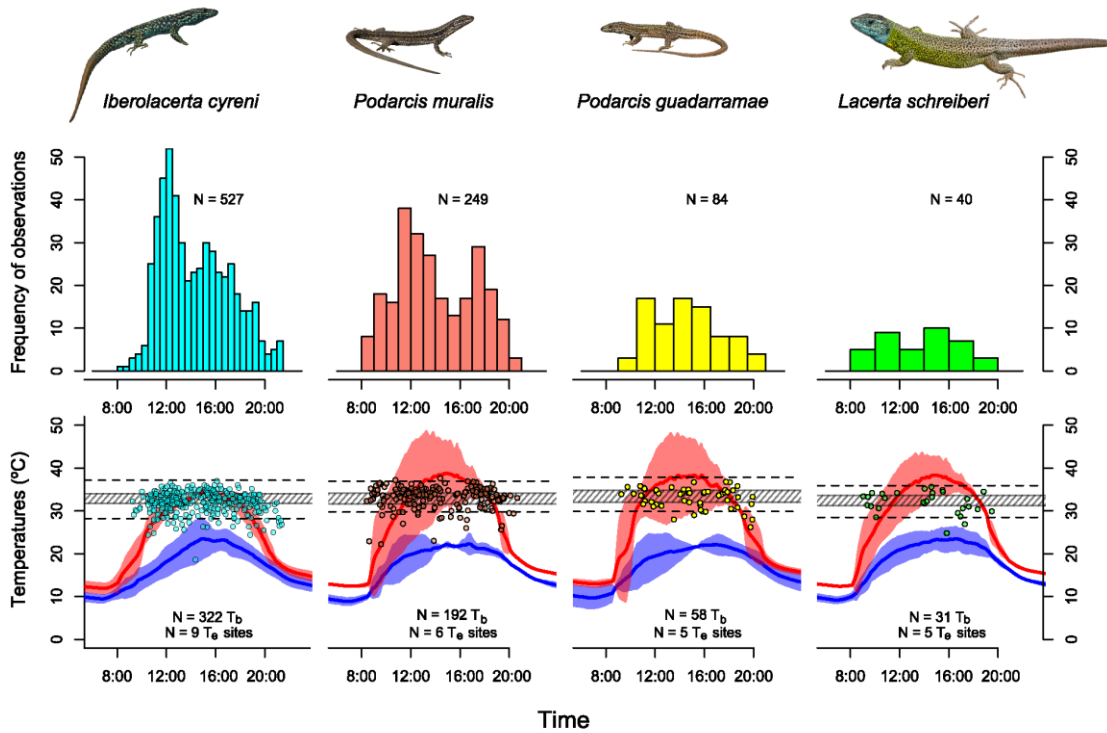
1 Table 1. Estimated metrics for assessing thermal preferences and thermoregulatory
2 parameters for the four Lacertidae species found at 1800–2150 m elevation in the Sierra
3 de Guadarrama, Spain. Median preferred temperature (T_{pref}), voluntary maximum
4 (T_{Vmax}), the upper and lower bounds of the set point range (T_{upSel} and T_{lowSel}),
5 emergence temperature (T_{emerge}), body (T_b) and operative (T_e) temperatures, deviation
6 of T_e from T_{set} (d_e) and deviation of T_b from T_{set} (d_b) and the two complimentary indices
7 of thermoregulation effectiveness d_e-d_b (Blouin-Demers & Weatherhead, 2001) and E
8 (Hertz et al., 1993). Mean \pm standard deviation, range (in parenthesis) and sample size
9 (N; in parenthesis the number of males, non-pregnant females and gravid females).).
10 Pairwise difference significances were assessed by post hoc Tukey tests and a bootstrap
11 comparison in the case of E and d_e-d_b . *cyr* refers to *I. cyreni*, *mur* to *P. muralis*, *gua* to
12 *P. guadarramae* and *sch* to *L. schreiberi*.
13

Species	Thermal preferences			Activity thresholds			Thermoregulation parameters				
	T _{pref} (°C)	T _{upSel} (°C)	T _{lowSel} (°C)	T _{vmax} (°C)	T _{emerge} (°C)	T _b (°C)	d _b (°C)	T _c (°C)	d _c (°C)	d _{c-d_b} (°C)	E
<i>Iberolacerta cyreni</i>	32.9 ± 1.7 (27.2-35.7) N=176 (105+29+42)	34 ± 1.6 (28.6-36.3)	31.8 ± 1.8 (25.5-34.8)	37.1 ± 1.2 (33.1-40.3)	28.21 N=310 (194+59+57)	31.9 ± 2.6 (18.6-37)	1.1 ± 1.7 (0-13.2)	28.8 ± 4.1 (15-39) N=198 (128+41+29)	5 ± 2.5 (0.2-16.8)	4 ± 2.7 (-2.5-13.6) N=135 (82+31+22)	0.7 ± 0.5 (-2.3-1)
<i>Podarcis muralis</i>	32.9 ± 1.7 (24-35.8) N=99 (37+29+33)	34.1 ± 1.4 (28.8-37)	31.6 ± 1.9 (22.5-34.9)	36.9 ± 1.2 (33.3-39.6)	29.73 N=191 (79+48+64)	33.2 ± 2.6 (22.2-37.6)	1 ± 1.5 (0-9.4)	29.2 ± 5.3 (13.7-40.9) N=118 (54+29+35)	6.7 ± 3.2 (1.6-18)	6.2 ± 3.2 (-0.4-15.3) N=87 (42+16+29)	0.9 ± 0.2 (-0.2-1)
<i>Podarcis guadarramae</i>	33.5 ± 1.6 (29.5-35.9) N=29 (15+5+9)	34.8 ± 1.5 (30.8-36.5)	32 ± 1.7 (27.4-35.2)	37.9 ± 1.5 (34.2-42)	29.87 N=57 (33+11+13)	33.1 ± 2.4 (26.2-36.8)	0.8 ± 1.3 (0-5.8)	31.3 ± 4.4 (18.8-38.6) N=52 (30+13+9)	6.3 ± 1.9 (2.9-13.2)	5.5 ± 1.8 (0.9-8.7) N=32 (19+7+6)	0.9 ± 0.2 (0.3-1)
<i>Lacerta schreiberi</i>	32.5 ± 1.3 (30-34.7) N=20 (11+7+2)	33.7 ± 1.3 (31.6-36.1)	31.3 ± 1.5 (28.9-34.1)	35.9 ± 1.3 (33.9-37.7)	28.5 N=30 (18+8+4)	31.8 ± 2.9 (24.8-35.6)	1.2 ± 1.8 (0-6.5)	32.1 ± 4.9 (23.6-39.5) N=17 (9+5+3)	6.3 ± 1.7 (3.2-9)	5.6 ± 2.9 (-0.1-8.7) N=11 (7+2+2)	0.8 ± 0.3 (0-1)
Statistics	F _{3,320} = 1.5 P = 0.214	F _{3,320} = 2.79 P = 0.041	F _{3,320} = 0.87 P = 0.457	F _{3,320} = 10.57 P < 0.001	F _{3,599} = 13.6 P < 0.001	F _{3,599} = 1.1 P = 0.353	F _{3,588} = 7.05 P < 0.001	F _{3,273} = 11.22 P < 0.001	F _{3,557} = 14.01 P < 0.001	F _{3,273} = 3.9 P = 0.009	
Groups	{cyr, mur, sch, gua}	{cyr, sch} < {cyr, mur, sch, gua}	{cyr, mur, sch, gua}	sch < {cyr, mur} < gua	cyr < {mur, gua}	{cyr, mur, sch, gua}	cyr < gua	cyr < {mur, gua}	cyr < sch < {gua, mur}	{cyr, sch, gua} < mur	
Pairwise comparisons			Tukey tests			bootstrap results					
cyr vs. mur					cyr < mur p < 0.001					cyr < mur p < 0.001	cyr < mur 100%
cyr vs. gua					cyr < gua p = 0.002					cyr < gua p = 0.02	cyr < gua 100%
cyr vs. sch					cyr > sch p < 0.001					cyr < sch 79.3%	cyr < sch 98.2%
mur vs. gua					mur < gua p = 0.002					mur > gua 69.4%	mur > gua 98.1%
mur vs. sch					mur > sch p = 0.005					mur > sch 86.9%	mur > sch 76.4%
gua vs. sch					sch < gua p < 0.001					gua > sch 94%	sch < gua 56.8%

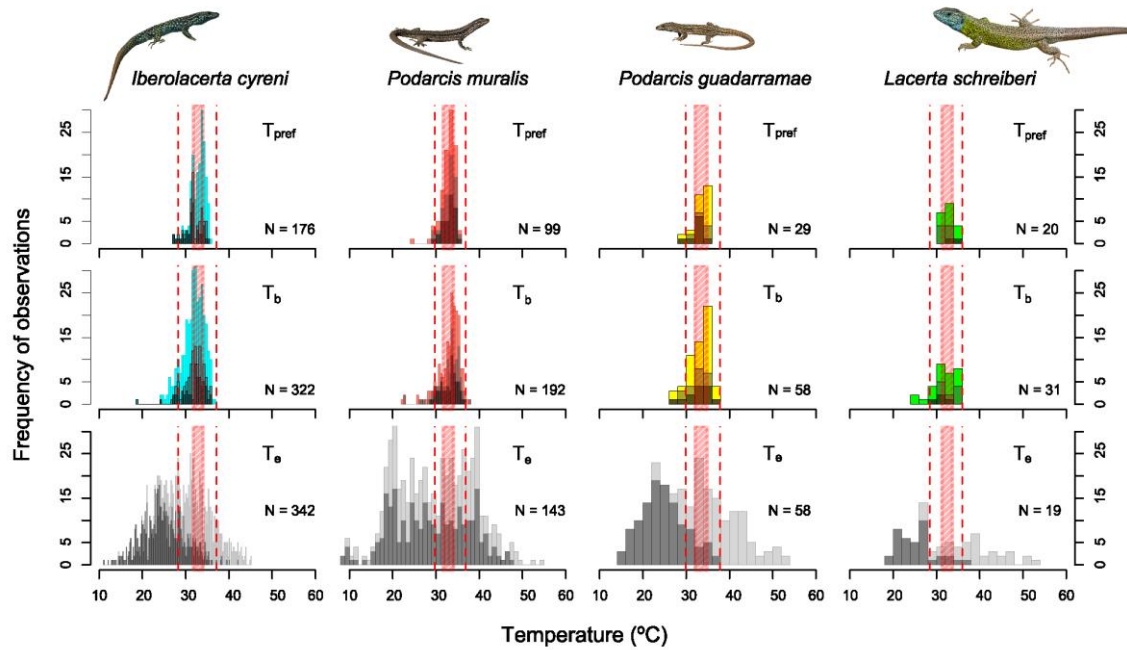


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Figure 1. Study area. A) Location of Sierra de Guadarrama in the Central System and the Iberian Peninsula. B) Study area within the Sierra de Guadarrama. C) Location of line transects of 200 m where we surveyed the lizard communities repeatedly during the springs of 2013 and 2014. Image modified from Google Earth

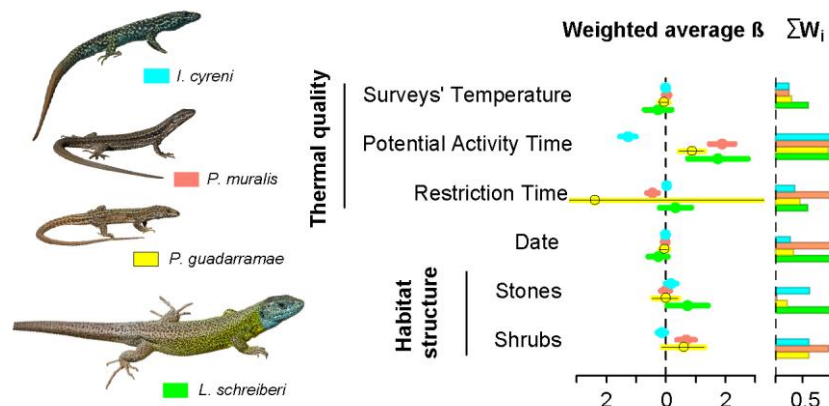


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2 Figure 2. Daily activity patterns of four Lacertidae and the operative temperatures (T_e)
3 in their habitats at 1800-2150 m in the Sierra de Guadarrama, Spain. In the second row,
4 the averaged maximum operative temperatures T_e are represented by a red line with
5 their 95% confidence intervals in red shade, and minimum operative temperatures are
6 analogously represented in blue. Dots represent records of body temperatures for each
7 species. Cross-hatched rectangles indicate the set point range T_{set} , measured in the
8 laboratory for every species, while the dashed horizontal lines are the thermal limits we
9 assumed to define activity: the upper one, mean voluntary maximum T_{Vmax} measured in
10 laboratory; the lower one, the 10 percentile of body temperatures observed in active
11 individuals in the field, which we used as a proxy of emergence temperature T_{emerge} .
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2 Figure 3. Distributions of body temperatures T_b measured in the field and operative
3 temperatures T_e in Lacertidae lizard populations of the Sierra de Guadarrama above 1800
4 m, during the May-August 2013 and 2014, illustrating the accuracy and effectiveness of
5 thermoregulation. In the first row, bright colours represent body temperatures measured
6 in males, while the darker parts are females, being the gravid ones even darker. In the
7 second row, the operative temperatures of plastic models simultaneous to active lizards
8 observations are represented in two grey intensities: light grey for models exposed to
9 full sun and dark grey for models in half shade conditions. Red cross-hatched rectangles
10 indicate the set point range T_{set} , measured in the laboratory for every species, while the
11 red dashed vertical lines are the thermal limits we assumed to define activity: the upper
12 one, mean voluntary maximum T_{Vmax} measured in laboratory; the lower one, the
13 percentile of body temperatures observed in active individuals in the field, which we
14 used as a proxy of emergence temperature T_{emerge} .

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 2 Figure 4. Graphic representation of the model averages from the sets of plausible
 3 ZIGLMM models (those with AICc two units lower than respective null models)
 4 explaining occurrences of the four lizard species present in the Sierra de Guadarrama
 5 above 1800 m: *Iberolacerta cyreni* (blue; averaged from 50 models), *Podarcis muralis*
 6 (*Podarcis muralis*; averaged from 30 models), *Podarcis guadarramae* (yellow; averaged from 20
 7 models) and *Lacerta schreiberi* (green; averaged from 3 models). In the left vertical
 8 axis, estimates of the weighted averages of standardized regression coefficients (dots),
 9 their unconditional standard errors (wider lines) and confidence intervals (thinner lines).
 10 In the right vertical axis, importance of variables contributing to explain variance of
 11 each species in lizard counts, defined as the sum of the AICc-based weights of plausible
 12 models in which a particular variable appears.
 13