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Lizard thermoregulation revisited after two decades of global warming

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Abstract

1. Although the effects of global warming on thermoregulation are usually explored using predictions of climate envelop modelling, such effects should best be analysed empirically, studying the same population with the same methods after a long enough period of temperature rise.

2. We used a 30-year long database about body temperatures (T_bs) of field-active *Psammodromus algirus* lizards inhabiting a well-conserved temperate open forest, and we focused on the summers of 1997 and 2017 to compare T_bs, environmental operative temperatures (T_es), their proximity to the selected thermal range (T_{sel}), and the selection of sunlit and shaded patches all along the day. From these data, we estimated the precision (standard deviation of T_bs), accuracy (average distance between T_bs and T_{sel}) and effectiveness (extent to which T_bs are closer to T_{sel} than T_es) of thermoregulation.

3. Of the highest 5% of all T_bs in the database, 95% were recorded in 2017, when the adjustment to T_{sel} was much better for T_bs selected in a laboratory thermogradient than for field T_bs (percentages of T_bs above T_{sel} of 2% and 52% respectively).

4. In 2017, especially after 12:00 h, the selection of shaded patches (87% of lizards in full shade vs. <1% in full sun) was more intense than in 1997, contributed more to overall thermoregulation, and produced a larger difference between T_es and T_bs. In spite of this, T_bs were lower—and closer to T_{sel}—in 1997 (when most shaded patches offered favourable thermal opportunities, with T_es within or below T_{sel}) than in 2017 (when only 33% of full shade T_es, and 8% of all T_es, were within or below T_{sel}). As a consequence, estimates of the accuracy and effectiveness of thermoregulation decreased over the 20-year period examined.

5. We conclude that given the low availability of T_es within or below T_{sel}, lizards cannot longer prevent the rise of their T_bs above T_{sel}, at least in hot summer days. Thus, the effects of global warming are already hindering the ability of lizards to buffer environmental change by behavioural means, even in temperate forests with a fine-grained mosaic of sun and shade patches.

1 | INTRODUCTION

Temperature is one of the most relevant environmental factors that control biological processes and determine the distribution of all life-forms (Angilletta, 2009). Thermal effects span all levels of biological organization, from the catalytic activity of enzymes (Daniel & Danson, 2010) to whole-organism performance traits such as sprint speed (Bauwens et al., 1995; Van Berkum, 1986; Zamora-Camacho et al., 2015), escape efficiency (Christian & Tracy, 1981) or foraging performance (Angilletta et al., 2002; Díaz, 1994; Hu et al., 2019; Van Damme et al., 1991). Temperature shapes both the relationship between phenotypic traits and performance (e.g., by controlling the velocity, force and duration of skeletal muscle contraction; Niu et al., 2021) and the effects of performance on fitness (e.g., by affecting growth, energy budgets, reproductive output and survivorship). Thus, thermal effects influence life histories, population dynamics and conservation prospects (Adolph & Porter, 1993; Buckley, 2008; Kearney et al., 2009; Sinervo et al., 2010). It is therefore not surprising that global warming stands with habitat loss as one of the most important causes of the current biodiversity crisis (Ceballos et al., 2015; Ceballos et al., 2020; Garcia et al., 2014). Warming has sped up in the past decade, with records of global surface temperature in 2016 and 2020 (Voosen, 2021).

Terrestrial ectotherms are particularly prone to suffer the consequences of global warming (Deutsch et al., 2008) because they rely on the environment, much more heterogeneous in space and variable over time than in aquatic habitats, to regulate their body temperature. Most species are projected to lose range due to their limited dispersal ability. For instance, loss of suitable climate space is likely to occur in southwestern Europe, where hot, dry conditions are projected to increase (Araújo et al., 2006). On the other hand, many terrestrial ectotherms can regulate their body temperature by behavioural means to values almost as high and stable as those of endotherms (Bauwens et al., 1995; Cowles & Bogert, 1944; Díaz & Cabezas-Díaz, 2004; Hertz et al., 1993). In fact, behavioural thermoregulation by ectotherms has been regarded as a factor that inhibits, rather than drives, adaptation to global warming, because it may reduce the impact of environmental change on organisms, thus minimizing the intensity of selection on the thermal sensitivity of physiological traits (Huey et al., 2003).

Studies of behavioural thermoregulation were fostered in the early 90s by the proposal of an elegant protocol to evaluate thermoregulation by small, field-active ectotherms (Hertz et al., 1993). The starting point was the long-held view that the mechanisms and extent of behavioural thermoregulation, and indeed the very existence of an active thermoregulatory process, cannot be evaluated without appropriate null hypotheses (Heath, 1964; Hertz, 1992; Hertz et al., 1993). Such null hypotheses can be obtained by estimating environmental operative temperatures (T_es), defined as the equilibrium temperatures of a population of inanimate objects with the same heat-transfer properties as the study animals (Bakken & Gates, 1975). These temperatures can be estimated directly using physical models of the study organism ('operative temperature thermometers'; Bakken & Angilletta Jr., 2014; Bakken & Gates, 1975; Shine & Kearney, 2001; Vickers & Schwarzkopf, 2016; Vitt & Sartorius, 1999). Thus, the random distribution of T_es in the environment describes the null distribution of body temperatures (T_bs) expected in nonregulating animals. Hertz et al. (1993) combined data about T_es, T_bs and selected thermal ranges (T_{sel}; the range of T_bs that lizards attempt to maintain in the absence of physical or biotic constraints; Licht et al., 1966) to estimate quantitative indexes of the precision (standard deviation of T_bs), accuracy (average distance between T_bs and T_{sel}) and effectiveness (extent to which T_bs are closer to T_{sel} than are T_es) of thermoregulation. Although some of these measurements, especially effectiveness, have been criticized (Blouin-Demers & Weatherhead, 2001), they still provide the standard parameters to evaluate thermoregulation in field studies.

Despite all these advances, there is a paucity of empirical studies comparing the thermal biology of a population inhabiting the same unmodified habitat, after a long enough period of global warming, with the same measuring protocol and analytical methods. Within this framework, we took advantage of a long-term database about T_bs of field-active lizards from a population of *Psammodromus algirus*, the commonest lacertid in many areas of the western Mediterranean region. The database includes records taken in 1987, 1992, 1994, 1997 and 2017, with the same protocol of capture, manipulation and measurement. More specifically, the procedure developed by Hertz et al. (1993) was replicated in the summers (July–August) of 1997 and 2017. This allowed us to analyse the effects of global warming on thermal biology by comparing the relevant statistics, instead of relying on predictions of climate envelop modelling. Importantly, our study area (Monte de El Pardo) is one of Europe's best preserved Mediterranean forests, because it was a royal hunting ground for centuries before it became part of Spain's national heritage. Therefore, the landscape has remained relatively unchanged, and between-year differences in the availability of sunlit and shaded patches (see Results) must be attributed to small variations in vegetation cover among the sampled transects (e.g., southern facing slopes are more open than northern facing ones). This is consistent with the fact that inter-annual variation in the availability of shade between 1997 and 2017 was of the same magnitude as seasonal variation in 1997 (Díaz et al., 2005; Díaz & Cabezas-Díaz, 2004). Thus, our methods allowed us to minimize confounding effects, providing a direct link between global warming and inter-annual differences in thermal biology.

Our specific goals were to address the following questions: (1) How much has the thermal environment changed after two decades

of global warming in a well-conserved Mediterranean forest? (2) How have these changes affected the thermoregulatory behaviour of lizards (microhabitat use and selection of sunlit or shaded patches) and their realized thermoregulatory performance (body temperatures and accuracy and effectiveness of thermoregulation)? (3) To what extent can behaviour buffer the effects of global warming on the temperature, and hence physiology, of these small ectotherms?

2 | MATERIALS AND METHODS

Because we were interested in making 1997 and 2017 data directly comparable, we used a revised version of the 1997 methods described in Díaz and Cabezas-Díaz (2004), which are summarized in the next sections.

2.1 | Study organism and study area

Psammodromus algirus is a medium-sized (adult snout-vent length 60–85 mm; mass 6–15 g) heliothermic lacertid that inhabits shrub and woodland habitats of the western Mediterranean (Díaz & Carrascal, 1991). Lizards were sampled at 'El Pardo' (Madrid, central Spain: 40°30′N, 03°45′W; 650–700 m elevation), a holm oak (*Quercus ilex*) perennial forest in which offshoots of *Q. ilex* dominate the shrub layer together with rockroses *Cistus ladanifer*. In July–August, mean ambient temperature is 25.2°C (daily mean temperatures from the nearby meteorological stations of Barajas-Aeropuerto and Cuatro Vientos, averaged for the 40-year period between 1978 and 2017), and mean daily maximum temperature is 33.0°C.

2.2 | Field sampling

In both 1997 and 2017, data about T_es, T_bs and use and availability of patches within different categories of sun exposure (full sun, sun filtered by vegetation, or full shade) were simultaneously collected during the daily activity period of this species. Animals were captured under licence of the 'Dirección General de Biodiversidad y Recursos Naturales' of the Community of Madrid, and their care and use were conducted in conformity with the principles approved by the Animal Experimentation Ethical Committee of the Universidad Complutense de Madrid. In 1997, sampling took place between 17 and 31 July on six different transects, one per sampling day (Díaz & Cabezas-Díaz, 2004). In 2017, sampling took place between 19 July and 25 August, again on six different transects, but this time each transect was sampled on two different sampling days. In 1997 we used 15 T_e thermometers per transect, that provided data about T_e and exposure to sun (full sun, sun filtered by vegetation, or full shade) covering the whole daily activity period of the species. For each transect, there was a new scatter of devices that were placed at randomly selected intervals (1–9 m, distance determined by one-digit numbers from a table of random numbers). In 2017, we used 20 T_e thermometers per transect (see below). Thus, T_e and exposure to sun were measured throughout the day on 90 different locations in 1997, and on 120 different locations in 2017.

In 1997, T_es were measured using unpainted copper cylinders (5 cm long × 1 cm wide × 1 mm thick) closed at both ends except for a small fissure that allowed inserting the sensing tip of an electronic digital thermometer (digi-thermo®; ±0.1°C precision; Díaz & Cabezas-Díaz, 2004). The performance of these models as T_e thermometers for this species was examined by Belliure et al. (1996), who showed that under the same conditions of radiant heat loads (100 W bulb at different heights), the mean temperatures at equilibrium of models and recently dead lizards were highly correlated and statistically indistinguishable ($r^2 > 0.99$; $p > 0.25$ for the assumptions of the identity regression line that the slope and intercept do not differ significantly from one and zero respectively). However, this validation method may be limited by the fact that absorption and emissivity may differ between recently dead lizards and living ones, and also because the thermal environment is much more complex under field conditions than in the laboratory. In fact, 17 years after we carried out field work in 1997, Bakken and Angilletta Jr. (2014) argued that physical models with simple geometries such as the ones we used may lead to systematic errors of 2°–4°C, and that T_e thermometers should match the shape, size and colour of live animals to avoid such errors. For that reason, in June 2022 we carried out a second calibration experiment in which we compared the T_es of a pair of simple models identical to the ones used in this study (and in Díaz & Cabezas-Díaz, 2004) with those of two models matching the detailed shape, size and colour of live animals. Such models were hollow lizard casts built with malleable 0.2 mm thick copper sheet, moulded to the contours of a museum specimen, and painted to visually match the colour of live lizards. The calibration experiment was done at the study area under field conditions, ensuring that our devices were validated in outdoor natural conditions and exposed to all modes of heat exchange. We chose 20 random sites (12 in full sun and 8 in full shade) to measure the temperatures of the two simple models, the two lizard casts and two tethered live lizards (one male and one female) between 08:00 and 14:00 h. Temperatures were measured with the same thermometers as in 1997 and 2017. To allow estimating heat exchange rates, temperatures were registered during 5 min, at 1-min intervals for T_e thermometers and at minutes 2 and 5 in the case of lizards. Equilibrium temperatures (i.e., heat exchange rates ≈ 0) were sometimes difficult to reach, particularly in full sun and at high temperatures, when live lizards heated more slowly than both types of devices, probably to prevent lethal overheating (in fact, we did not measure the T_bs of live lizards at the four sites with highest T_es [>50°C] to avoid their death). We averaged all the temperatures of each type of entity (simple models, lizard casts and live lizards) at each site, and we used the resulting mean values in subsequent statistical analyses. The mean temperatures of both types of devices were highly correlated with those of lizards (simple models: $r^2 = 0.980$; lizard casts: $r^2 = 0.974$; $N = 16$ and $p \ll 0.001$ in both cases). Importantly, both types of operative temperature thermometers produced highly correlated and statistically indistinguishable

datasets ($r^2 = 0.969$, $N = 20$; $p > 0.53$ for the assumptions of the identity regression line that the slope and intercept do not differ significantly from one and zero respectively; average difference between the mean temperatures of both types of models = 0.6°C; repeated measures ANOVA: $F_{1,19} = 2.92$, $p > 0.1$). These results support the conclusion that our thermoregulatory statistics and metrics are not only comparable between years, but also accurate.

Also, our 1997 data indicate that our simple models allow accurate quantitative prediction of seasonal shifts in thermoregulatory behaviour (Díaz & Cabezas-Díaz, 2004). Thus, in July lizards actively selected patches in full shade, and their mean T_b (35.9°C) was close to the mean T_e (35.3°C) of those patches (Díaz & Cabezas-Díaz, 2004). On the other hand, in May lizards used sunlit and shaded patches almost at random, shuttling frequently between different types of patches, and their mean T_b (33.5°C), rather than equilibrating to the T_e within any type of patch, was close to the grand mean (33.7°C) of T_es in full sun (46.7°C), filtered sun (29.8°C) and full shade (24.7°C; Díaz & Cabezas-Díaz, 2004). These results support Shine and Kearney's (2001) assumption that placement may have more influence than increased precision on predicted T_e, and they suggest that errors may be randomly distributed rather than consistent.

We registered T_e at hourly intervals between 08:00 and 20:00h, and we also recorded time of day and exposure to sun (full sun, filtered sun shade or full shade; occasional cloudy intervals were excluded from these analyses) to provide a null hypothesis against which lizards' selectivity for sunlit/shaded patches could be tested (Díaz, 1997; Díaz & Cabezas-Díaz, 2004). Lizards were lassoed or captured by hand, and their T_b was measured to the nearest 0.1°C with a Miller–Weber quick-reading cloacal thermometer. As for T_es, time of day and sun exposure at first sighting were recorded (also for lizards that were detected but not captured).

In 2017, T_es were measured between 19 July and 25 August in six different transects scattered across the same area as in 1997; data were taken throughout the lizards' activity period (08:00–20:00h). We used two types of devices. First, we used the same copper models described above, since we were interested in obtaining directly comparable datasets. Second, we also used Thermochron® iButtons (model DS1921G-F), which are small data loggers that monitor time and temperature. These loggers allowed measuring temperature every 5min, thus providing a much larger number of data and increased precision in estimates of T_e. We conducted a pilot study to establish the relationship between iButtons and models, so that both types of data could be directly compared (Vitt & Sartorius, 1999). For that purpose, we matched both types of devices by forming nine pairs of iButtons and models that were placed three in full sun, three in full shade and three in sun filtered by vegetation. Temperature values registered by iButtons and models were highly correlated ($r^2 = 0.978$, $p < 0.001$), allowing the accurate transformation of temperatures recorded by iButtons into model T_es with the resulting regression equation ($T_{e\,[model]} = 5.4069 + 0.895\,T_{iButton}$). For the measurement of T_e, 10 models and 10 iButtons were placed at randomly determined intervals along each transect line. Thermochrons were set to register temperature every 5min, whereas the temperature of models was registered every 2h (five models per hour). We averaged the 12 hourly temperature readings recorded by iButtons, leading to a single T_e estimate per iButton and hour. To obtain a null hypothesis of the availability of sunlit/shaded patches, we noted sun exposure of models when measuring their temperature, and of iButtons by means of a single focal observation at the middle of the hourly interval. Again, occasional cloudy intervals were excluded from these analyses.

The analysis of thermoregulation requires that data about T_es and T_bs are sympatrically and simultaneously collected. Because in 2017 all T_b data were obtained between 26 July and 3 August, we restricted to that period (transects 2 and 3) the analyses of T_es and derived indices of thermoregulation, although conclusions would have remained unchanged had we used the complete dataset (see Results). However, data on the use and availability of patches within different categories of sun exposure were gathered throughout the entire study period, to increase sample sizes for selectivity (i.e., log-linear) analyses.

2.3 | Selected temperatures

The previously published selected temperature range (T_{sel}, defined as the central 80% of all T_bs selected in a thermogradient) in this species is 32.8–36.9°C in July (Díaz & Cabezas-Díaz, 2004; Díaz et al., 2006). In 2017, we captured four males and four females to look for possible changes in preferred temperatures. Lizards were transported to the laboratory and individually housed in terraria ($40 \times 60 \times 30$cm) with white, opaque walls and with their tops covered with a green net (0.5-cm mesh) that prevented escape and created a shrubby-like shelter. The laboratory had natural daylight and ventilation. Terraria were filled with moistened earth and covered with a leaf litter layer. Some rocks and thin fallen wood increased structural complexity and provided lizards with additional shade and refuge. Food and water were supplied ad libitum. A thermogradient was created in the terraria by a 100W bulb suspended above one end at a height of c. 20cm. This gradient offered a wide range of available temperatures (24.3–47.7°C), and T_b was measured three times per day (at 10:30–11:00, 13:00–13:30 and 15:00–15:30h CET), with the same thermometers used in the field, on 2 and 4 August 2017 (six data per lizard). In five occasions T_bs could not be measured because the lizard was hidden under cover at the cool end of the thermogradient, and it was thereby considered to be inactive (not thermoregulating). Thus, final sample size was 43 T_b readings that could be compared with T_{sel} and with the T_b data recorded in the field.

2.4 | Data analyses and thermoregulation statistics

For the long-term analysis of T_bs, we recovered previously published data about T_bs measured in July–August at the study area with Miller–Weber quick-reading cloacal thermometers. This allowed us to compare the mean summer T_bs of this lizard population in 1987,

1989, 1994, 1997 and 2017 (Carrascal & Díaz, 1989; Díaz, 1992; Díaz, 1997, Díaz & Cabezas-Díaz, 2004; and results of this study).

In 1997 and 2017, the thermal quality of the habitat was measured by the proportion of T_e values within T_{sel} and by the mean $(\overline{d_e})$ of the absolute values of deviations of T_es from T_{sel} (d_es). Similarly, the accuracy of thermoregulation was quantified by the proportion of T_bs within T_{sel} and by the mean $(\overline{d_b})$ of the absolute values of deviations of T_bs from T_{sel} (d_bs). The precision of thermoregulation (i.e., the actual variability of T_bs) was estimated by the standard deviations of the distributions of T_bs. Finally, the effectiveness of lizard thermoregulation with respect to nonregulating models was evaluated with two indexes: (1) the original formula proposed by Hertz et al. (1993), $E = 1 - (\overline{d_b}/\overline{d_e})$; and (2) the difference $\overline{d_e} - \overline{d_b}$, proposed by Blouin-Demers and Weatherhead (2001) as a mathematically simpler, better alternative.

We evaluated the relative importance of the selection of sun and shade patches as a thermoregulatory behaviour by comparing the random distribution of models (T_es and d_es) with the same distribution weighted by the lizards' hourly patterns of sun and shade selection (Bauwens et al., 1996; Díaz & Cabezas-Díaz, 2004). While the first distribution represents the T_bs and d_bs of a lizard population with a use of sun and shade patches proportional to their availability throughout the day (i.e., the 'no thermoregulation' hypothesis), the second one represents the T_bs and d_bs of a population using the selection of sun and shade patches as its only thermoregulatory behaviour. The weighting coefficients for each hourly period were L_i/M_i, where L_i and M_i are the proportions of lizards and models in the ith category of sun exposure during that period. Descriptive data are presented as mean ± one standard deviation.

3 | RESULTS

3.1 | Long-term temperature trends

Both mean and maximum air temperatures, averaged for July–August and for the nearby meteorological stations of Barajas-Aeropuerto and Cuatro Vientos (Figure S1; data available at http://www.aemet.es), increased significantly during the 40-year period spanning from 1978 to 2017 (mean of daily mean temperatures: $T = -82.82 + 0.054 \times \text{year}$, $F_{1,38} = 24.33$, $p < 0.001$; mean of daily maximum temperatures: $T = -60.14 + 0.047 \times \text{year}$, $F_{1,38} = 12.20$, $p = 0.001$). Thus, ambient temperatures during summer showed a warming trend of ca. 0.05°C/year (2.16 and 1.86°C, respectively, over the 40-year period examined; Figure S1).

Mean lizard T_bs also showed a consistent rising trend over the 30-years period examined (mean $T_b = -174.26 + 0.104 \times \text{year}$, $F_{1,3} = 131.84$, $p = 0.0014$), of 0.11°C/year, or 3.3°C between 1987 and 2017 (Figure S2). Lizard T_bs differed significantly among years (one-way ANOVA: $F_{4,327} = 11.42$, $p < 0.001$), reaching their highest values in 2017 (Figure 1). The percentage of lizards with T_bs above T_{sel} (32.8–36.9°C; see Díaz et al., 2005) was much higher in 2017 (52%) than in previous years (6, 9, 7 and 9% in 1997, 1994, 1989 and
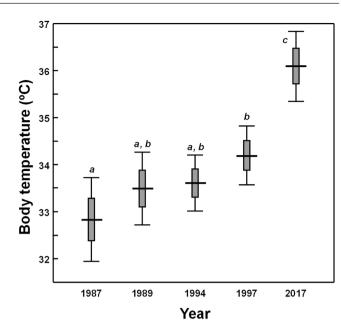

FIGURE 1 Mean values (with standard errors and 95% confidence intervals) for body (cloacal) temperatures of active lizards recorded in the same open forest ('Montes de El Pardo y Viñuelas') during the summers of different sampling years between 1987 and 2017. Letters indicate homogeneous groups according to the results of a Newman–Keuls post-hoc test following one-way ANOVA.

1987 respectively). Moreover, 18 of 19 (94.7%) T_bs above 38.2°C (the 95th percentile of the distribution of 332 summer T_bs recorded between 1987 and 2017) belonged to lizards captured in 2017, including eight T_bs above 39°C.

3.2 | Body temperatures

On average, lizards had higher T_bs in 2017 than in 1997 (two-way ANOVA with year and time of day as factors; year: $F_{1,108} = 21.43$, $p < 0.001$; time of day: $F_{11,108} = 12.64$, $p < 0.001$; interaction: $F_{11,108} = 2.07$, P = 0.029; Table 1; Figure 2). In both years, T_bs raised during the early morning basking period to remain stable within T_{sel} between 09:00 and 12:00h (Figure 2; Figure S5). Therefore, mean T_bs before 12:00h did not differ significantly between years ($F_{1,42} = 0.41$, $p = 0.524$; Table 1). After that time, however, T_bs differed clearly between years ($F_{1,86} = 54.74$, $p < 0.001$; Table 1). Whereas in 1997 lizards managed to keep their T_bs within T_{sel} during the rest of the day, in 2017 mean T_bs exceeded T_{sel} between 13:00 and 18:00h (Figure 2; Figure S5). In fact, all T_bs above 38.2°C obtained in 2017 and mentioned in the previous paragraph were taken after 12:00h. Given this pattern, and the significant interaction between year and time interval (a factor with two levels, before vs. after 12:00h) in a two-way ANOVA ($F_{1,128} = 6.11$, $p = 0.015$), many of the following analyses use time interval instead of time of day as a categorical predictor to facilitate the interpretation of results.

The observed rise in T_bs could not be attributed to a concomitant shift in T_{sel}, because field T_bs were higher and more variable than T_bs

TABLE 1 Summary of thermoregulation statistics in 1997 and 2017: mean±SD, with sample sizes between parentheses, of body temperature ($\overline{T_b}$), accuracy of thermoregulation ($\overline{d_b}$), environmental operative temperature ($\overline{T_e}$), thermal quality of the environment ($\overline{d_e}$), amount of thermoregulation achieved ($\overline{d_b} - \overline{d_e}$) and effectiveness of thermoregulation (E), equal to $1 - (\overline{d_b}/\overline{d_e})$. All values are given in °C except for E that has no dimension. Means are given separately for time intervals before 12:00h (08:00–12:00h), after 12:00h (12:00–20:00h) and total daily activity period (08:00–20:00h)

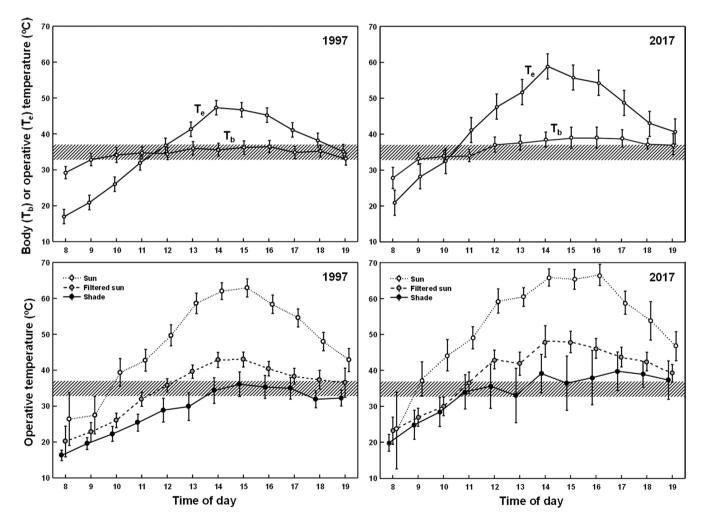|	1997			2017		
	08:00–12:00h	12:00–20:00h	Total	08:00–12:00h	12:00–20:00h	Total
$\overline{T_b}$	32.5±3.0	35.0±2.0	34.2±2.6	33.1±3.2	37.7±1.4	36.1±3.1
$\overline{d_b}$	1.2±2.2	0.3±0.7	0.6±1.4	1.2±2.1	1.1±0.9	1.1±1.4
(N)	(22)	(45)	(67)	(22)	(43)	(65)
$\overline{T_e}$	24.0±8.3	41.4±12.1	35.6±13.7	30.7±10.0	50.0±11.7	43.6±14.4
$\overline{d_e}$	10.6±5.3	7.8±9.6	8.7±8.50	7.4±5.2	13.3±11.5	11.3±10.2
(N)	(360)	(720)	(1080)	(120)	(240)	(360)
$\overline{d_e} - \overline{d_b}$	9.3	7.5	8.1	6.3	12.2	10.2
E	0.882	0.964	0.932	0.844	0.918	0.902

FIGURE 2 Mean values (with 95% confidence intervals) for body (cloacal) temperatures (T_bs) and environmental operative temperatures (T_es) as a function of time of day in 1997 and 2017. The upper panels show the mean T_bs of active lizards and the overall means of available T_es. The lower panels show the mean T_es available for full sun, filtered sun and full shade locations. The selected temperature range (T_{sel}) is represented by the dashed areas.

selected in a laboratory thermal gradient (field: 36.1±2.1°C, N = 65; thermogradient: 34.5±1.7, N = 43; $F_{1,106}$ = 9.60, p = 0.002; Levene´s test: $F_{1,106}$ = 7.18, p = 0.009). Moreover, in 2017 deviations from T_{sel}

(32.8–36.9°C; Díaz et al., 2006) were much smaller for T_bs measured in the thermogradient (14, 84, and 2% below, within and above T_{sel} respectively) than for field T_bs (14, 34, and 52% below, within and

above T_{sel} respectively; $\chi^2 = 31.9$, df = 2, $p<0.001$). This result is even clearer if we restrict it to lizards captured after 12:00h (0%, 23%, and 77% below, within and above T_{sel} respectively; $\chi^2 = 50.8$, df = 2, $p<0.001$).

3.3 | Operative temperatures

Because in 2017 T_bs were measured on 26–27 July (transect 2) and 2–3 August (transect 3), the T_e data we present are restricted to those days and transects to fulfil the assumption of thermoregulation studies that T_es and T_bs must be collected simultaneously and at the same sites (Bauwens et al., 1996; Hertz et al., 1993). However, conclusions would have remained unchanged if we had used the complete dataset, even if transects 2 and 3 might have been sampled during some of the hottest summer days (see Appendix in Supplementary Material). In both years, T_es showed a similar rising trend between 08:00 and 14:00–15:00h, followed by a slower decrease after that peak (Figure 2; Figure S5). Overall, T_es were higher in 2017 than in 1997 (two-way ANOVA; year: $F_{1,1416} = 181.32$, $p<0.001$; time of day: $F_{11,1416} = 109.23$, $p<0.001$; interaction: $F_{11,1416} = 1.42$, $p = 0.156$; Table 1; Figure 2). Sun exposure had a marked effect on the variation of T_es. In both years, T_es reached a maximum at noon, and they were higher in full sun than in filtered sun and full shade, with differences between sun and shade peaking at midday (two-way ANOVAs with data on Figure 2; all ps<0.001 in both years for the effects of sun exposure, time of day and their interaction). In 1997, all mean T_es in full shade between 14:00 and 18:00h remained within T_{sel}, whereas in 2017 they were mostly above T_{sel} (Figure 2; Figure S5). More importantly, the frequencies of T_es below, within or above T_{sel} differed between years, specially after 12:00h and for T_es in full shade (Table 2). In 1997 after 12:00h, 51% of T_es in full shade were below T_{sel}, meaning that lizards could lower their T_bs by using those sites as 'heat sinks'. In 2017, however, 67% of full shade measurements

were above T_{sel}, and only 7% were below T_{sel}. Overall, the frequency of T_es above T_{sel}, pooling all categories of sun exposure, was higher in 2017 than in 1997, both before ($\chi^2 = 19.26$, df = 2, $p<0.001$) and after 12:00h ($\chi^2 = 93.02$, df = 2, $p<0.001$). However, the thermal environment became truly challenging only after 12:00h, when 92% of T_es were above T_{sel} (Table 2).

3.4 | Thermoregulation statistics

Precision of thermoregulation sensu Hertz et al. (1993) was high (Table 1): standard deviations were much smaller for T_bs than for T_es both in 1997 (Levene's test: $F_{1,1145} = 70.36$, $p<0.001$) and 2017 ($F_{1,423} = 82.90$, $p<0.001$), indicating a high degree of precision that was similar in both years (Levene's test for standard deviations of T_bs in 1997 and 2017: $F_{1,130} = 0.75$, $p = 0.389$).

Thermal quality was higher in 1997 than in 2017 because $\overline{d_e}$ (mean of the absolute values of deviations of T_es from T_{sel}) was higher in 2017 than in 1997 (Table 1; but see Appendix in Supplementary Material). However, a better picture of thermal differences between years is obtained by considering the effects of year, time interval (before vs. after 12:00h) and their interaction (two-way ANOVA; year: $F_{1,1436} = 4.10$, $p = 0.043$; time interval: $F_{1,1436} = 7.37$, $p = 0.007$; interaction: $F_{1,1436} = 57.00$, $p<0.001$). The most significant effect is by far that of the interaction: whereas before 12:00h T_es were on average 3.2°C closer to T_{sel} in 2017 than in 1997, after 12:00h the opposite was true, thermal quality being 5.5°C lower in 2017 due to much higher T_es.

Thermoregulation was more accurate in 1997 than in 2017 (one-way ANOVA with the absolute values of deviations of T_bs from T_{sel}, or $\overline{d_b}$s: $F_{1,130} = 4.44$, $p = 0.037$; Table 1). Although the interaction between the effects of time interval and year on the variation of d_bs was marginally non-significant (two-way ANOVA: $p = 0.078$), accuracy of thermoregulation was higher in 1997 only after 12:00h (one-way ANOVA: $F_{1,86} = 22.91$, $p<0.001$), when T_bs were on average

TABLE 2 Frequencies of environmental operative temperatures (T_es) below, within or above T_{sel}, with percentages between parentheses, as a function of year, sun exposure (full sun, filtered sun or full shade), and time interval (before vs. after 12:00h). The two last columns show values of the χ^2 statistic comparing frequencies between years

	1997			2017			χ^2 (df = 2)	p
	Below T_{sel}	Within T_{sel}	Above T_{sel}	Below T_{sel}	Within T_{sel}	Above T_{sel}		
08:00–12:00h								
Full sun	13 (34.2)	6 (15.8)	19 (50.0)	3 (12.5)	1 (4.2)	20 (83.3)	7.04	0.030
Filtered sun	95 (83.3)	7 (6.1)	12 (10.5)	43 (76.8)	7 (12.5)	6 (10.7)	2.04	0.360
Full shade	207 (100.0)	0 (0.0)	0 (0.0)	39 (97.5)	0 (0.0)	1 (2.5)	—	—
Total	315 (87.7)	13 (3.6)	31 (8.6)	85 (70.8)	8 (6.7)	27 (22.5)	19.26	<0.001
12:00–20:00h								
Full sun	4 (2.1)	7 (3.7)	176 (94.1)	0 (0.0)	1 (1.0)	96 (99.0)	3.90	0.142
Filtered sun	62 (22.2)	54 (19.4)	163 (58.4)	1 (0.9)	7 (6.2)	105 (92.9)	45.73	<0.001
Full shade	77 (51.0)	52 (34.4)	22 (14.6)	2 (6.7)	8 (26.7)	20 (66.7)	41.00	<0.001
Total	143 (23.2)	113 (18.3)	361 (58.5)	3 (1.25)	16 (6.7)	221 (92.1)	93.02	<0.001

0.8°C closer to T_{sel} than in 2017, but not before 12:00h ($F_{1,42} = 0.02$, $p = 0.887$), when such difference was only of 0.1°C (Table 1). After 12:00h the frequencies of T_bs below, within or above T_{sel} differed clearly between years ($\chi^2 = 42.8$, df = 2, $p < 0.001$). In 1997, 34 of 45 captured lizards (75.6%) had T_bs within T_{sel}, 7 (15.5%) had T_bs below T_{sel} and only 4 (8.9%) had T_bs above T_{sel}. In 2017, no lizard had its T_b below T_{sel}, 10 of 43 lizards (23.3%) had T_bs within T_{sel} (15.5%) and the remaining 33 (76.7%) had T_bs above T_{sel}.

In both years, T_bs were much closer to T_{sel} than were T_es (Table 1), that is, $\overline{d_b}$ was significantly smaller than $\overline{d_e}$ (1997: $F_{1,1145} = 61.72$, $p < 0.001$; 2017: $F_{1,423} = 64.31$, $p < 0.001$; Table 1), providing un-equivocal evidence of active thermoregulation. This conclusion is independent of the fact that $\overline{T_b}$ may or may not differ significantly from $\overline{T_e}$; $\overline{T_b}$ and $\overline{T_e}$ did not differ significantly in 1997 ($F_{1,1145} = 0.69$, $p = 0.407$), whereas $\overline{T_e}$ was substantially higher than $\overline{T_b}$ in 2017 ($F_{1,423} = 17.16$; $p < 0.001$).

The effectiveness of thermoregulation, after controlling for the effects of time of day in a repeated measures ANOVA with year as the within-subjects factor (Table 3 and Appendix in Supplementary Material), was higher in 1997 ($E = 0.932$) than in 2017 ($E = 0.902$), although the difference was marginally non-significant ($F_{1,11} = 4.42$, $p = 0.059$) due to the confounding effect of the last 1-hour period, whose low value for E in 1997 (Table 3) was caused by a higher ther-mal quality in 1997 than in 2017 rather than by minor differences in the accuracy of thermoregulation. Finally, the total amount of ther-moregulation achieved, as estimated by the difference $\overline{d_e} - \overline{d_b}$, was higher in 1997 than in 2017 before 12:00h, whereas the opposite was true after 12:00h (interaction effect in a repeated measures ANOVA with 1997 vs. 2017 as the within-subjects factor, time inter-val as the between-subjects factor and hourly estimates of $\overline{d_e} - \overline{d_b}$ as data: $F_{1,10} = 25.34$, $p < 0.001$).

3.5 | Selection of patches in full sun, filtered sun or full shade

Selection of sun and shade patches (Figure 3) was analysed by means of a log-linear analysis on the complete dataset of lizard and model observations, classified according to year, time interval and exposure to sun. The final model obtained (maximum likelihood $\chi^2 = 1.92$, df = 4, $p = 0.751$) included three interactions, which we report in decreasing order of contribution to the model's goodness-of-fit (Figure S3). The first interaction (model-lizard x sun exposure x time interval; partial association: $\chi^2 = 313.48$; marginal associa-tion: $\chi^2 = 313.08$; df = 2 and $p < 0.001$ in both cases) shows that in both years our system followed the basic pattern of heliothermic thermoregulation, because the proportion of lizards (models) in full sun tended to decrease (increase) after the early morning. Thus, se-lectivity for sunlit patches was positive before 12:00h and negative after that time, whereas the opposite was true for shaded patches (Figure 3). The second and more relevant interaction (model-lizard x sun exposure x year; partial association: $\chi^2 = 78.60$; marginal as-sociation: $\chi^2 = 70.49$; df = 2 and $p < 0.001$) shows that selectivity for shaded patches increased from 1997 to 2017, whereas selectivity for sunlit patches decreased (Figure 3). Finally, the third interaction (model-lizard x time interval x year) seems to reflect small sample-size biases; although its own independent contribution is small (marginal association: $\chi^2 = 0.03$; df = 2 and $p = 0.865$), it helps to improve the fit of the model (partial association: $\chi^2 = 10.83$; df = 1 and $p < 0.001$; Figure S3).

Before 12:00h, lizards used sunlit patches less frequently, and shaded patches more frequently, in 2017 than in 1997 (Figure 3: $\chi^2 = 17.89$, df = 2, $p < 0.001$), although the availability of sunlit and shaded patches did not change significantly between years

TABLE 3   Variation of thermoregulation statistics in 1997 and 2017 as a function of time of day (1-hour periods between 08:00 and 20:00h): mean ± SD (with sample sizes between parentheses) of accuracy of thermoregulation ($\overline{d_b}$), thermal quality of the environment ($\overline{d_e}$), effectiveness of thermoregulation (E) and amount of thermoregulation achieved ($\overline{d_e} - \overline{d_b}$). All values are given in °C except for E that has no dimension

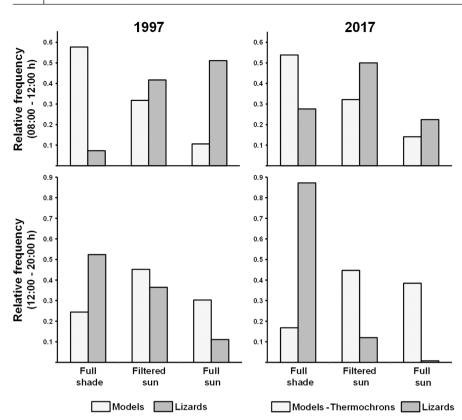| Time of day | Accuracy of thermoregulation ($\overline{d_b}$) | | Thermal quality ($\overline{d_e}$) | | $E = 1 - (\overline{d_e}/\overline{d_b})$ | | $\overline{d_e} - \overline{d_b}$ | |
	1997	2017	1997	2017	1997	2017	1997	2017
08:00–09:00h	3.6 ± 3.1 (6)	5.0 ± 2.5 (2)	15.8 ± 2.9 (90)	11.9 ± 2.6 (30)	0.772	0.580	12.2	6.9
09:00–10:00h	0.6 ± 0.9 (6)	1.1 ± 1.1 (7)	12. 1 ± 3.1 (90)	6.3 ± 2.4 (30)	0.948	0.830	11.5	5.2
10:00–11:00h	0.3 ± 0.6 (4)	1.1 ± 2.5 (7)	8.3 ± 4.0 (90)	5.1 ± 4.1 (30)	0.964	0.794	8.0	4.1
1100–12:00h	0.2 ± 0.4 (6)	0.1 ± 0.2 (6)	6.1 ± 4.8 (90)	6.4 ± 7.3 (30)	0.975	0.984	5.9	6.3
12:00–13:00h	0.7 ± 1.2 (6)	0.7 ± 1.0 (4)	6.5 ± 7.7 (90)	11.3 ± 10.0 (30)	0.900	0.940	5.8	10.7
13:00–14:00h	0.0 ± 0.0 (5)	0.9 ± 0.7 (4)	9.1 ± 9.5 (90)	15.1 ± 12.2 (30)	1.000	0.944	9.1	14.2
14:00–15:00h	0.0 ± 0.1 (5)	1.4 ± 0.6 (4)	12.1 ± 11.2 (90)	21.7 ± 12.9 (30)	0.997	0.937	12.0	20.3
15:00–16:00h	0.0 ± 0.0 (5)	1.9 ± 0.1 (2)	11.1 ± 12.3 (90)	18.9 ± 11.3 (30)	1.000	0.902	11.1	17.0
16:00–17:00h	0.4 ± 0.5 (6)	1.9 ± 0.3 (2)	9.5 ± 9.8 (90)	17.4 ± 11.7 (30)	0.960	0.891	9.1	15.5
17:00–18:00h	0.3 ± 0.7 (6)	2.0 ± 0.8 (9)	7.3 ± 9.2 (90)	11.7 ± 9.0 (30)	0.961	0.832	7.0	9.8
18:00–19:00h	0.0 ± 0.0 (6)	0.7 ± 0.6 (11)	4.5 ± 6.3 (90)	5.9 ± 5.9 (30)	1.000	0.890	4.5	5.3
19:00–20:00h	0.8 ± 1.1 (6)	0.4 ± 0.6 (7)	2.6 ± 3.9 (90)	3.9 ± 4.0 (30)	0.706	0.898	1.8	3.5

FIGURE 3 Use (lizards) and availability (models) of patches in full sun, filtered sun or full shade as a function of time interval (before vs. after 12:00 h) in 1997 and 2017. Sample sizes in 1997 before 12:00 h: 96 (lizards) and 359 (models); in 1997 after 12:00 h: 189 (lizards) and 617 (models); in 2017 before 12:00 h: 58 (lizards) and 327 (models-thermochrons); in 2017 after 12:00 h: 133 (lizards) and 624 (models-thermochrons).

($\chi^2 = 4.28$, df = 2, $p = 0.118$). After 12:00 h, the difference between years became more pronounced. Although the availability of patches in full shade was lower in 2017 ($\chi^2 = 16.07$, df = 2, $p < 0.001$), lizards used those patches much more frequently than in 1997 ($\chi^2 = 44.17$, df = 2, $p < 0.001$), up to the point that in 2017, 87.2% of lizards (vs. 52.4% in 1997) were in full shade when first sighted, and only one (0.8%, vs. 11.1% in 1997) was in full sun.

In both years, the selection of sun and shade patches had a significant contribution to lizard thermoregulation, because the mean deviations from T_{sel} of a lizard population using patch selection as its only thermoregulatory behaviour (d_es weighted by the selection of sun and shade patches, or $\overline{d_{sun-shade}}$; 5.3 ± 6.1°C in 1997, vs. 3.4 ± 4.2°C in 2017) were smaller than $\overline{d_e}$ both in Díaz et al. (2005) ($F_{1,1950} = 131.56$, $p < 0.001$) and in 2017 ($F_{1,718} = 185.92$, $p < 0.001$). In addition, $\overline{d_{sun-shade}}$ was smaller in 2017 than in 1997 ($F_{1,1334} = 32.26$, $p < 0.001$), indicating a more effective use of patch selection as a thermoregulatory mechanism in 2017. The contribution of this mechanism ($\overline{d_e} - \overline{d_{sun-shade}}$) to overall thermoregulation ($\overline{d_e} - \overline{d_b}$) was 3.4°C in 1997 (41.8% of the difference $\overline{d_e} - \overline{d_b}$) and 8.0°C in 2017 (77.9% of the difference $\overline{d_e} - \overline{d_b}$).

4 | DISCUSSION

Overall, the thermoregulatory behaviour of lizards was similar in 1997 and 2017, because in both cases the selection of sunlit versus shaded patches was the most important thermoregulatory behaviour (Díaz & Cabezas-Díaz, 2004, and results of this study). However, differences between years were also remarkable. In 1997,

lizards were active at midday despite low overall thermal suitability by selecting shaded patches with favourable thermal opportunities (Table 2: about one third of the models in full shade had T_es within T_{sel}, and more than half of them had T_es below T_{sel}, indicating potential heat sinks). Moreover, the mean T_b of lizards between 13:00 and 16:00 h (35.9 ± 1.5°C) matched the mean T_e of models in full shade (35.3 ± 3.6°C), and both were within T_{sel} (Díaz & Cabezas-Díaz, 2004).

On the other hand, in 2017 the selection of shaded patches reached its peak, especially after 12:00 h (i.e., during most of the daily activity period), when only one lizard of 133 (<1%) was in full sun when first sighted, whereas 87% were in full shade. This is consistent with the availability of T_es below, within and above T_{sel}, with 67% of full shade T_es above T_{sel} (vs. 15% in 1997). Thus, in 2017 most shaded patches were no longer available as heat sinks for active lizards. Not surprisingly, most lizards (67%, vs. 7% in 1997) had T_bs above T_{sel}, despite the very strong selection of shaded patches. As in 1997, at midday hours (13:00–18:00 h; see Figure 2) the mean T_b of lizards (38.5 ± 0.9°C) was similar to the mean T_e of models in full shade (37.8 ± 2.5°C), but this time both values were above the upper limit of T_{sel}. These results, that confirm the utility of our devices to predict the mean T_b of lizards in the field, cannot be attributed to a concomitant rise in T_{sel}, because T_bs selected in the laboratory were lower, less variable and much closer to T_{sel} than field T_bs (especially after 12:00 h).

Our data indicate that the contribution of the selection of sun and shade patches to the regulation of T_b was larger in 2017 (when a population of models matching the lizards' pattern of exposure to sunlight produced a distribution of T_es that would be 8°C closer to T_{sel} than were randomly distributed T_es) than in 1997 (when such difference would be of 3.4°C). Moreover, the difference $\overline{d_e} - \overline{d_b}$

(Table 1), an alternative index of the effectiveness of thermoregulation (Blouin-Demers & Weatherhead, 2001), was also higher. However, in 2017, despite all the above evidence of active thermoregulation, the high proportion of T_bs above T_{sel} led to indexes of accuracy and effectiveness (sensu Hertz et al., 1993) that indicated poorer thermoregulatory performance than in 1997. Thus, some of our findings indicate a more careful thermoregulation in 2017, because T_bs departed further from T_es, selection of sun and shade patches was more intense, and its contribution to thermoregulation was larger. However, lizard T_bs were closer to T_{sel} in 1997 than in 2017 (i.e., $\overline{d_b}$ was lower), and as a consequence the effectiveness of thermoregulation (i.e., the E index) was larger. As noted by Hertz et al. (1993), no single index is adequate, because the information they provide is complementary; in our system, all measures ($\overline{d_b}$, $\overline{d_e}$ and the derived indexes E and $\overline{d_e} - \overline{d_b}$) were necessary to describe our populations thermal ecology and its inter-annual variation.

These discrepancies can be explained, at least in part, by considering that in high-temperature environments thermoregulatory effort should increase as T_es rise and thermal quality declines (Neel & McBrayer, 2018; Vickers et al., 2011) to avoid the high performance costs of overheating (Huey & Kingsolver, 1993). However, the accuracy and effectiveness of thermoregulation can only increase if lizards can gain access to sites with T_es within T_{sel}. If T_es below the upper limit of T_{sel} are scarce, these statistics will decrease until thermal constraints provoke the cessation of activity (Grant & Dunham, 1988; Jørgensen et al., 2021). In 2017, as long as nearly all available patches were above T_{sel} after 12:00h, the options for behavioural thermoregulation were limited. One possibility would be to move between shaded patches (i.e., shrubs, and perhaps tree shades) until finding one with temperatures within T_{sel} (5% of all T_es, and 32% of T_es in full shade) or below T_{sel} (1% of all T_es, and 8% of T_es in full shade). However, this would entail a relatively long search, a high exposure to overheating while crossing open patches (Díaz, 1991; Lagarde et al., 2012), and possibly an increased risk of predation (Christian & Tracy, 1981; Díaz, 1992; Herr et al., 2020). Another possibility would be to climb trees to increase perch height, because air temperature decreases, and wind speed increases, far from the ground (Adolph, 1990; Bakken, 1989; Geiger, 1965). In addition, trees tend to be more shaded, and to offer surfaces favouring vertical body orientation and hence lowered T_es (Díaz et al., 1996; Heath, 1964). Occasional but not infrequent observations of climbing lizards suggest that such behaviour was much more widespread in 2017 than in previous years. Thus, it seems that lizards were exhausting their heat loss capacity either by microhabitat selection or postural orientation (Adolph, 1990; Brewster & Beaupre, 2019; Díaz et al., 1996; Martin et al., 1995), in spite of which they basically failed to maintain T_bs within T_{sel}.

Our data allowed us to test the predictions of several contrasting hypotheses about the relationships between thermoregulatory effectiveness and environmental thermal quality. The original cost–benefit model of lizard thermoregulation (Huey & Slatkin, 1976) assumed that ectotherms have T_bs below T_{sel}, and incur in costs of raising T_b that make thermoregulation less effective in cooler habitats (e.g., closed forests) than in warmer and more open ones (Huey, 1974).

Thus, Huey and Slatkin (1976) explicitly made clear that their model was centred on T_bs below T_{sel}, although they acknowledged that in warmest habitats there should also be a cost of seeking cooler microhabitats. Afterwards, the model was modified to note that in cool forests the physiological costs of thermoconformity may be higher than those of thermoregulation, which could explain observations of effective thermoregulation in these habitats (Blouin-Demers & Nadeau, 2005; Blouin-Demers & Weatherhead, 2001). Finally, Vickers et al. (2011) extended the original model to high-temperature environments, showing that thermoregulatory effort should increase as T_es rise and thermal quality declines, to avoid the disproportionally high performance costs of overheating (Huey & Kingsolver, 1993). Thus, the models predict lower effectiveness at lower thermal quality for T_es $< T_b$ (Huey & Slatkin, 1976), similar or higher effectiveness at lower thermal quality for T_es $< T_b$ (Blouin-Demers & Nadeau, 2005) or higher effectiveness at lower thermal quality for T_es $> T_b$ (Vickers et al., 2011). Our results provide partial support for the classical cost–benefit model of lizard thermoregulation (Huey & Slatkin, 1976), because lizards thermoregulated with higher accuracy and effectiveness in 1997 than in 2017, that is, when T_es were closer to T_{sel}. However, this was due to a lack of thermal opportunities to keep T_b below the upper limit of T_{sel} rather than to an increased time and energy cost of rising T_b, as postulated in the original model. For the same reason, our data did not support an alternative model for high-temperature environments that predicts higher effectiveness at higher T_es (Vickers et al., 2011), because lizards thermoregulated less effectively in 2017, when T_es were higher. Instead, our results confirm that under unfavourably hot environmental temperatures lizards thermoregulated precisely, and as accurately and effectively as possible, independently of associated costs (Neel & McBrayer, 2018).

We must remark that our study site was an open forest that offered a fine-grained mosaic of sun and shade patches (Figure S4), which should allow lizards to thermoregulate more accurately, move less and expend less energy than they would have done in a coarser grained habitat. This is because ectotherms achieve a better balance between accuracy of thermoregulation and energy expenditure when thermal resources are spatially dispersed than when they are clumped (Sears et al., 2016). In our thermal landscape, T_es in the shade, although mostly above T_{sel}, were always below the critical thermal maximum for this species (43.5°C; Bauwens et al., 1995), and the arrangement and interspersion of sun and shade patches (Figure S4) should allow lizards to minimize costs while shuttling between sun and shade. In fact, the selection of the appropriate compass directions around shrub patches allows lizards to use sunlit patches within short reach (<50cm) from the security of shrubs (Díaz, 1992), minimizing time and energy losses (Huey, 1974; Huey & Slatkin, 1976). However, all these claims assume that at least some patches offer T_es within T_{sel}, and this assumption was hardly met in 2017, when such patches were very scarce, regardless of the spatial structure of the thermal mosaic.

The design of our study allowed us to assess the effects of the rise in temperature per se, disentangled from those of changes in vegetation cover (that might alter the availability of shade; Grimm-Seyfarth et al., 2017; Kearney et al., 2009) or in the methods used

to measure and analyse T_es, T_bs or T_{sel}. Thus, the negative effects of global warming on lizard thermoregulation were not attributable to a pronounced loss of shaded microhabitats, because most lizards were in full shade when first sighted, and inter-annual variation in the availability of shade was of the same magnitude as seasonal variation (Díaz et al., 2005; Díaz & Cabezas-Díaz, 2004). Instead, and in contrast with previous research (Grimm-Seyfarth et al., 2017, Kearney et al., 2009), the impact of climate warming on these lizards was seemingly due to the rise in temperature itself rather than to habitat changes that alter the availability of shade.

Our 2017 data show that for this population the primary thermal challenge was to stay cool, thus resembling arid continental climates more than temperate forests in that behaviour could buffer the impact of warming only by restricting activity to shaded locations (Huey & Tewksbury, 2009; Kearney et al., 2009). Nevertheless, shaded patches, although frequently exceeding T_{sel}, still offered a security margin of at least 2.5°C below the critical thermal maximum. Therefore, and in contrast with desert environments (Grant, 1990; Grant & Dunham, 1988; Lara-Resendiz et al., 2014), lizards could remain active in the shade during midafternoon, but at the cost of accepting T_bs higher than T_{sel} (Grant, 1990). Unexpectedly, we did not observe a peak of activity after the early morning basking period, when thermal quality was high. Perhaps lizards delayed the onset of activity to avoid risk of predation in sunlit patches while their T_bs were still low (Christian & Tracy, 1981; Herr et al., 2020), especially when they could soon attain T_bs within T_{sel} by selecting shaded patches without leaving the security of shrubs (Díaz, 1992).

Our data were collected in the postbreeding season, when gonadal cycles and activity levels decrease, and hepatic lipogenesis increases to fuel fat body cycles (Díaz et al., 1994). A pilot study carried out on 9 May 2017 suggests that global warming has caused thermal environmental conditions to move ahead seasonally (Buonaiuto & Wolkovich, 2021; Menzel et al., 2006). Thus, our preliminary data indicate that spring conditions in 2017 resembled summer conditions in 1997, because after 12:00h lizards selected shaded locations (with T_es within or just below T_{sel}) and rejected sunlit patches (with T_es well above T_{sel}). This is in contrast with the strategy observed in May 1997, when shuttling between sun and shade, rather than selecting sun or shade, was the main mechanism of behavioural thermoregulation between 11:00 and 17:00h (Díaz & Cabezas-Díaz, 2004), and lizards moved randomly among patches as required by the high activity levels typical of the breeding season. If normal shuttling activity is restricted not only in summer but also in spring, this might interfere with reproduction, eventually leading to demographic declines (Cadby et al., 2010; Falaschi et al., 2019). A world-wide correlation between the extent of local warming and lizard extinction rates was reported by Sinervo et al. (2010), who attributed such correlation to energetic shortfalls during spring caused by thermally imposed time constraints on activity. However, summer heat stress may also be important, if it curtails the recovery of energy reserves (Díaz et al., 1994), thereby compromising the next season's reproductive cycle (Derickson, 1976), or if it restricts juvenile dispersal (Massot et al., 2008). Anyway, our T_e data in the summers of 1997 and 2017 (Figure 2) accurately mirrored predicted effects of global warming on the time window available for lizard activity (Huey et al., 2010), although the consequence of such effects was not cessation of activity but elevation of T_bs above T_{sel} for most of the day.

To summarize, our results, based on empirical data rather than on predictions of climate envelop modelling, suggest that the effects of global warming on the thermal biology of lowland lizard populations are already crossing the threshold, because behavioural thermoregulation is losing its ability to buffer environmental change and to weaken the intensity of selection on physiological traits (the so called 'Bogert effect'; Huey et al., 2003). The reason is simple: at least in mid-summer, the availability of T_es within the preferred range is very low, behavioural adjustments cannot prevent overheating, and T_bs rise above T_{sel}. If we consider that our study site was a temperate open forest with a highly heterogeneous mosaic of sun and shade patches (Sears et al., 2016), and that our model organism is the commonest and most widely distributed lizard in the Mediterranean region of the Iberian peninsula (Díaz & Carrascal, 1991), we can conclude that vulnerability of temperate lizards to climate warming may be higher than predicted by global-scale studies already forecasting a dark future (Kearney et al., 2009; Sinervo et al., 2010). In spite of this, and to end with a less negative message, it is also true that our comparison was restricted to a relatively short part of the mid-summer season, and that no demographic effects were apparent (e.g., on population size or numbers of juveniles). Thus, the limited seasonal duration of our sampling period could have affected our conclusions. For instance, lizards could compensate the detrimental effects of climate change during mid-summer by being active earlier in the year and/or enlarging their daily activity time in early spring or late autumn. Future research should focus on a wider seasonal window to fully appreciate the real impact of global warming on behavioural thermoregulation by these lizards.

AUTHOR CONTRIBUTIONS
José A. Díaz conceived the ideas and designed methodology; José A. Díaz, Raúl Izquierdo-Santiago and Alejandro Llanos-Garrido collected and analysed the data; José A. Díaz led the writing of the manuscript; and all authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

We declare no conflict of interest in connection with the work submitted.

DATA AVAILABILITY STATEMENT

Data for this study are available in the Zenodo repository https://doi.org/10.5281/zenodo.7108399 (Díaz et al., 2022).

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REFERENCES

Adolph, S. C. (1990). Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology*, 71, 315–327. https://doi.org/10.2307/1940271

Adolph, S. C., & Porter, W. P. (1993). Temperature, activity, and lizard life histories. *The American Naturalist*, 142, 273–295. https://doi.org/10.1086/285538

Angilletta, M. J. (2009). Thermal adaptation: A theoretical and empirical synthesis. https://doi.org/10.1093/acprof:oso/9780198570875.001.1

Angilletta, M. J., Hill, T., & Robson, M. A. (2002). Is physiological performance optimized by thermoregulatory behavior? A case study of the eastern fence lizard, *Sceloporus undulatus. Journal of Thermal Biology*, 27, 199–204. https://doi.org/10.1016/S0306-4565(01)00084-5

Araújo, M. B., Thuiller, W., & Pearson, R. G. (2006). Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, 33, 1712–1728. https://doi.org/10.1111/j.1365-2699.2006.01482.x

Bakken, G. S. (1989). Arboreal perch properties and the operative temperature experienced by small animals. *Ecology*, 70, 922–930. https://doi.org/10.2307/1941359

Bakken, G. S., & Angilletta Jr., M. J. (2014). How to avoid errors when quantifying thermal environments. *Functional Ecology*, 28(1), 96–107.

Bakken, G. S., & Gates, D. M. (1975). Heat-transfer analysis of animals: Some implications for field ecology, physiology, and evolution. In *Perspectives of biophysical ecology* (pp. 255–290). Springer.

Bauwens, D., Garland Jnr, T., Castilla, A. M., & Van Damme, R. (1995). Evolution of sprint speed in lacertid lizards: Morphological, physiological, and behavioral covariation. *Evolution*, 49, 848–863. https://doi.org/10.1111/j.1558-5646.1995.tb02321.x

Bauwens, D., Hertz, P. E., & Castilla, A. M. (1996). Thermoregulation in a lacertid lizard: The relative contributions of distinct behavioral mechanisms. *Ecology*, 77, 1818–1830. https://doi.org/10.2307/2265786

Belliure, J., Carrascal, L. M., & Díaz, J. A. (1996). Covariation of thermal biology and foraging mode in two mediterranean lacertid lizards. *Ecology*, 77, 1163–1173. https://doi.org/10.2307/2265585

Blouin-Demers, G., & Weatherhead, P. J. (2001). Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology*, 82, 3025–3043. https://doi.org/10.1890/0012-9658(2001)082[3025:teobrs]2.0.co;2

Blouin-Demers, G., & Nadeau, P. (2005). The cost-benefit model of thermoregulation does not predict lizard thermoregulatory behavior. *Ecology*, 86, 560–566. https://doi.org/10.1890/04-1403

Brewster, C. L., & Beaupre, S. J. (2019). The effect of body posture on available habitat and activity-time in a lizard: Implications for thermal ecology studies. *Journal of Thermal Biology*, 82, 10–17. https://doi.org/10.1016/j.jtherbio.2019.03.006

Buckley, L. B. (2008). Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *The American Naturalist*, 171, E1–E19. https://doi.org/10.1086/523949

Buonaiuto, D. M., & Wolkovich, E. M. (2021). Differences between flower and leaf phenological responses to environmental variation drive shifts in spring phenological sequences of temperate woody plants. *Journal of Ecology*, 109, 2922–2933. https://doi.org/10.1111/1365-2745.13708

Cadby, C. D., While, G. M., Hobday, A. J., Uller, T., & Wapstra, E. (2010). Multi-scale approach to understanding climate effects on offspring size at birth and date of birth in a reptile. *Integrative Zoology*, 5, 164–175. https://doi.org/10.1111/j.1749-4877.2010.00201.x

Carrascal, L. M., & Díaz, J. A. (1989). Thermal ecology and spatio-temporal distribution of the Mediterranean lizard *Psammodromus algirus. Holarctic Ecology*, 12, 137–143. https://doi.org/10.1111/j.1600-0587.1989.tb00832.x

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, 1, e1400253. https://doi.org/10.1126/sciadv.1400253

Ceballos, G., Ehrlich, P. R., & Raven, P. H. (2020). Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 13596–13602. https://doi.org/10.1073/pnas.1922686117

Christian, K. A., & Tracy, C. R. (1981). The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia*, 49, 218–223. https://doi.org/10.1007/BF00349191

Cowles, R. B., & Bogert, C. M. (1944). A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History*, 83, 261–296.

Daniel, R. M., & Danson, M. J. (2010). A new understanding of how temperature affects the catalytic activity of enzymes. *Trends in Biochemical Sciences.*, 35, 584–591. https://doi.org/10.1016/j.tibs.2010.05.001

Derickson, W. K. (1976). Lipid storage and utilization in reptiles. *Integrative and Comparative Biology.*, 16, 711–723. https://doi.org/10.1093/icb/16.4.711

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 6668–6672. https://doi.org/10.1073/pnas.0709472105

Díaz, J. A. (1991). Temporal patterns of basking behaviour in a Mediterranean Lacertid lizard. *Behaviour*, 118, 1–14. https://doi.org/10.1163/156853991X00166

Díaz, J. A. (1992). Choice of compass directions around shrub patches by the heliothermic lizard *Psammodromus algirus. Herpetologica*, 48(3), 293–300.

Díaz, J. A. (1994). Effects of body temperature on the predatory behaviour of the lizard *Psammodromus algirus* hunting winged and wingless prey. *Herpetological Journal*, 4(4), 145–150.

Díaz, J. A. (1997). Ecological correlates of the thermal quality of an ectotherm's habitat: A comparison between two temperate lizard populations. *Functional Ecology*, 11, 79–89. https://doi.org/10.1046/j.1365-2435.1997.00058.x

Díaz, J. A., Alonso-Gómez, A. L., & Delgado, M. J. (1994). Seasonal variation of gonadal development, sexual steroids, and lipid reserves in a population of the lizard *Psammodromus algirus. Journal of Herpetology*, 28(2), 199–205. https://doi.org/10.2307/1564621

Díaz, J. A., & Cabezas-Díaz, S. (2004). Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. *Functional Ecology*, *18*, 867–875. https://doi.org/10.1111/j.0269-8463.2004.00916.x

Díaz, J. A., Cabezas-Díaz, S., & Salvador, A. (2005). Seasonal changes in the thermal environment do not affect microhabitat selection by *Psammodromus algirus* lizards. *Herpetological Journal*, *15*(4), 295–298.

Díaz, J. A., & Carrascal, L. M. (1991). Regional distribution of a Mediterranean lizard: Influence of habitat cues and prey abundance. *Journal of Biogeography*, *18*, 291. https://doi.org/10.2307/2845399

Díaz, J. A., Díaz-Uriarte, R., & Rodriguez, A. (1996). Influence of behavioral thermoregulation on the use of vertical surfaces by Iberian wall lizards *Podarcis hispanica*. *Journal of Herpetology*, *30*, 548.

Díaz, J. A., Iraeta, P., & Monasterio, C. (2006). Seasonality provokes a shift of thermal preferences in a temperate lizard, but altitude does not. *Journal of Thermal Biology*, *31*(3), 237–242.

Díaz, J. A., Izquierdo-Santiago, R., & Llanos-Garrido, A. (2022). Lizard thermoregulation revisited after two decades of global warming. *Zenodo*, https://doi.org/10.5281/zenodo.7108399

Falaschi, M., Manenti, R., Thuiller, W., & Ficetola, G. F. (2019). Continental-scale determinants of population trends in European amphibians and reptiles. *Global Change Biology*, *25*, 3504–3515. https://doi.org/10.1111/gcb.14739

Garcia, R. A., Cabeza, M., Rahbek, C., & Araújo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, *344*(6183), 1247579. https://doi.org/10.1126/science.1247579

Geiger, R. (1965). *The climate near the ground*. Harvard University Press.

Grant, B. W. (1990). Trade-offs in activity time and physiological performance for thermoregulating desert lizards, *Sceloporus merriami*. *Ecology*, *71*(6), 2323–2333. https://doi.org/10.2307/1938643

Grant, B. W., & Dunham, A. E. (1988). Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology*, *69*, 167–176. https://doi.org/10.2307/1943171

Grimm-Seyfarth, A., Mihoub, J. B., & Henle, K. (2017). Too hot to die? The effects of vegetation shading on past, present, and future activity budgets of two diurnal skinks from arid Australia. *Ecology and Evolution*, *7*(17), 6803–6813. https://doi.org/10.1002/ece3.3238

Heath, J. E. (1964). Reptilian thermoregulation: Evaluation of field studies. *Science*, *146*, 784–785. https://doi.org/10.1126/science.146.3645.784

Herr, M. W., Avery, J. D., Langkilde, T., & Howey, C. A. F. (2020). Trade-off between thermal quality and predation risk at timber rattlesnake gestation sites. *Journal of Herpetology*, *54*, 196–205. https://doi.org/10.1670/18-073

Hertz, P. E. (1992). Evaluating thermal resource partitioning by sympatric lizards *Anolis cooki* and *A. cristatellus*: A field test using null hypotheses. *Oecologia*, *90*, 127–136. https://doi.org/10.1007/BF00317818

Hertz, P. E., Huey, R. B., & Stevenson, R. D. (1993). Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *The American Naturalist*, *142*, 796–818. https://doi.org/10.1086/285573

Hu, Y. C., Lu, H. L., Cheng, K. M., Luo, L. G., & Zeng, Z. G. (2019). Thermal dependence of feeding performance and resting metabolic expenditure in different altitudinal populations of toad-headed lizards. *Journal of Thermal Biology*, *80*, 16–20. https://doi.org/10.1016/j.jtherbio.2019.01.001

Huey, R. B. (1974). Behavioral thermoregulation in lizards: Importance of associated costs. *Science*, *184*, 1001–1003. https://doi.org/10.1126/science.184.4140.1001

Huey, R. B., Hertz, P. E., & Sinervo, B. (2003). Behavioral drive versus behavioral inertia in evolution: A null model approach. *The American Naturalist*, *161*, 357–366. https://doi.org/10.1086/346135

Huey, R. B., & Kingsolver, J. G. (1993). Evolution of resistance to high temperature in ectotherms. *The American Naturalist*, *142*, S21–S46. https://doi.org/10.1086/285521

Huey, R. B., Losos, J. B., & Moritz, C. (2010). Are lizards toast? *Science*, *328*, 832–833. https://doi.org/10.1126/science.1190374

Huey, R. B., & Slatkin, M. (1976). Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology*, *51*, 363–384. https://doi.org/10.1086/409470

Huey, R. B., & Tewksbury, J. J. (2009). Can behavior douse the fire of climate warming? *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 3647–3648. https://doi.org/10.1073/pnas.0900934106

Jørgensen, L. B., Malte, H., Ørsted, M., Klahn, N. A., & Overgaard, J. (2021). A unifying model to estimate thermal tolerance limits in ectotherms across static, dynamic and fluctuating exposures to thermal stress. *Scientific Reports*, *11*, 12840. https://doi.org/10.1038/s41598-021-92004-6

Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 3835–3840. https://doi.org/10.1073/pnas.0808913106

Lagarde, F., Louzizi, T., Slimani, T., El Mouden, H., Ben Kaddour, K., Moulherat, S., & Bonnet, X. (2012). Bushes protect tortoises from lethal overheating in arid areas of Morocco. *Environmental Conservation.*, *39*, 172–182. https://doi.org/10.1017/S0376892911000634

Lara-Resendiz, R. A., Jezkova, T., Rosen, P. C., & Méndez-De La Cruz, F. R. (2014). Thermoregulation during the summer season in the Goode's horned lizard *Phrynosoma goodei* (Iguania: Phrynosomatidae) in Sonoran Desert. *Amphibia-Reptilia*, *35*, 161–172. https://doi.org/10.1163/15685381-00002938

Licht, P., Dawson, W. R., Shoemaker, V. H., & Main, A. R. (1966). Observations on the thermal relations of western Australian lizards. *Copeia*, *1966*, 97. https://doi.org/10.2307/1440766

Martin, J., Lopez, P., Carrascal, L. M., & Salvador, A. (1995). Adjustment of basking postures in the high-altitude Iberian rock lizard (*Lacerta monticola*). *Canadian Journal of Zoology*, *73*, 1065–1068. https://doi.org/10.1139/z95-126

Massot, M., Clobert, J., & Ferrière, R. (2008). Climate warming, dispersal inhibition and extinction risk. *Global Change Biology*, *14*, 461–469. https://doi.org/10.1111/j.1365-2486.2007.01514.x

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aaasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Finn, M., … Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, *12*, 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Neel, L. K., & McBrayer, L. D. (2018). Habitat management alters thermal opportunity. *Functional Ecology*, *32*, 2029–2039. https://doi.org/10.1111/1365-2435.13123

Niu, Z., Li, M., Pu, P., Wang, H., Zhang, T., Tang, X., & Chen, Q. (2021). Effects of temperature on the locomotor performance and contraction properties of skeletal muscle from two *Phrynocephalus* lizards at high and low altitude. *Journal of Comparative Physiology B*, *191*, 907–916. https://doi.org/10.1007/s00360-021-01391-9

Sears, M. W., Angilletta, M. J., Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., Rusch, T. W., & Mitchell, W. A. (2016). Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 10595–10600. https://doi.org/10.1073/pnas.1604824113

Shine, R., & Kearney, M. (2001). Field studies of reptile thermoregulation: How well do physical models predict operative temperatures? *Functional Ecology*, *15*, 282–288. https://doi.org/10.1046/j.1365-2435.2001.00510.x

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M. L., Meza-Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Victoriano Sepulveda, P., Rocha, C. F., Ibargüengoytía, N., Aguilar Puntriano, C., Massot, M., … Sites Jr., J. W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, *328*, 894–899. https://doi.org/10.1126/science.1184695.

Van Berkum, F. H. (1986). Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution*, *40*, 594–604. https://doi.org/10.1111/j.1558-5646.1986.tb00510.x

Van Damme, R., Bauwens, D., & Verheyen, R. F. (1991). The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. *Functional Ecology*, *5*, 507. https://doi.org/10.2307/2389633

Vickers, M., Manicom, C., & Schwarzkopf, L. (2011). Extending the cost-benefit model of thermoregulation: High-temperature environments. *The American Naturalist*, *177*, 452–461. https://doi.org/10.1086/658150

Vickers, M., & Schwarzkopf, L. (2016). A simple method to predict body temperature of small reptiles from environmental temperature. *Ecology and Evolution*, *6*, 3059–3066. https://doi.org/10.1002/ece3.1961

Vitt, L. J., & Sartorius, S. S. (1999). HOBOs, Tidbits and lizard models: The utility of electronic devices in field studies of ectotherm thermoregulation. *Functional Ecology*, *13*, 670–674. https://doi.org/10.1046/j.1365-2435.1999.00357.x

Voosen, P. (2021). Global temperatures in 2020 tied record highs. *Science*, *371*, 334–335. https://doi.org/10.1126/science.371.6527.334

Zamora-Camacho, F. J., Rubiño-Hispán, M. V., Reguera, S., & Moreno-Rueda, G. (2015). Thermal dependence of sprint performance in the lizard *Psammodromus algirus* along a 2200-meter elevational gradient: Cold-habitat lizards do not perform better at low temperatures. *Journal of Thermal Biology*, *52*, 90–96. https://doi.org/10.1016/j.jtherbio.2015.06.003

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