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Interaction of hydric and thermal conditions drive geographic variation in thermoregulation in a widespread lizard

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Abstract. Behavioral thermoregulation is an efficient mechanism to buffer the physiological effects of climate change. Thermal ecology studies have traditionally tested how thermal constraints shape thermoregulatory behaviors without accounting for the potential major effects of landscape structure and water availability. Thus, we lack a general understanding of the multifactorial determinants of thermoregulatory behaviors in natural populations. In this study, we quantified the relative contribution of elevation, thermal gradient, moisture gradient, and landscape structure in explaining geographic variation in thermoregulation strategies of a terrestrial ectotherm species. We measured field-active body temperature, thermal preferences, and operative environmental temperatures to calculate thermoregulation indices, including thermal quality of the habitat and thermoregulation efficiency for a very large sample of common lizards (*Zootoca vivipara*) from 21 populations over 3 yr across the Massif Central mountain range in France. We used an information-theoretic approach to compare eight a priori thermo-hydroregulation hypotheses predicting how behavioral thermoregulation should respond to environmental conditions. Environmental characteristics exerted little influence on thermal preference with the exception that females from habitats with permanent access to water had lower thermal preferences. Field body temperatures and accuracy of thermoregulation were best predicted by the interaction between air temperature and a moisture index. In mesic environments, field body temperature and thermoregulation accuracy increased with air temperature, but they decreased in drier habitats. Thermoregulation efficiency (difference between thermoregulation inaccuracy and the thermal quality of the habitat) was maximized in cooler and more humid environments and was mostly influenced by the thermal quality of the habitat. Our study highlights complex patterns of variation in thermoregulation strategies, which are mostly explained by the interaction between temperature and water availability, independent of the elevation gradient or thermal heterogeneity. Although changes in landscape structure were expected to be the main driver of extinction rate of temperate zone ectotherms with ongoing global change, we conclude that changes in water availability coupled with rising temperatures might have a drastic impact on the population dynamics of some ectotherm species.

Key words: body temperature; elevational gradient; landscape heterogeneity; moisture gradient; non-avian reptiles.

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INTRODUCTION

In a climate changing world, as average temperatures and frequency of heatwaves increase (IPCC 2014), organisms are exposed to repeated challenges in their capacity to regulate their body temperature in order to optimize their physiological performance and fitness (Angilletta et al. 2002). Behavioral thermoregulation (i.e., regulation of body temperature through behavioral means; Angilletta 2009) is essential for ectotherms to rapidly adjust performance level to temperature fluctuations (Kearney et al. 2009, Huey et al. 2012, Buckley et al. 2015, Gunderson and Stillman 2015). These behaviors involve flexible changes in activity patterns (Porter et al. 1973, Grant 1990), microhabitat selection (Kleckova et al. 2014), movement decisions (Vickers et al. 2016), or adjustments in body posture (Barton et al. 2014). The suitability of a habitat for ectotherms depends on the spatial variation in local temperatures and the tradeoffs associated with the costs and benefits of thermoregulatory behaviors (Sunday et al. 2014). For example, differences in body temperature along elevational gradients can be small or even nonexistent in some ectotherms despite substantial changes in ambient temperatures (Van Damme et al. 1989, Zamora-Camacho et al. 2013), because behavioral compensation allows animals to attain their optimal body temperatures even in cold environments by increasing their thermoregulation effort (Adolph 1990, Gvoždík 2002). However, the predictors of these costs and benefits from thermoregulation are diverse, and we lack multivariate studies of geographic variation in thermoregulatory behaviors (Angilletta 2009).

The classical cost and benefit model of thermoregulation predicts that behavioral strategies of ectotherms should range from active thermoregulation (i.e., maintaining a constant body temperature despite environmental variation) to thermoconformity (i.e., body temperature matches environmental conditions) depending on the costs of thermoregulation imposed by local thermal conditions (Huey and Slatkin 1976). When local thermal conditions deviate from an organism's preferred body temperature, the model predicts that ectotherms should lower their thermoregulation effort and accuracy (Huey and Slatkin 1976, Herczeg et al. 2006, 2008). However, when benefits of active thermoregulation increase in poor quality habitats and there is a risk of overheating, increased thermoregulation effort and accuracy can be beneficial for ectotherms despite costs due to missed opportunities for foraging or other behaviors (Blouin-Demers and Weatherhead 2002, Blouin-Demers and Nadeau 2005, Vickers et al. 2011). Thus, terrestrial ectotherms often increase thermoregulation effort in poor thermal environments to realize the benefits of attaining preferred temperatures or avoiding lethal overheating (Sunday et al. 2014, Buckley et al. 2015, Artacho et al. 2017). Given that mean thermal conditions change with elevation, latitude, or time of the year, an implicit prediction of the cost and benefit model of thermoregulation is that thermoregulatory behaviors should change along an elevational or latitudinal gradient (Hypothesis 1, Table 1; Adolph 1990, Caldwell et al. 2017) or in response to short-term changes in ambient temperatures (Hypothesis 2, Table 1; Blouin-Demers and Weatherhead 2002). The relative importance of short-term changes in thermoregulatory behaviors vs. stable differences across a geographic gradient is not yet clear and can only be elucidated with multiyear studies of several populations (Samietz et al. 2005, Huey et al. 2012, Caldwell et al. 2017).

Recent models and experiments have suggested that the spatial heterogeneity of thermal conditions within a habitat might be a better predictor of the costs of thermoregulation than the mean thermal environment (Caillon et al. 2014, Sears and Angilletta 2015, Sears et al. 2016, Basson et al. 2017). Heterogeneity of thermal conditions at a small spatial scale can be caused by differences in vegetation height or topography (i.e. shade availability) within the home ranges of animals. One prediction from these recent models is that spatial heterogeneity reduces the costs of thermoregulation by allowing energy-free investment in basking through shuttling of an individual between different thermal microhabitats (Sears and Angilletta 2015, Sears et al. 2016). Thus, behavioral thermoregulation should be more efficient in heterogeneous habitats than in homogeneous habitats even when the mean thermal quality of the habitat is poor (e.g., Goller et al. 2014). Based on the individual-based model of thermoregulatory behavior in a ground dwelling ectotherm of Sears and Angilletta (2015), a low thermoregulation efficiency should, for example, evolve in more homogeneous habitats (Hypothesis 3, Table 1). In addition, the importance of landscape heterogeneity should be more critical under strong thermal constraints, whether cold or hot, because landscape heterogeneity favors a greater reduction in the costs of thermoregulation when mean conditions deviate from the preferred temperature range (Hypothesis 4, Table 1; Herczeg et al. 2003, Sears et al. 2016). Unfortunately, support for both predictions are rare, since most comparative studies of behavioral thermoregulation are based on the mean thermal quality at the population level without consideration of the spatial distribution of microhabitats within a landscape (Gvoždík 2002, Herczeg et al. 2003, Blouin-Demers and Nadeau 2005). As suggested by Sears et al. (2016), we need an explicit map of operative environmental temperatures (T_e, i.e., steady-state temperature of the animal without behavioral or physiological regulation; Bakken et al. 1985) from each habitat to reach a full understanding of the costs of thermoregulation across an environmental gradient.

Ongoing climate change is not only modifying the thermal quality of the environment, but also affects the water availability, through changes in precipitation rates and frequency and magnitude of drought (Field et al. 2012). Water availability, in the form of moisture or free-

Table 1. Our sampling protocol aims to quantify the relative importance of climate and habitat factors in explaining the geographical variation in thermoregulation statistics of the common lizard (*Zootoca vivipara*).

No.	Hypotheses	Explanation	Variables in statistical models	References
1	elevational variation	Thermoregulation strategies are shaped by thermal clines and differences in duration of seasonal activity correlated with elevation.	elevation (ELE) of the study site	Adolph (1990), Caldwell et al. (2017)
2	annual thermal conditions	Thermoregulation strategies respond flexibly to annual changes in thermal conditions (hot years, cold years).	average daily minimal (respectively, maximal) air temperatures $T_{\min}$ (respectively, $T_{\max}$) of the year and study site	Blouin-Demers and Weatherhead (2002)
3	thermal landscape	Different thermal landscapes occur among sites because of differences in forest cover and the spatial distribution of vegetation. The spatial distribution of shade and full-sun patch dictates thermoregulation strategies.	evenness in operative temperature microhabitats (TE), forest cover index (FCI), homogeneity in the thermal landscape (*H*) of the study site	Sears and Angilletta (2015), Sears et al. (2016)
4	condition-dependent thermal landscape	The effect of thermal landscape on thermoregulation strategies depends on persistent differences in temperature (thermal cline) or yearly differences in temperature, such that for example spatial heterogeneity is critical only in hot or cold conditions.	ELE × (TE, FCI or H) $T_{\min}$ × (TE or H) $T_{\max}$ × (THE, FCI or H)	Sears and Angilletta (2015), Sears et al. (2016)
5	historical climate aridity	If water is a limiting factor, persistent differences in water availability or habitat moisture caused by climate differences in rainfall and temperatures should be the main predictor of thermoregulation statistics. Dry climate and habitat should select for water conservation strategies in dry environments.	Emberger pluviometric quotient (Q, an aridity index) or the presence/absence index of free water (FW) of the study site	Davis and DeNardo (2009), Lillywhite et al. (2012), Rozen-Rechels et al. (2020)
6	annual moisture conditions	The instantaneous risk of desiccation is correlated with dry environmental conditions. Site specific, annual, variation in air moisture select for plastic changes in thermoregulation strategies and explain most of their variation.	average daily maximum in air moisture ($P_{\max}$) of the year	Rozen-Rechels et al. (2020)
7	thermo-hydroregulation	If thermoregulation at high body temperatures compromises water balance, thermoregulation strategies should respond differently to short-term changes in temperature or thermal clines depending on water availability of the site or moisture conditions of the year.	ELE × (Q, FW, $\mathrm{P}_{\max}$) $T_{\min}$ × (Q, FW, $\mathrm{P}_{\max}$) $T_{\max}$ × (Q, FW)	Rozen-Rechels et al. (2019)
8	thermo-hydroregulation landscape	The use of diverse thermal microhabitats could also be dictated by differences in water loss rates. A wet and hot homogeneous habitat could be of lower cost than a dry one if water loss is the main thermoregulation costs	Q × (TE, FCI, H) FW × (TE, FCI, H) $P_{\max}$ × (TE, FCI, H)	Rozen-Rechels et al. (2019)

Note: This table summarizes our working hypotheses and defines how these working hypotheses were tested with statistical models.

standing water in the environment, is another predictor of the costs of thermoregulatory behavior. Water restriction can compromise the regulation of water balance and the accuracy of thermoregulation at high body temperatures (e.g., Dupoué et al. 2015, Lourdais et al. 2017, Pirtle et al. 2019). Water restriction in the environment is therefore expected to decrease behavioral activity (Lorenzon et al. 1999, Kearney et al. 2018, Pirtle et al. 2019) and to change microhabitat selection such that ectotherms avoid the risks of dehydration (Pintor et al. 2016, Pirtle et al. 2019). In addition, thermal performance curves are often maximized at lower body temperatures in dehydrated compared to fully-hydrated animals, which may select for lower preferred body temperature and thermal depression in more xeric environments (e.g., Ladyman and Bradshaw 2003, Muir et al. 2007, Anderson and Andrade 2017). The number of studies focusing on the effect of water availability and water balance on behavioral thermoregulation in ectotherms is growing (Pintor et al. 2016, Rozen-Rechels et al. 2020), but few have quantified the joint effects of water availability and the thermal environment on thermoregulation strategies to date. Variation in water availability in the environment may be described by persistent differences in the presence or absence of free water (Dupoué et al. 2017*b*, 2018) or by moisture gradients (Tieleman et al. 2003). When population sites have consistent differences in the availability of permanent water, adaptive shifts towards lower optimal body temperatures can be expected to limit water loss in dry environments where the water debt cannot be recovered by drinking (Hypothesis 5 in Table 1; Davis and DeNardo 2009, Lillywhite et al. 2012). Moreover the magnitude of change in thermoregulation strategies should be greater in xeric than in mesic habitats as the environment gets warmer (Hypothesis 7, Table 1) and in homogeneous landscapes (Hypothesis 8 in Table 1) as proposed by the concept of thermo-hydroregulation (Rozen-Rechels et al. 2019). Another possibility is that variation in water availability in the environment is caused by short-term changes in air moisture or rainfall due to weather fluctuations. Rainfall variability has for example been shown to drive changes in behavioral activity of ectotherms or to change their microhabitat selection (Davis and DeNardo 2009, Ryan et al. 2016, Kearney et al. 2018). This variability can be described by year to year differences in the risk of dehydration for which atmospheric water vapor pressure is an accurate predictor (Spotila 1972, Lourdais et al. 2017). In this context, one can therefore predict that dry local conditions, favoring dehydration and characterized by low water vapor pressure in the air, should alter thermoregulation strategies just as surface water would (Rozen-Rechels et al. 2020; Hypothesis 6 in Table 1).

All things considered, quantifying the relative importance of thermal conditions, hydric conditions and habitat heterogeneity thus requires comparative, multiyear studies to understand the key drivers of geographic variation in thermoregulatory behavior. Here, we surveyed geographical variation in the thermoregulation strategies of a cold-adapted vertebrate species, the common lizard (*Zootoca vivipara*, Lacertidae, Lichtenstein, 1823) over three years. The sampled sites included in our study are located at the southern margin of the distribution of the species. Previous work has demonstrated that climate warming induces changes in life-history strategies in these populations (e.g., Chamaillé-Jammes et al. 2006). Annual variability in the phenology of reproduction as well as reproductive effort correlates with changes in ambient temperature (Le Galliard et al. 2010, Rutschmann et al. 2016*a*,*b*). Moreover, geographic variation in water availability influences the species' thermal ecology and water balance (Lorenzon et al. 1999, 2001, Dupoué et al. 2017*a*, 2018) as well as their physiological sensitivity to extreme thermal conditions (Dupoué et al. 2018). Thermal and water conditions further interact in predicting dispersal and population extinctions (Massot et al. 2002, 2008, Dupoué et al. 2017*b*). The common lizard has been described as an active, efficient thermoregulator relying on flexible changes in microhabitat selection and basking behavior to regulate its body temperature (Gvoždík 2002, Herczeg et al. 2003). Although body temperatures vary among populations due to differences in local temperature, previous comparative studies have suggested that thermal preferences and indices of thermoregulation do not differ between low and high elevation populations with contrasted mean thermal conditions (Van Damme et al. 1990, Gvoždík 2002). Here, we moved a step forward to sample 21 populations and ca. 2000 lizards along an elevational gradient at a regional scale (Massif Central, France) over three summers to gather data across 31 population–year combinations. We used an information-theoretic approach to test the eight hypotheses summarized in Table 1 and evaluate how the thermal and hydric quality of the environment may explain variation in behavioral thermoregulation of the common lizard.

Material and Methods

Study species and sampling

The common lizard (*Zootoca vivipara*) is a widespread Eurasian ectotherm species distributed from the southern European mountains up to Finland and from Western Europe to the Pacific Coast of Russia. This species inhabits wetlands (e.g., peatbogs and marshes), mesic meadows, and heathlands where persistence of local populations depends on cool climates and high soil moisture conditions (Lorenzon et al. 2001, Massot et al. 2002, Dupoué et al. 2018). Most of the natural populations outside of the southern Europe refugia are characterized by ovoviviparous reproduction, including the focal populations of in this study. In our study area, males emerge from hibernation in April. Yearlings and adult females emerge later from end of April to early May. Mating occurs soon after the emergence of adult females and gestation lasts approximately two months. Parturition occurs between early July and early August depending on weather conditions (Bleu et al. 2013, Rutschmann et al. 2016*b*).

Our focal populations are located in the mountain ranges of Massif Central in south-central France on a 500-m elevation gradient clustering most of the species population in the area (see Appendix S1: Table S1). The study sites are located in a variety of habitat types and include: wet meadows, heathlands, and glades within dense forest patches. The habitat may also include open forest with dispersed trees or shrubby vegetation (pine trees, *Pinus* spp.; juniper trees, *Juniperus* spp.; scotch broom, *Cytisus scoparius*; and gorse, *Ulex* spp.) or low-growth shrubs (heather, *Caluna vulgaris*; and blueberry, *Vaccinium* spp.) that offer contrasting thermal microhabitats and shelters. We sampled 21 populations between 2016 and 2018. Most populations were sampled at least twice in differing years, but some were only sampled once (Appendix S1: Table S1). Sites ranged in size from 0.6 to 12 ha and occurred in a diversity of habitats ranging from open meadows without permanent access to water to forest clearing with free-standing water (Fig. 1 and Appendix S1: Table S1). The two closest sites were more than 700 m away from each other, and the landscape in the region is fragmented by roads, closed forest, pasture, and other unsuitable habitats for the species.

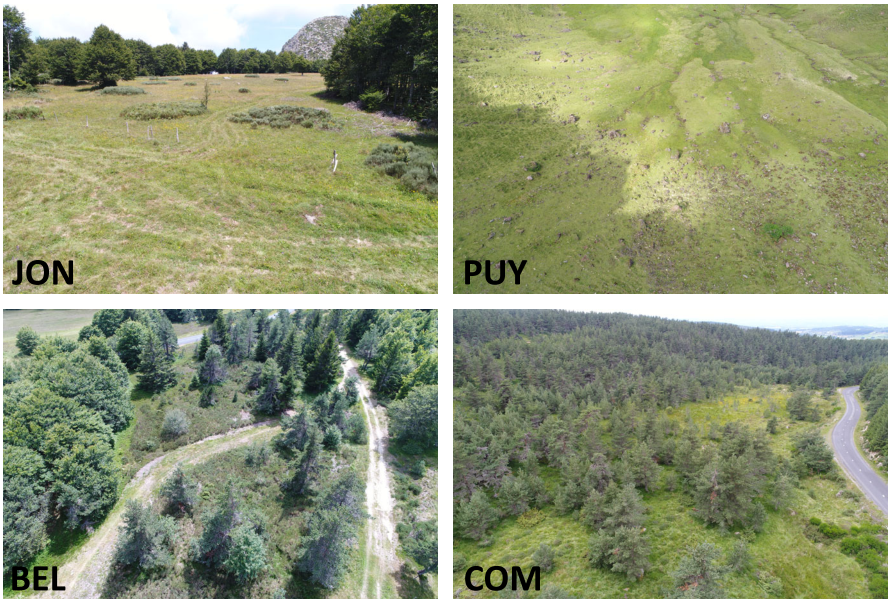

FIG. 1. Aerial views of four contrasting sites. JON and PUY are two open habitats. The former is situated in a clearing, whereas the latter is a vast grassland within the crater of the extinct volcano. BEL and COM are two populations with substantial forest cover. The availability of water differs among the locations. Streams traverse PUY and COM and the soil is saturated with water in portions of the site; other areas are peat bogs. In contrast, free water is not available at JON and BEL; both are much drier than COM and PUY, especially during the summer time. No bogs can be found at JON and BEL. Photographs were taken in 2017 with a Phantom 4 Pro drone (DJI, Shenzen, China) concomitant with a separate project to generate vegetation maps (Appendix S4: Fig. S1) of each sample site.

The probability that two sites are connected by a permanent flow of migrants is thus low. Capture dates in focal populations varied to accommodate current weather conditions within each sample year. Our capture dates occurred from 20 June to 29 June 2016, from 12 June to 26 June 2017 and from 9 June to 28 June 2018. In each population, we captured yearlings (less than 2 yr old), adult gravid females and adult males (2 yr old or more). We attempted to capture 20–24 adult females, 10 adult males, and 20 yearlings (sex ratio 1:1) per population (see Appendix S2: Table S1). We measured snout–vent length (average SVL ± SD; yearlings 43 ± 6 mm, adult females 62 ± 5 mm, adult males 55 ± 4 mm) and body mass (BM; yearlings 1.50 ± 0.57 g, adult females 4.47 ± 1.32 g, adult males 3.35 ± 0.67 g).

Adult gravid females and adult males were then brought to the laboratory and housed in individual terraria (females 25 × 15 × 16 cm, males 18 × 11 × 12 cm) with peat soil and a shelter. A temperature gradient of 20–35°C, which is representative of the gradient of temperatures found in natural population sites, was created in the terraria for 6 h in the day (from 09:00 to 12:00 and from 14:00 to 17:00) with 25 W incandescent bulbs placed above one side of each of the terrarium to allow thermoregulation. Water was supplied to individuals by misting the terraria three times per day at 09:00, 12:00, and 17:00. Individuals were not fed for two days after capture to ensure a post-absorptive state during the thermal preference tests (see *Thermal preferences and thermoregualtion traits*). Lizards were fed once every two days with two domestic crickets (*Acheta domestica*) until they were released (after parturition for females or after measurements for males; Rutschmann et al. 2016*b*, Dupoué et al. 2018). In one population subject to a long-term mark–recapture study (ROB; Appendix S2: Table S1), we also brought yearlings back to the laboratory to assess age-related differences in thermal preferences.

Description of climate and habitat characteristics

We described the focal sites using well-defined meteorological, microhabitat and landscape variables to test our hypotheses (summarized in Appendix S1: Table S1, with locations and area of the sites). First, elevation ELE and the Emberger pluviometric quotient Q (Daget 1977, see below, Fig. 2) were scored in order to test for consistent differences among populations along the elevational cline and along a historic climatic cline. The calculation of elevation allowed us to test for potential trends of thermoregulatory strategies variations from the lowest altitude populations in this geographic area up to mountain tops. The elevation gradient in our study area ranged from 1,099 to 1,527 m. In addition, the calculation of the pluviometric quotient Q allowed us to test for a consistent trend along a historic, climatic gradient of aridity (lower precipitations and higher temperatures). To calculate the pluviometric quotient,

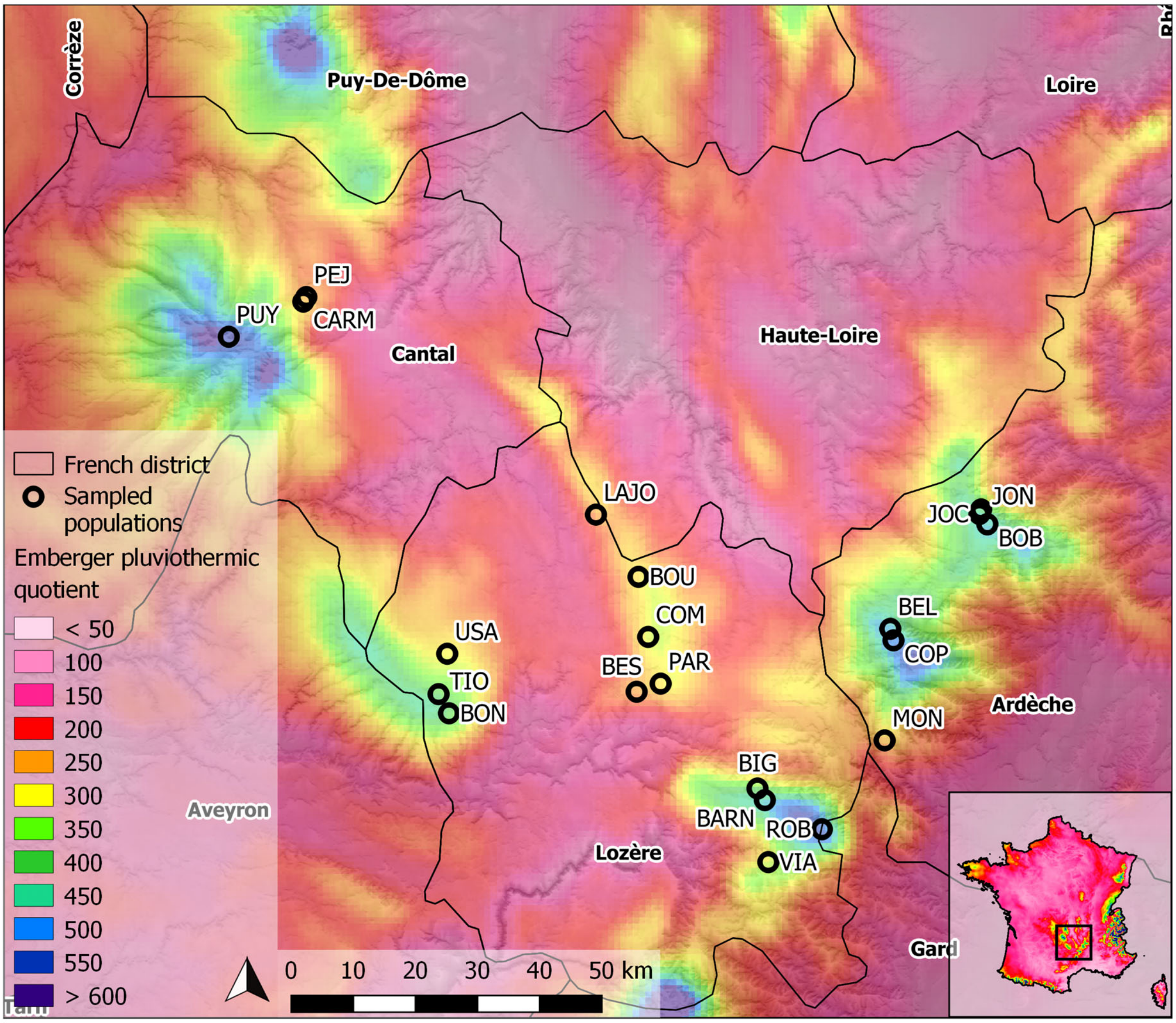

FIG. 2. Geographic location of studied populations in the Massif Central mountain range from France (see also Appendix S1: Table S1) with a heat map of the Emberger pluviometric quotient Q measuring long-term historical differences in climate dryness among sites (low values of Q indicate more arid climates).

meteorological variables were extracted from the AURELHY database of temperature and precipitation records over France from 1971 to 2000 extrapolated at a 1-km^2 scale (provided by Meteo France, see Bénichou and Breton [1987] for a description of the data set). This database has the finest resolution grid and accounts for relief differences in interpolating the data, which is important for extracting correct statistics for each population in this geographic area. From these data, the Emberger pluviometric quotient for each site was given by

$$Q = \frac{100 \times P}{T^2_{\mathrm{ARLmax}} - T^2_{\mathrm{ARLmin}}}$$

where P is the average annual precipitation in cm and T_{ARLmin} (respectively, T_{ARLmax}) the average of daily minimum temperature of the coldest month (respectively, average of daily maximum temperature of the warmest month). The pluviometric quotient among the focal sites ranged from 228.1 to 563.3. None of the sites could thus be characterized as arid.

Second, we obtained local weather conditions for each year at each site including air temperature and water vapor pressure. These variables allowed us to measure both geographic and temporal changes in the microclimate conditions, and therefore quantify the specific meteorological conditions during the study period instead of long-term historical trends. We measured local weather conditions at each site and each year with one to three temperature and humidity data loggers placed on the ground in the shade of the representative vegetation (Hygrochron iButtons, Maxim Integrated Products, Sunnyvale, California, USA, ± 0.5°C and 5% relative humidity [RH]). At one site (ROB), we placed an additional 18 temperature loggers in different types of vegetation to calculate spatial variation in thermal conditions. For each sample site, we calculated the average 10:00 to 18:00 minimal and maximal air temperatures (hereafter called T_{min} and T_{max}) and the average 10:00 to 18:00 maximal water vapor pressure (hereafter called P_{max}; see Appendix S3 for further information on measurements, calculations, and choice of variable as well as Rutschmann et al. 2016*a* and Dupoué et al. 2018). We restricted these calculations from 10:00 to 18:00 in order to compare local microclimatic conditions during the diurnal activity period of the lizards, because this interval is the most relevant to thermal quality of the environment during thermoregulation.

Third, we characterized habitat attributes including the presence of free water (permanent access or temporary access, hereafter called FW, see Dupoué et al. 2017*b*), an index of forest cover, the evenness in thermal microhabitat diversity and the homogeneity of the thermal landscape. Sixteen sites had permanent sources of water, either streams or ponds, whereas five sites had access to temporary pools or streams. To characterize the landscape, we took aerial georeferenced digital photographs of all sites with a Phantom 4 Pro drone (DJI, Shenzen, China). In most cases except for small sites (BARN, MON, LAJO), we took a georeferenced grid of pictures centered on each site with Pix4Dcapture (Pix4D SA, Prilly, Switzerland) and then reconstructed a georeferenced orthophoto with the Maps Made Easy application (*available online*).[12] For small sites, the map was created from one picture and we aligned georeferencing with control points accurately geolocated on Google Earth maps (version 7.3.2, Google 2019). From each georeferenced orthophoto, we then generated an eight-level vegetation map by creating a vector layer where each polygon corresponds to a patch of one of eight predefined vegetation types (grass, heather, bilberry, tree, bush, rock, naked soil, and dead tree). Vector layers were constructed in QGIS (version 2.18; QGIS Development Team 2018) and downscaled to a 1-m accuracy map (Appendix S4: Fig. S1).

We assessed the thermal quality of each vegetation type (i.e., each thermal microhabitat) by recording operative temperatures in all vegetation types and sites. To do so, we placed between 6 and 24 physical copper tube models fitted with HOBO Pro v2 U23-003 (ONSET Cape Cod, Massachusetts, USA) temperature loggers in representative vegetation types at each site. Sampled vegetation types were chosen in order to characterize as much as possible the vegetation diversity observed at each site. Each copper tube was 6 cm long and painted to mimic the dorsal coloration of a common lizard to match the biophysical, heat exchange properties of the species and record operative environmental temperatures (T_{e}) in a diversity of vegetation types (Dzialowski 2005). Indeed, operative environmental temperatures provide the best estimate for microhabitat thermal quality (Bakken et al. 1985, Angilletta 2009, Sears and Angilletta 2015). The loggers recorded temperatures every minute during each capture episode. We calibrated the temperatures made with operative temperatures models by comparing the temperatures with dead individuals (Appendix S4). In subsequent calculations, we averaged these measurements in 15-minute bins in order to compensate for short time changes in microclimatic conditions (e.g., due to wind or cloud cover). This time scale was also chosen because it captures heat exchange properties, i.e., thermal inertia, of small lizards such as the common lizard (Fraser and Grigg 1984). The average operative environmental temperature score of each site per year (hereafter called T_{e}) over 15-minute bins was calculated from the average T_{e} of all loggers in the site weighted by the abundance of the vegetation types in the site.

We also calculated an average T_{e} score, independent from site and year, for each of the 8 vegetation types, in order to obtain an objective estimate of thermal differences across all microhabitats (see Appendix S4 for details). The chosen vegetation types represented a diversity of thermal microhabitats with short vegetation (grass), short bush (heather or bilberry), bush, shade under a tree, full sun (rock, bare soil), and dead tree. We then constructed a "thermal map" of operative temperatures at each site by linking each pixel of our rasterized map to the average T_e score of the corresponding vegetation type. From the vegetation map and the thermal map, we then calculated three different indices of landscape heterogeneity. First, we calculated a forest cover index defined as the proportion of trees within the site (hereafter called FCI). This index is a proxy of the proportion of shade in the habitat and has been often used to quantify habitat constraints on thermoregulation in heliothermic lizards (Huey and Slatkin 1976). It ranges from 0 (open landscape) to 1 (closed forest). In the focal sites, FCI ranges from 0 (open prairies, mainly grass) to 0.75 (sites in forest environments). Second, we calculated an index of thermal evenness (hereafter called TE). This index measures the diversity of average operative temperatures available in the landscape, corrected by the abundance of each microhabitat. TE ranges from 0 (low diversity and/or large dominance of a close range of operative temperatures) to 1 (diversified and equally abundant operative temperatures in the landscape). This index ranges from 0.01 to 0.46 indicating a low diversity of operative temperatures in the landscape. The lowest scored sites are those mainly covered in grass and open with few bushes. Third, we calculated an index of homogeneity based on the vegetation dissimilarity between adjacent pixels corrected by the difference of average operative temperatures between these pixels (hereafter called *H*). This index ranges from 0 (heterogeneous thermal landscape) to 1 (homogeneous thermal landscape). The focal sites were relatively homogeneous, with an index ranging from 0.80 to 0.98. All methods and calculations are described in detail in Appendix S4.

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[12] https://www.mapsmadeeasy.com/

Thermal preferences and thermoregulation traits

Immediately after capture, we measured cloacal body temperature T_b using a K-type thermocouple connected to a digital thermometer (Ecoscan PT100, Eutech Instruments Pte Ltd, Singapore) inserted ~1 cm within the cloaca. We also obtained T_b data on additional individuals in the field that were not included in the laboratory studies. Two days after capture, we measured the thermal preferences (T_{pref}) of all lizards returned back to the laboratory. Thermal preference represents the selected body temperature of an individual in an environment free of costs for thermoregulation and is assumed to match the optimal body temperatures for physiological performance (Hertz et al. 1993, Angilletta et al. 2002). Here, thermal preferences were measured in 20 separate thermal gradients (120 × 25 × 20 cm) with a substrate of dried peat soil. One side of each gradient was heated with a 60 W incandescent bulb in order to approach the species critical thermal maximum CT_{max} (43.9° ± 4.8°C, Gvoždík and Castilla 2001) and the other end of the gradient was maintained at ambient temperature (24.1° ± 2.0°C). The range of temperatures provided in the thermal gradient therefore allowed the lizards to select a body temperature with low thermoregulatory costs (Angilletta 2009). A plastic shelter was placed under the heat bulb and water was supplied continuously during the experiment with a permanently filled small petri dish on the cold side in order to limit the stress of individuals in the terrarium. We note that this can confound measurements of thermal preferences with shelter or water preferences, but the design was the same for all populations. Two UVB 30 W neon tubes provided natural white light above each gradient. Heat bulbs were turned on at approximately 08:00 in the morning. At 09:00 in the morning or at 14:00 in the afternoon, two individuals of the same age, sex, and SVL (±3 mm maximum in the same gradient) were placed in each gradient to acclimate for 30 minutes. Both individuals were identified with a drop of nail polish placed on the dorsum side between the pelvis and tail. We did not observe any aggressive behavior between individuals during any run. In addition, it was not unusual to observe the lizards basking at the same spot, indicating that avoidance behaviors may not strongly influence our measurements. After acclimation, the temperature of the dorsal surface T_{pref} of each lizard was measured with an infrared thermometer (Raytek, Raynger MX2, Fluke Corporation, Everett, Washington, USA) every 15 minutes for 3 h and 15 minutes. We calculated the corresponding core body temperature from a calibration curve performed with additional data on the same species (Artacho et al. 2013; $R^2 = 0.96$; $T_{core} = (-4.50 \pm 0.5) + (1.17 \pm 0.03) \times T_{pref}$ [mean ± SE]). We excluded from analyses the extremes of T_{core} (lower than 25°C and higher than 41°C) with consideration that they corresponded to failed measurements aimed at the substratum instead of the lizard back (results were similar qualitatively with all data included). T_{pref} referred to T_{core} in the following parts of the manuscript.

Variation of T_{pref} with the time of the day, date or individual status was investigated (see *Statistical analyses*, Appendix S5, and Appendix S6). We further tested for differences between thermal preferences of yearlings and adults at the same time of the year in one population (ROB). These data showed that thermal preferences of yearlings (regardless of sex) and adult males were not different (Fig. 4A, Appendix S5: Table S1, all details in Appendix S5). Thus, we assume that thermal preferences of males in each population were a good proxy of the thermal preferences of yearlings. For each population and year, we calculated the average thermal preferences of adult females and adult males/yearlings hereafter called $\overline{T_{pref}}$ (average of all T_{pref} measurements for each year, population, and age–sex category of individuals). To quantify how field body temperatures of lizards deviate from their thermal preferences, we calculated the thermoregulation inaccuracy, defined as the absolute difference between body temperature during activity in the field and thermal preferences $D_b = |\overline{T_{pref}} - T_b|$, for each T_b measurement (Hertz et al. 1993, Blouin-Demers and Nadeau 2005). For each individual record, we used the average $\overline{T_{pref}}$ from the same category of individuals (age and sex class) in the same population of the same year.

We further calculated thermal quality of the habitat, defined as the absolute difference between operative temperatures and thermal preferences $D_e = |\overline{T_{pref}} - T_e|$, for each age–sex category of lizards in each population each year and each 15 minute time bin (Hertz et al. 1993, Blouin-Demers and Nadeau 2005). The ability of an individual to reach their thermal preference given the thermal quality of the habitat is called thermoregulation efficiency or effectiveness of thermoregulation. For each capture event, we calculated the index of thermoregulation efficiency, E ($E = D_e – D_b$; Blouin-Demers and Nadeau 2005) based on the D_b calculated with T_b at capture and the D_e for the same population during the 15 minute time bin of the capture time. When $E = 0$, the body temperature of the lizard is the same as that of a physical model that is not thermoregulating and there is therefore no evidence that individuals are active thermoregulators. If $E > 0$, individuals are thermoregulating as they reach their preferred temperature even though the thermal environment is not of sufficient quality for a thermoconformer. If $E < 0$, individuals are avoiding thermally suitable microhabitats.

Statistical analyses

All analyses were performed with R version 3.4.4 (R Core Team 2018). We analysed variation of T_b, T_{pref}, D_b, D_e, and E using linear mixed models with the function lme from the package nlme (Pinheiro and Bates 2006) after assessment of homoscedasticity and normality of residuals. As the distribution of D_b was not Gaussian, we used a square-root transformation. For each variable, we followed the same logic for model selection procedure. We first fit a full model including all individual and time covariates as fixed effects and then selected a first minimum adequate model using backward model selection based on likelihood ratio tests (LRT). Time covariates included year (categorical, all response variables), hour of the day (continuous, for T_b, D_b, and E), and time of the day (morning or afternoon session, T_{pref}). Individual covariates were age and/or sex (categorical, for T_b, T_{pref}, and D_b) or category (categorical, adult females vs. adult males and both sexes yearlings, D_e, E, see Appendix S5 and Fig. 4A for motivation). Full models included additive effects of all covariates and two-way interaction terms between all individual covariates. For T_{pref} data, we analysed all temperatures recorded for each individual rather than a composite variable (e.g. mean or variance), unpublished data from the team showed that thermal preferences sometimes change depending on the hour of the day but also with the time spent in the gradient (*unpublished data*). We therefore also fit a two-way interaction between the time of the day the experiment was run (morning vs. afternoon) and the time spent since the beginning of the test (i.e., end of habituation). Population identity was included as a random effect. Individual identity nested in the population identity was also included as a random effect to account for repeated measurements on the same individual (T_{pref} data).

When a minimum adequate model was selected, we determined whether the traits differed across populations. We tested the significance of the population identity random effect with log-likelihood ratio test comparison of models fitted by REML (Pinheiro and Bates 2006, Bell et al. 2019). We subsequently compared the relative importance (sum of AIC_c over all models in which the variable appears) of environmental variables related to elevation, Emberger pluviometric quotient, microclimatic conditions, and habitat features (see Appendix S7: Table S1) using the Akaike information-based criterion (AIC_c) comparison procedure (Burnham and Anderson 2004) and a model averaging procedure from maximum likelihood estimates of model parameters (Burnham and Anderson 2002). Models were constructed from the best model selected during the first step described above (hereafter, called our null model) in which we added the environmental variables alone as fixed effects, or in two-way interactions. The main effects and interaction terms were selected based on our working hypotheses (Table 1). In order to test for sex- or age-dependent effects, when sex, age, or the age–sex category of individuals was retained in the null model, we also added to our list of models the two-way interactions as well as the three-way interactions of environmental characteristic with the sex and/or the age variables. Correlations among the environmental variables tended to be low (see Appendix S3: Table S2), but we excluded models with significant collinear variables ($r > 0.5$). We also removed the few models that showed no convergence (listed in Appendix S7: Table S1). For the purpose of model averaging calculations, all continuous covariates were mean centered and scaled by the standard deviation and categorical covariates (FW, sex, and age) had their contrasts summed to zero. We selected the main effects and interaction terms with significant contributions to the variability of the traits based on the AIC_c difference between models, the relative weight of the models and the importance as well as conditional averages from model averaging procedure.

RESULTS

Measured and calculated thermoregulation statistics for each population are presented in Appendix S2: Table S1. Detailed results of the model selection procedures are presented in Appendix S7: Table S1. Conditional averages of the most important environmental variables from model averaging are presented in Table 2.

Variation in body temperature

Field body temperature of lizards varied significantly among populations (proportional variance explained = 41%; LRT = 487.4, df = 1, $P < 0.0001$). The average body temperature also changed with the hour of the day following a quadratic function and was significantly explained by the interactions between age × sex and sex × year. Average adult female T_b was 27.8° ± 0.5°C, whereas female yearlings T_b were 1.5° ± 0.1°C warmer than adult females ($t_{1963} = 10.0$, $P < 0.0001$). Adult males T_b were 1.2° ± 0.3°C warmer than adult females ($t_{1963} = 4.2$, $P < 0.0001$). Male yearlings had approximately the same body temperatures as female yearlings and adult males (yearlings × males: $t_{1945} = -7.5$, $P < 0.0001$). The most important environmental variables explaining geographic variation of body temperature included the pluviometric quotient Q (relative importance, RI = 0.97) and T_{max} (RI = 0.94) and the two-way interaction $Q \times T_{max}$ (RI = 0.93, Fig. 3A and B, Appendix S7: Table S1). According to the best supported model, mean body temperatures were higher in populations characterized by a mesic environments (higher Q coefficient) with high T_{max} (Table 2, Fig. 3A). In drier environments (low Q), body temperatures were almost consistent with minimal air temperatures T_{max}, whereas T_b increased with T_{max} in mesic environments (high Q).

Variation in thermal preference

We identified significant differences in records from thermal gradient T_{pref} measurements among populations; however, the variance explained among populations was quite low (variance explained = 2%; LRT = 48.2, df = 1, $P < 0.0001$) compared to the variation among individuals (proportional variance explained = 24%). Variation in T_{pref} was also significantly explained by an interaction of sex × year, and between time of day (morning vs. afternoon) when the T_{pref} was measured with the time since beginning of the

TABLE 2. Conditional average of selected variables from the model averaging procedure (Appendix S7: Table S1).

Trait and variable	Estimate	SE	Adjusted SE	z	P
T_b					
Intercept	30.2	0.35	0.35	85.1	<0.0001
Q	−0.9	0.4	0.4	2.1	0.03
T_{max}	1.2	0.2	0.2	4.8	<0.0001
$Q \times T_{max}$	0.7	0.2	0.2	3.5	0.0005
T_{pref}					
Intercept	35.3	0.1	0.1	350.6	<0.0001
FCI	0.3	0.1	0.1	2.7	0.006
Female	−0.9	0.1	0.1	13.9	<0.0001
FCI × Female	0.2	0.1	0.1	3.8	0.0002
$\sqrt{D_b}$					
Intercept	2.1	0.1	0.1	27.4	<0.0001
Q	0.2	0.1	0.1	1.8	0.07
T_{max}	−0.4	0.1	0.1	8.1	<0.0001
$Q \times T_{max}$	−0.3	0.05	0.05	6.0	<0.0001
D_e					
Intercept	4.8	0.8	0.8	5.7	<0.0001
T_{min}	−4.0	0.3	0.3	11.7	<0.0001
P_{max}	3.2	0.3	0.3	12.2	<0.0001
$T_{min} \times P_{max}$	−2.7	0.3	0.3	10.4	<0.0001
E					
Intercept	−0.4	0.9	0.9	0.4	0.66
P_{max}	2.9	0.3	0.3	10.7	<0.0001
T_{min}	−4.4	0.4	0.4	12.1	<0.0001
$P_{max} \times T_{min}$	−3.1	0.2	0.2	12.3	<0.0001

Notes: Continuous variables are scaled and centered. Categorical variables had their contrasts summed to zero, i.e., the intercept is the average trait for average continuous variable and for a theoretical average level of the categorical variables. Effects are obtained from the deviation from this average. T_b, cloacal body temperature in field-active lizards; T_{pref}: mean body temperature measured in thermal preferences tests in the laboratory; D_b, thermoregulation inaccuracy; D_e, thermal quality of the habitat; E, thermoregulation efficiency.

test. Despite little quantitative variation among populations, our model comparison procedure uncovered that the forest cover index FCI as well as the two-way interaction between FCI and sex were significant variables explaining geographic variation in T_{pref} (RI of 0.85 and 0.84, respectively, Table 2). T_{pref} of females significantly increased with FCI (Fig. 4B).

Variation of thermoregulation inaccuracy

The inaccuracy of thermoregulation D_b differed among populations (proportional variance explained = 39%; LRT = 519.1, df = 1, $P < 0.0001$). Variation in D_b followed a quadratic function of the hour of the day and was also significantly explained by a three-way interaction of sex × age × year. Values of mean D_b among males and yearlings did not differ from adult females in 2016 (males, $t_{1959} = -0.3$, $P = 0.79$; yearlings, $t_{1959} = -1.1$, $P = 0.27$; males × yearlings, $t_{1959} = 0.9$, $P = 0.34$) and in 2018 (males, $t_{1959} = -1.7$, $P = 0.09$; yearlings, $t_{1959} = -0.3$, $P = 0.76$; males × yearlings, $t_{1959} = -0.9$, $P = 0.37$). However, in 2017, males displayed mean $\sqrt{D_b}$ values 0.2° ± 0.1°C higher than females ($t_{1959} = 2.0$, $P = 0.05$) and yearlings of both sexes displayed mean $\sqrt{D_b}$ values 0.4° ± 0.1°C higher than females (yearlings, $t_{1959} = 3.7$, $P = 0.0003$; males × yearlings, $t_{1959} = -2.4$, $P = 0.02$). They were thus less precise in their accuracy during that year. Geographic variation in D_b was mostly explained by T_{max} (RI = 1), pluviometric quotient Q (RI = 0.1), and their two-way interaction (RI = 0.1, Appendix S7: Table S1). Thermal inaccuracy (D_b values) was lowest in drier (low Q) and cooler habitats (low T_{max}) and higher in more mesic (high Q) and low T_{max} (Table 2). The inaccuracy of thermoregulation (D_b) increased with pluviometric quotient at low minimal air temperature T_{max}, and decreased with pluviometric quotient at high T_{max} (Fig. 3B).

Variation in thermal quality of the habitat

Thermal quality of the habitat D_e differed among populations (proportional variance explained = 37%; LRT = 652.7, df = 1, $P < 0.0001$). Values for D_e varied following a quadratic function of the hour of the day. Geographic variation in D_e was mostly explained by P_{max} (RI = 1), T_{min} (RI = 1), and their two-way interactions (RI = 1, Appendix S7: Table S1). In populations with average T_{min}, D_e increased with an increase of P_{max}. This effect vanished and was even inverted with an increase in local minimal air temperature (Table 2). In

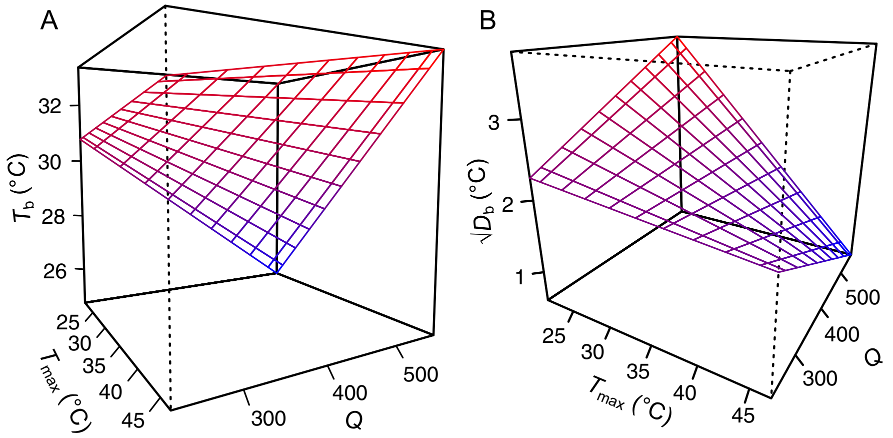

FIG. 3. Variation of (A) cloacal body temperatures at capture T_b and (B) thermoregulation inaccuracy D_b in the field as a function of the pluviometric quotient Q and mean daily maximum temperatures during the study year T_{max}. The surface is drawn from the conditional average of the best predictors estimated from the model averaging procedure (Table 2). The color gradient highlights the values of T_b in panel A, from low (blue) to high body temperatures (red); and the values of D_b in panel B, from low inaccuracy (blue) to high inaccuracy (red).

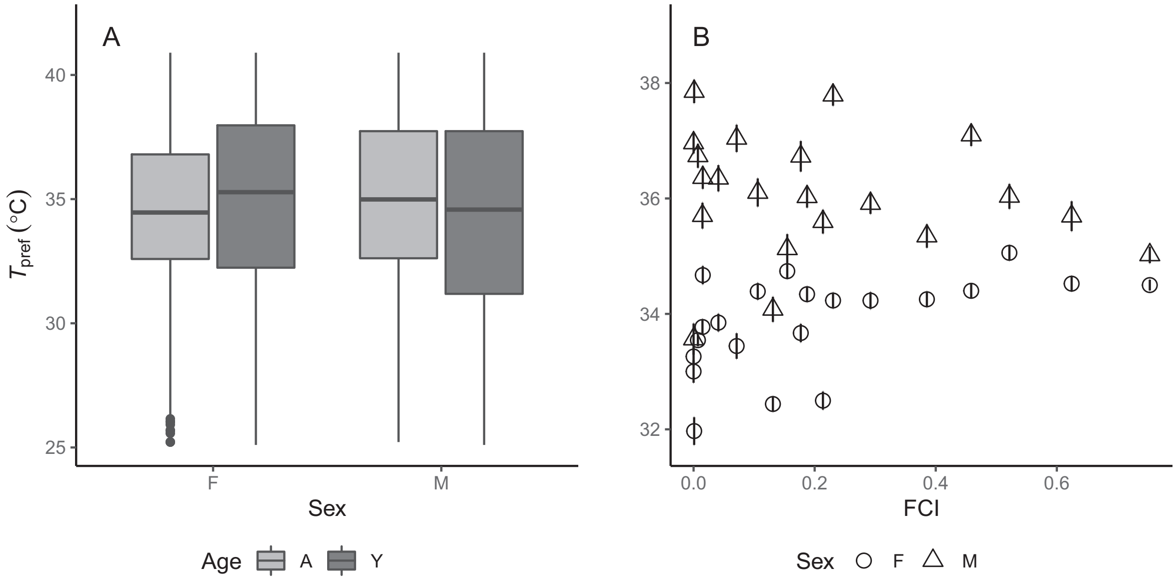

FIG. 4. Variation of preferred body temperatures measured in the laboratory T_{pref} (A) as a function of sex and age in the ROB population and (B) as a function of sex and forest cover (FCI) in all populations with adults only. The box plots display the median and the quantile distribution of raw data in panel A. Points and error bars in panel B represent the average and the standard error of raw data for each population and each sex. A, adults; Y, yearlings; FCI, forest cover index.

most cases, T_e were below thermal preferences, i.e., thermal quality of the habitat was in average too cold (Appendix S4: Figs S3 and S4).

Variation in thermoregulation efficiency

The D_b values increased significantly with D_e (Fig. 5, slope 0.2 ± 0.02, intercept 6.5 ± 0.4; $F_{1,1811} = 141.4$, $P < 0.0001$). Variation in thermoregulation efficiency E followed a quadratic function of the hour of the day (decreased with the hour of the day after which it increased again). In addition, E differed among populations (proportional variance explained = 47%; LRT = 744.3, df = 1, $P < 0.0001$). Geographic variation in E was significantly explained by T_{min} (RI = 1), P_{max} (RI = 1), and the two-way interaction $P_{max} \times T_{min}$ (RI = 1, Appendix S7: Table S1, Fig. 5). In other words, thermoregulation efficiency E increased with minimal air temperature T_{min} in populations with higher water vapor pressure P_{max}, whereas it decreased with $T_{\min}$ in populations with high $P_{\max}$ (Table 2, Fig. 6).

Discussion

In this study, we tested whether geographic differences in elevation or climate dryness, year- and site-specific differences in air temperature and moisture, habitat differences in water availability, and habitat differences in spatial landscape features of the vegetation influenced thermoregulation strategies across multiple populations of a widespread lizard species. Our results highlight that thermoregulation behaviors are mainly shaped by interactions between local site- and year-specific air temperatures, historical differences in the Emberger pluviometric quotient and the local annual air moisture conditions, supporting the thermo-hydroregulation hypothesis (hypothesis 7; results supporting each hypothesis are summarized in Table 3). Body temperature, and as a consequence thermoregulation inaccuracy, was influenced by an interaction between local air temperatures and the historical differences in climate dryness of the site. Preferred temperature of lizards was significantly lower for adult females and in populations with permanent access to water. Finally, thermoregulation efficiency and the quality of the thermal habitat, were highly variable among populations and were influenced by the interaction between air temperature and air moisture, which were calculated for each site and each year. In contrast, persistent, historical differences in weather conditions and habitat features had little effects on these thermoregulation statistics. Thermoregulation traits were not influenced by elevation or by the thermal landscape of the sites, rejecting hypotheses 1, 3, 4, and 8 (Table 3).

Thermo-hydroregulation as a driver of the geographic trends in thermoregulatory behaviors

Geographic variation in body temperature and in thermoregulation accuracy was best explained by the interaction between the local ambient thermal conditions quantified each year at each population and the pluviometric quotient (Q score, an index of the dryness of the climate) calculated from historical weather data for each population. As expected, body temperatures of lizards increased with local air temperatures at the study site, but this correlation was evident in only the most mesic climates (high Q score). In addition, the thermoregulation inaccuracy decreased with local air temperatures. However, the pattern was stronger in more mesic climates, as indicated by a high value of Q. We note that, on average, field-active body temperatures were below the thermal preference sets and field thermoregulation behavior was "suboptimal." However, according to our best supported statistical models, we predicted that thermal preferences of lizards should be almost attained in the warmer local climate conditions and in the sites occurring in the most historically mesic climates.

According to the thermo-hydroregulation hypothesis (hypothesis 7 in Table 1), the costs of thermoregulation depend on the risks of desiccation and overheating, which are generally more important in drier climates (e.g., Dupoué et al. 2017*b*, 2018) and should increase in warmer climatic conditions (e.g., Lourdais et al. 2017, Rozen-Rechels et al. 2019). We thus expect thermoregulation to be more accurate in sites with lower costs of desiccation when local climate conditions are warmer (Rozen-Rechels et al. 2019). Our results are concordant with these expectations, which emphasizes the importance of non-energetic costs of thermoregulation due to a higher risk of dehydration in populations with long-term patterns of a dry climate accompanied by high ambient temperature. One explanation is that selection favoring behavioral thermoregulatory strategies to limit dehydration led to either plastic or genetic adaptive responses in lizard populations occupying historically drier climate conditions. To our knowledge, this is the first demonstration that a climate dryness index, calculated from rainfall and temperature data, accurately predicts geographic variation in thermoregulation strategies in an ectotherm (see Tieleman et al. 2003 in endotherms). This complements recent data by Kearney et al. (2018), who observed that activity patterns in another species of lizard were also sensitive to both local temperature and rainfall patterns.

In addition, we found that the thermoregulation inaccuracy had a positive correlation with the thermal quality of the habitat with a slope < 1 (Fig. 5), suggesting that in our study system, the common lizard is intermediate between a perfect thermoregulator and a perfect thermoconformer (Hertz et al. 1993). Variation in thermoregulation efficiency, calculated from the difference between the thermal inaccuracy of the lizard and the thermal quality of the habitat, was best explained by an interactive effect between ambient thermal conditions and local air moisture, which provides additional support to the thermo-hydroregulation hypothesis (hypothesis 7 in Table 1). Air moisture, another measure of the hydric quality of the habitat, explained geographic variation in the thermal quality of the habitat (D_e) and in thermoregulation efficiency (E), whereas the historical aridity index (Q score) best explained the thermoregulation inaccuracy. In low air moisture conditions, thermoregulation efficiency exhibited a slight increase with minimal air temperature. In contrast, in high air moisture conditions, thermoregulation efficiency was maximal at low air temperatures and displayed a striking decrease as air temperatures increased. These results suggest that the relation between air temperature and thermoregulation efficiency is constrained at low air moisture conditions, i.e. when local microclimatic conditions at the site are more desiccating. They further indicate that variation in thermoregulation efficiency are mainly explained by local and yearly moisture-driven

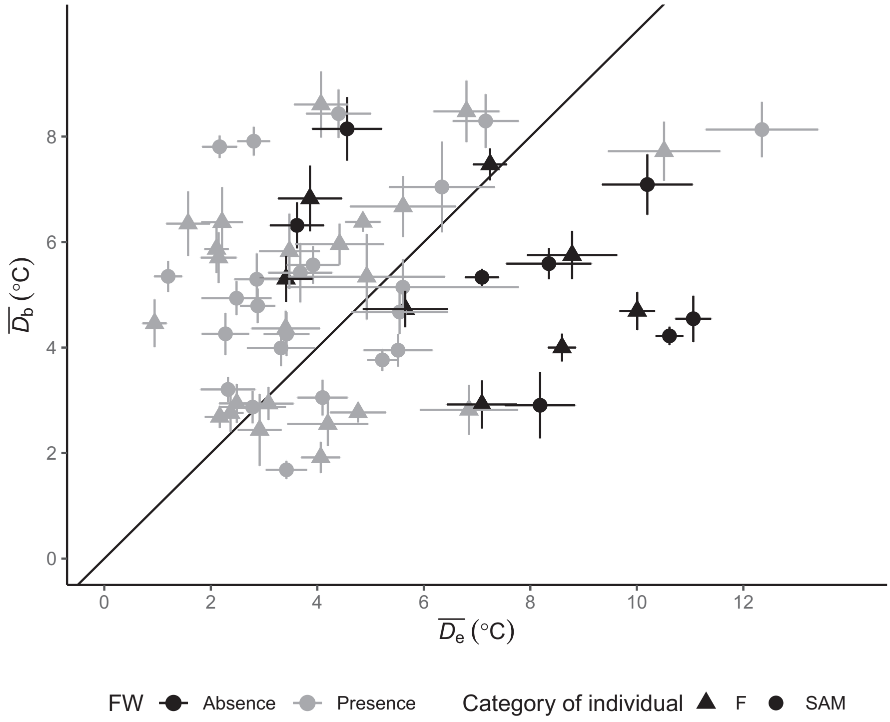

FIG. 5. Variation of thermoregulation inaccuracy D_b as a function of the thermal quality of the habitat D_e. Points are for $\overline{D}_b$ and $\overline{D}_e$ per population per year per age-sex group. Colors represent the presence of free-standing water (FW) at the site and symbols represent the age-sex category of individuals. The black line is the line of equation $\overline{D}_b = \overline{D}_e$. This graph shows that lizards from some dry sites without permanent access to free-standing water have high D_e compared to wet sites because we measured lower T_e in these populations (Appendix S8: Fig. S1). Error bars represent standard error.

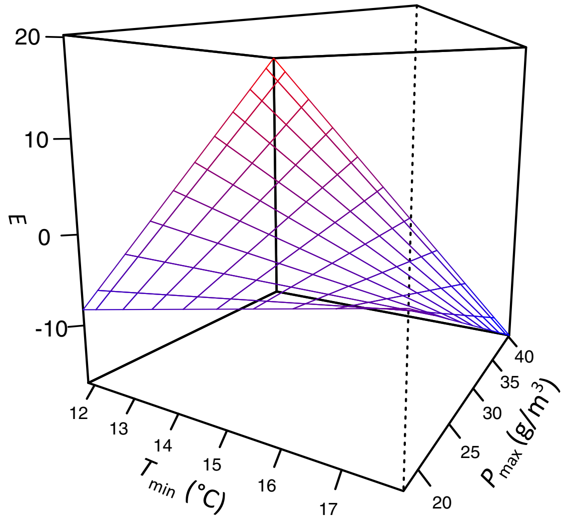

FIG. 6. Variation of thermoregulation efficiency E as a function of the mean daily maximum air moisture during the study year $P_{\max}$ and mean daily minimum temperatures during the study year $T_{\min}$. The surface is drawn from the predictions of the conditional average of the best predictors estimated from the model averaging procedure. The color gradient highlights the values of E: from low (blue) to high (red).

changes in the thermal quality of the habitat rather than historical differences in climatic conditions characterizing each population (as described by the pluviometric quotient Q). However, geographic variation of thermoregulation accuracy was best explained by long-term and historical weather conditions rather than local annual weather conditions. We note that this was not due to some model inconsistency due to a collinearity between variables because the pluviometric quotient and the moisture conditions of a site were uncorrelated ($F_{1,29} = 0.32$, $P = 0.57$, $R = -0.13$). Furthermore, differences in air moisture are mainly associated with potential differences in total rates of water loss from lizards in each site and each year (Spotila 1972, Mautz 1982), whereas differences in historical pluviometry may further influence soil moisture, availability of free-standing water throughout the year and ecosystem productivity. One potential interpretation of our findings is therefore that the risk of dehydration, which is typically enhanced in drier air conditions (Rozen-Rechels et al. 2019), decreased thermoregulation efficiency, which indicates that some non-energetic costs linked to water loss act as a constraint to thermoregulatory behaviors. Altogether, these results provide strong support for the thermo-hydroregulation hypothesis (Rozen-Rechels et al. 2019, hypothesis 7 in Table 1), which posits that

TABLE 3. Our sampling protocol aims to quantify the relative importance of climate and habitat factors in explaining the geographical variation in thermoregulation statistics of the common lizard (*Zootoca vivipara*).

No.	Hypotheses	Supporting results	Potential explanation	Supported by our study
1	Elevational variation	None	Local relief or other site properties affect local thermal and hydric conditions more than elevation per se blurring any elevation effect.	No
2	Annual thermal conditions	T_b increases with T_{max}; D_b decreases with T_{max}; D_e and E decrease with T_{min}	Higher local temperatures lead to a wider range of environmental temperatures allowing attainment of thermal preference. Thermoregulation behavior becomes more accurate and the habitat is of higher thermal quality.	Yes
3	Thermal landscape	None	In the absence of a cost of overheating, landscape features might not affect thermoregulation behaviors. Sites may also be too homogeneous on average.	No
4	Condition-dependent thermal landscape	None	In the absence of a cost of overheating, landscape features might not affect thermoregulation behaviors. Sites may also be too homogeneous on average.	No
5	Historical climate dryness	T_b decreases with Q	When climatic conditions are historically more mesic, this relaxes the water constraints on thermoregulation on average, thus allowing field-active individuals to reach higher body temperature.	Yes
6	Annual moisture conditions	D_e and E increase with P_{max}	Air moisture could cool down local operative temperatures for lizards, reducing the thermal quality of the habitat.	Yes
7	Thermo-hydroregulation	T_b increases faster with T_{max} at high Q; D_b decreases faster with T_{max} at high Q; D_e and E decrease strongly with T_{min} at high P_{max} but are almost constant at low P_{max}	In more xeric conditions, an increase of temperature is riskier in terms of water loss, the benefits of thermoregulation are more constrained. In more mesic conditions, these constraints are relaxed. These constraints may have shaped the evolution of thermoregulation behaviors in these populations. Thermal quality of the habitat is modulated by moisture conditions. When moist, cold air conditions make the environment too cold. When warmer, the refreshing effect of moisture might be attenuated.	Yes
8	Thermo-hydroregulation landscape	None	In the absence of a cost of overheating, landscape features might not affect thermoregulation behaviors. Sites may also be too homogeneous on average.	No

Note: This table summarizes our working hypotheses and defines how these working hypotheses were tested with statistical models.

the thermoregulatory behavior of common lizards is shaped by a trade-off between body temperature regulation and water balance regulation.

Low geographical variability of thermal preferences

Thermal preferences exhibited the lowest geographic variation among all thermoregulation statistics investigated in this study. A striking pattern was that intra-population variation in thermal preferences (24%) was unexpectedly higher than inter-population variation (2%). The low geographic variability of thermal preference is consistent with previous findings in the same species comparing populations at low and high elevations (Van Damme et al. 1990, Gvoždík 2002, but see Trochet et al. 2018 for oviparous populations of *Z. vivipara*). The low inter-population variability of thermal preference also supports earlier findings that thermoregulatory preferences exhibit limited variation compared to field-active body temperature (generally a standard deviation of 1.7°C compared to 2.9°C for the body temperature range among Lacertidae species based on Clusella-Trullas and Chown 2014). It is also consistent with the observation that thermal preferences vary less than field body temperatures across elevational ranges or along climate gradients in many lizard species (Van Damme et al. 1990, Angilletta et al. 2002, but see Gilbert and Miles 2019 for a counter-example in an arid zone lizard). Interestingly, average thermal preferences reported here were surprisingly high, especially for gravid females, compared to previous values reported for the same species in other study sites (gravid females 34.0° ± 3.2°C, males 35.8° ± 3.4°C; see Gvoždík [2002] who used a different method at higher latitude, in the Czech Republic, Le Galliard et al. [2003], Artacho et al. [2013], Rozen-Rechels et al. [2020] with similar methods in an experimental set-up, Trochet et al. [2018] using oviparous populations located in the Pyrénées, in the southwestern European range). Methodological differences, in part, between these studies may contribute to this contrast. However, an alternative is that the differences may be real and the high values reported in our study might suggest directional selection for higher thermal preference along the warmer, southern margin of the species distribution, which is under warming pressure (Chamaillé-Jammes et al. [2006] and Gilbert and Miles [2017] for another example in an other species). Overall, our results suggest higher variation in thermal preferences at a greater spatial scale than the one investigated here. Further latitudinal comparisons of populations spanning a broader geographic range than this study are needed to confirm this pattern.

The only noticeable geographic trend in thermal preference that we detected was a significant shift towards higher thermal preference in females from populations with a high forest cover. We suggest the shift is an indirect response associated with differences in the stage of gestation of females among populations rather than a direct effect of forest cover per se. Indeed, thermal preference has a higher correlation with the stage of gestation, which overwhelmed the effect of the forest cover index (see Appendix S6). The geographic difference between populations with low vs. high forest cover was mostly driven by one site (ROB, the population with the highest forest cover), where females were more intensively sampled early in pregnancy (Appendix S6: Fig. S1). In addition, a delayed timing of parturition in populations with higher forest cover had also been demonstrated in a smaller sample of our study sites (Rutschmann et al. 2016*a*). In the common lizard, advancement of gestation is associated with a shift toward lower thermal preferences, which is more obvious at the end of pregnancy (ca. 29–30°C at the end vs. 33–4°C before gestation; see Le Galliard et al. 2003). As we sampled a larger number of females early in gestation in sites with high forest cover, differences in the timing of sampling and timing of parturition provided the best explanation for why females had lower thermal preference in more open habitats.

Absence of thermal landscape effects

An unexpected result of our geographic comparison was that indices of the spatial heterogeneity of the thermal landscape made no significant contribution to population variation in body temperature and thermoregulation accuracy contra our hypotheses 3 and 4 (see Tables 1 and 3). According to recent individual-based models of thermoregulatory behavior (Sears and Angilletta 2015), which were confirmed by detailed experiments of heterogeneous thermal landscapes with desert lizards (Sears et al. 2016), we expected a higher thermoregulation accuracy for lizards in more heterogeneous landscapes because more heterogeneous thermal environments entail lower costs of behavioral thermoregulation. For example, optimality models of thermoregulation predict that opportunities for behavioral thermoregulation are weaker in more homogeneous habitats and the energetic costs of thermoregulation are higher in homogeneous habitats when contrasting habitats of different thermal quality are highly segregated in space.

A first potential explanation for the pattern of thermoregulation behavior of common lizards to be similar in homogeneous and heterogeneous thermal landscapes, is that the costs of thermoregulation in homogeneous environments are not as high as hypothesized in optimality models of thermoregulation. For example, Basson et al. (2017) showed that the energetic cost of locomotion between microhabitats are negligible for Oelofsen’s Girdled lizards *Cordylus oelofseni* moving inside their typical home ranges. Similar results may apply to common lizards because these are actively foraging, ground dwelling lizards with a relatively good endurance capacity (Garland and Losos 1994, Vitt and Pianka 2014; D. B. Miles *unpublished data*).

A second potential explanation is that the ambient temperatures during capture were below the thermal preference set of common lizards as opposed to the desert lizard species in previous theoretical and empirical studies, where there was a significant risk of overheating (Sears et al. 2016). In the cool temperature range of our geographic area and study sites and at the time of sampling (Appendix S4: Fig. S3), the risks of overheating were in general negligible with the exception of a few populations over short time periods of the day. In cool climate conditions, the benefits of thermoregulation imply faster and more prolonged access to the thermal preference set by selection of warmer microhabitats. Given the asymmetric shape of the thermal performance curves of reptiles and the generalist (wide thermal breadth) thermal physiology of the common lizard (Van Damme et al. 1991, Artacho et al. 2013), the benefits of thermoregulation by microhabitat selection of warm sites are smaller in cool climates on average in this species than the benefits of thermoregulation by microhabitat avoidance of warm sites in warm climates. This is because individual physiological performances, such as maximal locomotor capacities, are weakly ascending and reach a plateau over the body temperature range of 32°–36°C including most of the observed variation in temperature conditions in the vegetation. Since, a heterogeneous landscape would be beneficial when it allows for behavioral shifts among contrasted cold and hot microhabitats in order to heat faster in cool weather conditions and to avoid overheating in warm weather conditions; heterogeneity would thus be critical only when the habitat overlaps the critical thermal limits of the species, which is not the case in our study focal period in the focal sites.

A third potential explanation is that our methods failed to characterize the complete range of variation in the thermal landscape despite substantial differences in vegetation characteristics and heterogeneity (Sears et al. 2011, Caillon et al. 2014). Our methods showed that the thermal landscapes had limited variation. Our estimates of the homogeneity index (*H*) varied between 0.75 and 1. Most of the study sites were covered in large expanses of grass and other vegetation of short stature. We could not characterize and quantify the fine-scale, spatial variability of thermal conditions within vegetation patches inside each pixel of our vegetation maps. It is obvious from field observations that active lizards can take advantage of the varying shade levels and vertical thermal structure within a vegetation patch, and this fine-scale heterogeneity to which lizards are familiar might be more critical determinants of their thermoregulation behavior than vegetation homogeneity at the scale of meters or tens of meters. Quantifying the very fine details of the vegetation thermal landscape, however, represents a strong methodological challenge that is beyond the scope of this study.

Implications for ecological responses to climate change

Future risks of extinction for temperate lizard species as a result of global warming are expected to show a dramatic increase due to a reduction in the availability of shade and an increase in the risks of overheating. However, there is an ongoing debate about the critical determinants of population loss from global warming for these species (Sinervo et al. 2010, Kearney 2013). In the common lizard, climate warming in our study area has led to simultaneous changes in stress physiology, ageing, life history, reproduction phenology, and trajectories of population extinction in the warmest sites (Chamaillé-Jammes et al. 2006, Rutschmann et al. 2016*a*,*b*, Dupoué et al. 2017*a*,*b*, 2018). In parallel, we found no evidence of a reduction of shade availability in our study sites, contrary to predictions of global mechanistic models (Kearney 2013). Stasis in forest cover (shade) is a result of little or no change in vegetation among some study sites or an expansion of forest cover in other sites during the past 15 yr due to changes in land use (J. Clobert, *personal observations*). The increase of availability of shade in some populations could benefit the common lizard in the context of global warming because tall and dense vegetation ameliorates the risk of overheating (Grimm-Seyfarth et al. 2017). Our study suggests, however, that thermoregulation strategies in these populations are more strongly constrained by changes in hydric conditions and temperature than by landscape features, and are best explained by an hypothesis that assume a trade-off between behavioral thermoregulation and hydroregulation. The role of water balance is underappreciated in current studies of thermoregulation. Our understanding of ectotherm responses to global change would benefit from further studies that evaluate the role of water balance regulation in modulating thermoregulatory behaviors (Rozen-Rechels et al. 2019).

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1440/full

Data Availability Statement

Analyses reported in this article can be reproduced using the data provided at Zenodo https://doi.org/10.5281/zenodo.4030491