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

3 **Running head:** Water driven thermoregulation strategies

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30

31 **Abstract**

32 Behavioral thermoregulation is an efficient mechanism to buffer the physiological effects of climate
33 change. Thermal ecology studies have traditionally tested how thermal constraints shape
34 thermoregulatory behaviors without accounting for the potential major effects of landscape
35 structure and water availability. Thus, we lack a general understanding of the multifactorial
36 determinants of thermoregulatory behaviors in natural populations. In this study, we quantified the
37 relative contribution of elevation, thermal gradient, moisture gradient and landscape structure in
38 explaining geographic variation in thermoregulation strategies of a terrestrial ectotherm species. We
39 measured field active body temperature, thermal preferences and operative environmental
40 temperatures to calculate thermoregulation indices, including thermal quality of the habitat and
41 thermoregulation efficiency for a very large sample of common lizards (*Zootoca vivipara*) from 21
42 populations over 3 years across the Massif Central mountain range in France. We used an
43 information-theoretic approach to compare eight *a priori* thermo-hydroregulation hypotheses
44 predicting how behavioral thermoregulation should respond to environmental conditions.

45 Environmental characteristics exerted little influence on thermal preference with the exception that
46 females from habitats with permanent access to water had lower thermal preferences. Field body
47 temperatures and accuracy of thermoregulation were best predicted by the interaction between air
48 temperature and a moisture index. In mesic environments, field body temperature and
49 thermoregulation inaccuracy increased with air temperature, but they decreased in drier habitats.
50 Thermoregulation efficiency (difference between thermoregulation inaccuracy and the thermal
51 quality of the habitat) was maximized in cooler and more humid environments and was mostly

52 influenced by the thermal quality of the habitat. Our study highlights complex patterns of variation
53 in thermoregulation strategies, which are mostly explained by the interaction between temperature
54 and water availability, independent of the elevation gradient or thermal heterogeneity. Although
55 changes in landscape structure were expected to be the main driver of extinction rate of temperate
56 zone ectotherms with ongoing global change, we conclude that changes in water availability
57 coupled with rising temperatures might have a drastic impact on the population dynamics of some
58 ectotherm species.

59 **Introduction**

60 In a climate changing world, as average temperatures and frequency of heatwaves increase (IPCC
61 2014), organisms are exposed to repeated challenges in their capacity to regulate their body
62 temperature in order to optimize their physiological performance and fitness (Angilletta et al. 2002).
63 Behavioral thermoregulation (i.e., regulation of body temperature through behavioral means;
64 Angilletta 2009) is essential for ectotherms to rapidly adjust performance level to temperature
65 fluctuations (Kearney et al. 2009, Huey et al. 2012, Gunderson and Stillman 2015, Buckley et al.
66 2015). These behaviors involve flexible changes in activity patterns (e.g., Porter et al. 1973, Grant
67 1990), micro-habitat selection (e.g., Kleckova et al. 2014), movement decisions (e.g., Vickers et al.
68 2016) or adjustments in body posture (e.g., Barton et al. 2014). The suitability of a habitat for
69 ectotherms depends on the spatial variation in local temperatures and the tradeoffs associated with
70 in the costs and benefits of thermoregulatory behaviors (Sunday et al. 2014). For example,
71 differences in body temperature along elevational gradients can be small or even non-existent in
72 some ectotherms despite substantial changes in ambient temperatures (Van Damme et al. 1989,
73 Zamora-Camacho et al. 2013), because behavioral compensation facilitates the ability of animals to
74 attain physiological optimal body temperatures even in cold environments (Adolph 1990, Gvoždík
75 2002). However, the predictors of these costs and benefits from thermoregulation are diverse, and
76 we lack multivariate studies of geographic variation in thermoregulatory behaviors (Angilletta
77 2009).

78 The classical cost and benefit model of thermoregulation predicts that behavioral strategies of
79 ectotherms should range from active thermoregulation (i.e., maintaining a constant body
80 temperature despite environmental variation) to thermoconformity (i.e., body temperature matches
81 environmental conditions) depending on the costs of thermoregulation imposed by local thermal
82 conditions (Huey and Slatkin 1976). When local thermal conditions deviate from an organism's
83 preferred body temperature, the model predicts that ectotherms should lower their thermoregulation

84 effort and accuracy (Huey and Slatkin 1976, Herczeg et al. 2006, 2008). However, when benefits of
85 active thermoregulation increase in poor quality habitats and there is a risk of overheating,
86 increased thermoregulation effort and accuracy can be beneficial for ectotherms despite costs due to
87 missed opportunities for foraging or other behaviors (Blouin-Demers and Weatherhead 2002,
88 Blouin-Demers and Nadeau 2005, Vickers et al. 2011). Thus, terrestrial ectotherms often increase
89 thermoregulation effort in poor thermal environments to realize the benefits of attaining preferred
90 temperatures or avoiding lethal overheating (Sunday et al. 2014, Buckley et al. 2015). Given that
91 mean thermal conditions change with elevation, latitude, or time of the year, an implicit prediction
92 of the cost and benefit model of thermoregulation is that thermoregulatory behaviors should change
93 along an elevational or latitudinal gradient (Hypothesis 1, Table 1, Adolph 1990, Caldwell et al.
94 2017) or in response to short-term changes in ambient temperatures (Hypothesis 2, Table 1, Blouin-
95 Demers and Weatherhead 2002). The relative importance of short-term changes in thermoregulatory
96 behaviors versus stable differences across a geographic gradient is not yet clear and can only be
97 elucidated with multiyear studies of several populations (Samietz et al. 2005, Huey et al. 2012,
98 Caldwell et al. 2017).

99 Recent models and experiments have suggested that the spatial heterogeneity of thermal conditions
100 within a habitat might be a better predictor of the costs of thermoregulation than the mean thermal
101 environment (Caillon et al. 2014, Sears and Angilletta 2015, Sears et al. 2016, Basson et al. 2017).
102 Heterogeneity of thermal conditions at a small spatial scale can be caused by differences in
103 vegetation height or topography (i.e. shade availability) within the home ranges of animals. One
104 prediction from these recent models is that spatial heterogeneity reduces the costs of
105 thermoregulation by allowing energy-free investment in basking through shuttling of an individual
106 between different thermal microhabitats (Sears and Angilletta 2015, Sears et al. 2016). Thus,
107 behavioral thermoregulation should be more efficient in heterogeneous habitats than in
108 homogeneous habitats even when the mean thermal quality of the habitat is poor (e.g., Goller et al.

109 2014). Based on the individual-based model of thermoregulatory behavior in a ground dwelling
110 ectotherm of Sears and Angilletta (2015), a low thermoregulation efficiency should, for example,
111 evolve in more homogeneous habitats (Hypothesis 3, Table 1). In addition, the importance of
112 landscape heterogeneity should be more critical under strong thermal constraints, whether cold or
113 hot, because landscape heterogeneity favors a greater reduction in the costs of thermoregulation
114 when mean conditions deviate from the preferred temperature range (Hypothesis 4, Table 1,
115 Herczeg et al. 2003, Sears et al. 2016). Unfortunately, support for both predictions are rare, since
116 most comparative studies of behavioral thermoregulation are based on the mean thermal quality at
117 the population level without consideration of the spatial distribution of micro-habitats within a
118 landscape (Gvoždík 2002, Herczeg et al. 2003, Blouin-Demers and Nadeau 2005). As suggested by
119 Sears et al. (2016), we need an explicit map of operative environmental temperatures (T_e , i.e.,
120 steady-state temperature of the animal without behavioral or physiological regulation, Bakken et al.
121 1985) from each habitat to reach a full understanding of the costs of thermoregulation across an
122 environmental gradient.

123 Ongoing climate change is not only modifying the thermal quality of the environment, but also
124 affects the water availability, through changes in precipitation rates and frequency and magnitude of
125 drought (Field et al. 2012). Water availability, in the form of moisture or free-standing water in the
126 environment, is another predictor of the costs of thermoregulatory behavior. Water restriction can
127 compromise the regulation of water balance and the accuracy of thermoregulation at high body
128 temperatures (e.g., Dupoué et al. 2015, Lourdais et al. 2017, Pirtle et al. 2019). Water restriction in
129 the environment is therefore expected to decrease behavioral activity (Lorenzon et al. 1999,
130 Kearney et al. 2018, Pirtle et al. 2019) and to change micro-habitat selection such that ectotherms
131 avoid the risks of dehydration (Pintor et al. 2016, Pirtle et al. 2019). In addition, thermal
132 performance curves are often maximized at lower body temperatures in dehydrated compared to
133 fully-hydrated animals, which may select for lower preferred body temperature and thermal

134 depression in more seric environments (e.g., Ladyman and Bradshaw 2003, Muir et al. 2007,
135 Anderson and Andrade 2017). The number of studies focusing on the effect of water availability
136 and water balance on behavioral thermoregulation in ectotherms is growing (Pintor et al. 2016,
137 Rozen-Rechels et al. 2020), but few have quantified the joint effects of water availability and the
138 thermal environment on thermoregulation strategies to date. Variation in water availability in the
139 environment may be described by persistent differences in the presence or absence of free water
140 (Dupoué et al. 2017b, 2018) or by moisture gradients (Tieleman et al. 2003). When population sites
141 have consistent differences in the availability of permanent water, adaptive shifts towards lower
142 optimal body temperatures can be expected to limit water loss in dry environments where the water
143 debt cannot be recovered by drinking (Hypothesis 5 in Table 1, Davis and DeNardo 2009,
144 Lillywhite et al. 2012). Moreover the magnitude of change in thermoregulation strategies should be
145 greater in xeric than in mesic habitats as the environment gets warmer (Hypothesis 7, Table 1) and
146 in homogeneous landscapes (Hypothesis 8 in Table 1) as proposed by the concept of thermo-
147 hydroregulation (Rozen-Rechels et al. 2019). Another possibility is that variation in water
148 availability in the environment is caused by short-term changes in air moisture or rainfall due to
149 weather fluctuations. Rainfall variability has for example been shown to drive changes in behavioral
150 activity of ectotherms or to change their micro-habitat selection (Davis and DeNardo 2009, Ryan et
151 al. 2016, Kearney et al. 2018). This variability can be described by year to year differences in the
152 risk of dehydration for which atmospheric water vapor pressure is an accurate predictor (Spotila
153 1972, Lourdais et al. 2017). In this context, one can therefore predict that dry local conditions,
154 favoring dehydration and characterized by low water vapour pressure in the air, should alter
155 thermoregulation strategies just as surface water would (Rozen-Rechels et al. 2020, Hypothesis 6 in
156 Table 1).
157 All things considered, quantifying the relative importance of thermal conditions, hydric conditions
158 and habitat heterogeneity thus requires comparative, multi-year studies to understand the key

159 drivers of geographic variation in thermoregulatory behavior. Here, we surveyed geographical
160 variation in the thermoregulation strategies of a cold-adapted vertebrate species, the common lizard
161 (*Zootoca vivipara*, Lacertidae, Lichtenstein, 1823) over three years. The sampled sites included in
162 our study are located at the southern margin of the distribution of the species. Previous work has
163 demonstrated that climate warming induces changes in life-history strategies in these populations
164 (e.g., Chamaillé-Jammes et al. 2006). Annual variability in the phenology of reproduction as well as
165 reproductive effort correlates with changes in ambient temperature (Le Galliard et al. 2010,
166 Rutschmann et al. 2016b, 2016a). Moreover, geographic variation in water availability influences
167 the species' thermal ecology and water balance (Lorenzon et al. 1999, 2001, Dupoué et al. 2017a,
168 2018) as well as their physiological sensitivity to extreme thermal conditions (Dupoué et al. 2018).
169 Thermal and water conditions further interact in predicting dispersal and population extinctions
170 (Massot et al. 2002, 2008, Dupoué et al. 2017b). The common lizard has been described as an
171 active, efficient thermoregulator relying on flexible changes in microhabitat selection and basking
172 behavior to regulate its body temperature (Gvoždík 2002, Herczeg et al. 2003). Although body
173 temperatures vary among populations due to differences in local temperature, previous comparative
174 studies have suggested that thermal preferences and indices of thermoregulation do not differ
175 between low and high elevation populations with contrasted mean thermal conditions (Van Damme
176 et al. 1990, Gvoždík 2002). Here, we moved a step forward to sample 21 populations and ca. 2000
177 lizards along an elevational gradient at a regional scale (Massif Central, France) over three summers
178 to gather data across 31 population-year combinations. We used an information-theoretic approach
179 to test the eight hypotheses summarized in Table 1 and evaluate how the thermal and hydric quality
180 of the environment may explain variation in behavioral thermoregulation of the common lizard.

181 **Material and methods**

182 ***Study species and sampling***

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

194 Our focal populations are located in the mountain ranges of Massif Central in south-central
195 France on a 500 meters elevation gradient clustering most of the species population in the area (see
196 Table S1). The studiy sites are located in a variety of habitat types and include: wet meadows, heath
197 lands, and glades within dense forest patches. The habitat may also include open forest with
198 dispersed trees or shrubby vegetation (pine trees, *Pinus* spp., juniper trees, *Juniperus* spp., scotch
199 broom, *Cytisus scoparius* and gorse, *Ulex* spp.) or low growth shrubs (heather, *Calluna vulgaris*, and
200 blueberry, *Vaccinium* spp.) that offer contrasting thermal micro-habitats and shelters. We sampled
201 21 populations between 2016 and 2018. Most populations were sampled at least twice in differing
202 years, but some were only sampled once (Table S1). Sites ranged in size from 0.6 to 12 ha and
203 occurred in a diversity of habitats ranging from open meadows without permanent access to water
204 to forest clearing with free standing water (Figure 1 and Table S1). The two closest sites were more
205 than 700 meters away from each other and the landscape in the region is fragmented by roads,
206 closed forest, pasture and othe unsuitable habitats for the species. The probability that two sites are
207 connected by a permanent flow of migrants is thus low. Capture dates in focal populations varied to

208 accommodate current weather conditions within each sample year. Our capture dates occurred from
209 June 20th to June 29th, 2016, from June 12th to June 26th, 2017 and from June 9th to June 28th, 2018.
210 In each population, we captured yearlings (less than 2 years old), adult gravid females and adult
211 males (2 years old or more). We attempted to capture 20-24 adult females, 10 adult males and 20
212 yearlings (sex ratio 1:1) per population (see Table S2). We measured snout-vent length (average
213 SVL \pm SD; yearlings: 43 ± 6 mm; adult females: 62 ± 5 mm; adult males: 55 ± 4 mm) and body
214 mass (BM: yearlings: 1.50 ± 0.57 g; adult females: 4.47 ± 1.32 g; adult males: 3.35 ± 0.67 g).
215 Adult gravid females and adult males were then brought to the laboratory and housed in individual
216 terraria (females: $25 \times 15 \times 16$ cm, males: $18 \times 11 \times 12$ cm) with peat soil and a shelter. A
217 temperature gradient between 20 to 35°C, which is representative of the gradient of temperatures
218 found in natural population sites, was created in the terraria for 6 hours in the day (from 09:00 to
219 12:00 and from 14:00 to 17:00) with 25W incandescent bulbs placed above one side of each of the
220 terrarium to allow thermoregulation. Water was supplied to individuals by misting the terraria three
221 times per day at 09:00, 12:00 and 17:00. Individuals were not fed for two days after capture to
222 ensure a post-absorptive state during the thermal preference tests (see below). Lizards were fed
223 once every two days with 2 domestic crickets (*Acheta domestica*) until they were released (after
224 parturition for females or after measurements for males; Rutschmann et al. 2016b, Dupoué et al.
225 2018). In one population subject to a long-term mark-recapture study (ROB; Table S2), we also
226 brought yearlings back to the laboratory to assess age-related differences in thermal preferences.

227 **Description of climate and habitat characteristics**

228 We described the focal sites using well-defined meteorological, microhabitat and landscape
229 variables to test our hypotheses (summarized in Table S1, with accurate locations and area of the
230 sites). First, elevation ELE and the Emberger pluviometric quotient Q (Daget 1977, see below,
231 Figure 2) were scored in order to test for consistent differences among populations along the
232 elevational cline and along a historic climatic cline. The calculation of elevation allowed us to test

233 for potential trends of thermoregulatory strategies variations from the lowest altitude populations in
234 this geographic area up to mountain tops. The elevation gradient in our study area ranged from 1099
235 to 1527 meters. In addition, the calculation of the pluviometric quotient Q allowed us to test for a
236 consistent trend along a historic, climatic gradient of aridity (lower precipitations and higher
237 temperatures). To calculate the pluviometric quotient, meteorological variables were extracted from
238 the AURELHY database of temperature and precipitation records over France from 1971 to 2000
239 extrapolated at a 1 km² scale (provided by Meteo France, see Bénichou and Le Breton (1987) for a
240 description of the dataset). This database has the finest resolution grid and accounts for relief
241 differences in interpolating the data, which is important for extracting correct statistics for each
242 population in this geographic area. From these data, the Emberger pluviometric quotient for each
243 site was given by:

$$244 Q = \frac{100 \times P}{T_{ARLmax}^2 - T_{ARLmin}^2}$$

245 where P is the average annual precipitation in cm and T_{ARLmin} (respectively T_{ARLmax}) the average of
246 daily minimum temperature of the coldest month (respectively average of daily maximum
247 temperature of the warmest month). The pluviometric quotient among the focal sites ranged from
248 228.1 to 563.3. None of the sites could thus be characterized as arid.

249 Second, we obtained local weather conditions for each year at each site including air temperature
250 and water vapor pressure. These variables allowed us to measure both geographic and temporal
251 changes in the microclimate conditions, and therefore quantify the specific meteorological
252 conditions during the study period instead of long-term historical trends. We measured local
253 weather conditions at each site and each year with 1 to 3 temperature and humidity dataloggers
254 placed on the ground in the shade of the representative vegetation (Hygrochron iButtons, Maxim
255 Integrated Products, Sunnyvale, CA, USA, ± 0.5 °C and 5% relative humidity—RH). At one site
256 (ROB), we placed an additional 18 temperature loggers in different types of vegetation to calculate
257 spatial variation in thermal conditions. For each sample site, we calculated the average 10:00 to

258 18:00 minimal and maximal air temperatures (hereafter called T_{\min} and T_{\max}) and the average 10:00
259 to 18:00 maximal water vapor pressure (hereafter called P_{\max} ; see Supplementary Information 1 for
260 further information on measurements, calculations and choice of variable as well as Rutschmann et
261 al. 2016A and Dupoué et al. 2018). We restricted these calculations from 10:00 to 18:00 in order to
262 compare local microclimatic conditions during the diurnal activity period of the lizards, because this
263 interval is the most relevant to thermal quality of the environment during thermoregulation.

264 Third, we characterized habitat attributes including the presence of free water (permanent access or
265 temporary access, hereafter called FW, see Dupoué et al. 2017b), an index of forest cover, the
266 evenness in thermal micro-habitat diversity and the homogeneity of the thermal landscape. Sixteen
267 sites had permanent sources of water, either streams or ponds, whereas 5 sites had access to
268 temporary pools or streams. To characterize the landscape, we took aerial georeferenced digital
269 photographs of all sites with a Phantom 4 Pro drone (DJI, Shenzen, China). In most cases except for
270 small sites (BARN, MON, LAJO), we took a georeferenced grid of pictures centered on each site
271 with Pix4Dcapture (Pix4D SA, Prilly, Switzerland) and then reconstructed a georeferenced
272 orthophoto with the Maps Made Easy application (<https://www.mapsmadeeasy.com/>). For small
273 sites, the map was created from one picture and we aligned georeferencing with control points
274 accurately geolocated on Google Earth maps (version 7.3.2, Google Inc. 2019). From each
275 georeferenced orthophoto, we then generated an 8-level vegetation map by creating a vector layer
276 where each polygon corresponds to a patch of one of 8 pre-defined vegetation types (grass, heather,
277 bilberry, tree, bush, rock, naked soil, and dead tree). Vectors layers were constructed in QGIS
278 (version 2.18; QGIS Development Team, 2018, QGIS Geographic Information System. Open
279 Source Geospatial Foundation Project. <http://qgis.osgeo.org>) and downscaled to a 1-meter accuracy
280 map (Figure S2).

281 We assessed the thermal quality of each vegetation type (i.e, each thermal microhabitat) by
282 recording operative temperatures in all vegetation types and sites. To do so, we placed between 6

283 and 24 physical copper tube models fitted with HOBO® Pro v2 U23-003 (ONSET Cape Cod,
284 Massachusetts) temperature loggers in representative vegetation types at each site. Sampled
285 vegetation types were chosen in order to characterize as much as possible the vegetation diversity
286 observed at each site. Each copper tube was 6 cm long and painted to mimic the dorsal coloration of
287 a common lizard to match the biophysical, heat exchange properties of the species and record
288 operative environmental temperatures (T_e) in a diversity of vegetation types (Dzialowski 2005).
289 Indeed, operative environmental temperatures provide the best estimate for microhabitat thermal
290 quality (Bakken et al. 1985, Angilletta 2009, Sears and Angilletta 2015). The loggers recorded
291 temperatures every minute during each capture episode. We calibrated the temperatures made with
292 operative temperatures models by comparing the temperatures with dead individuals
293 (Supplementary Information 2). In subsequent calculations, we averaged these measurements in 15-
294 minute bins in order to compensate for short time changes in microclimatic conditions (e.g., due to
295 wind or cloud cover). This time scale was also chosen because it captures heat exchange properties,
296 i.e., thermal inertia, of small lizards such as the common lizard (Fraser and Grigg 1984). The
297 average operative environmental temperature score of each site per year (hereafter called T_e) over
298 15-minute bins was calculated from the average T_e of all loggers in the site weighted by the
299 abundance of the vegetation types in the site.
300 We also calculated an average T_e score, independent from site and year, for each of the 8 vegetation
301 types, in order to obtain an objective estimate of thermal differences across all microhabitats (see
302 Supplementary Information 2 and Figure S3 for details). The chosen vegetation types represented a
303 diversity of thermal microhabitats with short vegetation (grass), short bush (heather or bilberry),
304 bush, shade under a tree, full sun (rock, bare soil) and dead tree. We then constructed a “thermal
305 map” of operative temperatures at each site by linking each pixel of our rasterized map to the
306 average T_e score of the corresponding vegetation type. From the vegetation map and the thermal
307 map, we then calculated three different indices of landscape heterogeneity. First, we calculated a

308 forest cover index defined as the proportion of trees within the site (hereafter called FCI). This
309 index is a proxy of the proportion of shade in the habitat and has been often used to quantify habitat
310 constraints on thermoregulation in heliothermic lizards (Huey and Slatkin 1976). It ranges from 0
311 (open landscape) to 1 (closed forest). In the focal sites, FCI ranges from 0 (open prairies, mainly
312 grass) to 0.75 (sites in forest environments). Second, we calculated an index of thermal evenness
313 (hereafter called TE). This index measures the diversity of average operative temperatures available
314 in the landscape, corrected by the abundance of each microhabitat. TE ranges from 0 (low diversity
315 and/or large dominance of a close range of operative temperatures) to 1 (diversified and equally
316 abundant operative temperatures in the landscape). This index ranges from 0.06 to 0.47 indicating a
317 low diversity of operative temperatures in the landscape. The lowest scored sites are those mainly
318 covered in grass and open with few bushes. Third, we calculated an index of homogeneity based on
319 the vegetation dissimilarity between adjacent pixels corrected by the difference of average operative
320 temperatures between these pixels (hereafter called H). This index ranges from 0 (heterogeneous
321 thermal landscape) to 1 (homogeneous thermal landscape). The focal sites were relatively
322 homogeneous, with an index ranging from 0.78 to 0.96. All methods and calculations are described
323 in detail in Supplementary Information 2.

324 ***Thermal preferences and thermoregulation traits***

325 Immediately after capture, we measured cloacal body temperature T_b using a K-type thermocouple
326 connected to a digital thermometer (Ecoscan PT100, Eutech Instruments Pte Ltd) inserted ca. 1 cm
327 within the cloaca. We also obtained T_b data on additional individuals in the field that were not
328 included in the laboratory studies. Two days after capture, we measured the thermal preferences
329 (T_{pref}) of all lizards returned back to the laboratory. Thermal preference represents the selected body
330 temperature of an individual in an environment free of costs for thermoregulation and is assumed to
331 match the optimal body temperatures for physiological performance (Hertz et al. 1993, Angilletta et
332 al. 2002). Here, thermal preferences were measured in 20 separate thermal gradients (120 × 25 × 20

333 cm) with a substrate of dried peat soil. One side of each gradient was heated with a 60W
334 incandescent bulb in order to approach the species critical thermal maximum CT_{max} ($43.9 \pm 4.8 ^\circ C$,
335 Gvoždík and Castilla 2001) and the other end of the gradient was maintained at ambient
336 temperature ($24.1 \pm 2.0 ^\circ C$). The range of temperatures provided in the thermal gradient therefore
337 allowed the lizards to select a body temperature with low thermoregulatory costs (Angilletta 2009).
338 A plastic shelter was placed under the heat bulb and water was supplied continuously during the
339 experiment with a permanently filled small petri dish on the cold side in order to limit the stress of
340 individuals in the terrarium. We note that this can confound measurements of thermal preferences
341 with shelter or water preferences, but the design was the same for all populations. Two UVB 30W
342 neon tubes provided natural white light above each gradient. Heat bulbs were turned on at
343 approximately 08:00 in the morning. At 9:00 in the morning or at 14:00 in the afternoon, two
344 individuals of the same age, sex and SVL (± 3 mm maximum in the same gradient) were placed in
345 each gradient to acclimate for 30 minutes. Both individuals were identified with a drop of nail
346 polish placed on the dorsum side between the pelvis and tail. We did not observe any aggressive
347 behavior between individuals during any run. In addition, it was not unusual to observe the lizards
348 basking at the same spot, indicating that avoidance behaviors may not strongly influence our
349 measurements. After acclimation, the temperature of the dorsal surface T_{pref} of each lizard was
350 measured with an infrared thermometer (Raytek, Raynger MX2) every 15 minutes for 3h15. We
351 calculated the corresponding core body temperature from a calibration curve performed with
352 additional data on the same species (Artacho et al. 2013; $R^2 = 0.96$; $T_{core} = -4.50 (\pm 0.5 SE) + 1.17$
353 $(\pm 0.03 SE) \times T_{pref}$). We excluded from analyses the extremes of T_{core} (lower than $25^\circ C$ and higher
354 than $41^\circ C$) with consideration that they corresponded to failed measurements aimed at the
355 substratum instead of the lizard back (results were similar qualitatively with all data included). T_{pref}
356 referred to T_{core} in the following parts of the manuscript.

357 Variation of T_{pref} with the time of the day, date or individual status was investigated (see the
358 Statistical Analyses section, Supplementary Information 3 and 4). We further tested for differences
359 between thermal preferences of yearlings and adults at the same time of the year in one population
360 (ROB). These data showed that thermal preferences of yearlings (regardless of sex) and adult males
361 were not different (Figure 4A, Table S5, all details in Supplementary Information 3). Thus, we
362 assume that thermal preferences of males in each population were a good proxy of the thermal
363 preferences of yearlings. For each population and year, we calculated the average thermal
364 preferences of adult females and adult males/yearlings hereafter called $\overline{T_{\text{pref}}}$ (average of all T_{pref}
365 measurements for each year, population and age-sex category of individuals). To quantify how field
366 body temperatures of lizards deviate from their thermal preferences, we calculated the
367 thermoregulation inaccuracy, defined as the absolute difference between body temperature during
368 activity in the field and thermal preferences $D_b = |\overline{T_{\text{pref}}} - T_b|$, for each T_b measurement (Hertz et al.
369 1993, Blouin-Demers and Nadeau 2005). For each individual record, we used the average $\overline{T_{\text{pref}}}$
370 from the same category of individuals (age and sex class) in the same population of the same year.
371 We further calculated thermal quality of the habitat, defined as the absolute difference between
372 operative temperatures and thermal preferences $D_e = |\overline{T_{\text{pref}}} - T_e|$, for each age-sex category of
373 lizards in each population each year and each 15 minutes' time bin (Hertz et al. 1993, Blouin-
374 Demers and Nadeau 2005). The ability of an individual to reach their thermal preference given the
375 thermal quality of the habitat is called thermoregulation efficiency or effectiveness of
376 thermoregulation. For each capture event, we calculated the index of thermoregulation efficiency, E
377 ($E = D_e - D_b$; Blouin-Demers and Nadeau 2005) based on the D_b calculated with T_b at capture and
378 the D_e for the same population during the 15 minutes' time bin of the capture time. When $E = 0$, the
379 body temperature of the lizard is the same as that of a physical model that is not thermoregulating
380 and there is therefore no evidence that individuals are active thermoregulators. If $E > 0$, individuals
381 are thermoregulating as they reach their preferred temperature even though the thermal environment

382 is not of sufficient quality for a thermoconformer. If $E < 0$, individuals are avoiding thermally
383 suitable microhabitats.

384 **Statistical analyses**

385 All analyses were performed with R version 3.4.4 “Someone to Lean On” (R Core Team 2018). We
386 analysed variation of T_b , T_{pref} , D_b , D_e , and E using linear mixed models with the function *lme* from
387 the package nlme (Pinheiro and Bates 2006) after assessment of homoscedasticity and normality of
388 residuals. As the distribution of D_b was not Gaussian, we used a square root transformation. For
389 each variable, we followed the same logic for model selection procedure. We first fit a full model
390 including all individual and time covariates as fixed effects and then selected a first minimum
391 adequate model using backward model selection based on likelihood ratio tests. Time covariates
392 included year (categorical, all response variables), hour of the day (continuous, for T_b , D_b , and E),
393 and time of the day (morning or afternoon session, T_{pref}). Individual covariates were age and/or sex
394 (categorical, for T_b , T_{pref} and D_b) or category (categorical, adult females versus adult males and both
395 sexes yearlings, D_e , E , see Supplementary Information 3 and Figure 4A for motivation). Full
396 models included additive effects of all covariates and two-way interaction terms between all
397 individual covariates. For T_{pref} data, we analysed all temperatures recorded for each individual
398 rather than a composite variable (e.g. mean or variance), unpublished data from the team showed
399 that thermal preferences sometimes change depending on the hour of the day but also with the time
400 spent in the gradient (unpublished data). We therefore also fit a two-way interaction between the
401 time of the day the experiment was run (morning vs. afternoon) and the time spent since the
402 beginning of the test (i.e., end of habituation). Population identity was included as a random effect.
403 Individual identity nested in the population identity was also included as a random effect to account
404 for repeated measurements on the same individual (T_{pref} data).
405 When a minimum adequate model was selected, we determined whether the traits differed across
406 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 AICc over all models in which the variable appears) of environmental variables related to elevation, Emberger pluviometric quotient, microclimatic conditions and habitat features (see Table S6) using the Akaike information-based criterion (AICc) 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 Table S4), but we excluded models with significant collinear variables ($r > 0.5$). We also removed the few models that showed no convergence (listed in Table S6). 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 AICc 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 Table S2. Detailed results of the model selection procedures are presented in Table S6. Conditional averages of the most important environmental variables from model averaging are presented in Table 2.

Variation in body temperature

432 Field body temperature of lizards varied significantly among populations (proportional variance
433 explained = 41%; LRT = 487.4, df = 1, $p < 0.0001$). The average body temperature also changed
434 with the hour of the day following a quadratic function and was significantly explained by the
435 interactions between age \times sex and sex \times year. Average adult female T_b was 27.8 ± 0.5 °C, whereas
436 female yearlings T_b were 1.5 ± 0.1 °C warmer than adult females ($t_{1963} = 10.0, p < 0.0001$). Adult
437 males T_b were 1.2 ± 0.3 °C warmer than adult females ($t_{1963} = 4.2, p < 0.0001$). Male yearlings had
438 approximately the same body temperatures as female yearlings and adult males (yearlings \times males:
439 $t_{1945} = -7.5, p < 0.0001$). The most important environmental variables explaining geographic
440 variation of body temperature included the pluviometric quotient Q (relative importance RI: 0.95)
441 and T_{\max} (RI = 0.95) and the two-way interaction Q \times T_{\max} (RI = 0.91, Figure 3A and B, Table S6).
442 According to the best supported model, mean body temperatures were higher in populations
443 characterized by a mesic environments (higher Q coefficient) with high T_{\max} (Table 2, Figure 3A).
444 In drier environments (low Q), body temperatures were almost consistant with minimal air
445 temperatures T_{\max} , whereas T_b increased with T_{\max} in mesic environments (high Q).

446 ***Variation in thermal preference***

447 We identified significant differences in records from thermal gradient T_{pref} measurements among
448 populations, however the variance explained among populations was quite low (variance explained
449 = 2%; LRT = 48.2, df = 1, $p < 0.0001$) compared to the variation among individuals (proportional
450 variance explained = 24%). Variation in T_{pref} was also significantly explained by an interaction of
451 sex \times year, and between time of day (morning versus afternoon) when the T_{pref} was measured with
452 the time since beginning of the test. Despite little quantitative variation among populations, our
453 model comparison procedure uncovered that the forest cover index FCI as well as the two-way
454 interaction between FCI and sex were significant variables explaining geographic variation in T_{pref}
455 (RI of 0.85 and 0.84 respectively, Table 2). T_{pref} of females significantly increased with FCI
456 (Figure 4B).

457 ***Variation of thermoregulation inaccuracy***

458 The inaccuracy of thermoregulation D_b differed among populations (proportional variance
459 explained = 39%; LRT = 519.1, df = 1, $p < 0.0001$). Variation in D_b followed a quadratic function
460 of the hour of the day and was also significantly explained by a three-way interaction sex \times age \times
461 year. Values of mean D_b among males and yearlings did not differ from adult females in 2016
462 (males: $t_{1959} = -0.3, p = 0.79$, yearlings: $t_{1959} = -1.1, p = 0.27$, males \times yearlings: $t_{1959} = 0.9, p =$
463 0.34) and in 2018 (males: $t_{1959} = -1.7, p = 0.09$, yearlings: $t_{1959} = -0.3, p = 0.76$, males \times yearlings:
464 $t_{1959} = -0.9, p = 0.37$). However, in 2017, males displayed mean $\sqrt{D_b}$ values 0.2 ± 0.1 °C higher than
465 females ($t_{1959} = 2.0, p = 0.05$) and yearlings of both sexes displayed mean $\sqrt{D_b}$ values 0.4 ± 0.1 °C
466 higher than females (yearlings: $t_{1959} = 3.7, p = 0.0003$, males \times yearlings: $t_{1959} = -2.4, p = 0.02$).
467 They were thus less precise in their accuracy during that year. Geographic variation in D_b was
468 mostly explained by T_{max} (RI=1), pluviometric quotient Q (RI=0.1) and their two-way interaction
469 (RI=0.1, Table S6). Thermal inaccuracy (D_b values) was lowest in drier (low Q) and cooler habitats
470 (low T_{max}) and higher in more mesic (high Q) and low T_{max} (Table 2). The inaccuracy of
471 thermoregulation (D_b) increased with pluviometric quotient at low minimal air temperature T_{min} ,
472 and decreased with pluviometric quotient at high T_{max} (Figure 3B).

473 ***Variation in thermal quality of the habitat***

474 Thermal quality of the habitat D_e differed among populations (proportional variance explained =
475 36%; LRT = 678.3, df = 1, $p < 0.0001$). Values for D_e varied following a quadratic function of the
476 hour of the day. Geographic variation in D_e was mostly explained by P_{max} (RI=1), T_{min} (RI=1) and
477 their two-way interactions (RI=1, Table S6). In populations with average T_{min} , D_e increased with an
478 increase of P_{max} . This effect vanished and was even inverted with an increase in local minimal air
479 temperature (Table 2). In most cases, T_e were below thermal preferences, i.e. thermal quality of the
480 habitat was in average too cold (Figures S3 and S4).

481 ***Variation in thermoregulation efficiency***

482 The D_b values increased significantly with D_e (Figure 5, slope: 0.2 ± 0.02 , intercept: 6.4 ± 0.4 ;
483 $F_{1,1836} = 144.5, p < 0.0001$). Variation in thermoregulation efficiency E followed a quadratic
484 function of the hour of the day (decreased with the hour of the day after which it increased again).
485 In addition, E differed among populations (proportional variance explained = 46%; LRT = 781.7, df
486 = 1, $p < 0.0001$). Geographic variation in E was significantly explained by T_{\min} (RI=1), P_{\max} (RI=1),
487 and the two-way interaction $P_{\max} \times T_{\min}$ (RI=1, Table S6, Figure 5). In other words,
488 thermoregulation efficiency E increased with minimal air temperature T_{\min} in populations with
489 higher water vapour pressure P_{\max} , whereas it decreased with T_{\min} in populations with high P_{\max}
490 (Table 2, Figure 6).

491 Discussion

492 In this study, we tested whether geographic differences in elevation or climate dryness, year- and
493 site-specific differences in air temperature and moisture, habitat differences in water availability
494 and habitat differences in spatial landscape features of the vegetation influenced thermoregulation
495 strategies across multiple populations of a widespread lizard species. Our results highlight that
496 thermoregulation behaviors are mainly shaped by interactions between local site- and year-specific
497 air temperatures, historical differences in the Emberger pluviometric quotient and the local annual
498 air moisture conditions, supporting the thermo-hydroregulation hypothesis (Hypothesis 7; results
499 supporting each hypothesis are summarized in Table 3). Body temperature, and as a consequence
500 thermoregulation inaccuracy, was influenced by an interaction between local air temperatures and
501 the historical differences in climate dryness of the site. Preferred temperature of lizards was
502 significantly lower for adult females and in populations with permanent access to water. Finally,
503 thermoregulation efficiency and the quality of the thermal habitat, were highly variable among
504 populations and were influenced by the interaction between air temperature and air moisture, which
505 were calculated for each site and each year. In contrast, persistent, historical differences in weather
506 conditions and habitat features had little effects on these thermoregulation statistics.

507 Thermoregulation traits were not influenced by elevation or by the thermal landscape of the sites,
508 rejecting hypotheses 1, 3, 4 and 8 (Table 3).

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

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

522 According to the thermo-hydroregulation hypothesis (hypothesis 7 in Table 1), the costs of
523 thermoregulation depend on the risks of desiccation and over-heating, which are generally more
524 important in drier climates (e.g., Dupoué et al. 2017b, 2018) and should increase in warmer climatic
525 conditions (e.g., Lourdais et al. 2017, Rozen-Rechels et al. 2019). We thus expect thermoregulation
526 to be more accurate in sites with lower costs of desiccation when local climate conditions are
527 warmer (Rozen-Rechels et al. 2019). Our results are concordant with these expectations, which
528 emphasizes the importance of non-energetic costs of thermoregulation due to a higher risk of
529 dehydration in populations with long-term patterns of a dry climate accompanied by high ambient
530 temperature. One explanation is that selection favoring behavioral thermoregulatory strategies to
531 limit dehydration led to either plastic or genetic adaptive responses in lizard populations occupying

532 historically drier climate conditions. To our knowledge, this is the first demonstration that a climate
533 dryness index, calculated from rainfall and temperature data, accurately predicts geographic
534 variation in thermoregulation strategies in an ectotherm (see Tieleman et al. 2003 in endotherms).
535 This complements recent data by Kearney et al. (2018), who observed that activity patterns in
536 another species of lizard were also sensitive to both local temperature and rainfall patterns.
537 In addition, we found that the thermoregulation inaccuracy had a positive correlation with the
538 thermal quality of the habitat with a slope < 1 (Figure 5), suggesting that in our study system, the
539 common lizard is intermediate between a perfect thermoregulator and a perfect thermoconformer
540 (Hertz et al. 1993). Variation in thermoregulation efficiency, calculated from the difference between
541 the thermal inaccuracy of the lizard and the thermal quality of the habitat, was best explained by an
542 interactive effect between ambient thermal conditions and local air moisture, which provides
543 additional support to the thermo-hydroregulation hypothesis (hypothesis 7 in Table 1). Air
544 moisture, another measure of the hydric quality of the habitat, explained geographic variation in the
545 thermal quality of the habitat (D_e) and in thermoregulation efficiency (E), whereas the historical
546 aridity index (Q score) best explained the thermoregulation inaccuracy. In low air moisture
547 conditions, thermoregulation efficiency exhibited a slight increase with minimal air temperature. In
548 contrast, in high air moisture conditions, thermoregulation efficiency was maximal at low air
549 temperatures and displayed a striking decrease as air temperatures increased. These results suggest
550 that the relation between air temperature and thermoregulation efficiency is constrained at low air
551 moisture conditions, i.e. when local microclimatic conditions at the site are more desiccating. They
552 further indicate that variation in thermoregulation efficiency are mainly explained by local and
553 yearly moisture-driven changes in the thermal quality of the habitat rather than historical
554 differences in climatic conditions characterizing each population (as described by the pluviometric
555 quotient Q). However geographic variation of thermoregulation accuracy was best explained by
556 long-term and historical weather conditions rather than local annual weather conditions. We note

557 that this was not due to some model inconsistency due to a collinearity between variables because
558 the pluviometric quotient and the moisture conditions of a site were uncorrelated ($F_{1,29} = 0.32$, $p =$
559 0.57, $R=-0.13$). Furthermore, differences in air moisture are mainly associated with potential
560 differences in total rates of water loss from lizards in each site and each year (Spotila 1972, Mautz
561 1982), whereas differences in historical pluviometry may further influence soil moisture,
562 availability of free-standing water throughout the year and ecosystem productivity. One potential
563 interpretation of our findings is therefore that the risk of dehydration, which is typically enhanced in
564 drier air conditions (Rozen-Rechels et al. 2019), decreased thermoregulation efficiency, which
565 indicates that some non-energetic costs linked to water loss act as a constraint to thermoregulatory
566 behaviors. Altogether, these results provide strong support for the thermo-hydroregulation
567 hypothesis (Rozen-Rechels et al. 2019, Hypothesis 7 in Table 1), which posits that the
568 thermoregulatory behavior of common lizards is shaped by a trade-off between body temperature
569 regulation and water balance regulation.

570 ***Low geographical variability of thermal preferences***

571 Thermal preferences exhibited the lowest geographic variation among all thermoregulation statistics
572 investigated in this study. A striking pattern was that intra-population variation in thermal
573 preferences (24%) was unexpectedly higher than inter-population variation (2%), as seen in
574 previous geographic comparisons of thermal preferences in this species (Trochet et al. 2018) but
575 also across lizard species (Clusella-Trullas and Chown 2014). The low geographic variability of
576 thermal preference is consistent with previous findings in the same species comparing populations
577 at low and high elevations (Van Damme et al. 1990, Gvoždík 2002, but see Trochet et al. 2018 for
578 oviparous populations of *Z. vivipara*). The low inter-population variability of thermal preference
579 also supports earlier findings that thermoregulatory preferences exhibit limited variation compared
580 to field active body temperature (generally a standard deviation of 1.7 °C compared to 2.9°C for the
581 body temperature range among Lacertidae species based on Clusella-Trullas and Chown 2014). It is

582 also consistent with the observation that thermal preferences vary less than field body temperatures
583 across elevational ranges or along climate gradients in many lizard species (Van Damme et al.
584 1990, Angilletta et al. 2002, but see Gilbert and Miles 2019 for a counter-example in an arid zone
585 lizard). Interestingly, average thermal preferences reported here were surprisingly high, especially
586 for gravid females, compared to previous values reported for the same species in other study sites
587 (gravid females: 34.0 ± 3.2 °C, males: 35.8 ± 3.4 °C; see Gvoždík 2002 who used a different
588 method at higher latitude, in the Czech Republic, Le Galliard et al. 2003, Artacho et al. 2013,
589 Rozen-Rechels et al. 2020 with similar methods in an experimental set-up, Trochet et al. 2018 using
590 oviparous populations located in the Pyrénées, in the South-Western European range).

591 Methodological differences, in part, between these studies may contribute to this contrast. However,
592 an alternative is that the differences may be real and the high values reported in our study might
593 suggest directional selection for higher thermal preference along the warmer, southern margin of the
594 species distribution, which is under warming pressure (Chamaillé-Jammes et al. 2006, Gilbert and
595 Miles 2017 for another example in an other species). Overall, our results suggest higher variation in
596 thermal preferences at a greater spatial scale than the one investigated here. Further latitudinal
597 comparisons of populations spanning a broader geographic range than this study is needed to
598 confirm this pattern.

599 The only noticeable geographic trend in thermal preference that we detected was a significant shift
600 towards higher thermal preference in females from populations with a high forest cover. We suggest
601 the shift is an indirect response associated with differences in the stage of gestation of females
602 among populations rather than a direct effect of forest cover *per se*. Indeed, thermal preference has
603 a higher correlation with the stage of gestation, which overwhelmed the effect of the forest cover
604 index (see Supplementary Information 4). The geographic difference between populations with low
605 versus high forest cover was mostly driven by one site (ROB, the population with the highest forest
606 cover), where females were more intensively sampled early in pregnancy (Figure S6). In addition, a

607 delayed timing of parturition in populations with higher forest cover had also been demonstrated in
608 a smaller sample of our study sites (Rutschmann et al. 2016a). In the common lizard, advancement
609 of gestation is associated with a shift toward lower thermal preferences, which is more obvious at
610 the end of pregnancy (ca. 29–30°C at the end versus 33–34°C before gestation; see Le Galliard et al.
611 2003). As we sampled a larger number of females early in gestation in sites with high forest cover,
612 differences in the timing of sampling and timing of parturition provided the best explanation for
613 why females had lower thermal preference in more open habitats.

614 ***Absence of thermal landscape effects***

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

626 A first potential explanation for the pattern of thermoregulation behavior of common lizards to be
627 similar in homogeneous and heterogeneous thermal landscapes, is that the costs of thermoregulation
628 in homogeneous environments are not as high as hypothesized in optimality models of
629 thermoregulation. For example, Basson et al. (2017) showed that the energetic cost of locomotion
630 between microhabitats are negligible for Oelofsen's Girdled lizards *Cordylus oelofseni* moving
631 inside their typical home ranges. Similar results may apply to common lizards because these are

632 actively foraging, ground dwelling lizards with a relatively good endurance capacity (Garland Jr
633 and Losos 1994, Vitt and Pianka 2014), Miles *unpublished data*).

634 A second potential explanation is that the ambient temperatures during capture were below the
635 thermal preference set of common lizards as opposed to the desert lizard species in previous
636 theoretical and empirical studies, where there was a significant risk of over-heating (Sears et al.
637 2016). In the cool temperature range of our geographic area and study sites and at the time of
638 sampling (Figure S4), the risks of overheating were in general negligible with the exception of a
639 few populations over short time periods of the day. In cool climate conditions, the benefits of
640 thermoregulation imply faster and more prolonged access to the thermal preference set by selection
641 of warmer microhabitats. Given the asymmetric shape of the thermal performance curves of reptiles
642 and the generalist (wide thermal breadth) thermal physiology of the common lizard (Van Damme et
643 al. 1991, Artacho et al. 2013), the benefits of thermoregulation by microhabitat selection of warm
644 sites are smaller in cool climates on average in this species than the benefits of thermoregulation by
645 microhabitat avoidance of warm sites in warm climates. This is because individual physiological
646 performances, such as maximal locomotor capacities, are weakly ascending and reach a plateau
647 over the body temperature range of 32–36°C including most of the observed variation in
648 temperature conditions in the vegetation. Since, a heterogeneous landscape would be beneficial
649 when it allows for behavioral shifts among contrasted cold and hot microhabitats in order to heat
650 faster in cool weather conditions and to avoid overheating in warm weather conditions;
651 heterogeneity would thus be critical only when the habitat overlaps the critical thermal limits of the
652 species which is not the case in our study focal period in the focal sites.

653 A third potential explanation is that our methods failed to characterize the complete range of
654 variation in the thermal landscape despite substantial differences in vegetation characteristics and
655 heterogeneity (Sears et al. 2011, Caillon et al. 2014). Our methods showed that the thermal
656 landscapes had limited variation. Our estimates of the homogeneity index (H) varied between 0.75

657 to 1. Most of the study sites were covered in large expanses of grass and other vegetation of short
658 stature. We could not characterize and quantify the fine-scale, spatial variability of thermal
659 conditions within vegetation patches inside each pixel of our vegetation maps. It is obvious from
660 field observations that active lizards can take advantage of the varying shade levels and vertical
661 thermal structure within a vegetation patch, and this fine scale heterogeneity to which lizards are
662 familiar might be more critical determinants of their thermoregulation behavior than vegetation
663 homogeneity at the scale of meters or tens of meters. Quantifying the very fine details of the
664 vegetation thermal landscape however represents a strong methodological challenge that is beyond
665 the scope of this study.

666

667 ***Implications for ecological responses to climate change***

668 Future risks of extinction for temperate lizard species as a result of global warming are expected to
669 show a dramatic increase due to a reduction in the availability of shade and an increase in the risks
670 of overheating. However, there is an ongoing debate about the critical determinants of population
671 loss from global warming for these species (Sinervo et al. 2010, Kearney 2013). In the common
672 lizard, climate warming in our study area has led to simultaneous changes in stress physiology,
673 ageing, life history, reproduction phenology and trajectories of population extinction in the warmest
674 sites (Chamaillé-Jammes et al. 2006, Rutschmann et al. 2016b, 2016a, Dupoué et al. 2017a, 2017b,
675 2018). In parallel, we found no evidence of a reduction of shade availability in the our study sites,
676 contrary to predictions of global mechanistic models (Kearney 2013). Stasis in forest cover (shade)
677 is a result of little or no change in vegetation among some study sites or an expansion of forest
678 cover in other sites during the past 15 years due to changes in land use (Clobert et al. *pers. obs.*).
679 The increase of availability of shade in some populations could benefit the common lizard in the
680 context of global warming because tall and dense vegetation ameliorates the risk of overheating
681 (Grimm-Seyfarth et al. 2017). Our study suggests, however, that thermoregulation strategies in

682 these populations are more strongly constrained by changes in hydric conditions and temperature
683 than by landscape features, and are best explained by an hypothesis that assume a trade-off between
684 behavioral thermoregulation and hydroregulation. The role of water balance is underappreciated in
685 current studies of thermoregulation. Our understanding of ectotherm responses to global change
686 would benefit from further studies that evaluate the role of water balance regulation in modulating
687 thermoregulatory behaviors (Rozen-Rechels et al. 2019).

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704 **Authors contributions**

705 DRR, J-FLG, AR, SM and JC designed the study. DRR, AR, AD, PB, JC, DBM, MR, AB, and J-
706 FLG participated to data collection and their formatting. VC produced the vegetation maps. MG

707 provided macroclimatic data and generated Figure 2. DRR analyzed the data with help of J-FLG.
708 DRR and J-FLG led the writing of the manuscript to which all authors significantly contributed.

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935 **Table 1** Our sampling protocol aims to quantify the relative importance of climate and habitat factors in explaining the geographical variation in
 936 thermoregulation statistics of the common lizard (*Zootoca vivipara*). This table summarises our working hypotheses and defines how these working
 937 hypotheses were tested with statistical models.

	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 at 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.	$ELE \times (TE, FCI \text{ or } H)$ $T_{\min} \times (TE \text{ or } H)$ $T_{\max} \times (THE, FCI \text{ or } H)$	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.	$ELE \times (Q, FW, P_{\max})$ $T_{\min} \times (Q, FW, P_{\max})$ $T_{\max} \times (Q, FW)$	(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.	$Q \times (TE, FCI, H)$ $FW \times (TE, H)$ $P_{max} \times (TE, FCI, H)$	(Rozen-Rechels et al. 2019)
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939 **Table 2** Conditional average of selected variables from the model averaging procedure (Table S6).

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

<i>Trait</i>	<i>Variable</i>	<i>Estimate</i>	<i>SE</i>	<i>Adjusted SE</i>	<i>z value</i>	<i>p value</i>
T_b	Intercept	30.2	0.38	0.38	85.2	< 0.0001
	Q	-0.9	0.4	0.4	2.1	0.03
	T_{max}	1.2	0.2	0.2	4.7	< 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	350.9	< 0.0001
	FCI	0.3	0.1	0.1	2.7	0.006
	Female	-0.9	0.1	0.1	13.9	< 0.0001
	$FCI \times Female$	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	4.9	0.9	0.9	5.9	< 0.0001
	T_{min}	-4.0	0.3	0.3	12.0	< 0.0001
	P_{max}	3.3	0.3	0.3	12.6	< 0.0001

	$T_{\min} \times P_{\max}$	-2.7	0.3	0.3	10.6	< 0.0001
<i>E</i>	Intercept	-0.2	0.9	0.9	0.3	0.78
	P_{\max}	2.8	0.3	0.3	10.6	< 0.0001
	T_{\min}	-4.5	0.4	0.4	12.8	< 0.0001
	$P_{\max} \times T_{\min}$	-3.1	0.2	0.2	12.6	< 0.0001

947 **Table 3** Our sampling protocol aims to quantify the relative importance of climate and habitat factors in explaining the geographical variation in
 948 thermoregulation statistics of the common lizard (*Zootoca vivipara*). This table summarizes our working hypotheses and defines how these working
 949 hypotheses were tested with statistical models.

	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 <i>per se</i> 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 modulate 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-	None.	In the absence of a cost of overheating, landscape features might not affect thermoregulation behaviors. Sites	No

hydroregulation landscape		may also be too homogeneous on average.	
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951 **Figure Legends**

952

953 **Figure 1** Aerial views of four contrasting sites. JON and PUY are two open habitats. The former is
954 situated in a clearing, whereas the latter is a vast grassland within the crater of the extinct volcano.
955 BEL and COM are two populations with substantial forest cover. The availability of water differs
956 among the locations. Streams traverse PUY and COM and the soil is saturated with water in
957 portions of the site; other areas are peat bogs. In contrast, free water is not available at JON and
958 BEL; both are much drier than COM and PUY especially during the summer time. No bogs can be
959 found at JON and BEL. Photographs were taken in 2017 with a Phantom 4 Pro drone (DJI,
960 Shenzhen, China) concomitant with a separate project to generate vegetation maps (Figure S2) of
961 each sample site.

962

963 **Figure 2** Geographic location of studied populations in the Massif Central mountain range from
964 France (see also Table S2) with a heat map of the Emberger pluviometric quotient Q measuring
965 long-term historical differences in climate dryness among sites (low values of Q indicate more arid
966 climates).

967

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

974

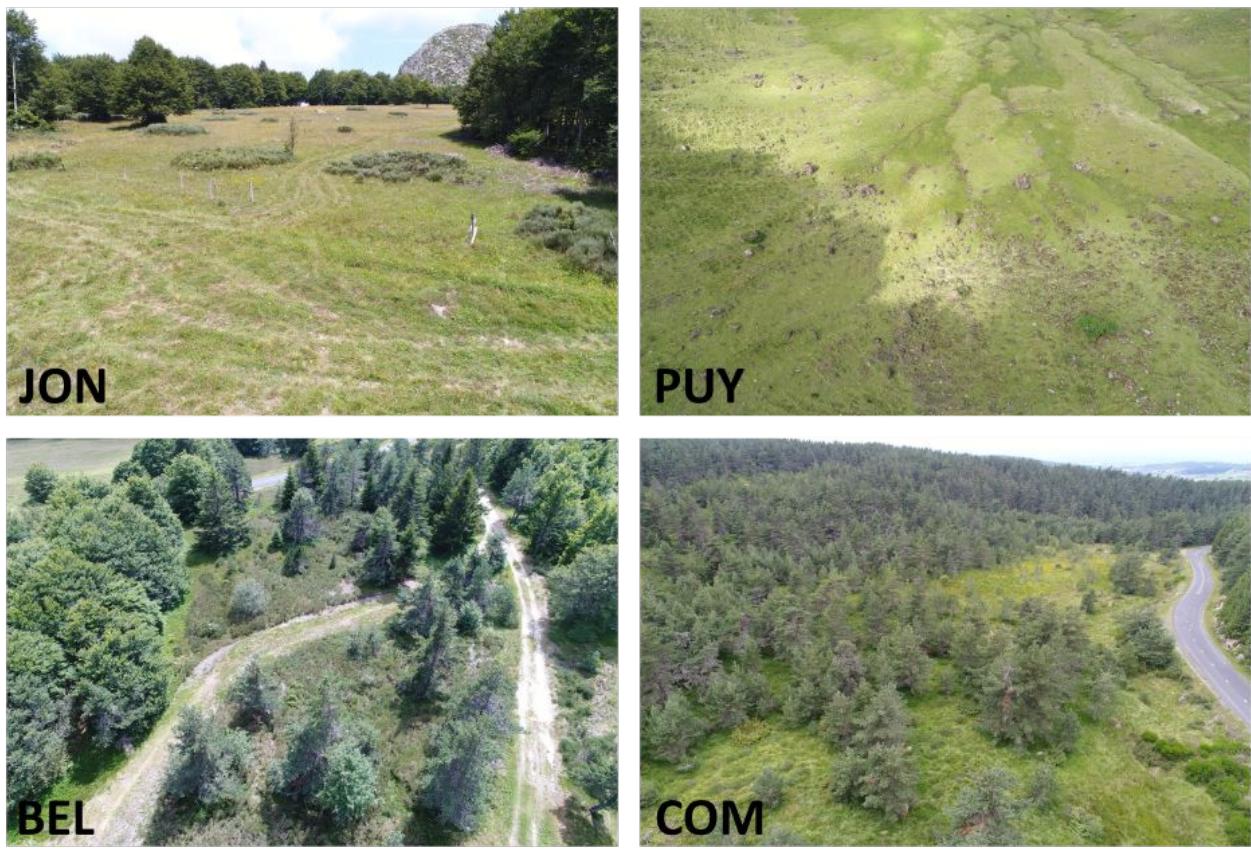
975 **Figure 4** Variation of preferred body temperatures measured in the laboratory T_{pref} as a function of
976 sex and age in the ROB population (**A**) and as a function of sex and forest cover (FCI) in all
977 populations with adults only (**B**). The boxplots display the median and the quantile distribution of
978 raw data in A. Points and error bars in B represent the average and the standard error of raw data for
979 each population and each sex. A: adults, Y: yearlings, FCI: forest cover index.

980

981 **Figure 5** Variation of thermoregulation inaccuracy D_b as a function of the thermal quality of the
982 habitat D_e (**A**). Points are for \bar{D}_b and \bar{D}_e per population per year per age-sex group. Colors
983 represent the presence of free-standing water (FW) at the site and symbols represent the age-sex
984 category of individuals. The black line is the line of equation $\bar{D}_b = \bar{D}_e$. This graph shows that
985 lizards from some dry sites without permanent access to free standing water have high D_e compared
986 to wet sites because we measured lower T_e in these populations (Figure S5). Error bars represent
987 standard error.

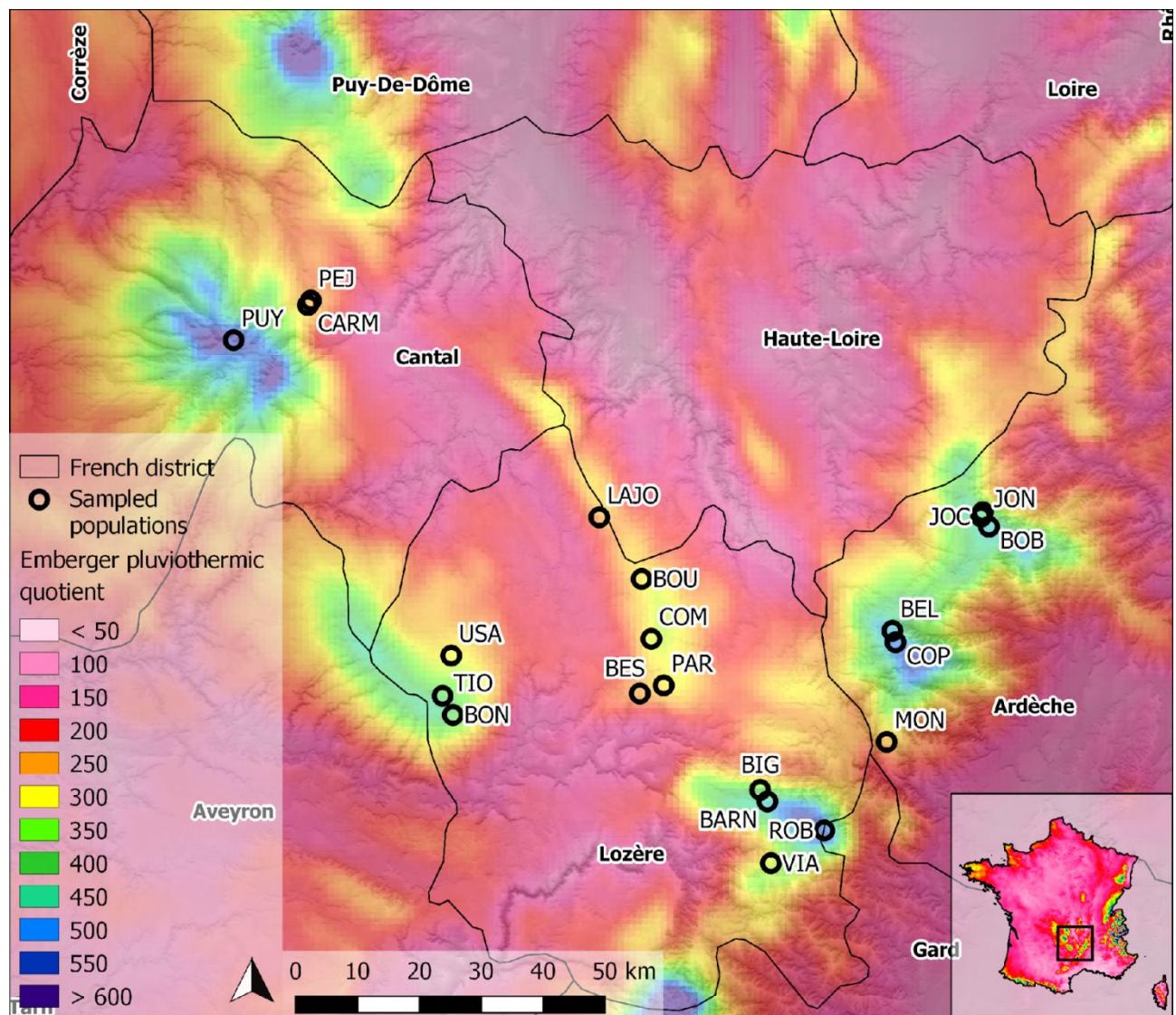
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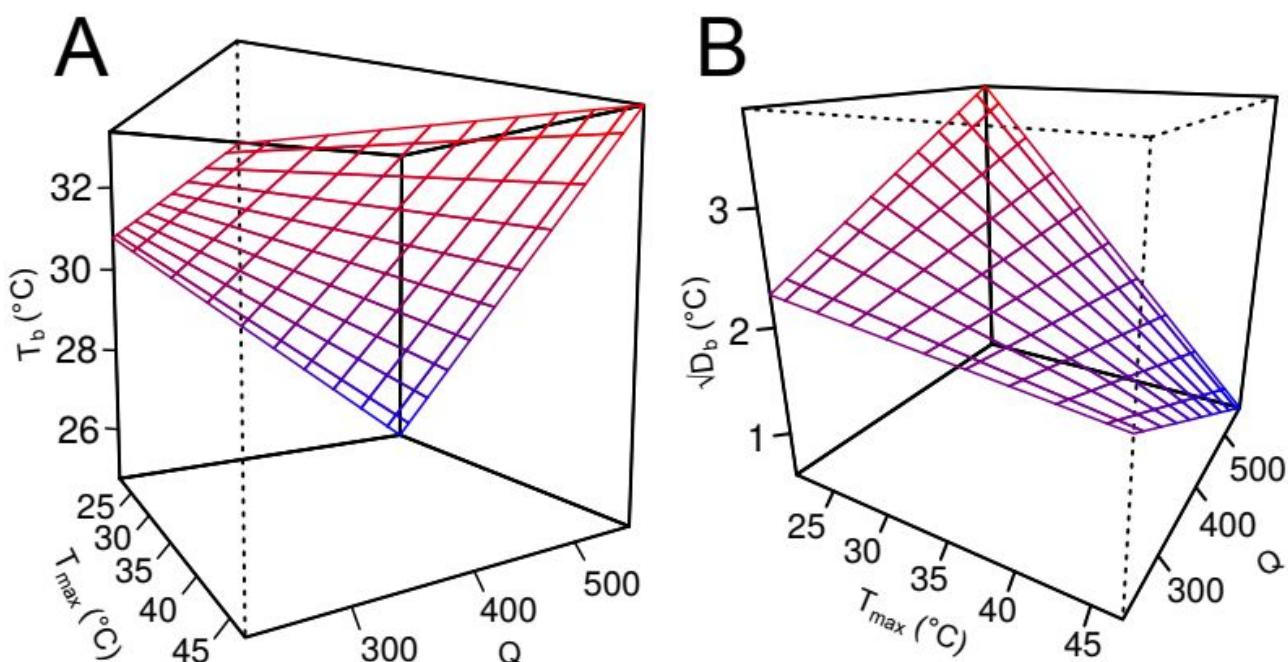
989 **Figure 6** Variation of thermoregulation efficiency E as a function of the mean daily maximum air
990 moisture during the study year P_{max} and mean daily minimum temperatures during the study year
991 T_{min} . The surface is drawn from the predictions of the conditional average of the best predictors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

994 **Figure 1**

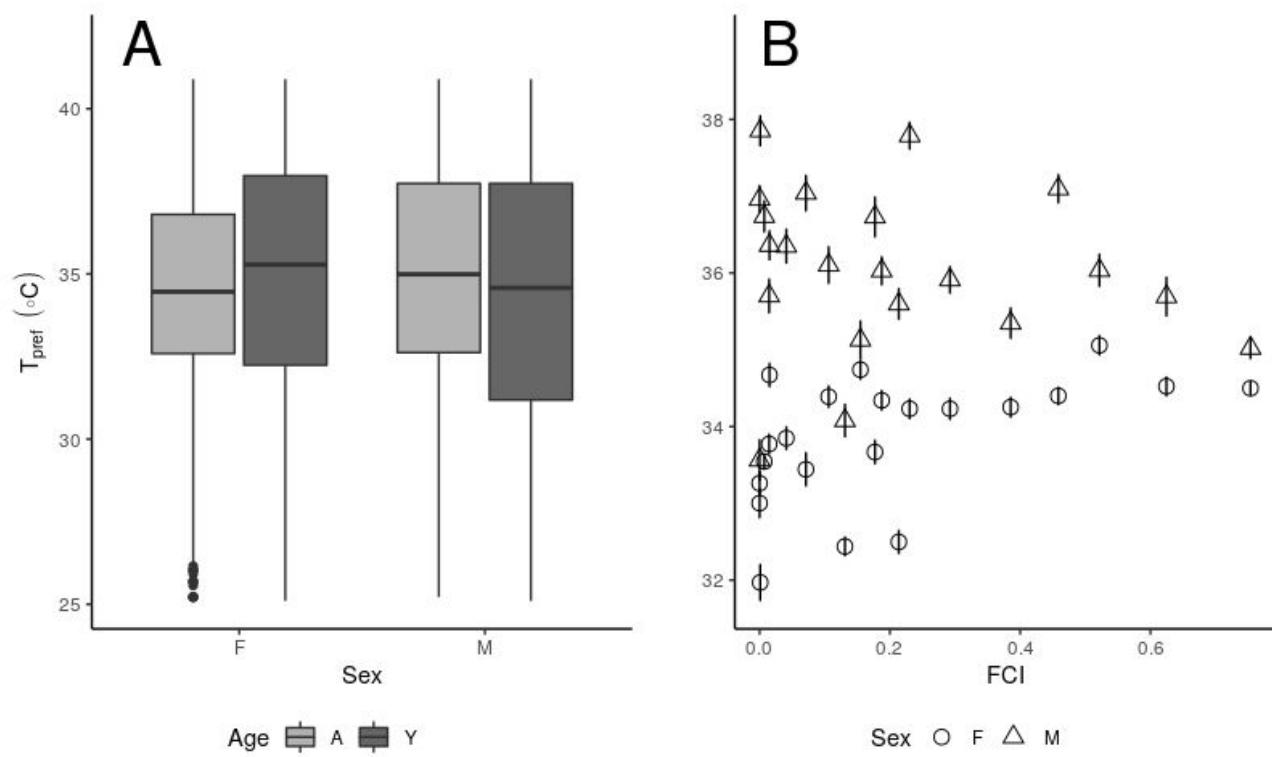
995

996 **Figure 2**

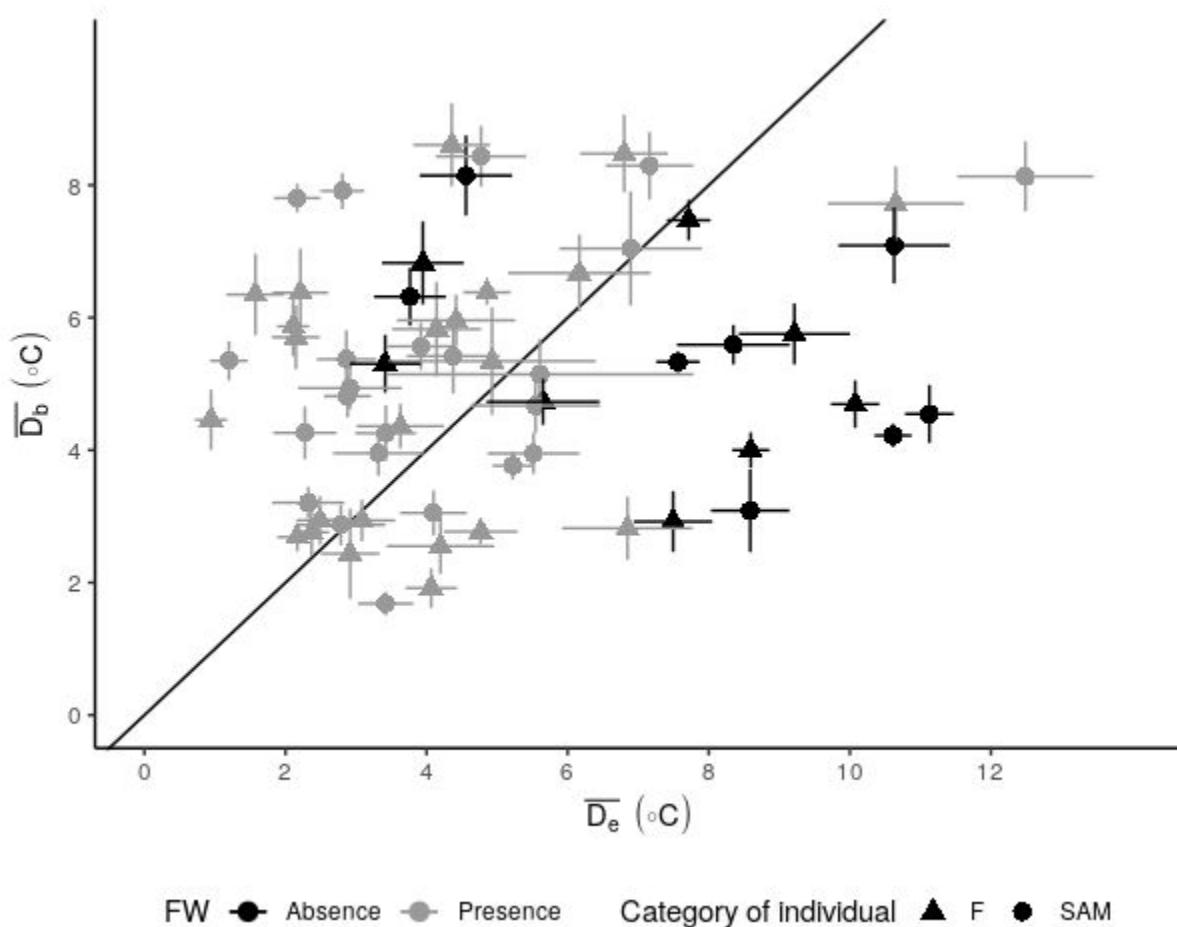


998 **Figure 3**

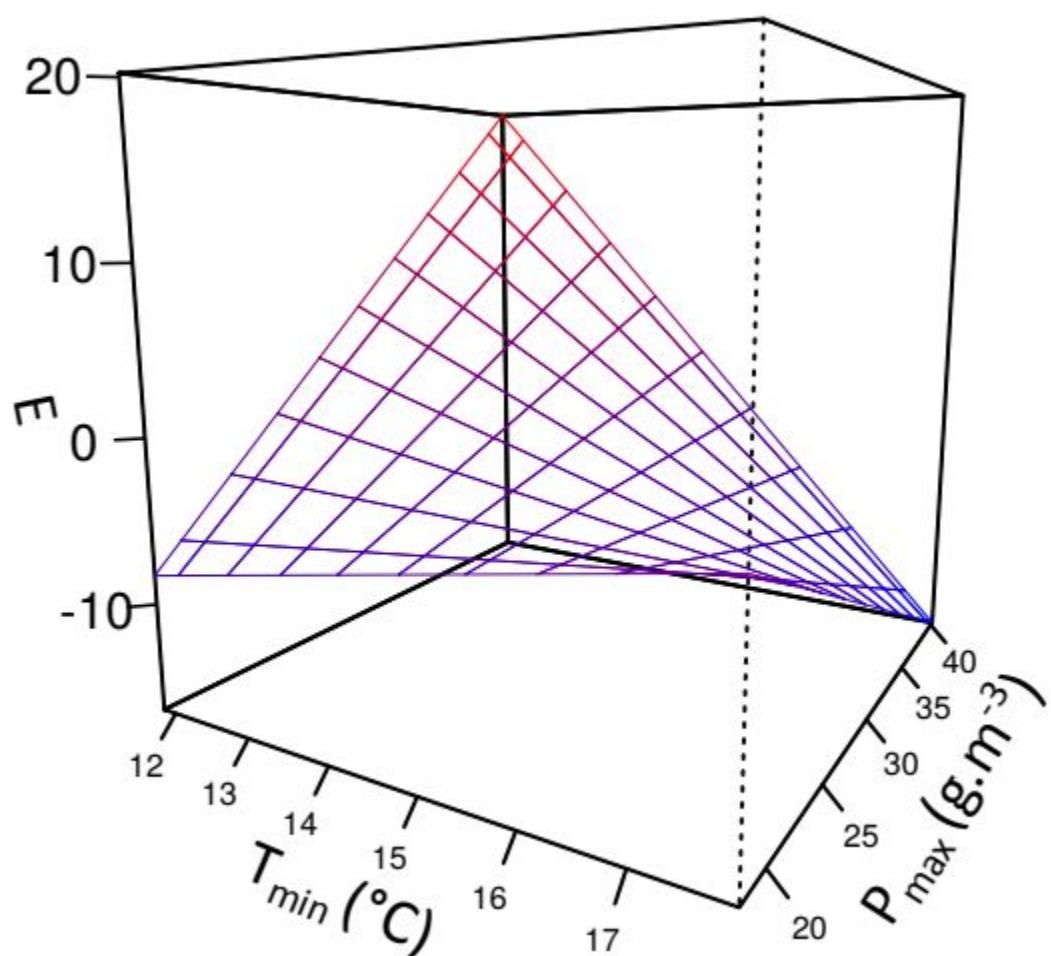
999

1000 **Figure 4**

1001

1002 **Figure 5**

1003

1004 **Figure 6**

1006 *Appendix*

1007 **Interaction of hydric and thermal conditions drive geographic variation in thermoregulation in a**
1008 **widespread lizard**

1009 Rozen-Rechels David^{1,*}, Rutschmann Alexis², Dupoué Andréaz³, Blaimont Pauline⁴, Chauveau
1010 Victor¹, Miles Donald B.⁵, Guillon Michael⁶, Richard Murielle⁷, Badiane Arnaud¹, Meylan
1011 Sandrine^{1,8}, Clobert Jean⁷, Le Galliard Jean-François^{1,9}

1012

1013

1014 **Supplementary Information 1:** Description of the microhabitat of each site

1015 **Supplementary Information 2:** Difference in operative environmental temperature among
1016 vegetation substrates and description of the thermal landscape

1017 **Supplementary Information 3:** Age and sex related differences in thermal preferences in
1018 individuals from the population ROB

1019 **Supplementary Information 4:** Effect of the presence of water on parturition date

1020

1021

1022 **Table S1** Environmental characteristics of sites for each year of study.

1023 **Table S2** Thermoregulation statistics measured and sample size in all populations of the study

1024 **Table S3** Correlations between micro-climate variables

1025 **Table S4** Correlations between environmental variables

1026 **Table S5** Summary of the best models explaining T_{pref} variation in ROB

1027 **Table S6** Model selection classification for each model averaging procedure

1028 **Figure S1** Variation in temperature T and water vapour density P for the three post-sampling
1029 periods

1030 **Figure S2** Vegetation map of the 21 populations

1031 **Figure S3** Hourly variation in operative temperature according to the substratum

- 1032 **Figure S4** Differences of operative environmental temperatures T_e among populations
- 1033 **Figure S5** Relationship between an alternative quality of the thermal habitat
- 1034 **Figure S56** Number of days between the capture of a females (2 days before we measured T_{pref}) and
- 1035 parturition for each population.

1036 **Table S1** Environmental characteristics of sites for each year of study. FW: 1 = permanent presence of free water / temporary presence of free water,
 1037 Q: Emberger pluviometric quotient, FCI: forest cover index, TE: index of thermal evenness, H: homogeneity index, T_{\min} : minimal day air temperature,
 1038 T_{\max} : maximal day air temperature, P_{\max} : maximal day air moisture.

Site	Massif	Latitude	Longitude	Surface (ha)	FW	Elevation (m)	Q	FCI	TE	H ($^{\circ}\text{C}^{-2}$)	Year	T_{\min} ($^{\circ}\text{C}$)	T_{\max} ($^{\circ}\text{C}$)	P_{\max} (g.m^{-3})
BARN	Mont-Lozère	44.427913	3.763798	0.6	1	1527	459.8	0	0.18	0.96	2017	14.1	30.1	25.1
BEL	Mont du Velay	44.672268	4.024641	1.8	0	1464	485.1	0.62	0.46	0.85	2016	13.5	32.4	31.9
											2018	12.5	35.5	31.8
BES	Margeride	44.587835	3.508084	1.5	1	1277	234.0	0.39	0.43	0.86	2016	15.1	37.4	36.3
											2018	15.5	39.1	39.0
BIG	Mont-Lozère	44.4449	3.749366	3.4	0	1463	398.8	0.46	0.28	0.81	2017	12.4	26.1	23.0
BOB	Mont du Viverais	44.820279	4.226584	1.3	1	1450	473.3	0.19	0.43	0.82	2016	13.8	32.8	26.7
											2018	17.1	28.8	27.2
BON	Mont d'Aubrac	44.560054	3.127512	2.0	1	1397	406.6	0	0.29	0.92	2017	15.1	28.1	21.8
BOU	Margeride	44.754214	3.515408	1.3	1	1461	277.9	0.15	0.44	0.86	2016	12.7	33.4	23.1
											2018	13.5	34.8	26.6
CARM	Mont du Cantal	45.1575	2.83787	1.9	1	1267	272.5	0	0.06	0.96	2018	17.9	35.2	28.1
COM	Margeride	44.66701	3.53321	2.4	1	1454.2	289.5	0.21	0.42	0.82	2017	13.2	21.2	19.9
											2018	14.8	28.6	27.1
COP	Mont du Velay	44.655493	4.03064	1.9	1	1421	514.0	0.04	0.36	0.91	2017	14.1	29.6	28.0
JOC	Mont du Viverais	44.835167	4.211043	1.5	1	1282	460.2	0.11	0.47	0.82	2017	15.8	23.6	19.7
JON	Mont du Viverais	44.841699	4.214639	0.4	0	1385	432.7	0.23	0.23	0.90	2017	15.7	22.8	17.9
LAJO	Margeride	44.84475	3.43069	0.6	0	1383	228.1	0.52	0.26	0.78	2016	13.4	27.3	21.8
											2018	13.8	39.7	31.1
MON	Mont du Velay	44.510983	4.008337	0.9	1	1099	240.7	0.13	0.24	0.86	2017	16.4	32.6	32.4
											2018	17.7	33.2	28.4
PAR	Margeride	44.599056	3.556981	3.6	1	1454.5	277.0	0.29	0.45	0.80	2016	14.2	36.9	40.3
											2018	13.9	46.9	38.5
PEJ	Mont du Cantal	45.164138	2.844013	1.1	1	1254	262.9	0.02	0.02	0.98	2017	16.2	31.6	29.6
PUY	Mont du Cantal	45.107208	2.684955	2.8	1	1471	561.5	0.01	0.25	0.91	2017	13.9	26.7	28.7

ROB	Mont-Lozère	44.38418	3.877859	1.2	0	1411	563.3	0.75	0.42	0.87	2017	11.8	39.2	31.3
											2018	12.3	42.3	32.4
TIO	Mont d'Aubrac	44.587934	3.106771	5.8	1	1321	407.9	0.01	0.42	0.88	2016	16.2	39.7	26.4
											2018	16.4	38.3	37.3
USA	Mont d'Aubrac	44.64629	3.125162	12	1	1274	306.9	0.07	0.13	0.96	2017	16.0	24.6	19.5
VIA	Mont-Lozère	44.33807	3.768619	0.6	1	1191	318.5	0.18	0.31	0.83	2017	13.0	33.3	30.5

1039 **Table S2** Thermoregulation statistics and sample size for each population for all years combined. In addition to thermoregulation statistics used in our
 1040 study, we provided alternative statistics also used in the literature (Hertz et al. 1993). T_{set} is the range defined by the interquartile range (25% and 75%
 1041 quartiles) of T_{pref} . D'_b (respectively D'_e) is the absolute difference of T_b (respectively T_e) to the limits of this range and equals 0 if in the range.

1042 Thermoregulation efficiency E' is then calculated as $1 - \frac{D'_b}{D'_e}$. T_b : cloacal body temperature in field active lizards, T_{pref} : mean body temperature

1043 measured in thermal preference tests in the laboratory, D_b : thermoregulation inaccuracy, D_e : thermal quality of the habitat, E : thermoregulation
 1044 efficiency. N_{15min} : number of 15 bouts with exploitable T_e for all years combined. N_{pref} : number of individuals with exploitable T_{pref} for all years
 1045 combined. $N_{capture}$: number of individuals with exploitable T_{body} for all years combined.

Population	Category of individual	N_{15min}	\overline{T}_e	\overline{D}_e	\overline{D}'_e	N_{pref}	\overline{T}_{pref}	T_{set}	$N_{capture}$	\overline{T}_{body}	\overline{D}_b	\overline{D}'_b	E	E'
BARN	Adult females	9	31.4 ± 6.5	4.9 ± 4.4	3.2 ± 4.4	22	33.3 ± 2.8	[31.5 – 35.2]	21	27.9 ± 3.8	5.3 ± 3.8	3.8 ± 3.6	0.6 ± 2.4	-0.2
	Adult males + yearlings			5.6 ± 6.5	4.4 ± 6.3	10	37.0 ± 2.1	[35.5 – 38.4]	24	31.8 ± 2.6	5.1 ± 2.6	3.6 ± 2.6	-2.0 ± 4.8	0.2
BEL	Adult females	35	26.2 ± 2.7	8.1 ± 2.8	6.5 ± 2.8	45	34.5 ± 3.2	[32.5 – 36.9]	46	30.5 ± 2.6	4.2 ± 2.6	2.7 ± 2.5	4.5 ± 2.2	0.6
	Adult males + yearlings			9.3 ± 2.8	6.6 ± 3.3	18	35.7 ± 3.8	[33.7 – 38.4]	42	30.8 ± 2.9	5.1 ± 3.4	3.2 ± 3.3	4.5 ± 2.9	0.5
BES	Adult females	53	32.2 ± 4.1	3.6 ± 3.4	2.3 ± 3.3	45	34.3 ± 3.3	[32.0 – 36.7]	45	30.3 ± 3.0	4.3 ± 2.9	2.7 ± 3.0	-0.5 ± 2.5	-0.2
	Adult males + yearlings			4.1 ± 3.6	2.6 ± 3.4	23	35.3 ± 3.4	[32.9 – 38.1]	67	30.9 ± 2.6	4.6 ± 2.7	2.7 ± 2.8	1.6 ± 2.7	0
BIG	Adult females	20	28.7 ± 3.6	5.7 ± 3.6	4.4 ± 3.6	24	34.4 ± 2.2	[33.2 – 35.7]	23	29.7 ± 1.7	4.7 ± 1.7	3.5 ± 1.7	1.2 ± 3.9	0.2
	Adult males + yearlings			8.3 ± 3.6	7.3 ± 3.6	10	37.1 ± 2.2	[36.1 – 38.6]	30	31.5 ± 1.6	5.6 ± 1.6	4.6 ± 1.6	4.3 ± 3.5	0.4
BOB	Adult females	43	28.4 ± 6.4	7.7 ± 5.8	6.1 ± 5.8	45	34.3 ± 3.3	[32.2 – 36.7]	45	27.6 ± 2.4	6.7 ± 2.5	4.8 ± 2.7	-0.0 ± 6.0	0.2

	Adult males + yearlings			8.6 ± 6.8	7.6 ± 6.9	27	36.0 ± 3.5	[34.1 – 38.7]	61	29.5 ± 2.2	6.5 ± 2.6	4.8 ± 3.1	-1.9 ± 5.1	0.4
BON	Adult females	22	36.7 ± 2.4	4.8 ± 2.4	3.3 ± 2.3	15	32.0 ± 3.5	[29.8 – 33.5]	25	29.2 ± 1.0	2.8 ± 1.0	0.7 ± 0.7	2.2 ± 2.5	0.8
	Adult males + yearlings			2.2 ± 1.5	1.1 ± 1.3	8	37.9 ± 2.0	[36.7 – 39.4]	30	30.0 ± 1.2	7.8 ± 1.2	6.6 ± 1.2	-5.7 ± 2.2	-5
BOU	Adult females	53	31.3 ± 5.5	5.2 ± 3.2	3.5 ± 3.0	46	34.7 ± 3.3	[32.7 – 37.3]	46	26.2 ± 3.1	8.5 ± 2.9	6.6 ± 3.0	-3.3 ± 4.1	-0.9
	Adult males + yearlings			5.6 ± 3.6	3.6 ± 3.3	22	35.1 ± 4.1	[32.1 – 38.6]	70	27.2 ± 3.3	8.4 ± 2.9	6.0 ± 3.1	-1.6 ± 4.1	-0.7
CARM	Adult females	17	32.4 ± 2.7	2.2 ± 1.6	0.6 ± 1.2	24	33.0 ± 3.5	[31.0 – 35.3]	24	26.6 ± 3.3	6.4 ± 3.3	4.3 ± 3.2	-3.7 ± 3.5	-6.2
	Adult males + yearlings			2.3 ± 1.8	0.7 ± 1.3	13	33.6 ± 3.5	[31.3 – 36.0]	34	29.3 ± 2.3	4.3 ± 2.3	2.2 ± 2.0	-2.1 ± 2.6	-2.1
COM	Adult females	32	32.8 ± 3.2	2.2 ± 1.8	0.9 ± 1.3	32	32.5 ± 3.2	[30.3 – 34.5]	32	27.1 ± 3.6	5.4 ± 3.2	3.4 ± 3.0	-2.8 ± 3.5	-2.8
	Adult males + yearlings			3.4 ± 2.3	1.8 ± 2.2	23	35.6 ± 3.5	[33.3 – 38.1]	59	31.1 ± 3.0	4.6 ± 2.3	2.8 ± 2.0	-0.6 ± 2.7	-0.6
COP	Adult females	17	39.9 ± 5.2	6.8 ± 3.9	5.0 ± 3.6	25	33.8 ± 2.8	[32.0 – 36.0]	24	31.1 ± 2.4	2.8 ± 2.3	1.4 ± 2.0	4.0 ± 6.2	0.7
	Adult males + yearlings			5.5 ± 2.7	3.4 ± 2.6	10	36.3 ± 2.6	[34.3 – 38.6]	38	32.4 ± 1.9	3.9 ± 1.9	1.9 ± 1.8	1.2 ± 3.2	0.4
JOC	Adult females	34	30.7 ± 5.4	4.4 ± 4.9	2.9 ± 4.6	24	34.4 ± 2.7	[32.5 – 36.5]	24	28.4 ± 1.9	6.0 ± 1.9	4.0 ± 1.9	-0.9 ± 4.7	-0.4
	Adult males + yearlings			5.5 ± 5.3	4.0 ± 5.1	10	36.1 ± 2.8	[34.3 – 38.4]	30	31.4 ± 2.3	4.7 ± 2.3	2.9 ± 2.2	-0.1 ± 4.4	0.3
JON	Adult females	20	34.2 ± 4.2	3.4 ± 2.2	2.0 ± 1.9	25	34.2 ± 2.5	[32.7 – 36.0]	25	28.9 ± 2.2	5.3 ± 2.2	3.8 ± 2.2	-2.7 ± 3.4	-0.9
	Adult males + yearlings			4.6 ± 2.9	3.5 ± 2.9	10	37.8 ± 2.1	[36.7 – 39.3]	30	29.8 ± 3.6	8.1 ± 3.3	7.0 ± 3.3	-2.5 ± 4.7	-1.0
LAJO	Adult females	53	30.0 ± 8.0	7.4 ± 3.8	5.4 ± 3.4	48	35.1 ± 3.3	[32.8 – 37.6]	46	29.3 ± 2.3	5.6 ± 2.5	3.5 ± 2.6	2.7 ± 4.5	0.4
	Adult males + yearlings			7.9 ± 4.2	6.2 ± 3.7	20	36.0 ± 3.4	[34.5 – 38.7]	68	30.8 ± 2.6	5.5 ± 2.7	4.0 ± 2.9	1.7 ± 4.5	0.4
MON	Adult females	55	33.0 ± 4.1	3.2 ± 2.1	1.3 ± 1.6	50	32.4 ± 3.3	[30.0 – 34.8]	53	29.2 ± 3.6	3.7 ± 2.8	1.8 ± 2.2	-0.9 ± 3.6	-0.4
	Adult males + yearlings			3.2 ± 2.1	1.2 ± 1.7	27	34.1 ± 4.0	[31.7 – 36.9]	84	31.2 ± 3.8	3.3 ± 2.7	1.7 ± 2.4	0.3 ± 3.0	-0.4
PAR	Adult females	40	32.6 ± 5.5	5.6 ± 4.9	4.3 ± 4.7	45	34.2 ± 3.6	[31.5 – 37.3]	47	29.8 ± 2.6	4.6 ± 3.3	3.2 ± 3.1	0.6 ± 3.4	0.3

	Adult males + yearlings			5.6 ± 5.1	4.5 ± 5.2	22	35.9 ± 3.0	[34.0 – 38.3]	45	31.4 ± 2.0	4.1 ± 2.5	2.6 ± 2.6	-0.6 ± 2.5	0.4
PEJ	Adult females	33	32.1 ± 5.4	3.1 ± 2.7	2.0 ± 2.2	17	34.7 ± 2.4	[33.1 – 36.5]	25	31.8 ± 1.6	2.9 ± 1.6	1.5 ± 1.4	1.0 ± 2.5	0.3
	Adult males + yearlings			4.1 ± 2.7	2.4 ± 2.7	11	36.4 ± 2.4	[34.7 – 38.4]	30	33.5 ± 2.2	3.1 ± 1.9	1.6 ± 1.7	0.5 ± 2.2	0.3
PUY	Adult females	39	37.7 ± 3.3	4.9 ± 2.1	3.7 ± 2.1	25	33.5 ± 1.9	[32.2 – 34.7]	24	27.2 ± 0.9	6.4 ± 0.9	5.1 ± 0.9	-1.5 ± 2.5	-0.4
	Adult males + yearlings			2.8 ± 2.0	1.1 ± 1.6	10	36.7 ± 2.5	[34.9 – 38.9]	31	28.8 ± 1.5	7.9 ± 1.5	6.0 ± 1.5	-4.9 ± 2.7	-4.5
ROB	Adult females	157	26.5 ± 2.5	8.2 ± 2.5	6.1 ± 2.6	97	34.5 ± 3.2	[32.6 – 36.8]	123	28.8 ± 3.3	5.9 ± 1.9	3.7 ± 2.6	2.4 ± 3.5	0.4
	Adult males + yearlings			9.2 ± 2.9	7.2 ± 3.1	236	34.6 ± 3.8	[31.9 – 37.7]	318	29.8 ± 3.1	4.9 ± 2.2	2.5 ± 2.1	4.3 ± 3.2	0.7
TIO	Adult females	25	34.3 ± 3.7	2.1 ± 2.0	0.9 ± 1.5	45	33.8 ± 3.3	[31.7 – 36.1]	46	29.3 ± 2.5	4.4 ± 2.0	2.4 ± 1.9	-1.8 ± 3.2	-1.7
	Adult males + yearlings			2.9 ± 1.8	1.0 ± 1.5	27	35.7 ± 3.8	[33.3 – 38.9]	54	30.6 ± 1.9	4.9 ± 1.8	2.7 ± 1.7	-1.5 ± 2.5	-1.5
USA	Adult females	38	33.7 ± 2.8	2.4 ± 1.5	1.0 ± 1.1	16	33.4 ± 3.3	[31.3 – 35.0]	26	30.8 ± 2.0	2.8 ± 1.8	1.0 ± 1.4	-0.1 ± 2.9	0
	Adult males + yearlings			3.4 ± 2.7	2.2 ± 2.3	8	37.0 ± 2.4	[35.4 – 38.9]	28	32.8 ± 2.2	4.3 ± 2.2	2.6 ± 2.2	-1.2 ± 1.6	-0.2
VIA	Adult females	22	31.5 ± 1.4	2.2 ± 1.4	0.5 ± 0.9	24	33.7 ± 2.9	[31.4 – 35.4]	25	31.3 ± 1.6	2.7 ± 1.1	0.7 ± 0.9	-0.6 ± 1.4	-0.4
	Adult males + yearlings			5.2 ± 1.4	3.1 ± 1.4	10	36.7 ± 3.0	[34.6 – 39.0]	32	33.1 ± 1.6	3.8 ± 1.2	1.7 ± 1.2	2.2 ± 1.9	0.5

1047 Supplementary Information 1

1048 We measured micro-habitat temperature and moisture conditions at each site by recording local
1049 temperature and relative humidity with temperature-humidity loggers (Hygrochron iButtons,
1050 Maxim Integrated Products, Sunnyvale, CA, USA, $\pm 0.5^{\circ}\text{C}$ and 5% relative humidity—RH) at 1
1051 hour interval during approximately one month every year. A total of 1 to 3 loggers were set under
1052 cover at each site in diverse substrates, away from full sun in order to avoid high temperatures.
1053 Each logger was placed in a net in a T-shaped PVC plumbing connection, in which air could
1054 circulate. This set-up enabled us to measure air temperature and relative humidity at approximately
1055 2 cm from the soil. As part of another study, we deployed 18 temperature and temperature-humidity
1056 loggers on one of our focal site (ROB) and used these data for calculating relative micro-habitat
1057 characteristics in this study. We calculated the water vapor density at each sample point using
1058 temperature and relative humidity data, following the equation provided by Tieleman et al. (2002).
1059 This calculation was made in three steps:

1060 1. Calculation of the dew point DP: $DP = (\text{RH}/100)^{1/8} \times (112 + 0.9 \times T) + 0.1 \times T - 112$ with T the
1061 temperature ($^{\circ}\text{C}$) and RH the relative humidity (%).

1062 2. Saturation vapor pressure PWS calculation:

1063 $PWS = [a + b \times DP + c \times DP^2 + d \times DP^3 + e \times DP^4 + f \times DP^5 + g \times DP^6 + h \times DP^7 + i \times DP^8]/10$

1064 Where:

1065 $a = 6.11583699$

1066 $b = 0.444606896$

1067 $c = 0.0143177157$

1068 $d = 0.000264224321$

1069 $e = 0.00000299291081$

1070 $f = 0.0000000203154182$

1071 $g = 0.000000000702620698$

1072 $h = 0.000000000000037953431$

1073 $i = -3.21582393 \times 10^{-16}$

1074 3. Water vapor density P calculation:

1075 $P = [216.7 \times PWS \times 10 / (DP + 273.15) \times (1013 \times (DP + 273.15))] / [1013 \times 273.15]$

1076 Variation in the environmental conditions for each site are plotted in Figure S1.

1077 For each focal site and each sample year, we calculated the average 10:00 to 18:00 minimal, mean,
1078 and maximal temperatures (hereafter called T_{\min} , T_{mean} , T_{\max} respectively) and the average 10:00 to
1079 18:00 minimal, mean and maximal water density (i.e., water vapor pressure, hereafter called P_{\min} ,
1080 P_{mean} , P_{\max} respectively) during periods of approximately one month each year (Figure S1A and B).

1081 To do this we extracted each variable for each day in the period for all loggers in the same site, the
1082 same year (maximal and minimal were thus the maximal and minimal values recorded from all
1083 loggers combined) and averaged it over the entire period to obtain a yearly mean allowing relative
1084 comparison of populations. Cross-correlation coefficients of these microclimatic variables were
1085 calculated (Table S3). We selected the microclimatic variables of interest based on these
1086 correlations. T_{\min} is only highly correlated to P_{\min} . As Dupoué et al. (2018) previously showed the
1087 importance of T_{\min} for lizard biology, we retained it and excluded P_{\min} from our analyses. We also
1088 kept T_{\max} over T_{mean} as previous studies showed that maximum daily temperatures can significantly
1089 impact the physiology and phenology of the lizards in these populations (Rutschmann et al. 2016b,
1090 Dupoué et al. 2017b). We also kept P_{\max} , because we considered to be the best proxy of air
1091 moisture.

1092

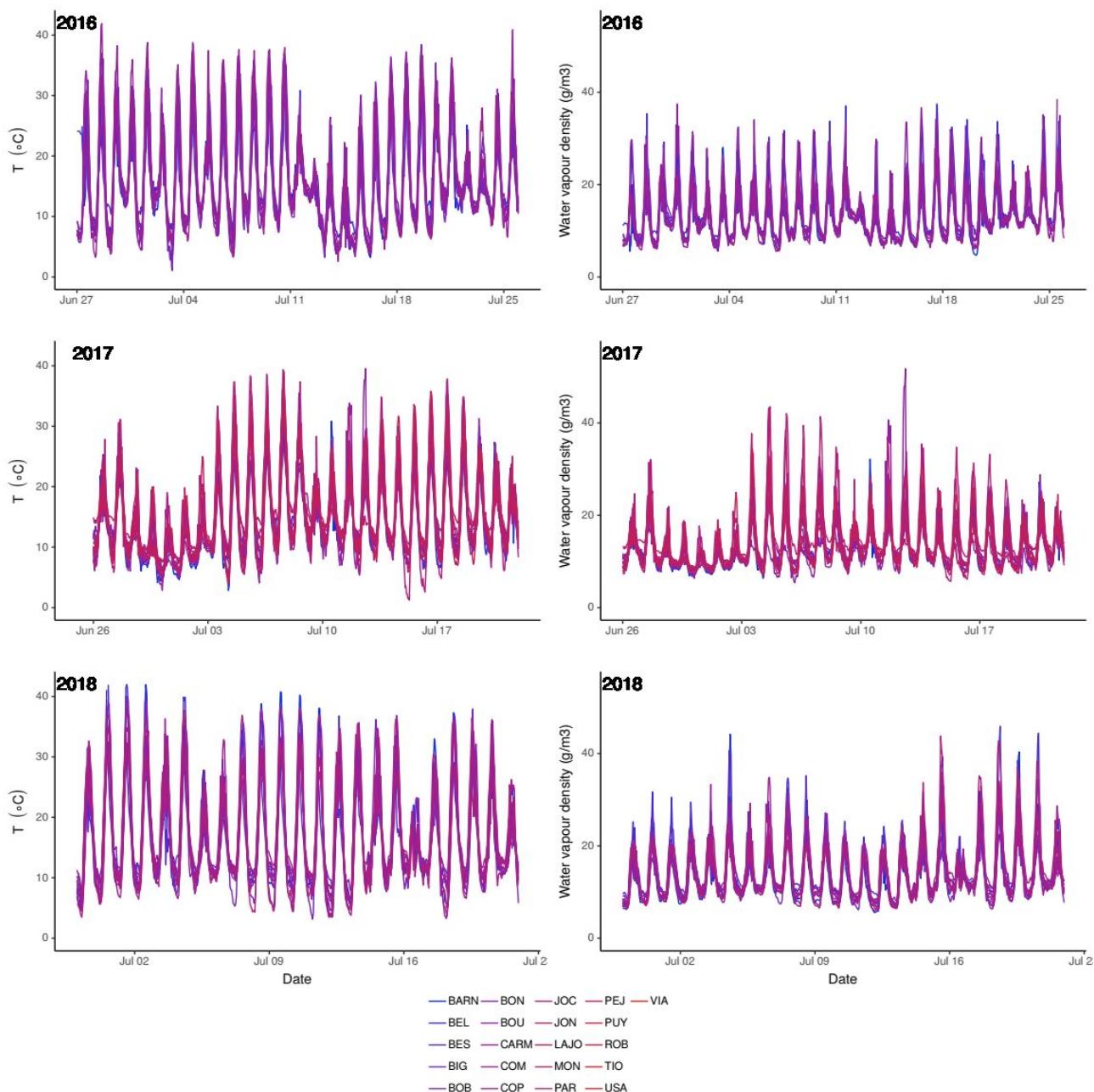
1093 Dupoué, A., A. Rutschmann, J. F. Le Galliard, D. B. Miles, J. Clobert, D. F. DeNardo, G. A.
1094 Brusch, and S. Meylan. 2017. Water availability and environmental temperature correlate with
1095 geographic variation in water balance in common lizards. *Oecologia* 185:561–571.

- 1096 Dupoué, A., A. Rutschmann, J. F. Le Galliard, J. Clobert, P. Blaimont, B. Sinervo, D. B. Miles, C.
1097 Haussy, and S. Meylan. 2018. Reduction in baseline corticosterone secretion correlates with climate
1098 warming and drying across wild lizard populations. *Journal of Animal Ecology* 87:1331–1341.
- 1099 Rutschmann, A., D. B. Miles, J.-F. Le Galliard, M. Richard, S. Moulherat, B. Sinervo, and J.
1100 Clobert. 2016. Climate and habitat interact to shape the thermal reaction norms of breeding
1101 phenology across lizard populations. *Journal of Animal Ecology* 85:457–466.
- 1102 Tieleman, B. I., J. B. Williams, and M. E. Buschur. 2002. Physiological adjustments to arid and
1103 mesic environments in larks (Alaudidae). *Physiological and Biochemical Zoology* 75:305–313.
- 1104

1105 **Figure S1A** Variations of temperature T and water vapor density P for the three post-sampling
1106 periods during which T_{\min} , T_{\max} , T_{mean} , P_{\min} , P_{\max} and P_{mean} were calculated (temperature and vapor
1107 density were averaged over the loggers present at the same time in the site for graphical purposes).

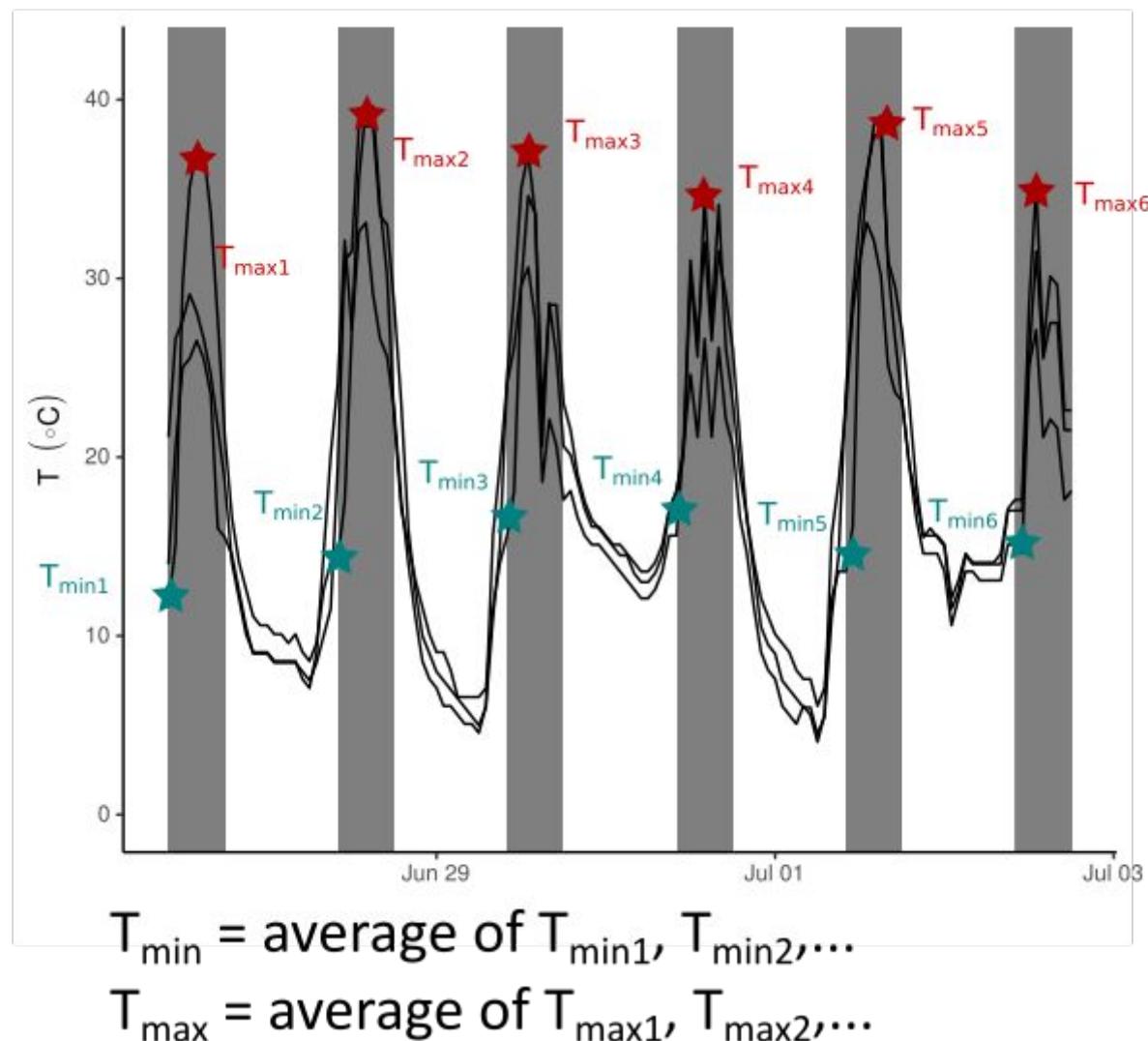
1108

1109



1110

1111 Figure S1B Graphical explanation of the calculations of T_{\min} and T_{\max} . For each activity period
1112 (10:00 to 18:00, gray areas) we measured the minimal and maximal temperatures. Each line
1113 corresponds to a logger on the site. We averaged these values over the whole measurement period
1114 to obtain T_{\min} and T_{\max} . A similar procedure was used for T_{mean} , P_{\min} , P_{mean} , and P_{\max} .



1115 **Table S3** Pearson's correlation coefficients R between each micro-climatic variable.

	T _{min}	T _{mean}	T _{max}	P _{min}	P _{mean}	P _{max}
T _{min}		0.22	-0.11	0.77	0.25	-0.02
T _{mean}			0.84	0.16	0.73	0.77
T _{max}				-0.06	0.60	0.80
P _{min}					0.53	0.18
P _{mean}						0.88

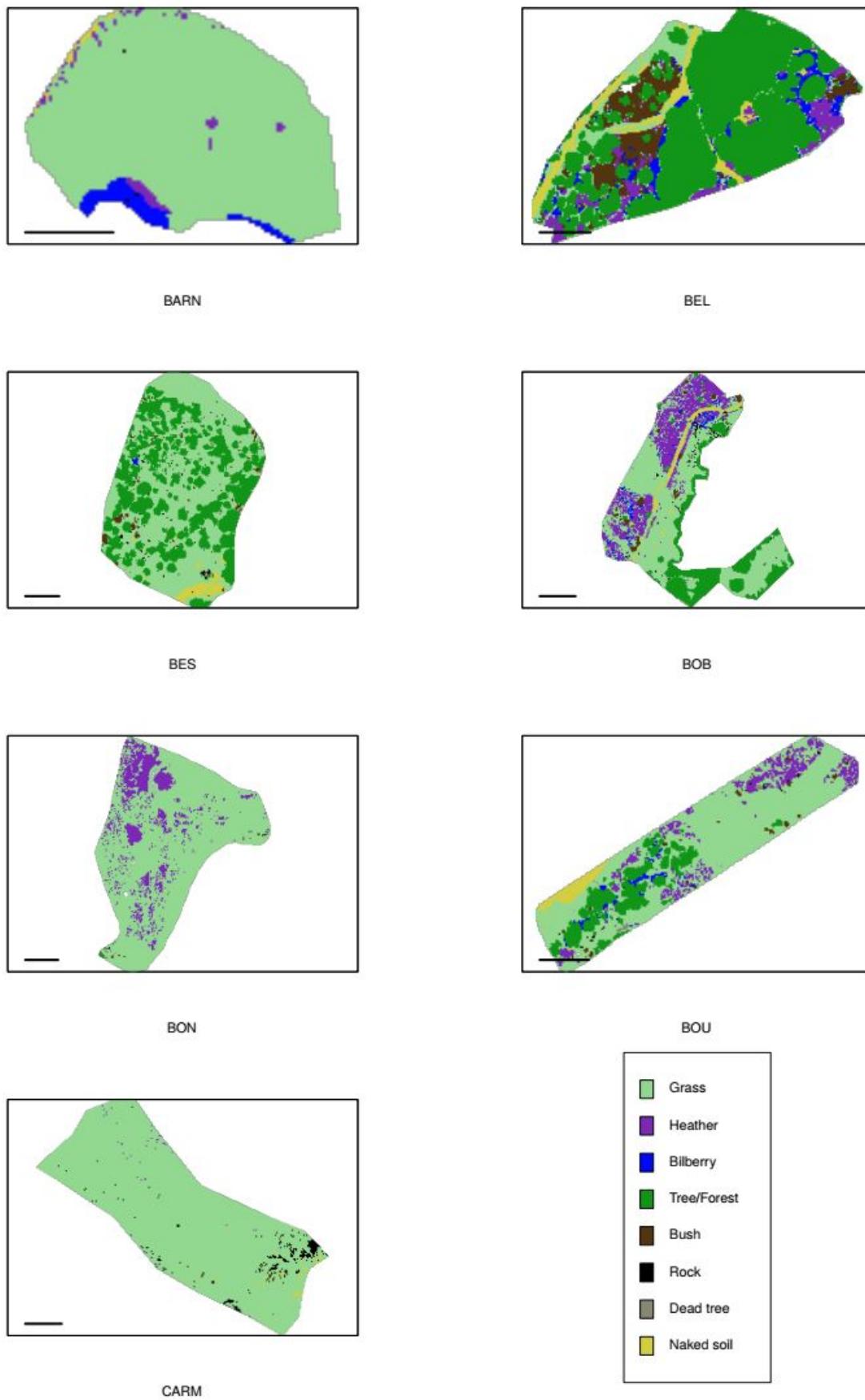
1116

1117 **Table S4** Pearson's correlation coefficients R between each selected environmental variable.

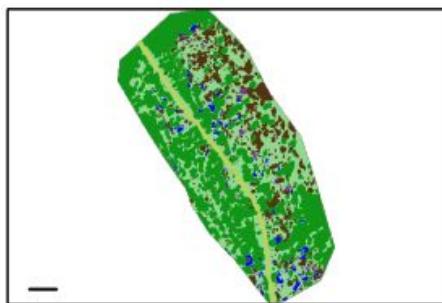
	T _{min}	T _{max}	Elevation	P _{max}	Q	FCI	TE	H
T _{min}		-0.11	-0.60	-0.02	-0.30	-0.62	-0.40	0.37
T _{max}			-0.07	0.80	-0.11	0.34	0.28	-0.16
Elevation				-0.12	0.45	0.25	0.40	-0.16
P _{max}					-0.13	0.28	0.28	-0.19
Q						0.17	0.35	0.18
FCI							0.40	-0.49
TE								-0.63

1118

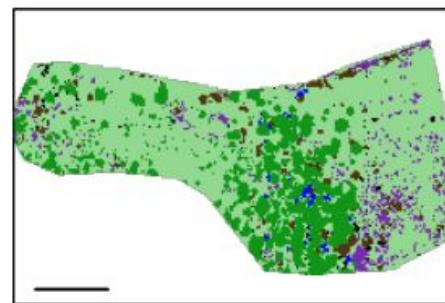
1119 **Figure S2** Raster vegetation map of the 21 populations. Blank pixels stand for water pans or



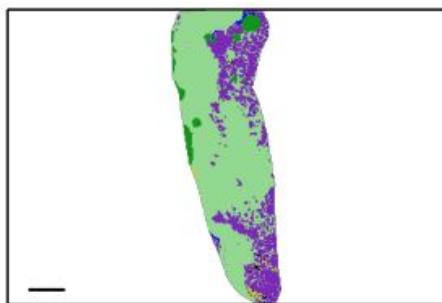
1120 streams in the population. The scale stands for 50 meters.



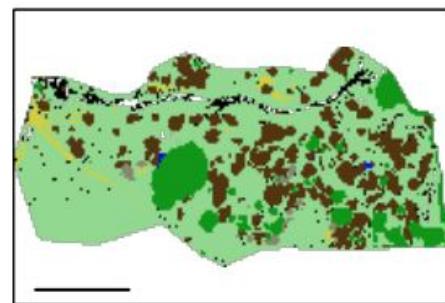
CHA-BIG



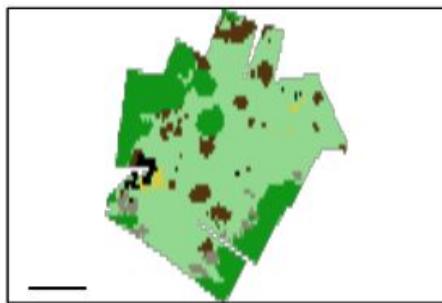
COM



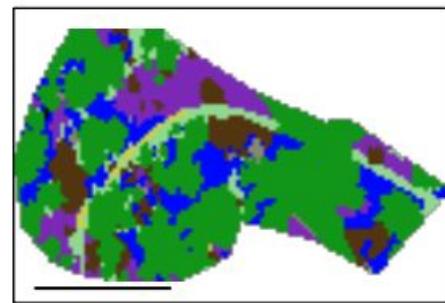
COP



JOC

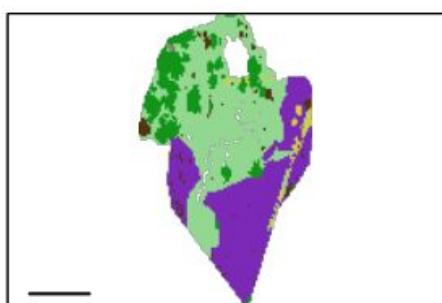


JON

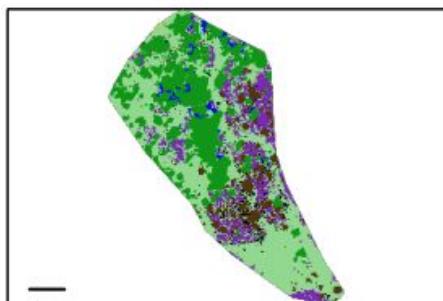


LAJO

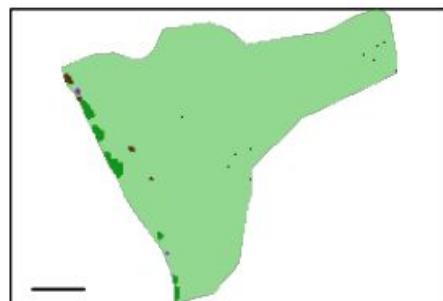
- [Green square] Grass
- [Purple square] Heather
- [Blue square] Bilberry
- [Dark Green square] Tree/Forest
- [Brown square] Bush
- [Black square] Rock
- [Grey square] Dead tree
- [Yellow square] Naked soil



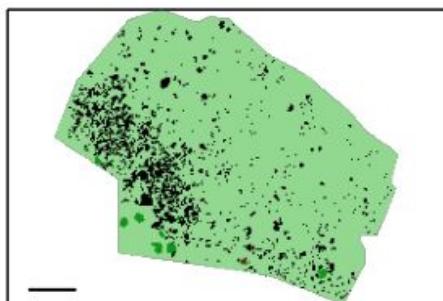
MON



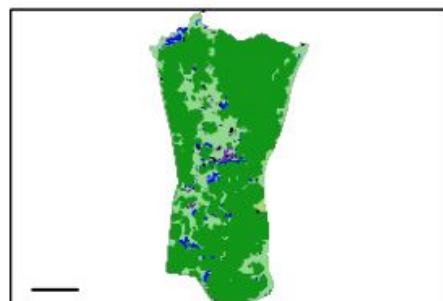
PAR



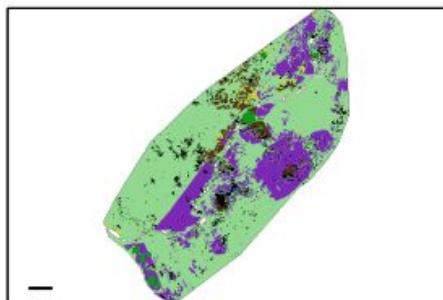
PEJ



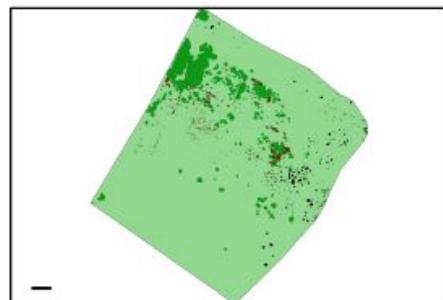
PUY



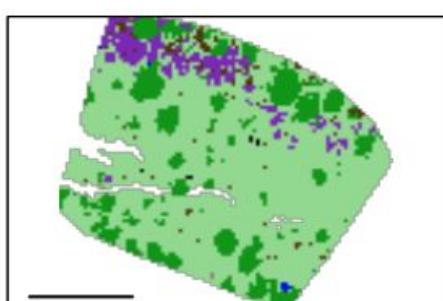
ROB



TIO



USA



VIA



1123 **Supplementary Information 2**

1124 During field census, we put between 4 and 12 HOBO® Pro v2 U23-003 (ONSET Cape Cod,
1125 Massachusetts) temperature probes inside a painted 6cm long copper tube to measure a lizard
1126 operative temperatures in a diversity of substratum (Dzialowski 2005). The loggers recorded
1127 operative temperatures every minute in each substratum. In further calculations, we averaged these
1128 measures over 15-minute time bins (hereafter called T_e) in order to compensate for short-time
1129 changes in weather conditions such as wind, clouds, etc. The operative temperatures data were
1130 calibrated in September 2016 in CEREEP-Ecotron ÎleDeFrance, France facilities ($48^{\circ} 17' N$, $2^{\circ} 41' E$)
1131 by temperature records inside the painted copper tube with those of a dead adult individual at the
1132 exact same location side by side without contact. We calibrated the operative temperatures under
1133 two different conditions (under sun radiation or on a shady patch) and used the calibration curve to
1134 transform records from the copper tube model into those representative of core body temperatures
1135 of a common lizard.

1136 Under sun radiation: $T_e = -0.933331 + 1.035632 \times T_{\text{copper tube}}$

1137 Under shade: $T_e = 2.589795 + 0.878049 \times T_{\text{copper tube}}$

1138 We then analyzed variation in operative temperatures across the hour of the day for each substrate
1139 in each site (see Figure S3). We fitted the non-linear variation in operative temperature to the hour
1140 of the day using a Generalized Additive Model (*gam* from the package *mgcv*, Wood 2017). We took
1141 into account the local site conditions (which could either be specific to the site or to the weather
1142 during capture) by adding a site-day fixed effect, which had as many levels as different capture days
1143 for each population. To assess average differences between substratum corrected by hour of the day
1144 and site-day, we also fitted a substratum fixed effect. We then extracted the estimated operative
1145 temperature score per substrate from the model and created temperature raster maps for each site by
1146 attributing the estimated operative temperature to each pixel based on the main substratum
1147 presence. In order to describe the thermal structure of the landscape we calculated two indices of

1148 the functional diversity of the landscape. The first one, called TE for Thermal Evenness, was
 1149 calculated by analogy to the functional evenness from Villéger et al. (2008). Initially, this score was
 1150 defined to measure the diversity and regularity of the distribution of functional traits in an
 1151 ecological community. It was used here to provide a measure of the diversity and regularity of the
 1152 distribution of operative temperature across the landscape, where

$$1153 \quad TE = \frac{\sum_{i=1}^{S-1} \min \left(PEW_{i,i+1}, \frac{1}{S-1} \right) \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

1154 with S the number of substrates, substrates were ranked in the ascending order of operative
 1155 temperatures and

$$1156 \quad PEW_{i,i+1} = \frac{EW_{i,i+1}}{\sum_{i=1}^{S-1} EW_{i,i+1}}$$

1157 and

$$1158 \quad EW_{i,i+1} = \frac{|T_{i+1} - T_i|}{A_{i+1} + A_i}$$

1159 with T_i as the operative temperature score of the substratum i of abundance A_i in the landscape. As a
 1160 general rule, TE is close to 1 when operative temperatures across the landscape are diverse and
 1161 equally abundant. It is close to 0 when temperatures are poorly diversified or when one temperature
 1162 is over-abundant compared to the others.

1163 The other landscape structure H index measures the spatial homogeneity of temperatures by
 1164 assessing the probability of having different substrata between adjacent pixels corrected by the
 1165 difference of temperature between these substrata. We followed Tuanmu and Jetz (2015) method
 1166 who calculated spatial heterogeneity index for vegetation features, where

$$1167 \quad H = \sum_{i,j=1}^S \frac{P_{i,j}}{1 + (T_i - T_j)^2}$$

1168 with P_{ij} the probability that substrata i and j are adjacent.

1169

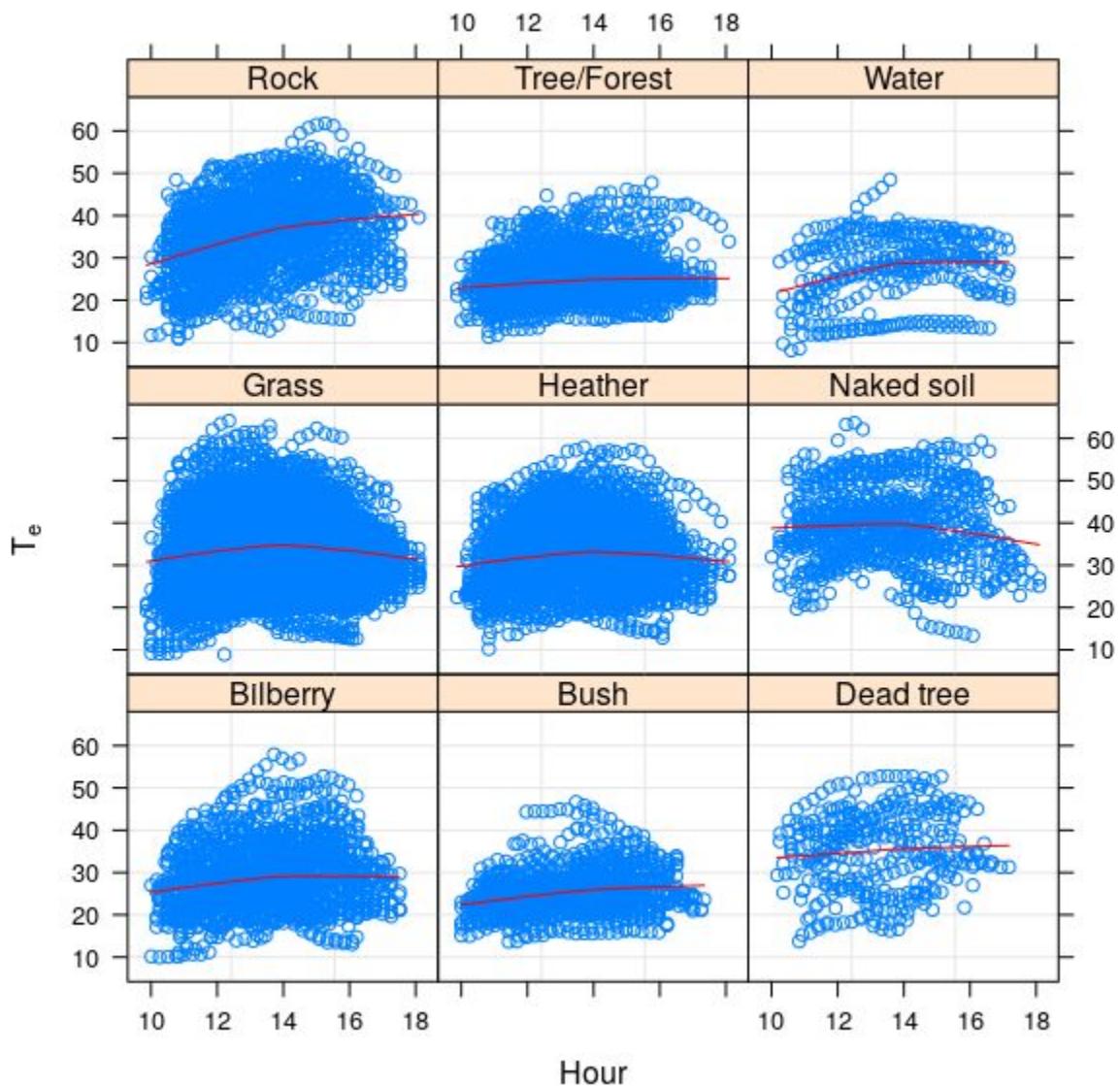
1170 Dzialowski, E. M. 2005. Use of operative temperature and standard operative temperature models
1171 in thermal biology. *Journal of Thermal Biology* 30:317–334.

1172 Wood, S. N. 2017. Generalized additive models: an introduction with R. Chapman and Hall/CRC.

1173

1174 **Figure S3**

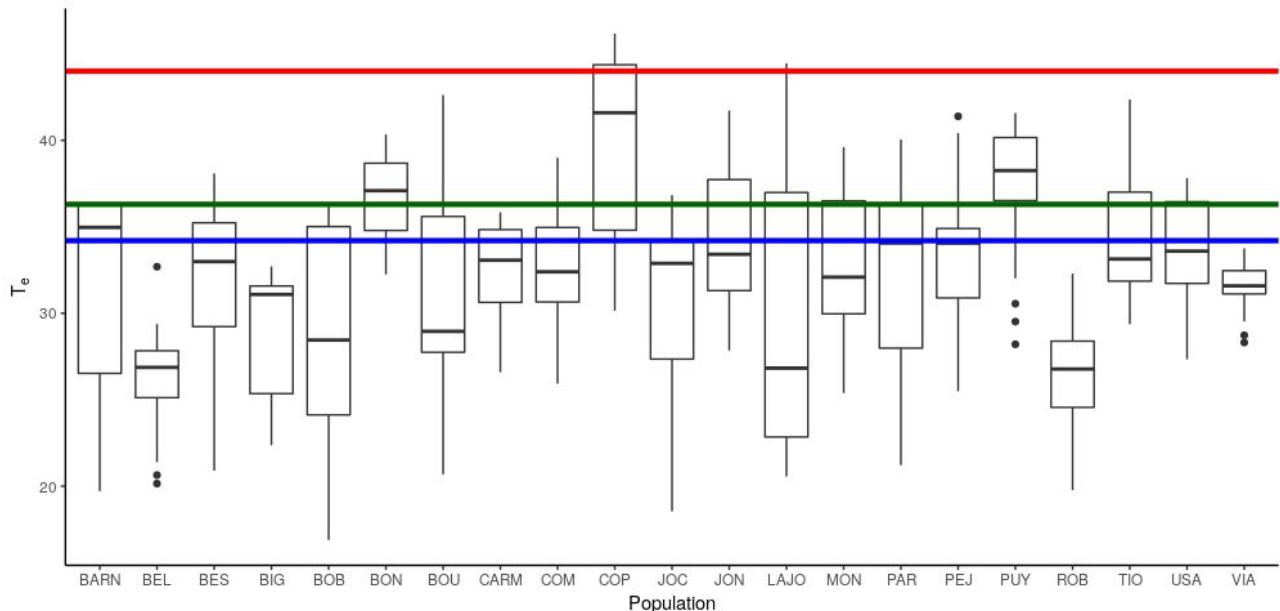
1175 Variation in operative temperatures as a function of the hour of the day, depending on the substrate.
1176 Each blue circle is one log of operative temperatures; red lines are loess regressions of T_e against
1177 time.



1178

1179 **Figure S4**

1180 Differences in operative temperatures T_e between sites. The blue line is the gravid females $\overline{T_{pref}}$,
1181 the green line is the adult males and yearlings $\overline{T_{pref}}$ and the red line is the species CT_{max} (Gvozdik
1182 and Castilla 2001).

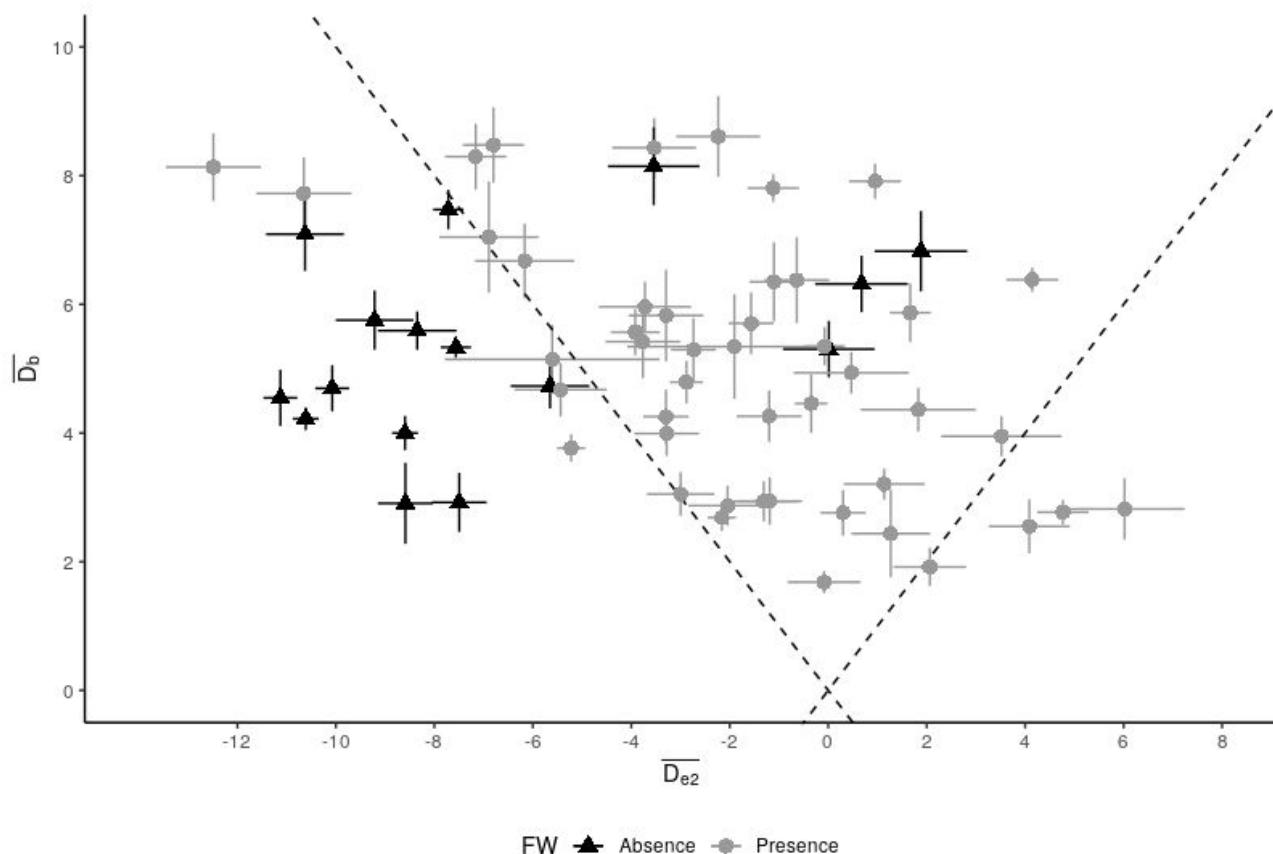


1183

1184

1185 **Figure S5**

1186 Relationship between the inaccuracy of thermoregulation D_b measured in individual lizards inside
 1187 each population and year and the quality of the thermal habitat $D_{e2} = T_e - \bar{T}_{pref}$ measured with
 1188 loggers over the same 15-minute time bin for the lizard. Each point represents the average D_b and
 1189 D_{e2} values calculated for each population, each age-sex category of individual, each year. Error bars
 1190 are standard errors. Dashed lines are $D_b = D_{e2}$ and $D_b = -D_{e2}$ lines.



1191

1192 **Supplementary Information 3**

1193 We fitted the variation of T_{pref} calculated for all age and sex classes in the ROB population to the
1194 addition of the two-way interaction of the age and sex of individuals and the two-way interactions
1195 of sex and age with the year with a linear mixed-model using the function *lme* from the package
1196 *nlme* (Pinheiro and Bates 2006). We also took into account the time of the day by adding the two-
1197 way interaction of the time since habituation with the moment of day (morning vs. afternoon). To
1198 assess intrapopulation and intraindividual variances, we nested an individual identity random effect
1199 in a populational identity random effect. We then proceeded to perform a backward model selection
1200 based on log-likelihood ratio tests. T_{pref} variation was significantly explained by the two-way
1201 interaction of the sex and the age ($F_{1,325} = 4.04, p = 0.045$) as well as the two-way interactions
1202 between the sex and the year ($F_{1,325} = 10.2, p = 0.002$) and between the age and the year ($F_{1,325} =$
1203 $15.3, p = 0.0001$). Adult male T_{pref} as well as both sexes yearlings T_{pref} were higher than females.
1204 Yearlings and adult males T_{pref} are not strongly different on average (Table S5, Figure 3A). In our
1205 study, we thus supposed that yearling $\overline{T_{pref}}$ is equivalent to adult males from the same population.
1206
1207 Pinheiro, J., and D. Bates. 2006. Mixed-effects models in S and S-PLUS. Springer Science &
1208 Business Media.
1209
1210

1211 **Table S5.** Summary of estimated effects in the best model explaining variation in T_{pref} of ROB in
 1212 comparison of the reference: adult female in 2017 during the afternoon. SE: standard error, DF:
 1213 degree of freedom.

Effect	Value	SE	DF	<i>t</i>	<i>p</i>
<i>Intercept</i>	35.1	0.3	3624	102.8	< 0.0001
<i>Yearling</i>	1.5	0.4	325	3.8	0.0002
<i>Male</i>	1.5	0.5	325	3.3	0.001
<i>2018</i>	-1.0	0.4	325	-2.8	0.006
<i>Morning</i>	0.2	0.2	325	0.9	0.35
<i>Time since habituation</i>	-0.8	0.1	3624	-10.4	< 0.0001
<i>Yearling : Male</i>	-0.9	0.4	325	-2.0	0.045
<i>Yearling : 2018</i>	-1.8	0.4	325	-3.9	0.0001
<i>Male : 2018</i>	-1.5	0.5	325	-3.2	0.002
<i>Time since habituation : Morning</i>	0.3	0.1	3624	3.1	0.002
<i>Time since habituation : Male</i>	0.3	0.1	3624	3.0	0.003

1215 **Table S6.** Classification of the 10 best models in the model averaging classification procedure
 1216 based on AICc. Model weights indicate the relative evidence in favor of one model over all other
 1217 models included in the set and models are unlikely to represent the “truth” when weight is smaller
 1218 than ca. 5-10%. The best models based on this rule and the $\Delta\text{AICc} < 2$ rule are in boldface. T_b :
 1219 cloacal body temperature at capture, T_{pref} : body temperature measured in the thermal preferences
 1220 set-up, D_b : thermoregulation inaccuracy, D_e : thermal quality of the habitat, E: thermoregulation
 1221 efficiency. Models that showed wrong convergence were removed (FW, FW \times TE and Q \times ELE in
 1222 T_{pref} analyses).

Response	Model	DF	Log-likelihood	AICc	ΔAICc	Weight
T_b	$Q \times T_{\max}$	15	-4536.30	9102.84	0	0.91
	$Q \times T_{\min}$	15	-4539.46	9109.16	6.33	0.04
	$H \times T_{\max}$	15	-4540.24	9110.72	7.89	0.02
	$ELE \times P_{\max}$	15	-4541.33	9112.90	10.07	0.01
	$T_{\max} \times \text{Age}$	14	-4542.62	9113.46	10.63	0
	$FCI \times \text{Sex} \times \text{Age}$	16	-4540.72	9113.71	10.88	0
	$TE \times T_{\max}$	15	-4541.76	9113.76	10.93	0
	$FW \times \text{Sex} \times \text{Age}$	16	-4540.91	9114.10	11.26	0
	$FCI \times \text{Age}$	14	-4543.55	9115.31	12.48	0
T_{pref}	$FCI \times \text{Sex}$	15	-35171.37	70372.77	0	0.84
	$FW \times \text{Sex}$	15	-35173.10	10376.24	3.47	0.15
	FCI	14	-35178.52	70385.07	12.30	0
	$ELE \times FW$	16	-35176.68	70385.41	12.64	0
	$FCI \times T_{\max}$	16	-35176.87	70385.78	13.01	0
	$FCI \times ELE$	16	-35177.14	70386.65	13.55	0
	$T_{\max} \times FW$	16	-35177.52	70387.08	14.30	0

	FW × FCI	16	-35177.60	70388.24	14.48	0
	FW × TE	16	-35177.68	70387.40	14.63	0
	FW × H	16	-35177.97	70387.98	15.21	0
D_b	Q × T_{max}	19	-1551.76	3141.90	0	1
	Q × T _{min}	19	-1559.97	3158.33	16.43	0
	TE × T _{max}	19	-1563.38	3165.14	23.24	0
	H × T _{max}	19	-1565.32	3169.02	27.12	0
	ELE × P _{max}	19	-1566.34	3171.07	29.17	0
	T _{max}	17	-1572.67	3179.66	37.75	0
	T _{max} × Sex × Age	20	-1569.82	3180.06	38.16	0
	T _{max} × Sex	18	-1572.33	3181.00	39.09	0
	Age × T _{max}	18	-1572.52	3181.40	39.49	0
	T _{max} × FCI	19	-1572.03	3182.45	40.55	0
D_e	P_{max} × T_{min}	11	-4046.11	8114.39	0	1
	TE × T _{max}	11	-4070.09	8162.35	47.96	0
	FW × T _{max}	11	-4076.64	8175.45	61.06	0
	FCI × P _{max}	11	-4081.76	8185.69	71.30	0
	FCI × T _{max}	11	-4092.67	8207.51	93.12	0
	Q × T _{max}	11	-4096.94	8216.04	101.65	0
	H × P _{max}	11	-4097.24	8216.64	102.26	0
	T _{max}	9	-4099.50	8217.10	102.72	0
	H × T _{max}	11	-4098.14	9218.44	104.05	0
	AgeSex Category × T _{max}	10	-4099.23	8218.59	104.20	0
	Q × T _{min}	11	-4098.77	8219.71	105.32	0
E	P_{max} × T_{min}	13	-4778.58	9583.35	0	1

	FW × T _{max}	13	-4812.36	9650.91	67.55	0
	FE × T _{max}	13	-4813.72	9653.64	70.29	0
	FCI × T _{max}	13	-4818.76	9663.71	80.36	0
	T _{max} × H	13	-4819.91	9666.01	82.65	0
	T _{max}	11	-4822.98	9668.11	84.76	0
	AgeSex Category × T _{max}	12	-4822.33	9668.84	85.48	0
	H × T _{min}	13	-4821.85	9669.90	86.55	0
	FCI × P _{max}	13	-4836.97	9700.14	116.79	0
	Q × T _{min}	13	-4837.96	9702.1	118.76	0

1223

1224

1225 **Supplementary Information 4**

1226 We estimated stage of gestation for adult females when we measured T_{pref} by calculating the
1227 number of days between the measure date and parturition date. As breeding conditions were the
1228 same for all females after capture, differences in the stage of gestation are likely consequences of
1229 differences in individual state variables among females and environmental conditions among
1230 natural populations as indicated in previous studies (Le Galliard et al. 2010, Rutschmann et al.
1231 2016b). We analyzed whether the T_{pref} of a gravid females differed according to the stage of
1232 gestation and FCI with a linear mixed model (*lme* from package “nlme”). We fitted inter-population
1233 and inter-individual deviance by adding the individual identity nested in the population identity as a
1234 random effect. As weather conditions in spring were different across years, we also fitted an
1235 additive year effect to account for yearly differences in average stage of gestation. We selected the
1236 best model with a backward model selection procedure based on loglikelihood.

1237 T_{pref} significantly decreased with the progress of pregnancy ($F_{1,619} = 75.4, p < 0.0001$) and average
1238 body temperature did not change according to the forest cover index ($F_{1,19} = 1.5, p = 0.23$).
1239 Populations with high forest cover were on average sampled at earlier stage of pregnancy especially
1240 because we sampled the population ROB first in 2018, in which we sampled more individuals and
1241 gestation is usually delayed compared to other populations.

1242 As a supplement, we also tested if adult male thermal preferences changed with the date. We
1243 calculated the difference in days between the date of capture and the earliest date at which a male
1244 had been captured for all year combined, which we will call the “date”. We used the same starting
1245 mixed effect model as described in the Methods, removing the sex effect and adding the year ×
1246 date. The male T_{pref} did not change according to the date, whatever the year (year×date: $F_{2,334} =$
1247 0.01, $p = 0.99$; date: $F_{1,334} = 0.2, p = 0.64$).

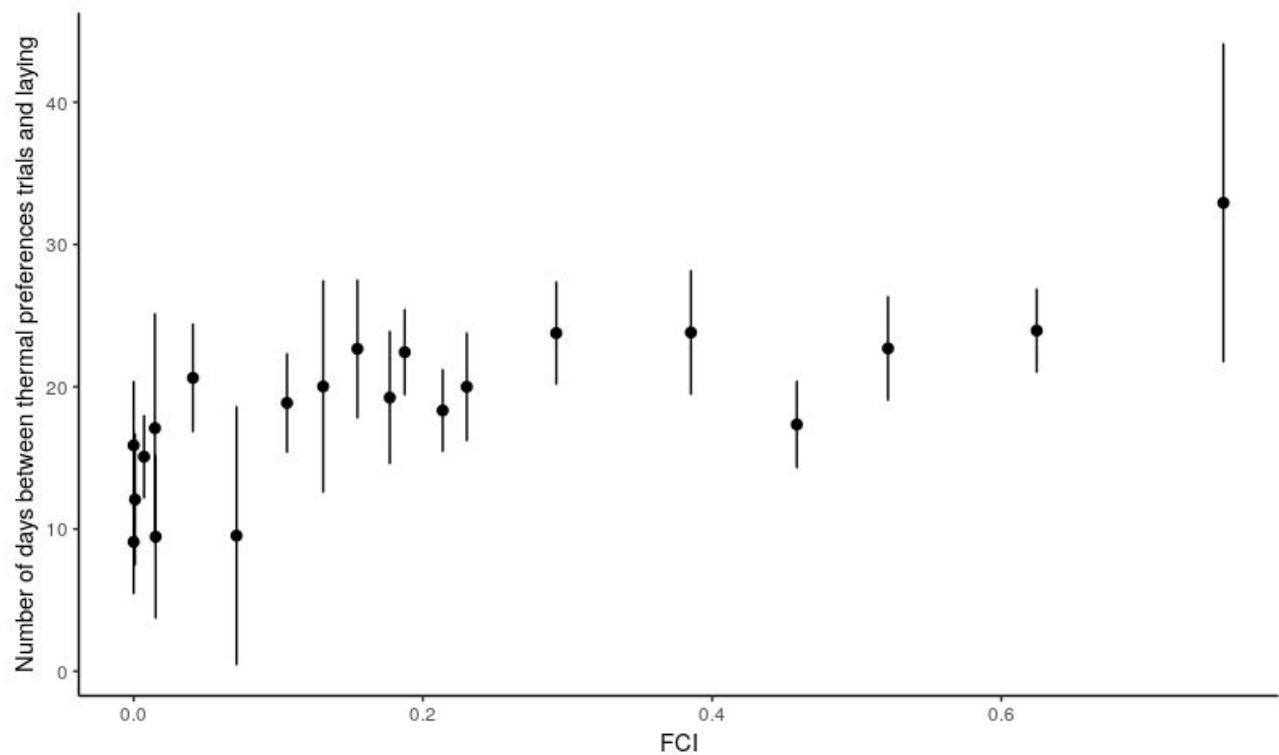
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- 1254

1255 **Figure S6**

1256 Number of days between the measurement of Tpref and laying for each population as a function of
1257 forest cover index. Error bars are for standard deviations.



1258