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Preferred temperature in the warmth of cities: body size, sex and development stage matter more than urban climate in a ground-dwelling spider

Valentin Cabon^{1,2}, Sylvain Pincebourde³, Hervé Colinet¹, Vincent Dubreuil⁴, Romain Georges^{1,2}, Maud Launoy¹, Julien Pétilion^{1,5}, Hervé Quéno⁴, Benjamin Bergerot^{1,2}

1. University of Rennes, CNRS, ECOBIO [(Ecosystèmes, biodiversité, évolution)] - UMR 6553, Rennes, France

2. LTSER ZA Armorique, F-35000 Rennes, France

3. Institut de Recherche sur la Biologie de l'Insecte, UMR 7261, CNRS – Université de Tours, Tours, France

4. University of Rennes 2, CNRS, LETG - UMR 6554, Rennes, France

5. Institute for Coastal and Marine Research – Nelson Mandela University – Port Elizabeth – South Africa

Corresponding author: Valentin Cabon, valentin.cabon@univ-rennes.fr

Abstract:

Most ectotherms rely on behavioural thermoregulation to maintain body temperatures close to their physiological optimum. Hence, ectotherms can drastically limit their exposure to thermal extremes by selecting a narrower range of temperatures, which includes their preferred temperature (T_{pref}). Despite evidence that behavioural thermoregulation can be adjusted by phenotypic plasticity or constrained by natural selection, intraspecific T_{pref} variations across environmental gradients remain overlooked as compared to other thermal traits like thermal tolerance. Here, we analysed T_{pref} variation of spider populations found along a gradient of urban heat island (UHI) which displays large thermal variations over small distances. We measured two components of the thermal preference, namely the mean T_{pref} and the T_{pref} range (i.e., standard deviation) in 557 field-collected individuals of a common ground-dwelling spider (*Pardosa saltans*, Lycosidae) using a laboratory thermal gradient. We determined if T_{pref} values differed among ten populations from contrasting thermal zones. We showed that endogenous factors such as body size or sex primarily determine both mean T_{pref} and T_{pref} range. The T_{pref} range was also linked to the UHI intensity to a lesser extent, yet only in juveniles. The absence of relationship between T_{pref} metrics and UHI in adult spiders suggests a Bogert effect according to which the ability of individuals to detect and exploit optimal microclimates weakens the selection pressure of temperatures (here driven by UHI) on their thermal physiology. Alternatively, this lack of relationship could indicate that temperature patterns occurring at the scale of the spiders' micro-habitat differ from the measured UHI. This study shows the importance of considering both inter-individual and inter-population variations of the T_{pref} range when conducting T_{pref} experiments, and supports T_{pref} range as being a relevant measure to inform on the strength of behavioural thermoregulation in a given population.

Key words: behavioural thermoregulation, Bogert effect, climate change, ectotherm, *Pardosa saltans*, urbanization, selected temperature

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29

30 **Introduction**

31 Ectothermic animals depend on external heat to regulate their body temperature, which directly drives
32 their physiological performance, from metabolism, growth, reproduction or movement, to interaction
33 strength and distribution (Angilletta, 2009; Huey et al., 2012). Ectotherms are thus widely affected by
34 climate change (Deutsch et al., 2008; Sinclair et al., 2016). To maintain their body temperature close
35 to their physiological optimum and maximize their performance and fitness, ectotherms' ability to
36 behaviourally thermoregulate is of critical importance (Martin & Huey, 2008). This mechanism consists
37 in moving within a specific range of temperatures that bring the organism near its optimum for a given
38 performance metric across heterogeneous thermal environments. Thus ectotherms evolved particular
39 adaptations to select temperatures within this range, hence the term of preferred temperature (T_{pref}),
40 which limits the exposure to deleterious thermal extremes and maximize energetic and physiological
41 benefits (Angilletta, 2009; Martin & Huey, 2008).

42 Among the variety of thermal traits, T_{pref} and related metrics are considered as the most relevant trait
43 to assess behavioural thermoregulation (Gvoždík, 2012; Hertz et al., 1993; Kearney et al., 2009; Porter
44 et al., 1973; Stevenson, 1985). T_{pref} reflects the selected temperature within a controlled thermal
45 environment, in absence of confounding factors interacting with the thermoregulatory behaviour (e.g.,
46 foraging opportunities or predator avoidance) (Huey & Slatkin, 1976). Traditionally, the mean of the
47 T_{pref} was mostly used (Labra et al., 2009) but the range of T_{pref} is also an informative component to
48 characterize thermoregulation capacities. The inter-individual variability of T_{pref} often displays
49 contrasting levels between species. For example, all the tested individuals selected temperatures
50 within a narrow range of only 2-3 °C in the common brown shrimp (Reiser et al., 2014) and in the León
51 rock lizard (Ortega et al., 2016). By contrast, the T_{pref} distribution encompassed a range of >10°C in
52 several drosophilids (MacLean et al., 2019). Several studies showed that intraspecific T_{pref} variations
53 are sex- and size-dependant (Berec et al., 2014; Dillon et al., 2009; Forsman, 2000), as well as being
54 driven by developmental or reproductive stages (Dillon et al., 2009; MacLean et al., 2019). Although
55 the drivers of such differences, both at the inter and intra specific levels, are not well understood, the
56 range of T_{pref} can be used as an indicator of a population's ability to buffer against temperature
57 extremes like heat waves events (Brandt et al. 2020). In general, thermal ecology theory predicts that
58 a narrow T_{pref} range improves the ability to buffer environmental extremes as long as the targeted
59 temperature remains in some microclimates (Woods et al., 2015). However, a narrow T_{pref} range can
60 reduce selection pressure on thermal limits, thereby making the species particularly vulnerable when
61 the adequate temperature is not present anymore in the environment (Muñoz et al., 2016). Thus, the
62 T_{pref} range and mean are often expected to vary along environmental gradients such as altitude but
63 available studies suggest that this relation is more complex and species specific than anticipated
64 (Gvoždík, 2012; Trochet et al., 2018).

65 Most of the complex and highly variable responses of T_{pref} to temperature variations along
66 geographical clines were derived from studies on vertebrate ectotherms (Llewelyn et al., 2016; Muñoz,
67 2022; Trochet et al., 2018). Three types of ectotherms' responses can be drawn from these studies
68 that mostly focused on the median or mean of T_{pref} (Figure 1). Firstly, the adaptation of local optima
69 hypothesis, according to which individuals from colder environments select lower T_{pref} relative to
70 conspecifics from warmer environments, following a co-gradient response (Brattstrom, 1965;
71 Levinton, 1983; Mitchell & Lampert, 2000). Secondly, the counter-gradient relationship hypothesis
72 predicts that individuals experiencing extreme temperatures should be more sensitive to adverse
73 thermal conditions (Llewelyn et al., 2016), and therefore they select lower temperatures (i.e., lower
74 T_{pref}) when they are given the opportunity. Hence, individuals from cold environments select higher
75 T_{pref} to compensate for lower opportunities to find favourable temperatures within the thermal
76 environment (Conover & Schultz, 1995; Fanguie et al., 2009; Hodgson & Schwanz, 2019; Llewelyn et al.,
77 2016; McElroy, 2014). Thirdly, the Bogert effect (Bogert, 1949) suggests that behavioural
78 thermoregulation inhibits the plastic response of T_{pref} (Huey et al., 2003; Marais & Chown, 2008). This
79 behavioural inertia is suspected to buffer selection pressure and thus to reduce plastic or evolutive
80 adaptation to changing thermal environments. Consequently, this process involves the absence of
81 correlation between geographical clines and T_{pref} . Alternatively, an absence of correlation could also
82 indicate that patterns of temperature measured along the geographical cline do not occur at the scale
83 of the microhabitat occupied by the investigated taxa. Different patterns can apply in closely related
84 species; for instance, the variation of T_{pref} in a community of *Drosophila* species along geographical
85 clines illustrated a co-gradient pattern (Nevo et al., 1998), a counter-gradient pattern (Yamamoto &
86 Ohba, 1984) as well as an absence of T_{pref} response to elevation (Krstevska & Hoffmann, 1994)
87 depending on the species. Here, we applied this framework to test if one of these mechanisms prevail

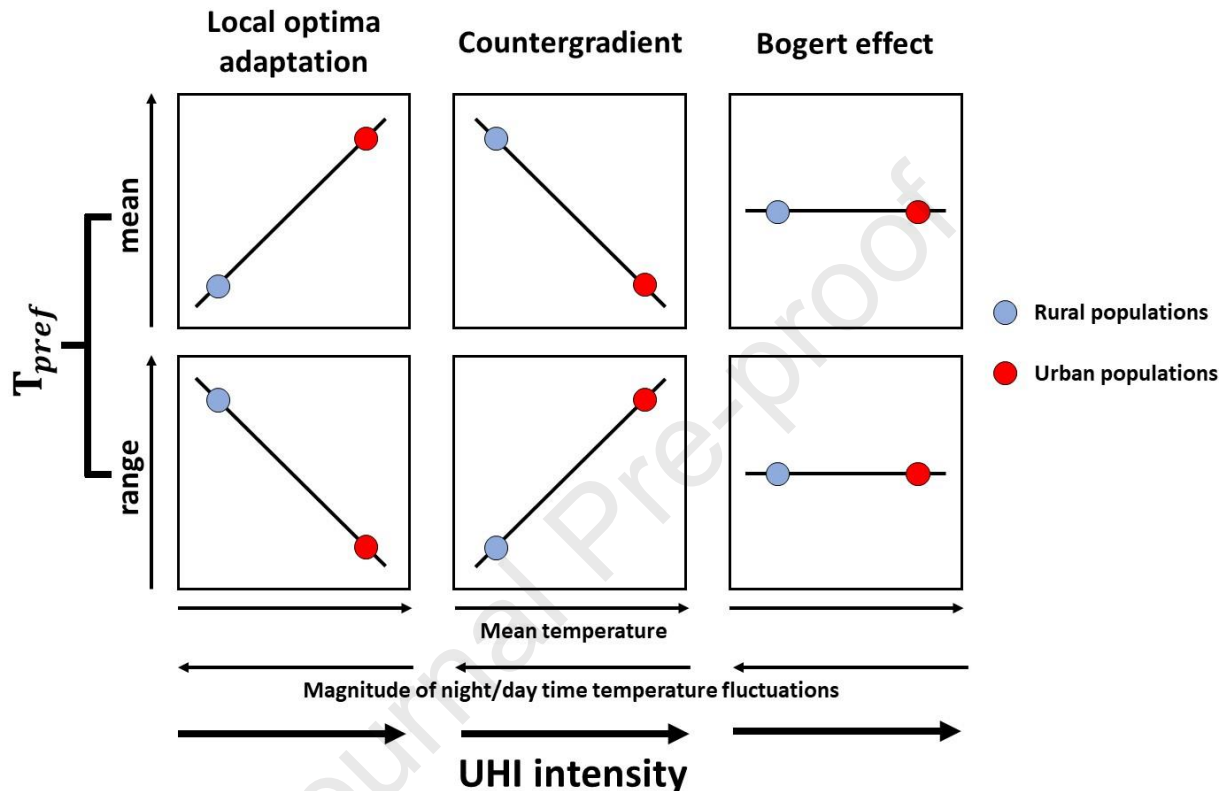
88 in the variation of T_{pref} (both mean and range) of a spider species along a broad thermal cline
89 generated by the urban heat island.

90 Urbanisation gradients, alongside with their strong deleterious impacts on local biodiversity (Fenoglio
91 et al., 2020; Groffman et al., 2014; McKinney, 2008), have been recently recognised as promising open-
92 sky laboratories to surrogate climate change impacts on arthropods (Lahr et al., 2018; Youngsteadt et
93 al., 2015). During the night, the mean air temperature in cities is higher than in the countryside due to
94 the combination of heat-absorbing impervious materials, reduction of vegetation cover and associated
95 water vapor flux, canyon-like urban morphology, and accumulations of anthropogenic heat sources
96 (such as traffic or heating) (Heisler & Brazel, 2010). This phenomenon, commonly referred to as the
97 atmospheric urban heat island (UHI) (Oke et al., 2017), provides multiple advantages for conducting
98 thermal ecology studies, particularly on ectothermic species such as arthropods (Verheyen et al.,
99 2019). A first interesting component of the UHI lies in the steep slope of the thermal gradient (Oke et
100 al., 2017). Differences in average temperatures can reach 4°C between locations separated by less than
101 10 km, providing a broad thermal gradient within a narrow geographic area (Verheyen et al., 2019).
102 The second component of interest lies in the magnitude of night/day time temperature fluctuations
103 which is modulated by the UHI's intensity. Much of the increased average temperatures in urban areas
104 is the result of warmer nocturnal temperatures relative to adjacent rural areas (Dubreuil et al., 2020;
105 Foissard et al., 2019; Oke et al., 2017). Therefore, the magnitude of temperature variations between
106 day- and night-time is lower in urban areas than in rural surroundings (Oke et al., 2017). An urban
107 dwelling animal living under intense UHI conditions thus experience a narrower range of night/day
108 time temperature fluctuations than its rural conspecific. If multiple studies on arthropods
109 demonstrated the existence of plastic or evolutive responses of thermal tolerance to the UHI
110 (Angilletta et al., 2007; Brans et al., 2017; Diamond, Chick, Perez, Strickler, & Martin, 2018; Diamond,
111 Chick, Perez, Strickler, & Zhao, 2018; Sato & Takahashi, 2022), almost no studies aimed at linking
112 arthropods' thermal preferences across a UHI gradient to infer the impact of temperature variations
113 on their thermoregulatory behaviour (but see Youngsteadt et al., 2023). Although fine-scale surface
114 temperatures are likely to be an important driver of the T_{pref} response to the thermal environment,
115 repeating investigations into the potential effects of large-scale warming through atmospheric UHI on
116 rural-urban thermal gradients represents a first step in providing crucial information on how climate
117 change relates to the physiology and behaviour of ectotherms. If large-scale temperature patterns
118 across geographical clines (i.e., atmospheric UHI) cannot be linked to T_{pref} variations, surface
119 temperature may better match the scale at which arthropods experience their thermal environment
120 and therefore be the determining metric. In addition, we lack information on the variation of the range
121 of T_{pref} along these environmental gradients. By applying the same reasoning than for the mean,
122 however, we expect a positive relationship between the T_{pref} range and the magnitude of the
123 night/day time temperature fluctuations in the local optima adaptation hypothesis, and therefore a
124 negative relationship between the mean and range of T_{pref} (Figure 1). By contrast, we expect the
125 range of T_{pref} to decrease with the magnitude of the night/day time temperature fluctuations under
126 the counter-gradient hypothesis, while no change is anticipated in the Bogert effect hypothesis (Figure
127 1).

128 In this study, we determined the variation of thermal preference in a free-moving wolf-spider along an
129 UHI gradient to infer which mechanism (Figure 1) is at play. Lycosids are relevant models for such a
130 study because (i) they are dominant ground-dwelling predators in many habitats, including along
131 urbanization gradients (Varet et al., 2011), and (ii) previous studies showed the relationship between
132 local abiotic factors and micro-habitat partitioning (e.g., for temperature and humidity, see Frick et al.,
133 2007 and DeVito et al., 2004, respectively), suggesting they adjust their local distribution according to
134 their T_{pref} , including in the field (Humphreys, 1974). We collected individuals along an UHI gradient to

135 measure their T_{pref} in the lab under standardized conditions. We conducted individual-based and
 136 repeated measurements of T_{pref} over time, which permitted to calculate both mean T_{pref} and T_{pref}
 137 range for every individual. We then tested if mean T_{pref} and T_{pref} range co-vary with the UHI intensity.
 138 We further tested whether the response to UHI dominates the influence of three endogenous factors
 139 on mean T_{pref} and T_{pref} range, namely body size, sex and life stage (juveniles versus adults). This
 140 comparison can be useful to infer the relative biological importance of any effect of the UHI on T_{pref} .

141



142

143 Figure 1 - Conceptual hypothesis framework displaying predicted responses on thermal preferences (mean T_{pref} : top line
 144 and T_{pref} range: bottom line) according to the urban heat island intensity (UHI). The UHI intensity axis is characterized by
 145 an increase in mean temperature and a concomitant decrease of magnitude in night/day time temperature fluctuations.
 146 The three columns describe the local optima adaptation, the counter-gradient hypothesis and the behavioural inertia
 147 hypothesis (Bogert effect) respectively.

148 Material and methods

149 Model species and sampling sites

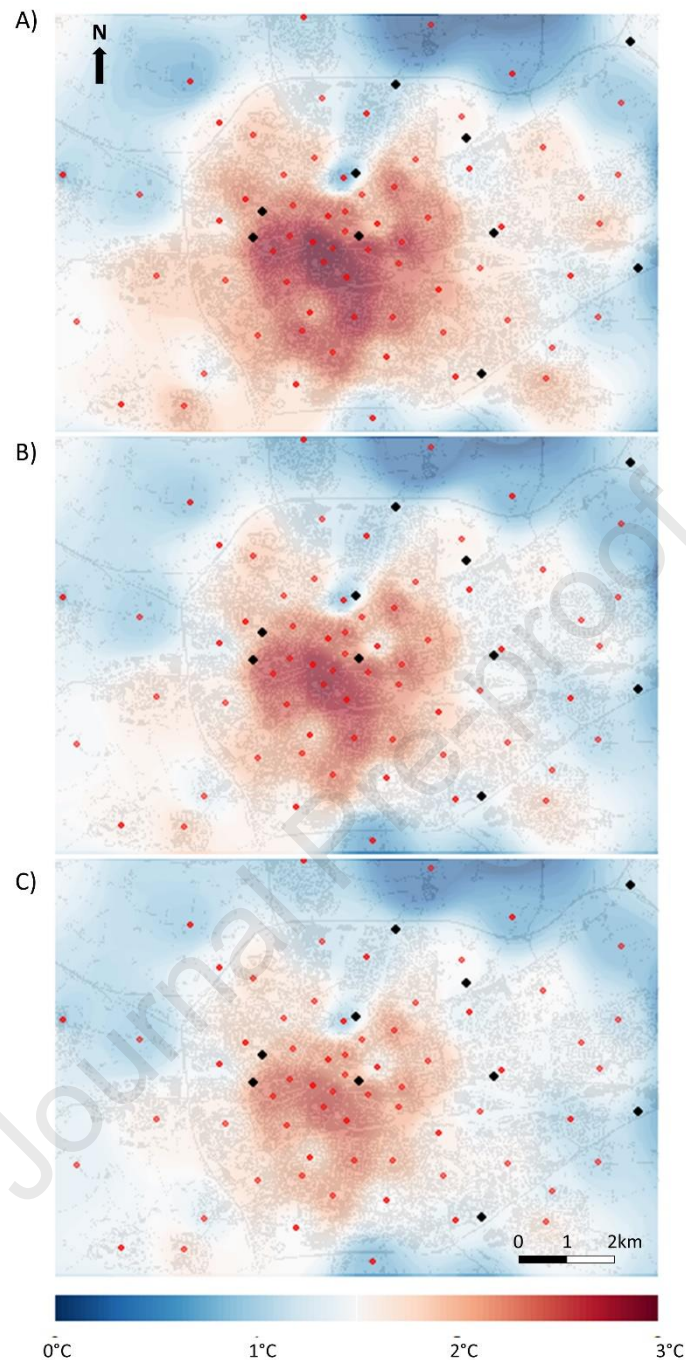
150 The wolf spider *Pardosa saltans* (Töpfer-Hofmann et al., 2000) (Araneae: Lycosidae) is widely
 151 distributed across Europe. This spider completes its life cycle over two years. Spiderlings emerge during
 152 summer in year N, to spend winter exclusively in the leaf litter. Individuals reach the subadult stage in
 153 September of N+1 and overwinter a second time as subadults. Finally, subadults reach the adult stage
 154 between early March and the end of April of the year N+2. Since mating occurs as soon as the adult
 155 stage is reached, most females are carrying egg-sacs by the end of May and spiderlings start to emerge
 156 in July (Edgar, 1971). If adults are active on the leaf-litter during daytime in woody habitats (Edgar,
 157 1971; Hendrickx et al., 2001; Pétilion et al., 2011), males commonly explore a wider range of habitats
 158 than females and can also be found in clearings, hedgerows, or thickets (Ruhland et al., 2016; Tralalon,
 159 2022). In urbanised areas, *P. saltans* can be found in woody patches such as parks, wastelands, and

160 natural remnants. These spiders use the litter layer to behaviourally thermoregulate and protect
161 themselves from high temperature variations (Trabalon, 2022). Due to its abundance in urban habitats
162 and its thermoregulatory capacity, *P. saltans* represents an excellent model species to study if
163 temperature changes induced by the UHI modulate the ability of arthropods to behaviourally
164 thermoregulate.

165 We collected adults and juveniles (subadults) from both sexes by visual inspection of the litter of ten
166 deciduous woodlots located across a gradient of UHI in the area of Rennes, France (coordinates:
167 48°06'41.6"N 1°40'46.5"W), using 200 ml plastic tubes. Spiders were all collected in similar woody
168 habitats regardless of the corresponding UHI intensity. For females, only individuals without egg-sac
169 where collected. To account for spiders' acclimation to field temperature variation over the season,
170 we conducted two sampling sessions, respectively in March and April 2022, between 10 am and 3 pm,
171 during sunny conditions. To ensure that individuals remained acclimated to field temperature
172 conditions, spiders were brought to the laboratory and experiments began within two hours following
173 field collection (Reynolds & Casterlin, 1979).

174 **Urban heat island (UHI)**

175 In Rennes, a long-term climate observation network was established in 2004 with the aim to
176 characterize the UHI intensity across space and time (Dubreuil et al., 2020; Foissard et al., 2019). Since
177 2004, the Rennes Urban Network (<https://run.letg.cnrs.fr>) has grown from 12 to 30 DAVIS Vantage-
178 Pro-2 automatic weather stations, to which 93 connected temperature sensors were added in 2020
179 (Dubreuil et al., 2022). The weather stations and temperature sensors are spread over rural, suburban
180 and city-centre areas, collecting data at a 60- and 15-minutes frequency, respectively. We used this
181 database to calculate the UHI intensity for each month between June 2021 and June 2022, as the mean
182 difference between minimal daily temperatures measured at the cold reference station and the
183 minimal daily temperatures measured by each other sensor. Therefore, this UHI intensity corresponds
184 to a temperature anomaly of a particular site, i.e., the number of degrees C above the cold reference
185 that is necessarily outside the urban landscape. These temperature difference values were used to
186 spatialize the UHI intensity by inverse distance weighting interpolation to the entire city area at a 100m
187 resolution. The UHI intensity is known to vary over the year, so we averaged the monthly raster maps
188 to calculate UHI value corresponding to three periods that are ecologically relevant for our study
189 species (Figure 2): (1) the exact period of the T_{pref} measurements (i.e., March and April 2022), (2) the
190 period corresponding to the entire time spent by the collected *P. saltans* individuals since they reached
191 the subadult stage (i.e., September 2021 to April 2022), and (3) the winter period before the
192 experiment (i.e., December 2021 to February 2022), during which individuals overwintered as
193 subadults. At last, we extracted the UHI intensity values corresponding to the raster cells on which the
194 ten sampling sites were located for those 3 periods defined above.



195

196 **Figure 2** - Location of the 10 sampling sites (black dots) within the city borders of Rennes and surroundings according to the
 197 spatialized UHI mean intensity obtained from the sensor network (red dots) during A) the experiment period (March and
 198 April 2022), B) the entire period *P. saltans* individuals have spent as subadults or adults before and during the
 199 experimentation (September 2021 to April 2022), C) the winter period preceding the experiment (December 2021 to
 200 February 2022). The UHI is depicted by a colour gradient ranging from blue (low intensity) to red (high intensity).
 201 Transparent grey patches represent build-up areas.

202 Thermal preference

203 We determined the T_{pref} of each individual collected at the ten sites using two home-made thermal
 204 gradient systems in the laboratory. Each unit was composed of an aluminium plate (dimensions L x l x
 205 h: 50 x 18 x 1 cm), heated at one side using a thermal resistance and cooled at the other side with a
 206 cryostat bath (Polystat CC3, Huber Kältemaschinenbau AG, Germany) filled with heat transfer fluid

207 (Thermofluid SilOil, Huber, Germany), creating a linear temperature gradient orientated along the
208 plates' length (Figure S1). A system of 14 ramps was created on top of the plate (along the length) by
209 applying 15 aluminium bars of 1 cm height, 35 cm length and separated by 1 cm from each other. Each
210 spider was placed individually in one of the ramps. The grid of ramps was covered with a transparent
211 acrylic plate to avoid the animals to escape. The two units therefore allowed us to determine the T_{pref}
212 of 28 individuals at a time.

213 We conducted preliminary tests to set the temperature range of the gradient at 14-39°C, in accordance
214 to the range of preferred temperatures of spiders, thereby avoiding an edge effect with individuals
215 stuck at one end of the gradient. We then measured the temperature distribution over the two
216 gradients using thermocouples (Type-K) connected to Testo 175T3 temperature data loggers (Testo
217 SE& Co. Germany) that were placed every centimetre along the plates (the edge of gradients was
218 graduated at a 5 mm resolution), and checked for temperature stability over time. The temperatures
219 measured as a function of the distance to the warmer end allowed us to generate calibration curves
220 that were used for post-conversions of distance (location of a spider in a ramp) to temperature.
221 Conjointly, air humidity was measured along the gradient using five iButton Hygrochron
222 Temperature/Humidity Logger (DS1923, Dallas Semiconductor/Maxim, Dallas, USA). First trials
223 revealed humidity proportions ranging from 20% at the warm side, to 100% at the cold extremity. To
224 avoid a temperature-humidity co-gradient effect and enable the decoupling of preferred temperatures
225 from humidity preference, we placed a fragment of wet sponge at each ramp's warm extremity. This
226 method maintained the relative humidity above 70% along the whole gradients.

227 At the time of an experimental run, the set-up was turned on one hour prior to experiment's start to
228 ensure the thermal gradient is stable. Then, the collected spiders were individually sexed, weighted
229 (to the nearest 0.01 mg using a Sartorius A200S Analytical Balance) and randomly placed individually
230 in the ramps in the centre of the gradient (where surface temperature was about 27°C). Stabilization
231 times exceeding one hour have already been observed in arthropods (Refinetti, 1984). Therefore, we
232 monitored spiders' position every minute during 90 minutes with cameras (AKASO Brave 7) suspended
233 above the set-up. Light was maintained in the lab at the minimum level so that the position of spiders
234 in the images could be clearly observed. At the end of the experiment, each spider was numbered and
235 kept in a separate Eppendorf tube, in 70° alcohol, for morphological measurements. All spiders were
236 individually checked under binocular magnifier to confirm the prior identification of species, sex and
237 development stage (juvenile or adult). In addition, we took pictures of the cephalothorax and the right
238 leg IV (Pétillon et al., 2018) using the software Leica LAS X, and used ImageJ to measure the length of
239 cephalothorax and leg as proxies of body size.

240 **Data analysis**

241 We extracted the position in the ramps of each individual obtained each minute during the 90 min
242 experimental period, and converted them in temperature values using the gradient calibration curves
243 (Figure S2). We tested if the T_{pref} varied over the 90 minutes by dividing the temperature
244 measurements into 10 min intervals. We then calculated a mean T_{pref} per spider and per 10 min
245 interval. We performed generalized mixed models (GLMM) to test the effect of time (fixed effect),
246 while accounting for spider individuals as random effect. We computed multiple models considering
247 at first the whole experiment time (i.e., 90 min), and successively removed 10 min time intervals to
248 allow for the determination of a breakpoint at which spiders reached their (stable) final T_{pref} . To
249 estimate the spiders' stabilized T_{pref} considered in further analyses, we determined the mean and
250 range values based on all temperature measurements available after this breakpoint.

251 To determine mean T_{pref} and T_{pref} range, we fitted a Gaussian distribution curve to each individual's
 252 temperature distribution by maximum likelihood (mle). Based on the obtained estimates, we
 253 attributed a mean and a range value calculated as the standard deviation value of the mean of the
 254 fitted Gaussian distribution. A low T_{pref} range indicates that a spider explored a narrow range of the
 255 thermal gradient, whereas a high value corresponds to an individual exploiting a large portion of the
 256 ramp. To reduce the risk of including individuals for which the movement was inhibited by low
 257 temperatures at the cold end of the gradient (see Dillon et al. 2009), we removed outliers with median
 258 T_{pref} values outside the 95% dispersion interval, after pooling all individuals.

259 Statistically, we tested separately the response of mean T_{pref} and T_{pref} range to endogenous variables
 260 and UHI intensity. We computed generalized linear mixed models (GLMM) and included
 261 developmental stage (juvenile versus adult), sex, two morphological measurements (length of
 262 prosoma and leg) and a measure of UHI intensity (i.e., March to April 2022) as predictors. As habitat
 263 and behaviour are likely to differ strongly in juveniles and adults of *P. saltans*, we added an interaction
 264 term between developmental stage and each other predictor. We selected the best models using the
 265 dredging procedure from the 'MuMin' package (Bartoń, 2016). In cases where interactions were
 266 retained in the final models, we computed post hoc tests to identify the underlying significant
 267 relationships. We performed Tukey tests using the 'emmeans' R-package (Lenth, 2023) in the case of
 268 categorical variables and linear models for continuous data. Additional similar models were
 269 independently tested to verify that the predictive power of the two other UHI metrics (i.e., September
 270 2021 to April 2022 and December 2021 to February 2022) remained unchanged. In each model, we
 271 defined all the endogenous and environmental variables as fixed effects and sampling session (March
 272 or April) as a random effect. We also calculated the coefficient of determination (marginal r-squared)
 273 to assess the proportion of variation explained by the fixed effects.

274 All statistical analyses were performed in R version 4.0.3, using the package 'fitdistrplus' for gaussian
 275 distribution fitting (Delignette-Muller & Dutang, 2015), 'lme4' for GLMMs computing (Bates et al.,
 276 2015) and 'performance' (Lüdtke et al., 2021) for computing marginal r-squared values from mixed
 277 effects models.

278 Results

279 Sampled individuals

280 The number of collected individuals at each sampling site ranged from 27 to 71 for a total number of
 281 557 individuals that were assayed. We obtained the T_{pref} for every minute during 90 minutes on 522
 282 individuals of *P. saltans*, including 259 males (102 juveniles and 157 adults) and 263 females (117
 283 juveniles and 146 adults) after removing only 35 outliers in the complete dataset. Globally, spiders had
 284 a mean T_{pref} of $33.4 \pm 2.0^\circ\text{C}$ and a T_{pref} range of $1.8 \pm 1.7^\circ\text{C}$ (Table 1). The average UHI intensity of
 285 the study sites ranged from 0.85°C to 2.5°C when calculated over the exact sampling period (March
 286 2022 – April 2022), from 0.83°C to 2.1°C when considering the preceding winter period (Dec. 2021 –
 287 March 2022) and from 0.93°C to 2.8°C when calculated over the entire previous year (July 2021 – June
 288 2022).

289 **Table 1** – Summary of individual parameters for two development stages (adults and juveniles) in males and females of
 290 *Pardosa saltans*. Mean and standard deviation values are indicated for each variable, except in the case "count", where the
 291 number of individuals and the corresponding percentage are indicated. Values related to T_{pref} (mean and range) in this table
 292 were calculated on the experimental time ranging from the 31st to 90th minute.

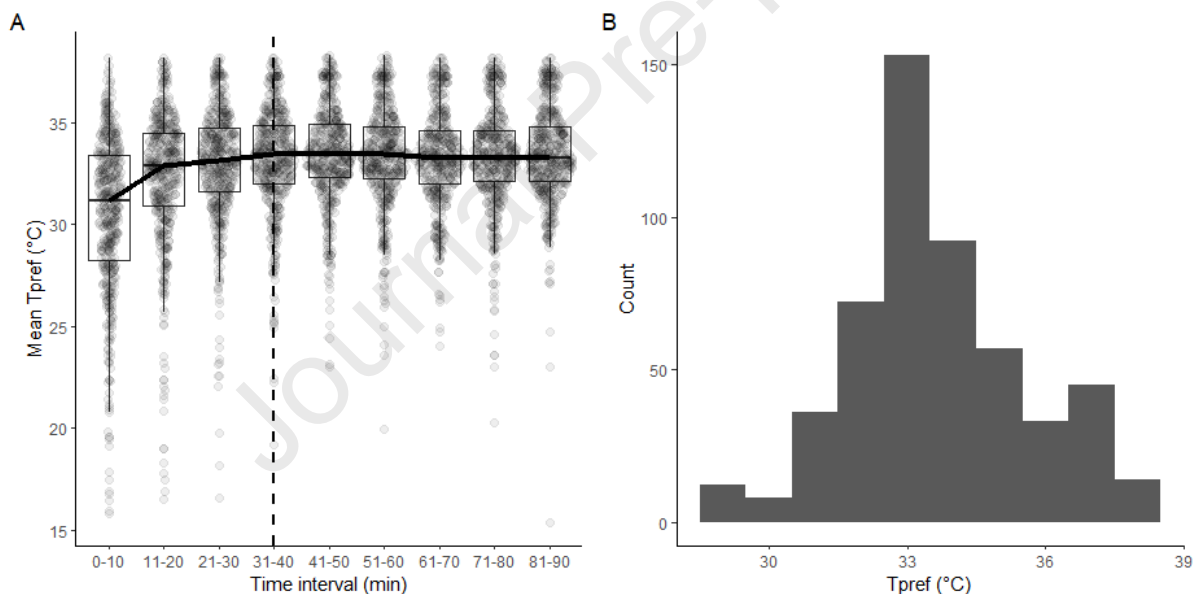
| | | Males | Females | Total |
|--------|---------------------|----------------|----------------|----------------|
| Adults | Count | 157 (30%) | 146 (28%) | 303 (58%) |
| | Prosoma length (mm) | 2.3 ± 0.3 | 3.6 ± 0.7 | 2.9 ± 0.8 |
| | Leg length (mm) | 10.2 ± 0.9 | 12.4 ± 1.2 | 11.3 ± 1.5 |

| | | | | |
|------------------|---------------------|-------------|-------------|------------|
| | Mean Tpref (°C) | 32.8 ± 2.0 | 34.3 ± 2.3 | 33.5 ± 2.3 |
| | Tpref range (°C) | 2.6 ± 1.6 | 2.3 ± 1.5 | 2.1 ± 1.6 |
| Juveniles | Count | 102 (19.5%) | 117 (22.5%) | 219 (42%) |
| | Prosoma length (mm) | 2.7 ± 0.3 | 3.0 ± 0.4 | 2.9 ± 0.4 |
| | Leg length (mm) | 8.6 ± 0.9 | 9.4 ± 1.3 | 9.0 ± 1.2 |
| | Mean Tpref (°C) | 33.4 ± 1.7 | 33.0 ± 1.5 | 33.2 ± 1.6 |
| | Tpref range (°C) | 1.2 ± 1.5 | 1.4 ± 1.8 | 1.3 ± 1.6 |
| Total | Count | 259 (49.6%) | 263 (50.4%) | 522 (100%) |
| | Prosoma length (mm) | 2.5 ± 0.3 | 3.4 ± 0.6 | 2.9 ± 0.7 |
| | Leg length (mm) | 9.6 ± 1.2 | 11.0 ± 2.0 | 10.3 ± 1.8 |
| | Mean Tpref (°C) | 33.0 ± 1.9 | 33.7 ± 2.1 | 33.4 ± 2.0 |
| | Tpref range (°C) | 2.0 ± 1.7 | 1.5 ± 1.6 | 1.8 ± 1.7 |

293

294 **Period selection for Tpref parameters**

295 Spiders' Tpref was influenced by experimental time (GLMM, $p < 0.001$, Figure 3A, Table S1). Mean
 296 Tpref values were lower during the first three time-intervals considered (0-10 min: $32.9 \pm 3.0^\circ\text{C}$, 11-
 297 20 min: $33.2^\circ\text{C} \pm 2.7^\circ\text{C}$, 21-30 min: $33.3 \pm 2.5^\circ\text{C}$), but stabilized after 30 minutes and remained
 298 unchanged until the end of the experiment (31-90 min: $33.4 \pm 2.0^\circ\text{C}$, Figure 3B). Consequently, we
 299 excluded Tpref data collected during the exploration phase, and considered only stabilized Tpref values
 300 measured after the 30th minute of the experiment.



301

302 **Figure 3** – A) Variation of the mean Tpref of 522 individuals of *Pardosa saltans* over 90 minutes in an experimental thermal
 303 gradient. Tpref data were divided and averaged into 10 minutes intervals. Semi-transparent points represent individual values
 304 of averaged Tpref. The central line of each box indicates the median of the averaged Tpref and the black line connecting these
 305 values represents its variation through time. The dashed line indicates the 10 min interval from which Tpref values remained
 306 stable in time and were considered in analyses. B) Histogram displaying the global distribution of Tpref values within the 31-
 307 90 min time interval considered in further analysis.

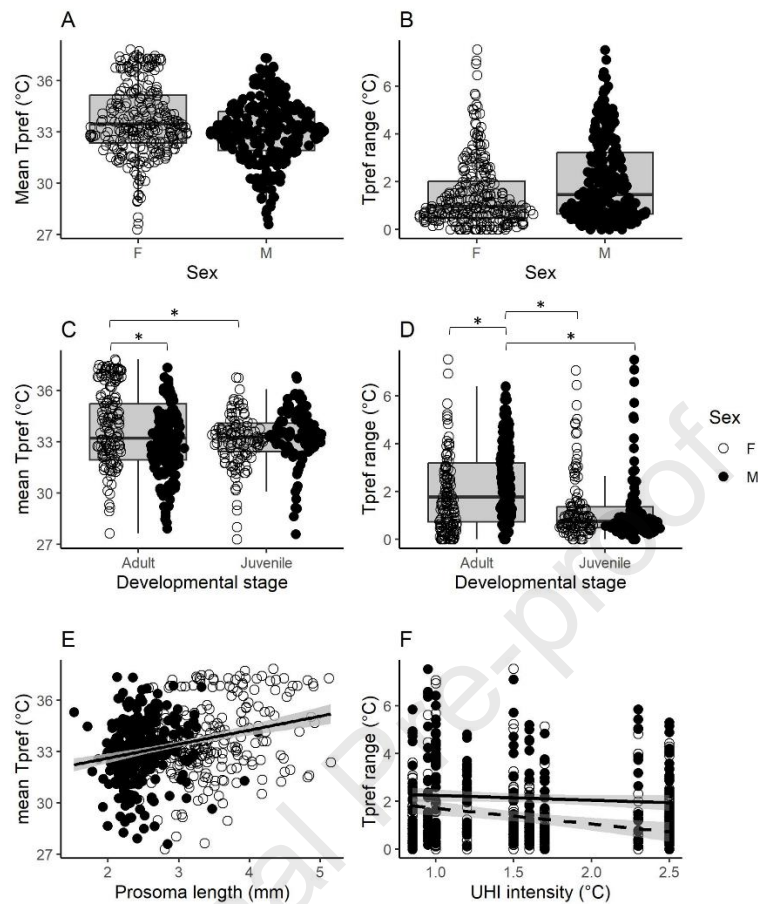
308 **Influence of endogenous factors and UHI on Tpref**

309 We found that females had a warmer mean Tpref (Table 2, Figure 4A) and a narrower Tpref range
 310 (Table 2, Figure 4B) than males. Post hoc analyses revealed that these two relationships were present
 311 in adults, but not in juveniles (Table S2, Figures 4C and 4D). In addition, larger individuals (i.e., adult
 312 females) had warmer mean Tpref (Table 2, Figure 4E). We detected an interaction between
 313 development stage and UHI intensity on Tpref range (Table 2). Post hoc tests on interactions showed

314 that Tpref range became more precise, as UHI intensity increased, but only in juveniles (Table S3, Figure
 315 4F). Models fitted with UHI intensities measured over longer time periods showed similar relationships
 316 between the interaction of UHI intensity and developmental stage, and the Tpref range (Table S4,
 317 Figure S3).

318 **Table 2** - Effects of endogenous (development stage, sex, prosoma length), environmental factors (UHI intensity) and their
 319 interactions on mean Tpref and Tpref range estimated by generalized linear mixed models (GLMM). Significant results
 320 (P<0.05) are in bold. Results of models after variable selection are displayed.

| | Est. | SE | P-val | R ² |
|-----------------------------------|---------------|--------------|------------------|----------------|
| Mean Tpref | | | | 0.105 |
| Development stage | -1.005 | 0.260 | <0.001 | |
| Sex | -0.876 | 0.327 | 0.007 | |
| Prosoma length | 0.491 | 0.185 | 0.008 | |
| Development stage : Sex | 1.401 | 0.384 | <0.001 | |
| Tpref range | | | | 0.140 |
| Development stage | 0.834 | 0.438 | 0.057 | |
| Sex | 1.053 | 0.180 | <0.001 | |
| UHI intensity | -0.128 | 0.148 | 0.387 | |
| Development stage : Sex | -1.420 | 0.279 | <0.001 | |
| Development stage : UHI intensity | -0.580 | 0.238 | 0.015 | |



321

322 **Figure 4** – Graphs representing significant relationships between Tpref parameters (mean Tpref and Tpref range) and the
 323 tested endogenous and environmental factors. White dots represent females and black dots are males. A and B show the
 324 differences in Tpref among sexes. C and D display relationships observed between Tpref parameters and developmental
 325 stage, as well as significant interactions (*: p-value < 0.05) between developmental stage and sex. E represents the positive
 326 relationship between mean Tpref and the prosoma length. F represents the relationship between Tpref range, the significant
 327 interaction of the UHI intensity (from March to April 2022) and developmental stage (solid line represents adults, dashed line
 328 represents juveniles).

329 Discussion

330 While the plasticity of thermal tolerance limits across urban gradients has received attention (Brans et
 331 al., 2017; Diamond et al., 2017), little is known on the plasticity of Tpref in ectotherms. In this study,
 332 we showed that Tpref varies only marginally (and only in juveniles) along an UHI gradient in a common
 333 spider species. *Pardosa saltans* showed a preferred temperature of 33.40 °C (\pm 2.0°C), which is in line
 334 with previous results obtained on lycosids spiders (Humphreys, 1978; Nørgaard, 1951; Sevacherian &
 335 Lowrie, 1972). Tpref is more strongly modulated by endogenous factors such as sex, life stage and body
 336 size than the UHI gradient. This result implies that traits may be more important than the environment
 337 in defining the parameters of behavioural thermoregulation. Our results further imply that the Bogert
 338 effect may prevail in this spider system, although we cannot exclude that the thermal optima
 339 hypothesis rules the response in juveniles.

340 1 – Role of endogenous factors

341 Sex and body size are generally identified as an important determinant of several thermal traits
342 (Angilletta 2009). Our study confirms the importance of sex and body size on thermal responses. Sex
343 was the only factor, among the predictors we tested, to explain part of the variance for both the mean
344 T_{pref} and the T_{pref} range. The effect, however, was opposite for the two parameters. If mean T_{pref}
345 was warmer in females, their T_{pref} range was narrower. The difference of T_{pref} range among sexes
346 suggests that females, which tend to be larger than males, choose more accurately the temperatures
347 to which they expose themselves. Hence, this observation coupled with the warmer mean T_{pref}
348 observed in females suggests that they tend to be 'specialist' thermoregulators, placing themselves
349 accurately in the mosaic of thermal environments where temperatures are rather high. Contrastingly,
350 smaller male individuals may be more 'generalists', having lower preferred temperature but exploring
351 a wider range of thermal conditions. These patterns of variation in T_{pref} mean and T_{pref} range in adult
352 spiders may be linked to the framework 'suboptimal is optimal' (Martin & Huey, 2008). This theory
353 relates the asymmetric shape of temperature-performance curves to the expected T_{pref} mean, which
354 should shift below optimal temperature to avoid exposure to challenging temperatures. This should
355 be especially true for thermal specialists, like *Lycosid* females, for which the temperature range
356 between optimum and critical maximal temperature is particularly narrow. Nevertheless, we lack data
357 on this spider thermal biology (e.g., optimum) to test this theory any further. Similar complexity was
358 already observed in the relationship between body size (or mass) and thermal tolerance traits in
359 arthropods, yet with a general pattern suggesting a positive association between body size and heat
360 tolerance (Blanckenhorn, 2000; Klockmann et al., 2016; Nielsen & Papaj, 2015). Given that the CT_{max},
361 the optimal temperature and T_{pref} (mean) are often related to some extent (Angilletta 2009), our
362 result on a similar positive relationship between T_{pref} and body size is not surprising. Yet, contrasting
363 patterns of body size effect on other thermoregulation traits such as the onset temperature for refuge
364 seeking were also observed (Nielsen & Papaj, 2015). More experimental studies are needed to identify
365 a general pattern between body size and T_{pref} metrics and the functional underpinnings of this
366 relation.

367 Further, the observed divergence between the mean T_{pref} of males and females in *P. saltans* contrasts
368 with previous observations in other *Lycosids* (Frick et al., 2007; Nørgaard, 1951). However, the mean
369 T_{pref} of *Lycosids* is well known to strikingly vary in adult females carrying an egg-sac (Sevacherian &
370 Lowrie, 1972), as they select warmer microhabitats that are more suitable for their cocoon. Our results
371 suggest that females *P. saltans* are already more thermophilic than males prior to egg laying. In
372 addition, the difference of T_{pref} range between sexes has never been revealed before in *Lycosids*. We
373 propose that the higher variability of T_{pref} in males is related to their exploratory behaviour. In
374 *Pardosa* spiders, males and females display contrasting movement and exploratory behaviours.
375 Heydemann (1960) reported that populations with high abundance are structured with females mainly
376 located within optimal biotopes whereas males move across adjacent marginal biotopes where density
377 is lower. Further, *P. saltans* males can be twice as active as females and they can explore larger surfaces
378 (Trabalon, 2022). Indeed, adult males start to actively search for females during the reproductive
379 period (Cady, 1983; Hallander, 1967; Vlijm & Richter, 1966), which can in turn be accompanied by an
380 increase of their T_{pref} range. More experimental works are needed to generalize (or not) this effect,
381 especially by comparing species with various activity levels and contrasting exploratory behaviours.

382 Our study further brings evidence that T_{pref} range might increase, especially in males, once individuals
383 reach sexual maturity in response to a change in their ecology relative to juveniles. Previous studies
384 on species from the genus *Pardosa* have pointed out that habitats used by conspecifics are stage-
385 dependant (Edgar, 1971; Hallander, 1967, 1970). For example, juveniles of *P. pullata* were shown to
386 hide in grass tussocks, whereas adults stayed at the surface of the meadow vegetation (Hallander,
387 1970). Sub-adults of *P. lugubris* (former name of *P. saltans*) were reported to overwinter until March

388 in shady parts of forest leaf litter, whereas adults explore a broader habitat range (Edgar, 1971). These
389 relationships between habitat preferences across spiders' life stages are likely to be accompanied by
390 shifts in experienced thermal environments and could explain why T_{pref} range and development stage
391 are closely related.

392 **2 – Role of the urban heat island**

393 **2.1 Mean T_{pref} suggests Bogert hypothesis**

394 We found no relationship between the mean T_{pref} values and the thermal environment measured as
395 UHI intensities. This result gives therefore support to the Bogert effect hypothesis which states that
396 adjustments of traits to local climate conditions can be inhibited by thermoregulatory behaviour. *P.*
397 *saltans* relies on behavioural thermoregulation in its usual habitat that displays high thermal
398 heterogeneity during spring and summer. Its thermophilic nature makes it particularly active and
399 abundant in sunny patches such as wood clearings and hedges (Trabalon 2022). Therefore, this
400 thermoregulatory ability could constrain the evolution of T_{pref} mean as long as favourable thermal
401 microenvironments are available in its habitats across the urban landscape.

402 *P. saltans* is active on the leaf-litter during daytime in the growth season. Despite soil surfaces are
403 often considered as relatively homogenous and buffered thermal environments (Lembrechts et al.,
404 2020), they can display higher thermal heterogeneity at small spatial scales. Indeed, local (i.e., spider-
405 scale) thermal heterogeneity may be of primary importance because the UHI gradient studied results
406 in an increase in mean air temperatures of up to 2.5°C (no sampling sites were available in the city
407 centre, where the UHI intensity reaches 3°C). The amplitude of the UHI gradient (0 - 2.5°C) may be too
408 weak to cause adaptation or acclimation leading to a change in behaviour that can be detected in the
409 T_{pref} assay. In contrast, Pincebourde & Salle (2020) measured soil surface temperature over the
410 horizontal ground layer of a temperate forest using thermal cameras and loggers and reported
411 temperature ranges of up to 16°C within less than 1 meter. This small scale heterogeneity results from
412 the interaction between multiple factors, including sun exposure, leaf litter microtopography and
413 shading effects by above-ground vegetative elements (Pincebourde & Salle, 2020). The scale at which
414 this variability is perceptible in forest litter surface matches the scale corresponding to the size of many
415 arthropods, i.e., an area of about 20 cm in length (Pincebourde & Woods, 2020). Therefore, there is
416 plenty of thermal opportunities for *P. saltans* to thermoregulate behaviourally over fine spatial scales
417 on the leaf litter in semi-open areas that are typical in wood patches across urban landscapes. Future
418 studies need to integrate more deeply temperatures at micro-scale that are pertinent for those
419 arthropods at the soil surface, to infer the role of this microclimatic mosaic on the thermoregulation
420 behaviour and ability to escape extremes (Woods et al. 2015). The fact that *P. saltans* has a
421 predominantly diurnal activity may explain its particular ability to take advantage of a thermally
422 heterogeneous diurnal environment to actively thermoregulate. However, the nocturnal nature of air
423 warming in an urban environment challenges the theory that daytime temperatures release
424 evolutionary constraints on T_{pref} . Although active during daytime, *P. saltans* individuals experience
425 the nocturnal temperature increase in a thermal microhabitat that is much more homogeneous than
426 during the day, because sun exposure and associated shading effects disappear. However, apart from
427 a Bogert effect or a low explanatory power of the UHI metric considered, several other factors may
428 explain T_{pref} lack of response to urban warming. Among these, T_{pref} may exhibit a lack of plasticity or
429 heritable variation in *P. saltans* (but see Paranjpe et al., 2013). In addition, urban conditions may rarely
430 allow spiders to experience their preferred temperatures as predator, prey or even humidity
431 distribution may force individuals to thermoconform, as observed by Stork et al. (2021) in a Lycosid
432 spider.

433 2.2 Tpref range suggests hypothesis of local optima adaptation for juveniles only

434 Although results for adults and the Tpref mean suggest the Bogert hypothesis, another scenario is
435 observed for the Tpref range of juveniles. We observed that the Tpref range decreased significantly
436 with increasing UHI intensity, corresponding to the local optima adaptation (Figure 1, left-side, bottom
437 line). This indicates that, while the mean of Tpref remains similar across urban populations, the spiders
438 are more selective relative to temperature (or more precise) under more intense UHI conditions
439 compared to rural areas. This result can be explained by the microclimate conditions that juveniles
440 experience during the winter. As previously mentioned, *P. saltans* individuals overwinter as juveniles
441 in forests' dry-leaves litter. Indeed, in their natural environment, low-mobile juveniles spend most of
442 their lifetime under relatively shady and thermally homogeneous conditions. These
443 microenvironments offer limited opportunities to behaviourally thermoregulate and favour therefore
444 selection pressure on thermoregulation traits. Hence, the overwintering period might be responsible
445 for shifts in Tpref range among rural and urban populations since also winters are marked by UHI
446 events in Rennes (Dubreuil et al., 2020). These winter UHI events could have driven beneficial local
447 acclimation in juveniles' Tpref ranges by imposing novel selective pressure. The observed inter-
448 population variations in Tpref range might disappear as soon as sub-adults moult to reach their final
449 adult stage, and thereby start exploring broader thermal conditions. Endogenous variations in thermal
450 traits are likely to occur in arthropods in which a single stage overwinters, or in which development
451 stages differ in habitat preference and mobility (Marais & Chown, 2008). However, to date only few
452 studies explicitly considered life-stages when testing for intra-specific differences in arthropod's Tpref
453 response across geographic clines (but see MacLean et al. 2019). To infer the factors affecting
454 behavioural thermoregulation under natural conditions, we tested individuals collected in the field,
455 i.e., non-acclimated to controlled temperatures. Experiments combining field and laboratory approach
456 are ideal for conducting behavioural experiments, although multiple factors may still be confounding
457 (Calisi & Bentley, 2009), as the limited part of variation explained in our study (14%) suggests. To
458 further our interpretations, conducting experiments in common gardens and comparing
459 thermoregulatory patterns along a UHI gradient could provide additional information to elucidate how
460 phenotypic plasticity and adaptive changes interact in thermal preference under rapid urban
461 development for different life stages.

462 Conclusion

463 We showed that contrasting thermoregulatory behaviour patterns along an UHI gradient were
464 modulated by the developmental stage in populations of *P. saltans*. We propose the hypothesis of
465 Bogert effect to be relevant for adult individuals and the adaptations of local optima in juveniles. Our
466 proposed conceptual framework further brings evidences that the mean Tpref and the Tpref range can
467 respond differently. Considering both parameters in future studies could help to better predict
468 complex and variable responses of ectotherms' Tpref along geographic clines. If we further brought
469 evidence that urban thermal macro-conditions can trigger changes in thermoregulatory behaviour, our
470 interpretations also suggest microclimates, and particularly their local heterogeneity, to be a major
471 driver of arthropods' thermal preferences. Including fine-scale local temperature data (e.g., from
472 thermal imagery) to compare the implication of the thermal environment for arthropods'
473 thermoregulatory behaviour at multiple scales would therefore be a promising approach.

474 Author contributions

475 BB, HC, HQ, RG, SP and VC conceived and designed the study. ML, VC and VD conducted the field
476 work and analyzed the data. VC wrote the first draft of the manuscript. BB, HC, HQ, JP, RG, SP and VD
477 contributed substantially to revisions.

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 487 the sampling of spiders in green spaces.

488 **Competing interest**

489 We declare no competing financial interest.

490 **Data accessibility**

491 The data set is available at: <https://doi.org/10.48579/PRO/AF5COX>

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Author contributions for “Preferred temperature in the warmth of cities: body size, sex and development stage matter more than urban climate in a ground-dwelling spider”

BB, HC, HQ, RG, SP and VC conceived and designed the study. ML, VC and VD conducted the field work and analyzed the data. VC wrote the first draft of the manuscript. BB, HC, HQ, JP, RG, SP and VD contributed substantially to revisions.

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Highlights

- Preferred temperature (T_{pref}) and related metrics are relevant to assess how ectotherms' behavioural thermoregulation vary along geographical clines.
- Three types of ectotherms' responses are expected: the local optima adaptation hypothesis (co-gradient response), the counter-gradient relationship hypothesis and the Bogert effect (behavioural inertia)
- Cities and their associated urban heat islands (UHI) are promising open-sky laboratories to surrogate climate change impacts on arthropods
- We determined the variation of thermal preference in 557 wolf-spider individuals (*Pardosa saltans*) along an UHI gradient to infer which mechanism is at play
- We show that T_{pref} varies only marginally along an UHI gradient and is mainly modulated by ontogenetic factors such as sex, life stage and body size
- Ontogenetic factors may be more important than the environment in defining the parameters of behavioural thermoregulation and the Bogert effect may prevail in *P. saltans*
- The mean T_{pref} and the T_{pref} range respond differently to the tested factors, suggesting that both T_{pref} parameters should be considered in future studies

Competing interest

We declare no competing financial interest.

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