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RESEARCH ARTICLE

Body size responses to urban temperature variations are driven by life history traits in spiders

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Abstract

1. Urban ecosystems exhibit altered environmental conditions compared to the rural surroundings, including higher temperatures, the so-called urban heat island (UHI) effect. Along urbanisation gradients, temperature variations occur at various scales ranging from the landscape to the microhabitat, with possible consequences on living organisms. As ectothermic animals, arthropods are particularly affected by UHIs because warming may directly induce physiological effects on their metabolism.
2. Body size is a commonly used metric to investigate arthropod responses to thermal stress, but the scale-dependent role of temperature variation as predictor of body size remains unclear. To assess temperature–size relationships across spatial scales and test if a common pattern to several species emerges, we performed morphological measurements on 2283 individuals representing 11 spider species belonging to Hahniidae, Linyphiidae, Lycosidae and Tetragnathidae. Spiders were collected on 36 grasslands distributed along a broad UHI gradient.
3. Intraspecific shifts in body size were related to temperature in the Lycosids *Pardosa prativaga* and *Pardosa pullata* at the landscape and local scales, respectively, whereas no clear effects were observed regarding the other examined species. In both species, sex was an important endogenous factor that modulated individual responses; females were more affected than males by temperature.
4. The contrasting amplitudes of the responses observed among Lycodids and the other species indicate that large, low dispersive and univoltine species are under a stronger influence of temperature than small bivoltine species that can disperse aurally. Our results on spiders highlight that considering species-specific life history traits helps to understand contrasting responses among species, and this may be essential for drawing general patterns of phenotypic changes among arthropods under anthropogenic warming.

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KEYWORDS

Araneae, climate warming, intraspecific trait variation, morphological traits, urban ecology, urban heat island

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1 | INTRODUCTION

In cities, temperature increase not only contributes to global warming but is also exacerbated by it and is commonly referred to as the urban heat island (UHI) phenomenon (Oke et al., 2017). UHIs are characterised by an elevation of mean temperatures in urban centres relative to nearby rural areas and regional average temperatures (Foissard et al., 2019). Assessing changes in body size is a recognised efficient method to investigate adaptations of individuals under environmental thermal stress, notably in UHI contexts (Johnson et al., 2019, 2020). In a recent meta-analysis, Lövei and Magura (2022) summarised body size as having crucial ecological implications from the individual to the ecosystem level. Body size is closely related to several functional and life history traits such as morphology, physiology, survival or fecundity, with consequences on the fitness, ecological niches and spatial distribution of individuals (Wanninger, 2015). In addition, body size influences biotic interactions, and in turn community dynamics, food webs and ecological networks (Lövei & Magura, 2022). Among other organisms, arthropods are critical players in urban ecosystems (Johnson et al., 2019), by providing a wide range of ecosystem services (e.g. pollination, decomposition and predation). As ectotherms, urban arthropods are particularly sensitive to warming because increased temperature has a physiological effect on their metabolism (Angilletta et al., 2007; Brans et al., 2017; Diamond, Chick, Perez, Strickler, & Martin, 2018; Diamond, Chick, Perez, Strickler, & Zhao, 2018; Sato & Takahashi, 2022). Therefore, investigating changes in the body size of arthropods may provide a better understanding of urbanisation-induced stress and instability, including the consequences of UHIs on arthropod species (Merckx, Souffreau, et al., 2018).

Ecological and evolutionary body size responses to temperature have been observed across geographical thermal gradients (latitudinal and altitudinal ones; Ameline et al., 2018; Beckers et al., 2020; Yang et al., 2018) for many arthropods—for example spiders—and more recently across thermal gradients in urban areas (Johnson et al., 2019; Malmos et al., 2021). Thermal variations can be measured at various scales ranging from the broad landscape to the microhabitat along urbanisation gradients (Cabon, Quéno, Dubreuil, et al., 2024). Air temperature 3 m above the surface is commonly recorded to monitor UHIs (Foissard et al., 2019), that is large areas of heat at the landscape scale (Foissard et al., 2019; Oke et al., 2017). Yet, arthropods also experience their thermal microenvironment near to the ground level, where fine-scale temperature variations can be highly heterogeneous due to habitat microstructures (Harvey et al., 2020, 2023; Ma et al., 2021; Pincebourde & Woods, 2020). However, these two scales are rarely considered simultaneously in studies on body size because sensor networks dedicated to the monitoring of temperature at the landscape and local scales are rarely available.

The body size responses of arthropods to thermal gradients also vary according to the life history strategies and ecological characteristics of the species (Fenberg et al., 2016; Forster et al., 2012; Horne et al., 2015; Wilson-Brodie et al., 2017). For instance, the dispersal strategy determines how body size is linked to UHI in several

arthropod groups (Merckx, Souffreau, et al., 2018). Since escaping from adverse conditions within a fragmented environment requires high dispersal capacities, increased mobility should enhance the chances of survival of a focus taxon (Merckx, Kaiser, et al., 2018). Among arthropod groups, positive and negative size-dispersal links can be found and this parameter has been evidenced to play a central role in the way community-averaged body size respond to UHI (Merckx, Souffreau, et al., 2018). Accordingly, taxa showing negative size-dispersal links should become smaller within warm fragmented urban environments. In addition, life history strategies can influence how the environment constrains the development of individuals. For example, the developmental time may determine whether growing larger should be prioritised at the expense of early maturity under harsh thermal conditions (Wilson et al., 2019), or if a converse trade-off occurs. Voltinism is expected to be an important explanatory factor of interspecific patterns of temperature–size relationships (Horne et al., 2015). Terrestrial arthropods with a univoltine life cycle (i.e. one generation *per* year) and long developmental times are expected to respond differently to warming than bivoltine and multivoltine species (i.e. two or more generations *per* year, respectively; Blanckenhorn & Demont, 2004; Opell, 2010). At the intraspecific level, body size changes along temperature clines may also vary seasonally because individuals from distinct generations may grow at different rates and experience contrasting thermal conditions (Wilson et al., 2019). For instance, spiders that emerge early in the season can be larger than those that emerge later (Masumoto, 1994). In addition, the body size response of spiders to temperature has been repeatedly found to be sex biased (Bowden et al., 2013; Høye & Hammel, 2010), possibly due to contrasting activity patterns (Harvey & Dong, 2023).

The present study aims to (1) explore which temperature–size patterns occur in common spider species along urban thermal clines, (2) evaluate the respective roles of temperature (at the landscape and microhabitat scales), the biotic environment and endogenous factors in shaping intraspecific variations in body size and (3) determine if trait syndromes explain interspecific differences in the temperature–size rule followed by different species. To reach these objectives, we conducted morphological measurements on 11 spider species collected along urban temperature gradients. Spiders are a particularly well suited model because communities are highly abundant and diverse in cities (Meineke et al., 2017; Piano et al., 2020; Varet et al., 2014). Moreover, urban populations exhibit diversified behavioural and/or physiological responses to UHIs (Johnson et al., 2019, 2020). According to recent results on Lycosid spiders obtained in natural areas (Ameline et al., 2018), and to the general trend observed in univoltine arthropods, we expected intraspecific relationships to vary according to species-specific trait syndromes. For instance, we expect positive relationships between body size and urban temperature within large, univoltine and low dispersive species. Although knowledge is still scarce regarding spiders from other families, we hypothesized, based on the reported importance of life history traits for temperature–size relationships (Horne et al., 2015), that negative size–temperature relationships will prevail

in small, highly dispersive and multivoltine species (Blanckenhorn & Demont, 2004) such as Linyphiids.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling design

We conducted this study in Rennes (northwestern France, 48°06' N–1°40' W) and its surroundings. Rennes is a city of 227,000 inhabitants under a strong oceanic climate influence. According to a long-term urban climate monitoring programme, Rennes faces regular and strong UHI events (Dubreuil et al., 2020) that provide ideal experimental conditions to investigate if morphological changes occur along a thermal gradient. We chose grasslands as a model ecosystem because they represent a major part of urban green spaces in Rennes (445 ha, 56%; Chollet et al., 2018) and are available from the centre to the outskirts of the city. Furthermore, the diversified management strategies applied across Rennes result in grassland structures ranging from short and dense to high and heterogeneous vegetation. These conditions provide a broad range of microclimatic conditions, a determinant ecological driver of arthropod fauna (Harvey et al., 2020, 2023; Ma et al., 2021; Pincebourde & Woods, 2020). Finally, grasslands support abundant spider communities along a broad UHI gradient in Rennes (Cabon, Quénel, Dubreuil, et al., 2024) ensuring a suitable sampling size to perform morphological comparisons. Our site selection procedure aimed to maintain the confounding effect of urbanisation at a low level, in order to focus on the effects of temperature. To do so, we first performed a spatial correlation procedure allowing for the identification of areas where urbanisation (i.e. the proportion of built-up areas) and UHIs are weakly correlated ($p < 0.05$), as thoroughly described in Cabon, Quénel, Dubreuil, et al. (2024). Then, we identified all grassland patches (dataset ocsge_rm_2017; geo.data.gouv.fr;

accessed on 1 December 2021) overlapping the areas previously identified as 'weakly correlated' and selected 36 accessible sites encompassing a broad gradient of UHI (Figure 1). Three pitfall traps per sampling site were installed and opened 15 days per month from March to September 2022. We used plastic cups (85 mm in diameter and 115 mm in height), filled with 150 mL of saline solution at a concentration of 100 g.L⁻¹ to improve spider preservation and a drop of neutral soap to prevent floating. The three traps were placed 5 m apart and oriented north, southeast and southwest, forming a triangle to ensure capture efficiency (Ward et al., 2001). Each month, spiders were sorted and stored in individual vials containing 70% ethanol. All mature spiders were identified to the species level using identification keys (Roberts, 1985, 1987). Nomenclature followed the World Spider Catalogue version 22 (<https://wsc.nmbe.ch/>; accessed on 1 December 2022). Prior to the start of the fieldwork, sampling authorisations were granted by each city council and land owner concerned. Our study did not require ethical approval.

2.2 | Species selection

We analysed the distribution of the spider species and selected the most abundant species evenly distributed along the UHI gradient. To do so, we sorted the sites according to their UHI intensity in three classes labelled 'high', 'medium' and 'low', using quantiles as cut-off values. Then, we selected the species with at least 20 individuals per UHI class. The selection resulted in six Linyphiid species, three Lycosids, one Tetragnathid and one Hahniid (Table 1). The species' life history traits related to dispersal (i.e. ballooning capacity) and voltinism were retrieved from the literature (Table 1). Species selection resulted therefore to two main trait syndromes: (1) small, highly dispersive, bivoltine species and (2) large, low dispersive, univoltine species. In addition, one species (*Pachygnatha degeeri*) shared characteristics with both groups (Table 1).

FIGURE 1 Map of the study area. The atmospheric urban heat island (UHI; from 1 March to 30 September 2022) is illustrated by a coloured gradient ranging from blue (low intensity; minimum = 0°C) to red (high intensity; maximum = 3°C). Small black dots, temperature sensors at 3 m height used to record the atmospheric UHI. Large coloured dots, sampling sites with near-ground temperature measured at 5 cm height, ranging from blue (low intensity; minimum = 0°C) to red (high intensity; maximum = 5°C). Grey, impervious surfaces.

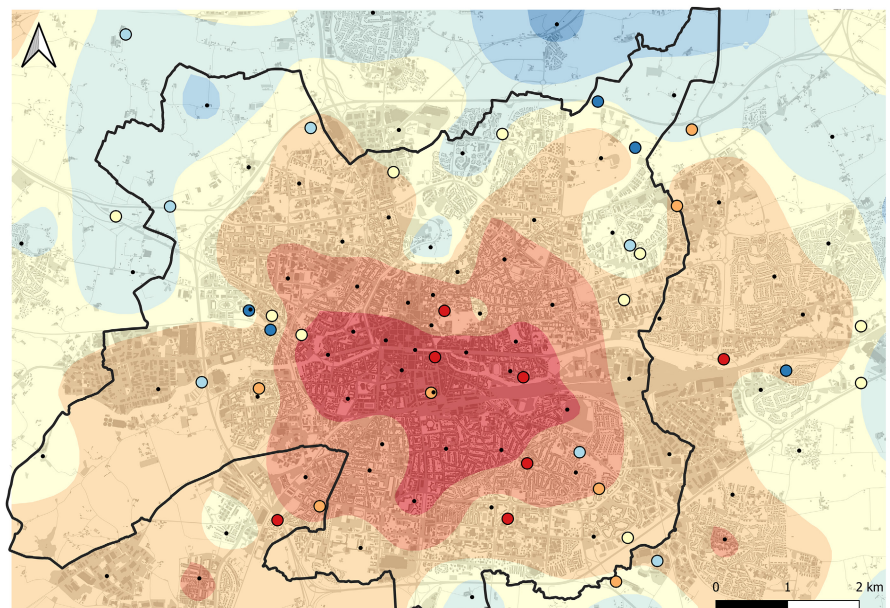


TABLE 1 Summary of the characteristics of the 11 selected species.

Family	Species	Ballooning capacity (Simonneau et al., 2016)	Voltnism (Alderweireldt & De Keer, 1988, 1990, De Keer & Maelfait, 1987a, 1987b, 1988a, 1988b, Duffey, 1956, Hallander, 1970, Hollander, 1971)	Sex	Generation (G) or cohort (C)	Intraspecific competition (total number of individuals trapped per sampling site)
Linyphiidae	<i>Bathypantes gracilis</i>	High	Bivoltine	m / f	G2	19.97 ± 17.92
Linyphiidae	<i>Diplostyla concolor</i>	High	Bivoltine	m/f	G2	14.03 ± 18.42
Linyphiidae	<i>Erigone dentipalpis</i>	High	Bivoltine	m	G2	36.19 ± 57.76
Hahniidae	<i>Hahnina nava</i>	High	Bivoltine	m	G1	16.25 ± 17.87
Linyphiidae	<i>Oedothorax fuscus</i>	High	Bivoltine	m/f	G1/G2	29.94 ± 89.68
Linyphiidae	<i>Oedothorax retusus</i>	High	Bivoltine	m	G2	24.53 ± 87.43
Tetragnathidae	<i>Pachygnatha degeeri</i>	High	Univoltine	m	C1/C2	137.14 ± 120.72
Lycosidae	<i>Pardosa cf. tenuipes</i>	Low	Univoltine	m/f	C1/C2	72.31 ± 110.21
Lycosidae	<i>Pardosa prativaga</i>	Low	Univoltine	m/f	–	8.75 ± 14.72
Lycosidae	<i>Pardosa pullata</i>	Low	Univoltine	m/f	–	18.06 ± 28.73
Linyphiidae	<i>Tenuiphantes tenuis</i>	High	Bivoltine	m/f	G2	33.58 ± 24.74

Note: 'Ballooning capacity' and 'Voltnism' columns, possible interspecific comparisons. 'Sex' and 'Generation/Cohort' columns, possible intraspecific comparisons. The generation of each multivoltine species is indicated by the number following the letter G. The cohort of each univoltine species showing cohort splitting is indicated by the number following the letter C. 'Intraspecific competition' column, mean number (and standard deviation) of co-occurring individuals from a same species at the sampling sites.

2.3 | Morphological measurements

We conducted morphological measurements in the laboratory with a stereomicroscope (Leica M205 C) equipped with a binocular camera (Leica DMC4500). For each individual of each selected species, we took pictures of the prosoma and right leg IV (Cabon et al., 2023; Pétilion et al., 2018) using software LEICA LAS X. The length and width of the prosoma and the length of the leg segments were measured to the nearest 0.01 mm with software ImageJ (Rasband, 2007; Figure 2).

2.4 | Explanatory variables

2.4.1 | Atmospheric UHI

Thanks to a long-term climate observation network established in Rennes in 2004 (Rennes Urban Network; <https://run.letg.cnrs.fr>), the UHI can be accurately measured across space and time (Dubreuil et al., 2020; Foissard et al., 2019). Since 2020, temperatures have been monitored by 30 DAVIS Vantage-Pro-2 automatic weather stations (Davis Instruments Corporation, Hayward, CA 94545, USA) and 93 RisingHF RHF1S001 connected temperature sensors (LoRaWAN Solutions RisingHF, Shenzhen 518057, China) distributed across rural, suburban and city centre areas and collecting data at a standardised 3 m height and at 60 (Vantage-Pro-2) and 15 min (RisingHF) frequencies. We calculated the UHI from the 2022 dataset as the mean difference between the minimum daily temperatures measured by each sensor and the minimum

daily temperatures measured at a rural reference station. The rural reference station is located about 11 km in the north of Rennes (Melesse, 48°12'18.1"N 1°40'52.8"W). It is characterised by agricultural land with hedges and the local climate is considered as not influenced by urbanisation (Foissard et al., 2019). Therefore, the resulting metric corresponds to the number of °C above the temperature measured at the rural reference station located outside the city. Using these differences, we spatialised the UHI by inverse distance weighting interpolation to the entire study area at 100 m resolution. As seasonal variations in UHI are known to occur, we averaged monthly raster maps to generate a single UHI map corresponding to the exact period of the T_{pref} measurements (i.e. March to September 2022). Finally, we extracted the UHI values corresponding to the raster cells on which the 36 sampling sites were located.

2.4.2 | Near-ground temperature

At the microclimate scale, we monitored near-ground temperature 5 cm above the ground using a specific network of temperature loggers composed of 21 Lascar EL-USB-2+ (Lascar Electronics Ltd., Whiteparish, Wiltshire SP5 2SJ, UK) and 15 Tinytag Talk 2 TK-4023 (Gemini Data Loggers Ltd., Chichester, West Sussex PO198UJ, UK). At each sampling site, the logger was placed in the direct vicinity of the north-headed pitfall trap and recorded temperature every 15 min. As for the atmospheric UHI, we calculated the differences between the daily minimum temperatures obtained from the station showing the lowest averaged near-ground temperature

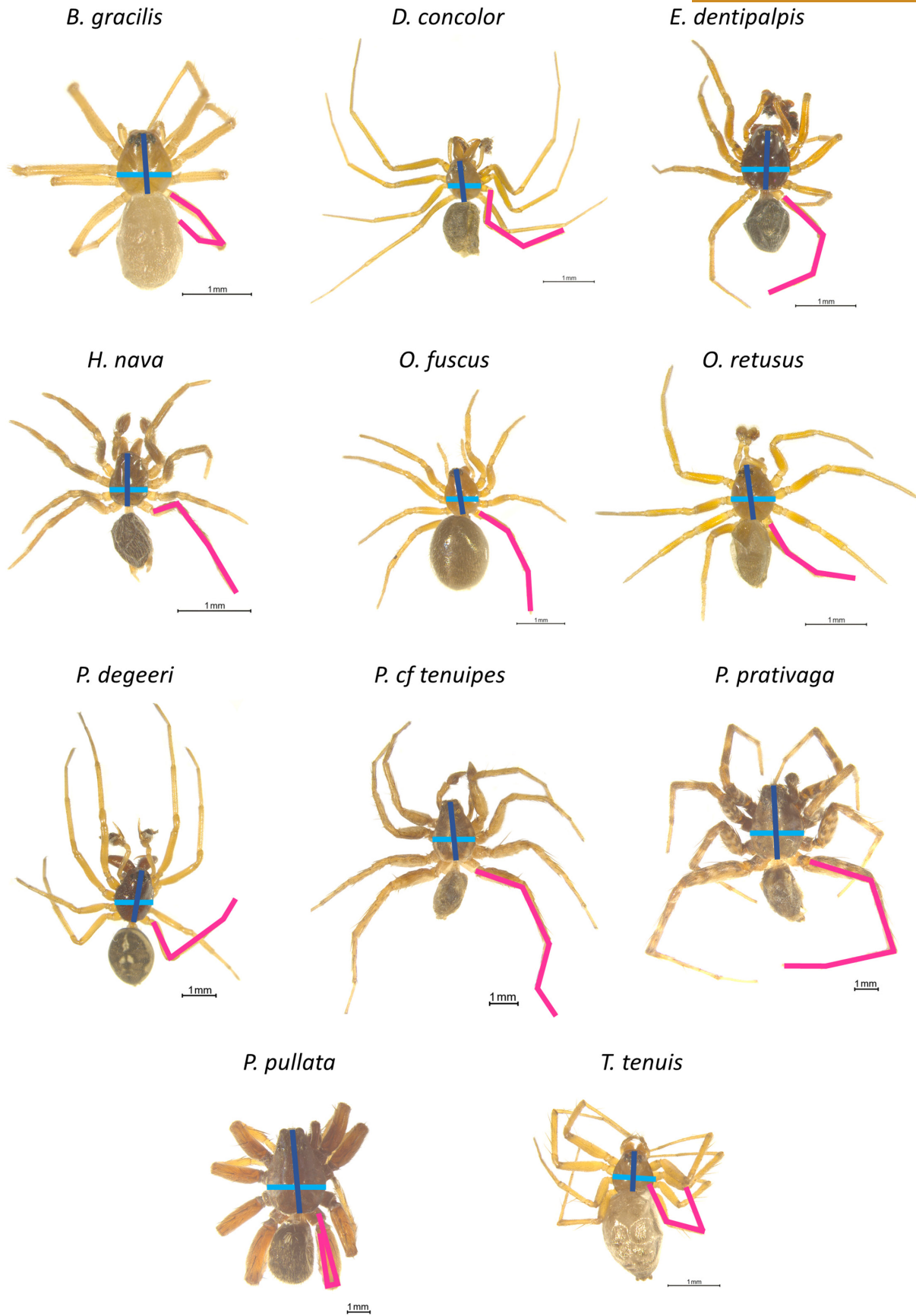


FIGURE 2 Laboratory morphological measurements of the 11 selected spider species. Blue segments, prosoma measurements (light blue, width; dark blue, length). Pink segments, measurements of right legs IV.

(Cesson-Sévigné, 48°06'36.6"N-1°36'29.9"W) and that of each of the other sites. We obtained a single near-ground temperature value by averaging daily differences throughout the study period.

2.4.3 | Intraspecific competition

To account for the possible effects of intraspecific competition and test if local abundance affected body size, we estimated the population density at each sampling site. To do so, we calculated the total number of trapped individuals of a given species *per* sampling site throughout the study period (Beckers et al., 2020).

2.4.4 | Endogenous factors

Considering the sex-biased response of body size to temperature reported in previous studies (Bowden et al., 2013; Høye et al., 2009; Høye & Hammel, 2010), we included male and female individuals whenever both sexes were sufficiently represented. Out of 11 selected species, only males were considered in *Hania nava*, *Erigone dentipalpis* and *Oedothorax retusus* because females were underrepresented. *Pachygnatha degeeri* females were not considered because their internal epigyne did not allow for reliably checking maturity. In addition, we analysed the phenological variations of species abundance to control for possible seasonal changes in body size throughout the year. All individuals from a monthly peak and those from the previous and next months were selected for measurement, except for *Pardosa prativaga*, whose peak was not clear so that we had to select 5 months instead of three to consider enough individuals (Figure S.1). By doing so, we also characterised individuals according to their generation in the case of bivoltine species, or their cohort when univoltine species exhibited cohort splitting (Samu et al., 1998).

2.5 | Data analysis

2.5.1 | Correlations among traits

All statistical analyses were performed in R version 4.2.2 (R Core Team, 2022). We first performed an analysis of correlations among the measured morphological attributes to determine if prosoma width could be considered as a reliable proxy of the body size of each selected species. The prosoma is widely considered as a reliable proxy of spiders' body size because this sclerotised body part is less prone to deformation and damage than their unsclerotised soft abdomen (Beckers et al., 2020). Prosoma width was significantly positively correlated to all other attributes in every species (except to femur length in *O. retusus*; Table S.1). Therefore, we considered prosoma width as an overall proxy of body size and referred to it as body size (Ameline et al., 2018; Beckers et al., 2020; Hein et al., 2019; Høye et al., 2009).

2.5.2 | Effects of environmental and endogenous factors on body size

First, we pooled all individuals *per* species and sex, and removed outliers with median body size values outside the 95% confidence interval to reduce statistical noise in the dataset (Cabon et al., 2023). Then, we assessed the effect of environmental variables and endogenous factors on body size by computing one generalised linear mixed model (GLMM) *per* species for a total 11 models, using the 'lmer' function in 'lme4' package. 'Intraspecific competition', 'near-ground temperature' and 'UHI' were included as fixed effects, and so were 'sex' and/or 'generation' whenever available. 'Sampling site' was added as a random effect to correct for a potential site-specific bias. As the body size response to environmental changes is likely to differ strongly among sexes and generations of spiders (Bowden et al., 2013; Høye et al., 2009; Yang et al., 2018), we added an interaction term between 'sex', 'generation' and every other explanatory variable included as a fixed effect. In the case of *Oedothorax fuscus*, generation G1 was only represented by females, whereas G2 had individuals from both sexes available. Therefore, we split the data related to this species by (1) excluding G1 individuals to include 'sex', but not keeping 'generation' as an explanatory variable in a first sub-model (*O. fuscus* (A), Table 2), and (2) excluding G2 male individuals to include 'generation', but not 'sex' in a second sub-model (*O. fuscus* (B), Table 2). We selected the best models among all possible candidate models using the 'dredge' function and averaged the top-ranking models showing a delta AIC <2, using the 'model.avg' function in 'MuMin' package (Bartoń, 2016). When the final models included interactions involving 'sex' or 'generation', we computed linear models to identify the underlying significant relationships. We tested the significance of the explanatory variables by performing type III ANOVA tests using the 'Anova' function in 'car' package (Fox et al., 2007). Finally, we calculated the coefficients of determination to assess the proportion of variation explained by the selected models, shown in Table 2.

3 | RESULTS

3.1 | Sampling results

The morphological attributes of 2283 adult spiders were measured on the 36 sampling sites, and data from 2174 individuals were kept in the dataset for analysis after removing 109 outliers. The largest species in averaged size were *P. prativaga* (2.19 ± 0.13 mm), *P. pullata* (2.03 ± 0.09 mm) and *P. cf. tenuipes* (1.98 ± 0.28 mm), whereas the smallest ones were *Bathyphantes gracilis* (0.66 ± 0.05 mm) and *Hahnina nava* (0.66 ± 0.05 mm) (Table S.2). The UHI at the sampling sites ranged from 0.8 to 2.9°C, whereas near-ground temperature ranged from 0 to 5.1°C.

TABLE 2 Effects of temperature variables ('UHI' and 'near-ground temperature'), intraspecific concurrence, 'sex' (two levels: female/male) and 'generation' (two levels: G1/G2) and their interactions, on body size estimated by GLMMs.

	UHI	Near-ground temperature	Intraspecific competition	Sex	Generation/cohort	UHI: Sex	Near-ground temperature: Sex	Intraspecific competition: Sex	Generation: Sex	Intraspecific competition: Generation	Conditional R ²	Marginal R ²
<i>Bathypantes gracilis</i>	0.006	0.007	0.004	-0.041 (*)	NA	-0.020 (*)	-0.009	-	NA	NA	0.39	0.35
<i>Diplostyla concolor</i>	0.007	0.005	-	0.031 (**)	NA	-	-	-	NA	NA	0.24	0.15
<i>Erigone dentipalpis</i>	-0.014	-0.007	-0.007	NA	NA	NA	NA	NA	NA	NA	0.15	0.03
<i>Hahnina nava</i>	0.024	-0.01	0.004	NA	NA	NA	NA	NA	NA	NA	0.19	0.08
<i>Oedothorax fuscus</i> (A)	0.006	0.004	0.004	-0.134 (***)	NA	-	-	0.007	NA	NA	0.84	0.84
<i>Oedothorax fuscus</i> (B)	-	-	-	NA	-0.018 (***)	NA	NA	NA	NA	-	0.07	0.07
<i>Oedothorax retusus</i>	-	0.004	-0.006	NA	NA	NA	NA	NA	NA	NA	0.13	0.06
<i>Pachygnatha degeeri</i>	-0.009	-0.004	0.007	NA	-0.026 (***)	NA	NA	NA	NA	-	0.2	0.11
<i>Pardosa cf. tenuipes</i>	-	0.023	-0.035	-0.190 (***)	-0.405 (***)	-	-	0.026	-0.036	-0.018	0.74	0.69
<i>Pardosa prativaga</i>	0.125 (**)	0.01	-0.025	0.116	NA	-0.132 (**)	-	-	NA	NA	0.3	0.27
<i>Pardosa pullata</i>	0.032	-0.017	0.012	-0.030 (*)	NA	-	0.034 (*)	-	NA	NA	0.21	0.09
<i>Tenuiphantes tenuis</i>	-0.009	-0.004	-	-0.074 (***)	NA	-	-	-	NA	NA	0.41	0.39

Note: Estimates are indicated, followed by significance levels between brackets (*0.01 < p < 0.05; **0.001 < p < 0.01; ***p < 0.001). Significant results (p < 0.05) are in bold. Results of averaged models after variable selection. '-', non-selected variables; 'NA', variables not included in the full models.

3.2 | Predictors of body size

3.2.1 | Effect of the thermal environment

Thermal conditions were found related to the body size of specific species (Table 2). The body size of *B. gracilis* and *P. prativaga* was significantly related to the 'UHI:sex' interaction. In accordance with the procedure described in the 'data analysis' section, we computed linear models to identify the underlying significant relationships, since these final models included interactions involving 'sex'. The linear models computed separately on both sexes of *B. gracilis* revealed that neither males ($\alpha = -0.006$; $p > 0.05$), nor females ($\alpha = 0.002$; $p > 0.05$) were significantly related to the UHI. In *P. prativaga*, only females were positively related to the UHI ($\alpha = 0.06$; $p < 0.001$, Figure 3). The body size of *P. pullata* was significantly related to the 'near-ground temperature: sex' interaction, with only females negatively related to near-ground temperature ($\alpha = -0.02$; $p = 0.05$, Figure 3).

3.2.2 | Effect of endogenous factors

'Sex' had a predominant independent effect on body size in all species with individuals from both sexes available, except *P. prativaga* for which 'sex' was only significant in interaction with the UHI (Table 2). The males of all species were smaller than the females, except *Diplostyla concolor*, in which females were smaller (Figure S.2). 'Generation' was another determinant driver of body size in all three

species for which a comparison among generations was possible (i.e. *O. fuscus*, *P. degeeri* and *P. cf. tenuipes*; Table 2), and the second-generation individuals were consistently the smallest (Figure S.2).

4 | DISCUSSION

Urbanisation is hypothesized to induce changes in body size within arthropod populations through the UHI effect (Merckx, Kaiser, et al., 2018; Merckx, Souffreau, et al., 2018). In a previous study conducted in the same area, the community-averaged body size of spiders was found to be reduced in urban areas compared to adjacent rural areas due to the exclusion of individuals from large-bodied species in response to intense UHI conditions (Cabon, Quéno, Dubreuil, et al., 2024). While communities consisting of smaller species are thought to result from increased metabolic rates and associated costs for a given body size (Brown et al., 2004; Scheffers et al., 2016), intraspecific shifts in body size within urban populations match the community-level pattern in flying arthropod species (Merckx, Kaiser, et al., 2018). The present study shows that general conclusions on patterns of temperature-related shifts in body size cannot reliably be drawn for spiders, as already observed in non-urban areas (Ameline et al., 2018; Hein et al., 2019). Indeed, we found body size response to temperature gradients to be mediated by species' trait syndromes, with only large, low dispersive, univoltine species showing response patterns.

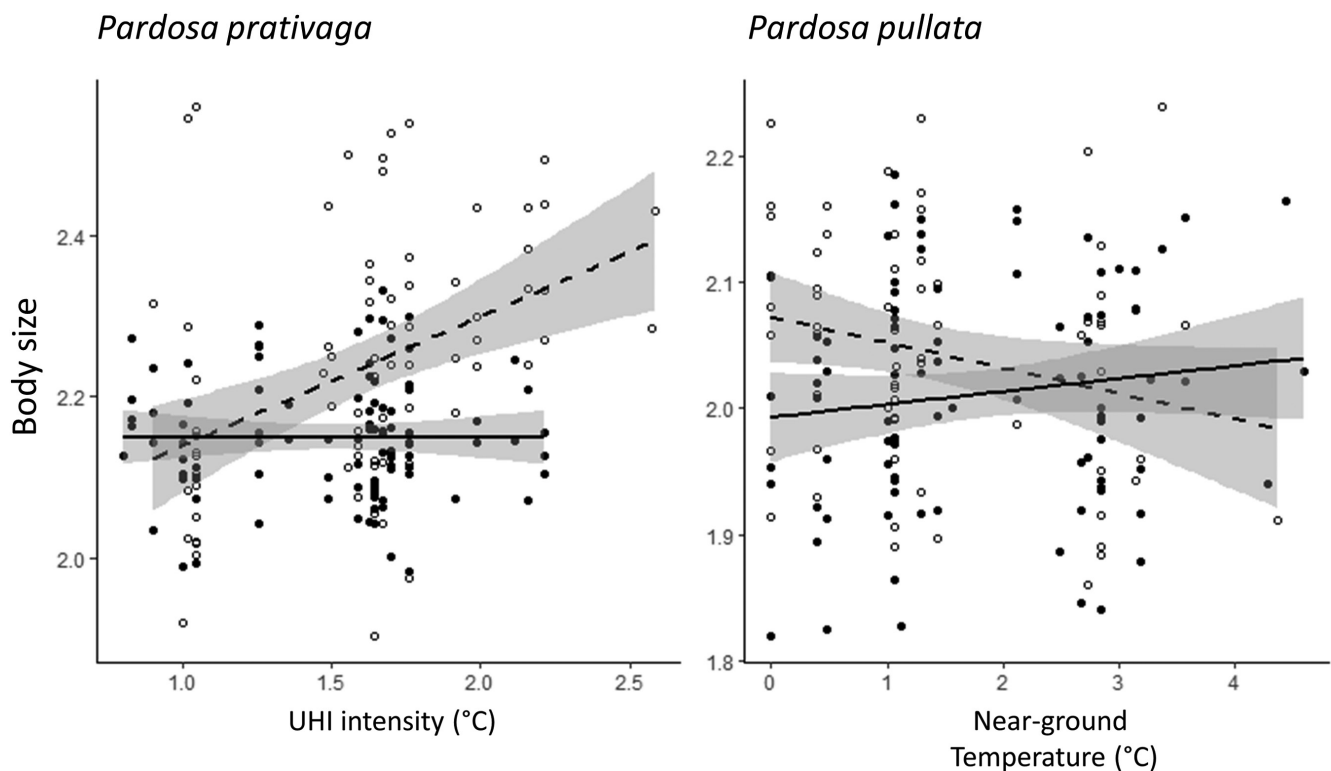


FIGURE 3 Relationships between *Pardosa prativaga* and *Pardosa pullata* body size and temperature variables. Relationships were only significant in females (white dots, dashed regression lines). Black dots, males (solid regression lines).

The thermal response of body size has been repeatedly identified as size dependent (Blanckenhorn & Demont, 2004; Klok & Harrison, 2013). That only the largest species tested here (*P. prativaga* and *P. pullata*) are involved in temperature–size relationships contradicts the general pattern of terrestrial arthropods according to which larger species are less sensitive to warming than smaller ones (Forster et al., 2012; Klok & Harrison, 2013). Among spiders, the general pattern might not be applicable, since size is negatively related to the species' capacity to use large-scale aerial dispersal. Small spider species weighing less than 2.0 mg (i.e. 8 out of the 11 species tested in the present study) can be lifted easily by the wind due to biomechanical constraints, and this mass threshold is not reached by adult linyphiids (Foelix, 2011; Simonneau et al., 2016). Accordingly, Simonneau et al. (2016) noticed that several Linyphiids and Tetragnathid species also tested in our study were dominant ballooners (e.g. *B. gracilis*, *E. dentipalpis*, *O. fuscus*, *O. retusus*, *Tenuiphantes tenuis* and *P. degeeri*). In addition, aerial dispersal almost systematically occurred during 'hot' days (i.e. with a mean daily atmospheric temperature above 19°C) and reduced wind speed conditions (below $\sim 4 \text{ m.s}^{-1}$; Simonneau et al., 2016). These parameters also match the conditions observed during intense UHI events in our study area (Dubreuil et al., 2020). Therefore, small Linyphiid, Tetragnathid and Hahniid species should be able to escape unfavourable thermal habitats caused by UHI events by using large-scale aerial dispersal (Samu et al., 1999). This capacity to escape adverse temperatures might explain why UHI exerts a low selection pressure on the body size of these species, compared to adult Lycosids that can only cover distances of up to 100 m (Morse, 1997, 2002; Richter, 1970). The smallest species investigated here, which were also the bivoltine ones (Table 1), were less constrained by temperature than the univoltine species, as shown in previous studies on arthropods (Horne et al., 2015).

Thanks to a low time pressure during their developmental cycle, univoltine species are expected to exploit their developmental time to grow larger over the season and improve their fecundity (Horne et al., 2015). Therefore, we expected positive size–temperature relationships for univoltine species. We observed this pattern in *P. prativaga*, possibly resulting from enhanced development rates under intense UHI conditions, yet only in females. Sex-biased responses have also been observed along altitudinal clines (Bowden et al., 2013; Høye & Hammel, 2010). These authors found that the males of several wolf spider species remained unchanged in body size in response to elevation, whereas females grew smaller. Our results bring additional support to the rule stating that the body size of female terrestrial arthropods is more plastic than that of males in relation to constraining environments (Stillwell et al., 2010). Intensified UHI conditions in urban areas may extend the growing seasons compared to rural adjacent areas owing to elevated daily minimum temperatures in early spring and late autumn (Dubreuil et al., 2020; Foissard et al., 2019) and a reduced number of frost days *per* year. Consequently, the sex-biased body size response to UHI variations that we report in *P. prativaga* may result from sex-dependent growth strategies (Høye

& Hammel, 2010; Uhl et al., 2004). Urban females may increase their number of moults over the season (Esperk et al., 2007) or increase their growth increments between moults (Blanckenhorn et al., 2007) compared to their rural counterparts. In Lycosids, fecundity is known to be limited by female body size, and larger females produce more and/or larger eggs (Simpson, 1993). Therefore, intensified UHI conditions appear to allow females to become more fecund by growing larger. In males, body size may not be constrained by the environment because no fecundity–size relationship is involved and the growth strategy might consist in becoming mature earlier instead of reaching a larger size (Uhl et al., 2004).

Contrary to our expectations, *P. pullata* females grew smaller with increasing near-ground temperature. In this species, the constraints of large-scale atmospheric temperatures, as estimated by the UHI, were overridden by the microclimatic cline. Variations of the body size response to environmental factors across closely related Lycosid species has been reported (Ameline et al., 2018; Bowden et al., 2013). However, to our knowledge, this is the first time that diverging body size responses to temperature are highlighted to be scale-dependent among Lycosids. This might be due to the contrasting habitat preferences of closely related species. Indeed, although *P. prativaga* is mainly found in buffered microhabitats, *P. pullata* prefers poorly grown herbaceous vegetation with low-growth plants, where temperature at the ground level is directly influenced by solar radiation and wind velocity (Hollander & Lof, 1972). Given that Lycosid spiders are known to locally use locomotion to select a specific temperature range across their thermal microhabitat (Cabon et al., 2023; Humphreys, 1974), the body size of *P. pullata* may primarily be constrained by near-ground temperatures: this species might be a more active and precise thermoregulator than *P. prativaga* due to its complex thermal microenvironment.

5 | CONCLUSIONS

Our results support that interspecific differences in spider life history traits (e.g. spider mobility or voltinism) determine whether intraspecific body size variations are related to urban temperature clines or not, as previously suggested along altitudinal and latitudinal gradients (Beckers et al., 2020; Bowden et al., 2013; Hein et al., 2019). The body size of large and low dispersive univoltine species (Lycosids) was particularly sensitive to temperature changes. For *Pardosa* species, both positive (in *P. prativaga*) and negative (in *P. pullata*) responses occurred, with body size variations associated to temperature measured at the landscape ('UHI') and microhabitat ('near-ground temperature') scales, respectively. In small and highly dispersive bivoltine species (Linyphiids, Hahniids and Tetragnathids), body size variations were mainly associated with endogenous factors ('sex', 'generation/cohort'), but were not constrained by the environment. These results based on a large number of spider individuals belonging to 11 species with contrasting trait syndromes

provide a new understanding on why a general pattern of the relationship between body size and urbanisation-induced warming cannot be drawn. We conclude that predictions on species responses to thermal stress generated by cities should consistently be made with regard to species life history characteristics.

AUTHOR CONTRIBUTIONS

B.B., H.Q. and V.C. conceived and designed the study. V.D. and V.C. conducted the field work. B.D. and L.C. made the laboratory measurements. B.B. and V.C. analysed the data. V.C. wrote the first draft of the manuscript. All authors contributed substantially to revisions and agreed to the published version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the data.InDoRES digital repository: <https://doi.org/10.48579/PRO/UDLVCA> (Cabon, Quénel, Deletre, et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S.1. Distribution of the number of females and males collected of the 11 selected species according to the sampling month.

Table S.1. Results of correlation tests between prosoma width and three other measured morphological attributes.

Table S.2. Summary of the individual parameters of the 11 selected species after excluding outliers, arranged by sex and generation/cohort.

Figure S.2. Differences in body size between male and female individuals as well as differences between body size of individuals from generations/cohorts.

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