



RESEARCH PAPER

Urbanisation reduced body size but potentially improved flight performance in bees and wasps

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ARTICLE INFO

Keywords:

Urbanisation

Wild bees

Wasps

Body size

Wing morphology

ABSTRACT

Urbanisation is a main driver of land-use change, leading to rising in temperatures and fragmentation and reduction of green areas. Bees and wasps, which are important insect groups due to the ecosystem services they provide, may respond to this disturbance via changes in morphological traits which are functionally relevant. To date, studies focusing on this aspect only investigated few social bee species, and often gave contrasting results even at intra-generic level. Here, we studied how body size, wing loading, wing aspect ratio and wing fluctuating asymmetry vary in a social ground-nesting bee (*Halictus scabiosae*), a solitary hole-nesting bee (*Osmia cornuta*) and a social paper wasp (*Polistes dominula*) along an urbanisation gradient within Milan (Italy). By assessing the effects of temperature, green areas fragmentation and vegetation productivity on the above-listed functional traits, we found the three species to variably respond to increasing urbanisation, albeit the driving environmental parameters differed among species. More specifically, smaller individuals were sampled in warmer (for bees) and in less productive (for wasps) areas along the urbanisation gradient. Furthermore, greater wing aspect ratio values were recorded at warmer locations for *H. scabiosae*, lower wing loading was recorded at more fragmented sites for *O. cornuta*, and greater wing loading was recorded at locations with greater productivity for *P. dominula*. *H. scabiosae* and *P. dominula* showed greater wing fluctuating asymmetry at more fragmented sites. Although distinct species seemed sensitive to different driving factors, our results point toward a consistent response: smaller body but potentially improved flight performance in more urbanised environments.

Introduction

Urbanisation drives the replacement of natural cover with cemented surfaces (Kalnay & Cai, 2003). This change in land-use has consequences such as rising in temperatures, reduction and fragmentation of green areas (Cheela et al., 2021). The rise in temperature within cities is called the “Urban Heat Island Effect” (hereafter, UHI effect) and makes cities hotter compared to the neighbouring non-urban areas (Deilami et al., 2018). The UHI effect is mainly due to the impervious (i.e., concrete) surface that acts as heat sink in cities (Cheela et al., 2021). The replacement of natural cover has also consequences on the urban vegetation, mainly producing a reduction of it, e.g. a lowering of the so-called NDVI (Normalised Different Vegetation Index, a measure of health and density of vegetation) (Moreno et al., 2020). In addition, roads and other infrastructures reduce the connectivity between different urban green patches leading to a fragmentation of green areas,

e.g. increasing the edge density of green areas (Li et al., 2019).

Lately, insects have been studied in urban settings due to the ecosystem services they provide (e.g., Wagner et al., 2021). Among insects, bees (Hymenoptera: Apoidea) are widely investigated in cities from a community ecology point of view (e.g., Biella et al., 2022; Ferrari & Polidori, 2022; Geppert et al., 2022) since they are the major pollinators (Lowenstein et al., 2015). To a lesser extent, also communities of predatory wasps (Hymenoptera: Vespoidea) are studied in cities due to their abundance and ecosystem services provided (e.g. pest control) (Barbosa et al., 2020; Brock et al., 2021; Corcos et al., 2019). However, urbanisation can affect insects at the intraspecific level, involving morphological traits that influence insects’ fitness (i.e., functional traits, Aguirre-Gutiérrez et al., 2016; Violle et al., 2007). Nonetheless, only recently the scientific community has started to focus on how urbanisation affects insects at individual level. The variation in functional traits may be described as phenotypic plasticity (Baldwin, 1896;

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<https://doi.org/10.1016/j.baae.2023.11.010>

Received 21 June 2023; Accepted 30 November 2023

Available online 2 December 2023

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Whitman & Agrawl, 2009). Alternatively, these changes can be the result of genetic adaptations of insects to urban environments (Diamond et al., 2022). Both cases lead to intraspecific trait variation that only recently has been acknowledged for its ecological importance (Des Roches et al., 2018). In fact, functional traits are important to determine the organisms' potential adaptation to urbanisation and to shape their biotic interactions, possibly driving changes in the ecosystem services provided (Fontana et al., 2021).

Despite the ecological importance of intraspecific variation, previous studies focused essentially on body size (Buchholz & Egerer, 2020). Temperature is known to affect body size in animals, often leading to smaller individuals in hotter areas (Bergmann's rule, Bergmann (1847)). The UHI effect was shown to elicit a reduction in body size in few bee species (e.g., Tommasi et al., 2022). This is seen as an adaptation to reduce the risk of overheating (Gérard et al., 2020), although it may have negative consequences for the bee since body size is positively correlated with several fitness-related traits (e.g., Araújo et al., 2004; Benjamin et al., 2014). Conversely, no studies tested the UHI effect on wasp body size but higher temperatures due to climate change were shown to elicit a reduction in body size in a *Dolichovespula* species across the last century (Polidori et al., 2020).

Intraspecific trait variations across environmental gradients may also occur in wings. Environmental changes can affect their morphometric properties (Hayes et al., 2019; Hoffmann et al., 2005) potentially altering flight performances (Gilchrist & Huey, 2004). For example, a reduced wing loading was found in bees inhabiting colder environments (Lozier et al., 2021). Lower wing loading minimizes the energetic costs of flight and improves flight manoeuvrability and take-off with a load (Dudley, 2000; Polidori et al., 2013). More elongated wings (greater aspect ratio) are also typically associated with better flight manoeuvrability (Ellington, 1984) and increase dispersal abilities (Hughes et al.,

2007). Despite their importance, wing loading and wing aspect ratio have not been investigated yet along urbanisation gradients.

Environmental gradients can also affect the bilateral symmetry of wings (Møller & Swaddle, 1997). Deviations from bilateral asymmetry can occur through directional asymmetry (DA) when one side is larger than the other within a population, or fluctuating asymmetry (FA) when random deviations from perfect symmetry are present (Van Valen, 1962). While DA may be explained by genetic factors (Graham et al., 1993), FA is commonly considered to reflect developmental instability and it is used as an indicator of environmental stress. Analysis of fluctuating asymmetry along urbanisation gradients have yielded contrasting results both in bees and wasps (e.g., Polidori et al., 2018; Tommasi et al., 2022).

Here, we present the first study that investigates urbanisation effects on different intraspecific traits in two wild bee and one wasp species. We focused on how urbanisation, estimated through temperature, edge density of green areas and NDVI, affects body size, wing loading, wing aspect ratio and wing asymmetry. Based on the above considerations, we predicted that more heavily urbanised areas (i.e. hotter, more fragmented and with lower vegetation productivity) should filter for small-bodied individuals. We also hypothesized that the urban matrix increases fluctuating asymmetry because of more stressful conditions (e.g., higher temperatures) during larval development, and that fragmentation of green areas and lower NDVI may reduce wing loading and enhance aspect ratio to improve flight performance.

Materials and methods

Study city and landscape characterization

The study area is the metropolitan city of Milan (45°28'01" N;

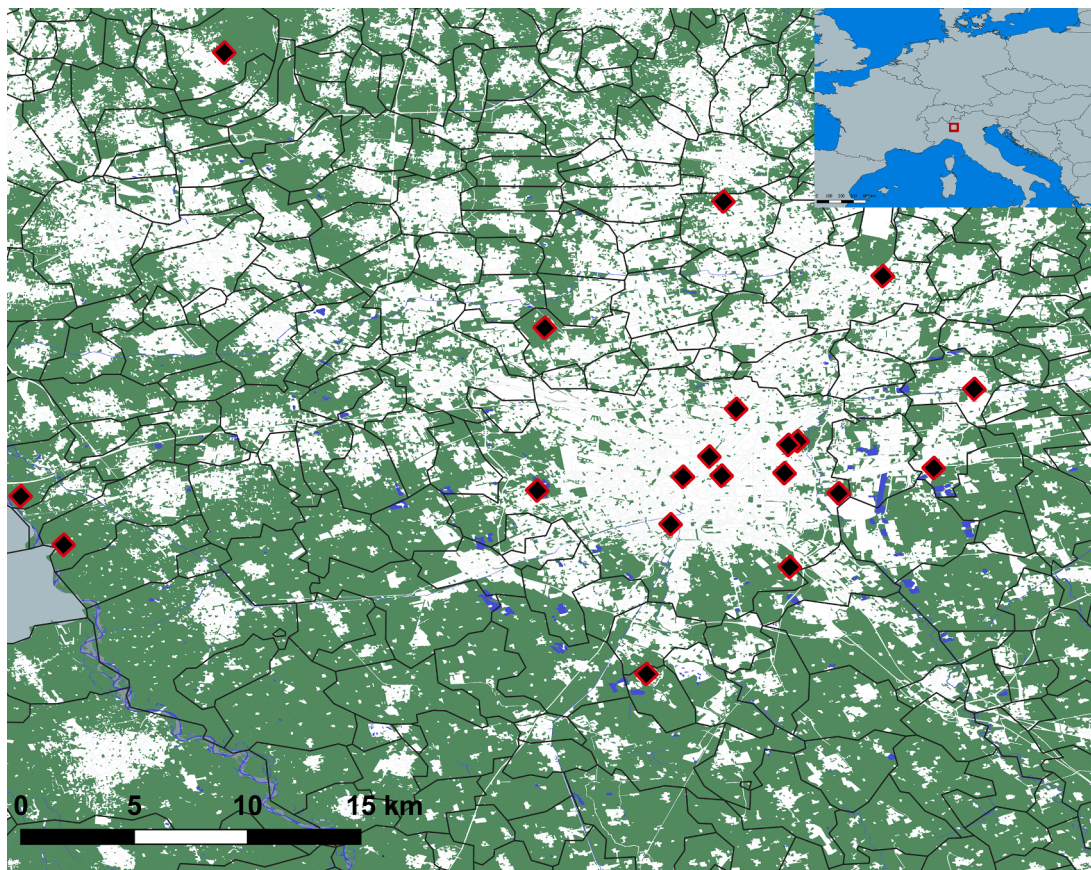


Fig. 1. Diamonds represent the sampling sites (in the metropolitan city of Milan). Top-right panel shows the location of the study area (Italy, Lombardy). White: impervious surfaces, green: vegetated surfaces, blue: water, black: cities' borders.

9°11'24" E) and the nearest semi-natural outskirts situated in Lombardy, northern Italy (Fig. 1). We selected a total of 21 sites (Appendix C: Table S1) along an urbanisation gradient, with at least 1 km between each other to as this would be a reasonable foraging distance of the studied species (Greenleaf et al., 2007). We visually scanned through the map and the site selection was based on a widely used proxy of urbanisation: the amount of impervious surface. We selected these sites to maximise the distance between each other, thus reducing as much as possible the probability of autocorrelation.

Land-use data were obtained from DUSAF6.0 (<https://www.dati.lombardia.it/Territorio/Dusaf-6-0-Uso-del-suolo-2018/7rae-fng6>) that exploits aerial photogrammetry. DUSAF contains a 1:10,000 scale land-use map of the entire region Lombardy with a resolution of 20 m (in form of .shp file). The shapefile in DUSAF6.0 was imported in QGIS v3.16.15 (QGIS.org, 2022. QGIS Geographic Information System. QGIS Association. <http://www.qgis.org>) and buffers with a radius of 500 m centred on the geographical coordinates of each sampling site were created. From this circular cut-out, we extracted the landscapes metrics. This radius has been widely used before (e.g., Glaum et al., 2017; Greenleaf et al., 2007; Grüter & Hayes, 2022). These buffers were never overlapping, so that the environmental variables were never shared among sites. From DUSAF6.0 we extracted the proportion of green and impervious surfaces (see Appendix B) for each site, and calculated the Edge Density of green areas as the ratio between the total perimeter and surface of green patches. This metric quantifies the degree of fragmentation of green areas, i.e., higher edge density values indicate more fragmented green areas (e.g., Theodorou et al., 2020).

Land surface temperature was estimated using the product MOD11A2 (<https://modis.gsfc.nasa.gov/data/dataproduct/mod11.php>) downscaled from the original resolution of 1 km to a finer resolution of 100 m through bilinear interpolation. Mean land surface temperatures were calculated for each sampling site within a 500 m radius buffer (as in Tommasi et al., 2022). NDVI was retrieved through the product MOD13A1-061 (<https://modis.gsfc.nasa.gov/data/dataproduct/mod13.php>), which provides NDVI values recorded every 16 days within a 500 m radius. NDVI is a vegetation productivity index and describes the amount of plant biomass in a place. The higher its value, the higher the primary productivity of the green area is. Mean temperature has been widely proved to be a key factor affecting the size of bees and wasps and previously used in urban bee studies (e.g., Polidori et al., 2020; Tommasi et al., 2022). NDVI has been recently used in a study on urban wild bees (Casanelles-Abella et al., 2022) and it was shown to be a driver of arthropod diversity in cities (Turrini & Knop, 2015). How green-/impervious, edge density, temperature and NDVI correlate with each other along the urbanisation gradient is presented in Appendix C: Fig. S1.

Study species and sampling methods

Insects (all females and only workers for social species) were hand-netted, placed in 1.5 mL plastic vials and stored in cool-bags in the field. All the specimens were then stored in the lab at −20 °C for the morphological analyses. We chose three abundant hymenopteran species across urban landscapes, which present different ecological traits. The first is *Osmia cornuta* (Latreille, 1805) (Megachilidae), a solitary bee that nests in pre-existing cavities. It is polylectic, and in temperate areas females flight period lasts from March to April (Bosch, 1994). After egg hatching, the larval development lasts until around late August, when the pupa metamorphoses into a dormant adult that overwinters until the next spring (Bosch et al., 2008). Conversely, *Halictus scabiosae* (Rossi, 1790) (Halictidae) is a social, ground-nesting and polylectic species (Ulrich et al., 2009). In this species, only queens overwinter and start nesting activity in April. After nest foundation, two cohorts of workers are produced: the first in May and the second in June-July (Brand & Chapuisat, 2012). Finally, *Polistes dominula* (Christ, 1791) (Vespidae) is a social paper wasp that builds nests from chewed wood fibres

(Bagriacik, 2012). This species is a generalist predator, hunting different orders of insects (Nonacs & Reeve, 1993). Mated queens overwinter and start the nest in April while between May and June, a first brood of workers is produced. Then, later in summer new gynes and males are produced, the colony starts to wear off and new mated queens start to hibernate (Dapporto et al., 2010).

Overall, 193 individuals of *O. cornuta* from 9 sites, 132 individuals of *H. scabiosae* from 13 sites and 104 individuals of *P. dominula* from 11 sites were sampled during the study.

Morphological traits

We measured fresh body weight (BW) and intertegular distance (ITD) as a proxy for body size (Cane, 1987), and calculated wing loading (WL) and wing aspect ratio (AR). Except for body size, six individuals (three *H. scabiosae* and three *O. cornuta*) were excluded from the morphological analyses of wings due to the wings being severely damaged. See Appendix B for further methodological details.

First, we weighed each specimen two times with a digital scale (accuracy 0.001 g) and took the mean of the two measures. ITD was measured as the minimum linear distance between the tegulae under a LEICA MZ75 stereomicroscope mounted with a LEICA flexacam C3 camera (accuracy 0.001 mm); each sample was measured three times and we then took the mean of these measures. We calculated wing loading and wing aspect ratio as follows: $WL = BW / \text{Wing Area}$ (Lozier et al., 2021) and $AR = 4 \text{ Wing Length}^2 / \text{Wing Area}$ (Ellington, 1984).

We evaluated the asymmetry of both fore wings and hind wings with a traditional morphometric approach (hereafter, FAT) and, only for fore wings, a geometric morphometric approach (hereafter, FAG). For FAG, we followed the method presented in Section 4 of Benítez et al. (2020) that was recently used in other similar studies (e.g., Hernandez et al., 2022; Orrego et al., 2022). To do so, we firstly selected 11 landmarks on the fore wing and 5 on the hind wing (Banaszak-Cibicka et al., 2018). To standardize the process, the landmarks were selected to be all homologous for the three studied species (Fig. 2). In addition, we selected these landmarks in the basal part of the wing to avoid biases due to the degradation of the margin of the wings. For the traditional morphometric approach, we selected 7 linear traits (F) on the fore wing and 3 (H) on the hind wing as distances between certain pairs of landmarks (EMS3, Table S3, similarly to Banaszak-Cibicka et al., 2018). We used the same 11 landmarks on fore wings to evaluate the fluctuating asymmetry in terms of shape (FAG).

Statistical analysis

First, we conducted a series of statistical checks to verify the goodness of the measure taken as explained in Appendix B (see also Appendix C: Tables S4 to S11, Fig. S1 to S3). For FAT, analyses were carried out at the population level (i.e., sampling site). We calculated the mean FAT (absolute difference R-L) for each site for the traits considered. The correlation between the mean value of FAT and the three environmental variables selected (T, ED, and NDVI) was then tested using the Spearman index. For a better statistical robustness, we only tested traits with FAT present in >10 sites for *H. scabiosae* and *P. dominula* and 9 for *O. cornuta* (since the latter species was only sampled in 9 sites).

The analysis of morphological functional traits (BW, ITD, WL, and AR) and FAG was done using simple or Generalized Linear Mixed Models (LMM or GLMM) after checking for normality of the tested parameters (Appendix C: Fig. S3). For those that highly deviated from normality, either we transformed the variable (square of ITD for *O. cornuta*), or we assigned a Gamma distribution from the Cullen-Frey graphs (Appendix C: Fig. S4, Delignette-Muller & Dutang, 2015). Before analysis, the three chosen environmental variables were scaled (Schielzeth, 2010). For each tested parameter, we built seven different models (similarly to Bishop et al., 2016) testing the three chosen variables singularly and every combination of them plus the null model as control (i.e.,

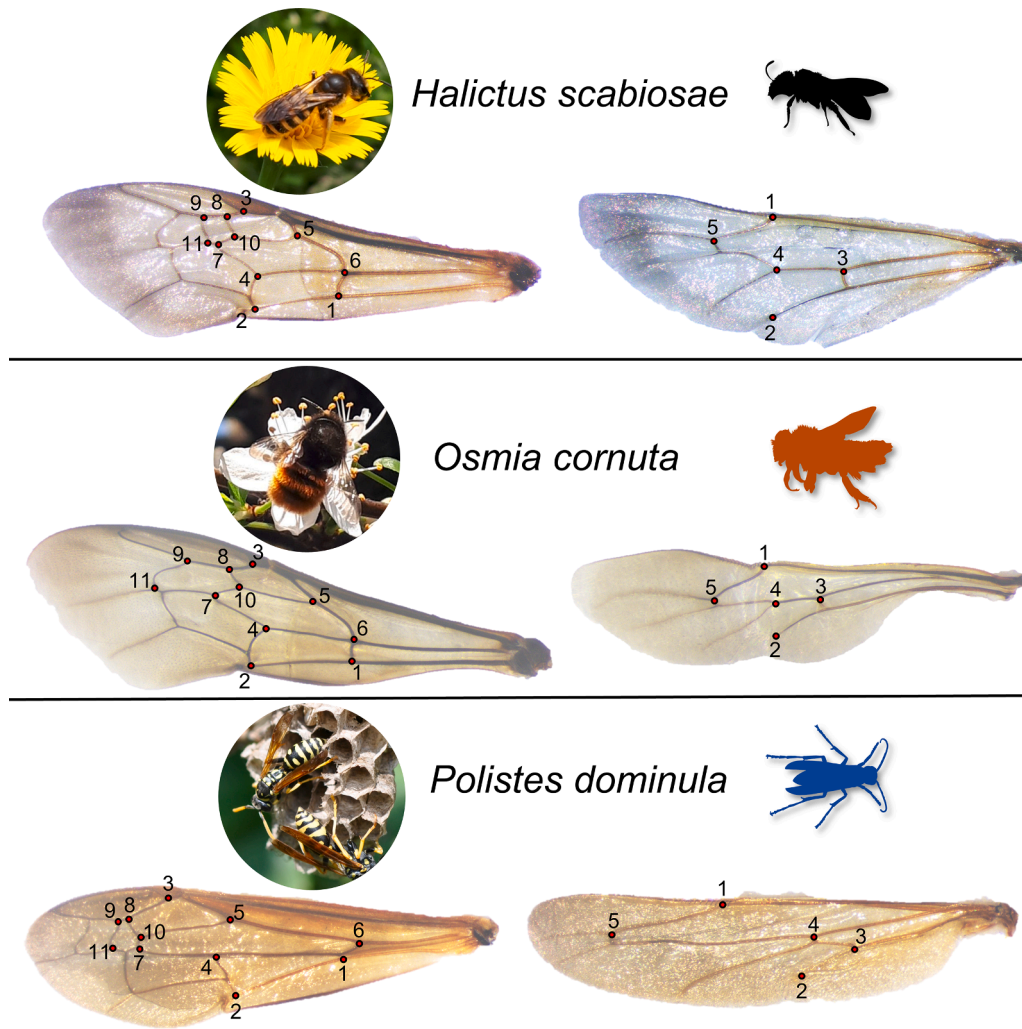


Fig. 2. Position on the fore and hind wings of the landmarks used for the assessment of fluctuating asymmetry.

dependent variables tested against the random effect; Appendix C: Table S12, Felderhoff et al., 2023). In each model, the sampling site was added as random effect to account for local site effects (Lozier et al., 2021). For *O. cornuta* and *P. dominula* we added the number of nicks in the AR model since the number of nicks significantly correlated with this latter variable (Appendix C: Table S2). An information theoretic approach was used to choose the best model for each tested parameter. We predict the best model to be the one to minimize the bias-corrected Akaike information criterion (AIC_c) while maximising marginal (due to fixed effects only) and conditional (due to fixed effects and random effects) R^2 (Barton, 2009; Nakagawa & Schielzeth, 2013). For each final model, with the function “*check_model()*” from the package *performance* (Lüdtke et al., 2021), we visually checked the assumptions of residual normality (Cheng et al., 2010), homoscedasticity (Schielzeth et al., 2020), normality of random effects and multicollinearity with VIFs all below 3 (variance inflation factors) (Felderhoff et al., 2023).

All the analyses were carried out in R 4.2.2 (R Core Team, 2021). Along with the core functions, we used the following packages: *ggplot2* (Wickham, 2016) and *ggcorrplot* (Kassambara, 2019) for graphics; *lme4* (Bates et al., 2015) and *sjPlot* (Lüdtke, 2020) for mixed models; *car* for VIFs (Fox et al., 2012) and *fitdistrplus* for checking distributions (Delignette-Muller & Dutang, 2015). In the following text, average values are expressed \pm Standard Error.

Results

Overall, we found the three species to variably respond to increasing urbanisation, albeit the driving environmental parameters differed among species.

Intertegular distance in *H. scabiosae* ranged from 2.219 to 3.418 mm (2.899 ± 0.022 on average), while body mass ranged from 0.035 to 0.107 g (0.070 ± 0.001 on average). Smaller individuals were sampled at warmer sites, in terms of both measures (Table 1, Fig. 3A-B). We found wing aspect ratio (5.242 – 7.000, 5.838 ± 0.028 on average) to increase (Table 1, Fig. 3C) with increasing temperature across sites, while wing loading (0.0008 – 0.0015, 0.0011 ± 0.0001 on average) was unaffected by these variables (Table 1). We found higher shape asymmetry (FAg) (0.015– 0.042, 0.027 ± 0.0005 on average) at sites with greater edge density (Table 1, Fig. 3D). We also found one trait of FA (F1) to increase with increasing NDVI (EMS3, Table S13, Fig. S5A).

Intertegular distance in *O. cornuta* ranged from 3.216 to 5.243 mm (4.180 ± 0.023 on average), while body mass ranged from 0.066 to 0.179 g (0.125 ± 0.002 on average). Intertegular distance (Table 1, Fig. 3E), but not body mass, was reduced at warmer sites. Wing loading (0.0016 – 0.0027, 0.0021 ± 0.00001 on average) was also lower at warmer sites (Table 1, Fig. 3F). Aspect ratio (6.052 – 8.106, 7.147 ± 0.026 on average) was higher at more fragmented sites, albeit this trend was only marginally significant (Table 1). Finally, FAg (0.014 – 0.046, 0.026 ± 0.0004 on average) did not vary significantly with the environmental predictors (Table 1). However, smaller individuals presented

Table 1

Best fitting (G)LMM of the five functional traits analysed: ITD: intertegular distance (mm), BW: body weight (g), WL: wing loading (g/mm²), AR: aspect ratio, and FA: fluctuating asymmetry. The environmental predictors are: Temperature (°C), NDVI: Normalized Difference Vegetation Index, ED: edge density. *d.f.*: degrees of freedom, *N*: number of samples, *R*_M²: amount of variation explained by the fixed effects, *P*: p-value. Significant results are in bold.

Species	Trait	Distribution	<i>d.f.</i>	<i>N</i>	<i>R</i> _M ²	Predictor-	<i>t</i>	<i>P</i>
<i>H. scabiosae</i>	ITD	Normal	124	129	0.063	Temperature	−2.058	0.042
						NDVI	−0.245	0.807
	BW	Normal	124	129	0.104	Temperature	−2.803	0.006
						NDVI	−1.078	0.283
	WL	Normal	124	129	0.062	Temperature	−1.930	0.056
<i>O. cornuta</i>						NDVI	−1.420	0.158
	AR	Gamma	125	129	0.006	Temperature	−2.425	0.016
	FA Score	Normal	122	126	0.089	ED	3.487	0.001
	ITD ²	Normal	189	193	0.065	Temperature	−2.203	0.029
	BW	Normal	188	193	0.052	Temperature	−1.428	0.155
						NDVI	0.740	0.460
	WL	Normal	185	190	0.075	ED	−2.728	0.007
	AR	Normal	184	190	0.110	ED	1.721	0.087
						Nicks	−3.034	0.003
	FA Score	Gamma	182	189	0.409	Temperature	−1.072	0.285
<i>P. dominula</i>						NDVI	1.009	0.314
						ED	1.046	0.297
	ITD	Normal	100	104	0.032	NDVI	1.039	0.301
	BW	Normal	99	104	0.221	NDVI	3.294	0.001
						ED	1.979	0.051
	WL	Normal	99	104	0.183	Temperature	−1.297	0.198
						NDVI	2.816	0.006
						Nicks	−0.613	0.541
	AR	Normal	100	104	0.022	Temperature	1.519	0.132
	FA Score	Normal	99	104	0.140	Temperature	−0.743	0.419
						ED	3.236	0.002

higher values of shape asymmetry (Table S5). In this species, we found some correlations between FA and either NDVI or temperature (Appendix C: Table S13, Fig. S5B-F).

Intertegular distance in *P. dominula* ranged from 2.604 to 3.575 mm (3.171 ± 0.018 on average), while body mass ranged from 0.054 to 0.146 g (0.1096 ± 0.002 on average). We sampled larger individuals at sites with greater NDVI in terms of body weight (Table 1, Fig. 3G) but not intertegular distance. Wing loading ($0.0008 - 0.0014$, 0.0010 ± 0.00001 on average) was greater at sites with greater NDVI (Table 1, Fig. 3H). In this species, we did not find any variation in aspect ratio ($6.221 - 7.701$, 96.975 ± 0.025 on average) (Table 1). We found higher shape asymmetry (FAg) ($0.010 - 0.025$, 0.017 ± 0.0003 on average) in more fragmented sites (Table 1, Fig. 3I). Also in this species we found some correlations between FA and the three environmental variables used (EMS3, Table S13, Fig. S5G-J).

Discussion

In this study, we focused on relevant traits of three hymenopteran species with contrasting biology that are associated with dispersal abilities and thermoregulatory capacities (body size, Gathmann & Tscharntke, 2002; May, 1979), flight performance (wing loading and aspect ratio, Dudley, 2000) or that are possible indicators of larval development stress (fluctuating asymmetry, Graham et al., 2010). Overall, we found strong intraspecific trait variability along gradients of temperature, green areas' fragmentation and productivity, all representative of the urbanisation degree. Such environmental factors were found to be the drivers of morphological variations often in a species- and trait-dependent way. This highlights how, beside community-level analysis, more attention should be paid to intraspecific trait variability.

We found smaller individuals of *H. scabiosae* and *O. cornuta* in hotter sites, while for *P. dominula* we found a reduction in body size in sites with lower vegetation productivity. Body size reduction in urban landscapes due to UHI effect was already reported in bees (e.g., Garlin et al., 2022, Tommasi et al., 2022). For example, different *Bombus* species coping with higher temperatures due to the UHI effect have shown a reduced body size (Theodorou et al., 2021), though not in all studies and

species (Tommasi et al., 2022). Thus, our results confirm this hypothesis also for other bees. Bees, as ectothermic insects, heavily rely on external temperatures (Deutsch et al., 2008). Specifically, higher temperatures, associated with the UHI effect, may have accelerated the larval development of the bees, resulting in the emergence of smaller individuals (Howe, 1967). Nonetheless, this body size reduction could also be an adaptation to hotter urban landscapes. In fact, accordingly to Bergmann's rule, smaller individuals show a higher surface area-to-volume ratio which facilitates heat loss (Peat et al., 2005), and thus smaller bees may be subject to reduced overheating risk in urban heat islands. This is even more important since bees modulate their activities according to ambient temperature (de Farias-Silva & Freitas, 2021).

We also found smaller *P. dominula* in more urbanised sites, but vegetation properties rather than temperature emerged as driver of the variation observed. *P. dominula* can build nests hanging from shaded artificial structures (Pérez-Bote & Mora-Rubio, 2020) and exhibit thermoregulatory social behaviours (Jones & Oldroyd, 2006) such as fanning or cooling the nest with water drops (Stabentheiner et al., 2022). Together, these behaviours may result in a better shielding from high urban temperatures, explaining at last partially why temperature did not affect body size of this species in our analysis. Instead, the body size of *P. dominula* is positively influenced by increasing NDVI (associated with less urbanised sites). A lush and more cohesive vegetation can correlate with greater arthropod diversity in cities (Turrini & Knop, 2015). The increase in size could therefore be due to a greater availability of trophic resources (prey for larvae), since in predatory wasps the quality of the prey is important during offspring development (Judd & Fasnacht, 2017).

Altogether, our results on body size point towards a size reduction in all three species in more urbanised landscapes. This can have in turn impacts on the fitness of these species. Bees and wasps are central-place foraging insects (Field, 2005), and their foraging efficiency is directly affected by body size since bigger individuals can fly further, load more pollen (Goulson et al., 2002), or hunt and carry bigger prey (Polidori et al., 2005, 2013). However, smaller individuals require less resources, and this can be an advantage in urban environments, where there may be a reduction in flower resources for bees (Matteson et al., 2013) or

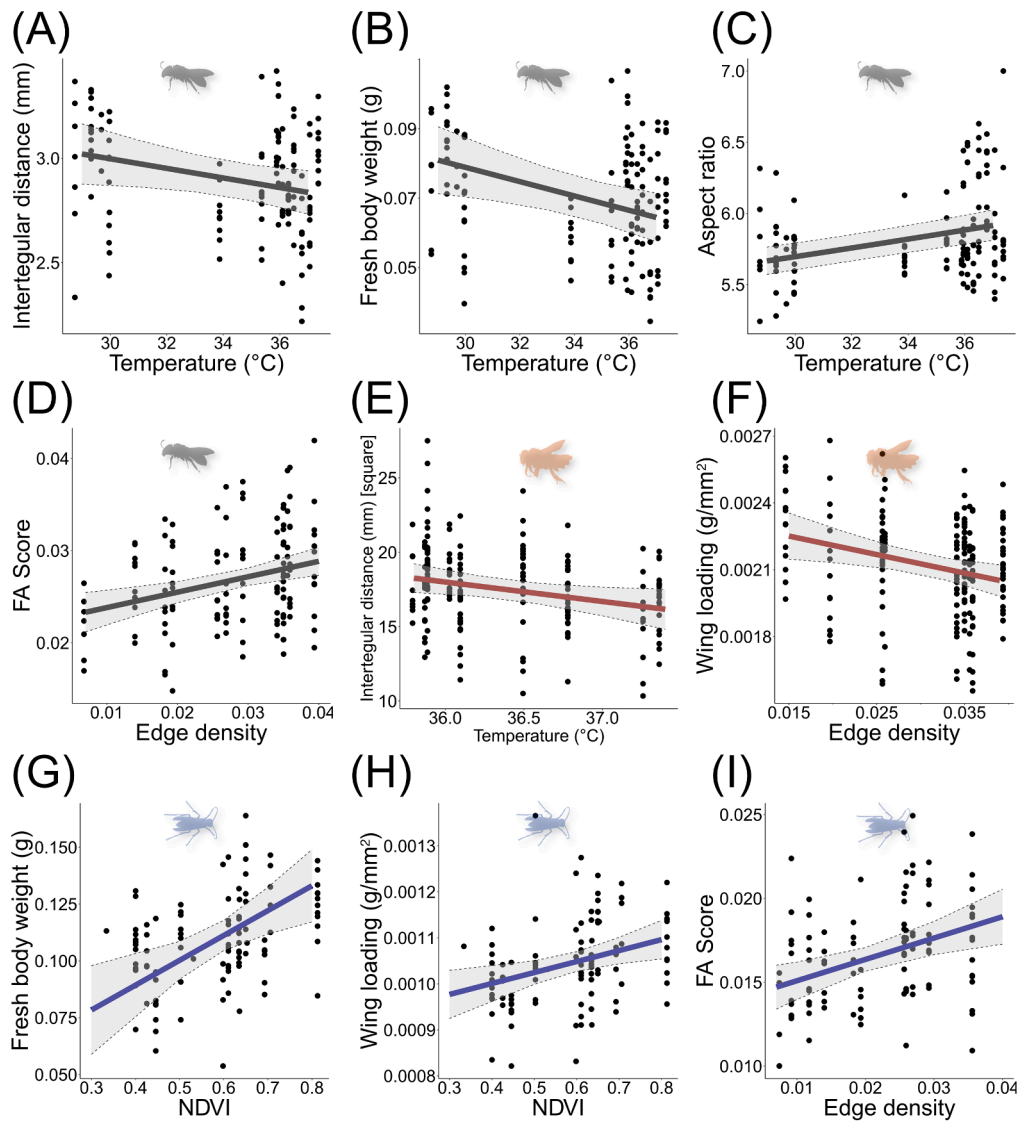


Fig. 3. Scatterplots showing the effect of temperature on intertegular distance (A), fresh body weight (B), aspect ratio (C), and the effect of edge density on FA Score (D) in *H. scabiosae*. The effect of temperature on intertegular distance (E) and on wing loading (F) in *O. cornuta*. Finally, the effect of NDVI on fresh body weight (G) and wing loading (H), and the effect of edge density on FA Score (I) in *P. dominula*. Dots represent the actual values measured; the line is the representation of the Linear Mixed Model used, along with 95 % confidence intervals in light grey.

prey for wasps (Turrini & Knop, 2015).

We also analysed variation in flight-related traits such as wing loading and wing aspect ratio. Again for *H. scabiosae*, temperature emerged as the key driver, while for *O. cornuta* this was not the case. For *H. scabiosae* we found higher aspect ratio (longer, tapered wings) in hotter sites. This is in contrast with some previous studies. For example, wing aspect ratio decreases with increasing temperature in *Drosophila melanogaster* (Diptera: Drosophilidae) (Azevedo et al., 1998) but this variation is probably more complex than just a thermal response (Pitchers et al., 2013). However, Anderson et al. (2008) found an increase in aspect ratio values over the past century in a moth species, albeit links with increasing temperatures (climate change) were only suggested. Even if longer wings in hotter climates may be explained by Allen's rule (Shelomi & Zeuss, 2017), whether this increase in aspect ratio is an adaptation to increasing temperatures or just driven by body size shifts remains to be better explored. In *O. cornuta* we found lower wing loading in more fragmented green patches (higher edge density). This can be read as a possible adaptation to urbanisation. Reduced wing loading is associated with better flight performances and dispersal abilities (Dudley, 2000). Thus, bees with increased aspect ratio should

be favoured in urban fragmented green patches with possibly scattered floral resources (Matteson et al., 2013). Again, consistent with what had been found for body size, *P. dominula* is sensitive to NDVI variations. Despite body size reduction – which may negatively affect the range of prey potentially hunted – *P. dominula* could adapt to effectively collect resources in impoverished green areas (low NDVI, urbanized) through reduced wing loading.

Interestingly, once again the responses are consistent between the three species. That is, even though variations were driven by distinct environmental predictors, all the three species showed better flight performance (with higher aspect ratio and/or lower wing loading) in more urbanized areas. Especially for *O. cornuta* and *P. dominula*, better flight performances were linked with the configuration of the vegetation and thus with the need to forage effectively in the urban context. In the light of the body size reduction we just showed, there seems to be a possible trade-off between size reduction (worse dispersion capabilities) and changes in wing loading and aspect ratio (better flight performance).

Finally, we analysed fluctuating asymmetry both in the traditional and in the geometric morphometric approach. However, mixed results

emerged from our studied species, in accordance with previous literature. For example, Tommasi et al. (2022) found a positive association between increasing urbanisation and FA values in two *Bombus* species, while Banaszak-Cibicka et al. (2018) (for the solitary bee *Anthophora plumipes* Pallas, 1772) and Polidori et al. (2018) (for *P. dominula*) found no relevant alterations of wing symmetry in urban contexts. Although other studies found shape asymmetry to be less susceptible to stressors than size asymmetry (Gérard et al., 2018), we found higher shape asymmetry in more fragmented sites for *H. scabiosae* and *P. dominula*. Wing asymmetry is considered a proxy for larval development stress (Parsons, 1992), so we could expect higher asymmetry in more urbanized landscapes and these results, despite regarding only two species, are in accordance with other studies on bees which found higher fluctuating asymmetry in relation to more urbanised conditions (e.g., Leonard et al., 2018; Tommasi et al., 2022). Conversely, we could not find any consistent significant relationships between traditional fluctuating asymmetry and environmental conditions. Interestingly, we found smaller *O. cornuta* to have significantly higher shape asymmetry as found in *Apis mellifera* by Łopuch and Tofilski (2016), albeit this association is not clear for other bees (Silva et al., 2009). We may hypothesize that body size reduction, due to either faster development or lack of pollen resources may stress the larvae, resulting in higher fluctuating shape asymmetry. Further experiments will be needed to elucidate the correlation between size and asymmetry in bees. In addition, in *O. cornuta* and *P. dominula* we found some correlations between traditional fluctuating asymmetry and environmental variables. However, these variations are not consistent as there is not a clear trend towards an increase (or decrease) in fluctuating asymmetry in more urbanized sites. This inconsistency was also found by other studies on wild bees along urbanisation gradients (Banaszak-Cibicka et al., 2018). Altogether, these results show how wing fluctuating asymmetry may not be sensitive enough to pick up variations on such a small scale, or that the environmental gradient we chose for this study may not be long enough to allow such subtle differences to be identified. Again, this contrasting evidence may be the result of the investigated species. In fact, other factors may be involved in shaping such responses, such as genetic background, thermal limits or, in general, resilience to different conditions found across the urbanisation gradient. However, both the traditional and the morphometric approach could constitute an effective integrated framework for future studies aiming to use fluctuating asymmetry as proxy for environmental stressors in insects (De Anna et al., 2013).

In conclusion, our study showed how environmental conditions associated with urbanisation affect different functional traits of wild bees and wasps, and how they seem to respond similarly to increasing urbanisation, when the latter is quantified through different parameters. We found smaller insects but with potentially better flight abilities in more urbanised sites. Urbanisation seemed also to increase fluctuating asymmetry. Albeit this study highlighted considerable variation in morphological functional traits, we cannot infer whether these changes are due to phenotypic plasticity or a genetic adaptation. However, Austin et al. (2022) concluded, in a similar context, that phenotypic plasticity, rather than genetic adaptation, may underlie the phenotypic clines observed across urbanisation gradients. Nonetheless, our study suggests how individual-level trait variability may constitute a powerful tool to understand how urbanisation shapes organism before community-level variations may occur. The outcomes of our study may address important conservation perspectives. As cities will expand in the future, better green management practices should be implemented to counteract the negative effects of the urban environment. For example, practices such as urban forestry can mitigate the UHI effect (Ren et al., 2018), the creation of corridors between green patches (Zhang et al., 2019) may help dispersal and foraging in such insects and the reduction of mowing regimes may overall boost the arthropod communities in more urbanised areas (Proske et al., 2022), and thus the prey availability for wasps.

Data availability

All raw data are available in Ferrari_et_al_Appendix A.

Funding

Project funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 - Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – NextGenerationEU, Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP, H43C22000530001 Project title “National Biodiversity Future Center - NBFC”

Authors' contributions

CP conceived and designed the study. AF and NT sampled the insects and collected the data. AF and CP analyzed the data. AF wrote the first draft of the manuscript. All authors read, improved, and approved the manuscript.

Declarations of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank our students Simone Briatico, Linda Polidori, Alessio Polastri, and Beatrice Colombo for their help during the sampling period and in the initial stages of the work.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.11.010.

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