



# Urban landscapes affect wild bee maternal investment and body size

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Accepted: 16 May 2023

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## Abstract

Urbanization is considered one of the major threats to biodiversity worldwide, with a special concern for native species decline, including wild bees. Through the increase of impervious surfaces, urbanization diminishes, fragments, and warms city environments, significantly reducing nesting and foraging resources for bees. Understanding the response of wildlife to urbanization in terms of reproduction, foraging efficiency, and offspring provisioning is important to species conservation in the face of continued urban development. In this study, we investigated how different levels of urbanization affect individual foraging effort, survival, brood productivity, and fitness in *Ceratina calcarata*. Our findings show that low urbanization levels favour larger-bodied adults, but foraging efforts (determined by wing wear) were higher at moderate disturbance levels. Larger-bodied mothers produced more numerous offspring (clutch size), mainly in medium disturbance sites. Likewise, larger-bodied mothers produced a larger-bodied offspring at low urbanization levels. Our results indicate that wild bees benefit from low and medium levels of urbanization indicated by maternal and offspring fitness in terms of body size and the number of brood, respectively. This suggests significant effects of urbanization on the fitness and stability of wild bee populations. This study provides novel insights into the impact of urban land use and highlights the importance of conserving and providing green spaces for pollinators.

**Keywords** Urbanization · Clutch size · Wing wear · Disturbance · Small carpenter bees · Apidae

## Introduction

Approximately half of the world's population resides in urban areas, a number estimated to reach nearly 68% by the year 2050 (United Nations 2018). With rapidly expanding cities, urban ecology, and biodiversity conservation in these landscapes are of growing interest, as increasing sprawl and urban density are considered one of the major threats to biodiversity worldwide (Grimm et al. 2008; Seto et al. 2012). Critical concerns regarding increased urbanization are related to the depletion of native species in response to habitat loss, fragmentation, and degradation (Simkim et al. 2022). The decrease in natural vegetation cover associated with the development of infrastructure, roads, and other impervious surfaces, and the increase in the number and pervasiveness of invasive species, position cities as low-quality habitats for many native species (McDonnell and Hahs 2008; Geslin et al. 2016; Larson et al. 2021). Moreover, the warmer and

drier impervious surface present in urban landscapes contribute to a phenomenon known as the Urban Heat Island (UHI) effect, which can raise temperatures up to four degrees Celsius within cities (Klysik and Fortuniak 1999; McCarthy et al. 2010; Zipper et al. 2017). All of these factors have been associated with increased urbanization having negative consequences for global biodiversity and species persistence (Brant et al. 2022; Hernandez et al. 2009; Seto et al. 2012).

Urbanization has been shown to negatively impact pollinators, particularly bee species (Brant et al. 2022; Harrison et al. 2019; Hernandez et al. 2009). Cities convert natural habitat into paved landscapes, which contribute to a depletion of provisioning and nesting resources that affects bee foraging, fecundity, and overall species richness and abundance (Ayers and Rehan 2021; Cardoso and Gonçalves 2018; Geslin et al. 2016; Potts et al. 2010). Several studies have noted declines in bee abundance and richness attributed to urbanization. For instance, a 35-year study from Brazil revealed species richness declines of up to 45% in response to urbanization (Cardoso and Gonçalves 2018). Similarly, a study in Paris, France, found that wild bee abundance and species richness significantly decreased in response to

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increased impervious surfaces (Geslin et al. 2016). Moreover, a study in Stockholm, Sweden, found a decrease in bumble bee (*Bombus* spp.) diversity with increasing urbanization (Ahrné et al. 2009). Comparisons across land use types in Michigan, USA, revealed that *Bombus* and *Lasioglossum* (*Dialictus*) are negatively affected by urbanization, whereas rural sites (with less than 40% of impervious surface) better support these groups (Wilson and Jamieson 2019). Urban warming can also affect bees as high proportions of impervious surface intensifies heat at the local scale, changing plant phenology, affecting emergency synchrony, reducing survival rates, and hindering flight activity due to thermal limitation within a city (Ferrari and Polidori 2022; Hamblin et al. 2017, 2018; Zipper et al. 2017). As urban expansion continues to increase, it is imperative to understand the role that urban land use has in providing security for this important group of pollinators.

While rapid urbanization around the globe has high impact on wild bee populations (Cardoso and Gonçalves 2018; Geslin et al. 2016; Hernandez et al. 2009; Zipper et al. 2017; Harrison et al. 2019), cities can also support bee diversity, providing refuges for a considerable number of managed and wild bees (Hall et al. 2017; Threlfall et al. 2015; Wilson and Jamieson 2019, reviewed in Ayers and Rehan 2021). In fact, more bees visit residential and community gardens in the UK than other land types, thus urban areas may be considered pollinator hotspots (Baldock et al. 2019). Similarly, the foraging activity of stingless bees in Australian urban gardens is reported to be higher than in natural habitats (Kaluza et al. 2016). Some cities can host greater bee richness than other landscapes such as agricultural ones (Baldock et al. 2015; Banaszak-Cibicka et al. 2018; Prendergast et al. 2021; Sirohi et al. 2015). Urban bee diversity is thought to be supported by an increase in plant variety across urban green areas such as remnant vegetation, city parks, and residential yards, which increase floral diversity and foraging possibilities for bees (Ayers and Rehan 2021; Baldock et al. 2019; Banaszak-Cibicka et al. 2018). Bees may be able to locate suitable floral resources and nesting sites despite environmental changes, allowing them to overcome the negative impacts of land use change and instead persist in urban fragments (Banaszak-Cibicka et al. 2018; Buchholz and Egerer 2020).

Bee response to urbanization is dependent upon the functional traits displayed by certain species (Ayers and Rehan 2021; Ferrari and Polidori 2022). For example, cities with highly fragmented green areas seem to support a community with large-bodied bees, probably due to lower patch connectedness and higher isolation, favouring large-bodied bees over small-bodied (Ferrari and Polidori 2022) given that small-bodied bees often present limited flying ranges (Greenleaf et al. 2007). In bees, the body size is highly influenced by the quantity and quality of food provided during

larval development (Bosch and Vicens 2002; Chole et al. 2019; Lawson et al. 2016; Quezada-Euán et al. 2011). Additionally, smaller bees tend to carry less pollen and nectar, affecting brood cell provisioning and offspring survival (Chole et al. 2019). Interestingly, extensive land use across the globe has shifted bee body size towards smaller-bodied individuals, with the declines being prominent in species exhibiting narrow dietary and phenological breadth as well as larger body size (Bartomeus et al. 2013). Such outcomes are highly associated with the global increase in human population from 140 people/km<sup>2</sup> to 325 people/km<sup>2</sup> and the consequent anthropogenic land use transformation across biomes, possibly limiting food and nesting resources for pollinators (Bartomeus et al. 2013; Ellis et al. 2010). Thus, smaller body size in adults and offspring is expected to be associated with lower resource availability. Urbanization also significantly enhances the susceptibility and spread of parasites largely due to habitat fragmentation, local isolation, and urban heat islands, all of which favor pathogen and parasite transmission (Borowska and Pyza 2011; Bradley and Altizer 2007; Goulson et al. 2012). Indeed, along an urbanization gradient, parasites on social bees' have been responsible for a threefold decline in workers' survival (Youngstead et al. 2015).

Sex ratio may also be affected in wild bees along an urbanization gradient. Male offspring are often smaller in wild bees and thus require less provisioning than female offspring ((Rehan and Richards 2010b). Urbanization has been related to male-biased in wild bees across 143 species in Michigan, potentially related to a decrease in local resources (Fitch et al. 2019). Sex allocation in bees has been previously related to food resource availability for the leaf-cutter bees *Megachile apicalis* and *Osmia lignaria*, where bias toward larger female offspring was related to higher food availability (Kim 1999; Tepedino 1982). Food availability also influences foraging activity in cities, mainly associated with impervious surfaces that intensify foraging effort, especially for small bees. An accurate measure of flight frequency and foraging efforts is wing wear, occurring when an insect collides with foliage while foraging, producing damage to its wings (Cartar 1992; Foster and Cartar 2011). In bumble bees, increased wing wear has been shown to increase the probability of mortality (Cartar 1992). The reproductive capabilities of bees are also affected by foraging, as increased wing wear poses more physical demands on bees (O'Neill et al. 2015).

Small carpenter bees, genus *Ceratina*, are among the top 20 most economically important wild bees (Kleijn et al. 2015) and have been significantly affected by land use change (Kelemen and Rehan 2021; Nooten and Rehan 2019). For example, naturalized areas support larger *Ceratina calcarata* mothers and offspring compared to mowed and tilled landscapes (Nooten and Rehan 2019).

As small-bodied central-place foragers that likely only forage less than 200 m from their stem nests, this species also might be more susceptible to natural habitat conversion (Rehan and Richards 2010a; Zurbuchen et al. 2010a). The sex ratio of *C. calcarata* has been found to be significantly male-biased (57%; Rehan and Richards 2010b). However, due to the larger size of females, the investment ratio (the ratio between resources that the mother provides to the male vs. female offspring) has also been found to be even between the sexes ((Rehan and Richards 2010b). Consideration of how bees' body size, sex ratio, and the number of offspring vary across an urban gradient is thus important to assess how these bees are investing resources in a highly modified habitat.

This study examined the small carpenter bee *Ceratina calcarata* Robertson (Hymenoptera: Apidae: Xylocopinae), a native species widely distributed across eastern North America (Shell and Rehan 2016). *C. calcarata* is a subsocial species with mother-offspring interaction throughout development and into adulthood, where the amount of pollen provisioned by the mother dictates adult offspring survival and body size (Lawson et al. 2016; Rehan and Richards 2010a). These bees are generalist pollinators, collecting pollen from hundreds of floral species (Lawson et al. 2016), and construct their nests in broken stems of raspberry (*Rubus sp.*) and sumac (*Rhus sp.*). After collecting pollen, the mother separates each brood cell in the nest by scraping pith to form a wall (Rehan and Richards 2010a; Rehan et al. 2014). Following oviposition, the mother will remain in the nest entrance (gallery) and guard the nest from parasites and predators until her offspring are fully developed (Rehan and Richards 2010a; Rehan et al. 2014). This species is also reported to display prolonged maternal care, revisiting brood cells within the nest and breaking down and rebuilding cell partitions to lick and groom offspring (Rehan and Richards 2010a; Arsenault et al. 2018).

There is abounding evidence that urbanization allows some species to flourish and others to decline, though the effects of urbanization on maternal bee quality and its subsequent effects on offspring for wild bees it is still largely unknown. As impervious surfaces continue to increase worldwide, it is important to know how this could affect species' survival. In this study, we investigated how *C. calcarata*'s maternal and offspring traits respond to different levels of urbanization and the influence of an urbanization gradient on adult and offspring bee health and survival. The aims of this study were to assess the effects of urbanization on (1) adult body size and foraging efforts; (2) offspring fitness and survival; and (3) the combined effects of maternal fitness and investment on offspring. We hypothesize that lower levels of urbanization would favour adults with larger body sizes and favour the production of more and larger offspring.

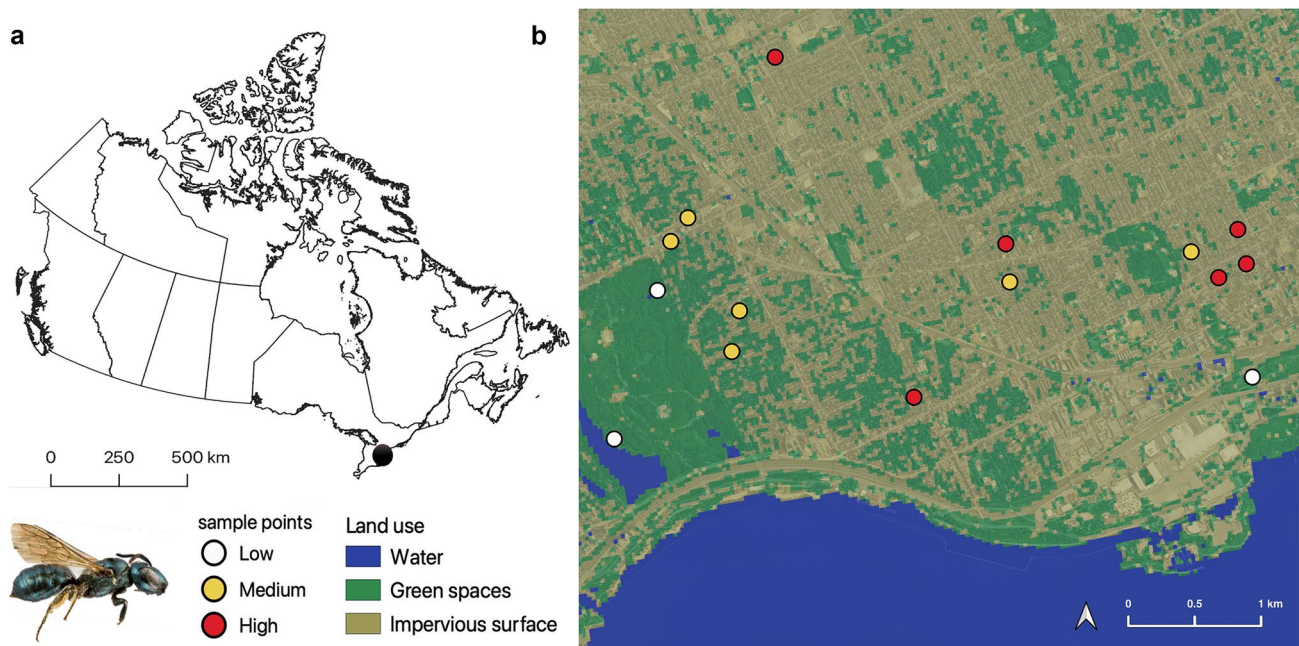
## Materials and methods

### Urbanization metrics

This study was conducted in Toronto, Canada, which is among the top four largest cities in North America (Statistics Canada 2016). The Ontario Land Cover Compilation (OLCC, Land Information Ontario 2019) in ArcMap v.10.7.1 was used to select fifteen study plots according to urbanization intensity and situated at least 200 m apart, according to the foraging range of small-bodied solitary bees (Zurbuchen et al. 2010b) (Fig. 1). The urbanization intensity threshold was determined based on the percentage of impervious surface within a 250 m diameter buffer, where low-intensity impervious surface sites were classified under 25% land development, medium intensity between 26% and 75% land development, and high intensity were sites with over 76% land development.

### Nest collection and measurements

A total of 454 raspberry stems were collected during early Spring and deployed under sumac trees in April 2021 outside Toronto. Nests were translocated from initial occupancy sites in June 2021 into a bare soil or grass at least two feet apart from each other to three low-intensity sites ( $n = 150$ ), six medium intensity ( $n = 152$ ), and six high-intensity sites ( $n = 152$ ). During the translocation, nest entrance holes were taped to prevent escape and transported on ice prior to deployment at the study sites. Once all translocations were completed, weekly visits to sites were made to ensure the stems were placed firmly into the ground and remained in the study sites. All 454 raspberry stems were collected from July 27–August 6 prior to 8:00 h when *Ceratina* foraging activity begins (Rehan and Richards 2010a) and followed dissection. After dissection, nests were categorized based on the Daly (1966) classification system. Hibernacula (H) nests are distinguished by the presence of a darkened interior of the nest with pollen residue from the previous breeding season (Rehan and Richards 2010a). Founding nests (FN) are newly formed nests indicated by lighter interior walls of nests without any residue (Daly 1966; Rehan and Richards 2010a). Active Brood (AB) nests contain one or more pollen balls or immature bees, with the outermost brood cell containing a pollen ball (Daly 1966; Rehan and Richards 2010a). In Full Brood (FB) nests the outermost cell contains a pupa or larva with no remaining pollen ball, also classified as “complete” since the mother has finished laying eggs (Rehan and Richards 2010a). Mature Brood (MB) nests contain only adult bees, the youngest of which are callow



**Fig. 1** Classification map and sample collection points for the study area. **a** Location of all sample points (black dot) within Canada. **b** White dots represent a low percentage of impervious surface (0–25%), yellow dots represent the medium percentage of impervious surface (26–75%), and red dots represent a high percentage of imper-

vicious surfaces (76–100%). **c** Land use classification showing the amount of water, green space, and impervious surface. Bee picture: *C. calcarata* female. Photo credit: Laurence Packer; Map of Canada retrieved from <https://open.canada.ca>

adults, young adults with incompletely hardened wings (Rehan and Richards 2010a).

For each nest we recorded maternal presence, the total number of brood cells (clutch size) and their developmental stage, the number of bee offspring (live brood), and any parasites detected. All larvae and pupae were placed in 200  $\mu$ L microcentrifuge tubes and then reared in the lab at room temperature (25°C) with an air hole poked in the lid of the tube to allow for natural ventilation upon rearing. For every adult and reared offspring, we ensured to identify the correct species, determined the sex and measured the head width. Head width was measured using a microscope (Nikon SMZ1270) across the widest part of the head to the outer margins of the compound eyes. To assess wing wear data, we actively (sweep net and vacuum) and passively (pan traps) collected bees during the months of May to September – 2021. Wing wear was measured by the presence of tears on the margins of the wings and recorded on a scale from 0 to 5, with 0 having no wing wear (no tears on the outer margin of the wing) and 5 having the highest wing wear (the outer margin of the wing completely worn away) (Mueller and Wolf-Mueller 1993). All adults (including mothers) were placed in cryogenic tubes and flash frozen in a Dewar containing liquid nitrogen, and then stored in a -80 °C freezer.

## Statistical analyses

We used the Shapiro-Wilk test to see whether our data were normally distributed, and we then generated a quantile-quantile (Q-Q) plot to determine whether the residuals were normally distributed. To test the effect of urbanization on adult body size and foraging efforts, we tested the relation between adult head width and wing wear, and urbanization level using ANOVA in R (R Core Team 2022 v 4.2.1) with a significant level set to  $p < 0.05$ . Results that had a significant  $p$ -value were further analyzed by a Tukey posthoc to test between differences among the three urbanization intensities. We used generalized linear models (GLMs) with different family distributions to investigate urbanization effects on offspring fitness and survival. We tested the relation of brood parasites, maternal presence and sex-ratio across different urbanization intensities and among nest stages using binomial distribution. To assess the combined effects of maternal fitness and investment on offspring, we used the Poisson family distribution to model counting variables (clutch size) and Gaussian for continuous variables (offspring head width) of maternal quality across the urbanization gradient. We performed a post-hoc test for our GLMs results using the *ghlt* function from the package multcomp in R (Hothorn et al. 2016). To gather values to each

level of urbanization for every model, we used the GLM function *relevel*. We used *ggplot2* (Wickham et al. 2016) to graph double scatterplots displaying relationships between maternal and daughters' head widths, as well as maternal and sons' head widths across urbanization categories, and to graph the sex ratio of offspring in nests.

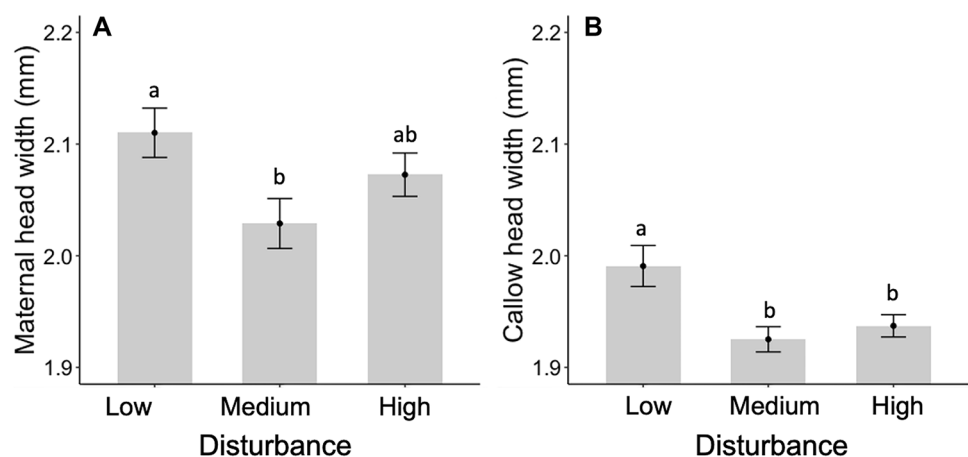
## Results

Out of the total 454 stems collected, 242 of the nests contained *C. calcarata*, with the rest of the stems either being empty or containing other insects. Out of these, 70 were from low (29%), 78 were from medium (32%), and 94 were from high disturbance level (39%) sites. The total number of *C. calcarata* individuals collected from all 242 nests was 1561, where 471 bees were collected from the low (30%), 553 in the medium (35%), and 537 from the high disturbance level (34%).

### Urbanization effects on clutch size and body size

The maternal head width ranged from 1.58 to 2.46 mm with means of 2.11 ( $\pm 0.02$ , low), 2.02 mm ( $\pm 0.02$ , medium) and 2.07 mm ( $\pm 0.02$ , high), varying significantly across disturbance levels ( $F=3.30$ ,  $df=2$ ,  $p=0.03$ ) (Fig. 2A). The higher values of maternal head width were found at the low urbanization level. We found a significant effect of urbanization on offspring head width ( $F=4.18$ ,  $df=2$ ,  $p=0.01$ , Fig. 2B), where low intensity was the factor in determining offspring head width (Tukey  $p=0.01$ ). Offspring head width (callows) varied from 1.39 to 2.57 mm, with means being 1.99 mm ( $\pm 0.02$ , low), 1.92 mm ( $\pm 0.01$ , medium), and 1.93 mm ( $\pm 0.01$ , high). Overall, both the maternal and offspring head width was larger in low disturbance sites when compared to medium and high urbanization sites (Fig. 2).

**Fig. 2** Mean ( $\pm$ SE) of **A** maternal and **B** callow head width collected from all *C. calcarata* nests at low, medium, and high levels of urbanization. Small letters indicate statistical significance



We found a significant correlation between the maternal-daughter head width across all disturbance gradients ( $F=30.62$ ,  $df=2$ ,  $p<0.001$ ). Tukey's posthoc results revealed low intensity to have a significantly higher maternal and daughter body size ( $p<0.001$ ). Similarly, we also found significant correlation between maternal-son head width across the gradient levels (Fig. 3) ( $F=19.9$ ,  $df=2$ ,  $p<0.001$ ). In both maternal daughter/son relationships, the medium intensity yielded smaller-bodied offspring (Fig. 3). There was a significant deviation from the expected even (50/50) sex ratio, where the sex ratio per nest (counted as every cell within a nest) was female-biased (65% female, Fig. 4). According to GLM results, the sex ratio was not significantly related to urbanization levels (Table 1). We tested clutch size (i.e., the total number of brood cells) against disturbance levels alone and together with maternal head width. Clutch size was correlated with maternal head width (t-value=4.22,  $p<0.001$ ; Table 2) and was largest at medium disturbance levels (t-value=2.64,  $p=0.008$ ; Fig. 5).

### Urbanization effects on foraging effort, parasitism, and maternal presence

Wing wear was higher at medium urbanization sites ( $2.93 \pm 0.25$ ) than low ( $1.81 \pm 0.19$ ) and high disturbance ( $1.74 \pm 0.36$ ), differing significantly among urbanization levels ( $F=7.30$ ,  $p<0.001$ , Fig. 5). Parasites were present in 12.4% (30/242) of the nests. Parasite presence was higher at the high disturbance sites (17/30) compared to medium (8/30) and low (5/30); however, parasite presence did not differ significantly among disturbance levels or nest stages (Table 1). Maternal presence was noted in 60.3% of the nests ( $n=146/242$ ). A higher percentage of maternal presence was noted under low disturbance sites where 64% of the nests were guarded by a mother ( $n=45/70$ ), followed by high (55%,  $n=59/94$ ) and medium disturbance (54%,  $n=42/78$ ). Narrowing to the maternal presence among nest stages, we found mothers to be present in 70.5% (12/17) of AB nests, 68% (34/50) of FB nests, and 79% (100/126) of MB stage. We did not find a significant

**Table 1** Summary results from generalized linear models (GLM) for clutch size, daughters' head width, and sons' head width across different urbanization levels and maternal head width

Variable	Parameter	Estimate	SE	t-value	Pr(> t )
<b>Clutch size</b>	Low	0.10637	0.0796	1.336	0.1814
	<b>Medium</b>	0.2856	0.1083	2.638	<b>0.0084</b>
	High	-0.10637	0.0796	-1.336	0.1814
	<b>Maternal head width</b>	1.2275	0.2909	4.219	<b>0.0000</b>
<b>Daughters' head width</b>	<b>Low</b>	0.0673	0.019	3.541	<b>0.0004</b>
	Medium	0.03661	0.01902	1.924	0.0547
	High	-0.03661	0.01902	-1.924	0.0547
	<b>Maternal head width</b>	0.25549	0.05553	4.601	<b>0.0000</b>
<b>Sons' head width</b>	<b>Low</b>	0.68184	0.33486	2.036	<b>0.0424</b>
	Medium	-0.2003	0.28878	-0.694	0.4884
	High	0.2003	0.28878	0.694	0.4884
	<b>Maternal head width</b>	0.14660	0.06318	2.32	<b>0.0209</b>

Significant values ( $p < 0.05$ ) are highlighted in bold

correlation between disturbance levels or nest stages on the maternal presence (Table 1).

## Discussion

In a densely urbanized area, we tested individual fitness, and maternal and offspring responses to different levels of urbanization of an important pollinator, the small carpenter bee,

**Table 2** Summary results from generalized linear models (GLM) for sex ratio and parasite presence across different urbanization levels and nest stage levels

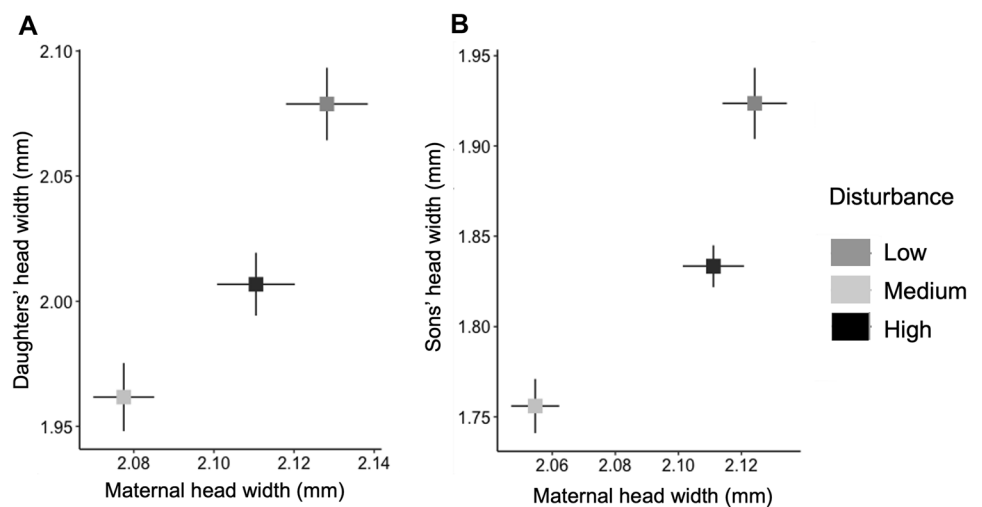
Variable	Parameter	Estimate	SE	t-value	Pr(> t )
<b>Parasites</b>	Low	-0.0654	0.0673	-0.973	0.3323
	Medium	-0.0631	0.0677	-0.932	0.3530
	High	0.0631	0.0677	0.932	0.3530
	Stage AB	0.1436	0.1010	1.421	0.1575
	Stage FB	-0.1209	0.1120	-1.079	0.2823
	Stage MB	-0.1436	0.1010	-1.421	0.1575
<b>Maternal presence</b>	Low	0.0871	0.4543	0.192	0.8479
	Medium	0.4295	0.4176	1.028	0.3037
	High	-0.4295	0.4176	-1.028	0.3037
	Stage AB	0.4090	0.5832	0.701	0.4831
	Stage FB	0.2589	0.6717	0.386	0.6998
	Stage MB	-0.4090	0.5832	-0.701	0.4831
<b>Sex ratio</b>	Low	0.3368	0.4597	0.733	0.464
	Medium	0.1995	0.4603	0.433	0.6648
	High	0.3218	0.4598	0.7	0.4841
	Stage AB	-0.0404	0.0588	-0.687	0.4923
	<b>Stage FB</b>	<b>0.1352</b>	<b>0.0678</b>	<b>1.994</b>	<b>0.0464</b>
	Stage MB	0.0404	0.0588	0.687	0.4923

Significant values ( $p < 0.05$ ) are highlighted in bold  
 AB active brood, FB full brood, MB mature brood

*Ceratina calcarata*. Moderate levels of urbanization seem to benefit bee clutch size and increase foraging effort, as indicated by greater wing wear. We found low urbanization sites to possess both larger-bodied mothers and offspring, with body size decreasing in medium urbanized sites. We did not find any relationship between urbanization levels and brood parasitism or sex ratio, although our results revealed a female-biased ratio across all levels. Overall, our results indicate a potential drive of urbanization intensity on *C. calcarata* body size, offspring investment, and foraging efforts.

In this system, low urbanization levels are benefiting larger bees according to their increased body size. Given that in bees, body size is highly influenced by the quantity and quality of food provided during larval development, individuals that receive high-quality diets with abundant and diverse floral resources tend to have larger body sizes, offering advantages in terms of reproductive success and survival (Bosch and Vicens 2002; Chole et al. 2019; Lawson et al. 2016; Quezada-Euán et al. 2011). Stem-nesting bees such as *C. calcarata* or ground-nesting bees, may benefit from areas with low human activity and more green spaces, helping maintain suitable nesting sites and protect them from potential predators or disturbances. Areas with simplified green spaces such as intense agriculture have contributed to the reduced body size of *Andrena nasonii*, a ground-nesting wild bee, compared to low development areas (roadsides, forests, and scrublands) (Renauld et al. 2016). Possible mechanisms underlying this include the decrease in resource quantity (proportion of flowers) and quality (flower richness) occurring in such simplified landscapes, and the increased exposure to pesticides. The same conditions could be expected in urbanized areas where the limited resources cities provide impact foraging efficiency in bees generally. This was observed in genus level investigations across Chicago, Illinois where small-bodied ground-nesting bees of the genus *Halictus* decreased in abundance with reduced flower

**Fig. 3** Two-dimensional plots of the relationship between **A** maternal daughters and **B** maternal sons head width in low, medium, and high disturbance levels. Error lines indicate the standard error ( $\pm$  SE) of the mean

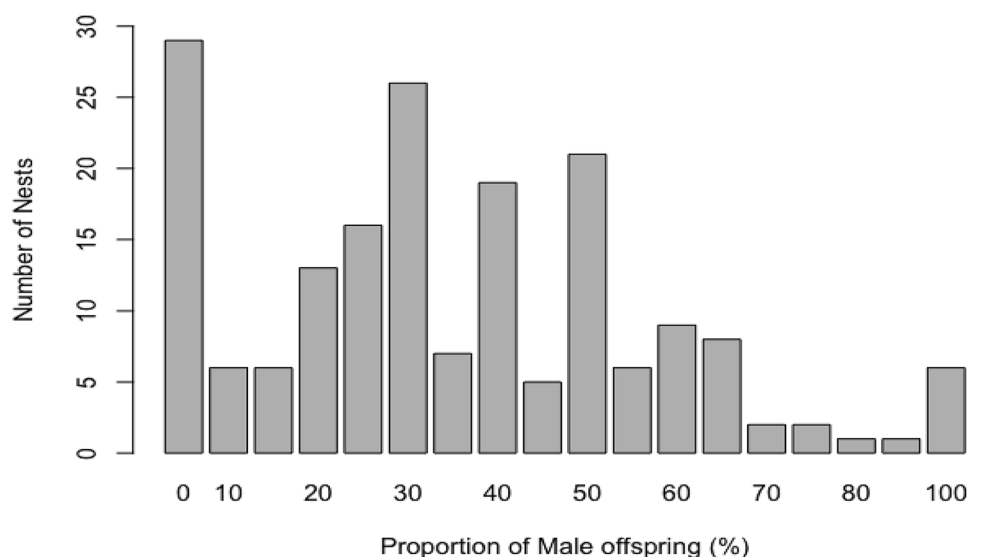


cover in sites with increased impervious surface at a 500 m threshold (Bennett and Lovell 2019). Urban landscapes can limit foraging efficiency even in long-distance flyers such as euglossine bees (Lopez-Urbe et al. 2008). Thus, increasing amounts of impervious cover likely translate to reduced resource availability and increased patch distances making access to favourable resources difficult for small stem nesting bees such as *C. calcarata*. Additionally, these factors may not only impact individual body size and foraging effort but the development of subsequent generations.

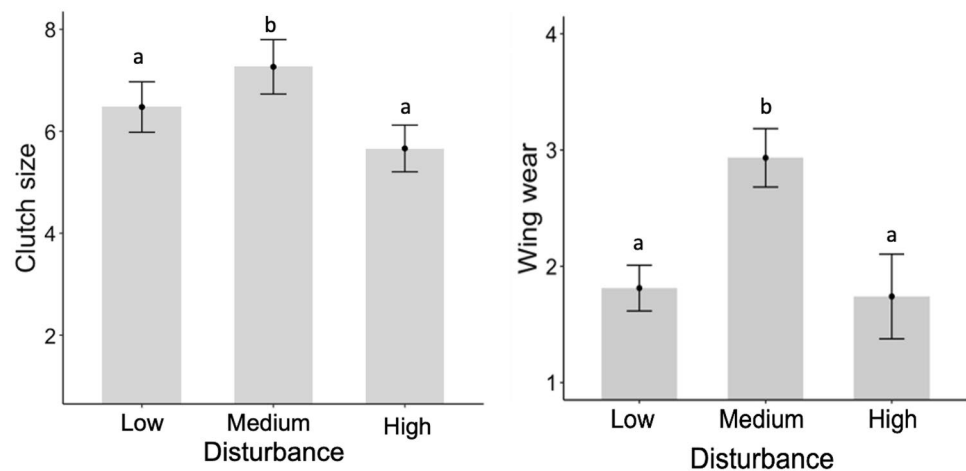
We found mother size to be significantly correlated with offspring body size in lower levels of urbanization (areas with lower proportions of surrounding impervious surface). *C. calcarata* is a small-bodied bee and central-place forager, meaning that mothers must forage and return to the nest multiple times to provide food for their brood (Rehan and Richards 2010a). According to optimal foraging theory,

bees are expected to forage shorter distances in environments with higher floral cover available near the nest site (Westphal et al. 2006). This would produce more efficiency in foraging (reduced time and energy spent foraging) and less damage from flight activity. *C. calcarata* have been reported to have a larger brood body size and larger clutch size when nests were surrounded by natural areas (Mikát et al. 2017). Seemingly, close proximity to pollen resources enables mothers to provide larger and higher quantity provision masses when compared to distant blooming options found in managed landscapes, where the body size of both mother and offspring was smaller (Nooten and Rehan 2019). A similar maternal investment was found in *Ceratina chalcites* where larger-sized mothers produced significantly larger female and male offspring in areas with abundant surrounding nesting substrates (Mikát et al. 2019). Another benefit of bigger body sizes on impervious surfaces is related

**Fig. 4** The sex ratio of *Ceratina calcarata* nests ranges from all females (0% male) to all males (100%), with an overall 65% female-biased (35% male) sex ratio at the population level



**Fig. 5** Average of *C. calcarata* nests clutch size and wing wear at low, medium, and high levels of urbanization. Small letters indicate statistical significance



to the amount of pollen and nectar a bee can carry at once. Under a highly human-modified landscape, larger females of the ground-nesting bee *Andrena nasonii* carried around 40% more pollen loads than smaller females (Renauld et al. 2016). This is likely to impact subsequent offspring production and fitness as the quantity and quality of food given by the mother is highly associated with larval development and adult body size (Chole et al. 2019; Quezada-Euán et al. 2011). In fact, pollen manipulation in *C. calcarata* has a conspicuous effect on offspring body size, where bee larvae provided with a smaller pollen ball are smaller than their siblings (Lawson et al. 2016). Smaller body size is also associated with temperature for the primitively eusocial bee *Lasioglossum zephyrum*, where higher temperatures produce smaller-bodied bees (Kamm 1974). As urbanization is leading to warmer environments (the Urban Heat Island effect; Zipper et al. 2017), it is likely playing an important role in wildlife development highlighting there need for future studies investigating the effects of microclimate on offspring body size and survivorship.

We found maternal presence to be prominent at low urbanization sites. Less-managed sites have been previously reported to have a higher proportion of attacked brood cells and mortality of bees due to natural enemies compared to intensively managed sites (Albrecht et al. 2007). *C. calcarata* guard their nests from the end of cell provision until the offspring reaches maturity (Rehan and Richards 2010a), thus nesting guarding strategy seems to aim to protect the nest from natural enemies that are presumably higher at lower levels of urbanization. Nesting guarding in *Ceratina* has been previously related to increased brood survival (Sakagami and Maeta 1977), meaning that this strategy is highly advantageous for offspring survival. We also found a higher proportion of maternal presence in mature brood nests. In the mature brood stage, nests will contain only adult bees with the youngest being the callow ((Rehan and Richards 2010b). It is expected that early nest stages such as active brood

(which contains only pollen balls or immature bees) and full brood (outermost cell containing a pupa or larva with no pollen ball) would have a higher maternal presence (Rehan and Richards 2010a). Our results are showing an apparent prolonged guarding and maternal care from *C. calcarata*, where the mother is present until all cells are fully mature. Existing literature on this matter has found a percentage of only 29% of mature brood to have a maternal presence, compared to over 98% of full brood nests ((Rehan and Richards 2010b), although the opposite has also been found for other *Ceratina* species where only 34% of mothers were present in full brood nests (Mikát et al. 2019). The sex ratio was female-biased across all sites. *C. calcarata* are known for precisely manipulating the sex ratio of offspring ((Rehan and Richards 2010b). A female-biased sex ratio was also found under high urbanization levels for the sweat bee *Agapostemon virescens* dwelling in the highly populous Toronto, Canada (Brasil et al. 2023). The strategy of producing more females here is likely related to improving foraging efficiency in a gradient of impervious surfaces, since females are thought to be better effective pollinators than males (Ne'eman et al. 2006).

Medium urbanized sites yielded more numerous offspring, indicating that maternal investment was allocated most successfully at moderate disturbance sites. In many species, a larger offspring offer advantages in terms of survival, fertility, territorial defense, and mating opportunities (Seidelmann 2018). Medium disturbance sites have been reported to hold higher levels of wild bee species diversity across urban landscapes (Fortel et al. 2014), therefore there seems to exist a trade-off between resource limitation found in highly urbanized areas and the competitive exclusion of low disturbance areas (Svensson et al. 2012; Wignall et al. 2020). Additionally, given that moderate human-disturbed landscapes provide a mosaic of different habitat types causing high heterogeneity (Fahrig 2017), bees might have access to more possibilities for food and nesting resources, as compared to simplified landscapes.



Although wing wear has been previously associated with declining clutch size, we found wing wear to be also higher at moderate disturbance sites. Following the same premises as above, moderate sites might be less challenging for an adult bee, giving it enough resources for food and nesting while reducing competition and predators. An example can be found in *Apis mellifera* which showed no alterations of flight performance even under a high reduction of wing area, during non-challenging flight conditions (Vance and Roberts 2014). The same was reported for *Bombus flavifrons* where loss of wing area had little effect on flight behavior, demonstrating a remarkable resilience to wing damages (Haas and Cartar 2008). Another possibility is that these bees are minimizing the effects of wing wear by increasing wingbeat during flights. This strategy has been previously reported for large carpenter bees of the genus *Xylocopa* and for the eastern bumblebee *Bombus impatiens* (Roberts et al. 2004; Roberts and Cartar 2015).

This study presents novel findings on the effects of urbanization gradients on fitness and offspring investment in a wild bee, *C. calcarata*, emphasizing the importance of providing green spaces within highly impervious landscapes. Our results also indicate that a moderate urbanization can be beneficial for bees, as these sites were correlated with larger offspring. This study also provides a foundation for future studies that examine the effects of urbanization on the nesting and fitness of other wild bee species. From a conservation standpoint, future studies on *C. calcarata* urban flower preferences (pollen and nectar) are necessary to know which plant species can be prioritized in parks and private and community gardens. As urbanization expands, it is essential to note that even in a highly urban environment, an adequate habitat could safeguard the future of these pollinators. Drawing attention to species living in cities, especially charismatic species such as bees, is a fantastic opportunity to highlight the value of wildlife conservation in an urban environment.

**Acknowledgements** We thank members of the Rehan lab for providing valuable feedback on earlier versions of this manuscript. Thanks to Mariam Shamekh and Phuong Nguyen for assistance with nest dissections and processing of bee specimens.

**Author contributions** ACA, JLH and MMRK performed material preparation and data collection. SNRB, MMRK and SMR performed data analysis. SNRB and SMR wrote the manuscript. SMR conceived and funded the study. All authors reviewed the manuscript.

**Funding** Funding for this study was provided by NSERC Discovery grants, supplements, and an E.W.R. Steacie Memorial Fellowship to SMR.

**Data availability** Raw data that support the findings of this study are available upon request.

## Declarations

**Conflict of interests** The authors declare no competing interests.

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