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Do Bee Wings Adapt for Flight in Urban Environments?

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Abstract - Understanding how organisms respond to urban-associated environmental changes is key to protecting vulnerable species. Bees, in particular, have gained interest due to their economic and ecological roles. We used a geometric morphometric approach to describe changes in wing shape and size in the solitary bee *Andrena barbara* (Barbara's Miner) collected across an urban landscape. We found that, although the wing morphology suggests a limited dispersal ability in its short and narrow frame, the urban landscape did not significantly explain how wing shape or size vary. Our findings are consistent with other studies that show little variation in wing morphology in urban solitary bees, and suggests that urban habitats may potentially serve an important role in bee conservation.

Introduction

As the terrestrial environment becomes increasingly urban, understanding organismal responses to urban-associated change is key to predicting future changes in global biodiversity. Urban environments are characterized by patchy landscapes, variation in vegetation abundance and diversity, and higher ambient temperatures—a phenomenon known as the urban heat-island effect (Wilby and Perry 2006). Many species, including insects, have shown variable responses to urban conditions in morphology, behavior, and physiology that may reflect adaptability in a rapidly changing environment (Angilletta et al. 2007, Czaczkes et al. 2018, Lundquist and Zhu 2018, Pérez et al. 2018, Weaver et al. 2018).

Urban environments can directly impact insect populations by imposing environmental stressors on development and physiology or indirectly by favoring pathogens or disrupting key species interactions (Raupp et al. 2010). Conversely, the same urban conditions that impose stress on some populations may favor other species via positive effects on development rates and generation turnover (Meineke et al. 2013). For instance, ant populations have been shown to switch towards eating human-associated food sources in urban centers, and those species become abundant (Penick et al. 2015). Similarly, periodical cicadas collected in urban areas in northern latitudes were recently shown to be larger than rural counterparts (Beasley et al. 2018).

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Understanding how bees, in particular, respond to urban conditions has become a major priority for conservation and economic purposes because of their role as pollinators of a large number of plant species. For *Apis mellifera* L (Honey Bee), colony conditions including foraging behavior, immunocompetence, and disease status have been shown to vary across urban landscapes (Appler et al. 2015, Hamblin 2017, López-Urbe et al. 2015, Youngsteadt et al. 2015). Although many studies have looked at the response of bee species richness and abundance across urban gradients (Banaszak-Cibicka and Żmihorski 2012, Cariveau and Winfree 2015), less is known about morphological variation within species across these same gradients. Changes in morphological traits of bees have been demonstrated in response to elevational changes, agriculture, and heavy-metal pollution (Classen et al. 2017, Pinto et al. 2015, Szentgyörgyi et al. 2017); the same might be true in response to urban conditions (Beasley et al. 2013, Nunes et al. 2015, Prudhomme et al. 2016). Specifically, we might expect increasing temperatures and concentrated resources to cause wing morphology in urban bees to become shorter and narrower as the flight distances shorten (Hamblin et al. 2017, Simao et al. 2018, Taylor and Merriam 1995). Conversely, if urban habitats favor longer flight distances, wing morphology may become longer and wider. The aim of our study was to investigate changes in wing shape and size of bees in response to urbanization. We focused our study on *Andrena barbara* Bouseman & LaBerge (Barbara's Miner), a solitary mining bee that is a key pollinator of early spring blooming plants in rural and urban habitats of eastern North America.

Field-site Description

Raleigh, NC, is a southeastern US city that has experienced rapid urban growth resulting in a population size of 464,758 as of 2017 (World Population Review 2019). It is the second largest city in North Carolina and covers a land area of 369.9 km² (142.8 mi²). It is located in the northeast-central region of the state and has landscape features reflecting the Piedmont and Atlantic Coastal Plain regions.

Methods

Bee collection

We collected a total of 102 *A. barbara* individuals during Spring 2015 from nest aggregations across 7 locations in Raleigh, NC (Fig. 1) and stored samples in a -20 °C freezer until analysis. These sites were located in areas that varied from 0.2% to 36% impervious surface—a proxy for the level of urbanization at each site—at a 500-m radius around each nest aggregation (Table 1).

Wing slide preparation

We removed both the left and right wings at the closest point on the body, used a template to wet-mount them on microscope slides to ensure consistency across mounting, and placed a cover slip secured with clear nail polish over wing samples. We captured images using a flatbed scanner at a resolution of 4800 dpi (Epson

Perfection V550). Due to the fragile nature of the wings we could not assess mounting error.

Geometric morphometric analysis

We employed tpsDIG (Rohlf 2005) to capture 14 landmarks on wing-vein interactions. We only selected landmarks in the center of the wing to avoid damaged areas along the wing edges (Fig. 2). We independently captured landmarks 3 times to test repeatability. Following Procrustes superimposition, which standardizes shape across position, rotation, and size, we extracted Procrustes coordinates and centroid size from raw landmark coordinates using MorphoJ (Klingenberg 2011). We assessed measurement error using a Procrustes ANOVA. We detected and removed outliers by visualizing the deviation of the individual from the average in MorphoJ (Klingenberg 2011). We ran a principal components analysis (PCA) of Procrustes coordinates to quantify variation in shape across an urban environment. We also used a generalized linear model (GLM) with a Poisson distribution to assess change in wing size (centroid size) as a function of percent impervious surface in R Studio (R Core Team 2013). The amount of area covered by impervious surface serves as a measure of landscape modification due to urbanization (Yuan and Bauer 2007).

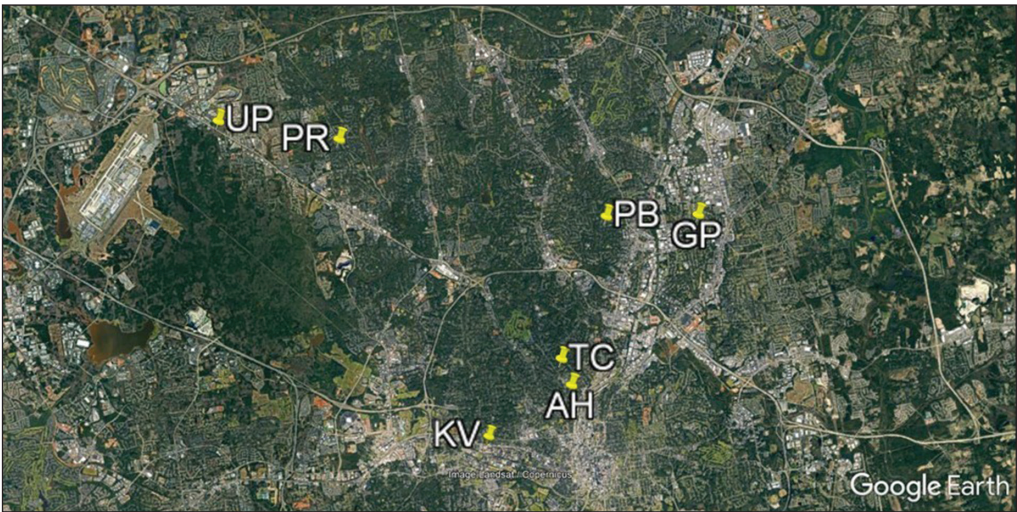


Figure 1. Location of 7 collection sites across Raleigh, NC.

Table 1. Bee collection sites with percent impervious surface values.				
Site	# of bees collected	Latitude (°N)	Longitude (°W)	Impervious surface (%)
UP	16	35.890	78.750	0.172
PB	20	35.845	78.622	4.979
PR	5	35.879	78.710	15.484
TC	15	35.808	78.646	15.531
GP	14	35.841	78.591	19.716
AH	18	35.799	78.645	23.377
KV	14	35.789	78.676	35.446

Results

Procrustes ANOVA indicated no significant measurement error ($P > 0.05$). Therefore, we only used 1 measure of Procrustes coordinates and centroid size for each specimen for the final shape and size analysis. Most shape variation was captured in PC1 (11.2% variance) and PC2 (9.3% variance). The first PCA suggested most of the variation indicated a lengthening of the basal and cubitus veins and a contraction of the third discal cell, resulting in a relatively short and narrow wing (Fig. 3A). However, the degree of the shape variation was not explained by collection location of individual bees within the urban environment (Fig. 3B). Similarly, wing size did not significantly vary as a function of percent impervious surface (coefficient = -2.46×10^{-4} ; SE = 5.33×10^{-4} ; $t = -0.46$; $P = 0.65$; Fig. 4).

Discussion

Understanding how organisms adapt to environmental change is key to identifying which species are vulnerable (or resilient) to these changes. Urbanization is associated with changes in landscape structure, temperature, and species interactions, and may pose novel challenges to biodiversity (McKinney 2008). Understanding how these changes impact bee adaptation is of particular interest due to their economic and ecological role in food production and pollination (Losey and Vaughan 2006). Specifically, flight ability may be the first to respond to urban-associated factors because it plays critical roles in resource acquisition, mate finding, and overall survivorship (Legagneux and Ducatez 2013, Møller 2008). We describe changes in wing morphology in *A. barbara* collected across an urban landscape. While the *A. barbara* wing appears to be adapted for short flight distances (short and narrow wing), the urban landscape did not significantly predict how wing shape or size vary.

Our results do not support the hypothesis that urbanization imposes selective pressure on flight ability in this particular population. Wing veins are responsible

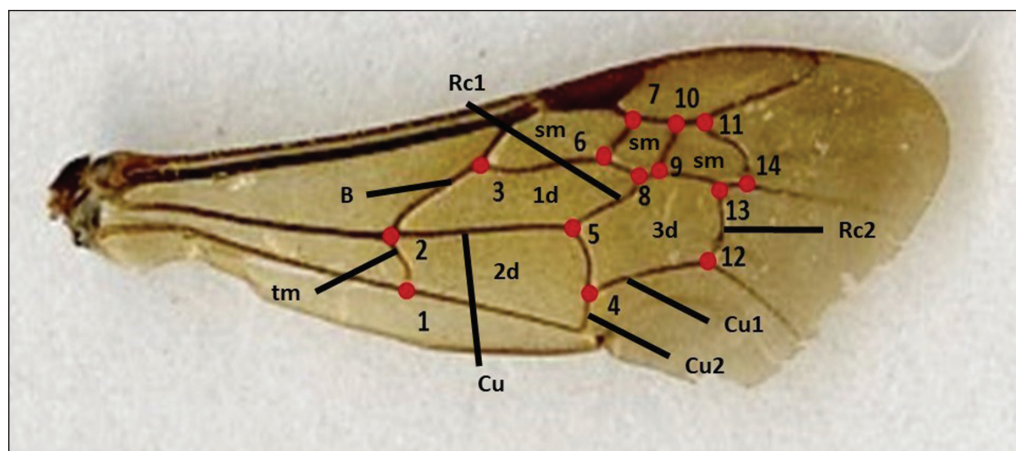


Figure 2. Landmark positions (1–14) on an *Andrena barbara* wing with relevant veins and cells. Veins: B = basal, Cu = cubitus, Rc1 and Rc2 = first and second recurrenents, and tm = transverse medial. Cells: 1d, 2d, 3d = 1st, 2nd, and 3rd discal cells; sm = submarginal cells.

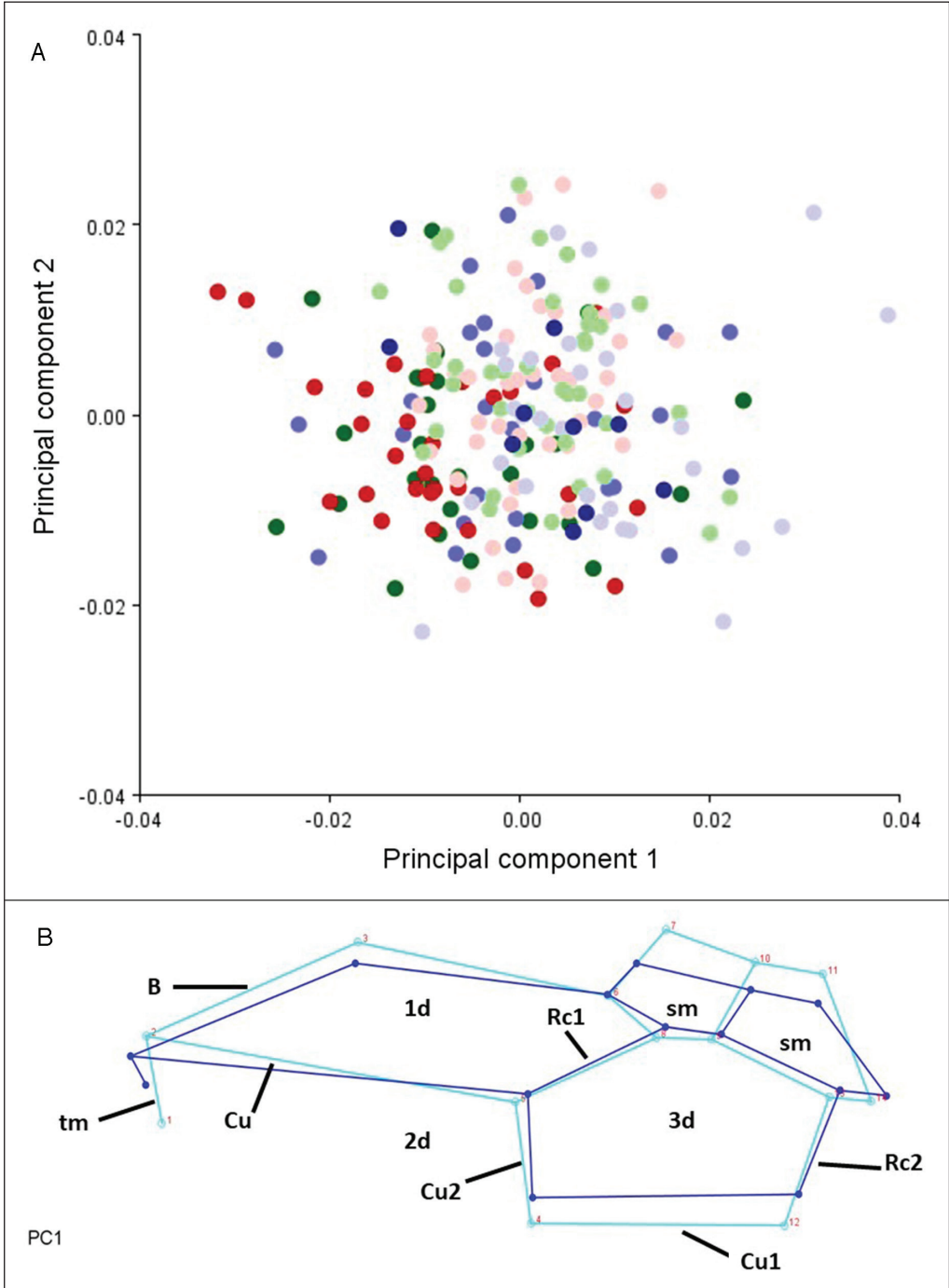


Figure 3. (A) Principal components graph of Procrustes coordinates depicting changes in wing shape. Data is color coded by bee collection location. (B) Shape frame depicting greatest variation in wing shape captured by PC1. Light blue lines indicate landmark positions with relevant wing veins and cells marked. Dark blue lines indicate overall change in shape in study population.

for aerodynamic stability and transporting hemolymph throughout the structure (Wootton 1992). Larger wings can generate more lift and allow organisms to fly longer distances (Taylor and Merriam 1995). We hypothesized that urban habitats may favor adaptations associated with shorter flight distances due to concentrated floral resources associated with urban gardens or restricted areas for foraging due to high ambient temperatures. This may especially be the case due to *A. barbara*'s behavior. Studies on other *Andrena* species show that the ground-nesting species displays sedentary behavior with short dispersal ranges (Franzén et al. 2009). Our study presents a possibility that *Andrena* species' limited dispersal makes them well adapted to urban habitats. Therefore, we might expect *A. barbara* to experience weak selective pressure on wing morphology. Alternatively, the degree of variation in wing shape and size in the population may serve as an adaptive response to urbanization: large-winged individuals have relatively greater dispersal ability across fragmented resources, whereas small-winged individuals can survive in fragmented habitats once populations are established (Kotze and O'Hara 2003). Comparing across bee species with varying dispersal abilities and foraging strategies will provide further insight in how bee wings adapt to urban environments.

Our sample size was modest and the city we studied, Raleigh, is relatively low density (compared, for example, to New York City), we caution against extrapolating any broad generalizations from our particular result. For instance, other urban

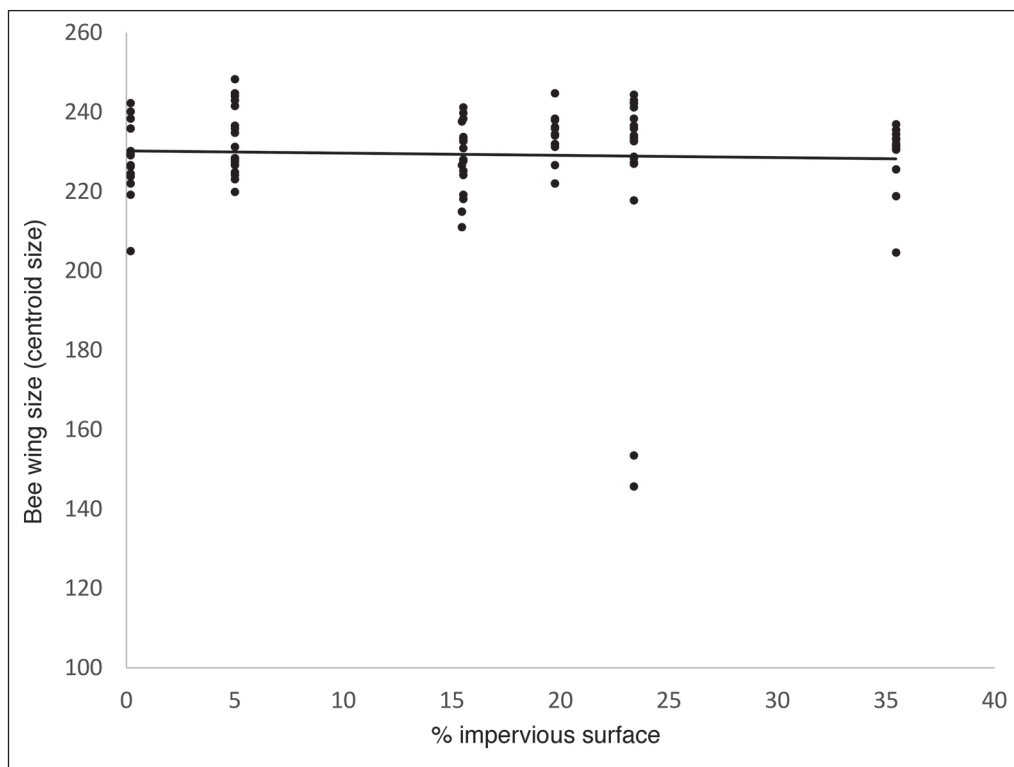


Figure 4. Regression analysis of bee wing size across an urban gradient. Wing size did not significantly vary with increasing urbanization ($n = 102$, $r^2 = 0$, $P = 0.65$).

landscape features such as diversity and size of vegetation patches, nest site availability, and floral resources would provide a more nuanced picture of the urban bee morphology. However, our finding is consistent with a recent study that found that body size and asymmetry varied little in the solitary bee *Anthophora plumipes* (Pallas) (Hairy-footed Flower Bee) collected in urban areas compared to rural areas (Banaszak-Cibicka et al. 2018). In light of cities becoming a prominent feature in terrestrial ecosystems, our study highlights the need for further research on how city design can potentially drive morphological adaptation in bees.

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