

Opposing pressures of climate and land-use change on a native bee

Evan P. Kelemen  | Sandra M. Rehan 

Department of Biology, York University,
Toronto, ON, Canada

Correspondence

Evan P. Kelemen and Sandra M. Rehan,
Department of Biology, York University,
Toronto, ON M3J 1P3, Canada.

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Abstract

Anthropogenic activities are rapidly changing the environment, and species that do not respond face a higher risk of extinction. Species may respond to environmental changes by modifying their behaviors, shifting their distributions, or changing their morphology. Recent morphological responses are often measured by changes in body size. Changes in body size are often attributed to climate change, but may instead be due to differences in available resources associated with changes in local land-use. The effects of temperature and land-use can be uncoupled in populations of the small carpenter bee *Ceratina calcarata*, which have experienced changes in agricultural and urban cover independent of climate change. We studied how the morphology of this bee has changed over the past 118 years (1902–2019) in relation to climate change and the past 45 years (1974–2019) in relation to agricultural and urban cover. Over this time, summer temperatures increased. We found that male and female size decreased with increasing temperature. Male size also decreased with agricultural expansion. Female size, however, increased with agricultural expansion. These results suggest that rising temperatures correlate with a decrease in female body size, while, opposite to predicted, agricultural land-use may select for increased female body size. These opposing pressures act concurrently and may result in bee extirpation from agricultural habitats if selection for large sizes is unsustainable as temperatures continue to increase. Furthermore, this study emphasizes the need to consider multiple environmental stressors when examining the effects of climate change due to their interactions.

KEYWORDS

historic data, land-use change, latitudinal range, museum specimens, wild bees

1 | INTRODUCTION

Anthropogenic activities have caused rapid changes in the environments in which species find themselves (Stocker et al., 2013). These environmental changes threaten a species' chances of survival (Dirzo et al., 2014), and those species that do not respond are likely to go extinct (McCarty, 2001). Species have responded by changing the timing of major life-history events and by shifting their distribution

(Walther et al., 2002). Species have also responded morphologically, often observed as changes in body size (Caruso et al., 2014; Merilä & Hendry, 2014; Oliveira et al., 2016; Tseng et al., 2018; Weeks et al., 2019; Yom-Tov & Geffen, 2011). Body size is an ecologically important trait of a species (Bennett, 1984; Calder, 1996), as it correlates with many ecological and physiological features, including metabolism (Brown et al., 2004), fecundity (Paine, 1990), dispersal distance (Jenkins et al., 2007), and survival (Lindstedt & Boyce, 1985).

In animals, body size has been reported to decrease with climate change (Caruso et al., 2014; Polidori et al., 2020; Tseng et al., 2018; Van Buskirk et al., 2010; Weeks et al., 2019), but the mechanism by which climate change drives the change in body size remains elusive.

There is generally a negative relationship between environmental temperature and body size. This relationship is often exhibited due to a plastic response by an organism developing under different temperatures, known as the temperature-size rule (Atkinson, 1994). Smaller body sizes at warmer temperatures are attributed to increased metabolic rates, which shorten development times, and cause adults to achieve smaller sizes at maturity (Davidowitz et al., 2004; Gillooly et al., 2001, 2002). This temperature-size rule has been suggested to cause geographic gradients in body size resulting in large-body species in colder environments and smaller size species in warmer environments (Bergmann's rule) (Bergmann, 1847). Therefore, recent changes in body size that correlate with changes in temperature are often attributed to climate change (Caruso et al., 2014; Polidori et al., 2020; Tseng et al., 2018; Van Buskirk et al., 2010; Weeks et al., 2019). However, the exact causes of these patterns remain highly debated (Merilä & Hendry, 2014; Yom-Tov & Geffen, 2011), as recent changes in body size may be due to climate-driven changes in resource abundance (Goodman et al., 2012). Therefore, rising temperatures may only indirectly influence body size by reducing available resources (De Boeck et al., 2008). Reduced resources may result in smaller body sizes through selection or by stunting growth during development (Davidowitz et al., 2004; Gienapp et al., 2008). From a conservation standpoint, understanding whether species are responding to changes in climate or resource abundance will help inform efforts to mitigate the effects of these anthropogenic threats.

One group that is under particular threat from anthropogenic changes includes bees. Worldwide native bees are declining (Bartomeus et al., 2013; Freitas et al., 2009; Jacobson et al., 2018; Mathiasson & Rehan, 2019). These losses are widespread and occur in both social and solitary species (Mathiasson & Rehan, 2020) and are projected to accelerate (Sirois-Delisle & Kerr, 2018). Bees face myriad threats, with climate change being of ubiquitous concern (Bommarco et al., 2011; Cameron & Sadd, 2019; Kennedy et al., 2013; Potts et al., 2010). Populations are also facing changes in local resource abundances and community dynamics brought on by urbanization and expansion of agricultural lands (Kennedy et al., 2013; McCune et al., 2020; Potts et al., 2010). Wild bees are important pollinators, and declines in their populations have potentially widespread ecological and economic impacts (Fijen et al., 2018; Garibaldi et al., 2016; Hoehn et al., 2008; Klein et al., 2007). Bees have been responding to these anthropogenic changes through shifts in their phenology, range, and behavior (Bartomeus et al., 2011; Mathiasson & Rehan, 2020; Schweiger et al., 2010). Furthermore, bees have been responding morphologically. Over the past century, the size of bees broadly has decreased (Bommarco et al., 2011; Miller-Struttman et al., 2015; Nooten & Rehan, 2020; Oliveira et al., 2016), but this response is not universal, and some have even increased in size (*Bombus* spp queens in Belgium; Gérard et al., 2020).

In bees, body size is closely related to their mobility and resource use. Larger bees can forage further (Greenleaf et al., 2007), at lower temperatures (Peters et al., 2016), and collect more floral resources than smaller bees (Spaethe & Weidenmüller, 2002). However, larger bees need more resources to survive and produce offspring (Müller et al., 2006). Temperature and resource abundance, therefore, are especially powerful drivers of body size evolution, as these factors create size-dependent trade-offs and give rise to size-dependent selective pressures. Indeed, changes in these selective pressures may explain why wild bees have been decreasing in body size over the past century (Miller-Struttman et al., 2015). Warming local temperatures may relax selection for larger bees (Bishop & Armbruster, 1999), or decreasing floral abundance may select for smaller bees (Oliveira et al., 2016). Additionally, smaller body sizes may be environmentally induced by developing under warmer temperatures (Radmacher & Strohm, 2011) or with fewer nutrients (Radmacher & Strohm, 2010). Bees have experienced reduced wildflower resources due to increases in agricultural cover (Langlois et al., 2020; Nooten & Rehan, 2019). Therefore, changes to bee body size may be due to differences in land-use (Falcone et al., 2018). To decouple the effects of changing climate and land-use on body size, a system is needed where both factors can be measured separately. The small carpenter bee (*Ceratina calcarata*) provides the opportunity to uncouple the intertwined effects of temperature and land-use.

The small carpenter bee, *C. calcarata*, is well represented in museum collections, including populations that have experienced different levels of anthropogenic change. *C. calcarata* is a stem nesting bee endemic to eastern North America (Rehan & Sheffield, 2011) that is among the top 10 most common species in the Northeast (Nooten et al., 2020). It is a polylectic bee, visiting 27 plant families, with the most common family being *Anacardiaceae* which is also their nesting substrate (Lawson et al., 2016). This species is subsocial, with prolonged maternal care and mother-offspring interactions (Rehan & Richards, 2010). This abundant bee is present in museum collections with populations sampled across its range dating back 118 years. These populations exist across a thermal gradient and have experienced different land-use regimes. The extensive collection of museum specimens provides an unrivaled opportunity to investigate the morphological response of *C. calcarata* to climate change among populations experiencing different levels of agricultural land-use and urbanization.

This study provides a rare opportunity to determine if body size is changing due to increases in temperature or changes in land-use. Using museum specimens of *C. calcarata*, we investigate if (a) temperature or (b) agricultural and urban cover influence adult size. If temperature affects bee body size, then body size should decrease with increasing temperatures. If agricultural land-use and urbanization affect bee body size by reducing available resources, then body size should decrease with increasing agricultural and urban cover. Consequently, this study will advance our understanding of the selective pressures shaping animal morphology in anthropogenically changing environments, with implications for land-use restoration and wild bee conservation.

2 | MATERIALS AND METHODS

2.1 | Morphological measurements

Specimens of *C. calcarata* were collected or loaned from 29 museums and personal collections (Table S1). Prior to inclusion in this study, we verified each specimen's taxonomic identification and sex according to Rehan and Sheffield (2011). Samples included 2,460 individuals (883 males and 1577 females) and covered 118 years (1902–2019), an elevation gradient of 1397 m (0–1397), and a geographic extent of eastern North America; covering approximately 2155 km north to south, from Michigan to Florida (47.38 to 27.99 N), and 3287 km east to west, from Nova Scotia to Oklahoma (60.75 to 97.71 W) (Figure 1; Figure S1; Table S1). For each specimen, we measured (a) head width, measured as the distance between the outer margins of the eye (Nooten & Rehan, 2020; Rehan & Richards, 2010), (b) intertegular width, measured as the distance between tegulae in a straight line across the bee's thorax (Greenleaf et al., 2007; Spaethe & Weidenmüller, 2002), and (c) right- and left-wing lengths, measured as the length of the intercostal veins (Nooten & Rehan, 2020) with a Nikon SMZ800n stereomicroscope with an ocular micrometer to an accuracy of 0.01 mm.

2.2 | Spatial data

Insects, including wild bees, are intimately tied to their microclimate and are sensitive to ever-changing environments (Radmacher & Strohm, 2010). *Ceratina calcarata* develop over the summer and overwinter in their natal nests above ground in dead pithy stems

as adults (Rehan & Richards, 2010). Therefore, *C. calcarata* experience an annual lag in response to resources and temperature. We analyzed climatic and spatial data for each specimen for the year prior to their collection. In particular, we examined average summer climates (June–August) as an indicator of the environment under which the bees developed. In parts of their range, *C. calcarata* may begin their development earlier than June, but, without detailed life-history studies from across their range, we conservatively used summer climate (Lawson et al., 2018). We obtained monthly temperature data with a resolution of 0.5° latitude by 0.5° longitude global grid (avg. 55 km²) from 1901 to 2019 from the Climate Research Unit (University of East Anglia, U.K.) as well as the monthly precipitation data, as precipitation can influence local floral abundances (Lambert et al., 2010). These monthly datasets were averaged per year to provide average summer temperatures and precipitations at each specimen's location.

Agricultural expansion and urbanization can reduce the abundance of wildflower resources (Steffan-Dewenter & Tscharntke, 2001). We obtained decadal land-use data for the United States from 1974 to 2012 (Falcone, 2015) and for Canada from 1990 to 2010 (Agriculture and Agriculture Food Canada, 2015) at a resolution of 60 m and 30 m, respectively. For analyses using land-use data, we only included specimens ($n = 1316$) that occurred within the decadal timeframe of available data for each location (1974 to 2019 US and 1990 to 2019 Canada). Specimens were binned by the intervals of the land-use data. We determined the foraging habitat of each specimen by calculating the percentage of land within a circular buffer of 500 m centered on each specimen's location that was classified as agricultural land (Production, Crops, Cropland), as well as the percentage that was urbanized (Developed, Semi-Developed,

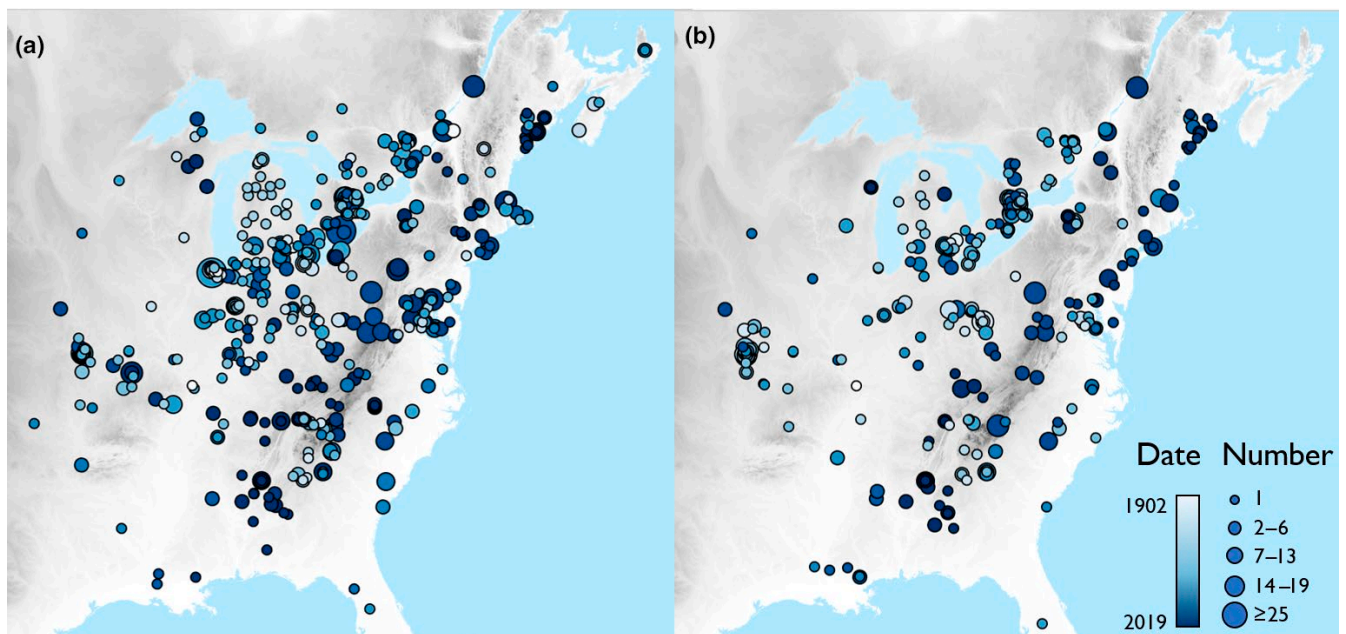


FIGURE 1 The distribution of (a) female and (b) male *Ceratina calcarata* specimens analyzed across their eastern North American range and dating back 118 years (1902–2019). The maps show elevation from white at sea level to dark grey at high elevation (Fick & Hijmans, 2017) [Colour figure can be viewed at wileyonlinelibrary.com]

Settlement, and Roads). Small bees like *C. calcarata* have short foraging ranges, on average 100–200 m (Zurbuchen et al., 2010). However, there is some evidence that bees increase their foraging range when flowering plant species richness is low (Jha & Kremen, 2013). Therefore a 500 m radius around a sampling location provides an estimate of the foraging range for each specimen.

Furthermore, elevation can influence shifts in bee body size (Nooten & Rehan, 2020). To control for effects of elevation, we obtained elevation data from WorldClim 2.0 dataset with a 30 second resolution (avg. 72.25 m) (Fick & Hijmans, 2017). We analyzed all spatial data in ArcGIS pro 10.7 (ESRI, 2011).

2.3 | Statistical analyses

Our statistical analyses were conducted in R 3.2.5 (R Development Core Team, 2013). This study aimed to use the morphological measurements to elucidate if any changes in specimens over time are associated with summer temperature or agricultural and urban cover. We determined the co-linearity between these morphological measurements by calculating Pearson's correlation coefficient (r). We also tested if summer temperature and agricultural and urban cover changed over time across the geographic extent of the specimens collected. This geographic extent was the smallest rectangle that included all the specimens in this study. We tested for changes in summer temperature over time by regressing the average yearly summer temperature against year. We tested for changes in land-cover over time using a linear mixed model with the percentages of target land-cover (agricultural or urban) as the response variable, year as the predictor variable, and country as a random factor. For the linear mixed model, we used the package nlme (Pinheiro et al., 2017) and calculated the pseudo- r^2 using the package piecewiseSEM (Lefcheck, 2016).

We analyzed the effects of temperature, precipitation, land-cover (agricultural or urban), and year on morphology using linear mixed models. The periods for which we have data for climate (1901–2019) and agriculture cover (1974–2018) are not the same, and therefore we used two models for our analyses. The morphological measurement was our response variable, and the test variables (summer temperature, precipitation, and year; agricultural cover, urban cover, and year), and sex were our predictor variables. We controlled for spatial and altitudinal effects by including elevation and a residual auto covariate (RAC), as a substitute of latitude and longitude to address spatial autocorrelation (Cruse et al., 2012) in our models. Collection site was included as a random factor to control for the measurement of multiple individuals at a given location. We included the interaction between the test variable and sex as a predictor variable when doing so generated a model with a lower AIC compared to a model excluding this interaction (Burnham & Anderson, 2002). These models differed from the next closest model by $>2\Delta\text{AIC}$. We also analyzed if the variation in body size we observed increased over time. We used a log-likelihood ratio test to test if a model with heterogeneous variance better fit the data than a nested model without heterogeneous variance (Zuur et al., 2009). We modeled heterogeneous variances over time using

the weight function (varFixed). Following Zuur et al. (2009), we verified the underlying assumptions of all models by visually inspecting the residuals.

3 | RESULTS

Summer temperature and urbanization increased over time (Figure 2). The average summer temperature across the geographic extent of the specimens collected increased by 0.83°C over 118 years (1901–2018) ($F_{116} = -3.78$, $R^2 = .10$, $p < 0.001$). The average summer monthly precipitation increased by 10.61 mm over the 118 years ($F_{116} = 2.86$, $R^2 = .06$, $p = 0.01$). Urbanization increased by 1.91% over the 38 years (1974–2012) ($F_5 = 4.74$, conditional $R^2 = .03$, marginal $R^2 = .99$, $p = 0.005$). However, agricultural cover did not increase over the 38 years ($F_5 = -2.04$, $p = 0.10$), likely due to expansions in croplands west of the Mississippi River being offset by losses in the east from urbanization (Falcone et al., 2018).

3.1 | Effect of climate on body size

Measures of intertegular width, and right- and left-wing measurements were all correlated with head width (Pearson's correlation, $r = .94$ – $.96$). Therefore, we selected one measure—head width—for the analyses (although for other measurements see Table S2 and Table S3), as head width is strongly correlated with both adult bee live weights and dry weights and is a common measure of total body size in this species (Rehan & Richards, 2010). Henceforth, we refer to head width as “body size.”

Individuals of *C. calcarata* were smaller at warmer temperatures. *Ceratina calcarata* females ranged in head width from 1.44 to 2.35 mm with a coefficient of variation (CV) of 8.40%; males ranged from 1.31 to 2.08 mm with a CV of 6.86%. The body size of *C. calcarata* decreased with increasing summer temperatures (effect size -0.081 ± 0.0015 mm per 1°C increase, $F_{1932} = -5.28$, $p < 0.001$; full model Table S4; Figure 3). Female body size decreased by approximately 0.42%, and males by 0.45% per 1°C increase. Female body size did not change significantly with elevation. Males were found to be smaller than females (effect size -0.2240 ± 0.0066 mm, $F_{1932} = -33.8$, $p < 0.001$). Male body size was on average 12.44% smaller than female size. The body size of *C. calcarata* was not affected by precipitation ($F_{1931} = -1.34$, $p = 0.18$; Table S4). These results were robust when analyzing the sexes separately, however, male size decreases less with temperature than females (Table S5 and S6).

3.2 | Effect of local agricultural and urban cover on body size

The body size of males and females was affected by agricultural cover but not by urbanization (Figure 4). Body size increased with agricultural cover (effect size 0.0007 ± 0.0003 mm per percent

FIGURE 2 Temperature and land-use change through time. Summer temperatures increased from (a) 1901–1921 to (b) 1998–2018. Urbanization but not agricultural cover increased across eastern North America from (c) historic data (1974–1990) and (d) contemporary land-use (2010–2012) [Colour figure can be viewed at wileyonlinelibrary.com]

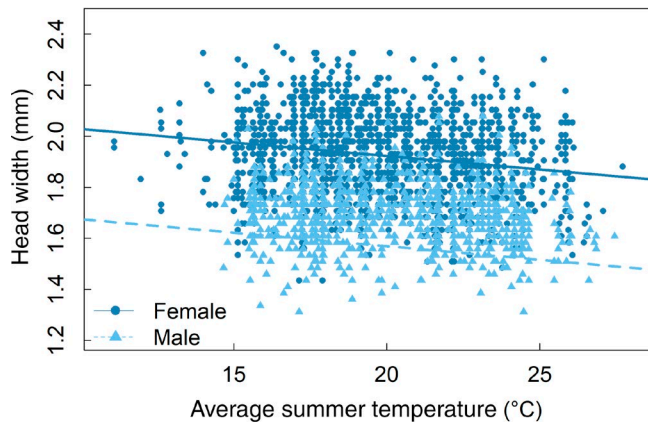
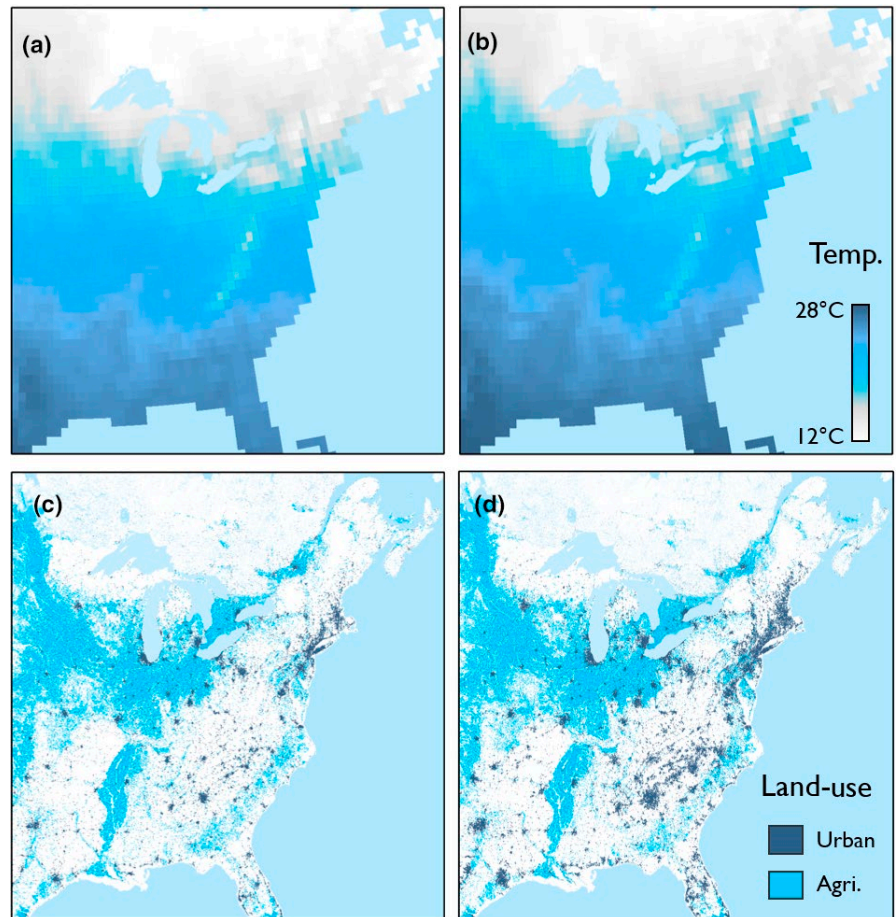


FIGURE 3 Body size of *Ceratina calcarata* was negatively correlated with summer temperature [Colour figure can be viewed at wileyonlinelibrary.com]

increase in agricultural land, $F_{1119} = 2.22$, $p = 0.03$; full model Table S7). This change equates to females and males collected in an agricultural landscape being 3.63% and 4.16% larger than those collected where there was no agricultural cover. Therefore, temperature and agricultural cover exert conflicting pressures on body size (Figure 5).

Interestingly, urbanization did not influence the size of *C. calcarata* males and females ($F_{1119} = 0.01$, $p = 0.31$; full model Table S7). When males and females were analyzed separately, only female

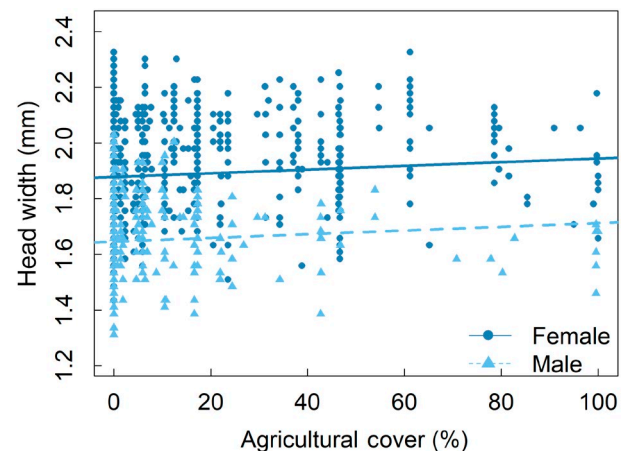


FIGURE 4 The body size of *Ceratina calcarata* increased with the percentage of agricultural land within 500 m of the collection location [Colour figure can be viewed at wileyonlinelibrary.com]

size increased with agricultural cover (Table S8 and Table S9). Male size also increased with elevation (Table S9).

3.3 | Temporal effects on body size

The average body size of *C. calcarata* has not changed over 118 years (1902–2019; $F_{1932} = -0.25$, $p = 0.80$; full model Table S3) (Figure S2).

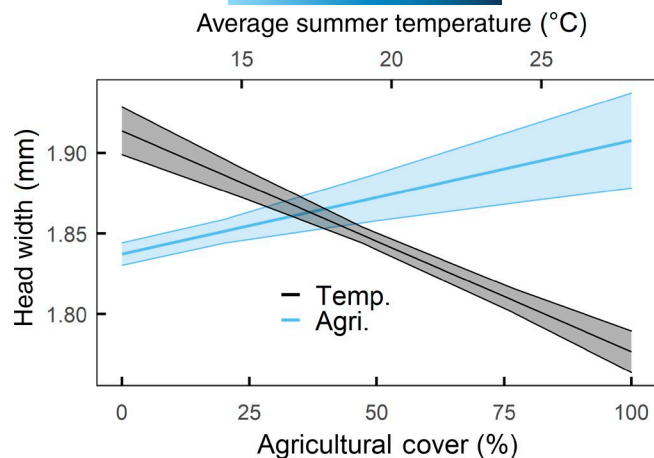


FIGURE 5 Summer temperature and agricultural cover exert conflicting pressures on body size. Lines represent the results of the linear mixed models (Table S4, S7), and the shaded region represents the standard errors [Colour figure can be viewed at wileyonlinelibrary.com]

Interestingly, body size has become more variable ($\chi^2_1 = 1.83$, $p < 0.001$).

4 | DISCUSSION

Here we show that the body size of *C. calcarata* is influenced by temperature and local agricultural cover. These two factors affected males and females differently. Male and female body size both decreased with increased summer temperatures. Greater agricultural cover also decreased male body size, but increased female body size. These opposing pressures on female body size may explain why the average size of *C. calcarata* has not changed over 118 years, but instead, *C. calcarata* has become more variable in size as summer temperatures have increased.

Our study provides an example of why, despite links between body size and temperature, body size does not always decrease with climate change (Baar et al., 2018; Matsuda et al., 2019). Female body size of *C. calcarata* did not decrease over time despite temperatures increasing across the studied range, likely due to opposing pressure from local agricultural cover. Often temporal studies focus on changes in body size associated with one environmental factor (Caruso et al., 2014; Oliveira et al., 2016; Polidori et al., 2020; Van Buskirk et al., 2010; Weeks et al., 2019). However, we show that multiple environmental factors are acting on body size. Local environmental differences among populations examined may explain why the body size of some bee species have been recorded to decrease (Oliveira et al., 2016) as well as to increase (Gérard et al., 2020). It may also explain why temporal changes in body size are more evident in vertebrates (Caruso et al., 2014; Merilä & Hendry, 2014; Sheridan & Bickford, 2011; Weeks et al., 2019) than in insects (Baar et al., 2018; Matsuda et al., 2019; Tseng et al., 2018). Due to their smaller size, insects experience the landscape at a finer scale than larger animals, and there is greater environmental heterogeneity among populations. This environmental heterogeneity, along with the

high body size plasticity in insects, creates considerable intrapopulation variation in body size that can make it hard to detect changes due to different environmental factors (Baar et al., 2018; Blanckenhorn, 2009).

Our findings support the negative relationship between body size and temperature. This result is in accordance with the temperature-size rule, as lower temperatures slow growth, and larger sizes are obtained at maturity (Atkinson, 1994). Larger sizes may also be found in colder climates because they benefit animals through minimizing heat loss by decreasing surface area to volume ratios or for non-thermoregulatory reasons such as differential dispersal rates, starvation resistance, genetics, or chance (Blackburn et al., 1999; Blackburn & Hawkins, 2004). Animals generally exhibit the geographic relationship between size and temperature with larger animals found in colder climates (Bergmann's rule), but it is not universal (Bergmann, 1847; Blackburn & Hawkins, 2004; Salewski & Watt, 2017; Shelomi, 2012). Previous work in *C. calcarata* has found similar patterns, with individuals in colder northern populations being larger on average than those in warmer southern populations (Lawson et al., 2018). Bees in general, mostly conform to Bergmann's rule (Gérard et al., 2018) with bumble bees being a notable exception (Ramírez-Delgado et al., 2016; however see Scriven et al., 2016), possibly due to their thermoregulatory ability and active incubation of their developing young (Heinrich, 1974).

Additionally, we found sex-specific differences in responses to temperature, as male size is affected less by temperature than females. This variation between males and females could be generated by sex-specific differences in the plasticity of their growth rate and development time, and the physiological controls of these processes (i.e. differences in their endocrine system) (Stillwell et al., 2010). Sex-specific differences in response to temperature may explain why males in this study and male bees more broadly have not decreased in size in recent history (Oliveira et al., 2016).

Our study was the first to examine the effect of agricultural expansion on the body size of both male and female bees. Interestingly, we found that males and females differ in their response to increasing agricultural cover. There was a positive relationship between agricultural cover and female body size. Larger females could also be advantageous in an agricultural landscape. In bees, foraging range correlates with body size (Greenleaf et al., 2007). Larger females can cover more distance when foraging and therefore find floral resources in the depauperate agricultural landscape (González-Varo et al., 2013). In bees more broadly, morphological responses to increased agricultural cover appear to be idiosyncratic. Species size has been found to increase in agriculture (*Bombus* spp. queens; Gérard et al., 2020; *Andrena favipes* and *A. haemorrhoea*; Warzecha et al., 2016), which may be a response to habitat fragmentation and the need for increased dispersal ability between habitat fragments (Hillaert et al., 2018). Species size is known to remain stable (*A. cineraria* (males) Van Reeth et al., 2018; *A. dorsata* and *A. nigroaenea*; Warzecha et al., 2016), possibly due to large species being already able to cover great distances and small species requiring only small patch sizes. However, species size has also decreased (*Bombus* spp. workers; Persson & Smith, 2011; *A. nasonii*; Renauld et al., 2016), due to reduced floral resources in

expansive agricultural landscapes. These shifts in bee body size have ecological implications as bees are important pollinators. Pollination efficiency increases with pollinator size (Jauker et al., 2016; Willmer & Finlayson, 2014). Therefore, the larger body sizes we observed in *C. calcarata* females across agricultural sites may be beneficial economically, assuming bee abundances remain the same (Gardiner et al., 2010; Kennedy et al., 2013; Tucker & Rehan, 2018; Tuell et al., 2009). Male size, however, did not change with agricultural cover. These sex differences in response to agriculture may be linked to sex differences in winter survival. Females but not males have a size threshold under which they are unable to survive through winter (Rehan & Richards, 2010). Therefore, while male and female offspring are smaller in an agricultural landscape (Nooten & Rehan, 2019), only the males make it through the winter and are collected in surveys the following summer (Rehan & Richards, 2010).

Urbanization did not affect the body size of *C. calcarata*. The body size of *C. calcarata* might not be affected because ornamental plants in residential gardens, community gardens, and city parks provide adequate floral resources and nesting sites for bees (Frankie et al., 2005), supporting increasing abundances of *C. calcarata* in more urbanized landscapes (Martins et al., 2017). Increasing *C. calcarata* abundances are not universal with urbanization (McCune et al., 2020). It is possible that when resources are inadequate, *C. calcarata* may be present at lower abundance than at smaller sizes. Similar to our results, another apid bee *Anthophora plumipes* did not show any changes in body size along the urban gradient (Banaszak-Cibicka et al., 2018). However, urban bumble bees were smaller on average than rural workers (Eggenberger et al., 2019). The difference in bumble bees may be due to their larger size. Urban environments have been found to filter out bees species with larger body sizes (Banaszak-Cibicka & Żmihorski, 2012; Buchholz & Egerer, 2020; Wray et al., 2014), and when the larger species are present, they tend to be in lower abundances (Banaszak-Cibicka, 2014; Banaszak-Cibicka & Żmihorski, 2012). The limited resources available in urban settings may not be enough for larger species to properly nourish their offspring, stunting growth during the larval stage (Radmacher & Strohm, 2010).

In conclusion, we found that both temperature and agricultural cover affect the adult size of *C. calcarata*. Our results suggest that climate change is correlated to overall decreases in body size, while opposite to predicted, increased agricultural land-use, a proxy for declining resource abundance, may select for increased female body size. These two anthropogenic factors, while influencing body size in opposite directions, are acting concurrently. Larger body sizes are more advantageous in agricultural landscapes due to their ability to forage longer distances (Greenleaf et al., 2007). Concomitantly, increasing temperatures are then likely harmful, as they result in individuals achieving smaller sizes as adults (Davidowitz et al., 2004). This raises the question of how long a species can remain viable in some parts of its range as these two environmental pressures continue to diverge with climate change. Furthermore, this study highlights the need to examine multiple environmental factors across species' ranges to distinguish the relative role of land-use and climate change.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Evan P. Kelemen  <https://orcid.org/0000-0003-3600-9878>

Sandra M. Rehan  <https://orcid.org/0000-0002-6441-5155>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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