ORIGINAL ARTICLE

Effects of land use type and seasonal climate on ground nesting wild bees

Sabine S. Nooten[1,2] | Sandra M. Rehan[1,3]

[1]Department of Biological Sciences, University of New Hampshire, Durham, New Hampshire, USA

[2]Department of Animal Ecology and Tropical Biology, University of Würzburg, Würzburg, Germany

[3]Department of Biology, York University, Toronto, Ontario, Canada

Correspondence
Sandra M. Rehan, Department of Biology, York University, Toronto, ON, Canada.
Email: sandra.rehan@gmail.com

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Abstract

1. Agricultural intensification leads to wide ranging changes in habitats along with reduction in nesting site availability and flower resources for wild pollinators. Yet, little is known about the impact of these changes on functional traits of communal ground-nesting bees.

2. This study assesses the abundance and body size of a common and widespread North American ground-nesting bee, *Agapostemon virescens*, throughout three consecutive years at three land use types: (i) unmowed meadows, (ii) conventional pesticide use and mowed agricultural and (iii) organic pesticide-free mowed landscapes.

3. We found no difference in abundance among the three land use types, but body size of spring bees was smaller at farmlands than meadow sites. Body size also varied among years, and bees were smaller in years that followed warm and dry summer seasons. Spring bees were particularly small at organic farms in years following dry and warm summers.

4. Our results suggest that the smaller size of overwintering bees at agricultural lands could compromise their long-term survival. This study indicates that a higher frequency of dry and warm summers as a consequence of climate change can impede bee populations in the future.

KEYWORDS
Agapostemon virescens, agriculture, body size, farming practise, management, season

INTRODUCTION

Wild bees provide vital services in virtually all ecosystems. However, they are rapidly declining along with the pollination service they provide, with considerable losses in economic and biodiversity value (Aguilar et al., 2006; Breeze et al., 2016; Goulson et al., 2015; Kleijn et al., 2015; Klein et al., 2007; Potts et al., 2010). These declines are attributed to a multitude of human-induced disturbances, such as pathogens, agrochemicals, climate change and landscape modifications (Brown et al., 2016; Goulson et al., 2015; Winfree et al., 2009). The large-scale conversions of natural landscapes to farm lands combined with agricultural intensification prompt the loss of habitat and resources for wild bees; both are considered as major threats to native pollinators (Brown et al., 2016; Williams et al., 2010). Climate change

additionally exacerbates these negative impacts (Settele et al., 2016). Many wild bee taxa have already shown changes in seasonal activity, distribution and abundance in recent decades (Bartomeus et al., 2013; Mathiasson & Rehan, 2019), but the full extent of these effects on wild pollinators and their services may not yet be fully apparent (Kerr et al., 2015; Potts et al., 2010).

Declines are not uniform. Certain species are more susceptible than others, and this is linked to ecologically relevant functional traits. Key traits of declining species include large body size, small dietary and phenological breadth, sociality and typically ground nesting habits (Bartomeus et al., 2013; Nooten & Rehan, 2019b; Oliveira et al., 2016; Scheper et al., 2014; Williams et al., 2010). However, these traits respond to different environmental disturbances. In agricultural systems, soil disturbance like tillage and grazing negatively

impact below-ground nesting bees (Stein et al., 2020; Williams et al., 2010), whereas land use intensity, loss of preferred host plants and climate change negatively affect wild bee body size (Bartomeus et al., 2013; Burkle et al., 2013; CaraDonna et al., 2018; Grab et al., 2019; Nooten & Rehan, 2019a; Renauld et al., 2016). Furthermore, larger-sized bees have experienced greater declines than smaller ones, and their loss could disproportionately hamper pollinations services (Bartomeus et al., 2013; Larsen et al., 2005; Nooten & Rehan, 2019b; Oliveira et al., 2016). As body size is a key trait that rapidly responds to environmental changes (Chown & Gaston, 2010), it is well suited for comparative studies assessing the effects of agricultural land use intensity on wild bees.

The majority of crop-pollination services are provided by a few dominant species in the bee community, and these vary across space and time (Kleijn et al., 2015; Winfree et al., 2015). In North America, the bicoloured striped-sweat bee, *Agapostemon virescens* Fabricius (Hymenoptera: Halictidae), is a very common and widespread pollinator that provides services across multiple agroecosystems (Gardiner et al., 2010; Gibbs et al., 2017; Kennedy et al., 2013; Tucker & Rehan, 2017, 2018). This sweat bee is also one of the largest-sized members of this group and builds nests in the soil, where large aggregations with more than 100 individuals are formed (Abrams & Eickwort, 1981; Eickwort, 1981; Roberts, 1973). Nests are elaborate structures (Abrams & Eickwort, 1981; Roberts, 1973) and are susceptible to land management and soil disturbances, thus the bicoloured striped-sweat bee is a good candidate for comparisons between land use types with varying management intensities.

Here, we assess the effects of land use types and seasonal variation on a ground-nesting bee in agricultural ecosystems. The following questions were addressed. (1) Are bees more abundant in less intensely managed landscapes? (2) Do more intensely managed land use types negatively affect body size? (3) Do climatic differences between years influence body size? (4) Do spring and summer bees differ in body size? Based on previous assessments of farming practice on body size, we expect that bees are smaller at more intensely managed land use types (Grab et al., 2019; Nooten & Rehan, 2019a; Renauld et al., 2016) and less abundant (Nicholson et al., 2017). We further expect that bee body size will fluctuate between years, and that bees will be smaller in warmer years (CaraDonna et al., 2018).

METHODS

Study area

Three agricultural land use types were chosen in Strafford County, New Hampshire, USA (43.2383°N, 71.0236°W). These were categorized as meadow, organic and conventional farmland. Sites were located 4.5 km apart (to ensure that different bee communities were targeted), similar in size (~8 ha) and surrounded by extensive forests.

Three replicate sites were established for each land use type to collect bees for 3 years. At each replicate site, bees were sampled along three 100 m transects, totalling nine sampling transects per land use type. Conventional farming sites were located on farmland on which pesticides were applied, transects were adjacent to fruit and vegetable crops (apple, squash and melon). Organic farming sites were on farmland that did not use pesticides and transects were adjacent to fruit crops (strawberries, raspberries and apples). Meadow sites were located on non-agricultural land and not mowed, whereas farmland sites were frequently mowed.

Bee sampling

Bees were collected biweekly from May–September in three consecutive years (2015–2017), using pan traps following the protocol described in (Tucker & Rehan, 2016). Nine pan traps per transect with alternating colours (blue, yellow and white) were filled with soapy water and left on the ground for 8 h (08:00–16:00 h) on sunny low wind days. The traps were placed along low vegetation strips that served as walking paths through the sites. The vegetation consisted of a mix of low cover clovers and vetch, and there was no vegetation overgrowth or tall grass to impede visibility of traps to pollinators. Traps were retrieved by straining the contents of the nine pans per transect through a sieve and transferred into a jar filled with 70% ethanol. In total, 105 sampling events were carried out throughout the 3 years, resulting in $n = 297$ transect samples ($n = 106$ at organic farm sites, $n = 102$ at conventional farm sites, and $n = 89$ at meadow sites). The uneven number of traps is a result of some traps lost or destroyed due to disturbances, including farming and animal activity. Bee processing and taxonomic identification were conducted as in (Tucker & Rehan, 2018).

Climate data

To assess the effects of climate variability on bee body size, we accessed annual and monthly mean temperature and total precipitation from the nearest weather station (Durham, NH) for the years 2014–2017 from the National Centres for Environmental Information (NOAA, 2020). Monthly data were used to calculate seasonal mean temperature and precipitation amount for summer, (May–September) and winter (October–April).

Study species

The bicoloured striped-sweat bee, *A. virescens*, is a soil-nesting, common, native bee species throughout North America (Roberts, 1973). In the northeast, bees hatch in late summer, overwinter as adults and emerge in the spring (mid-May) of the following year to found new colonies and die in summer (mid-June) (Abrams & Eickwort, 1981).

LAND USE AND CLIMATE IMPACT GROUND-NESTING BEES

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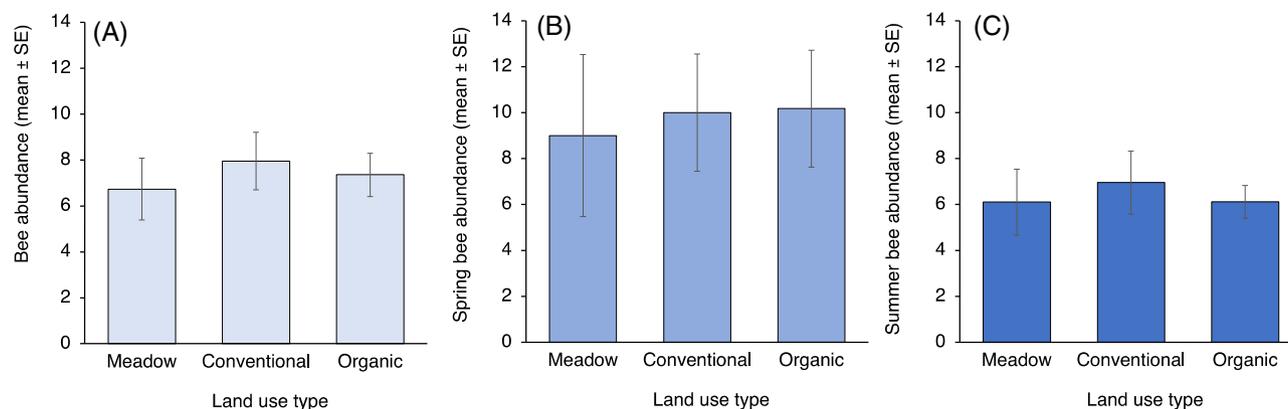
FIGURE 1 Abundance of *Agapostemon virescens* female bees at three land use types collected throughout three consecutive years (2015–2017), showing (mean $\pm$ SE per transect) for (a) overall bee, (b) spring and (c) summer bee abundance

The new brood emerges in July, mothers and daughters may overlap for about 3 weeks (Abrams & Eickwort, 1981). Thus, we categorized the bees collected from mid-May till mid-June as 'spring bees', representing bees enclosed in the previous year. Bees collected after mid-June till end-September were 'summer bees' hatched in the current year. Wing wear was scored to estimate age (Cartar, 1992) in increments from 0 to 5: young ('unworn') bees with no nicks or tears along the apical margins of their forewings were assigned a score of 0 and highly damaged ('worn') bees with completely shredded apical forewing margins a score of 5. Bees collected late spring with worn wings are 'spring' samples and those with unworn wings during this overlapping period are 'summer' samples.

Morphological trait measurements

A suite of morphological measurements was carried out on a range of *A. virescens* female specimens. A total of 840 individuals were measured for three body size traits: (1) head width, measured in full frontal view at the maximum width including the outer margins of both compound eyes (Rust, 1991); (2) inter-tegular distance (ITD), measured as the distance between both tegulae in a straight line across the bee's thorax (Cane, 1987) and (3) costal vein, measured in a straight line from the basal margin at the tegula to the distal end of the radial cell (Harder, 1982). The measurements were carried out using a Nikon SMZ800 stereomicroscope with an ocular micrometre to an accuracy of ~0.01 mm.

Data analyses

We calculated co-linearity between the three morphological measures using Pearson's *r*, to use one of these as a proxy for body size in the following analyses. To detect any influence of land use type or season on allometry, we calculated Pearson's *r* for each

morphological measure at each land use type and compared allometric slopes using an analysis of covariance (ANCOVA). To investigate the effects of land use type on body size, we used mixed effect models 'glmer' in *lme4*, with land use type as fixed effect and transects as random effects and nested in land use type (Bates et al., 2015; Zuur et al., 2009). Following the protocol by Zuur et al. (2010) for data distribution checks and model selection process based on the evaluation of model residuals, we selected a Gamma distribution for body size analyses. Effect of land use type on bee abundance was assessed in a similar fashion as described for body size but with a negative binomial distribution for overdispersed count data 'glmer.nb' (Zuur et al., 2010). We conducted each of these analyses for the abundance and body size of all, spring and summer female bees. Annual differences in bee body size for all, spring and summer bees were compared using mixed effect models, with a Gamma distribution 'glmer' in *lme4*, with years as fixed and transects nested in land use types as random factors (Bates et al., 2015; Zuur et al., 2009). Seasonal differences in body size were assessed in the same manner as described for annual differences but using season as the fixed effect. All statistical analyses were performed using the statistical software R (R Development CoreTeam, 2019).

RESULTS

Effect of land use type on abundance

Across 3 years, a total of 1310 *A. virescens* female bees were collected among three land use types. Bee abundance did not differ across the three land use types. There were on average (mean/transect) slightly fewer bees collected from meadow (mean $\pm$ SE; 6.73 ± 1.35) than from farm land sites (organic: 7.36 ± 0.94 and conventional: 7.95 ± 1.25, Figure 1a). This trend was repeated by spring bee (Figure 1b) and summer bee abundance (Figure 1c). Thus, there was no significant difference among the three land use types for overall
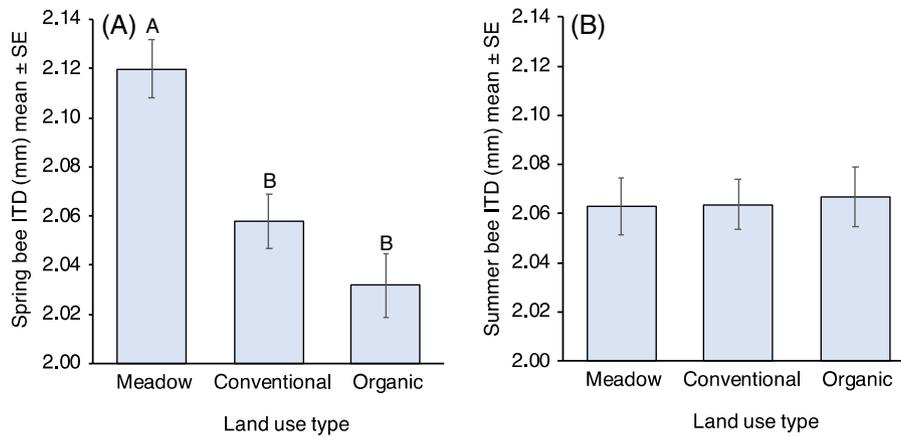
FIGURE 2 Body size of *Agapostemon virescens* female bees at three land use types including unmowed meadows, conventional pesticide application and mowed agricultural and organic pesticide free mowed landscapes. Inter-tegular distance (ITD) (mm) mean ± standard error (SE) for (a) spring bees and (b) summer bees is shown. Uppercase letters indicate statistical significance. Y-axis scales from 2.0

bee (Wald $\chi^2_2 = 0.476$, $p = 0.7882$), spring bee (Wald $\chi^2_2 = 0.083$, $p = 0.96$) and summer bee abundance (Wald $\chi^2_2 = 0.2124$, $p = 0.89$).

Effect of land use type on body size

The measures of head width and costa vein were closely correlated with ITD (Pearson's $r = 0.75$–0.85). As ITD is a commonly used measure of body size across a wide range of bee species (Bartomeus et al., 2013), this measure was used for the subsequent analyses and hereafter referred to as 'body size'. Overall, body size of *A. virescens* (measured as ITD) ranged from 1.53 to 2.54 mm and was not significantly different between land use types (Wald $\chi^2_2 = 3.12$, $p = 0.211$), and neither was summer bee body size (Wald $\chi^2_2 = 0.063$, $p = 0.97$; Figure 2b). Spring bees, however, were significantly smaller at farm lands (by 4%) than meadow sites (Wald $\chi^2_2 = 14.88$, $p < 0.001$; Table S1; Figure 2a).

We measured 840 *A. virescens* individuals comprising 315 spring and 525 summer bees. The measures of head width and costal vein were closely correlated with ITD (Pearson's $r = 0.75$–0.85). There was no effect of land use type on the allometric relationship between ITD and head width ($F_{2,834} = 1.982$; $p = 0.14$), ITD and costal vein ($F_{2,834} = 0.008$; $p = 0.91$) and head width and costal vein ($F_{2,834} = 2.853$; $p = 0.06$; Figure S1, upper panel). Season had a significant effect on the allometry for head width versus ITD ($F_{2,836} = 5.295$; $p = 0.02$), and versus costal vein ($F_{2,836} = 5.511$; $p = 0.02$),with spring bees having larger heads than summer bees. There was no significant effect for ITD versus costal vein ($F_{2,836} = 0.0195$; $p = 0.89$; Figure S1, lower panel).

Climatic variation among years and seasons

Temperature and precipitation varied annually and seasonally among the 3 years; 2015 and 2016 were drier (by 16%) in annual precipitation and warmer (by 5%) in mean summer temperature than 2014 and
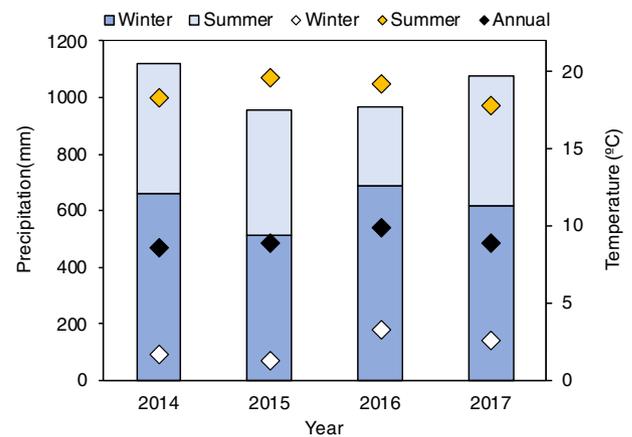
FIGURE 3 Climate data for Durham (NH, USA) for the years 2014–2017. Yearly amount of precipitation is shown as stacked bars, winter (dark blue) and summer (light blue), and mean temperature (°C) as diamonds, annual (black), winter (white) and summer (yellow) for each year

2017 (Figure 3, Table S2). Winter in 2015 was cooler and drier (Figure 3, Table S2).

Annual variation in body size

We found significant differences in bee body size among the 3 years. Bees in the first year of this study (2015) were on average significantly, by 3.2%, larger than in the following years (Wald $\chi^2_2 = 45.36$, $p < 0.0001$; Table S3; Figure 4a). Similarly, body size of summer bees was also, by 3.2%, significantly larger than in the other 2 years (Wald $\chi^2_2 = 25.59$, $p < 0.0001$; Table S3; Figure 4c). Spring bee body size differed significantly among years, with bees in 2015 being 3.1% larger than in 2017 and 4% larger than in 2016 (Wald $\chi^2_2 = 10.25$, $p = 0.006$; Table S3; Figure 4b). In addition, they showed a significant interaction between years and land use
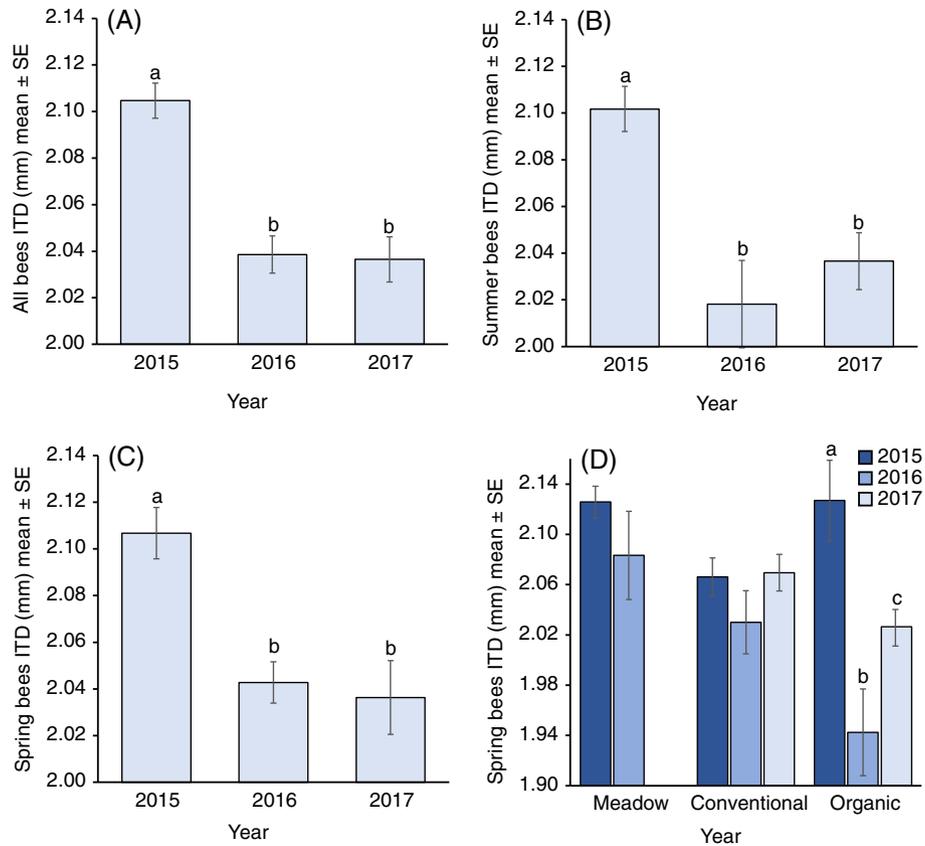
FIGURE 4 Body size of *Agapostemon virescens* throughout 3 years. Inter-tegular distance (ITD) (mm) mean ± standard error (SE) for (a) all female bees, (b) spring bees, (c) summer bees and (d) spring bees at three different land use types are shown. Uppercase letters indicate statistical significance. Y-axis scales from 2.0
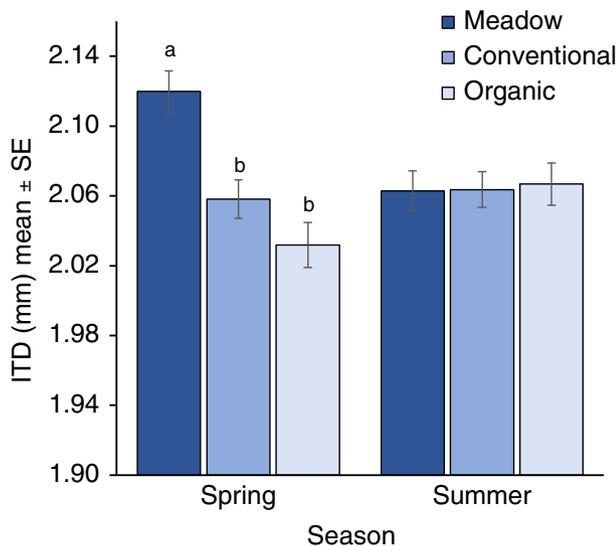
FIGURE 5 Body size of *Agapostemon virescens*. Inter-tegular distance (ITD) (mm) mean ± standard error (SE) for spring and summer female bees at three different land use types. Uppercase letters indicate statistical significance

types (Wald $\chi^2_2 = 10.25$, $p = 0.02$; Table S3; Figure 4d). Significant interactions were driven by size differences at organic farm land, where spring bees in 2016 were 9.5% smaller than in 2015 ($p < 0.001$), and 5% smaller than in 2017 ($p < 0.001$).

Seasonal variation in body size

On average, there was no significant difference in body size between spring and summer bees (Wald $\chi^2_1 = 0.001$, $p = 0.98$; 2.06 ± 0.01 mm). However, there was an interaction of season and land use type (Wald $\chi^2_1 = 12.21$, $p = 0.002$), with spring bees at meadow sites being 4% larger than spring bees at organic sites ($p = 0.018$) (Figure 5).

DISCUSSION

This study assessed the effects of land use type on the abundance and body size of *A. virescens*, a common and widespread ground-nesting wild bee in North America. We compared spring emerging and summer bees throughout three consecutive years between meadow, conventional and organic farm land. Contrary to our expectations, there was no difference in bee abundance among the three land use types. However, spring bees were smaller at farm lands, supporting previous trends of decreasing body size at intensely manged agricultural land use types (Grab et al., 2019; Nooten & Rehan, 2019a; Renauld et al., 2016). Body size varied annually, and bees were smaller in years that followed warm and dry summer seasons. This indicates that temperature extremes as a consequence of climate change can impede bee populations in the future (Graham et al., 2021; Settele et al., 2016).

Bees at agricultural land use types are smaller

Spring bees were 4% smaller at farms than at meadow lands, but there was no difference in the body size of summer bees among land use types. This indicates that any detrimental effects of agricultural land use might be particularly pronounced for overwintering individuals of this species. A reduction in body size in agricultural lands is also evident for other ground-nesting bees, for example, including the genera *Andrena*, *Halictus* and *Augochlorella* (Grab et al., 2019; Renauld et al., 2016). A separate study on an abundant stem-nesting bee (*Ceratina calcarata*) from the same region (NH, USA) showed a similar trend of smaller bees at farm land, but in summer bees rather than spring bees (Nooten & Rehan, 2019a). This supports previous findings on negative impacts of agricultural land use on wild bees and corroborates the importance of incorporating functional species traits, like body size, nesting habit and sociality in comparative analyses.

Bee body size underlies annual climatic variation

Body size fluctuated throughout the 3 years. Both spring and summer bees were 3% smaller in 2016–2017 than in 2015. There were also climatic variations among years; 2015 and 2016 were 16% drier in terms of annual precipitation and 5°C warmer as measured in summer mean temperatures than 2014. It is possible that the drier and warmer climate in 2015–2016 lead to smaller sized spring emerging bees in 2016–2017. In a separate study on the blueberry bee, *Osmia ribifloris*, rearing under warmer conditions resulted in decreased body mass (CaraDonna et al., 2018). Here, we found an interaction between years and land use types for bee body size. Spring bees were particularly small at organic farm land in 2016–2017. It is possible that other factors at organic farm land, such as flower strips as alternate forage and nesting sites, which were not investigated here, influenced the bees' size. In addition, incorporating other climatic parameters, such as precipitation patterns and severe weather events into future analyses would be beneficial, as wild bees are affected by drought, heat waves and cold spells (Graham et al., 2021; Settele et al., 2016). This suggests that there are many avenues to pursue for disentangling relationships between body size and environment, and future studies should combine a larger suite of climatic variables with nesting site and resource availability.

Allometry differs between spring and summer bees

The three measures of body size, ITD, head width and costal vein, scaled in a similar fashion at meadow and farm lands, indicate that land use type does not influence allometric relationships of these bees. However, allometric relationships differed between spring and summer bees for ITD versus head width and head width versus costal vein. This suggests that spring bees, which are predominantly overwintering females, have a different morphology than summer bees. However, no physiological caste differentiation was previously determined in this species (Abrams & Eickwort, 1981), and future studies could investigate allometric relationships more thoroughly by including additional body size traits, such as legs, wings and antennae alongside reproductive status, wing and mandibular wear among females.

CONCLUSION

Ground-nesting wild bees comprise the majority of the wild bee fauna in agroecosystems providing invaluable pollination services (Antoine & Forrest, 2020). However, management intensity of agricultural land use types has generally detrimental effects on wild bee diversity. This study shows that spring bees of the ground-nesting bicoloured striped-sweat bee are smaller at more intensely managed farm lands. In addition, body size fluctuates seasonally, and warmer and drier summer seasons can lead to smaller spring bees in the following year. Our results indicate that land use and climatic variables can significantly affect wild bees in each season and that it is vital to include functional traits in future studies.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

AUTHOR CONTRIBUTIONS

Sabine S. Nooten and Sandra M. Rehan designed the project, Sabine S. Nooten collected and analysed the data, Sabine S. Nooten wrote the paper and Sandra M. Rehan wrote and edited the article.

DATA AVAILABILITY STATEMENT

Specimens are avaialable upon request from the Rehan lab at York University

ORCID

Sabine S. Nooten https://orcid.org/0000-0002-1798-315X
Sandra M. Rehan https://orcid.org/0000-0002-6441-5155

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Table S1. Summary of mixed effect generalized linear models (glmer) for *A. virescens* spring female bee body size at three land use types. Shown are the model coefficient (Estimate), standard error (SE), z value, p value ($P(>|z|)$) of the Chi^2- Statistic; number of observations n = 315; transects n = 9.

Table S2. Climate data for Durham (NH). Summary of (A) annual mean temperature and yearly precipitation, and (B) summer and winter seasonal mean temperature and precipitation amount.

Table S3. Summary of mixed effect generalized linear models (glmer) for *A. virescens* body size for (A) all, (B) spring and (C) summer female bees for three years. Shown are the model coefficient (Estimate), standard error (SE), z value, p value ($P(>|z|)$) of the Chi^2- Statistic; number of observations: all (n = 850), spring (n = 315) and summer bees (n = 525); transects n = 9.

Figure S1. *A. virescens* allometry. Relationships between head width, costal vein and intertegular distance (ITD) of female bees at (A-C) three land use types and (D-F) in two seasons. The three body size measures are significantly correlated (Pearson's r = 0.75–0.85; $P < 0.0001$). There were no differences between land use types or seasons. Straight lines show significant relationship (at $P < 0.05$), grey shaded areas show 95% confidence interval.