

The Effect of Land Use Gradient on Adult Body Size of Bees in Eastern Tennessee

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ABSTRACT

With the intensification of agricultural practices, bee habitats are undergoing changes, impacting the nutritional quality of resources available to bee larvae and leading to variation in adult body sizes. Because larger bee species can forage at greater distances from their nests, we predicted that intraspecific body size would respond differently to agricultural land use gradient depending on bee size at the species level. Our study emphasizes the effect of a varying agricultural land use gradient on adult body sizes of bees. Our experiment took place in East Tennessee where we established twenty plots each containing 18 native plant species, at five sites of varying agricultural land-uses, ranging from 6-48% agriculture. During the summer, using an insect vacuum, we collected 11,183 insects representing 99 bee species interacting with these native plants. We then haphazardly selected adult bees from 13 species that were found at all sites to measure their body size via intertegular distance (ITD). We found that the intraspecific adult body size of larger bees, such as *Bombus impatiens*, increased along with agricultural land use in the surrounding landscape. The body size of small and medium sized bee species did not change along the agricultural land use gradient. This indicates that agricultural land use affects bee species differently. Larger bees are able to forage at greater distances from their nests and carry more provisions, which might make them more resilient to agricultural land use. Smaller bees may be less resilient because they cannot forage as far. This is critical to consider for future landscape management practices to best ensure the pollination of crops.

KEYWORDS

Pollinator Health; Wild Bees; Agriculture; Conservation; Spatial Ecology; Social Bees; Intertegular Distance; Land Use Change

INTRODUCTION

As the human population continues to grow, so does the demand for higher yielding agricultural areas, which are designed to produce the most food efficiently. However, there is a toll with this increased agricultural demand. To increase crop yield, most agricultural areas manage the land using pesticides and also decrease the amount of floral resources and wild habitat available to insects.^{1,2} These changes to the land can harm beneficial insects, such as the main pollinators for these agricultural areas.^{3,4} Wild insects, such as bees, provide a pollination service to 35% of the global crop production.⁵ Agricultural practices can affect bee species by reducing the amount of habitat available to them during agricultural intensification. However, not all bee species are equally impacted by these changes.⁶ In response to agricultural intensification, communities of some bee species are increasing, while others are declining⁴.

The different responses of bees to agricultural intensification could be linked to life history traits. For example, bees can be social, living in large colonies, or solitary, living independently. Social bees have a colony structure comprised of a queen bee, female worker bees, and their brood. Social bees are successful and abundant, with large populations.⁷ The larvae of social bees receive parental care until they pupate and eclose as adults to fill their new role in the colony.⁸ In a social bee colony, worker bees forage daily for pollen and nectar provisions for growing young.⁹

The larvae of solitary bees depend entirely on the quality and quantity of provisions provided by the nesting female and are not tended to by workers.^{10,11} A female solitary bee makes nest chambers in dirt, sand, logs, or other substrates to lay her eggs. She then packs the chambers with foraged pollen and nectar so the larvae can survive until the following season. The female bee does not return to the nest to care for her brood. Solitary bees are more diverse in terms of number of species.¹¹

In both social and solitary bee species, the higher the quantity and quality of nutrients the larvae obtain, the larger and healthier they will be when they mature.¹² Thus, adult body size in bees can be associated with the availability of nutritional resources in the

area surrounding the nest or colony site.^{13,14} When resources are limited or low in quality, larval provisions are smaller, resulting in smaller adult body sizes.¹³ Conversely, when there are plentiful, high quality floral resources within the foraging range, larval bee growth will improve due to the abundance of nutrients, resulting in larger adult bees.^{13,15} It is also possible that other attributes, such as specialization or sociality, of the bees themselves may affect their ability to collect high quality floral resources. Land use can have a large effect on the species richness, abundance, and identity of bee species.^{3,6} Habitat and landscape heterogeneity appear to support many species of pollinators. Increased agricultural habitat can limit floral diversity in bee-collected pollen provisions, which can lead to fewer bee offspring produced.¹⁶ Some bee species can tolerate high agricultural intensities because larger adult body size allows bees to forage farther distances.¹⁷ Overall, certain pollinators may be better adapted to urbanized areas while other pollinators are better adapted to agricultural areas.

Certain life history traits of bees can determine their response to land use.¹⁸ The large social bumblebees, *Bombus* spp., for example, can travel further in agricultural landscapes that have fragmented patches of floral habitat and hold more provisions than their smaller, solitary bee counterparts due to their larger body size.¹⁹ Some *Bombus* spp. can thrive in agricultural landscapes because they are resilient to habitat fragmentation.²⁰ Because they are generalist foragers, they may be collecting pollen both from the agricultural crops themselves and from surrounding patches of floral resources. Smaller bees, however, prefer areas with high species richness and abundance of floral display, like urban greenspaces.²¹ As the intensity of monocultural farming practices increases, habitat diversity decreases.²² Lack of habitat diversity can lead to decreases in richness and abundance in smaller bee species in high intensity land uses.²¹

Most studies focus on abundance and richness of pollinators in landscapes with high urban or agricultural land use. ^{6,18,22-29} Our goal was to test whether the intraspecific body size of adult bees was affected by different land uses because adult body size in bees is determined by the size and quality of the pollen provision that the larvae feed on, and agricultural land use can affect the size and quality of the pollen provision.^{16,19} We therefore included a range of different land use types, from agricultural to urban. We collected bees in research plots set in five different land use types that varied in the proportion of agricultural land use at 2 kilometers from 6-48%. Our hypotheses were: 1) that larger-sized bee species would perform better (increased intraspecific body size) in agricultural areas, because their larger body size would allow them to successfully forage longer distances, 2) that smaller-sized bee species would not perform as well (decreased intraspecific body size) in more agricultural landscapes, because they would be less resilient to the fragmented and resource-poor agricultural landscapes. To test these predictions, our methods included measuring the intertegular distance (ITD) of 13 bee species collected along an agricultural land use gradient.

Material and Methods

Site selection

We used ESRI ARC GIS mapping tools to select five sites in eastern Tennessee across an agricultural land use gradient at a 2 km radius.³⁰ The five sites were the UTK Gardens (UTG), UTK Arboretum (UTA), UTK Organic Crops Unit (UTO), and two sites at the Plateau AgResearch Station in Crossville, TN (UTP1 and UTP2). These locations ranged in agricultural land use from 6% (UTG) to 48% (UTP1) (Table 1).

Site	Meters	Proportion Agriculture	Proportion Urban	Proportion Seminalural	Location Description
UTG	2000	0.06	0.60	0.23	Downtown Knoxville
UTA	2000	0.12	0.29	0.55	Forest near Oak Ridge
UTO	2000	0.32	0.15	0.49	Organic agriculture
UTP2	2000	0.38	0.05	0.55	Mixed agriculture
UTP1	2000	0.51	0.06	0.41	Cattle pasture

Table 1. The proportion of agricultural, urban, and seminalural land use around the surveyed sites. Using GIS, and the NLCD, we classified land use within a 2 km radius around each site.

Plot design

At each site, we established four common garden plots of six species from each of three plant families (Asteraceae, Fabaceae, Lamiaceae), and a mixed plot containing two species from all three families. Each plot contained the same native, perennial flower species across different sites. Each plot contained four individuals of each of the six different plant species (Table 2).

Asteraceae	Fabaceae	Lamiaceae	Mixed
<i>Helianthus occidentalis</i> (Riddell)	<i>Amorpha herbacea</i> (Walter)	<i>Conradina verticillata</i> (Jennison)	<i>Helianthus occidentalis</i>
<i>Coreopsis lanceolata</i> (L.)	<i>Senna marilandica</i> (L.)	<i>Pycnanthemum muticum</i> (Michx.)	<i>Senna marilandica</i>
<i>Eurybia saxicastelli</i> (J.N. Campbell & M. Medley)	<i>Baptisia albens</i> (Small)	<i>Lycopus virginicus</i> (L.)	<i>Conradina verticillata</i>
<i>Stokesia laevis</i> (Hill)	<i>Lespedeza birta</i> (L.)	<i>Physostegia leptophylla</i> (Small)	<i>Baptisia. albens</i>
<i>Helianthus hirsutus</i> (Raf.)	<i>Baptisia tinctorial</i> (L.)	<i>Blephilia subnuda</i> (Simmers & Kral)	<i>Coreopsis lanceolata</i>
<i>Verbesina occidentalis</i> (Walter)	<i>Thermopsis villosa</i> (Walter)	<i>Collinsia canadensis</i>	<i>Pycnanthemum muticum</i>

Table 2. Plant species used in the experimental research plots.

Data collection

We observed each plant species in each plot once a week between the hours of 10 am and 4 pm as they bloomed over the summer season (May-August) for five-minute intervals in 2020 and 2021. Observations occurred on clear, sunny days above 12°C. During these five-minute intervals, we collected all insects that landed on the flower using an insect vacuum. The sampled insects were then placed into -20°C freezer for preservation and taxonomic sorting. Insects were pinned, labeled, and identified at the end of each season. Bees were identified to the species level and bee identifications were verified by Sam Droege (USGS). Specimens are vouchered at the University of Tennessee.

We haphazardly selected 25 - 134 females from 13 well-replicated (*i.e.*, at least 5 individuals present at each site) bee species from each of the five sites (between 93 – 171 females of all 13 species per site). The range is large because our lower limit to include a species was 25 females (5 at each site), but we measured as many individuals per species as possible. Some sites had many individuals of some species. The bee species included *Apis mellifera*, *Augochlorella aurata*, *Augochlorella persimilis*, *Augochloropsis metallica*, *Bombus impatiens*, *Ceratina calcarata*, *Ceratina strenua*, *Halictus confusus*, *Halictus ligatus/poeyi*, *Lasioglossum apocyni*, *Lasioglossum hitchensi*, *Lasioglossum imitatum*, and *Lasioglossum trigeninum*. In addition, we selected males from the two species for which males were most abundant, *Halictus ligatus/poeyi* (54 males measured) and *Halictus confusus* (47 males measured). In total, 744 individuals were selected. All species were considered eusocial, semi-social, or primitively social. No solitary bee species were included because they were not abundant enough to gain sufficient replication across all sites.

The length from the center of the left-wing base to the center of the right-wing base was measured and recorded for the results. Using LeicaS9D4DX microscope with an optical magnification of 40X, we measured the intertegular distance (ITD) in mm of each bee specimen. For smaller bee specimens, an increase of the magnification to 80X was needed. ITD has been shown to be a proxy for adult body size in bees.^{24,31} For each specimen, records of the collection plot, the species, the sex, and the ITD were transcribed. We found that the bees fell into three size classes: small (< 1.75 mm), medium (1.75 mm – 3 mm), and large (> 3 mm). Our preliminary analysis showed that the species in these size categories responded differently to land use, so we aggregated the bee species into these three categories and ran separate models for each size class. Each size class was represented by more than one species.

Data analysis

Using R version 4.3.2, we used generalized linear mixed effects models (GLMMs) in the package lme4 to analyze our data.^{32,33} We first built a model to see whether male and female bees (across all species) differed significantly from one another in body size. For this model, we used the ITD as the response variable, sex as the fixed effect, and the species identity as the random effect. For the purposes of this study, we were primarily interested in the effect of land use and did not expect the plot type or flower species where the bees were collected to directly affect their body size. Because there is a time lag of the effect of pollen quality on body size (*i.e.* the pollen determines the size of the next generation), the plant they are currently foraging on might not reflect the diet of the previous generation. We therefore used ITD as a response variable, agricultural land use at 2 km as a fixed effect, and bee species and sex as random effects. The agricultural land use at 2 km varied at the site level. We ran four separate models with this structure, one with all bees together and one for each size class of bees (small, medium, and large). Grouping bees in these size classes is commonly done in studies of the effect of land use.^{34,35} We did not test the effect of agricultural land use on each species individually because of low replication.

RESULTS

In the experiment, we collected a total of 11,183 insects over two seasons. Of those, 8,205 (~74%) were bees representing 99 species. From those collected bees, 13 species had enough specimens (i.e. at least 5 at each site) to obtain sufficient replication across the five sites. For each species, we recorded and measured the average ITD \pm standard deviation (SD) for both males and females (Table 3). Male bees were significantly smaller than female bees of the same species measured (effect size -0.13, $P < 0.001$, Figure 1).

Species	Female		Male	
	n	Average ITD	n	Average ITD
<i>Apis mellifera</i>	36	3.52 \pm 0.13		
<i>Augochlorella aurata</i>	43	1.79 \pm 0.17		
<i>Augochlorella persimilis</i>	57	1.40 \pm 0.11		
<i>Augochloropsis metallica</i>	25	2.58 \pm 0.17		
<i>Bombus impatiens</i>	48	4.23 \pm 0.53		
<i>Ceratina calcarata</i>	50	1.59 \pm 0.20		
<i>Ceratina strenua</i>	42	1.37 \pm 0.12		
<i>Halictus confusus</i>	36	1.65 \pm 0.12	47	1.50 \pm 0.12
<i>Halictus ligatus/poeyi</i>	134	1.91 \pm 0.12	54	1.79 \pm 0.15
<i>Lasioglossum apocyni</i>	37	1.01 \pm 0.09		
<i>Lasioglossum hitchensi</i>	49	1.19 \pm 0.10		
<i>Lasioglossum imitatum</i>	47	0.98 \pm 0.06		
<i>Lasioglossum trigeminum</i>	38	1.39 \pm 0.10		
Grand Total	643	1.87	101	1.67

Table 3. The 13 bee species measured, including the number of each species (n) and average ITD (mm) \pm standard deviation (SD), separated by sex.

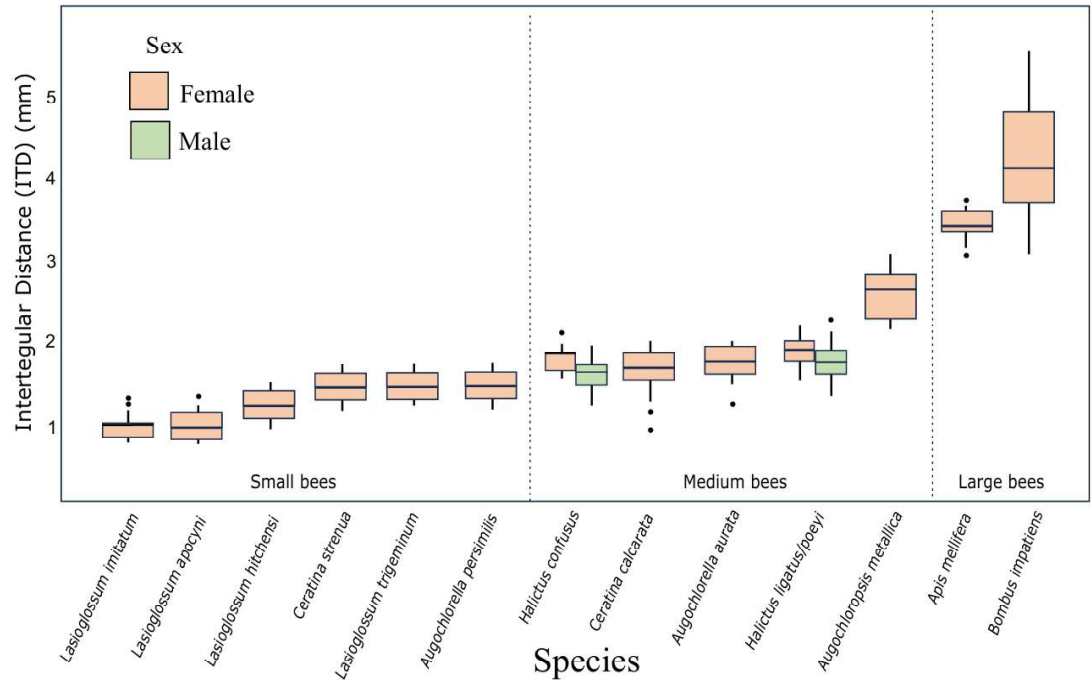


Figure 1. Box and whisker plot of the ITD of the 13 bee species measured in the three categories of bee species size (small, medium, and large), with differences between female (red) and male (green) ITD.

For the model that included all bees together, there was a significant positive relationship between agricultural land use at 2 km and bee ITD (effect size 0.11, $P = 0.02$, Table 4). However, most of the variation in body size was explained by the random

effects (species and sex, conditional $R^2 = 0.97$), while agricultural land use explained only an additional 0.03% (marginal $R^2 = 0.003$) of the variation in ITD across all bees (**Figure 2**). This was due to large differences in the responses of the species in the different size classes. Because we observed apparent differences in bees of different body sizes, we further categorized them into small, medium, and large, and repeated the analysis for each group (**Table 4**).

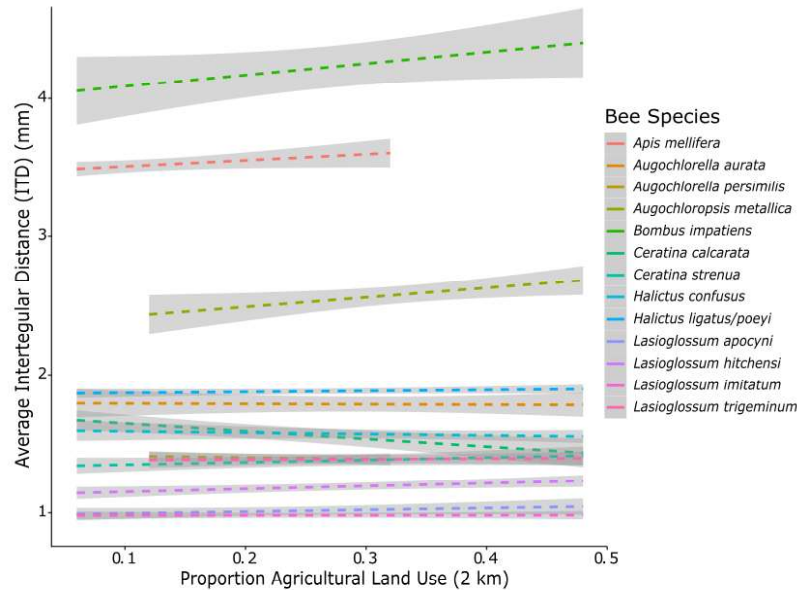


Figure 2. The relationship between ITD (mm) and agricultural land use (2 km) among the 13 bee species measured. We did not test the relationship between each species and land use, however across all species, there was not a significant effect of agricultural land use on adult body size.

Small and medium bees (i.e., bees with an ITD of less than 3 mm) were not significantly affected by agricultural land use at 2 km around the sites ($P > 0.05$, **Figure 3**). For these models, the random effects of sex and species still explained most of the variance in ITD (conditional $R^2 = 0.83$ (small), 0.90 (medium)). However, the ITD of large bees (> 3 mm ITD) increased significantly with surrounding agricultural land use (effect size = 0.77 $P = 0.02$, **Figure 3**). Agricultural land use at a 2 km radius explained 4% (marginal $R^2 = 0.04$, conditional $R^2 = 0.54$) of the variation in large bee ITD.

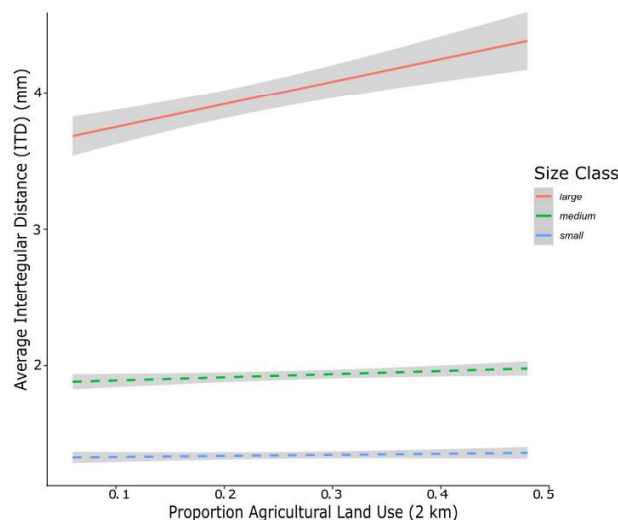


Figure 3. The relationship between agricultural land use in a 2 km radius around the site and average ITD by three size categories: small (< 1.75 mm), medium (1.75 mm – 3 mm), and large (> 3 mm). Dotted lines indicate relationships that were not significant, while solid lines indicate significant relationships.

Response	Fixed Effects	Random Effects	Observations	Effect Size	T Value	P Value	R ² m	R ² c
ITD (all bees)	Agricultural land use at 2 km	Species, Sex	744 obs, 13 Species, 2 Sexes	0.11	2.3	0.02	0.0003	0.97
ITD	Sex (F - M)	Species	744 obs, 13 Species	-0.13	-5.49	<0.001	0.002	0.97
ITD (small bees)	Agricultural land use at 2 km	Species, Sex	404 obs, 8 Species, 2 Sexes	-0.02	-0.38	0.71	<0.001	0.83
ITD (medium bees)	Agricultural land use at 2 km	Species, Sex	256 obs, 3 Species, 2 Sexes	0.11	1.85	0.06	0.001	0.9
ITD (large bees)	Agricultural land use at 2 km	Species	84 obs, 2 Species	0.77	2.42	0.02	0.04	0.54

Table 4. Generalized linear mixed-effects models of the relationship between ITD (mm) and agricultural land use at a 2 km radius around the site, including the fixed effects, random effects, and the number of observations. This reports effect size, T value, P value, and the marginal and conditional R², which explain the percentage of variation described by the fixed effects alone (R²m) and with the random effects (R²c).

DISCUSSION

Across diverse bee taxa, our research found agricultural land use had a significant effect on intraspecific body size on large bee species, but not small or medium bee species, in eastern Tennessee. The large bee species in our study, *Apis mellifera* and *Bombus impatiens*, had a significantly larger adult body size in sites with higher surrounding agricultural land use at a 2 km radius. Conversely, the ITD of small and medium bee species was not significantly affected by the land use gradient. Our hypothesis was that larger bee species would perform better in agricultural environments due to their extended foraging range.^{19,20,36} This hypothesis was based on the idea that larger species of bees can travel farther to get resources, and take advantage of patchy habitat in fragmented landscapes.¹⁷ Because the size and quality of the pollen provision affects adult body size in bees, we expected that the ability of larger bees to forage farther would make them more resilient to agricultural land use.^{13,15,16} These species are also generalists and can forage from many different plant species. While our findings appeared to confirm this hypothesis, it is worth noting that both larger-bodied bee species in our study are also sometimes managed for agricultural pollination.³⁷ Managed bees are sometimes given supplemental food, nesting habitat, and protection from diseases and parasites.³⁷ Our second hypothesis that smaller bee species would perform less well (have smaller adult body sizes) in agricultural landscapes did not receive support from our data. Moreover, we did not observe an effect of agricultural land use on the body size of medium-sized bee species. This could mean that the adult body size of small and medium bee species that were present at our sites was not affected by the land use, or that our study did not capture the effects of agricultural land use on these species. For example, we only used adult body size as a measure of bee health, while other aspects of bee health, such as survival and longevity, might have been affected by land use. We also did not factor in the effect of seasonality on bee health. In addition to this, urban land use surrounding the sites might have had a differential effect on the bee species. Across our sites, agricultural and urban land use were inversely related, so urban land use may have been contributing to some of the variation in body size. Indeed, other work has shown an effect of urban land use on bee body size.²⁷ Future work might look at other aspects of bee health and disentangle the effects of urban *versus* agricultural land use.

Furthermore, our research might observe varying results under increased agricultural activity levels. Within our study areas, agricultural land use peaked at 48% within a 2 km radius. Adverse consequences of agricultural land use may not be discernible at these lower levels of intensity.³⁸ Subsequent research could explore the relationship between solitary bee adult body size and more intense agricultural land usage, for our sites were more proportional to urban land use than monocultural agriculture by being in close proximity to Knoxville, TN.

Overall, our study supported other work showing that the impact of land use on adult body size varies across species.^{6,19,26,28-30,39} This suggests that managers interested in protecting the diversity of pollinators in agricultural landscapes might need to pay attention to different needs across different species. Some work has shown that native floral resource plantings (*i.e.*, flower strips) and access to natural habitat can improve the abundance and diversity of wild bees.¹⁴ While the large bee species had larger body sizes in more agricultural areas in our study, that could have also been related to urban land use, or support from managers in these areas.

In addition to body size, life history traits may play a role in determining the success of bee species in highly agricultural areas. All bee species examined in our study were social or eusocial species. We chose not to incorporate true solitary bee species into our analysis due to their relative rarity compared to social bee species.¹⁹ Consequently, we lacked sufficient replication across all sites to include solitary species in our analysis. It is plausible that the ITDs of solitary bee species could be negatively influenced by agricultural land use, given their life history characteristics.³⁹ However, there is a shortage of research investigating the impact of land use on solitary bee ITDs. Research that has been done has shown that solitary bees have smaller body sizes, different sex

ratios, and lower diversity and abundance in agricultural areas, suggesting land managers should consider the effects of land use on solitary bee body size as well.^{4,16}

CONCLUSION

Our findings offer ecologists and land managers a means to gauge bee health and foraging range by measuring the intertegular distance of adult bees. We observed larger adult body sizes in the large, generalist, eusocial, and managed bee species *Apis mellifera* and *Bombus impatiens*. However, it is not clear whether these bees are receiving additional support from land managers. We did not observe significant effects on small and medium sized bee species. However, ITDs might be a way for land managers to identify management approaches that optimize bee health and essential pollination services. Measuring adult body size in bees could be a proxy for bee health, which is important because bees provide free pollinating services and if agricultural land use destroys bee habitat, then crop yield could decrease, with economic and ecological consequences. Given our heavy reliance on agricultural products, specifically crops that rely on bee activity, it is crucial to adjust bee management practices to match the intensifying demands of agriculture and sustain both the agricultural industry and bee populations. Because the adult body size of bees is dependent on the amount and quality of pollen they forage, we recommend that land managers provide supplemental floral resources for bees in agricultural landscapes.

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PRESS SUMMARY

As agricultural practices intensify, native habitat could be altered, affecting the native insects that reside there, in particular native bees. Our research focused on agricultural land use and the effect it had on adult bee body size. In our study, there were five sites in eastern Tennessee that ranged in agricultural land-use intensification, i.e. a city garden to a cattle pasture. We collected bees on flowers within our replicated flower beds. After collecting and identifying the specimens, we then haphazardly selected female and male adult bees within 13 different species and measured and recorded their intertegular distance, indicating the body size of the bees. Our study showed that larger bees, like bumble bees, increased in body size as agricultural land-use in the surround landscape increased. This study is important because bees provide a free pollinating service and if agricultural companies destroy bee habitat, then crop yield will decrease. It is important for land management practices to ensure the best crop yield.