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A Large Aggregation of *Melissodes bimaculatus* (Hymenoptera: Apidae) Offers Perspectives on Gregarious Nesting and Pollination Services

Joseph Giulian[1,2,*], Bryan N. Danforth[1], and Jordan G. Kueneman[1]

Abstract - From the largest nesting aggregation ever recorded for the genus *Melissodes*, we took diverse bionomic measurements of *Melissodes bimaculatus* (Two-spotted Longhorn Bee). Our results show a protandrous reproductive strategy occurring from July through August in New York. We observed parasitism by the kleptoparasitic bee *Triepeolus simplex* as well as nest-architecture modifications to ease this burden that support the selfish-herd hypothesis. In this population, we also found a proclivity for grass (Poaceae) pollen, a previously undocumented diet preference for Two-spotted Longhorn Bees. We further showed that this bee species has widespread climatically suitable habitat, with expected range expansion under future climate conditions. Altogether, our results offer novel insights into the ecology of theTwo-spotted Longhorn Bee and its gregarious nesting behavior.

Introduction

Solitary native bees play a crucial role as pollinators in natural, agricultural, and urban ecosystems. Their effectiveness in providing pollination services has been well documented (Garibaldi et al. 2011, 2013; Park et al. 2020). It is also clear that more diverse assemblages of native bees lead to greater ecosystem and agricultural resiliency and yields (Rader et al. 2013, Winfree and Kremen 2009, Winfree et al. 2007). Ground-nesting bees themselves offer pollination efficiencies superior to honeybees, in part due to more reliable synchronization with blooms, and sometimes dense nesting aggregations (Cane 1997). Understanding the unique biology of these solitary native bees enhances our ability to integrate their pollination services and support ecosystem resilience.

Melissodes spp. (Hymenoptera: Apidae) (longhorn bees) are especially vital for many economically important crops (LaBerge 1956). They are among the most prevalent and effective pollinators of *Helianthus* (sunflowers) in the Great Plains (Mallinger et al. 2019). *Melissodes tepaneca* Cresson (Tepanec Longhorn Bee), and *M. bimaculatus* (Lepeletier) (Two-spotted Longhorn Bee) also readily pollinate *Gossypium* spp. (cotton) (Esquivel et al. 2020, 2021), which despite being able to self-pollinate, sees a 12% increase in fiber weight when native bees are present (Muhammad et al. 2020). Additionally, the Two-spotted Longhorn Bee, the focus of this study, has been shown to be an effective pollinator of crops like *Curcurbita* spp. (squash and pumpkin), *Cucumis* spp. (melon, cucumber, and

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gherkin), *Cannabis sativa* (Hemp), and cotton (Bomfim et al. 2016, Esquivel et al. 2021, Klein et al. 2018, Muhammad et al. 2020, O'Brien and Arathi 2019, Parys et al. 2020).

While all known *Melissodes* species are solitary, some species are known to nest in aggregations, where few to many females independently construct and provision each nest in a localized area. Aggregations of *Melissodes* generally occur in areas of sandy soil with little or no vegetative cover. As previously reported in the literature, these aggregations can vary between approximately 1 and 100 m² in area, limited to no more than a few hundred burrows (Buchmann and Jones 1980, Cameron et al. 1996, Clement 1973, Hurd and Linsley 1959, Miliczky 2000, Scullen 1928, Thorp and Chemsak 1964, Triplett and Gittins 1988). For example, *Melissodes persimilis* Cockerell was reported from a 4-m² site with about 100 active solitary burrows (Buchmann and Jones 1980), *Melissodes microsticta* Cockerell (Small Longhorn Bee), from a 16-m² site with at least 250 active nests (Miliczky 2000), and *Melissodes rivalis* Cresson (Western Thistle Longhorn Bee), along a ~6-m-long cliffside with ~60 scattered nests (Scullen 1928). *Melissodes druriellus* (Kirby) (Drury's Longhorn Bee), was observed at a 12-m² site with ~200 burrows (Cameron et al. 1996) and at a more extensive 33-m² site with at least 170 active burrows (Clement 1973). One of the largest aggregations reported for *Melissodes* hosted ~100 *Melissodes pallidisignatus* Cockerell nests in a 28-m² patch that was surrounded by an additional 93 m² of suitable nesting habitat (Thorp and Chemsak 1964). Triplett and Gittens (1988) discovered 2 sizeable aggregations of *Melissodes tepidus tepidus* Cresson (60 m^2 and 90 m^2) but did not report their densities. Additional descriptions of nesting aggregations are a crucial first step towards understanding the life history of bees, and reporting on nesting observations can aid in this process (Kueneman et al. 2024). A singular thorough bionomic description is lacking for most of the 143 known species of *Melissodes*.

Descriptions of bee-nesting biology also often include descriptions of their arthropod parasites. Direct and indirect evidence of brood parasitism has been frequently observed in *Melissodes*, especially by *Triepelous* (Hymenoptera: Apidae). For example the following interactions have been recorded: *Triepeolus lunatus* (Say) (Lunate Longhorn-cuckoo Bee) parasitizing Two-spotted Longhorn Bees (Mitchell 1962, Rightmyer 2008), *Triepeolus helianthi* (Robertson) (Sunflower Cuckoo Nomad Bee) parasitizing *Melissodes trinodis* Robertson (Dark-veined Longhorn Bee; Graenicher 1935, Thorp and Chemsak 1964), *Triepeolus occidentalis* (Cresson) parasitizing *Melissodes menuachus* Cresson (Clement 1973, Rightmyer 2008), both *Triepelous texanus* (Cresson) (Texas Cuckoo Bee) and *Triepeolus pectoralis* (Robertson) (Goldenrod Longhorn-Cuckoo Bee) parasitizing *M. druriellus* (Clement 1973, 1984; Rightmyer 2008), *Triepeolus* sp. parasitizing *M. microsticta* (Miliczky 2000), *Triepeolus michiganensis* Mitchell (Michigan Cuckoo Nomad Bee) parasitizing *Melissodes denticulatus* Smith (Denticulate Longhorn Bee; Rightmyer 2008), *Triepeolus donatus* (Smith) (Thistle Longhorn-Cuckoo Bee) parasitizing *M. desponsus* Smith (Rightmyer 2008), and both *Triepeolus helianthi* and *Villa* (Paravilla) sp. (Diptera: Bombyliidae) parasitizing *M. composita* Tucker (Hurd and Linsley 1959).

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Some *Melissodes* obscure their nest entrances to suppress these parasites (Danforth et al. 2019). Although covering or plugging a burrow entrance does not completely inhibit nest parasitism, it reduces the risk to varying degrees (Buchmann and Jones 1980; Clement 1973, 1984; Cameron et al. 1996; Thorp and Chemsak 1964). In *Melissodes* species for which burrow-plugging behavior has been observed, the trait shows little plasticity, with all females apparently employing burrow plugs. These observations are also restricted to relatively small aggregations where parasitism risk is likely similar among all nesting individuals. However, as aggregations expand in size, females who nest centrally should be increasingly less susceptible to parasitism. Thus, central nesters pass their risk of brood parasitism to more external nesters. External nesters could theoretically alleviate this risk by more frequently obscuring their burrow entrances, and internal nesters could forgo burrow plugging altogether, saving valuable time and energy. Selfish-herd patterns of this nature have yet to be observed in *Melissodes.* Our overall limited knowledge of their nesting behavior and parasite-avoidance strategies currently restricts our insight into the conditions that support the growth and maintenance of *Melissodes* aggregations.

The Two-spotted Longhorn Bee has a broad distribution encompassing most of the eastern US, extending west to North Dakota, Colorado, and Mexico. Individuals visit >60 different flower families across this range, collecting pollen from at least half of these families (LaBerge 1956). Despite their widespread and polylectic affinity for commercial crops, there are limited and cursory life-history notes on this species (Ashmead 1894, Banks 1902, LaBerge 1956). From the largest ever reported *Melissodes* aggregation, we characterize the following: (a) gregarious nesting behavior (b) nest density, (c) in-flight sex ratio, (d) wing wear and phenology, (e) prevalence of anti-parasite burrow covers and parasitic associations, (f) pollen collection, and (g) current and future distributions of Two-spotted Longhorn Bees.

Methods

Study area

The study site was a mostly sloping, 2400-m², southeast-facing residential lawn near Berne, Albany County NY. Most resident females nested in a 1100-m² unshaded region covered with grass and *Trifolium* spp. (clover), *Plantago major* L. (Broadleaf Plantain), and small, exposed dirt patches sparsely dispersed throughout. Vegetative height was maintained at ~5–8 cm throughout the summer by frequent residential mowing. An additional 1300-m² area uphill of our focal study area hosted nesting females, but to a lesser degree, as we saw many fewer females taking flight from that region. The uphill region had a steeper incline and vegetation height of ~8–10 cm. We studied the site from 21 July to 3 August 2021.

Aggregation density and frequency of burrow covers

To estimate burrow density and frequency of covered burrows at the aggregation site, we censused an 18-m² rectangular region within the aggregation from

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approximately 12:00 pm to 5:20 pm on 30 July 2021. We divided the surveyed region into 5 adjacent rows of ten 0.36-m² plots, each delimited by a square of four 2 cm x 5 cm x 60 cm wooden pieces bolted end-to-end (enclosing 0.36 m²). We inspected each plot for 5–7 minutes, noting the number and appearance of burrows as either open or covered. Burrows with a tumulus and detectable entrance of ~7–8 mm in diameter were counted as active burrows, while entrances that were not easily exposable by hand were excluded. The first 10 plots examined were located 60 cm below an area of highly unsuitable edge habitat, and the following 4 rows were placed progressively closer to the center of the aggregation. We excluded from our inspections burrows directly underneath the perimeter of the wooden frame to ease reproducibility. Our observations are visually presented in Excel (Microsoft, Redmond, WA) tables where red and blue represent the maxima and minima, and white represents the 50th percentile. Observations were scaled up to the size of our aggregation (1100 m²) for population estimates. We conducted a Kruskal–Wallis chi-squared and post-hoc Dunn test using R v. 4.3.2 (R Core Team 2023).

Phenology via in-flight sex ratios and wing-wear analysis

To assess the phenological change in this bee population, we utilized 2 methods: in-flight sex ratios and wing-wear analysis. For the sex-ratio assessment, we employed a standardized catch-and-release method to collect male and female bees. We swung a net 4 times 0.3–1 m from the ground, noting the number of males and females on every fourth swing until we reached 100 swings. We sampled in sunlit locations where bees were visibly in flight on 23 July (10:30 am–11:00 pm), 31 July (12:00 pm–12:30 pm), and 3 August (10:30 am–11:00 pm). We compared the ratios of total number of males and females collected each day using a 'VassarStats' chi-square analysis (Vassar College 2021).

For the wing-wear analysis, we captured and analyzed 152 females and 101 males from the site over 4 days. We determined their approximate age based on the level of damage to the hind margins of their anterior wings. We followed a scoring system previously outlined in Mueller and Wolf-Mueller (2005), whereby we assigned a score of 0–6 based on the number and depth of nicks on the wing margins. We collected a total of 8 females and 14 males on 21 July , 20 females and 19 males on 23 July, 40 females and 60 males on 30 and 31 July combined, and 84 females and 8 males on 3 August. We combined the specimens collected on 30 and 31 July to facilitate comparison, as they were consecutive collection dates near the midpoint of the sampling period. We calculated a "combined wing score" for each bee by averaging the scores for both wings and then compared the average combined wing score for males and females across all days sampled.

Nest excavations and parasitic associations

We conducted nest excavations to collect pollen brood samples and document cell contents (3 August 2021). We peeled away 2 square 1-m^2 layers of topsoil, and then carefully dug out each area of exposed soil to a depth of ~20 cm. We noted the presence and state of any brood cells encountered. We also measured soil temperature using a soil thermometer (Compost Wizard, Good Ideas, Inc., Erie, PA) at

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a depth of ~10 cm. We then collected soil samples adjacent to pollen-provisioned cells at the same depth. We collected 6 soil samples, placing each in a 1-qt Ziploc® bags (San Diego, CA), and randomly chose 3 samples to send to the Cornell Soil Health Lab for particle-size analysis.

Throughout the study, we collected voucher speciments of parasites of bees encountered both in flight and within brood cells. We took photographs to support identifications made using the following identification materials: Enns (1956), Mitchell (1962), Pinto (1991), and Rightmyer (2008). We also noted any excavated brood cells consumed by a black fungus. After dispatching bees in the field using a cyanide collection jar, we later preserved them on an insect pin and inspected all adult Two-spotted Longhorn Bees (n = 252) for mites or other potential parasites. All specimens are retained among authors.

Pollen collection by *Melissodes bimaculatus*

We examined the scopae of the 131 females collected between 23 July and 3 August, making initial observations under a stereoscope at 50x magnification. Pollen loads appeared in 1 of 4 states, either composed of: (1) predominately a yellow pollen morphotype, (2) predominately a white pollen morphotype, (3) a near-equal mix of yellow and white morphotypes, or (4) no scopal pollen. Yellow pollen grains were ~4–5x larger than white grains, easing morphotype discrimination. We then sampled the scopal loads from a subset of females with yellow (n = 10) and white (n = 10) scopal loads, attempting to select those with visually homogenous compositions. Evaluated bees were collected 23 July (n = 2), 30 July (n = 4), 31 July (n = 5), and 3 August (n = 9). We dislodged pollen with an insect pin, then slide-mounted the samples using glycerol gelatin and fuchsin dye. We examined slides under a compound microscope at 40x and 400x to view the diagnostic characters necessary for identification. Wodehouse (1935), Kapp (1969), Hufford (2004), Cornell Entomology Outreach and Extension's Pollen Grains Reference Library (Russo 2015), as well as the opinions of several experts, informed our pollen identifications.

Species-distribution model

We employed "maximum entropy" species-distribution models (Phillips et al. 2006) to estimate the current and future regions in North America where Two-spotted Longhorn Bees can offer pollination services. We used the R package 'ENmeval' v2.0.4 (Muscarella et al. 2014) to build models with 'MaxEnt' v3.4.4 (Phillips et al. 2006, 2017). We validated models using 4-fold block cross validation and compared model AUCs against those generated by null SDMs to assess performance (Kass et al. 2020, Muscarella et al. 2014). We downloaded occurrences from the Global Biodiversity Information Facility covering the span of 1 January 1988 to 31 December 2023 (GBIF 2024). We accepted only occurrences with 1 km of uncertainty. We used the R package 'CoordinateCleaner' v3.0.1 to remove problematic occurrences such as duplicates, imprecise records, etc. (Zizka et al. 2019). We thinned the final occurrence dataset to 25 km using the R package 'spThin' v0.2.0 to reduce spatial sampling biases (Aiello-Lammens et al. 2015). We

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deemed a total of 738 occurrence records to be eligible for use in the analysis after data cleaning.

We derived our model's predictor variables following the methods of Giulian et al. (2024). We downloaded open-source average monthly precipitation and temperature data from CHELSA (Karger et al. 2017) at 30-arcsecond resolution. These data spanned 1 January 1988 to 31 December 2018 (Giulian et al. 2024). We developed 19 bioclimatic variables common to ecological modeling using R package 'dismo' v1.3-14 (Hijmans et al. 2017, O'Donnel and Ignizio 2012). We resampled these variables to 2.5-arcminute resolution for analysis (Giulian et al. 2024). We performed variable selection to reduce collinearity with the R package 'usdm' v2.1-7 (Naimi et al. 2014). This process included using a threshold of 5 for variable inflation factors (VIFs) and 0.7 for Pearson correlation coefficients. These criteria allowed us to select 6 variables: annual mean diurnal range, temperature seasonality, maximum temperature of the warmest month, mean temperature of the wettest quarter, precipitation seasonality, and precipitation of the warmest quarter —all relevant to the biology of a summer emerging bee. We averaged all 5 GCMs predictions to produce a final prediction for habitat suitability. We also binarized current and future distribution maps using a suitability threshold of 50% to compare range-extent estimates. A more thorough description on the model workflow is available in Supplemental File 1 (available online at http://www.eaglehill.us/NENAonline/suppl-files/n31-3-N2098-Giulian-s1, and for BioOne subscribers, at https://www.doi.org/10.1656/N2098.s1).

Results

Assessing frequency of burrow covers, aggregation density, and population size

We found 1066 burrows in the 18-m² surveyed area (Fig. 1). Across all burrow entrances, 61.91% were open and 38.09% were covered. The average number within each 0.36-m² plot was 21.32 ± 7.73. Open burrows averaged 13.2 ± 7.17 per plot, while covered burrows averaged 8.12 ± 3.46. The frequency of covered burrows exhibited an edge effect. Covered and open burrow ratios were similar for rows 1 and 2, but both differed significantly from the ratios of interior rows (see Supplemental Table 1 in Supplemental File 1). The two edge rows had covered to open burrow ratios ~2.5 times higher than interior rows (Fig. 1; see also Supplemental Table 1 in Supplemental File 1). However, the three more interior rows hosted significantly more burrows than the two edge rows (Fig. 1; see also Supplemental Table 1 in Supplemental File 1).

The size and density of our study aggregation eclipses all others reported for the genus *Melissodes*. The total area occupied by this aggregation was 1100 m² if only areas similar and contiguous to the surveyed plot are considered (Fig. 1). Solitary bees provision anywhere from 7 to 35 offspring over the course of their lives (Danforth et al. 2019), so it is reasonably conservative to estimate Two-spotted Longhorn Bees provision around 10 offspring each. Thus, we estimated the following season's gross emergent population at 651,144 individuals from the primary area. This estimate does not include the uphill area, which hosted nesting

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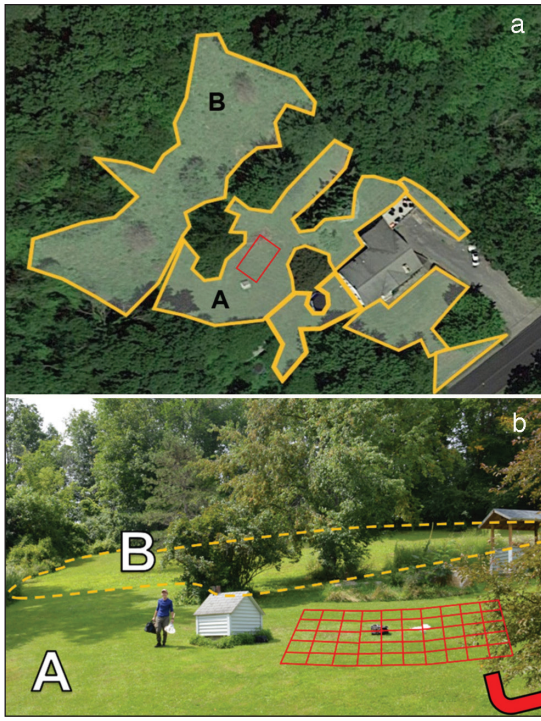
individuals but was not surveyed. After accounting for the 13% mortality rate estimated from nest excavations, we predict there are ~566,625 successful emergences from this site each year.

Capturing phenological change through in-flight sex ratios and wing-wear analysis

The ratio of females and males netted and released varied significantly across the days surveyed. On 23 July, 31 July, and 3 August, ratios were 64:230, 377:75, and 287:64, respectively ($\chi^2 = 358.05$, df = 2, $P < 0.0001$; see Supplemental Fig. 5 in Supplemental File 1). The in-flight sex ratio was male dominated by ~3.5 to 1 on 23 July 23, but by 31 July and 3 August, females dominated the sex ratio ~5 to 1 and ~4.5 to 1, respectively. Females that were collected in-flight for later examination consistently had reduced wing damage compared to males for each day sampled. Average wing scores for females across the sampling dates 21 July, 23 July, 30 and 31 July, and 3 August, were 1.3 ($n = 8$), 1.4 ($n = 20$), 1.9 ($n = 40$), and 2.3 ($n = 84$), respectively, while males' average wing scores were 3.1 ($n = 14$), 3.2 ($n =19$), 3.9 ($n = 40$), and 4.9 ($n = 9$), respectively (see Supplemental Fig. 5 in Supplemental



Concealed Burrows

Row	A	B	C	D	E	F	G	H	I	J	Total
1	2	2	3	6	12	17	9	12	12	10	85
2	11	10	10	14	15	11	5	8	7	9	100
3	12	7	4	8	9	6	9	8	10	5	78
4	2	4	6	4	6	4	10	5	11	6	58
5	9	5	8	12	8	7	5	8	11	12	85

Open Burrows

Row	A	B	C	D	E	F	G	H	I	J	Total
1	2	4	5	9	3	8	7	13	14	6	71
2	10	10	11	6	10	7	8	14	5	3	84
3	17	27	28	23	26	20	10	12	14	6	183
4	11	31	13	25	8	7	12	13	23	17	160
5	16	14	17	24	19	16	14	20	9	13	162

Total Burrows	Row	1	2	3	4	5
	Total	156	184	261	218	247

Ratio of Concealed to Open Burrows

Row	A	B	C	D	E	F	G	H	I	J	Avg.
1	1	0.5	0.6	0.6	4	2.1	1.2	0.9	0.8	1.6	1.362
2	1.1	1	0.9	2.3	1.5	1.5	0.6	0.5	1.4	3	1.401
3	0.7	0.2	0.1	0.3	0.3	0.3	0.9	0.6	0.7	0.8	0.522
4	0.1	0.1	0.4	0.1	0.7	0.5	0.8	0.3	0.4	0.3	0.43
5	0.5	0.3	0.4	0.5	0.4	0.4	0.3	0.4	1.2	0.9	0.565

Figure 1. (a) The 2400-m² region hosting females is encompassed by yellow borders, with a red rectangle representing the burrow survey area; the area labeled A (~1100 m²) indicates a region which hosted the most females, while the area labeled B (~1300 m²) hosted comparatively fewer females. (b) The burrow survey grid, visual differences between areas A and B, and the uninhabitable edge-habitat that separates the survey area from area B. Tables show the number and ratio of concealed and exposed burrow states in each 0.36-m² grid are; red and blue are maxima and minima, while white is the 50th percentile.

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File 1). Fifteen of 84 males were collected with extreme excisions where at least 1 wing's hind margin was destroyed beyond the veins of the 2nd marginal cell. No females were found with equivalent wing damage, with only 1 bee across all 134 females even scoring a 6, and her excisions ending far before the 2nd submarginal cell. Females with a wing score of 0 were also collected each day, while males scoring 0 were only detected on 21 July.

Parasitic associations and nest excavations

Across all 3 days visited, *Triepeolus simplex* Robertson (Simple Longhorn-Cuckoo Bee) was observed in flight nearby nest entrances, and sometimes nectaring on nearby garden flowers. This is the first record of *T. simplex* in association with a *Melissodes* species (Rightmyer 2008). These records, and 2 collected from the vicinity of Governeur on 13 and 19 July 2021 (C. Wilson, University of Arkansas, Fayetteville, AR, pers. comm.), are also the only reports of this species from New York. In total, 13 individuals of *T. simplex*, 2 *Zonitis bilineata* Say (Coleoptera: Meloidae) and 1 *Epicauta cinerea* (Forster) (Coleoptera: Meloidae; Clematis Blister Beetle), were collected as vouchers in areas central to the aggregation (see Supplemental Figs. 2 and 3 in Supplemental File 1). *Zonitis bilineata* was previously known to parasitize apid bees (Enns 1956), but the only hosts reported for Clematis Blister Beetles have been orthopterans (Pinto 1991). Of all 252 Two-spotted Longhorn Bee specimens inspected, 2 males were each discovered with 1 orange mite adhering to sternum 1 (see Supplemental Fig. 4 in Supplemental File 1). Our observations reveal diverse parasites of Two-spotted Longhorn Bees, but also that Two-spotted Longhorn Bees do not appear to suffer from extreme rates of parasitism.

During nest excavations on 3 August, brood cells were found at depths of 6–16 cm and soil temperatures between 20 and 22 °C. Larval pollen provisions were a

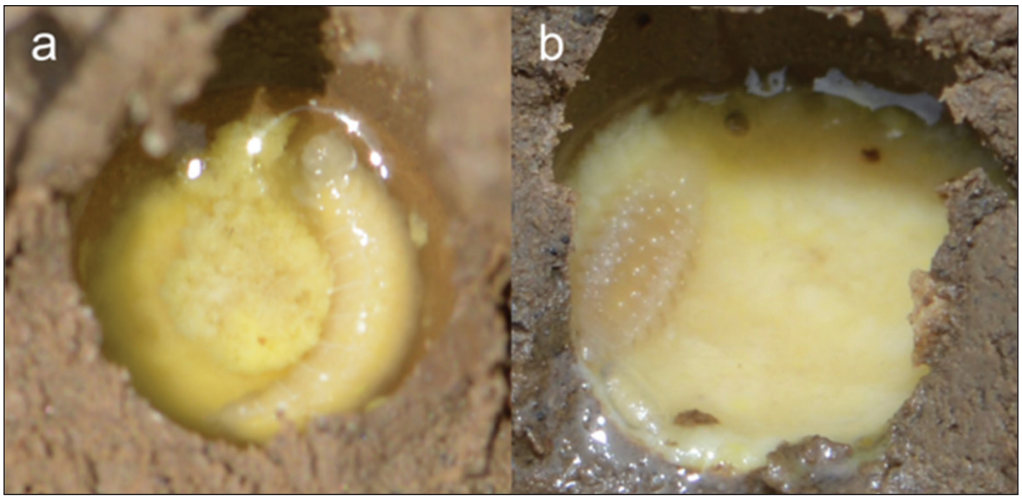

Figure 2. Photographs of excavated cells, with larval *Melissodes bimaculatus* (Two-spotted Longhorn Bee) (left) and it's kleptoparasite (right) both feeding on a nectar and pollen mixture.

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semi-liquid mixture of pollen and nectar (Fig. 2). Of the 53 cells uncovered, 1 (2%), had *Triepeolus* sp. (cf. *simplex*) larvae (Fig. 2), 6 had pollen provisions engulfed by an unidentified dark fungus, and the rest had healthy eggs or various larval stages of Two-spotted Longhorn Bees. A soil-texture analysis from the Cornell Soil Health Lab shows that 2 samples of nesting substrate were loam while the third was silt loam. The percentages of loam, silt, and sand between all samples were similar (see Supplemental Fig. 5 in Supplemental File 1).

Pollen collection by Two-spotted Longhorn Bees

Sixty-nine individuals (52.7%) had scopal loads composed of mostly large yellow pollen grains, while 25 (19.1%) had scopal loads composed of small white pollen grains, 25 (19.1%) had scopal loads with a near equal mixture of the first 2 categories, and 12 (9.2%) had no scopal loads. Slide evaluation of pollen in scopal categories 1 and 2 revealed samples varying from nearly homogeneous (Fig. 3a) to mixed (Fig. 3b), though each sample's minority morphotype still comprised far less than 50% of the sample volume. Our results indicate pollen mixing clearly occurs in this population, but the trait is apparently flexible among individuals or foraging bouts.

From the mounted slides inspected from category 1 (yellow morphotype), we found pollen was composed of single-pored pollen grains between 40 and 50 µm in diameter (Fig. 3a). These grains belong to the plant family Poaceae, according to Wodehouse (1935), Kapp (1969), and personal communications with Drs. Katherine R. Urban-Mead (Xerces Society for Invertebrate Conservation, Philadelphia, PA), Anna Edlund (Bethany College, Bethany, WV), and Pierre Lau (USDA-ARS, Stoneville, MS). From the 10 mounted slides inspected from category 2, we found at least 2 different tricolporate pollen types between ~10 and 20 µm (Fig. 3b). We suspect pollen from this morphotype to be from the plant family Hydrangeaceae. Unfortunately, Hydrangeaeceae has only disparate pollen resources available, not allowing for robust comparison. Our pollen keys out to the southern-central US Hydrangeaceae plant *Fendlera rupicola* Engelm. & A. Gray (Cliff Fendlerbrush; Kapp 1969:couplet 50a). Moreover, morphotype 2 pollen seems to match the morphological description of Hydrangeaceae presented by Hufford (2004), especially based on size, exine ornamentation, and the tricolporate nature. Our pollen grains also resemble *Hydrangea petiolaris* (= *H. anomala* ssp. *petiolaris*) Siebold & Zucc. in size, shape, and ornamentation, as pictured by Cornell Entomology Outreach and Extension's Pollen Grains Reference Library (Russo 2015). All visible morphological features, as well as the mid to late- July bloom period, suggest this pollen is most likely from the Hydrangeaceae family.

Current and future species distributions

Our model predictions show that climatically suitable habitat spans most of the eastern continental US (Fig. 4). Areas of highest habitat suitability generally occur along coastal areas and in the central and eastern US along the 40th parallel. Habitat suitability decreases in the north near the 45th parallel, and abruptly so in the west where eastern deciduous forest meets the Great Plains at the 100th meridian.

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Permutation variable importance shows the greatest driver of suitability is maximum temperature of the warmest month (59.5%), followed by diurnal temperature range (17.7%), precipitation of the warmest quarter (11.7%), precipitation seasonality (6%), and temperature seasonality (4.5%). Mean temperature of the wettest quarter had little effect on the model (0.6%). The AICc was 18457.88 and AUC was 0.89 ± 0.05. Our model had significantly better discrimination ability than null

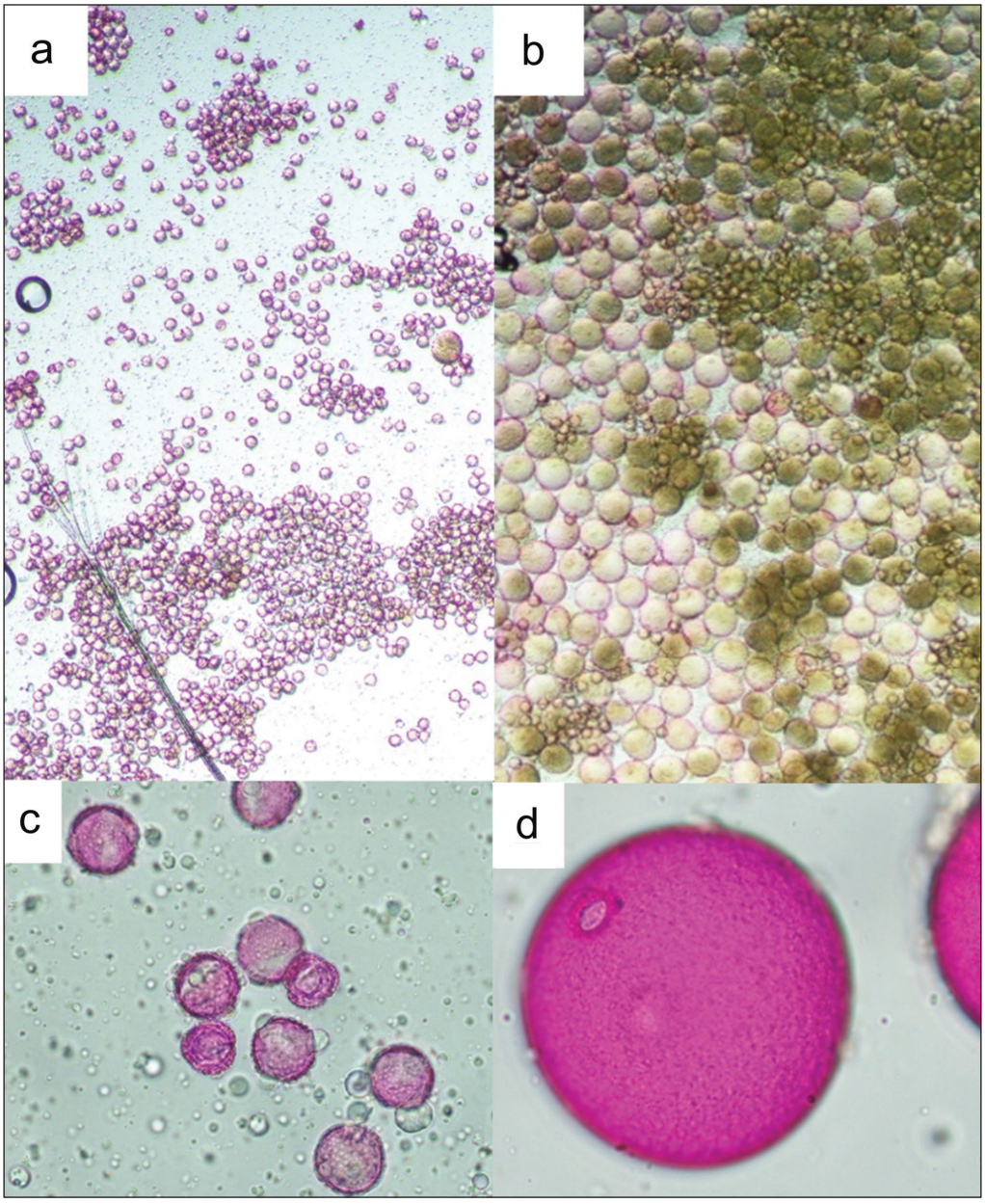

Figure 3. Microscopic photos of pollen identified as the white morphotype (a, c) and yellow Poaceae pollen (b, d).

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models (one-tailed t: $z = 1.851$; $P = 0.032$; see Supplemental Fig. 2 in Supplemental File 1).

Using a 50% suitability threshold for species' presence or absence, we illustrate a potential northerly expansion of suitable habitat by 2100, with some declines in southern and western regions (Fig. 4). Areas predicted to newly support Two-spotted Longhorn Bees extend from the eastern North American coast to approximately 100°W, 45°N, and 55°N. Regions of suitability predicted to remain above threshold were north of 36°N and east of 95°W. Most areas south and west of these boundaries fall below 50% suitability by 2100.

Discussion

Understanding native bee life histories is vital for managing landscapes and natural resources effectively. Native bees provide pollination, essential for agricultural crops and beneficial for all angiosperm genetic diversity and resilience. Though generally found in small populations across landscapes, some ground-nesting species like the Two-spotted Longhorn Bee form large, long-lasting aggregations. These aggregations could be incorporated into land-management practices to supplement localized pollination needs across eastern North America. Similar efforts have proved successful for *Nomia melanderi* Cockerell (Alkali Bee). This solitary ground-nesting bee provides yearly pollination services yielding an estimated 2240 kg of *Medicago sativa* L. (Alfafa) seeds per acre (Cane 2008, Danforth et al. 2019). New nesting beds can be seeded with as little as 0.3 m^3 of soil with pupae, as long as the new region has adequate soil texture, moisture, drainage, and alkali surface salt that the species requires (Cane 1997, Danforth et al. 2019).

Our observations demonstrate that large, naturally occurring Two-spotted Longhorn Bee aggregations can also appear under certain biotic and abiotic conditions. The aggregation we studied particularly thrived in an area lacking in canopy cover, allowing it to receive a full day of direct sun exposure. Some, but not all, nesting areas occurred along a northerly, southeast-facing incline, which likely increased

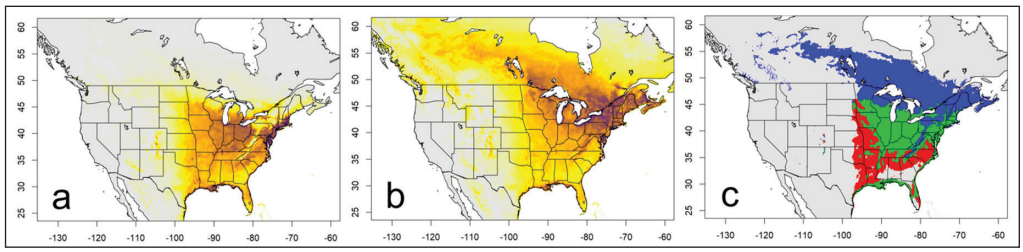

Figure 4. Species distribution model forecasts for *Melissodes bimaculatus* (Two-spotted Longhorn Bee) across North America ($n = 738$ occurrence points). (a) Current and (b) SSP 3-7.0 2071–2100 predictions of climatically suitable habitat range from 0 to 1. Suitability follows a color ramp where purple is most suitable and yellow is least suitable. (c) Range map shows areas predicted to be more than 50% suitable under current and future conditions in green, regions predicted to be above the 50% threshold under current conditions but not future conditions in red, and areas predicted to be above 50% suitability only under future conditions in blue.

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sun exposure and drainage. Nests mostly occurred where ground cover was below ~8 cm or where soil was exposed. The soil at this site was predominately loamy, offering superior drainage to silty and clayey soils but better moisture retention than sandy soils. Higher vegetation discouraged nesting, with residential mowing practices apparently sustaining a suitable vegetation height and not disrupting the aggregation. This naturally occurring aggregation of Two-spotted Longhorn Bees already covers 0.1 ha. With proper technique and matching conditions, we suspect this population, or others, could be managed to enhance the extensive supplementary pollination services already provided by Two-spotted Longhorn Bees for numerous mid-summer blooming crops (Bomfim et al. 2016, Esquivel et al. 2021, Klein et al. 2018, LaBerge 1956, Muhammad et al. 2020, O'Brien and Arathi 2019, Parys et al. 2020).

Aggregation phenology

The first major emergence of females occurred sometime between 23 and 30 July. This observation places the last week of July as the approximate start date for this species' pollination services in New York. Males emerged earlier than females to dominate the in-flight sex ratio during mid-July, also revealing a protandrous emergence pattern in New York. Early season male-biased sex ratios indicate a "race to be first" reproductive strategy, where early male emergence allows for access to unmated females who will mate only once early in life (Danforth et al. 2019). Our findings of females with near pristine wings across all days while pristine males were found only on 21 July also supports the hypothesis of significant protandry. However, late-flying males may also have a bet-hedging opportunity since newly emergent females seem to occur well past the shift in sex ratio.

Parasitic interactions and adaptations

The selfish-herd hypothesis is supported when individuals in a group reduce their own risk by competing for positions that place others between themselves and predators (Hamilton 1972). We observed nest density was indeed highest centrally, indicating higher spatial competition for internal positioning. We also found that internal nesters were buffered by external nesters that increasingly implemented covered burrows. This practice should alleviate some of the additional brood parasitism risk assumed by peripheral nesters, perhaps even offering an avenue for marginal nesters to redirect risk internally if externally approaching parasites must search for accessible burrows. Overall, the patterns of competition for safer internal positions and employment of risk-aversion strategies among peripheral nests support the hypothesis that this aggregation exhibits selfish-herd behavior (Hamilton 1972). Given this population has reached an exceptional density while still maintaining low overall parasitism rates, encounter-dilution effects (Mooring and Hart 1992) appear to also be occurring.

Estimating range and potential for pollination services

Two-spotted Longhorn Bees are predicted to have a wide range of climatically suitable habitats based on our model predictions. Most areas east of the 100th

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meridian and south of the 45th parallel in North America offer highly suitable climate for Two-spotted Longhorn Bees. These regions are thus the most likely to benefit from this species' pollination services at present. Suitability was mainly driven by maximum temperatures of the warmest month. For year 2100 predictions, climatically suitable habitats extend far into Canada. Midwestern and eastern coastal states along the 40th parallel show long-term climate suitability. However, southwest range edges are predicted to fall below 50% suitability by year 2100, so Two-spotted Longhorn Bees are likely to be less-viable long-term pollinators at this range edge.

Concluding remarks

Given the sheer number of bees, the scale of flower visitation from this population is huge. Based on our observations and model projections, the Two-spotted Longhorn Bee is a robust and widespread species that currently, and in the future, has the potential to contribute enormous pollinator services in eastern North America. Its ability to nest in large, dense aggregations while maintaining low parasitism rates via anti-parasite adaptations positions it as a resilient and highly productive pollinator. Propagation of this species may also be possible in the future. Our findings regarding nesting phenology and site preference will help inform how these bees may best be managed for use in agricultural systems to increase resilience in the farming sector and enhance food security.

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