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Original article

Emergence dynamics and host-parasite associations in a large aggregation of *Andrena regularis* (Hymenoptera: Apoidea: Andrenidae)

Steven T. Hoge[1,2], Jordan G. Kueneman[1], Rachel Fordyce[1], Cassidy Dobler[1], Katherine Odanaka[1], and Bryan N. Danforth[1]

[1] Department of Entomology, Cornell University, Ithaca, NY 14850, USA
[2] Division of Renal Medicine, Brigham and Women's Hospital, 75 Francis Street, Boston, MA 02115, USA

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Abstract – Ground-nesting solitary bees play a vital role in pollination, yet many aspects of their nesting ecology remain understudied, including population dynamics and interactions with brood parasites. We used emergence traps to estimate population size, emergence dynamics, sex ratio, and brood parasitism in a large aggregation of the ground-nesting solitary bee *Andrena regularis* Malloch at East Lawn Cemetery in Ithaca, NY. Over the course of the study, conducted from March 30th through May 16th, 2023, we collected 3251 individuals representing 16 species of bees, flies, and beetles, with *A. regularis* being the dominant species. Using emergence trap capture data over a 41-day emergence period, we document emergence phenology, sex ratio, and parasitism rate for *A. regularis* and its most abundant brood parasite, *Nomada imbricata* Smith. Our results provide insights into the population size, sex ratio, and timing of male and female emergence in a solitary, ground-nesting bee and its brood parasites. Our study demonstrates the effectiveness of emergence traps for studying existing ground-nesting bee populations. This study contributes to our knowledge of bee ecology and emphasizes the potential importance of cemeteries as refugia for ground-nesting bee populations.

solitary bees / emergence phenology / host-parasite interactions / emergence traps / cemeteries

1. INTRODUCTION

Solitary, ground-nesting bees comprise the vast majority of bee species on Earth and yet they remain poorly studied relative to their social relatives (Danforth et al. 2019). Some species (e.g., *Dasypoda plumipes* (Fabricius)) form massive nesting aggregations of millions of nests spanning over 30 hectares (Blagoveschenskaya 1963). Other species (e.g., *Centris caesalpiniae* Cockerell) build dense nesting aggregations with nest densities approaching 1252 nests/m^2 (Rozen & Buchmann 1990). These large and/or dense nesting aggregations support many natural enemies, including fly, beetle, and even bee parasites. The most impactful solitary bee parasites are the brood parasitic bees (Minckley and Danforth 2019), which lay their eggs in the nests of pollen-collecting hosts (Danforth et al. 2019; Chapter 10). Brood parasitism is well studied in birds, fish, and other insects (Sless et al. 2023), but we know relatively little about the interactions between solitary, ground-nesting bees and their brood parasites (Litman 2019; Minckley and Danforth 2019). Robust aggregations of ground-nesting bees, as well as the populations

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Corresponding author: J. G. Kueneman, jk2899@cornell.edu; B. N. Danforth, bnd1@cornell.edu
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of brood parasites that go with them, provide extraordinary opportunities for studying aspects of bee biology, including nesting biology, phenology, sex ratio allocation, and host-parasite interactions.

Because of the role these bees play in the pollination of both wild (Willmer et al. 2017) and managed (Garibaldi et al. 2013) flowering plants, large, stable bee nesting sites are also extraordinarily valuable from a conservation perspective (Kueneman et al. 2024). Giulian et al. (2024) recently calculated that a large aggregation of *Melissodes bimaculatus* (Lepeletier) (Apidae) in a single suburban lawn in upstate New York produces over 650,000 bees each year. *Melissodes bimaculatus* is known to be a valuable pollinator of squash, pumpkin, melon, cucumber, and cotton (see references in Giulian et al. 2024). Other high-value specialty crops, including apples, cherries, strawberries, blueberries, and cranberries, all rely heavily on wild, solitary bees for pollination (reviewed in Danforth et al. 2019). In many cases, such as in apples, the per-visit pollen deposition of solitary bees is considerably higher than that of managed social bees, such as honey bees (Park et al. 2015b). At the same time, these solitary, ground-nesting bees are at risk due to habitat loss, pesticide use, invasive species, pathogens, and parasites (Goulson et al. 2015; Lima et al. 2022; LeBuhn & Luna 2021).

In this study, we examined a large aggregation of the ground-nesting solitary bee *Andrena regularis* Malloch (Figure 1b–e) and its brood parasites, including the most common brood parasite, *Nomada imbricata* Smith (Figure 1f). *Andrena regularis* is a solitary, univoltine, ground-nesting bee active in the early spring (early April through June, depending on locality). It ranges across southern Canada from British Columbia to New Brunswick, and south into Pennsylvania, northern Ohio, Michigan, Wisconsin, and northern Minnesota in the USA (Bouseman and LaBerge 1979). Like many early spring members of the subgenus *Melandrena*, females are polylectic with a preference for diverse Rosaceae, including *Malus* (apples), *Prunus* (cherry, plum, peaches, etc.), *Amelanchier* (shadbush or serviceberry), and *Crataegus* (hawthorne) (Miliczky and Osgood 1995). Following mating, females build subterranean nests consisting of four to five brood cells at a depth of 10–22 cm (Schrader and LaBerge 1978). Lifetime reproductive success is unknown, but likely less than 10 offspring per female, as in many *Andrena* (Witt 1992; Danforth et al. 2019). Overwintering takes place in the adult stage (Schrader & LaBerge 1978; Miliczky and Osgood 1995). Miliczky and Osgood (1995) reported four species of *Nomada* attacking the nests of *Andrena regularis*: *N.* (*N.*) *imbricata* F. Smith, *N.* (*N.*) *cressonii* Robertson, *N.* (*N.*) *pygmaea* Cresson, and *N.* (*N.*) *armatella* Cockerell. At our study site *N. imbricata* was the most common *Nomada* based on surveys prior to the onset of this study.

By using a relatively underused sampling method (emergence traps or e-traps) to study the aggregation of *A. regularis* at the East Lawn Cemetery (ELC) in Ithaca, NY, we sought to answer the following questions: (1) what is the population size of both host (*A. regularis*) and brood parasite (*N. imbricata*), (2) what is the sex ratio of host and parasite, (3) how do temporal patterns of host and parasite emergence compare, and (4) what is the parasitism rate of bee (*N. imbricata*), fly, and beetle parasites of *A. regularis* at ELC? Finally, we examined the hypothesis of equal investment by combining numerical sex ratio data with body weight data to explore whether female offspring production in Spring 2022 (i.e., the year before our study) skewed significantly toward a more male or female-biased investment ratio.

Our study documents one of the largest, and possibly oldest, nesting aggregations of solitary bees ever recorded and provides novel insights into the emergence phenology of solitary bee hosts and their brood parasites.

2. METHODS

Our study was conducted from March 30th through May 16th, 2023, at the ELC, in Ithaca, NY, USA (42.43923, −76.46882). Originally a farm, the cemetery was established in 1878 and includes 10.1 hectares of land in total. Records

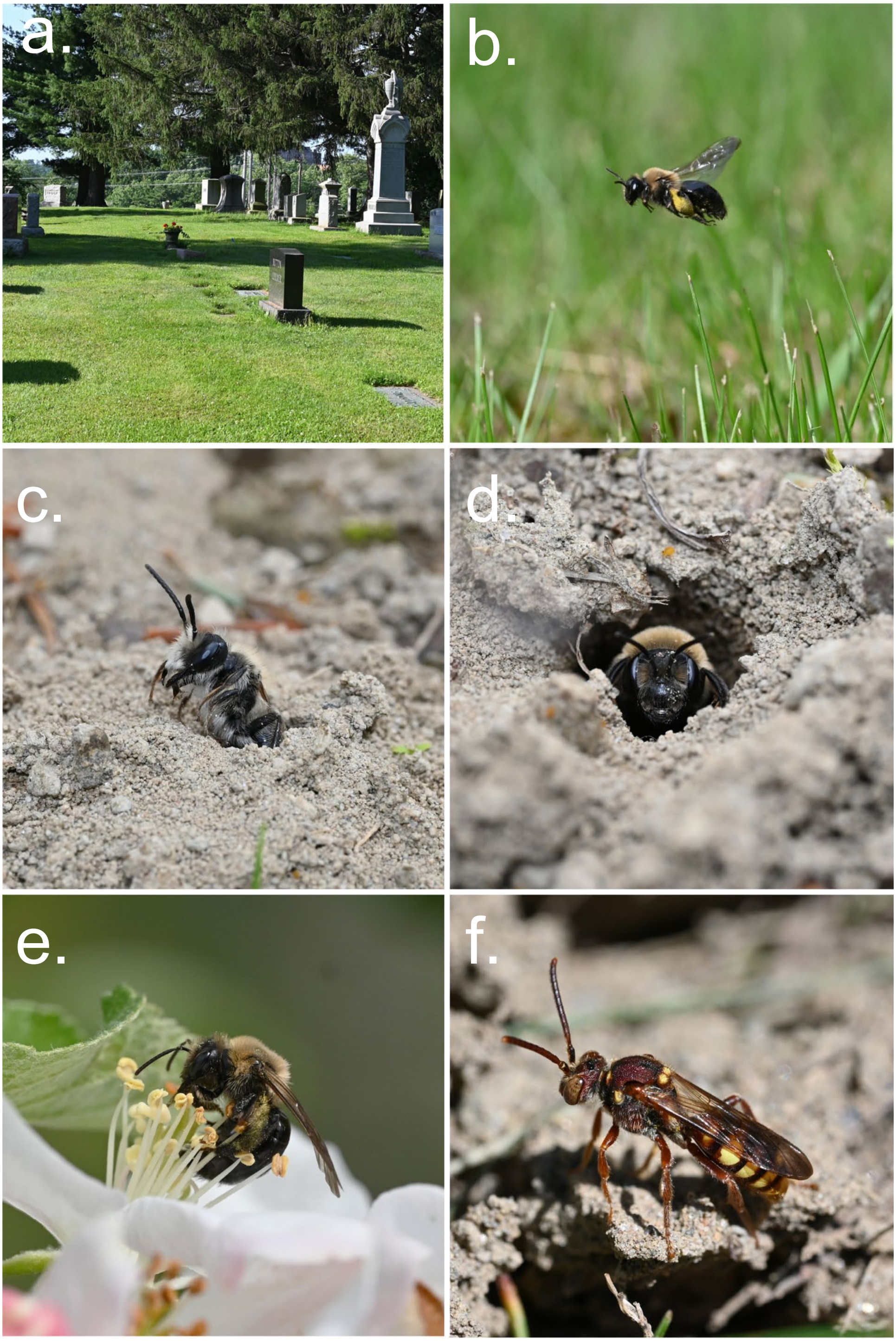

Figure 1. **a** East Lawn Cemetery showing area of high nest density, **b** female *Andrena regularis* in flight, **c** male *Andrena regularis* emerging from nest for first time, **d** female *Andrena regularis* at nest entrance, **e** female *Andrena regularis* on apple flower at Cornell Orchards, and **f** female *Nomada imbricata* inspecting nest entrance of *Andrena regularis*.

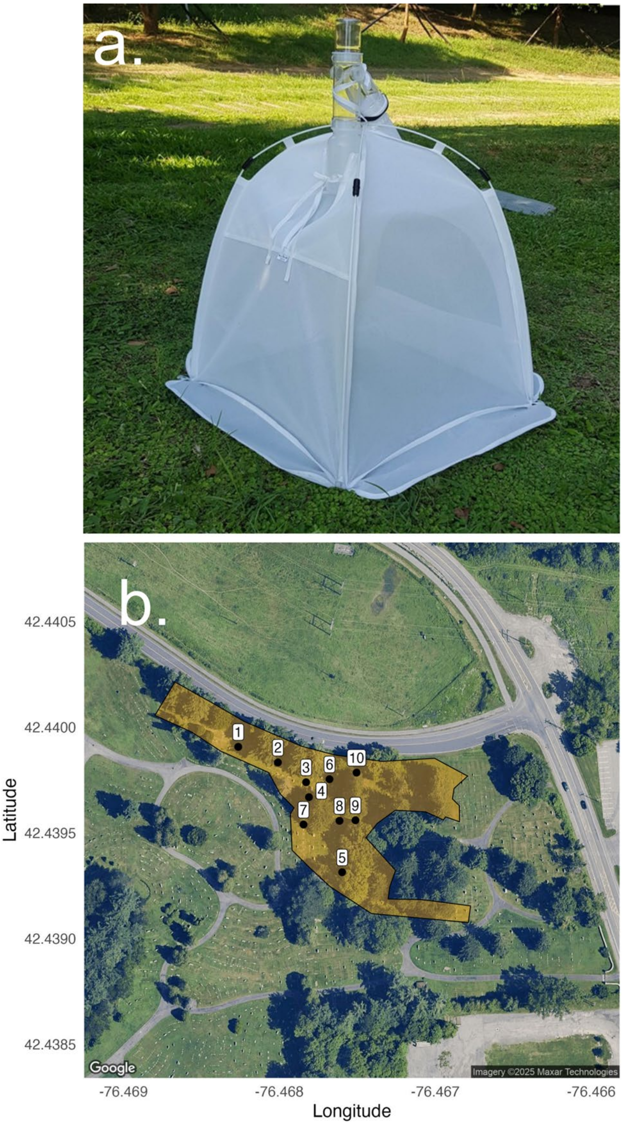

Figure 2. **a** Bug Dorm II emergence trap, **b** Aerial view of northeastern corner of East Lawn Cemetery showing area of aggregation (in yellow) and locations of emergence traps (numbered 1-10)

of *A. regularis* at ELC date back to 1935 (GBIF.org 2023); however, the massive nesting aggregation at ELC was not discovered until 2021, when numerous nests for this bee were located at the northeast corner of the cemetery, in a partly shady, regularly mowed lawn (Figures 1a and 2b). The floral composition of the site is similar to many northeastern suburban lawn landscapes, largely dominated by grasses (Poaceae). Flowering plants belonging to the families Asteraceae, Plantaginaceae, Caryophyllaceae, Lamiaceae, Fabaceae, and Polygonaceae are also present. Dominant tree species at the site include pines (*Picea glauca* (Moench) Voss, *Picea abies* (L.) H. Karst., *Pinus strobus* L.), maples (*Acer saccharum* Marshall, *Acer rubrum* L.), and cypresses (*Thuja occidentalis* L.). Sixty-eight percent of the 19 plant species at the site are non-native, but only one out of the six tree species (*Picea abies*) is non-native. The soil within the nesting site is primarily a sandy loam texture, with the average ratio composition from four samples being 66.5% sand, 23.5% silt, and 11% clay (Table S1 in Electronic Supplementary Material).

To sample emerging bees and other parasites across the known nesting site of *A. regularis*, we used 10 e-traps (Soil Emergence Trap II, Bugdorm) (Figure 2a). Due to the irregularity in the shape of the site, as well as other spatial barriers like trees and gravestones, traps were placed semi-randomly across the aggregation (Figure 2b), as determined from the previous year's observations of the limits of the aggregation. Traps were numbered, geolocated with Google Earth, and garden stakes were used to secure the traps as close to the ground as possible, preventing bee escape and entry. Each trap captured emerging bees from a 0.36 m^2 area. The lawn surrounding each trap was mowed on a regular basis by cemetery staff; however, the space under each trap was left untouched for the duration of the study. Importantly, e-traps were placed before the emergence of any *A. regularis* for the season.

Occurrence data within the Northeastern U.S. of *A. regularis* were downloaded from the Global Biodiversity Information Facility (GBIF.org 2023). Earliest records of this bee emerging in New York State were in early April, so we monitored the weather and decided to deploy the traps on March 30th to capture the earliest emerging bees. It should be noted that emergence was slightly (~5 days) delayed under the trap when compared to the surrounding soil, likely due to shading within the trap itself. Plastic collection jars attached to the e-traps were filled about halfway with 70% EtOH.

Due to the frequency and intensity of *A. regularis* emergence, daily visits to the aggregation were conducted once the first bees were detected. Exceptions to these daily visits included cold days (< 7.0 °C) and days of consistent rain. During each site visit, traps were visually inspected for insect specimens within the collection jars. Jars with insects (bees, beetles, flies) were poured through a sieve to separate the ethanol solution from the specimens. Specimens from each e-trap sample were added to small plastic storage bags, along with fresh 70% ethanol to cover the specimens. Collection jars were then re-filled with ethanol and re-attached to the e-trap. Once back in the lab, we replaced the ethanol in each storage bag with 95% ethanol to better preserve the specimens. Bags were carefully labeled with the date of collection, the trap number, and collection time (between 16:00 and 18:00 h).

After the collection period, the bagged samples were transferred to 50-mL conical centrifuge tubes for long-term storage in the laboratory refrigerator at 5 °C. For each trap and date, we recorded the number and sex of all *Andrena* and *Nomada* specimens collected. Species identifications for *Andrena*, *Nomada*, other bees, and non-bee parasitic insects were confirmed using a variety of print (Mitchell 1960, 1962; Selander 1960; Bouseman and LaBerge 1979) and online (Ascher and Pickering 2024) resources, and verified using the Cornell University Insect Collection (CUIC). Representative individuals were dried, pinned, and deposited in the CUIC. We compiled these data into a table summarizing the daily counts and sex ratio of each species across the collection period (Table S2 in Electronic Supplementary Material). Temperature data, including daily high temperature, were downloaded from NOAA for the Ithaca Cornell University weather station to relate daily emergence patterns with daily temperature. Statistical analyses were performed using R (R Core Team 2023) and Python (using the SciPy library).

The density of emerging bees within each trap was determined by dividing the total number of bees collected from each trap by the area under the trap (0.36 m^2), which yielded a measure of density in bees/m^2. To calculate the total population of emerging *A. regularis* and *N. imbricata*, we multiplied the area of the aggregation times the mean density of emerging bees. The area of the aggregation was determined by walking the periphery of the nest site and observing nest tumuli and foraging female bees during a warm day with peak bee activity (in mid-April). Using

Google Earth, we estimated the total area of the nest site as 6523 m^2 (Figure 2b).

To assess variation around our observed mean bee density for *A. regularis* and *N. imbricata*, we conducted a bootstrap analysis of our observed values with 1000 replicates. At each iteration, we resampled traps with replacement and recomputed the mean density (per m^2). To test for normality of our bootstrapped mean nest densities, we used a Shapiro-Wilk test of normality. Bootstrapping allowed us to estimate variance around the mean and to put upper and lower 95% confidence intervals on bee density. We calculated the mean and the upper and lower bounds on the total population size for both *A. regularis* and *N. imbricata* by multiplying density times the total area of the nest site.

In the classic model of sex ratio evolution, Fisher (1958) predicted that population-wide investment in male and female offspring (as measured by biomass) should approach equality in panmictic populations. In most bees, males are smaller than females, meaning that populations are expected to be numerically male-biased (Helms 1994), but to test the hypothesis of equal *investment*, one needs to consider differences between males and females in adult body weight, or some other measure of offspring "cost" (Danforth 1990). To calculate *investment* sex ratio in the emerging population of *Andrena regularis*, we combined numerical sex ratio data from emergence traps with body weight data for male and female *A. regularis*. Average weights of the male and female *A. regularis* were calculated by weighing 24 dried specimens of each sex (Table S3 in Electronic Supplementary Material). We tested the hypothesis of equal investment in males and females using a proportional (chi-square) test in R (R Core Team 2023).

To calculate the parasitism rate for *Nomada imbricata* and other known or presumed parasites of *Andrena regularis*, we divided the number of parasite specimens captured in the e-traps by the total number of adult *A. regularis* plus the number of other parasites captured. In solitary bees, brood parasites attack just one individual brood cell (or adult in the case of conopid flies) (Danforth et al. 2019).

To compare the mean date of emergence (in Julian days) for *A. regularis* males, *A. regularis* females, *N. imbricata* males, and *N. imbricata* females, we used a Mann-Whitney U test, a nonparametric method for comparing distributions. First, all Julian Day values for the four groups were combined and ranked, with average ranks assigned to tied values. The test statistic (U values) was compared against a null distribution to calculate a one-sided p-value, assessing whether (1) *A. regularis* males emerge significantly earlier than *A. regularis* females, (2) *N. imbricata* males emerge significantly earlier than *N. imbricata* females, (3) *A. regularis* females emerge significantly earlier than *N. imbricata* females, and (4) *A. regularis* males emerge significantly earlier than *N. imbricata* males. This latter comparison is of dubious biological relevance since male *Andrena* and male *Nomada* do not interact in any meaningful way, but we included it for completeness.

To assess phenological synchrony between *A. regularis* females and *N. imbricata* females, we used Spearman's rank correlation coefficient (ρ) to quantify the strength of the relationship between their daily emergence patterns. Specifically, we used Julian Day aligned counts of emerged individuals and then ranked these counts separately, assigning average ranks where ties occurred. Spearman's ρ was then calculated as the Pearson correlation of the rank-transformed variables, and a p-value which evaluates whether increases in one group's emergence are consistently and/or significantly associated with increases in the other.

3. RESULTS

3.1. E-trap results

Over the course of the 48-day sampling period, we collected 3251 individual insects across 16 insect species (Table I). *Andrena regularis* was by far the dominant species emerging during this period at the cemetery, followed by *Nomada imbricata*. We also detected other ground-nesting solitary bees (*Andrena*

Table I Summary of specimens collected in emergence traps, including bees, flies, and beetles. Parasitism rates are calculated by dividing the number of parasites recovered by the number of available brood cells that could have been parasitized. For example, the parasitism rate of *Nomada imbricata* is calculated as the number of *N. imbricata* individuals collected divided by the sum of the number of *A. regularis*, *Myopa vicaria*, and *Lytta aenea* collected. (Other sources of brood mortality exist [e.g., viruses, bacteria, fungi], but our methods cannot accurately measure below-ground mortality due to pathogens)

Order	Family	Species	Author	No. specimens collected	Parasitism rate (%)*
Hymenoptera	Andrenidae	*Andrena regularis*	Malloch, 1917	3070	
Hymenoptera	Andrenidae	*Andrena miserabilis*	Cresson, 1872	35	
Hymenoptera	Andrenidae	*Andrena forbesii*	Robertson, 1891	6	
Hymenoptera	Andrenidae	*Andrena rufosignata*	Cockerell, 1902	2	
Hymenoptera	Apidae	*Nomada imbricata*	Smith, 1854	43	1.380
Hymenoptera	Apidae	*Nomada "bidentate mandible"*		6	
Hymenoptera	Apidae	*Nomada maculata*	Cresson, 1863	2	
Hymenoptera	Apidae	*Nomada australis*	Mitchell 1962	1	
Hymenoptera	Apidae	*Nomada sayi*	Robertson, 1893	1	
Hymenoptera	Apidae	*Nomada illinoensis*	Robertson, 1900	1	
Hymenoptera	Colletidae	*Colletes inaequalis*	Say, 1837	21	
Hymenoptera	Halictidae	*Halictus* (*Seladonia*) *confusus*	Smith, 1853	15	
Hymenoptera	Halictidae	*Lasioglossum* (*Dialictus*) spp.		2	
Hymenoptera	Halictidae	*Sphecodes prosphorus*	Lovell and Cockerell, 1907	1	
Diptera	Conopidae	*Myopa vicaria*	Walker, 1849	30	0.959
Coleoptera	Meloidae	*Lytta aenea*	Say, 1824	15	0.477
		Total		3251	

*For known or presumed parasites of *A. regularis*

miserabilis Cresson, *A. forbesii* Robertson, *Colletes inaequalis* Say), ground-nesting social bees (*Lasioglossum* [*Dialictus*] sp., *Halictus* [*Seladonia*] *confusus* Smith), other species of *Nomada*, one conopid fly (*Myopa vicaria* Walker), and a meloid beetle (*Lytta aenea* Say). The other species of *Nomada* recovered in our e-traps (Table I) are believed to be parasites of *other* ground-nesting bee species, including *Andrena miserabilis* (*Nomada sayi* Robertson, *Nomada illinoensis* Robertson; KAO pers. obs.), *Agapostemon splendens* (Lepeletier) (*Nomada australis* Mitchell; Gibbs et al. 2023), other *Melandrena* (*Nomada maculata* Cresson; Gibbs et al. 2023), or their hosts are simply unknown (*Nomada* "bidentate mandible"). The close correlation between host and parasite body size observed in nomadine bees (Lim et al. 2022) would further support the view that *Nomada imbricata* is the primary bee brood parasite of *Andrena regularis* at the ELC. While *Nomada imbricata* is reported to attack multiple *Andrena* (*Melandrena*) (Hall & Ascher 2011) as well as *Halictus parallelus* Say (Alexander 1991), the only putative host present at ELC is *A. regularis*. Both conopid flies and meloid beetles are considered parasites of bees; however, conopid flies are endoparasites (or parasitoids) of adult bees whereas meloid beetles are brood parasites that consume pollen and nectar provisions within the bee brood cell (Minckley and Danforth 2019; Danforth et al. 2019).

Table II Emergence trap data for *Andrena regularis* and *Nomada imbricata* across the ten traps deployed with collection data and density/trap for each trap. Overall sex ratio of host and parasite is shown at the bottom

Trap #	*Andrena regularis* Males	*Andrena regularis* Females	*Andrena regularis* Total	*Andrena regularis* Density (bees/m^2)	*Nomada imbricata* Male	*Nomada imbricata* Female	*Nomada imbricata* Total	*Nomada imbricata* Density (bees/m^2)
1	346	176	522	1450.00	1	3	4	11.11
2	187	163	350	972.22	2	2	4	11.11
3	215	192	407	1130.56	0	1	1	2.78
4	52	28	80	222.22	2	3	5	13.89
5	206	98	304	844.44	4	2	6	16.67
6	0	0	0	0.00	1	0	1	2.78
7	6	7	13	36.11	0	0	0	0.00
8	186	74	260	722.22	4	6	10	27.78
9	378	367	745	2069.44	7	4	11	30.56
10	283	106	389	1080.56	1	0	1	2.78
	Total	**Total**	**Total**	**Average**	**Total**	**Total**	**Total**	**Average**
	1859	1211	3070	852.78	22	21	43	11.94
	Andrena regularis (% male)	***Andrena regularis*** (% female)			***Nomada imbricata*** (% male)	***Nomada imbricata*** (% female)		
Sex ratio	60.55	39.45			51.16	48.84		

3.2. Trap capture data and estimation of population size

Detailed collection data by trap for male and female *A. regularis* and *N. imbricata* are shown in Table II. Trap capture rates varied widely. For example, Trap 9 collected a total of 745 emerging *A. regularis* and 11 *N. imbricata*, whereas Trap 6 recovered just a single *N. imbricata*. For *A. regularis*, mean density across all ten traps was 852.78 bees/m^2 (Table II). For *N. imbricata*, mean density was 11.94 bees/m^2 (Table II). Extrapolating mean density to total emerging population size would indicate a total population of 5.56 million *A. regularis* and 77,914 *N. imbricata* emerging from ELC in Spring, 2023.

For *A. regularis*, the bootstrap distribution of means yielded a 95% confidence interval of 476.02–1230.56 bees/m^2, centered on a mean of 849.85 bees/m^2 (SD = 648.86; CV = 76.1%; range = 0–2069.44). The distribution of bootstrapped means did not significantly deviate from normality (Shapiro-Wilk W = 0.949, $p = 0.656$)**,** indicating that variation among traps was approximately normally distributed despite moderate heterogeneity in counts. The coefficient of variation (CV = 76%) reflects high spatial variability among traps, consistent with the patchy nest distributions characteristic of dense *Andrena* aggregations. Despite this variation, the bootstrap confidence interval provides an empirical estimate of plausible mean densities, thereby addressing uncertainty in extrapolated population size. Using our upper and lower 95% estimates of bee density, we estimate the total population of emerging *A. regularis* at ELC in the year of our study to be 3.1 to 8.0 million bees (Table S4 in Electronic Supplementary Material).

For *N. imbricata*, the bootstrap distribution of means yielded a 95% confidence interval of 5.6–18.6 bees/m^2, centered on a mean of 11.92 bees/m^2 (SD = 10.64; CV = 89.1%; range = 0–30.56). As for *A. regularis*, trap-level densities did not significantly deviate from normality (Shapiro-Wilk W = 0.889, $p = 0.164$). Using our upper and lower 95% estimates of bee density, we estimate the total population of emerging *N. imbricata* at ELC in the year of our study to be 36,528 to 121,393 bees (Table S4 in Electronic Supplementary Material). Other areas of the cemetery also had scattered *A. regularis* nests at low density, and we consider these numbers to be an underestimate of the total number of bees *A. regularis* and *N. imbricata* emerging at the ELC.

3.3. Sex ratio

Based on the emergence data for *A. regularis* (Table II), the numerical sex ratio is skewed toward males (60.6%). The same is true for *N. imbricata*, but the male-bias is less pronounced (51.2%). To test the hypothesis of equal investment in both sexes for *A. regularis*, we combined the dry body weight data with the numerical sex ratio data. The Fisherian expectation of equal investment (based on dry body weight) would predict a numerical sex ratio of 994 females and 2076 males (Fisher 1958). Our observed result (1211 females and 1859 males) was significantly female-biased (chi-square = 69.733; df = 1, $p < 0.001$).

3.4. Parasitism rate

Overall, the number of parasite individuals recovered in our sampling was relatively low. The most numerous species was *N. imbricata* ($n = 43$), which we determined to be the primary brood parasite of *A. regularis* at the ELC. The observed parasitism rate for *N. imbricata* was 1.4% (Table I). Parasitism rates for the fly (*Myopa vicaria*; rate = 0.959%) and beetle (*Lytta aenea*; rate = 0.477%) were lower (Table I).

3.5. Phenology of host (*Andrena regularis*) and parasite (*Nomada imbricata*)

Our sampling protocol, with e-trap placement prior to adult emergence, gives us a unique opportunity to examine temporal patterns of emergence in bee host and parasite. Figure 3 shows the temporal patterns of emergence for host (a) and parasite (b) over the 41-day collection period. Peaks in emergence for both *A. regularis* and *N. imbricata* coincide with warm days (Figure 3a, b), as one would expect. When temperatures exceeded 20 °C, both host and parasite bees emerged in large numbers. As expected for most ground-nesting, early spring, solitary bees, *A. regularis* is protandrous with males emerging significantly earlier than females (Table III; U statistic = 864,541.5, $p < 0.001$). Likewise, for *N. imbricata*, males emerge earlier than females, but the difference is much less pronounced (Table III; U statistic = 113.5, $p < 0.002$). Male *Andrena* emerged significantly earlier than male *Nomada* (Table III; U statistic = 4893.5, $p < 0.001$). Comparing host and parasite female emergence, which is biologically meaningful since female *N. imbricata* exploit the open brood cells of *A. regularis*, *Andrena* females emerge significantly earlier than *Nomada* females (Table III; U statistic = 2154.5, $p < 0.001$). While *Andrena* emergence largely occurs in the first few days of the emergence period, *Nomada* emergence is gradual and prolonged over the 41-day collection period (Figure 4). Based on the Spearman rank correlation coefficient comparing the daily emergence patterns of female *A. regularis* and female *N. imbricata*, there was no evidence of a significant correlation between host and parasite emergence ($\rho = 0.12$, $p = 0.66$).

4. DISCUSSION

4.1. Population size

Our study documented a total population size of between 3.1 and 8.0 million bees, with an average estimated total population of 5.56 million *A. regularis* emerging in 2023 from

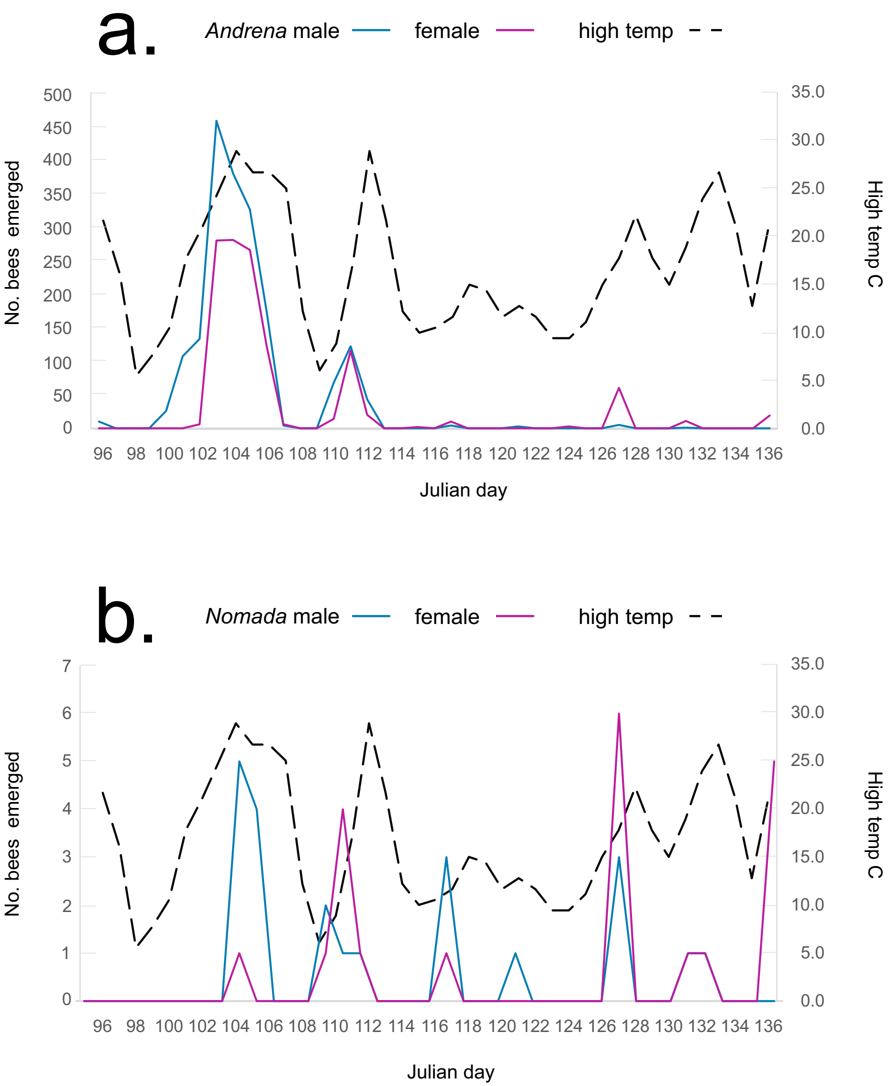

Figure 3. Phenology and emergence of (**a**) *Andrena regularis*, and (**b**) *Nomada imbricata*, with daily high temperatures (dashed lines) across the sampling period (in degrees C)

the ELC. Assuming a typical honey bee colony includes 20,000 to 40,000 workers, our mean value would be equivalent to 140 to 270 honey bee hives placed in an area of less than one hectare. Typical honey bee colony densities used by apple growers in New York are 2–3 colonies/hectare, so the ELC population of *A. regularis* represents an extraordinary abundance of bees, even when compared to honey bees.

It is difficult to find emergence data for comparison because most reports of solitary, ground-nesting bee population size refer to the total number of active *nests* rather than emerging individuals (see Table 6-2 in Danforth et al. 2019); however, three previous studies provide some data for comparison. Rozen and Buchmann (1990) documented a large aggregation of *Centris caesalpiniae* Cockerell (Apidae) in an area of 1290 m^2 along a power line right of way near

Table III Mean, median, and first date of emergence for male and female *Andrena regularis* and male and female *Nomada imbricata*, expressed in Julian days. See text for statistical comparisons among means

		Mean date of emergence (in Julian days)	Median date of emergence (in Julian days)	First date of emergence (in Julian days)
A. regularis	Male	104.701	104	96
	Female	107.121	105	102
N. imbricata	Male	114	110.5	105
	Female	123.476	127	105

Sahuarita, Arizona. Based on quantification of brood cell density multiplied by the total area occupied, they estimated that 1,615,000 *C. caesalpiniae* had emerged from the site in the year of their study (plus an additional 5160 *Ericrocis lata* (Cresson) [Apidae], the brood parasite of *C. caesalpiniae*). Giulian et al. (2024) documented a large aggregation of *Melissodes bimaculatus* (Apidae) in a suburban lawn in upstate New York. They calculated a total emerging population of 651,440 bees based on multiplying nest density (59.2 nests/m^2) times the area occupied by the nesting aggregation (1100 m^2) times the average number of offspring produced/female (10; deduced from the published literature on related species). Finally, Werneck and Campos (2020), using methods very similar to ours, studied phenology, natural enemies, and sex ratio in the solitary, ground-nesting bee *Epicharis picta* (Smith) (Apidae) in Brazil. They placed 10 e-traps (each covering a 0.25 m^2 area) over a roughly 160 m^2 nesting site of *E. picta* and recovered 211 emerging male and female *E. picta*, which translates to a total emerging population of 13,504 bees.

Not only is the aggregation at the ELC one of the largest nest sites ever recorded, we suspect that it also represents one of the oldest. Although the nest site was recently discovered, *A. regularis* collection records at the ELC date back to 1935, suggesting that the population could have existed for ~90 years. The ELC was originally set aside as a cemetery in 1878, so it is possible the aggregation is even older, as *Andrena* and other ground-nesting bee aggregations can persist for decades (Danforth et al. 2019). It should be noted that solitary bee populations can be ephemeral with significant year-to-year fluctuations in nesting population size (Martins et al. 2025) and local population extinction followed by recolonization (Bischoff 2003).

4.2. Sex ratio

While the numerical sex ratio of emerging *A. regularis* at ELC is male-biased (60.6%), the investment sex ratio (considering body size differences between males and females) is significantly female-biased. Female solitary bees (and wasps), because they can facultatively determine the sex of their offspring, are capable of altering offspring sex ratio in predictable ways in response to variation in resource availability, foraging distance, maternal size, and even age (Danforth et al. 2019). In most bees, including *A. regularis*, males are smaller than females and therefore “cheaper” to produce. When faced with low resource availability, long foraging distances, small female body size, or age-related decline in foraging efficiency, nesting females can adaptively shift to producing the “cheaper” sex: males (reviewed in Danforth et al. 2019). At the population level, the investment sex ratio can therefore provide insights into the overall health of a population. We infer from the female-biased investment sex ratio that the ELC population of *A. regularis* is healthy, thriving, and not suffering from obvious floral resource limitation, at least in Spring 2022 (the year prior to our study).

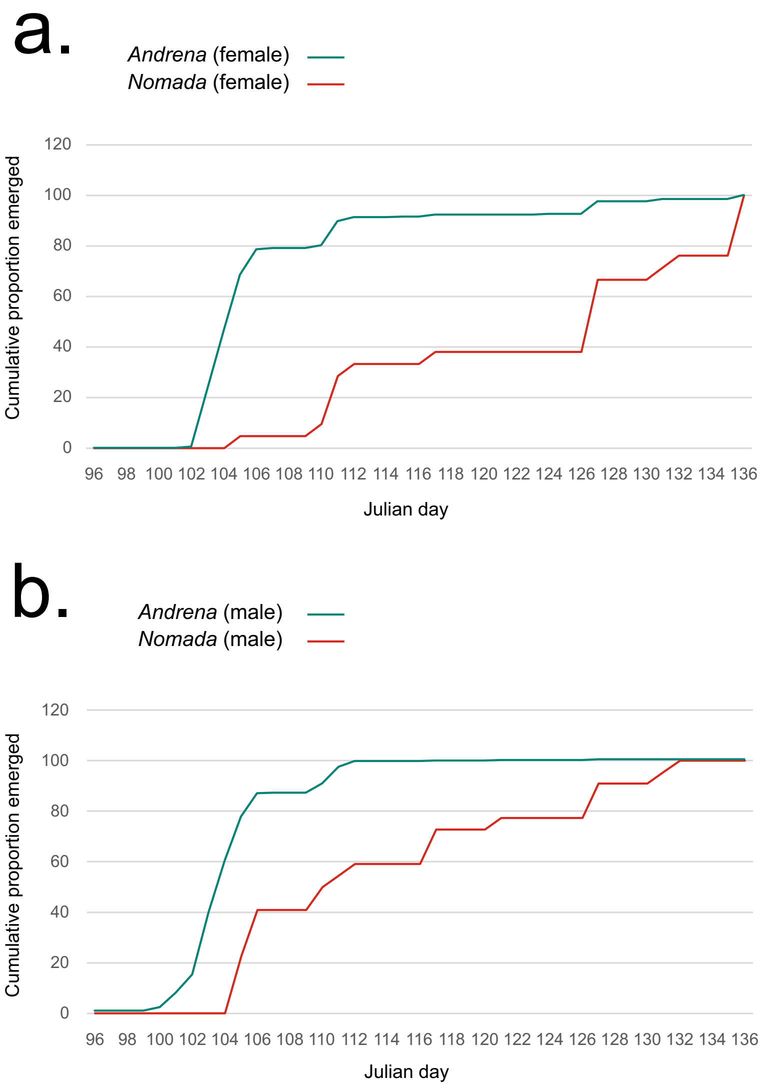

Figure 4. Cumulative emergence of (**a**) female *A. regularis* and female *N. imbricata*, and (**b**) male *A. regularis* and male *N. imbricata*

4.3. Parasites of Andrena regularis and parasitism rate by *Nomada imbricata*

Two non-bee parasitic associations were suggested by our study. First, a brood parasitic blister beetle, *Lytta aenea* ($n = 15$), was collected emerging from the nest site. Species of the genus *Lytta* are known brood parasites of a variety of bees, including ground-nesting Apidae, Colletidae, and Megachilidae (Selander 1960; Eickwort et al.1981), but this is the first observation to suggest that *Lytta* may also potentially parasitize andrenid bees. *Lytta aenea* would be a novel host-association if confirmed by future studies. We also collected a conopid fly, likely *Myopa vicaria* ($n = 30$). Conopid flies are parasitic on adult bees rather than their brood provisions (Danforth et al. 2019). Miliczky and Osgood (1995) reared *Myopa vicaria* Walker from adult *A. regularis*, further confirming the association between *Myopa vicaria* and *A. regularis*. The most abundant brood parasite observed in our study, *N. imbricata*, is a known brood parasite of *A. regularis* based on previous studies (Schrader and LaBerge 1978). Parasitism by *N. imbricata* was relatively low (1.4%) compared with other studies of solitary, ground-nesting bee brood parasites which, on average, cause 6.7% mortality (across the 52 studies reviewed by Minckley and Danforth 2019 [their Table 1]).

4.4. Phenology

Our study revealed significant differences in the temporal pattern of emergence between host (*A. regularis*) and brood parasite (*N. imbricata*) (Table III). Both species exhibit protandry, with males emerging before females (although this was more pronounced in *A. regularis*). Interestingly, the emergence patterns of host and parasite are strikingly different. Whereas *A. regularis* emerges *en masse* as soon as temperatures exceeded 20 °C, *N. imbricata* exhibits a more delayed, gradual emergence. A number of studies of early spring *Andrena* indicate that *Nomada* brood parasites, like their *Andrena* hosts, overwinter as adults (Linsley & MacSwain 1955; Witt 1992; Riddick 1993; Miliczky and Osgood 1995; Miliczky 2008), suggesting that differences in emergence phenology are not linked to differences in overwintering stage.

Whereas host and parasite are clearly emerging in bursts associated with warmer days (Figure 3a, b), the emergence of *N. imbricata* is much more prolonged than the emergence of *A. regularis* for both females (Figure 4a) and males (Figure 4b). The different patterns of temporal emergence may make sense given the biology of *Nomada* brood parasites. *Nomada* attack the open brood cells of their hosts, inserting a cryptic egg into the brood cell wall during cell provisioning (reviewed in Danforth et al. 2019, Chapter 10). There is a delay between when bees first emerge for the season and when females start to build nests, construct brood cells, and begin brood cell provisioning. We do not know the exact duration, but it is likely a week or two before emerged *A. regularis* have constructed their nests and are actively provisioning brood cells. From the perspective of female *Nomada*, delayed emergence makes sense as a way to maximize reproductive success. Riddick (1993) proposed the same idea based on his observations that *Nomada annulata* Smith emerges several days after peak emergence of its host *Andrena macra* Mitchell. To the best of our knowledge, no previous study has documented temporal patterns of emergence in bee host-parasite pairs with the level of detail provided by the e-traps in our study.

4.5. Utility of e-traps for population studies of ground-nesting bees

E-traps have been used extensively to estimate ground-nesting bee nest densities through random placement of traps across an area or habitat (Sardiñas & Kremen 2014, Pane & Harmon-Threatt 2017, Cope et al. 2019, Brokaw et al. 2023; Williams et al. 2024; reviewed in Antoine & Forrest 2020 and Hellerich et al. 2025). However, our use of emergence traps to document parasitism rates, emergence dynamics, and sex ratio of an existing aggregation of ground-nesting bees is novel. Most studies utilizing randomly placed e-traps report low levels of specimen capture. For example, Brokaw et al. (2023) reported an overall nest detection rate of 0.15 active nests/trap when comparing burned and unburned tall-grass prairie habitats in Minnesota. Similarly, low levels of trapping success have been reported in surveys of prairie habitats in Illinois (Pane & Harmon-Threatt 2017; 0.2 active nests/trap) and agricultural landscapes in Northern California (Williams et al. 2024; 0.22 active nests/trap).

We know of only two studies that have used e-traps to document the emergence dynamics of an existing population of ground-nesting bees. Minckley et al. (1994) used e-traps to document emergence phenology in *Dieunomia triangulifera* (Vachal) (Halictidae) in Kansas and Werneck and Campos (2020) used e-traps to document emergence phenology, sex ratio, and parasitism rates in *Epicharis picta* (Apidae) in the Atlantic Forest of Southeastern Brazil. Such an approach

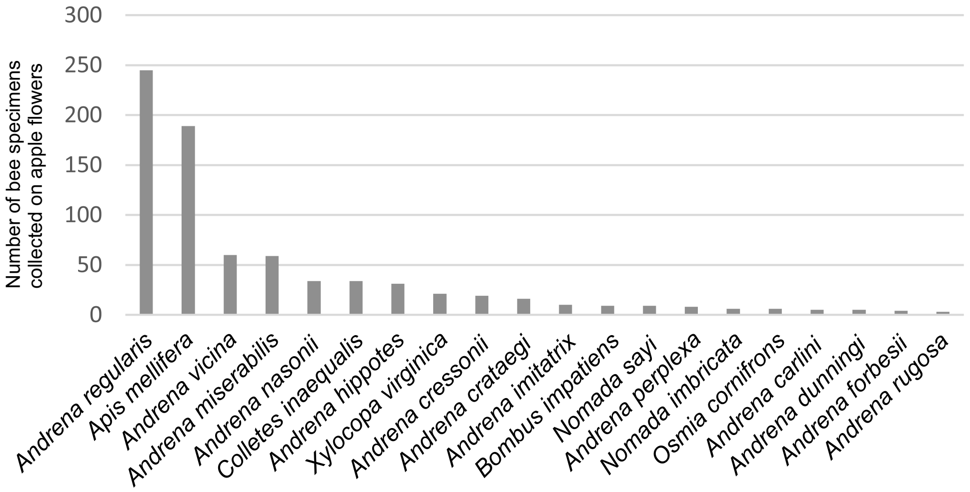

Figure 5. Abundance of the top 20 most common bee species visiting apple flowers at the CU Ithaca apple orchard from 2008-2016 (see Park et al. 2015a for detailed sampling protocols)

to studying ground-nesting bee aggregations has enormous potential to provide new insights into the nesting dynamics of ground-nesting bees. Future research should apply e-traps when sampling large aggregations of other bee species, as the direct sampling of emergence provides unique insight into species-specific nesting dynamics, host-parasite associations, and could be used to monitor population trends over time. However, caution should be taken to avoid significant mortality at valuable nest sites of rare or endangered bees.

4.6. *Andrena regularis* and apple orchard pollination

Andrena regularis is known to be a valuable blueberry (Schrader & LaBerge 1978) and apple (Park et al. 2015a; Russo et al. 2017; Russo & Danforth 2017) pollinator. Female *A. regularis* carry nearly pure apple pollen based on analysis of scopal and body loads (Russo et al. 2017; Russo & Danforth 2017) and contact the reproductive parts of *Malus* flowers at a high per-visit rate (Park et al. 2015b). Based on our surveys of apple orchards in New York state from 2008 to 2015, *A. regularis* also ranks in the top three most abundant bees in New York apple orchards and is the second most abundant native bee (second only to *Andrena crataegi*; Russo et al. 2015; supplementary Table 2). The Cornell University apple orchard (42.44406, −76.46197) is located just 600 m from the ELC and our surveys at that site from 2008 to 2015 revealed that *A. regularis* is the most abundant pollinator; even more common than managed honey bees (Figure 5). When these surveys were conducted, we were not aware of the massive *A. regularis* population at ELC. The discovery of the aggregation in 2021 provided the key to understanding why *A. regularis* was so common at the Cornell University apple orchard. The ELC population is likely the most important source of pollinators for the Cornell apple orchard. Therefore, our study highlights the importance of identifying and preserving large nesting aggregations of solitary bees for both ecosystem health and agricultural pollination, a perspective further supported by Kueneman et al. (2024), who demonstrate the power of community science to locate, study, and conserve ground-nesting bee aggregations across diverse landscapes.

4.7. The value of cemeteries as repositories of biodiversity

Cemeteries and other types of burial grounds are regarded as sacred places all over the world, closely linked to community history (Rugg 2000) and often functioning as "sentinels of biodiversity where the dead protect the living" (Barrett & Barrett 2001; Dybas 2025). Cemeteries are increasingly viewed as biodiversity preserves for native plants and animals (Shakeri et al. 2021; Kowarik et al. 2016; Löki et al. 2019; Itescu & Jeschke 2024), especially in heavily urbanized environments (Kowarick et al. 2016, Smith & Minor 2019). Cemeteries and burial places can also serve as refuges for rare and endangered species. In an urban cemetery in Berlin, Germany, for example, Kowarick et al. (2016) documented 604 species of flowering plants, bryophytes, lichens, bats, birds, spiders, and ground-beetles, 48 (7.9%) of which were identified as of conservation concern. Like urban parks and nature preserves, cemeteries can also serve as "cooling islands" that buffer high temperatures in urban habitats even more effectively than community gardens or parks (Stumpe et al. 2024). The ELC clearly serves as a valuable nesting site for one of the largest nesting aggregations of economically important solitary bees ever recorded.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at https://doi.org/10.1007/s13592-026-01256-6.

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AUTHOR CONTRIBUTION

STH, BND, and JGK conceived this research and designed the experiment; STH and RF conducted the fieldwork; BND, KO, and CD identified the insect specimens; STH curated and organized the data; STH, BND, and JGK analyzed the data; STH, BND, JGK, and KO wrote the paper and participated in the revisions of it. All authors read and approved the final manuscript.

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DATA AVAILABILITY

All data supporting the findings of this study are available within the paper and its Supplementary Information:

CODE AVAILABILITY

Not applicable.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

REFERENCES

Alexander B (1991) *Nomada* phylogeny reconsidered (Hymenoptera: Anthophoridae). J Nat Hist 25(2):315–30. https://doi.org/10.1080/00222939100770231

Antoine CM, Forrest JRK (2020) Nesting habitat of ground-nesting bees: a review. Ecol Entomol 46:143–159. https://doi.org/10.1111/een.12986

Ascher JS, Pickering J (2024) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Discover Life. Retrieved from www.discoverlife.org/bees. Accessed 1 July 2023

Barrett GW, Barrett TL (2001) Cemeteries as repositories of natural and cultural diversity. Conserv Biol 15:1820–1824. https://doi.org/10.1046/j.1523-1739.2001.00410.x

Bischoff I (2003) Population dynamics of the solitary digger bee *Andrena vaga* Panzer (Hymenoptera, Andrenidae) studied using mark-recapture and nest counts. Popul Ecol 45(3):197–204. https://doi.org/10.1007/s10144-003-0156-6

Blagoveshchenskaya NN (1963) Giant colony of the solitary bee *Dasypoda plumipes* PZ. (Hymenoptera, Melittidae). Entomol Rev 42:115–117

Bouseman JK, LaBerge WE (1979) A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part IX. Subgenus *Melandrena*. Trans Am Entomol Soc 104:275–389

Brokaw J, Portman ZM, Bruninga-Socolar B, Cariveau DP (2023) Prescribed fire increases the number of ground-nesting bee nests in tallgrass prairie remnants. Insect Conserv Divers 16:355–367. https://doi.org/10.1111/icad.12628

Cope GC, Campbell JW, Grodsky SM, Ellis JD (2019) Evaluation of nest-site selection of ground-nesting bees and wasps (Hymenoptera) using emergence traps. Can Entomol 151:260–271. https://doi.org/10.4039/tce.2019.3

Danforth BN (1990) Provisioning behavior and the estimation of investment ratios in a solitary bee, *Calliopsis* (*Hypomacrotera*) *persimilis* (Cockerell) (Hymenoptera: Andrenidae). Behav Ecol Sociobiol 27(3):159–68. https://doi.org/10.1007/BF00180299

Danforth BN, Minckley RL, Neff JL (2019) *The solitary bees: biology, evolution, conservation*. Princeton University Press, Princeton, xi+472 pp.

Dybas CL (2025) Sentinels of biodiversity: in cemeteries around the world, the dead protect the living. Bioscience 75:195–202. https://doi.org/10.1093/biosci/biae121

Eickwort GE, Mathews RW, Carpenter J (1981) Observations on the nesting behavior of *Megachile rubi* and *M. texana* with a discussion of the significance of soil nesting in the evolution of megachilid bees (Hymenoptera: Megachilidae). J Kans Entomol Soc 54:557–570

Fisher RA (1958) The genetical theory of natural selection, 2nd edn. Dover, New York, p 291

Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R et al (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339(6127):1608–11. https://doi.org/10.1126/science.1230200

GBIF.org (2023) GBIF Occurrence Download. https://doi.org/10.15468/dl.zwszss

Gibbs J, Hanuschuk E, Miller R, Dubois M, Martini M et al (2023) A checklist of the bees (Hymenoptera: Apoidea) of Manitoba, Canada. Can Entomol 155:e3:1-38. https://doi.org/10.4039/tce.2022.45

Giulian J, Danforth BN, Kueneman JG (2024) A large aggregation of *Melissodes bimaculatus* (Hymenoptera: Apidae) offers perspectives on gregarious nesting and pollination services. Northeast Nat 31(3):402–417. https://doi.org/10.1656/045.031.0314

Goulson D, Nicholls E, Botias C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347(6229):1255957. https://doi.org/10.1126/science.1255957

Hall HG, Ascher JS (2011) Surveys of wild bees (Hymenoptera: Apoidea: Anthophila) in organic farms of Alachua County in north-central Florida. Fla Entomol 94(3):539–552

Hellerich C, Klein A, Garratt M, Mix M, Mupepele A-C, Fornoff F (2025) Beneath the buzz: quantifying nest locations and densities of ground-nesting wild bees (Hymenoptera: Anthophila). Methods Ecol Evol 16:1334–1349. https://doi.org/10.1111/2041-210x.70062

Helms KR (1994) Sexual size dimorphism and sex ratios in bees and wasps. Am Nat 143:418–434. https://doi.org/10.1086/285611

Itescu Y, Jeschke JM (2024) Assessing the conservation value of cemeteries to urban biota worldwide. Conserv Biol 38:e14322. https://doi.org/10.1111/cobi.14322

Kowarik I, Buchholz S, von der Lippe M, Seitz B (2016) Biodiversity functions of urban cemeteries: evidence from one of the largest Jewish cemeteries in Europe. Urban For Urban Green 19:68–78. https://doi.org/10.1016/j.ufug.2016.06.023

Kueneman JG, Dobler CN, Danforth BN (2024) Harnessing community science to conserve and study ground-nesting bee aggregations. Front Ecol Evol 11:1347447. https://doi.org/10.3389/fevo.2023.1347447

LeBuhn G, Luna JV (2021) Pollinator decline: what do we know about the drivers of solitary bee declines? Curr Opin Insect Sci 46:106–111. https://doi.org/10.1016/j.cois.2021.05.004

Lim K, Lee S, Orr M, Lee S (2022) Harrison's rule corroborated for the body size of cleptoparasitic cuckoo bees (Hymenoptera: Apidae: Nomadinae) and their hosts. Sci Rep 12(1):1–12. https://doi.org/10.1038/s41598-022-14938-9

Lima MAP, Cutler GC, Mazzeo G, Hrncir M (2022) The decline of wild bees: causes and consequences. Front Ecol Evol 10:1027169. https://doi.org/10.3389/fevo.2022.1027169

Linsley EG, MacSwain JW (1955) The habits of *Nomada opacella* Timberlake with notes on other species (Hymenoptera: Anthophoridae). Wasmann J Biol 13:253–276

Litman JR (2019) Under the radar: detection avoidance in brood parasitic bees. Philos Trans R Soc Lond B Biol Sci 374:20180196. https://doi.org/10.1098/rstb.2018.0196

Löki V, Deák B, Lukács AB, Molnár VA (2019) Biodiversity potential of burial places – a review on the flora and fauna of cemeteries and churchyards. Glob Ecol Conserv 18:e00614. https://doi.org/10.1016/j.gecco.2019.e00614

Martins CF, dos Santos Neto VI, Aguiar CML (2025) Monitoring a nest aggregation of a solitary ground nesting bee (*Epicharis nigrita* Friese) in an urban area. Sociobiology 72(3):e11681–e11681. https://doi.org/10.13102/sociobiology.v72i3.11681

Miliczky E (2008) Observations on the nesting biology of *Andrena* (*Plastandrena*) *prunorum* Cockerell in Washington State (Hymenoptera: Andrenidae). J Kans Entomol Soc 81:110–121. https://doi.org/10.2317/jkes-611.12.1

Miliczky ER, Osgood EA (1995) Bionomics of *Andrena* (*Melandrena*) *vicina* Smith in Maine and Washington, with new parasite records for *A.* (*M.*) *regularis* Malloch and a review of *Melandrena* biology. J Kans Entomol Soc 68:51–66. https://doi.org/10.2307/25085560

Minckley RL, Wcislo WT, Yanega D, Buchmann SL (1994) Behavior and phenology of a specialist bee (*Dieunomia*) and Sunflower (*Helianthus*) pollen availability. Ecology 75:1406–1419. https://doi.org/10.2307/1937464

Minckley RL, Danforth BN (2019) Sources and frequency of brood loss in solitary bees. Apidologie 50:515–525. https://doi.org/10.1007/s13592-019-00663-2

Mitchell TB (1960) Bees of the Eastern United States, Vol. 1. N C Agric Exp Stn Tech Bull 141:1–538

Mitchell TB (1962) Bees of the Eastern United States, vol. 2. North Carolina Agricultural Experiment Station Technical Bulletin 152:1–557

Pane AM, Harmon-Threatt AN (2017) An assessment of the efficacy and peak catch rates of emergence tents for measuring bee nesting. Appl Plant Sci 5:1700007. https://doi.org/10.3732/apps.1700007

Park MG, Blitzer EJ, Gibbs J, Losey JE, Danforth BN (2015a) Negative effects of pesticides on wild bee communities can be buffered by landscape context. Proceedings of the Royal Society B: Biological Sciences 282:20150299. https://doi.org/10.1098/rspb.2015.0299

Park MG, Raguso RA, Losey JE, Danforth BN (2015b) Per-visit pollinator performance and regional importance of wild *Bombus* and *Andrena* (*Melandrena*) compared to the managed honey bee in New York apple orchards. Apidologie 47:145–160. https://doi.org/10.1007/s13592-015-0383-9

R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/; version 4.3.1

Riddick EW (1993) *Nomada annulata* Smith (Hymenoptera: Anthophoridae), a confirmed cleptoparasite of *Andrena macra* Mitchell (Hymenoptera: Andrenidae) and other *Nomada-Andrena* associations. Proc Entomol Soc Wash (USA) 95:107–112

Rozen JG, Buchmann SL (1990) Nesting biology and immature stages of the bees *Centris caesalpiniae*, *C. pallida*, and the cleptoparasite *Ericrocis lata* (Hymenoptera: Apoidea: Anthophoridae). Am Mus Novit 2985:1–30

Rugg J (2000) Defining the place of burial: what makes a cemetery a cemetery? Mortality 5:259–275. https://doi.org/10.1080/713686011

Russo L, Danforth B (2017) Pollen preferences among the bee species visiting apple (*Malus pumila*) in New York. Apidologie 48:806–820. https://doi.org/10.1007/s13592-017-0525-3

Russo L, Park M, Gibbs J, Danforth B (2015) The challenge of accurately documenting bee species richness in agroecosystems: bee diversity in eastern apple orchards. Ecol Evol 5:3531–3540. https://doi.org/10.1002/ece3.1582

Russo L, Park MG, Blitzer EJ, Danforth BN (2017) Flower handling behavior and abundance determine the relative contribution of pollinators to seed set in apple orchards. Agric Ecosyst Environ 246:102–108. https://doi.org/10.1016/j.agee.2017.05.033

Sardiñas HS, Kremen C (2014) Evaluating nesting microhabitat for ground-nesting bees using emergence traps. Basic Appl Ecol 15:161–168. https://doi.org/10.1016/j.baae.2014.02.004

Schrader MN, LaBerge WE (1978) The nest biology of the bees: *Andrena* (*Melandrena*) *regularis* Malloch and *Andrena* (*Melandrena*) *carlini* Cockerell

(Hymenoptera: Andrenidae). Illinois Natural History Survey Biological Notes 108:1–24. https://doi.org/10.5962/bhl.title.15182

Selander RB (1960) Bionomics, systematics, and phylogeny of *Lytta*, a genus of blister beetles (Coleoptera, Meloidae), vol 28. University of Illinois Biological Monographs, pp 1–295

Shakeri Z, Mohammadi-Samani K, Bergmeier E, Plieninger T (2021) Spiritual values shape taxonomic diversity, vegetation composition, and conservation status in woodlands of the Northern Zagros, Iran. Ecol Soc 26(1):30. https://doi.org/10.5751/es-12290-260130

Sless T, Danforth BN, Searle JB (2023) Evolutionary origins and patterns of diversification in animal brood parasitism. Am Nat 202:107–121. https://doi.org/10.1086/724839

Smith AD, Minor E (2019) Chicago's urban cemeteries as habitat for cavity-nesting birds. Sustainability 11:3258. https://doi.org/10.3390/su11123258

Stumpe B, Stuhrmann N, Jostmeier A, Marschner B (2024) Urban cemeteries: the forgotten but powerful cooling islands. Sci Total Environ 934:173167. https://doi.org/10.1016/j.scitotenv.2024.173167

Werneck H, Campos L (2020) A study of the biology of *Epicharis* (*Epicharoides*) *picta* using emergence-traps. J Hymenopt Res 80:147–167. https://doi.org/10.3897/jhr.80.56898

Williams NM, Buderi A, Rowe L, Ward K (2024) Wildflower plantings enhance nesting opportunities for soil-nesting bees. Ecol Appl 34(2):e2935. https://doi.org/10.1002/eap.2935

Willmer PG, Cunnold H, Ballantyne G (2017) Insights from measuring pollen deposition: quantifying the pre-eminence of bees as flower visitors and effective pollinators. Arthropod-Plant Interact 11(3):411–25. https://doi.org/10.1007/s11829-017-9528-2

Witt R (1992) Zur Bionomie der Sandbiene *Andrena barbilabris* (Kirby 1802) und ihrer Kuckucksbienen *Nomada alboguttata* Herrich-Schäffer 1839 und *Sphecodes pellucidus* Smith 1845. Drosera 92:47–81