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Article *in* The Canadian Entomologist · March 2019

DOI: 10.4039/tce.2019.3

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Evaluation of nest-site selection of ground-nesting bees and wasps (Hymenoptera) using emergence traps

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Abstract—Approximately 70% of the 30 000 known bee (Hymenoptera) species and most flower-visiting, solitary wasps (Hymenoptera) nest in the ground. However, nesting behaviours of most ground-nesting bees and wasps are poorly understood. Habitat loss, including nesting habitat, threatens populations of ground-nesting bees and wasps. Most ground-nesting bee and wasp studies implement trapping methods that capture foraging individuals, but provide little insight into the nesting preferences of these taxa. Some researchers have suggested that emergence traps may provide a suitable means by which to determine ground-nesting bee and wasp abundance. We sought to evaluate nest-site selection of ground-nesting bees and wasps using emergence traps in two study systems: (1) planted wildflower enhancement plots and fallow control plots in agricultural land; and (2) upland pine and hammock habitat in forests. Over the course of three years (2015–2017), we collected 306 ground-nesting bees and wasps across all study sites from emergence traps. In one study, we compared captures per trap between coloured pan traps and emergence traps and found that coloured pan traps captured far more ground-nesting bees and wasps than did emergence traps. Based on our emergence trap data, our results also suggest ground-nesting bees and wasps are more apt to nest within wildflower enhancement plots than in fallow control plots, and in upland pine habitats than in hammock forests. In conclusion, emergence traps have potential to be a unique tool to gain understanding of ground-nesting bee and wasp habitat requirements.

Introduction

Evidence suggests that ground-nesting pollinator populations (bees and wasps; Hymenoptera), particularly in Europe and North America, are in decline due to loss of habitat and floral resources (Thorp and Shepherd 2005; Goulson *et al*. 2008; Ollerton *et al*. 2014). In addition, wild bee abundance has declined 23% across the United States of America (Koh *et al*. 2016) and may be driven by habitat loss that is associated with land conversion to agriculture (Ricketts *et al*. 2008; Potts *et al*. 2010; Koh *et al*. 2016). Agricultural land use practices have contributed to the reduction of foraging resources and nesting substrate for ground-nesting bees (Ricketts 2004). Habitat fragmentation from agriculture can alter abundance and species richness of pollinators, as well as pollinator flight paths, leading to the reduction of pollination services provided by native bees (Powell and Powell 1987; Didham *et al*. 1996). Landscape complexity can affect abundance and richness of bees (Kennedy *et al*. 2013; Garratt *et al*. 2017). Additionally, Steffan-Dewenter (2002) showed that wasps especially rely on greater habitat diversity and landscape structure for nesting places and food resources.

Pollination services by ground-nesting bees are critical to sustain native plant species and crop production in natural and managed systems, respectively (Roubik 1995; Cane 1997; Klein *et al*. 2007). Furthermore, some wasp families

Received 6 May 2018. Accepted 10 October 2018. First published online 12 March 2019.

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Subject editor: Alejandro Zaldívar-Riverón
doi:10.4039/tce.2019.3

(*e.g.*, Hymenoptera: Scoliidae, Mutilidae) have morphological characteristics that permit them to collect pollen and, thereby, account for the pollination of specific plant species (Jervis 1998); wasps also can be important biological control agents, preying on many agricultural pest species (O'Neill 2001). Despite their importance, ground-nesting bees and wasps are far less studied for their susceptibility to habitat degradation than are other prolific plant pollinators such as honey bees (*Apis mellifera* Linnaeus; Hymenoptera: Apidae) (Koh *et al*. 2016).

Suitable nesting habitat for ground-nesting bees and wasps can include specific site characteristics, nesting substrate, and food plants (O'Neill 2001; Sardiñas and Kremen 2014). Suitability of nesting site characteristics for ground-nesting bees and wasps is influenced by soil texture, soil depth, slope, vegetation cover, soil moisture, and rewarding floral resource availability (Rubink 1979; Cane 2001; O'Neill 2001). Foraging behaviours to secure mud, leaves, and resins for partitioning of nests also affect habitat preference (O'Toole and Raw 1991). Bee community organisation is known to be linked closely to the respective foraging habits and resources of the population, but less is known about how nesting habitat and availability factor into the composition of pollinator communities in general, though suitable nesting habitat is often characterised by exposed bare ground and an abundance of potential nesting cavities (Potts *et al*. 2005). Loss of any of these resources within an ecosystem can impinge on the ability of ground-nesting bees and wasps to establish viable, local populations (Westrich 1996).

It can be challenging to study the effects of land conversion on ground-nesting bee and wasp populations and nesting locations without proper collecting methods. That said, trapping and monitoring methods for ground-nesting bees, wasps, and other pollinators can be accomplished via sweep netting at floral resources (Westphal *et al*. 2008), deploying coloured pans (Campbell and Hanula 2007), and vane traps (Stephen and Rao 2005). These methods can provide important information on relative abundances of ground-nesting bee and wasp species within a given habitat. However, these collecting methods lack the ability to trace ground-nesting bees and wasps back to their nests and provide little information on nest site preferences.

Kim *et al*. (2006) employed a trapping method of covering potential bee/wasp nesting sites with fabric propped up using metal hoops, as a supplement to pan trapping, to assess ground-nesting bee and wasp nesting sites. Historically this emergence trap technique has been used to sample aquatic insects (Mundie 1956), but in a similar fashion, ground-nesting bees and wasps have been collected with smaller-scale emergence traps (Sardiñas and Kremen 2014). With this method, ground-nesting bees and wasps can be sampled passively using soil emergence traps that cover a portion of the ground. To date, there is a paucity of studies in which emergence traps have been used to capture ground-nesting bees and wasps (Sardiñas and Kremen 2014). Agricultural practices are known to be detrimental to ground-nesting bee and wasp populations, whereas forested habitats can positively contribute to ground-nesting bee and wasp diversity (Ricketts 2004; Schuepp *et al*. 2012).

We used emergence traps in two case studies to examine ground-nesting bee and wasp abundance in agricultural and forested settings. In one study, we investigated the use of wildflower enhancement plots and fallow control plots as nest sites by ground-nesting bees and wasps, as determined by capture data using both emergence and pan traps. These habitats were chosen because native wildflower enhancement plots are becoming increasingly popular within intensive agriculture in an effort to augment wild pollinator abundance, diversity, and habitat conservation (Williams *et al*. 2015). Our objectives were to: (1) determine whether ground-nesting bees and wasps preferred to nest within the wildflower enhancement plots opposed to fallow control plots; and (2) compare between emergence trap and pan trap collection methods. We hypothesised that wildflower enhancement plots would have a greater abundance of ground-nesting pollinators than would fallow control plots because they would provide more foraging resources and prey items than would control plots. Additionally, we hypothesised that pan traps would collect more individuals of ground-nesting bees and wasps.

We conducted the second study in a forest ecosystem comprised of upland pine and hammock habitats. No previous studies have attempted to use emergence traps in a temperate forest. Forest habitats of the southeastern United States of America have been shown to contain a wide array of bee and wasp species, and relative abundance of these species can change due to alterations of forest habitat (Campbell and Hanula 2007). Upland pine habitat occurred on well-drained, elevated soil and experienced managed burns at three- to six-year intervals. Hammock habitat commonly occurs in north-central Florida, United States of America, and is characterised by poorly drained soil that is high in nutrients and organic material (Vince *et al.* 1989). Our objectives were to determine: (1) whether emergence traps could be used as a sampling method for ground-nesting bees and wasps in temperate forest habitats; and (2) whether upland pine and hammock ecosystems differed in nesting site availability for ground-nesting bees and wasps. We hypothesised that the upland pine habitat would have a greater abundance of ground-nesting bees and wasps than would the hammock habitat because it would be less likely to contain standing water due to soil characteristics (Vince *et al.* 1989).

Materials and methods

Trap types

We used emergence traps in both case studies to assess ground-nesting bee and wasp abundance in different habitats. Emergence traps (MegaView Science Company, Talchung, Taiwan) were comprised of an enclosed, four-sided mesh structure that tapered into a collection jar at its apex (Fig. 1). As pollinators emerged from their nests, they were trapped by the enclosed mesh. They were then funnelled into the collecting bottle that was partially filled with soapy water. Once emerged, ground-nesting bees and wasps were unable to exit the emergence trap because each edge of the trap remained flush with the ground. We determined trap position by random placement within each plot and ensured that the traps were at least 5 m apart. To minimise the chances of placing emergence traps over the same area, a random number generator was used to determine initial trap placement. Additionally, a different cardinal direction was designated for entrance to each plot for each monthly/weekly trap setup.

We also used two pan trap sets in each wildflower and fallow plot to assess the overall activity of bees and wasps in our study sites.

Fig. 1. Photograph of an emergence trap with dimensions used in our case studies to collect ground-nesting bees and wasps.

Pan trapping has been used as an efficient method for sampling pollinators in agricultural landscapes and forest ecosystems (Campbell and Hanula 2007; Westphal *et al.* 2008; Wilson *et al.* 2008). Each pan trap set consisted of a blue, yellow, and white bowl (355 mL Festive Occasion; Amscan International, Milton Keynes, United Kingdom) set on a rack system that allowed traps to be moved up as vegetation grew (see Campbell *et al.* 2016). The sets were placed 20 m apart in each wildflower and fallow plot. Pan traps were filled with soapy water, collected after 24 hours, and all bees and wasps were stored in ethanol for future identification. A synoptic set of voucher specimens for this study is deposited at the Florida State Collection of Arthropods, Gainesville, Florida, United States of America.

Case studies

Wildflower enhancement/fallow control study. We selected eight sites (hereafter "blocks") located within intensive agricultural areas (blueberry (*Vaccinium* Linnaeus; Ericaceae) and Cucurbitaceae, *etc.*) in northcentral Florida. Each block contained two plots (*e.g.*, treatments) (0.1 ha each) – one with a wildflower enhancement and a second as a fallow control plot. We located plots within a block approximately 500 m apart. The wildflower plots were prepared for seeding by application of glyphosate and mowing to minimise weed competition with the wildflowers (Bammer *et al.* 2017). In October/November 2014, we hand-broadcasted nine native annual and perennial herbaceous flowering plant species in each wildflower enhancement plot. We selected species for wildflower enhancement plots that had been shown to perform well in north Florida agricultural systems (Williams *et al.* 2015; see Campbell *et al.* 2017 for information on wildflower species, seeding rates, and maintenance). The unenhanced fallow control plots consisted primarily of grasses (Poaceae or Gramineae) and were similar in plant composition to that of the wildflower enhancement plots prior to manipulative seeding.

Once per month (April–November 2015 and April–October 2016), we placed 10 emergence traps within the wildflower enhancement and fallow control plots at dusk/night and collected samples the following morning. During the two-year experiment, we placed a total of 2400 emergence traps within the experimental plots (eight blocks × two plots per block × 10 emergence traps per plot × 15 sample periods). We also placed two sets of coloured pan traps within the fallow controls and wildflower enhancement plots; during the same days emergence traps were placed within the experimental plots [eight blocks x two plots per block x two sets of coloured pan traps per plot x 15 sampling periods (480 total coloured pan traps)].

Upland pine/hammock study. We studied ground-nesting bees and wasps in an upland pine stand and an area with hammock habitat (hereafter "block") within a managed tract of upland forest at the University of Florida Natural Area Teaching Laboratory in Gainesville, Florida (29.6354° N, 82.3677° W). Blocks were divided into 12 50 × 50 m plots using a pre-existing grid system based on north–south and east–west gridlines. We deployed sets of five emergence traps at dusk/night in four different plots at each block, respectively, for a total of 40 traps each sampling period per block. Each block was separated by approximately 200 m. To ensure that the same plot was not used in consecutive weeks, we rotated plot selection (four plots per block per week) on a constant interval. All traps were collected during mid-morning on the following day. From April–October 2017, these traps were active one day per week. A total of 840 emergence traps were placed within the experimental plots (two habitat types × four plots per block × five emergence traps per plot × 21 sample periods). Unlike the prior case study, pan traps were not used in tandem because we were primarily interested in whether emergence traps could capture ground-nesting bees and wasps within forested habitats, rather than surveying the overall bee and wasp community.

Statistical analysis

For each of the two case studies, we conducted generalised linear models with Poisson distributions with total count of ground-nesting bees and wasps per trap type as dependent variables to test treatment-level responses of ground-nesting bees and wasps to varying habitat types. For one case study, we also conducted Poisson generalised linear models with the same dependent variables to test for differences in the number of ground-nesting bee and wasp captures between emergence and pan traps. For all models, we tested for correlation among covariates and assumed overdispersion when the residual deviance divided by the residual degrees of freedom was > 1.0; we used quasipoisson generalised linear models when we detected overdispersion. For categorical treatment covariates in all models, we performed *post-hoc* Tukey's pair-wise comparisons of means using general linear hypothesis testing (glht function; single-step method) in the R package "multcomp" (Hothorn *et al.* 2013). We set $\alpha = 0.05$.

For each of the two case studies, we used treatment (*i.e.*, wildflower enhancement versus fallow control; upland pine versus hammock) as the experimental units and total number of captured individuals of ground-nesting bees and wasps in each treatment plot as dependent variables (Grodsky *et al.* 2018a, 2018b). For the wildflower enhancement/fallow control study, we pooled the number of captured individuals of ground-nesting bees and wasps over all emergence and pan traps, respectively, in each treatment plot (dependent variable). We first included a year × treatment interaction term, treatment, year, block, and Julian date (without year; *sensu* intra-annual, seasonal variation) as explanatory variables in each model. If we detected a significant year × treatment interaction, we consequently developed a model for each year separately and included treatment, block, and Julian date as explanatory variables. Otherwise, we included treatment, year, block, and Julian date as explanatory variables. For comparisons between emergence and pan traps used in the wildflower enhancement/fallow control study, we used treatment as the experimental unit and total number of captured individuals of ground-nesting bees and wasps pooled over all traps per trap type in each treatment as dependent variables. We then followed the same modelling procedure outlined to test treatment-level effects. For the upland pine/hammock study, we pooled the number of captured individuals of ground-nesting bees and wasps over all emergence traps in each treatment plot (dependent variable) and only included block and plot as explanatory variables.

Results

Wildflower enhancement/fallow control study

We captured 230 individual ground-nesting Hymenoptera (110 bees and 120 wasps) in emergence traps, which were comprised of eight ground-nesting bee species and 19 ground-nesting wasp species (Table 1). The fallow controls contained 18% of the ground-nesting bees and 30% of the ground-nesting wasps, whereas the wildflower enhancement plots contained 82% of the ground-nesting bees and 70% of the ground-nesting wasps. Ground-nesting bee (z-value = 3.94; $P < 0.001$) and wasp (z-value = 3.65; $P < 0.001$) relative abundance both were greater in wildflower enhancement plots than in fallow controls for the emergence traps (Fig. 2). Only 2.7% and 4.7% of the deployed emergence traps captured ground-nesting bees and wasps, respectively. Abundance of ground-nesting bees was greater in fallow controls than wildflower enhancement plots as collected by pan trap method (z-value = −2.16; $P = 0.03$) (Fig. 3A). This trend was primarily driven by two species: *Melissodes communis* Cresson (Hymenoptera: Apidae) and *Augochlorella aurata* (Smith) (Hymenoptera: Halictidae). Number of captures of ground-nesting bees in pan traps significantly decreased throughout the season (t-value = −6.42; $P < 0.001$). We detected a significant year × treatment interaction for ground-nesting wasps caught in pan traps. Abundance of ground-nesting wasps caught in pan traps in 2016 was greater in wildflower enhancement plots than in fallow controls (z-value = 4.13; $P < 0.001$) (Fig. 3B).

In contrast, we captured 617 ground-nesting bees and 495 ground-nesting wasps comprising 21 bee species and 16 wasp species in coloured pan traps (Table 2). Between the two methods of trapping exercised in the blocks, the coloured pan traps collected a greater abundance of ground-nesting bees (z-value = 35.76; $P < 0.001$) and wasps (z-value = 32.83; $P < 0.001$) than the emergence traps. Eighty three per cent of all ground-nesting bees and wasps were collected in pan traps, which is nearly five times more than those collected in emergence traps. We captured many species of ground-nesting bees and wasps with pan traps that we never captured in emergence traps and vice versa (Table 2). For example, two parasitic bee species from emergence traps (*Triepeolus lunatus* (Say) and *Triepeolus rufithorax* Graenicher (Hymenoptera: Apidae)) and one parasitic bee species from coloured pan traps (*Epeolus pusillus* Cresson; Hymenoptera: Apidae) were captured. Additionally, we captured six of the eight bee species collected from emergence traps in coloured pan traps and nine of the sixteen wasp species collected from emergence traps in coloured pan traps.

Upland pine/hammock study

We captured a total of 76 individual ground-nesting Hymenoptera (31 bees and 45 wasps) in emergence traps (Table 3). The upland pine habitat contained 84% of the ground-nesting bees and wasps collected (three bee families and six wasp families), while the hammock habitat contained 14% of the ground-nesting bees and 16% of the wasps (two families of bees and two families at wasps). Relative abundances of total ground-nesting bees (z-value = 1.94; $P = 0.049$) and ground-nesting wasps (z-value = 3.79; $P < 0.001$) were greater in the upland pine habitat than in the hammock habitat. We only captured ground-nesting bees and wasps in 3.7% and 5.4% of the total emergence traps we set, respectively. We captured one parasitic bee species from emergence traps (*Epeolus zonatus* Smith; Hymenoptera: Apidae).

Table 1. Ground-nesting bees and wasps collected from emergence traps from wildflower enhancement and fallow control plots, northcentral Florida, April–November 2015 and 2016

Family	Species/genera	Number of individuals trapped in control plots	Number of traps*	Number of individuals trapped in wildflower enhancement plots	Number of traps*
Bees					
Apidae	*Melissodes* species†	0	0	2	2
	Triepeolus lunatus	0	0	5	2
	Triepeolus rufithorax	0	0	1	1
Halictidae	*Agapostemon splendens* (LePeletier)†	0	0	6	6
	Augochlorella aurata†	0	0	4	4
	Halictus poeyi LePeletier†	8	2	55	26
	Halictus rubicundus (Christ)†	0	0	11	6
	Lasioglossum Curtis species†	12	9	6	5
Total		**20**	**11**	**90**	**52**
Wasps					
Crabronidae	*Cerceris* species Latreille	2	1	1	1
	Cerceris bicornuta Guérin-Méneville†	0	0	1	1
	Tachytes Panzer species	0	0	5	4
	Unknown species	10	10	34	32
Mutillidae†	*Dasymutilla* Ashmead species	5	5	4	4
	Ephuta Say species	0	0	2	2
	Pseudomethoca Ashmead species	0	0	1	1
	Sphaeropthalma Blake species	0	0	2	2
Pompilidae†		7	7	16	16
Scoliidae	*Campsomeris plumipes* (Drury)†	0	0	2	1
	Scolia nobilitata Fabricius†	1	1	2	2
	Trielis octomaculata (Say)†	0	0	2	2
Sphecidae	*Ammophila* Linnaeus species†	1	1	1	1
	Palmodes Kohl species†	1	1	1	1
	Sphex Linnaeus species†	0	0	3	3
Tiphiidae†	*Myzinium* Latreille species	4	4	2	2
	Tiphia Fabricius species	4	4	4	4
Vespidae	*Euodynerus hidalgo* (de Saussure)	1	1	1	1
Total		**36**	**35**	**84**	**80**

*Number of emergence traps out of 2400 traps deployed that contained ground-nesting bees or wasps.
†We also collected families, genera, or species of ground-nesting individuals in coloured pan traps.

Discussion

In our wildflower enhancement and fallow control study, as collected by emergence traps, ground-nesting bees and wasps were more abundant in wildflower enhancement plots, whereas fewer ground-nesting bees and wasps were collected in the fallow control plots. The positive association of bees and wasps with wildflower enhancement plots may be a result of more abundant floral resources that could potentially increase foraging behaviours and encourage nesting site selection (Gathmann and Tscharntke 2002). Fallow control plots may have contained scarce

Fig. 2. Mean number of ground-nesting bees (**A**) and wasps (**B**) captured in emergence traps set in fallow control and wildflower enhancement treatments in intensive agricultural areas, northcentral Florida, April–November 2015 and April–October 2016. Different letters indicate significantly different, pair-wise comparisons of treatment means at $\alpha = 0.05$. Errors bars = standard error.

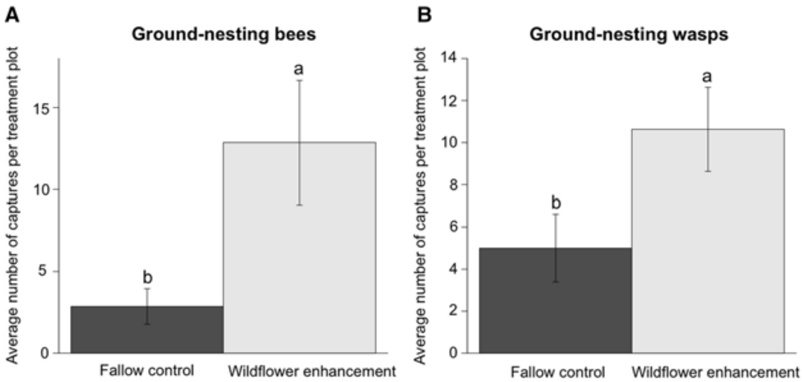
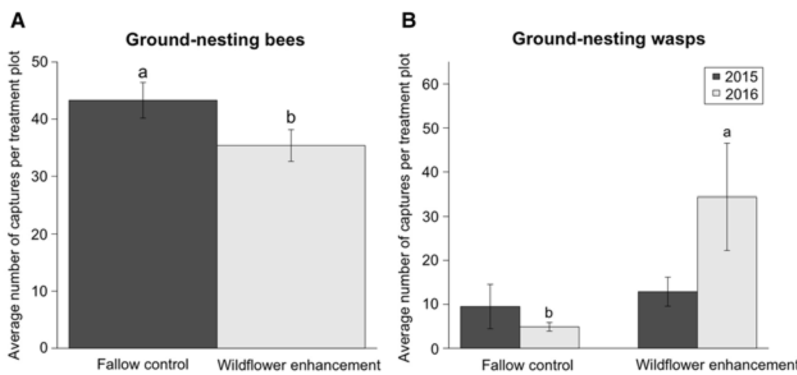


Fig. 3. Mean number of ground-nesting bees (**A**) and wasps (**B**) captured in pan traps set in fallow control and wildflower enhancement treatments in intensive agricultural areas, northcentral Florida, April–November 2015 and April–October 2016. Different letters indicate significantly different, pair-wise comparisons of treatment means at $\alpha = 0.05$. Years were analysed separately for ground-nesting wasps due to a significant year × treatment interaction. Error bars = standard error.



suitable nesting sites because soil moisture and texture may have been unsuitable for some ground-nesting species (Cane 1991).

The increased relative abundance of ground-nesting bees in fallow control plots in comparison to the wildflower plots by pan trapping could be related to bee body size and foraging distances. Many more large-bodied bees (*e.g.*, *Bombus* Latreille, *Melissodes* Latreille, *Svastra* Holmberg; Hymenoptera: Apidae) were captured within pan traps compared with emergence traps. Foraging ranges of bees tend to be greater for larger-bodied bees than for smaller-bodied bees (Greenleaf *et al.* 2007). Therefore, the bees collected in our pan traps may have been foraging, but not nesting, within our plots. Additionally, the two most common bee species collected by pan trapping within the fallow plots (*M. communis* and *A. aurata*) were both generalists and may have been attracted to grasses (Poaceae) and other plants that were growing within the fallow plots.

Increased wasp abundance in wildflower enhancement plots relative to fallow control plots, in 2016, may have been driven not only by increased forage but also by increased insect prey availability. The majority of ground-nesting wasps

Table 2. Ground-nesting bees and wasps collected in coloured pan traps from wildflower enhancement and fallow control plots, northcentral Florida, April–November 2015 and 2016

Family	Species/genera	Number of individuals trapped in control plots	Number of individuals trapped in wildflower enhancement plots
Bees			
Apidae	*Bombus bimaculatus* Cresson	1	1
	Bombus pensylvanicus (De Geer)	2	1
	Epeolus pusillus	1	0
	Melissodes bimaculata (LePeletier)	1	5
	Melissodes communis	35	13
	Melissodes comptoides Robertson	2	1
	Melissodes dentiventris Smith	0	1
	Melissodes manipularis Smith	1	1
	Melissodes species	7	0
	Melissodes trinodis Robertson	1	0
	Svastra aegis (LaBerge)	0	1
	Svastra compta (Cresson)	1	0
		7	4
Halictidae	*Agapostemon splendens*	0	5
	Augochlorella aurata	52	6
	Augochlorella gratiosa (Smith)	1	0
	Augochloropsis anonyma (Cockerell)	17	25
	Augochloropsis metallica (Fabricius)	0	2
	Halictus poeyi	20	65
	Halictus rubicundus	0	1
	Lasioglossum species	189	147
Total		**338**	**279**
Wasps			
Crabronidae	*Bicyrtes* LePeletier species	0	9
	Cerceris bicornuta	0	1
	Oxybelus Latreille species	0	6
	Unknown species	21	91
Mutillidae		12	39
Pompilidae		38	73
Sphecidae	*Ammophila* species	2	10
	Eremnophila aureonotata (Cameron)	0	3
	Palmodes species	0	1
	Podium Fabricius species	0	1
	Prionyx Vander Linden species	9	10
	Sphex species	0	5
Scoliidae	*Campsomeris plumipes*	2	13
	Campsomeris quadrimaculata (Fabricius)	2	2
	Scolia nobilitata	3	2
	Trielis octomaculata	2	0
Tiphiidae		26	112
Total		**117**	**378**

Table 3. Ground-nesting bees and wasps collected from emergence traps in upland pine and hammock habitats, University of Florida Natural Area Teaching Laboratory, Gainesville, Florida, April–October 2017

Family	Species/genera	Upland pine	Number of traps*	Hammock	Number of traps*
Bees					
Apidae	*Epeolus zonatus*	6	6	2	2
Halictidae	*Agapostemon splendens*	2	2	2	2
	Augochloropsis metallica	1	1	0	0
	Halictus poeyi	1	1	0	0
	Lasioglossum species	14	2	1	1
	Sphecodes ignitus Cockerell	1	1	0	0
Colletidae	*Colletes thoracicus* Smith	1	1	0	0
Total		**26**	**14**	**5**	**5**
Wasps					
Crabronidae		11	10	5	5
Mutillidae		7	7	0	0
Pompilidae		9	8	0	0
Sphecidae	*Prionyx parkeri* Bohart and Menke	1	1	0	0
	Sphex ichneumoneus (Linnaeus)	1	1	0	0
Tiphiidae	*Tiphia* Fabricius species	7	6	2	2
Vespidae	*Pachodynerus erynnis* (LePeletier)	2	2	0	0
Total		**38**	**35**	**7**	**7**

*Number of traps out of 840 traps deployed that contained ground-nesting bees or wasps.

collected in the wildflower and fallow plots collected by pan traps and emergence traps feed on a variety of insects, including Lepidoptera/Coleoptera larvae and spiders (Araneae). Wildflower plots have been shown to harbour increased arthropod abundance, including many that could act as prey items for ground-nesting wasps (Braman *et al*. 2002). Additionally, some ground-nesting wasp families (Hymenoptera: Mutillidae) use ground-nesting bees as hosts; therefore, increased ground-nesting wasp abundance could be dependent upon ground-nesting bee populations (Brothers *et al*. 2000).

As we hypothesised, ground-nesting bee and wasp abundances were greater in upland pine habitat than in hammock habitat, potentially owing to the soil composition of both respective ecosystems. Soil moisture, texture, and salinity varied between forest habitats, so ground-nesting bee and wasp abundances may have been driven by nest site selection in accordance with the preference of the species for certain soil characteristics (Cane 1991; O'Neill 2001). Soils in upland pine stands are well drained and loose, which may have provided more optimal nesting sites for certain species in comparison to highly compacted soils in hammocks. Furthermore, soils in hammocks are poorly drained and high in nutrients, which may have limited availability of suitable ground-nesting bee and wasp nest sites due to saturated soils.

Additionally, though there is no empirical data to show, there may have been more floral resource availability in upland pine stands compared with hammocks, owing to the greater bee abundance apparent in the upland pine habitat. Furthermore, greater wasp abundance in upland pine habitat than in hammock habitat may be explained by prey availability. Although adult wasps visit flowers, their young are fed other arthropods. Therefore, ground-nesting wasp abundance could also have been driven by greater prey and host abundance within the upland pine stands.

Emergence traps have been largely inefficacious at capturing species and are time-intensive to set; nevertheless, we were able to determine significant habitat-level differences in the abundance of ground-nesting bees and wasps in both studies. In contrast, Sardiñas and Kremen (2014) tested applications of emergence traps to sample ground-nesting bees and wasps and found them largely effective in identifying existing nesting sites and predicting other patterns of nesting for targeted ground-nesting bee populations. In our case studies, emergence traps had very low capture rates and, as seen in one case study, were less effective than coloured pan traps, a commonly implemented trapping method (Westphal *et al.* 2008; Morandin and Kremen 2013).

Many ground-nesting bees are communal nesters (Danforth *et al.* 1996) and, therefore, are not evenly spaced throughout the landscape. For example, we often captured numerous individual ground-nesting bees in one emergence trap, suggesting that the trap was near a communal nesting site. Thus, emergence traps not placed near communal nesting sites may underestimate abundance of many ground-nesting bees and wasps potentially present in an ecosystem. Accordingly, emergence traps placed near communal nesting sites may overestimate the abundance of many ground-nesting bees and wasps potentially present in the ecosystem. However, emergence traps captured a few parasitic bee species that were not captured in pan traps in wildflower enhancement and fallow control plots. Yet overall, we captured numerous ground-nesting bees and wasps with pan traps that we never captured in emergence traps. Our results suggest that emergence traps may not be an effective trapping method for studies using randomised trap placement to capture ground-nesting bees and wasps and that studies seeking to survey ground-nesting bee and wasp populations should use emergence traps as a supplement to other trapping methods.

In most other studies, pan traps were employed to survey ground-nesting pollinators (Campbell *et al.* 2007; Sardiñas and Kremen 2014; Campbell *et al.* 2016). Pan trapping may not provide information on the actual presence and location of nesting sites within a given area because it may capture transient, non-local foraging ground-nesting bees and wasps. As such, pan trapping may not be representative of nest site appropriateness and availability, especially for species of ground-nesting bees that have large foraging ranges. The efficiency of pan trapping can be limited because behavioural factors of foraging bees may not be evident; pan traps may be less attractive to bees and wasps in comparison to abundant floral resources (Cane *et al.* 2000). Unlike pan traps, emergence traps have the ability to give information on nesting site location and preferences for bees and wasps.

However, we found it time-intensive and resource-intensive to use emergence traps to study the abundance of ground-nesting bees and wasps. In previous studies that examined the characteristics of ground-nesting bee nests, active nesting sites had to be previously identified or artificially started with nesting blocks and provisions (Cane 1991; Cane and Neff 2011). We suggest that emergence traps that cover larger tracts of soil should be used, or simply deployed in larger quantity, to increase the potential of sampling active nesting sites. Furthermore, though the scale of emergence traps that we used may not be as effective as a singular method of sampling ground-nesting bees and wasps, they could be incorporated as a supplement to other insect-monitoring methods. Emergence traps may collect species that are not commonly captured in coloured pan traps, providing insight into which ground-nesting bees and wasps are nesting within a localised area that may be foraging locally or elsewhere. Additionally, emergence traps intentionally placed over different soil types in different habitat types may aid in the understanding of preferences of ground-nesting species.

Ground-nesting bee and wasp nesting sites remain largely understudied; however, our data support the concept that ground-nesting bees and wasps have specific preferences for nesting sites. Nevertheless, declines in wild bee abundances are a contemporary concern and have been associated with land conversion and habitat modification (Koh *et al.* 2016). Therefore, it is important to support a wider breadth of knowledge on nesting habitats and sites to advance the respective techniques of surveying ground-nesting bees and wasps for conservation purposes.

Acknowledgements

We thank Hennelly Irvin, Alyn Irvin, Alexandra Tsalickis, and Cherice Smithers for insect collection and data entry. The wildflower enhancement/fallow control portion of the study was funded by Syngenta, as part of the Operation Pollinator Initiative. The upland pine/hammock study was funded by a University of Florida Natural

Area Teaching Laboratory minigrant. We thank Anthony Abbate for constructive suggestions during manuscript development.

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