An Assessment of the Efficacy and Peak Catch Rates of Emergence Tents for Measuring Bee Nesting

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AN ASSESSMENT OF THE EFFICACY AND PEAK CATCH RATES OF EMERGENCE TENTS FOR MEASURING BEE NESTING[1]

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- *Premise of the study:* Emergence tents are a new tool used to understand nesting ecology of ground nesting bee species. However, many questions remain about how to use tents effectively. We assessed (a) variance in tent capture rates over time, (b) the effects of site characteristics on proportion of tents capturing bees, and (c) the effect of soil characteristics on nest site choice.
- *Methods:* Emergence tents were placed out for one week in May, June, and August and checked daily. Soil, bee, and floral characteristics were recorded.
- *Results:* Across all sites and months the average number of tents capturing bees was less than 20% during one week of sampling, but this varied between sites. Tent captures decreased after 48 h deployment, but accumulation differed seasonally, with slower accumulation of total bees caught in May than in June or August. Although capture rates were not affected by bee or floral abundance, soil moisture beneath a tent influenced where bees were captured.
- *Discussion:* Effective use of emergence tents may require adjusting the length of deployment depending on season and will require a minimum of 48 h installation to help maximize efficacy. The overall low capture rates demonstrate the need to optimize emergence tent use.

  Key words: bees; emergence tents; ground nesting.

Invaluable for the economic and ecological services they provide, bees are largely responsible for successful seed and fruit set of wild plant species and agricultural crops (Kremen et al., 2002; Potts et al., 2006; Klein et al., 2007; Ollerton et al., 2011). However, specific solutions to slow and reverse bee declines are lacking, often due to an incomplete understanding of the complex biotic and abiotic interactions bees have with their environment (Winfree et al., 2009). Aboveground resources like flower availability are well known to positively correlate with bee species richness (Potts et al., 2003; Kennedy et al., 2013), but research examining other resources that are necessary to support bees is limited.

In particular, adequate nesting resources are considered a primary limiting factor for many bee species (Potts et al., 2005), but the belowground nesting habits of most species (O'Toole and Raw, 1991; Michener, 2007) make it difficult to quantify the use and availability of nesting. Emergence tents (e-tents) are a recent tool used to help quantify ground nesting by bees and improve our understanding of bee resource use. E-tents are commercially available mesh traps, similar in appearance to small dome camping tents, with an open bottom and an opening at the top that feeds into a secured plastic insect kill jar. When securely placed on the ground, e-tents can capture two different groups of bees: new emergers from nests established the previous year, or female bees as they exit from nests they initiated. These two groups represent bees responding to conditions over two separate years, and depending on when and how long tents are deployed, one or both groups can be captured. Thus, e-tents can provide additional information on nesting and emergence, parts of the bee life cycle that are poorly understood and considered limiting for many bee populations.

Despite their utility and importance for understanding bee nesting, e-tents are relatively expensive and labor-intensive to install, which may limit the number used in any single project. To date, only a few studies have used these commercially available traps (Sardiñas and Kremen, 2014; Sardiñas et al., 2016a, 2016b), and published methods have varied widely in their use of e-tents, including altering the length of time they were deployed and the choice of locations in which they were placed. Developing methods to optimize efficiency is essential, as many questions remain about how effective e-tents are for capturing bees.

The first published assessment of e-tents deployed tents continuously for seven months (Sardiñas and Kremen, 2014), whereas the next study deployed e-tents for just 20 h (Sardiñas et al.,

2016a). These two methods (long and short deployment) capture bees responding to potentially different environmental variables when choosing nests. Long deployment blocks access to soil and only captures bees emerging from nests established the previous year, providing insights into nesting and reproductive success, but little information on when and why that nest location was chosen. Conversely, short deployment captures bees actively establishing and tending nests, but offers little information on the outcome of the nest and brood. While each of these methods have their utility, short deployment could better capture bees choosing nests based on current conditions. In areas that are undergoing rapid change, such as those that are disturbed or being restored, it may be more important to capture bees actively nesting in the site and responding to present conditions. Moreover, leaving e-tents out for long periods of time may be impractical in disturbed habitats (i.e., sites that are grazed, mowed, or on public lands) where this expensive and somewhat delicate equipment could be destroyed. To date, it is still unknown if there is an optimal deployment length for short-term studies that ensures e-tents have adequate opportunity to capture actively nesting bees.

Previous efforts have also attempted to target preferred nesting habitats (Sardiñas et al., 2016b); however, preferred characteristics (percent bare ground, variation of slope of the ground, surface soil compaction, and soil particle size) were established largely in Mediterranean ecosystems and may not translate to all habitats. Targeting nests based on preferred characteristics in other ecosystems could bias sampling against bee species that have other preferences. It may also be impractical when using e-tents for comparisons between sites with different treatments (e.g., grazed vs. ungrazed) that may affect site floral, soil, and ground characteristics used to identify potential nesting habitats. Given these limitations, placement without regard to previously observed preferences may be more practical in many habitats, but few studies have used tents in this manner or assessed whether site (e.g., floral or bee abundance) and soil (e.g., percent bare ground or soil moisture) characteristics that affect bee diversity and nesting in Mediterranean climates are important in other habitats. Additionally, nontargeted placement may help identify preferred nesting conditions in habitats not previously sampled for bee nesting preferences, thereby increasing our understanding of nesting preferences and the variability of ground nesting bees.

The diversity of previous methods used to implement e-tents leaves many questions regarding how to optimize tent deployment and improve catch rates of nesting bees. The objectives of this study were to: (1) assess variance in tent capture rates over time, (2) determine the effects of site characteristics on proportion of tents capturing bees, and (3) determine the effect of previously measured soil characteristics on nest site choice. Improved efficacy of e-tent use has far-reaching implications, possibly providing a new understanding of the resources required by these important pollinators and allowing for insights into the dynamics of bee populations and their declines.

MATERIALS AND METHODS

Study areas—All research was conducted on three managed, restored prairies owned by the University of Illinois at Urbana-Champaign in Champaign County currently known as Trelease Woods prairie buffer, Florida Orchard prairie restoration (4047 m²), and the Pollinatarium prairie restoration (5615 m²), herein referred to as Sites 1, 2, and 3, respectively. Two plots were

initially used at Site 1 during the May sampling period—Site 1-North (7532 m²) and Site 1-East (5785 m²)—but Site 1-East was replaced with Site 3 to capture more intersite variability. In each site, a 150-m² plot was established to ensure sampling occurred in a similar area. A 5-m buffer between the e-tents and the edges of each site was maintained to reduce the effects of edges on sampling. All sites were separated by a minimum of 500 m, which is outside the foraging distance of most bee species (Greenleaf et al., 2007), and established within the past 12 yr (Site 1 in 2005, Site 2 in 2012, and Site 3 in 2009).

Biotic sampling—Foraging bee communities at each site were assessed using 3.25-oz pan traps (Gordon Food Service, Wyoming, Michigan, USA) and blue vane traps (SpringStar, Woodinville, Washington, USA). Pan traps are a commonly used passive sampling method, utilizing small blue, fluorescent yellow, and white bowls filled with soapy water to capture foraging bees (Droege et al., 2010). Vane traps are a similar passive sampling method using a 64-oz fluorescent yellow container with a blue funnel to capture larger foraging bees not consistently trapped in pans (Stephen and Rao, 2005). One blue vane trap and six pan traps, two of each color, were placed at each site for 8 h (1100–1900 hours). The blue vane trap and one set of pan traps (blue, yellow, white) were elevated 1 m above the ground to increase visibility; the other set of pan traps were placed on the ground. At 1900 hours, the contents of each trap were placed in labeled Whirl-Paks (Nasco, Fort Atkinson, Wisconsin, USA) with 70% ethanol for later pinning and identification. This method was repeated during each of the three sampling periods (13–20 May [May], 24 June to 1 July [Jun], 26 August to 7 September [Aug]).

During each sampling period, 12 e-tents (BugDorm, Taichung, Taiwan; model BT2006), the same type and model used in the previous studies, were haphazardly placed beginning after 1900 hours. Haphazard tent placement was chosen to determine capture rates when targeting nest locations is impractical and to avoid the potential bias toward nesting characteristics observed in previous studies. Tents were placed in locations where vegetation permitted full contact with the ground while remaining within areas designated by the land managers. When possible, vegetation was bent and placed inside the tent. Placing the tents out at 1900 hours increased the probability that females finished foraging for the day and returned to their nest (Heinrich and Esch, 1994), while providing enough light to safely deploy the tents.

The kill jar of each e-tent was filled with soapy water to euthanize captured bees. The contents of each jar were visually inspected, and captured bees were placed in labeled Whirl-Paks with 70% ethanol for later pinning and identification. To determine whether tent capture rates peaked early or late in the day and how long tents should be deployed to capture bees, each e-tent was checked every 4 h beginning at 0700 hours and ending at 1900 hours on the first two days of deployment and daily at 1900 hours for the remainder of the week, resulting in tents being checked at 12, 16, 20, 24, 36, 40, 44, 48, 72, 96, 120, 144, and 168 h after deployment. Air temperature (°C), barometric pressure (inHg), and wind speed (mph) were collected at the first e-tent of each site during every check.

Bees were identified to species when possible using a forthcoming local taxonomic key (M. Arduser, Bees of the Tall Grass Prairie, unpublished). Two male bees and two parasitic bees were excluded from analysis because they do not participate in nest construction or provisioning.

Floral abundance and diversity were obtained for each site by taking six distributed 0.25-m² quadrats within the same 150-m² area where e-tents were distributed. All plants in bloom were counted, and the percentage of ground covered by flowering plants was determined for each quadrat. Flowers were identified to genus and, if possible, species.

Abiotic sampling—During May and August, when e-tents were removed, the percent bare ground and soil moisture were measured directly below each e-tent. June soil measurements were not obtained due to an inability to access the site in June. Percent bare ground is the percentage of ground (particularly soil) visible at the ground surface level below each tent (0.36 m²). One soil moisture reading was obtained below the center of each tent using a soil moisture meter (Extech, Nashua, New Hampshire, USA; model MO750), which measured the soil moisture percentage at a 20-cm depth.

Statistical analysis—Two generalized linear mixed-effects models (GLMM) with binomial errors were used to test the effect of characteristics previously observed to influence bee nesting: floral abundance, bee abundance, soil moisture, and bare ground. The first model assessed site-level characteristics (floral and bee abundance) that may increase the proportion of bees nesting.

Site-level characteristics were included as fixed effects and site as a random effect to account for multiple measurements taken during different months in some sites. Floral abundance was log transformed and one was added to meet model requirements. The second model examined the effects of soil characteristics (soil moisture and percent bare ground) on nest site location (marked as presence/absence). Site was treated as a random effect to account for multiple tents used in the same site. Interactions between fixed effects and sampling month were not significant and were excluded from the final models. R version 3.3.1 (R Core Team, 2016) was used to perform all statistical analyses with package lme4 version 1.1-12 (Bates et al., 2015) for the GLMM.

RESULTS

A total of 27 bees were captured in the e-tents over the three sampling periods: 24 in Site 2, 2 in Site 3, 1 in Site 1-North, and 0 in Site 1-East (Table 1). Across all sites and sampling periods, the proportion of tents capturing bees ranged from 0.000 to 0.416 with a mean of 0.166 ± 0.191 tents capturing bees (Table 2). Site 2 capture rates initially peaked within the first 24 h of deployment (Fig. 1), but the proportion of total captures over time varied by month. In May, more than half of total captures occurred by 20 h deployed but the total was not reached until 168 h (Fig. 2). In June, more than half of total captures occurred at 24 h deployed and the total was reached at 72 h (Fig. 2). In August, more than half of total captures occurred at 44 h and the total was reached at 96 h (Fig. 2). During each month, bee species richness in Site 2 accumulated at different rates, with e-tents continuing to capture new species until 168 h in May but 44 h in June and August.

A total of 69 foraging bees were captured in the pan and vane traps over the three sampling periods (Table 1). Bee species captured in both the e-tents and pan and vane traps were only observed in June, with two of the four e-tent species also represented in foraging traps (Table 3). No bee species captured in e-tents were also caught in foraging traps in May or August.

Floral abundance and richness differed between sites and varied within sites over time (Table 4). No flowering species were observed during the May sampling period, thus no flowers were observed at Site 1-East. Despite the differences in floral abundance and bee abundance among sites, these site factors did not significantly affect the number of tents capturing bees in each site. Soil moisture, but not percent bare ground, influenced the nesting of bees under individual tents, with more bees caught under tents with low soil moisture ($z = -2.885$, $P = 0.004$; see Fig. 3).

DISCUSSION

Improving e-tent methodology to optimize capture rates over short deployments could provide invaluable information on the nesting biology of bees across various geographic, management, treatment, and time gradients. The few studies including e-tents used drastically different methods, making it difficult to directly compare results. For example, the overall mean capture rate across all sites and sample periods in this study was less than 20%, highlighting how rare it is to capture bees with this method. Previous work recorded much higher mean capture rates (39–85%), but these studies targeted nesting locations or left tents in a single location for seven months, making comparison difficult (Sardiñas and Kremen, 2014; Sardiñas et al., 2016a). For studies in which it is impossible or impractical to target nests, the observed low capture rate may make this method unattractive despite the interesting information it yields. It is important to note, however, that the capture rate varied among sites, with Site 2 capturing more than double the overall mean during all sample periods (Table 2). The tents at other sites captured bees 0–8% of the time, suggesting strong site-level effects on captures. Large differences in captures over a short time period suggests that e-tents can be highly valuable in determining where and when bees are nesting in sites and how bees respond to gradients, but without a more standardized methodology, comparisons between locations and treatments are still limited.

Multiple captures were only observed in one site, thus limiting our ability to compare capture rates over time across sites. Despite the small sample size, interesting observations on time of captures and peak of captures suggest some ways to improve e-tent use in the future. Interestingly, no e-tents captured bees at the 0700 hours check time (12 and 36 h after deployment) and few bees were captured after the 1500 hours check time (20 and 44 h after deployment), suggesting that e-tents should be checked in the early afternoon or evening regardless of length of deployment to increase potential captures. This pattern is likely due to more bees attempting to exit the nests with increased midday temperatures. Additionally, the largest proportion of tents capturing bees always occurred within the first 24 h, but the rate at which tents continued to capture bees varied seasonally. The time required to reach total number of captured bees also varied between sampling periods; 72 h deployed in June, 96 h deployed in August, and 168 h deployed in May. The longer time frame in May could be due to lower average temperatures during the sampling period (13.0–20.2°C) vs. the June (24.4–31.1°C) and August (23.9–31.4°C) sampling periods; cooler daytime temperatures may have encouraged bees to stay within the nest.

Although capture rates peaked within the first 24 h, these peaks only accounted for roughly half of the total captures, suggesting e-tents should be deployed longer than one day. The number of captures increased rapidly between 24 and 48 h in June and August (Fig. 2), suggesting tents should be deployed at least 48 h during warm months. May, however, accumulated

TABLE 1. Foraging (pan/vane) and nesting (emergence tent) bee captures across site and month.

Site	May		June		August		Total captures/Site	
	Pan/vane	E-tent	Pan/vane	E-tent	Pan/vane	E-tent	Pan/vane	E-tent
Trelease East (Site 1-East)	7	0	NA	NA	NA	NA	7	0
Trelease North (Site 1-North)	13	1	6	0	4	0	23	1
Florida Orchard (Site 2)	4	8	14	7	7	9	25	24
Pollinatarium (Site 3)	NA	NA	4	1	10	1	14	2
Total captures							69	27

Note: NA = not applicable.

TABLE 2. Proportion of emergence tents[a] capturing bees across site and month.

Site	GPS coordinates	May	June	August
Trelease East (Site 1-East)	40°8′N, 88°8′W	0	NA	NA
Trelease North (Site 1-North)	40°8′N, 88°8′W	0.083	0	0
Florida Orchard (Site 2)	40°6′N, 88°13′W	0.417	0.417	0.417
Pollinatarium (Site 3)	40°5′N, 88°13′W	NA	0.083	0.083

Note: NA = not applicable.

[a] 12 e-tents per site per month.

bees much more slowly, suggesting that tents may need to be deployed longer in cooler periods of the year to maximize captures. This knowledge can be used in future studies to optimize e-tent captures by moving them every two to seven days depending on the season. Previous studies did not distinguish between catches over this short time frame, making this the first information on capture rates within a week and over each day. This is also the first study to use e-tents to capture nesting bees in a prairie habitat.

The lack of significant effect of percent bare ground on nest site occurrence challenges one of the most consistently observed characteristics related to bee nesting in Mediterranean habitats (Potts et al., 2005; Sardiñas and Kremen, 2014). This may not be surprising given that prairie habitats, which are grass and forb dominated, often contain significant leaf litter compared to Mediterranean areas where leaf litter accumulates more slowly. However, it is possible that by targeting bare areas, previous studies have placed more emphasis on this characteristic than is necessary or that this character is not important in other habitats, but further work is needed to elucidate this pattern. In accordance with other studies utilizing e-tents, we found increased bee nesting in areas with lower soil moisture (Sardiñas and Kremen, 2014; Sardiñas et al., 2016a) and no effect of floral availability (Sardiñas et al., 2016a), suggesting short deployment may capture similar important factors and
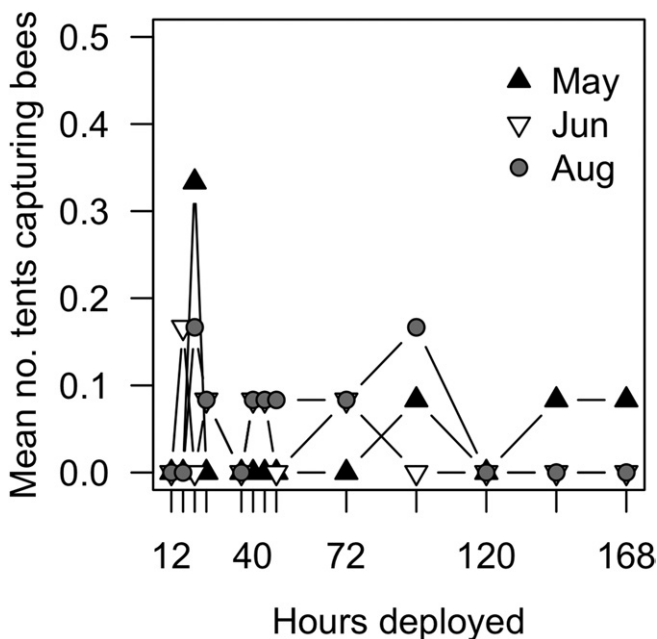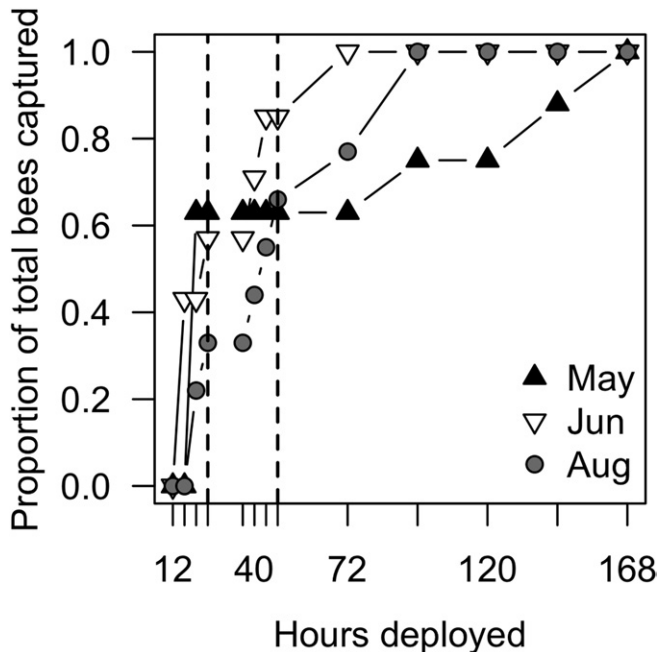

Fig. 2. Proportion of total bees captured in tents over time by month at Site 2. Tick marks are included to denote the sampling that occurred every 4 h for the first 2 d. Dotted vertical lines show 24 and 48 h deployed for comparison of how captures increase between 1 d and 2 d. Eight total bees were captured in May, seven in June, and nine in August.

some differences. It is possible that other characteristics previously observed to affect soil nesting (Sardiñas et al., 2016b), such as soil slope and soil compaction, which were not measured during our study, were also important for nest site location and that increasing sites sampled may provide more power to assess the importance of floral and bee abundance. These findings display the complexity of bee nesting ecology and the need to further improve methods to explore it in diverse habitats.

Although it was beyond the scope of this work, it is possible that the matrices surrounding each site affected nesting rates. The surrounding landscape can significantly affect bee diversity in many areas (Hines and Hendrix, 2005; Hinners et al., 2012; Kennedy et al., 2013), but this has yet to be extended to nesting. Site 1 and Site 3 were both surrounded by forest and agriculture, which could have offered suitable nesting resources outside of the site. Site 2, however, is surrounded by roads, buildings, and lawn, which may be less suitable nesting locations, potentially forcing bees to nest within the site. Bee diversity was previously found to be greater in suburban habitats such as these (Hinners et al., 2012), but nesting was not measured in these areas. Although the matrix is known to affect bee abundance and diversity, to date, no work has considered the effect matrices may have on nest location; future studies should consider matrix effects on nesting behavior. Additionally, the lack of fine-scale temporal data throughout the spring, summer, and fall makes it difficult to estimate when nest construction began for captured bees and how long nests were active; many halictid species begin nests in the spring to early summer and can be active for weeks to months (Michener, 2007). Future studies could record nest construction to help determine when nests are initiated.

Fig. 1. Proportion of tents capturing bees over time by month at Site 2.

TABLE 3. Identification of all captured bees at Site 2 across season (Florida Orchard prairie restoration).

Date captured	Capture method[a]	Family	Genus	Species[b]	Count	Primary nesting substrate[c]
May 13	Tent 27	Halictidae	*Lasioglossum*	*coreopsis*	1	Ground
May 13	Tent 33	Andrenidae	*Andrena*	sp. 1	1	Ground
May 13	Tent 35	Halictidae	*Lasioglossum*	*coreopsis*	1	Ground
May 13	Tent 35	Andrenidae	*Andrena*	sp. 1	1	Ground
May 13	Tent 36	Andrenidae	*Andrena*	sp. 1	1	Ground
May 16	Tent 35	Andrenidae	*Andrena*	sp. 2	1	Ground
May 18	Tent 26	Halictidae	*Lasioglossum*	*coreopsis*	1	Ground
May 19	Tent 27	Halictidae	*Lasioglossum*	*imitatum*	1	Ground
May 21	Vane	Halictidae	*Agapostemon*	*virescens*	1	Ground
May 21	Vane	Apidae	*Bombus*	*auricomus*	1	Ground
May 21	Pan	Halictidae	*Lasioglossum*	*anomalum*	2	Ground
June 24	Tent 64	Halictidae	*Lasioglossum*	*anomalum*	1	Ground
June 24	Tent 64	Halictidae	*Halictus*	*ligatus*	1	Ground
June 24	Tent 70	Halictidae	*Lasioglossum*	*coreopsis*	1	Ground
June 24	Tent 69	Halictidae	*Lasioglossum*	*anomalum*	1	Ground
June 25	Tent 64	Halictidae	*Halictus*	*ligatus*	1	Ground
June 25	Tent 64	Halictidae	*Lasioglossum*	*imitatum*	1	Ground
June 26	Tent 62	Halictidae	*Lasioglossum*	*anomalum*	1	Ground
June 25	Vane	Halictidae	*Augochlora*	*pura*	1	Wood
June 25	Vane	Halictidae	*Lasioglossum*	*bruneri*	1	Ground
June 25	Vane	Apidae	*Melissodes*	sp. 1	1	Ground
June 25	Pan	Halictidae	*Lasioglossum*	*anomalum*	3	Ground
June 25	Pan	Halictidae	*Augochlorella*	*aurata*	1	Ground
June 25	Pan	Halictidae	*Halictus*	*confusus*	1	Ground
June 25	Pan	Halictidae	*Lasioglossum*	*imitatum*	6	Ground
August 26	Tent 93	Halictidae	*Augochlorella*	*aurata*	1	Ground
August 26	Tent 92	Halictidae	*Lasioglossum*	*illinoense*	1	Ground
August 26	Tent 86	Halictidae	*Lasioglossum*	*versatum*	1	Ground
August 27	Tent 92	Halictidae	*Lasioglossum*	*illinoense*	1	Ground
August 27	Tent 92	Halictidae	*Lasioglossum*	*anomalum*	1	Ground
August 27	Tent 87	Halictidae	*Lasioglossum*	*anomalum*	1	Ground
August 28	Tent 93	Halictidae	*Augochlorella*	*aurata*	1	Ground
August 29	Tent 92	Halictidae	*Lasioglossum*	*illinoense*	1	Ground
August 29	Tent 91	Halictidae	*Augochlorella*	*aurata*	1	Ground
August 28	Vane	Apidae	*Bombus*	*bimaculatus*	1	Ground, trees
August 28	Vane	Halictidae	*Lasioglossum*	*hitchensi*	1	Ground
August 28	Vane	Halictidae	*Halictus*	*ligatus*	1	Ground
August 28	Vane	Apidae	*Melissodes*	sp. 1	1	Ground
August 28	Pan	Halictidae	*Lasioglossum*	*hitchensi*	2	Ground
August 28	Pan	Colletidae	*Hylaeus*	*mesillae*	1	Stems

[a] E-tent numbers distinguish the tents. E-tents were numbered 1–108: 1–36 in May, 37–72 in June, 73–108 in August.

[b] Species number was used when species could not be determined.

[c] Nest site designations are made by genus and retrieved from Packer et al. (2007).

The success of most current pollinator restoration projects centers on aboveground, biotic factors like floral abundance and composition (Williams and Kremen, 2007). Biotic factors are important, but bees use, and require, many more resources, and many questions remain about what those resources are and how bees respond to changes in their availability (Westrich, 1996). While the foraging bee community is often used to examine differences between sites (Potts et al., 2006), assessing nesting may be critical to fully understand the resources offered by sites and how degradation affects the bee community. Emergence tents may help fill in the significant gaps in knowledge about bee nesting, but increasing their efficacy, particularly with the very low capture rates observed here, is critical. This study provides some insights into how to more effectively use emergence tents to start exploring the complex ecology of bee nesting.

TABLE 4. Floral abundance and richness across site and month.

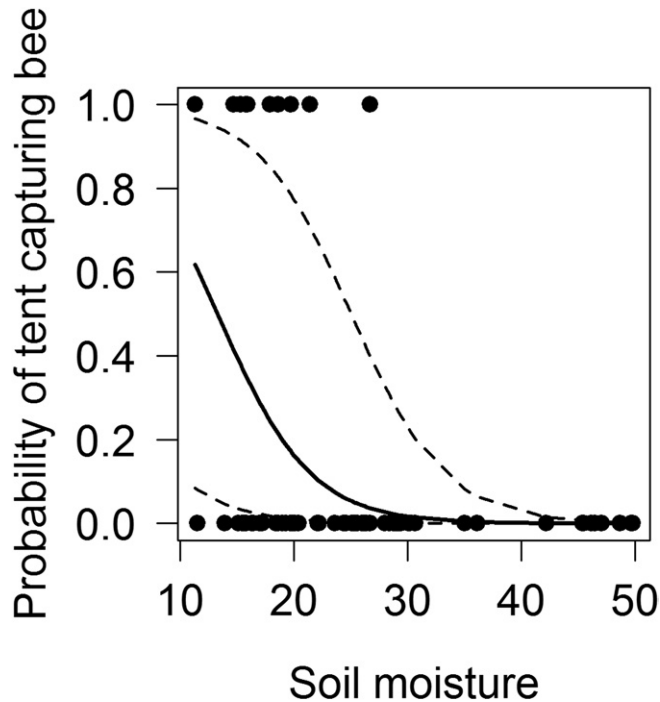|	May		June		August		Total	
Site	Richness	Abundance	Richness	Abundance	Richness	Abundance	Richness	Abundance
Trelease East (Site 1-East)	0	0	NA	NA	NA	NA	0	0
Trelease North (Site 1-North)	0	0	2	17	1	3	3	20
Florida Orchard (Site 2)	0	0	6	211	5	21	11	232
Pollinatarium (Site 3)	NA	NA	4	18	2	49	6	67
Total							20	319

Note: NA = not applicable.

Fig. 3. Relationship of the probability of an emergence tent capturing bees and soil moisture. The solid line shows fitted values from GLMM, and dotted lines show 95% confidence interval. Points denote measured soil moisture values for tents capturing (1.0) and not capturing (0.0) bees. Soil moisture is measured as a percentage.

LITERATURE CITED

BATES, D., B. M. BOLKER, AND S. WALKER. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.

DROEGE, S., V. J. TEPEDINO, G. LEBUHN, W. LINK, R. L. MINCKLEY, Q. CHEN, AND C. CONRAD. 2010. Spatial patterns of bee captures in North American bowl trapping surveys. *Insect Conservation and Diversity* 3: 15–23.

GREENLEAF, S. S., N. M. WILLIAMS, R. WINFREE, AND C. KREMEN. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153: 589–596.

HEINRICH, B., AND H. ESCH. 1994. Thermoregulation in bees. *American Scientist* 82: 164–170.

HINES, H. M., AND S. D. HENDRIX. 2005. Bumble bee (Hymenoptera: Apidae) diversity and abundance in tallgrass prairie patches: Effects of local and landscape floral resources. *Environmental Entomology* 34: 1477–1484.

HINNERS, S. J., C. A. KEARNS, AND C. A. WESSMAN. 2012. Roles of scale, matrix, and native habitat in supporting a diverse suburban pollinator assemblage. *Ecology* 22: 1923–1935.

KENNEDY, C. M., E. LONSDORF, M. C. NEEL, N. M. WILLIAMS, T. H. RICKETTS, R. WINFREE, R. BOMMARCO, ET AL. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters* 16: 584–599.

KLEIN, A.-M., B. E. VAISSIÈRE, J. H. CANE, I. STEFFAN-DEWENTER, S. A. CUNNINGHAM, C. KREMEN, AND T. TSCHARNTKE. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society, Series B. Biological Sciences* 274: 303–313.

KREMEN, C., N. M. WILLIAMS, AND R. W. THORP. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences, USA* 99: 16812–16816.

MICHENER, C. D. 2007. Bees of the world, 2nd ed. Johns Hopkins University Press, Washington, D.C., USA.

O'TOOLE, C., AND A. RAW. 1991. Bees of the world, 3rd ed. Blandford Publishing, London, United Kingdom.

OLLERTON, J., R. WINFREE, AND S. TARRANT. 2011. How many flowering plants are pollinated by animals? *Oikos* 120: 321–326.

PACKER, L., J. A. GENARO, AND C. S. SHEFFIELD. 2007. The bee genera of eastern Canada. *Canadian Journal of Arthropod Identification* 3: doi: 10.3752/cjai.2007.03.

POTTS, S. G., P. A. T. WILLMER, B. VULLIAMY, A. DAFNI, AND G. N. E. NE'EMAN. 2003. Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology* 84: 2628–2642.

POTTS, S. G., B. VULLIAMY, S. ROBERTS, C. O'TOOLE, A. DAFNI, G. NE'EMAN, AND P. WILLMER. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology* 30: 78–85.

POTTS, S. G., T. PETANIDOU, S. ROBERTS, C. O'TOOLE, A. HULBERT, AND P. WILLMER. 2006. Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. *Biological Conservation* 129: 519–529.

R CORE TEAM. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Website http://www.R-project.org/ [accessed 4 May 2017].

SARDIÑAS, H. S., AND C. KREMEN. 2014. Evaluating nesting microhabitat for ground-nesting bees using emergence traps. *Basic and Applied Ecology* 15: 161–168.

SARDIÑAS, H. S., L. C. PONISIO, AND C. KREMEN. 2016a. Hedgerow presence does not enhance indicators of nest-site habitat quality or nesting rates of ground-nesting bees. *Restoration Ecology* 24: 499–505.

SARDIÑAS, H. S., K. TOM, L. C. PONISIO, A. ROMINGER, AND C. KREMEN. 2016b. Sunflower (*Helianthus annuus*) pollination in California's Central Valley is limited by native bee nest site location. *Ecological Applications* 26: 438–447.

STEPHEN, W. P., AND S. RAO. 2005. Unscented color traps for non-*Apis* bees (Hymenoptera: Apiformes). *Journal of the Kansas Entomological Society* 78: 373–380.

WESTRICH, P. 1996. Habitat requirements of central European bees and the problems of partial habitats. *In* A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and J. H. Williams [eds.], The conservation of bees, 1–16. Academic Press, London, United Kingdom.

WILLIAMS, N. M., AND C. KREMEN. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications* 17: 910–921.

WINFREE, R., R. R. AGUILAR, D. P. VAZQUEZ, G. LEBUHN, AND M. A. AIZEN. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90: 2068–2076.