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The bee fauna of an Atlantic coastal plain tidal marsh community in southern New England, USA

Tracy A. Zarrillo¹ & Kimberly A. Stoner¹

Abstract. With growing evidence of changes in local abundance, geographical range, and species diversity of wild bees, it is imperative to document wild bee communities in representative habitats throughout North America. The Connecticut shoreline has historically been subject to many natural and anthropogenic disturbances, and there is a lack of baseline data regarding bee biodiversity in Connecticut's maritime habitats. In this study, we characterize the wild bee fauna of a discrete maritime habitat in Connecticut, USA, and examine salt-marsh, beach dune, and coastal scrub bee communities adjacent to Long Island Sound. We discuss patterns in relation to recent coastal surveys in New England. We conducted biweekly surveys at Grass Island (Guilford, CT) over a two-year period (2011–2012) using pan traps and effort-based (timed) net collecting from flowers. We collected 3928 individual bees, representing five families, 18 genera and at least 80 species. Floral records for 374 individuals resulted in associations of 35 bee species with 19 species of plants. Seventy percent of the bees captured in the net survey were visiting alien plants, with the exotic *Rosa rugosa* Thunb. having the highest level of bee diversity and relative abundance. The total number of bee species collected in this survey represents approximately 23% of the known Connecticut fauna, including four specialists associated with coastal and wetland habitats. The abundance and diversity of bees visiting alien plants on Grass Island, as well as the occurrence of these sand specialists, may prove to be of conservation concern as the Connecticut shoreline continues to be altered.

INTRODUCTION

Pollinators play a critical role in natural and agricultural ecosystems, both for the reproduction of native plants and for crop production (Buchmann & Nabhan, 1996; Ollerton *et al.*, 2011). Animal pollinators, mainly bees and other insects, transfer pollen from anther to stigma and are essential for 35% of global food production (Klein *et al.*, 2007). The economic value of wild pollinators to agricultural systems in the United States has been estimated to be greater than \$3 billion per year (Losey & Vaughan,

¹ The Connecticut Agricultural Experiment Station, 123 Huntington Street, New Haven, Connecticut 06511, USA (tracy.zarrillo@ct.gov, kimberly.stoner@ct.gov).

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2006), and \$190 billion per year globally (Gallai *et al.*, 2009).

The economic effect of honey bee losses (Kulhanek *et al.*, 2017) and the decline of several species of native bumble bees in North America (Colla *et al.*, 2012; Szabo *et al.*, 2012) have stimulated much interest in the status of wild bee populations occurring in many managed and natural ecosystems across the United States. In 2007, the National Research Council first drew attention to the lack of baseline information regarding the status of pollinators in North America (National Academy of Sciences, 2007). Since then, surveys have been conducted in urban port areas (Droege & Shapiro, 2011), green roofs, parks, and prairies (Smith *et al.*, 2012; Tonietto *et al.*, 2011), organic farms (Hall & Ascher, 2011), urban community gardens (Matteson *et al.*, 2008), suburban residential gardens and yards (Fetridge *et al.*, 2008; Lerman & Milam, 2016), commercial blueberry farms (Scott *et al.*, 2016; Tuell *et al.*, 2009), preserved natural areas (Giles & Ascher, 2006; Grundel *et al.*, 2011; Hall & Ascher, 2010; Tucker & Rehan, 2017), and transmission line corridors (Wagner *et al.*, 2014). Recently, the bee faunas of several states such as Maine, Pennsylvania, Michigan, Colorado, and Wisconsin have been documented (Dibble *et al.*, 2017; Donovall & vanEngelsdorp, 2010; Gibbs *et al.*, 2017; Scott *et al.*, 2011; Wolf & Ascher, 2008). Connecticut's primary checklist was published over 100 years ago by Viereck *et al.* (1916), with subsequent work by Britton (1920, 1938), Maier (2005, 2009), Wagner *et al.* (2014), Wagner & Ascher (2008), and Zarrillo *et al.* (2016). While other coastal habitats (notably from offshore islands) in New England and the Mid-Atlantic have been studied (Ascher *et al.*, 2014; Goldstein & Ascher, 2016; Orr, 2010; Rykken & Farrell, 2013; Scarpulla, 2013; Stage, 2009), bee communities in Connecticut maritime habitats have not been quantitatively surveyed. Sea level rise and an increase in storm surge because of climate change will have an effect on coastal areas and their fauna and flora (Nicholls & Cazenave, 2010). Several species of bees in Connecticut may be restricted to this coastal sand habitat and would be particularly vulnerable to local extirpation. The objectives of this inventory were to: (1) assemble a species list that would serve as an entry point for understanding Connecticut's coastal bee fauna by surveying bee biodiversity in salt-marsh, beach dune and coastal scrub communities; (2) augment and database the museum holdings in the insect collection of the Connecticut Agricultural Experiment Station to better serve the needs of future efforts to monitor the status of bee species in Connecticut, and; (3) contribute to the ongoing effort to database and map bee pollinators for regional and global assessment.

MATERIAL AND METHODS

SITE DESCRIPTION: Grass Island (12 ha) is an estuarine preserve located in New Haven County, Guilford, Connecticut, USA, in the Long Island Sound Coastal Lowland ecoregion (Griffith *et al.*, 2009), where the East and Neck Rivers empty into Long Island Sound. Although technically not a true island, the area can only be accessed by a narrow spit of land that is under the jurisdiction of the neighboring town of Madison. The preserve is primarily used by birdwatchers, nature enthusiasts, and fishermen, and unlike other Connecticut beaches, it is not frequented by large crowds. The flora of Grass Island is characterized by flowering plant species that are typical for New England coastal habitats, such as *Limonium carolinianum* (Walter) Britton (sea lavender), *Baccharis halimifolia* L. (eastern false willow), *Solidago sempervirens* L. (seaside goldenrod), *Althaea officinalis* L. (common marsh-mallow), *Lathyrus japonicus* Willd. (beach pea), *Cakile edentula* (Bigelow) Hook. (American sea-rocket), *Rosa rugosa* Thunb. (beach rose), *Teucrium canadense* L. (American germander), and *Hibiscus moscheutos* L. (swamp



Figure 1. Marsh bee bowl transect: New Haven County, Guilford, Connecticut, 41.2678°N, -72.6563°W: Gravel road through tidal marsh, transect orientation N-S (image taken 14 April 2012).

rose-mallow). Grass Island was selected as a study site because it is representative of minimally disturbed coastal habitat that had salt-marsh, beach dunes, and coastal scrub. We set up a single trap-line of 150 m in each of those habitats. The trap-line



Figure 2. Beach bee bowl transect: New Haven County, Guilford, Connecticut, 41.2666°N, -72.6593°W: Beach and dunes, transect orientation NNW-SSW (image taken 8 July 2012).

in the salt-marsh (41.2678°N, -72.6563°W) was linear, and to accommodate tidal fluctuations, was placed alongside a hedgerow at the edge of a gravel road that passed through its center (Fig. 1). The dominant flowering vegetation along the road was *R. rugosa* and *B. halimifolia*. Another trap-line (41.2666°N, -72.6593°W) followed the curve of the transition zone between the beach and the dunes, meandering through beach grasses, *L. japonicus*, and *Lonicera* spp. (honeysuckles) (Fig. 2). The last trap-line (41.2696°N, -72.6616°W) wove through the changing landscape of coastal scrub on the northwestern side of the preserve (Fig. 3), near plants such as *Celastrus orbiculatus* Thunb. (Oriental bittersweet), *Rhus typhina* L. (staghorn sumac), *Toxicodendron radicans* (L.) Kuntze (eastern poison ivy), *Phytolacca americana* L. (American pokeweed), *Elaeagnus umbellata* Thunb. (autumn olive), *R. rugosa*, and *Phragmites australis* (Cav.) Trin. Ex Steud. (common reed).

SAMPLING PROTOCOL, 2011: We conducted nine surveys on Grass Island at intervals of 14–28 days between 30 April and 20 August 2011. This survey ended prematurely in late August when Hurricane Irene severely damaged the study site and access was denied. We began each survey period between 0830 h and 0930 h and completed it the following day, generally between 1800 h and 1900 h. Within each habitat, we surveyed bees primarily by using bowl traps filled with soapy water (Droege, 2015). Bee bowls were 3.25 oz. SOLO® brand soufflé cups (Lake Forest, IL) either left original opaque white or painted entirely fluorescent blue (Ace Glo® Spray # 19716, Ace Hardware Corp., Oak Brook, IL) or fluorescent yellow (Ace Glo® Spray # 17052, Ace Hardware Corp., Oak Brook, IL). We placed 30 bowl traps at ground level along each trap-line



Figure 3. Scrub bee bowl transect: New Haven County, Guilford, Connecticut, 41.2696°N, -72.6616°W: Coastal scrub, transect orientation NNW-SSW (image taken 14 April 2012).

at a spacing of 5 m (Droege *et al.*, 2010a), alternating the pattern of white, blue, and yellow. On the second day of each trapping period, bees were strained from the bowl traps, and contents from each transect were pooled, placed into a whirlpak with 70% ethanol, and stored in a freezer (-17° C) until further processing. We also conducted opportunistic net-collecting throughout each zone to gain additional species and floral associations (Cane *et al.*, 2000; Nielsen *et al.*, 2011; Roulston *et al.*, 2007) between 1200 h and 1500 h. After we set up the bowls, we collected bees that visited blooms within each habitat. The amount of time spent net collecting per run per zone varied from 0 to 30 minutes, depending on the number of plants in bloom in each habitat, for a total of 9.6 h across the entire trapping season. We only collected a few specimens of the common *Bombus impatiens* Cresson and *Apis mellifera* L. for vouchers; therefore, their numbers in the net survey are underrepresented and do not reflect their true abundance. Bees captured at flowers were killed in vials with soapy water and subsequently placed into 70% ethanol to be stored in a freezer (-17° C) until further processing. Bee samples were sorted and processed using methods described by Droege (2015).

SAMPLING PROTOCOL, 2012: We conducted 12 surveys at intervals of 14 days between 14 April and 15 September 2012. We followed the sampling protocols described for 2011, with the addition of recording plant species in flower within one meter on each side of each pan trap in each zone. The amount of time spent net collecting per run varied from 0 to 60 minutes per zone, for a total of 15 h across the entire season. We made preliminary species identifications at the Connecticut Agricultural Experiment Station using published and online taxonomic resources (Ascher *et al.*, 2017;

Gibbs, 2010, 2011; Gibbs *et al.*, 2013; Mitchell, 1960, 1962; Rehan & Sheffield, 2011). The following bee taxonomists confirmed difficult determinations: Sam Droege of the U.S. Geological Survey, John Ascher of the National University of Singapore, Sandra Rehan of the University of New Hampshire, and Jason Gibbs of the University of Manitoba. Specimens are deposited in the insect collection housed in the Department of Entomology, Connecticut Agricultural Experiment Station (CAES), New Haven, Connecticut, USA, and collection data for at least one specimen of every species was entered into the American Museum of Natural History (AMNH), Division of Invertebrate Zoology Database using Arthropod Easy Capture Specimen Database Software (2013) and mapped (Schuh *et al.*, 2010) online at the biodiversity portal www.discoverlife.org.

STATISTICAL ANALYSES: We used Chi-square tests, using the Yates correction, to test the difference in capture rates of bowl traps and net collecting by genus (Snedecor & Cochran, 1980). Statistical estimates of species richness for bees captured by bowl traps in 2011 and 2012 were computed using the software package EstimateS[©] (Colwell, 2013), and were calculated using the nonparametric species richness estimators Chao 1 (Chao, 1984) and ACE (Abundance-based Coverage Estimator) (Chao & Lee, 1992; Chao *et al.*, 1993; Chazdon *et al.*, 1998). Chao 1 and ACE are both based on the frequencies of rare species in a sample. Chao 1 is a function of the ratio of singletons (species represented by a single individual) and doubletons (species represented by two individuals), and it uses this ratio to extrapolate beyond what has been observed to predict the lower bounds of the asymptotic number of species in an assemblage (Magurran, 2004). Greater relative frequency of singletons results in a greater difference between extrapolated and observed species richness (Magurran, 2004). Sampling is considered complete (no additional undetected species) once every species is represented by at least two or more individuals (Chao *et al.*, 2009). EstimateS userguide (Colwell, 2013) advises that estimated sample completeness be at least 50% (proportion of singletons should be less than 50%) when using Chao 1, and our dataset fulfilled this recommendation with the exception of the coastal scrub habitat in 2012 (singletons = 52%). ACE is a coverage estimator, which takes into account the variation in a species probability to be detected. It uses the number of species that have <10 individuals and the number of singletons to estimate the number of undetected species.

We excluded from the diversity analyses bees captured by net because the amount of time spent net collecting was dependent on floral availability and was not standardized. The following individuals were not included as their identity was uncertain: *Ceratina* sp. (n = 1), *Lasioglossum (Dialictus)* sp. (n = 39), *Lasioglossum (Dialictus) viridatum* species group (n = 63), *Lasioglossum (Dialictus) georgeickworti?* (n = 1), *Nomada* sp. (n = 1), and *Sphecodes* sp. (n = 2). The following taxa were treated as a single species in the analyses, as their taxonomy is unclear, and these groupings may be a repository for additional species: female *Hylaeus (Prosopis) affinis* or *modestus modestus* (Arduser, 2009; Shapiro & Droege, 2010; Sheffield *et al.*, 2009) and *Nomada (Gnathias) sp. sensu* Mitchell (1962) (Gibbs *et al.*, 2017; Shapiro & Droege, 2010). For each of the species captured, we also summarized from literature the type of pollen specificity and nesting habitat, as well as the level of sociality (Appendices 1, 2).

FLORAL ASSOCIATIONS: We depicted floral host associations for netted bees in a plant-pollinator interaction matrix using the R software package bipartite (Dormann *et al.*, 2008).

RESULTS & DISCUSSION

GENERAL OBSERVATIONS: We collected 3928 individual bees, representing five North

American families, 18 genera, and at least 80 species (Appendix 3). This survey captured 23% of the 349 described bee species known to occur in Connecticut (Zarrillo *et al.*, 2016). The Apidae had the most genera represented ($n = 7$), and the second highest number of species ($n = 24$) and individuals ($n = 846$; 21.5% of total), while the Halictidae exhibited the greatest number of species ($n = 27$) and individuals ($n = 2668$; 67.9% of total). The high proportion of halictines collected in this survey parallels other studies that employ bowl traps (Cane *et al.*, 2000; Hall & Ascher, 2010; Roulston *et al.*, 2007; Wilson *et al.*, 2008). Parasitic species within Halictidae (*Lasioglossum* Curtis, *Sphecodes* Latreille) and Apidae (*Nomada* Scopoli) comprised 17.5% of total species captured, but only 0.94% of total individuals, while eusocial species comprised 28.8% of total species captured and 68.6% of total individuals. Solitary species within all five families comprised 41.3% of total species captured, and 10.7% of total individuals. Six of the species captured in this survey were exotic, and except for *A. mellifera*, which was deliberately under-collected, all were present in small numbers.

Bowls caught a significantly higher proportion than net collecting of individuals of the genera *Lasioglossum* (66.5% of total bees in bowls, 14.5% of total bees in net; $\lambda^2 = 385.6$, $p < 0.01$, $df = 1$) and *Osmia* Panzer (6.0% bowls, 2.1% net; $\lambda^2 = 9.94$, $p < 0.01$, $df = 1$). The bowl samples were by far the richest in total species, with 59% of species ($n = 47$) collected only in bowls. Twenty-five percent of species ($n = 20$) were captured with bowls and netting, and 16% ($n = 13$) were captured only by netting. Forty-eight species (60% of total) were represented by 1–5 individuals (24 singletons, 12 doubletons), 16 species by 6–20 individuals, and 16 species by >20 individuals. *Lasioglossum ephialtum* Gibbs had the highest relative abundance overall, followed by *L. marinum* (Crawford), *L. oblongum* (Lovell), *Ceratina dupla* Say, *Augochlorella aurata* (Smith), *Osmia pumila* Cresson, *L. pilosum* (Smith), and *C. mikmaqi* Rehan & Sheffield. The remaining species (excluding the under-collected *B. impatiens* and *A. mellifera*) had less than 1% relative abundance.

Of the 696 one meter samples adjacent to the pan traps over the season, there were flowering plants in bloom in 152 (21.8%) of the samples in the marsh, 115 (16.5%) in the scrub, and 46 (6.6%) in the beach habitat. *Rosa rugosa* was the most common plant found in the samples, occurring in the marsh habitat in 5.9% of the samples, and in the scrub in 5.3% of samples. *Rosa rugosa* was also present in the beach habitat, but did not occur within one meter of the pan traps in the beach habitat. *Rosa rugosa* also had the longest bloom period, which spanned May through September. *Solidago sempervirens* was the second most common, occurring in the marsh in 3.0% of samples, 2.7% in the beach, and 1.1% in the scrub, but was sampled only once, on 15 September. *Lonicera* sp. was the third most common, found in 2.7% of scrub samples, 0.7% of marsh samples, and 0.1% of beach samples, and blooming from 5 May to 26 May.

FLORAL ASSOCIATIONS: In total, floral records for 374 individuals of netted bees resulted in associations of 35 bee species with 19 species of flowers (Fig. 4). *Rosa rugosa* had the highest level of bee diversity (20 species) and abundance (133 individuals). *Lonicera* spp. had the second highest level of bee diversity (15 species), followed by *L. carolinianum* (9 species) and *Sonchus arvensis* L. (field sow-thistle) (9 species). *Bombus impatiens* (23) was the most abundant bee species taken in the net survey despite intentional under-collecting ($n = 93$), and also visited the greatest diversity of flower species ($n = 8$), along with generalists *B. griseocollis* (DeGeer) (18) ($n = 35$) and *L. ephialtum* (15) ($n = 33$). Ninety-six percent of the bee species collected were polylectic. Only three known oligolectic species were captured, *Andrena violae* Robertson, *A. wilkella* (Kirby) [Palearctic origin], and *Peponapis pruinosa* (Say), and only one specimen of each.

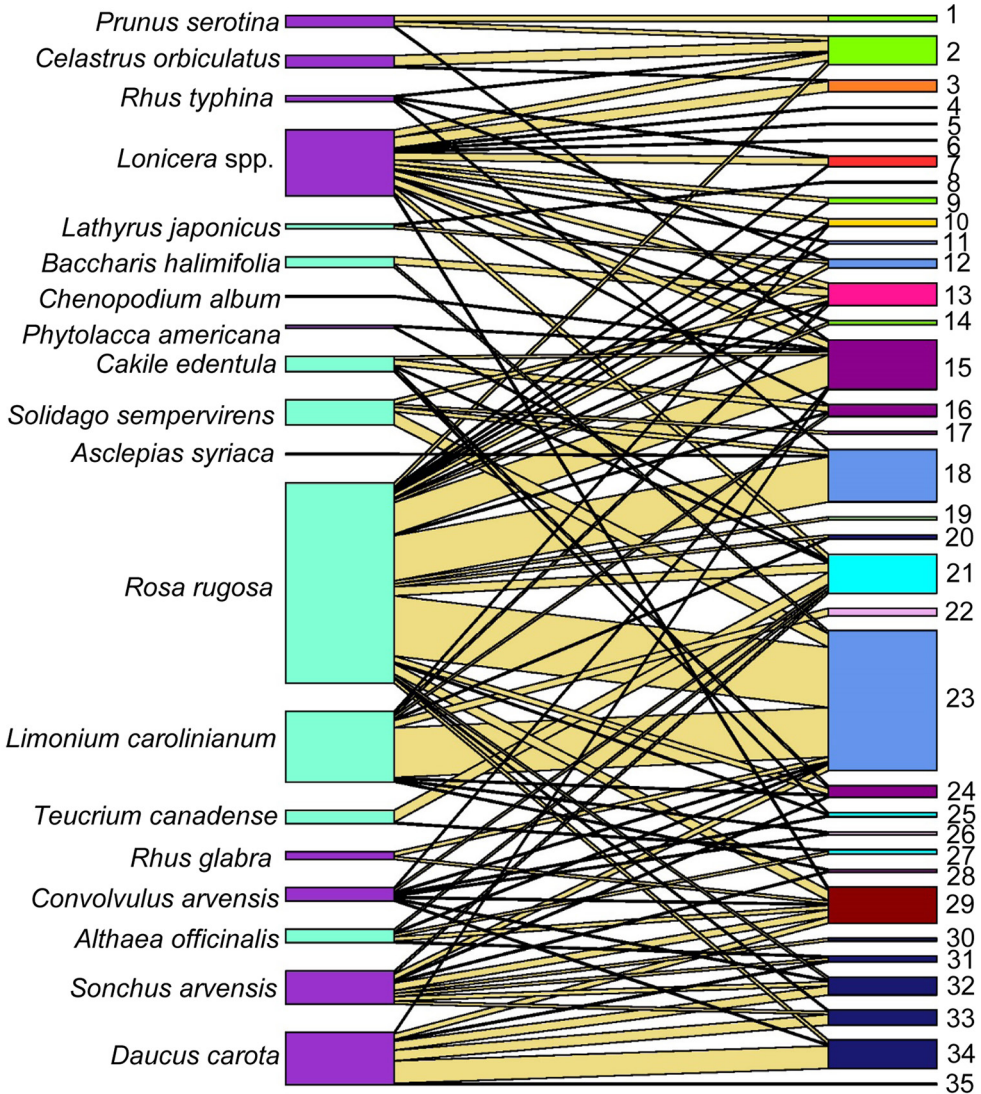


Figure 4. Bipartite network diagram depicting interaction strength between netted bee species and the species of plants visited in 2011 and 2012. The length of the plant blocks on the left represents total bee visitation observed on that plant species. The length of the bee species blocks on the right represents total bee visits observed to all flowers. The width of the diagonal lines connecting the bee species and plant species represents the number of bee/plant interactions observed. Coastal plant species are aqua and upland species are purple. Bee species are represented by numerals 1–35 (color coded by genus): 1. *Andrena forbesii*; 2. *Andrena crataegi*; 3. *Colletes thoracicus*; 4. *Bombus vagans*; 5. *Ceratina* sp.; 6. *Lasioglossum bruneri*; 7. *Osmia pumila*; 8. *Osmia simillima*; 9. *Andrena vicina*; 10. *Xylocopa virginica virginica*; 11. *Bombus perplexus*; 12. *Bombus bimaculatus*; 13. *Apis mellifera*; 14. *Andrena hipotes*; 15. *Lasioglossum ephialtum*; 16. *Lasioglossum marinum*; 17. *Lasioglossum viridatum*; 18. *Bombus griseocollis*; 19. *Andrena commoda*; 20. *Hylaeus schwarzii*; 21. *Ceratina dupla*; 22. *Agapostemon texanus*; 23. *Bombus impatiens*; 24. *Lasioglossum oblongum*; 25. *Ceratina mikmaqi*; 26. *Agapostemon virescens*; 27. *Ceratina calcarata*; 28. *Lasioglossum viridatum*; 29. *Augochlarella aurata*; 30. *Hylaeus illinoisensis*; 31. *Hylaeus* aff. *nelumbonis*; 32. *Hylaeus mesillae cressonii*; 33. *Hylaeus* sp. *affinis* or *modestus modestus*; 34. *Hylaeus modestus modestus*; 35. *Hylaeus leptocephalus*.

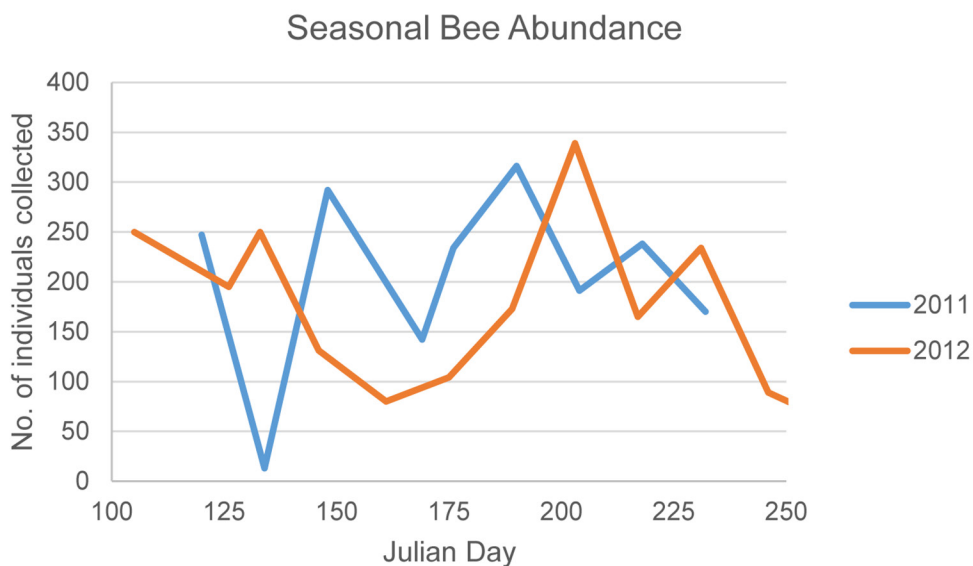


Figure 5. Total number of bees captured by bowl and net in the marsh, beach dunes, and scrub across the season in 2011 and 2012.

SEASONALITY: The month of capture for each bee species collected by net and bowl traps is depicted in Appendix 4 (2011) and Appendix 5 (2012). The families Colletidae, Halictidae, Megachilidae, and Apidae were represented throughout the entire trapping period, whereas individuals in the family Andrenidae were captured only in early to late spring. Certain species within Colletidae and Megachilidae, however, are vernal and were only active in the spring or early summer, such as *Colletes thoracicus* Smith (Colletidae) [May], *Osmia lignaria lignaria* Say [April], *O. cornifrons* (Radoszkowski) [April], *O. pumila* [April–early July], and *O. simillima* Smith (Megachilidae) [June].

There were three peaks in overall seasonal bee abundance (based on the number of individual bees captured on each of the sampling dates) in 2011 and 2012 (Fig. 5). The largest peak in 2011 ($n = 316$) occurred on 9 July, with sub-peaks occurring on 28 May ($n = 292$) and 6 August ($n = 238$). The largest peak in 2012 ($n = 339$) occurred on 21 July, with sub-peaks occurring on 12 May ($n = 250$) and 18 August ($n = 234$). Of the six most abundant species, four are primitively eusocial (*L. ephialtum*, *L. marinum*, *L. oblongum*, and *A. aurata*), one is considered subsocial (*C. dupla*) (Sandra Rehan, pers. comm.; Vickruck, 2010), and one is solitary (*O. pumila*). Seasonal bee abundance for each of these species is depicted in figure 6. The eusocial species were collected across the entire season, and were active when the surveys began in both years. High numbers of *C. dupla* were collected during the first sampling dates in 2011 and 2012, however in both years, the total number of individuals captured plummeted in the second sampling period. The large proportion of emerging males on the first sampling date (2011: males = 48, females = 7; 2012: males = 106, females = 41) may have skewed these initial, early spring catches. *Osmia pumila* was active before the first sampling period in April, and in both years, the first date had the highest number of individuals captured across the season. As this is a spring and early summer flying species, the number of individuals collected dropped to zero in early and mid-July in the two years as expected.

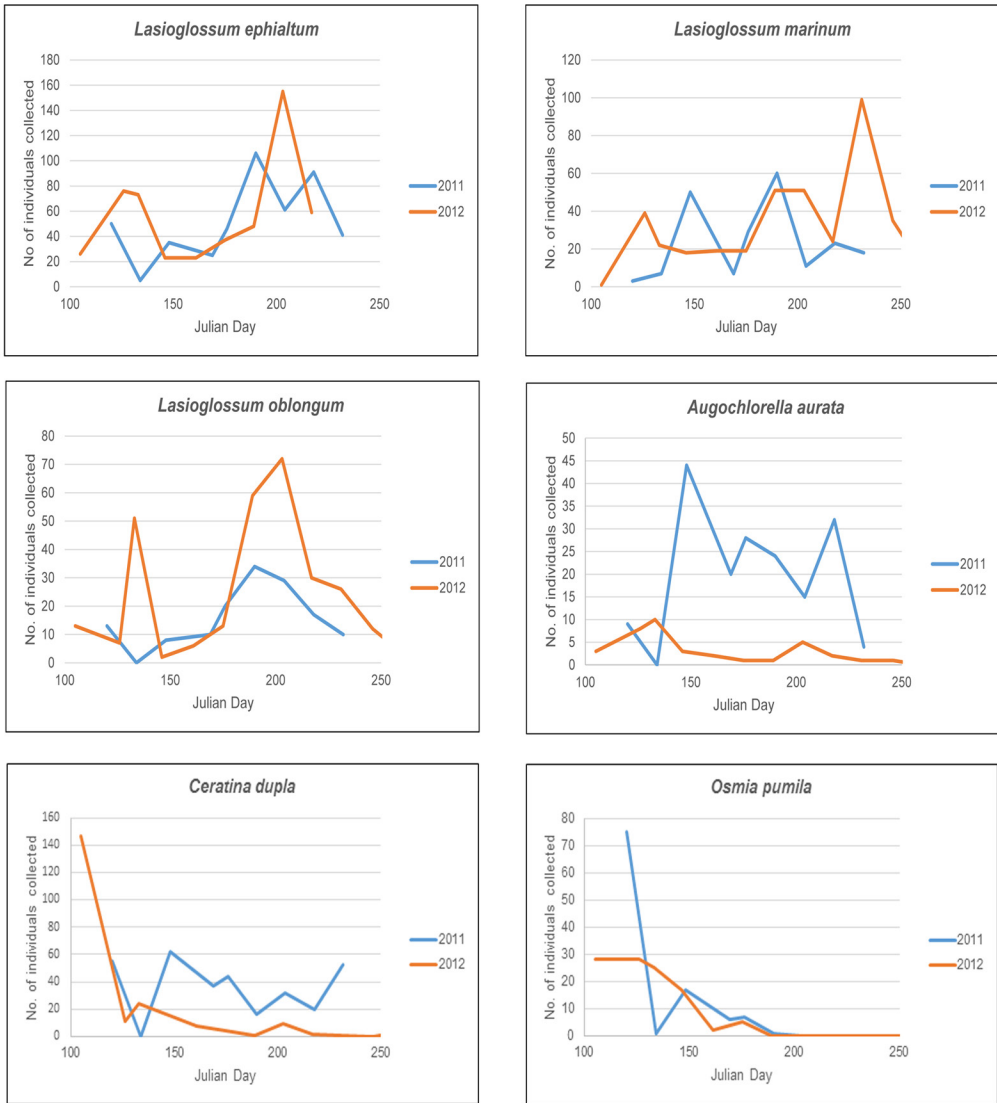


Figure 6. Total number of *Lasioglossum ephialtum*, *L. marinum*, *L. oblongum*, *Augochlorella aurata*, *Ceratina dupla*, and *Osmia pumila* captured by bowl and net in the marsh, beach dunes, and scrub across the season in 2011 and 2012.

Flight seasons of the bee species captured in this study generally matched the phenology found at two other New England coastal sites, Gardiner’s Island, NY, (Ascher *et al.*, 2014) and Martha’s Vineyard, MA (Goldstein & Ascher, 2016), with the following discrepancies: *H. aff. nelumbonis* (Robertson) was last captured 3 September, one month later than reported from Gardiner’s Island; *L. marinum* (Fig. 6) spanned 14 April–16 September, captured two weeks earlier and two weeks later than reported from Martha’s Vineyard; *L. oblongum* (Fig. 6) and *L. pilosum* were captured 14 April, two weeks earlier than reported from Martha’s Vineyard; *O. similima* was captured 10 June, approximately three weeks later than on Martha’s Vineyard and Gardiner’s Island; *C. mikmaqi* spanned 14 April–21 August, expanding the range documented at

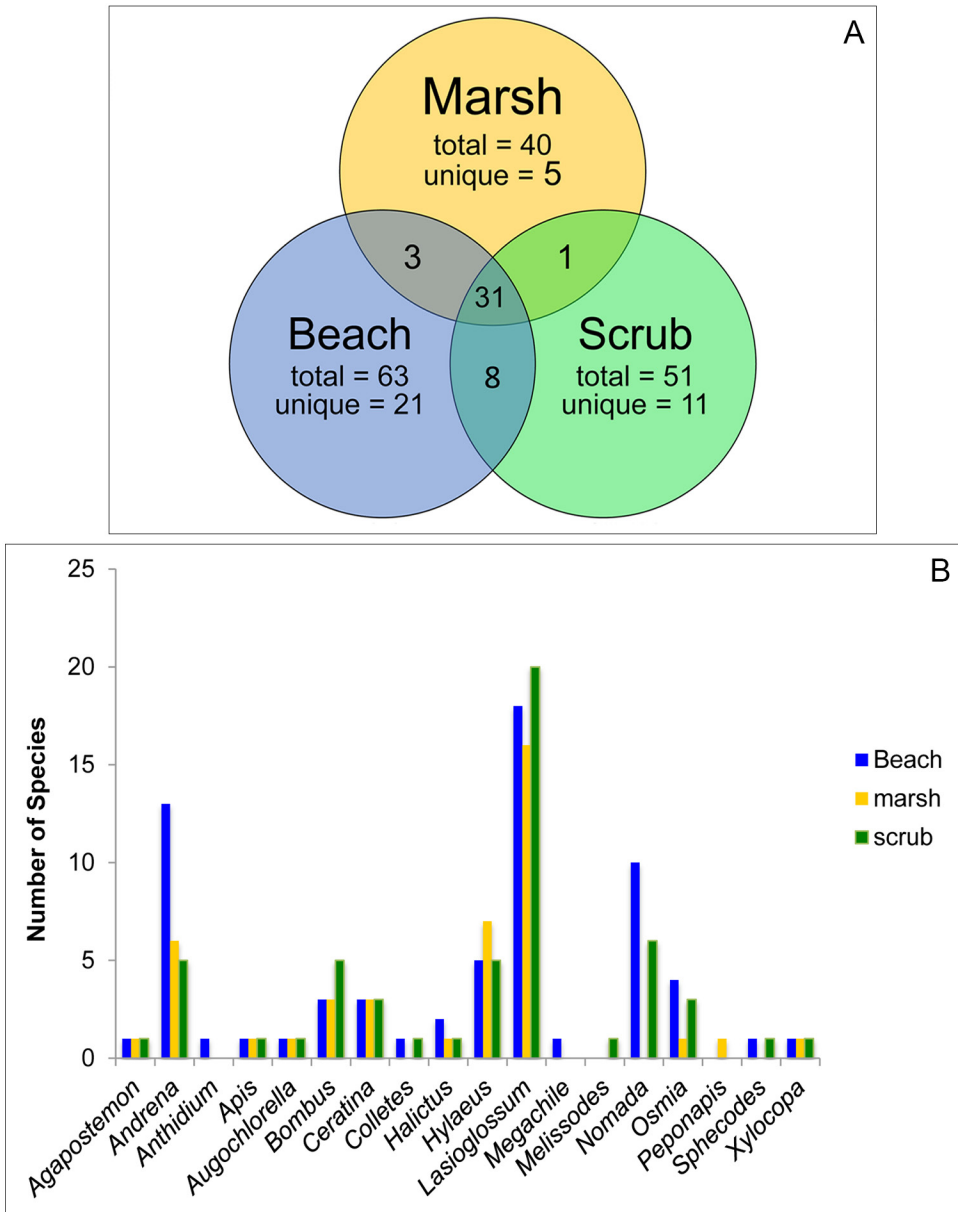


Figure 7. Number of shared and unique bee species captured by bowl and net in the marsh, beach dunes, and scrub habitats in 2011 and 2012 (A). Number of bee species captured per genus in the marsh, beach dunes, and scrub habitats in 2011 and 2012 (B).

Martha’s Vineyard. The flight seasons for species not captured in Ascher *et al.* (2014) and Goldstein & Ascher (2016) are: *A. violae* spanned 30 April–25 May; *L. ephialtum* (Fig. 6); *O. cornifrons* was captured 1 May; *O. lignaria lignaria* spanned 14 April–1 May.

HABITAT ASSOCIATION: The greatest proportion of total bee species was captured on the beach dunes (79%), with 21 species caught only in this habitat (Fig. 7A), including 8 of the 15 *Andrena* species collected in this survey. The coastal scrub habitat amassed 64% of the total bee species captured, with 11 species caught only in this area. The

Table 1. Comparison of species richness in each habitat measured with different estimators.

Trap-line	No. species observed	Chao 1 projected mean estimate	Chao 1 Proportion	ACE projected mean estimate	ACE Proportion
Marsh 2011	26	39.47	0.66	36.41	0.71
Beach 2011	40	76.03	0.53	72.48	0.55
Scrub 2011	29	30.8	0.94	31.88	0.91
Marsh 2012	16	16.5	0.97	17.09	0.94
Beach 2012	40	64.04	0.62	67.4	0.59
Scrub 2012	31	94.93	0.33	56.86	0.55

marsh habitat was the most depauperate in this survey, with only five unique species and only 50% of the total bee species collected (Fig. 7A). Eleven genera and thirty-one species were common to all three habitats (Fig. 7B). Although most bee species within the genera *Andrena* and *Agapostemon* Guérin-Méneville were captured in the marsh, their respective cleptoparasites in the genus *Nomada* (*ruficornis* group and *erigeronis* group, respectively) were not collected in this habitat. Four species of bees that were intercepted in this study are considered to be specialists of coastal and wetland areas (Appendix 3) — *L. marinum*, *Lasioglossum georgeickworti* Gibbs, *H. schwarzii* (Cockerell), and *H. aff. nelumbonis* (Ascher *et al.*, 2014; Gibbs, 2011; Goldstein & Ascher, 2016; Graenicher, 1930).

SPECIES RICHNESS: Projected species richness for each habitat in 2011 and 2012 are presented in Table 1. The observed number of species for the scrub in 2011 and the marsh in 2012 were within 90% of the estimated species richness with both estimators, indicating that few additional species would have been found with additional sampling intensity. The estimated species richness for the beach dunes in both years was considerably higher than the number of species observed, suggesting that additional sampling could have captured another 32–36 species in 2011 and 24–27 additional species in 2012. The estimated species richness was also 10–13 species higher than the observed species for the marsh transect in 2011, and 26–64 species higher for the scrub in 2012.

CONCLUDING REMARKS

COMPARISON TO OTHER NEW ENGLAND COASTAL SURVEYS: Our survey on Grass Island was conducted on a much smaller geographic and temporal scale than other surveys, such as the Boston Harbor Islands All Taxa Biodiversity Inventory (hereafter BHI) in Massachusetts (Rykken & Farrell, 2013), Gardiners Island (hereafter GI) in New York (Ascher *et al.*, 2014), and Martha’s Vineyard (hereafter MV) in Massachusetts (Goldstein & Ascher, 2016). However, 33–35% of the bee species we found on Grass Island also were reported in those studies, including a cryptic species of undetermined taxonomic status in the genus *Hylaeus* noted in Ascher *et al.* (2014). Of the shared species, the common ground-nesting augochlorine, *A. aurata*, was found in high numbers in all four surveys. The recently described sweat bee, *L. ephialtum*, aptly named from the Greek word “efialtis” or “nightmare” (Gibbs, 2010) due to its similarity to other species in the *L. (Dialictus) viridatum* species-group, was the most abundant species collected

at Grass Island, and was also found in modest numbers on seven of the 19 Boston Harbor Islands (Rykken & Farrell, 2013). This species is likely under reported from other regional surveys due to identification difficulties. Although not documented from GI or MV, it is an “expected” species on MV based on its occurrence in nearby counties in Massachusetts (Goldstein & Ascher, 2016), as is the late spring cleptoparasite, *Nomada bethunei* Cockerell, which was captured on Grass Island and BHI. *Lasioglossum georgeickworti*, an uncommon sweat bee associated with coastal areas and sand dunes (Gibbs, 2011), was found on Grass Island and MV, and another coastal specialist, the classic beach dune bee *L. marinum* (Gibbs, 2011), was documented in all four surveys. Late summer and fall species in the genera *Andrena* and *Colletes* and their cleptoparasites (autumnal species of *Nomada* and *Epeolus*, respectively) were noticeably absent in the Grass Island survey, even though composites such as *S. sempervirens* and *B. halimifolia* were in bloom and targeted, and sandy nesting sites were available in the beach dunes and scrub habitat. The genus *Colletes* was poorly represented in comparison to BHI, GI, and MV, having only one species, *C. thoracicus*, documented in our study. *Colletes thoracicus* flies later in the spring than the common *C. inaequalis* Say (Ascher *et al.*, 2014), and it is possible that the flight period for *C. inaequalis* was missed because the Grass Island surveys began too late, or because of insufficient early spring floral resources for net-collecting opportunities. Of the megachilids encountered, *O. similima*, *O. pumila*, and *M. mendica* were shared among all four locations. *Osmia simillima* is noteworthy, as unlike the others, it is generally scarce and localized in the northeastern USA, with most records from coastal locations (Dibble *et al.*, 2017; Schuh *et al.*, 2010; Zarrillo *et al.*, 2016; T.A. Zarrillo, [Napatree Point Conservation Area, Westerly, Rhode Island] unpubl. data). The native *O. lignaria lignaria* and its introduced relative *O. cornifrons* were unique to Grass Island.

Three species new to Connecticut were collected as part of this project and reported in Zarrillo *et al.* (2016): *Hylaeus illinoisensis* (Robertson) (1 male); *Lasioglossum michiganense* (Mitchell) (3 females, 1 male); *H. aff. nelumbonis* (Robertson) (9 females, 1 male). *Hylaeus illinoisensis* was also reported from Great Brewster Island, BHI (Rykken & Farrell, 2013), but this species was absent in other recent New England coastal surveys, such as GI (Ascher *et al.*, 2014) and MV (Goldstein & Ascher, 2016). *Lasioglossum michiganense*, a rare species and presumed social parasite or cleptoparasite of other nest-building *Lasioglossum* (*Dialictus*) (Gibbs, 2011; Giles & Ascher, 2006), was not reported in the three aforementioned coastal surveys.

Both *H. aff. nelumbonis* and closely related and very similar *H. schwarzii* were found on Grass Island but were not found together in other coastal surveys. *Hylaeus aff. nelumbonis* (reported as *H. cf. nelumbonis*) was first collected by Ascher *et al.* (2014) on GI. *Hylaeus schwarzii* has been recorded from MV, Penikese and Cuttyhunk Islands, BHI, and the Massachusetts mainland (Goldstein & Ascher, 2016; Rykken & Farrell, 2013; Stage, 2009), but not from GI (Ascher *et al.*, 2014). Our specimens of netted *H. aff. nelumbonis* were collected from *S. arvensis*, *A. officinalis*, and *D. carota*, plants not previously recorded for *H. nelumbonis* (Robertson), traditionally associated with wetland plants such as *Nelumbo* Adans., *Nymphaea* L. (Mitchell, 1960; Fowler, 2016), and *Pontederia* L. (Gibbs *et al.*, 2017), which were not found on Grass Island or GI (Ascher *et al.*, 2014; Burnham & Latham, 1917).

The males of *H. aff. nelumbonis* resemble *H. schwarzii* in that the first tergum is black, however these specimens lack basal elevations on the third and fourth sternite and have a rugose pleuron and metanotum, suggesting *H. nelumbonis*. The females of this dark form of uncertain taxonomic status have either a small red spot at the base of

the first tergum and/or a short, flat, finely rugose metanotum (Zarrillo *et al.*, 2016). Our specimens of *H. aff. nelumbonis* have more variation in color of the first tergum than is typical for *H. nelumbonis* (Mitchell, 1960).

Two female specimens from Grass Island, identified morphologically as *H. aff. nelumbonis* and *H. schwarzii*, were sent for DNA barcoding to the Packer Bee Collection at York University, Ontario, Canada, sequenced using cytochrome oxidase subunit 1 5' region, and both were identified as *H. nelumbonis* (BIN [Cluster ID]: BOLD: AAX2614). If these specimens are both *H. nelumbonis*, then there is more variation within the species both in coloration, rugosity of the metanotum, and in host plants than previously considered. One possibility could be that there is hybridization among these closely related species. The DNA barcoding uses a mitochondrial gene, which is passed down by the mother and therefore cannot pick up hybridization (Rubinoff *et al.*, 2006). Another possibility might be complications due to heteroplasmy, the coexistence of multiple mitochondrial haplotypes in a single organism, which means that the mitochondria of an individual may represent a sampling of alleles within a population, and these alleles could be overlapping with alleles of other closely related species (Rubinoff *et al.*, 2006).

The status, distribution, identification, genetics, and host plant utilization of the eastern North American species of the subgenus *Hylaeus* (*Prosopis*) require full integrative study, as Snelling's (1966) taxonomic revision treated only the western North American species. Such a study would need to address the confusion among *H. affinis*, *H. modestus modestus*, and *H. illinoisensis* (Arduser, 2009; Sheffield *et al.*, 2009; Shapiro & Droege, 2010; Zarrillo *et al.*, 2016), as well as *H. nelumbonis*, *H. aff. nelumbonis*, and *H. schwarzii*.

CONSERVATION: Tidal marsh-estuarine ecosystems are considered to be one of the most biologically productive environments in the world, next to tropical rain forests (CTDEEP, 2017a). The shoreline of Connecticut historically has been subject to many anthropogenic and natural disturbances, including grid-ditching of salt marshes for mosquito population control in the 1930's (Clarke *et al.*, 1984), thermal pollution (Hillman *et al.*, 1977), toxic contaminants from point and non-point sources (Balcom *et al.*, 2004; CTDEEP, 2017b), conflicting land usage and coastal development (filling/dredging, marinas/ports, commercial fishing, industrial complexes, water-front housing, waste-water treatment plants, landfills) (CTDEEP, 2017c), beach erosion, flooding and powerful tropical storms (CTDEEP, 2017d). Natural and cultural pressures continue to alter the stability of the Connecticut shoreline. Sudden Vegetation Dieback of salt marshes in Connecticut can decrease the amount of protection marshes provide against storm surge and wave erosion (Elmer *et al.*, 2013). Because climate change is causing sea level to rise, and tropical storms are increasing in frequency and severity (Hansen *et al.*, 2016), the four species of bees that are considered to be specialists of coastal areas or wetlands may be threatened in the future as extreme weather events intensify.

Alien plant species have been shown to have deleterious effects on native plant pollination (Brown *et al.*, 2002; Chittka & Schurkens, 2001; Grabas & Laverty, 1999; Jakobsson *et al.*, 2007; Morales & Traveset, 2009). The abundance and diversity of bees visiting alien plant species on Grass Island suggests that alien plants could be out-competing native plants for pollinators. Overall, 70% of the bees captured in the net survey were visiting alien plants. Bees were captured on 19 plant species during this survey, eight of which are not native to New England — *R. rugosa*, *Lonicera* spp., *Chenopodium album* L. (white goosefoot), *A. officinalis*, *C. orbiculatus*, *D. carota*, *Convolvulus*

arvensis L. (field bindweed), and *S. arvensis*. The remaining 11 plant species are native to Connecticut — *P. americana* L., *L. japonicus*, *Prunus serotina* Ehrh. (black cherry), *Asclepias syriaca* L. (common milkweed), *T. canadense*, *Rhus glabra* L. (smooth sumac), *R. typhina* L., *C. edentula*, *L. carolinianum*, *S. sempervirens*, and *B. hamilifolia* (Haines, 2011).

Rosa rugosa, a non-native shrub originally planted for erosion and dune control and now considered an invasive species in Connecticut (Connecticut Invasive Plant Working Group, 2014), had the highest level of bee diversity and relative abundance in this survey, despite the fact that flowers of *R. rugosa* do not offer a nectar reward to bees (Bruun, 2005). Possible explanations for this could be its prolific floral display, extended bloom period (May until the end of the survey in both years), and copious pollen, which contains methyleugenol, a substance known to be attractive to bumble bees (Bruun, 2005). Naturalized *R. rugosa* can be considered to be a threat to coastal ecosystem integrity because of its ability to outcompete other native plants in the community for resources (Kollmann *et al.*, 2007; USDA-NRCS, 2002) and pollination services (Stout & Morales, 2009). It is unclear to what extent this is happening at Grass Island.

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Appendix 1. Ecological table for bee species collected from Grass Island in the salt-marsh, beach dunes, and coastal scrub in 2011–2012. Ecological information for bee species was compiled from the primary literature, the *Catalogue of Hymenoptera* (Hurd, 1979), *Bees of the World* (Michener, 2007), and *Bumble Bees of North America* (Williams *et al.*, 2014). Ecological information for the genus *Lasioglossum* (*Dialictus*) was inferred based on phylogenetic data when unknown. Pollen specificity is categorized as polylectic (P) or oligolectic (O). Nests are categorized as ground burrows (G), cavity (C), wood (W), hive (H), and pithy stems or twigs (S). Sociality is categorized as solitary (S), communal (C), advanced eusocial (A), primitively eusocial (E), subsocial (SB), social parasite (SP), and cleptoparasite (CP).

Species	Pollen Specificity	Nesting Habit	Sociality
Family Colletidae			
<i>Colletes thoracicus</i> Smith	—	G	S
<i>Hylaeus (Prosopis) affinis</i> (Smith)/ <i>modestus</i> Say	—	C	S
<i>Hylaeus (Prosopis) illinoisensis</i> (Robertson)	—	C	S
<i>Hylaeus (Hylaeus) leptcephalus</i> (Morawitz)	P?	C	S
<i>Hylaeus (Hylaeus) mesillae cressonii</i> (Cockerell)	—	C	S
<i>Hylaeus (Prosopis) modestus modestus</i> Say	—	C	S
<i>Hylaeus (Prosopis) aff. nelumbonis</i> (Robertson)	—	C	S
<i>Hylaeus (Prosopis) schwarzii</i> (Cockerell)	—	C	S
Family Andrenidae			
<i>Andrena (Melandrena) barbara</i> Bouseman & LaBerge	—	G	S
<i>Andrena (Melandrena) carlini</i> Cockerell	P	G	S
<i>Andrena (Melandrena) commoda</i> Smith	P	G	S
<i>Andrena (Plastandrena) crataegi</i> Robertson	P	G	S/C
<i>Andrena (Holandrena) cressonii cressonii</i> Robertson	P	G	S
<i>Andrena (Trachandrena) forbesii</i> Robertson	P	G	S
<i>Andrena (Trachandrena) hippotes</i> Robertson	P	G	S
<i>Andrena (Andrena) mandibularis</i> Robertson	P	G	S
<i>Andrena (Simandrena) nasonii</i> Robertson	P	G	S
<i>Andrena (Tylandrena) perplexa</i> Smith	P	G	S
<i>Andrena (Melandrena) pruni</i> Robertson	—	G	S
<i>Andrena (Melandrena) vicina</i> Smith	P	G	S
<i>Andrena (Iomelissa) violae</i> Robertson	O (<i>Viola</i>)	G	S
<i>Andrena (Simandrena) wheeleri</i> Graenicher	—	G	S
<i>Andrena (Taeniandrena) wilkella</i> (Kirby)	O (Fabaceae)	G	S
Family Halictidae			
<i>Agapostemon (Agapostemon) texanus</i> Cresson	P	G	S
<i>Agapostemon (Agapostemon) virescens</i> (Fabricius)	P	G	S
<i>Augochlorella aurata</i> (Smith)	P	G	E/S
<i>Halictus (Seladonia) confusus confusus</i> Smith	P	G	E

Appendix 1. Continued.

Species	Pollen Specificity	Nesting Habit	Sociality
<i>Halictus (Odontalictus) ligatus</i> Say	P	G	E
<i>Lasioglossum (Dialictus) admirandum</i> (Sandhouse)	P	G	E
<i>Lasioglossum (Dialictus) albipenne</i> (Robertson)	—	W	E
<i>Lasioglossum (Dialictus) anomalum</i> (Robertson)	P	G	E
<i>Lasioglossum (Dialictus) bruneri</i> (Crawford)	P	G	E
<i>Lasioglossum (Dialictus) cressonii</i> (Robertson)	P	W	E
<i>Lasioglossum (Dialictus) ephialtum</i> Gibbs	P	G	E
<i>Lasioglossum (Dialictus) georgeickworti</i> Gibbs	P	G	E
<i>Lasioglossum (Dialictus) hitchensi</i> Gibbs	P	G	E
<i>Lasioglossum (Dialictus) leucomomum</i> (Lovell)	P	G	E
<i>Lasioglossum (Leuchalictus) leucozonium</i> (Schrank)	P	G	S
<i>Lasioglossum (Dialictus) marinum</i> (Crawford)	—	G	E
<i>Lasioglossum (Dialictus) michiganense</i> (Mitchell)	N/A	—	SP
<i>Lasioglossum (Dialictus) oceanicum</i> (Cockerell)	P	G	E
<i>Lasioglossum (Dialictus) oblongum</i> (Lovell)	P	W	E
<i>Lasioglossum (Hemihalictus) pectorale</i> (Smith)	P	G	S
<i>Lasioglossum (Dialictus) pilosum</i> (Smith)	—	G	E
<i>Lasioglossum (Dialictus) smilacinae</i> (Robertson)	P	G	E
<i>Lasioglossum (Dialictus) tegulare</i> (Robertson)	P	G	E
<i>Lasioglossum (Dialictus) versatum</i> (Robertson)	P	G	E
<i>Lasioglossum (Dialictus) viridatum</i> (Lovell)	P	G	E
<i>Sphecodes atlantis</i> Mitchell	N/A	—	CP
<i>Sphecodes cressonii</i> (Robertson)	N/A	—	CP
Family Megachilidae			
<i>Anthidium (Proanthidium) oblongatum</i> (Illiger)	P	C	S
<i>Megachile (Litomegachile) mendica</i> Cresson	P	C	S
<i>Osmia (Osmia) cornifrons</i> (Radoszkowski)	P	C	S
<i>Osmia (Osmia) lignaria lignaria</i> Say	P	C	S
<i>Osmia (Melanosmia) pumila</i> Cresson	P	C	S
<i>Osmia (Melanosmia) simillima</i> Smith	—	C	S/C
Family Apidae			
<i>Apis (Apis) mellifera</i> Linnaeus	P	H	A
<i>Bombus (Pyrobombus) bimaculatus</i> Cresson	P	H	E
<i>Bombus (Cullumanobombus) griseocollis</i> (DeGeer)	P	H	E
<i>Bombus (Pyrobombus) impatiens</i> Cresson	P	H	E
<i>Bombus (Pyrobombus) perplexus</i> Cresson	P	H	E
<i>Bombus (Pyrobombus) vagans</i> Smith	P	H	E

Appendix 1. Continued.

Species	Pollen Specificity	Nesting Habit	Sociality
<i>Ceratina (Zaodontomerus) calcarata</i> Robertson	P	S	SB
<i>Ceratina (Zaodontomerus) dupla</i> Say	P	S	SB
<i>Ceratina (Zaodontomerus) mikmaqi</i> Rehan & Sheffield	P	S	SB
<i>Melissodes (Melissodes) bimaculatus</i> (Lepeletier)	P	G	S
<i>Melissodes (Eumelissodes) agilis</i> Cresson/ <i>trinodis</i> Robertson	P	G	S
<i>Nomada articulata</i> Smith	N/A	1	CP
<i>Nomada australis</i> Mitchell	N/A	1	CP
<i>Nomada bethunei</i> Cockerell	N/A	2	CP
<i>Nomada cressonii</i> Robertson	N/A	3	CP
<i>Nomada illinoensis</i> Robertson	N/A	2	CP
<i>Nomada imbricata</i> Smith	N/A	4	CP
<i>Nomada maculata</i> Cresson	N/A	4	CP
<i>Nomada pygmaea</i> Cresson	N/A	2	CP
<i>Nomada sayi</i> Robertson/ <i>illinoensis</i> Robertson	N/A	2	CP
<i>Nomada valida</i> Smith	N/A	2	CP
<i>Nomada (Gnathias) sp. sensu</i> Mitchell	N/A	2	CP
<i>Peponapis (Peponapis) pruinosa</i> (Say)	oligolectic (<i>Cucurbita</i>)	G	S
<i>Xylocopa (Xylocopoides) virginica virginica</i> (Linnaeus)	P	W	S

¹ Nest of *Agapostemon*.² Nest of *Andrena*.³ Nest of *Andrena crataegi*, *A. vicina*, and *A. regularis*.⁴ Nest of *Andrena (Melandrena)*.

Appendix 2. Literature cited summary for each genus listed in Appendix 1.

Taxa	Reference
<i>Colletes</i>	Batra, 1980; Cane, 1991; Hurd, 1979
<i>Hylaeus</i>	Cane, 2003; Hicks, 1926; Hurd, 1979; Krombein, 1967; Rau, 1922, 1930; Torchio, 1984; Westrich, 1989
<i>Andrena</i>	Atwood, 1933; Bouseman & LaBerge, 1978; Gibbs <i>et al.</i> , 2017; Hurd, 1979; LaBerge, 1969, 1973, 1980, 1985, 1989; LaBerge & Bouseman, 1970; Miliczky, 1988; Miliczky & Osgood, 1995; Osgood, 1989; Schrader & LaBerge, 1978; Stephen, 1966; Wood & Roberts, 2017.
<i>Agapostemon</i>	Abrams & Eickwort, 1980; Eickwort, 1981; Roberts, 1969
<i>Augochlorella</i>	Hurd, 1979; Mueller, 1996; Ordway, 1966; Packer, 1990
<i>Halictus</i>	Cane, 1991; Eickwort, 1985; Michener & Bennett, 1977; Knerer & Atwood, 1962; Richards & Packer, 1995; Richards <i>et al.</i> , 2010
<i>Lasioglossum</i>	Ascher <i>et al.</i> , 2014; Atwood, 1933; Breed, 1975; Fetridge <i>et al.</i> , 2008; Gibbs, 2011; Gibbs <i>et al.</i> , 2012a, 2012b; Giles & Ascher, 2006; Goldstein & Ascher, 2016; Hurd, 1979; Knerer, 1969; Knerer & Atwood, 1966; McGinley, 1986; Mitchell, 1960
<i>Sphecodes</i>	Fetridge <i>et al.</i> , 2008; Michener, 1978, 2007
<i>Anthidium</i>	Cane, 2003; Hoebeke & Wheeler, 1999
<i>Megachile</i>	Hurd, 1979; Krombein, 1967; Medler, 1965
<i>Osmia</i>	Cane <i>et al.</i> , 2007; Hurd, 1979; Kraemer <i>et al.</i> , 2014; Krombein, 1967; Medler, 1967; Rau, 1937; Scott, 1993
<i>Apis</i>	Michener, 1974
<i>Bombus</i>	Michener, 1974; Williams <i>et al.</i> , 2014
<i>Ceratina</i>	Hurd, 1979; Rehan & Richards, 2010; Rutgers-Kelly, 2003; Vickruck & Richards, 2012; Vickruck <i>et al.</i> , 2011
<i>Melissodes</i>	Ashmead, 1894; Hurd, 1979
<i>Nomada</i>	Abrams & Eickwort, 1980; Droege <i>et al.</i> , 2010b; Eickwort, 1981; Gibbs <i>et al.</i> , 2017; Michener, 2007; Miliczky & Osgood, 1995; Osgood, 1989
<i>Peponapis</i>	Hurd, 1979; Hurd <i>et al.</i> , 1971, 1974; Mathewson, 1968
<i>Xylocopa</i>	Hurd, 1979

Appendix 3. Total number, method of collection, and habitat of capture of bees collected in the marsh, beach dunes and coastal scrub habitats at Grass Island in 2011–2012. Collection method: B = Bowl, N = Net. Habitat of capture: M = Marsh, D = Beach Dunes, S = Scrub. * denotes coastal/wetland specialist. E = denotes exotic. Exotic status was ascertained from Batra (1978), Cane (2003), Giles & Ascher (2006), Hoebeke & Wheeler (1999), Malloch (1918), Westrich (1989), and Zayed *et al.* (2007). Undetermined: Individuals that cannot be identified due to poor specimen quality or taxonomic difficulties.

Species	No. individuals	% total capture (n = 3928)	Collection method	Habitat of capture
Family Colletidae (2 genera, 8 species)	112	2.9		
<i>Colletes thoracicus</i> Smith, 1853	18	0.46	B, N	D, S
<i>Hylaeus (Prosopis) affinis</i> (Smith, 1853), (or <i>modestus modestus</i> Say, 1837)	29	0.74	N	D, M, S
<i>Hylaeus illinoisensis</i> (Robertson, 1896)	1	0.03	N	M
<i>Hylaeus leptcephalus</i> (Morawitz, 1870) ^E	1	0.03	N	M
<i>Hylaeus mesillae cressonii</i> (Cockerell, 1896)	27	0.69	B, N	D, M, S
<i>Hylaeus modestus modestus</i> Say, 1837	11	0.28	N	D, M
<i>Hylaeus (Prosopis) aff. nelumbonis</i> (Robertson, 1890)*	10	0.25	B, N	D, M, S
<i>Hylaeus schwarzii</i> (Cockerell, 1896)*	15	0.38	B, N	D, M, S
Family Andrenidae (1 genus, 15 species)	79	2.0		
<i>Andrena barbara</i> Bouseman & LaBerge, 1979	1	0.03	B	D
<i>Andrena carlini</i> Cockerell, 1901	2	0.05	B	D
<i>Andrena commoda</i> Smith, 1879	7	0.18	B, N	D, M, S
<i>Andrena crataegi</i> Robertson, 1893	19	0.48	N	D, M, S
<i>Andrena cressonii cressonii</i> Robertson, 1891	1	0.03	B	D
<i>Andrena forbesii</i> Robertson, 1891	4	0.10	N	M
<i>Andrena hippotes</i> Robertson, 1895	3	0.08	N	D
<i>Andrena mandibularis</i> Robertson, 1892	1	0.03	B	S
<i>Andrena nasonii</i> Robertson, 1895	27	0.69	B	D, M, S
<i>Andrena perplexa</i> Smith, 1853	2	0.05	B	D
<i>Andrena pruni</i> Robertson, 1891	1	0.03	B	D
<i>Andrena vicina</i> Smith, 1853	4	0.10	N	D, M, S
<i>Andrena violae</i> Robertson, 1891	6	0.15	B	D, M
<i>Andrena wheeleri</i> Graenicher, 1904	2	0.05	B	D
<i>Andrena wilkella</i> (Kirby, 1802) ^E	1	0.03	B	D
Family Halictidae (5 genera, 27 species)	2668	67.9		
<i>Agapostemon texanus</i> Cresson, 1872	5	0.13	N	S
<i>Agapostemon virescens</i> (Fabricius, 1775)	9	0.23	B, N	D, M
<i>Augochlorella aurata</i> (Smith, 1853)	213	5.42	B, N	D, M, S
<i>Halictus confusus confusus</i> Smith, 1853	1	0.03	B	D
<i>Halictus ligatus</i> Say, 1837	20	0.51	B	D, M, S

Appendix 3. Continued.

Species	No. individuals	% total capture (n = 3928)	Collection method	Habitat of capture
<i>Lasioglossum admirandum</i> (Sandhouse, 1924)	4	0.10	B	D, S
<i>Lasioglossum albipenne</i> (Robertson, 1890)	1	0.03	B	D
<i>Lasioglossum anomalum</i> (Robertson, 1892)	1	0.03	B	S
<i>Lasioglossum bruneri</i> (Crawford, 1902)	23	0.59	B, N	D, M, S
<i>Lasioglossum cressonii</i> (Robertson, 1890)	4	0.10	B	D, M, S
<i>Lasioglossum ephialtum</i> Gibbs, 2010	1082	27.55	B, N	D, M, S
<i>Lasioglossum georgeickworti</i> Gibbs, 2011*	10	0.25	B	D, M, S
<i>Lasioglossum hitchensi</i> Gibbs, 2012	1	0.03	B	M
<i>Lasioglossum leuocomum</i> (Lovell, 1908)	6	0.15	B	D, M, S
<i>Lasioglossum leucozonium</i> (Schrank, 1781) ^E	6	0.15	B	D, M, S
<i>Lasioglossum marinum</i> (Crawford, 1904)*	599	15.25	B, N	D, M S
<i>Lasioglossum michiganense</i> (Mitchell, 1960)	4	0.10	B	D, S
<i>Lasioglossum oceanicum</i> (Cockerell, 1916)	2	0.05	B, N	M, S
<i>Lasioglossum oblongum</i> (Lovell, 1905)	436	11.10	B	D, M, S
<i>Lasioglossum pectorale</i> (Smith, 1853)	2	0.05	B	D
<i>Lasioglossum pilosum</i> (Smith, 1853)	98	2.49	B	D, M, S
<i>Lasioglossum smilacinae</i> (Robertson, 1897)	2	0.05	B	S
<i>Lasioglossum tegulare</i> (Robertson, 1890)	8	0.20	B	D, M, S
<i>Lasioglossum versatum</i> (Robertson, 1902)	19	0.48	B	D, M, S
<i>Lasioglossum viridatum</i> (Lovell, 1905)	5	0.13	B, N	D, M, S
<i>Sphecodes atlantis</i> Mitchell, 1956	2	0.05	B	D
<i>Sphecodes cressonii</i> (Robertson, 1903)	1	0.03	B	S
Family Megachilidae (3 genera, 6 species)	223	5.7		
<i>Anthidium oblongatum</i> (Illiger, 1806) ^E	1	0.03	B	D
<i>Megachile mendica</i> Cresson, 1878	1	0.03	B	D
<i>Osmia cornifrons</i> (Radoszkowski, 1887) ^E	2	0.05	B	D, S
<i>Osmia lignaria lignaria</i> Say, 1837	6	0.15	B	D, S
<i>Osmia pumila</i> Cresson, 1864	212	5.40	B, N	D, M, S
<i>Osmia simillima</i> Smith, 1853	1	0.03	N	D
Family Apidae (7 genera, 24 species)	846	21.5		
<i>Apis mellifera</i> Linnaeus, 1758 ^E	24	0.61	B, N	D, M, S
<i>Bombus bimaculatus</i> Cresson, 1863	6	0.15	N	D, M, S
<i>Bombus griseocollis</i> (DeGeer, 1773)	36	0.92	B, N	D, M, S
<i>Bombus impatiens</i> Cresson, 1863	100	2.55	B, N	D, M, S
<i>Bombus perplexus</i> Cresson, 1863	2	0.05	N	S

Appendix 3. Continued.

Species	No. individuals	% total capture (n = 3928)	Collection method	Habitat of capture
<i>Bombus vagans</i> Smith, 1854	1	0.03	N	S
<i>Ceratina calcarata</i> Robertson, 1900	34	0.87	B, N	D, M, S
<i>Ceratina dupla</i> Say, 1837	545	13.87	B, N	D, M, S
<i>Ceratina mikmaqi</i> Rehan & Sheffield, 2011	48	1.22	B, N	D, M, S
<i>Melissodes bimaculatus</i> (Lepeletier, 1825)	1	0.03	B	S
<i>Melissodes (Eumelissodes) agilis</i> Cresson, 1878 (or <i>trinodis</i> Robertson, 1901)	1	0.03	B	S
<i>Nomada articulata</i> Smith, 1854	4	0.10	B	D
<i>Nomada australis</i> Mitchell, 1962	1	0.03	B	S
<i>Nomada bethunei</i> Cockerell, 1903	5	0.13	B	D
<i>Nomada cressonii</i> Robertson, 1893	1	0.03	B	D
<i>Nomada illinoensis</i> Robertson, 1900	1	0.03	B	S
<i>Nomada imbricata</i> Smith, 1854	2	0.05	B	D, S
<i>Nomada maculata</i> Cresson, 1863	3	0.08	B	D, S
<i>Nomada pygmaea</i> Cresson, 1863	2	0.05	B	D
<i>Nomada (Gnathias) sp. sensu</i> Mitchell (1962)	5	0.13	B	D, S
<i>Nomada sayi</i> Robertson, 1893 (or <i>illinoensis</i> Robertson, 1900)	1	0.03	B	D
<i>Nomada valida</i> Smith, 1854	1	0.03	B	D
<i>Peponapis pruinosa</i> (Say, 1837)	1	0.03	B	M
<i>Xylocopa virginica virginica</i> (Linnaeus, 1771)	12	0.31	B, N	D, M, S
Undetermined	111	2.83		

Appendix 4. Bee species captured in 2011 and their abundance by month.

Species	April	May	June	July	August	Total
Family Colletidae	0	1	10	20	24	55
<i>Hylaeus leptocephalus</i>	0	0	0	0	1	1
<i>Hylaeus mesillae cressonii</i>	0	1	5	10	5	21
<i>Hylaeus modestus modestus</i>	0	0	0	4	4	8
<i>Hylaeus aff. nelumbonis</i>	0	0	0	3	2	5
<i>Hylaeus schwarzii</i>	0	0	3	2	2	7
<i>Hylaeus affinis/modestus</i>	0	0	2	1	10	13
Family Andrenidae	1	23	5	0	0	29
<i>Andrena commoda</i>	0	1	3	0	0	4
<i>Andrena crataegi</i>	0	5	0	0	0	5
<i>Andrena hippotes</i>	0	1	0	0	0	1
<i>Andrena nasonii</i>	0	14	2	0	0	16
<i>Andrena vicina</i>	0	1	0	0	0	1
<i>Andrena violae</i>	1	0	0	0	0	1
<i>Andrena wilkella</i>	0	1	0	0	0	1
Family Halictidae	101	163	219	419	272	1174
<i>Agapostemon texanus</i>	0	0	0	0	5	5
<i>Agapostemon virescens</i>	0	0	4	1	1	6
<i>Augochlorella aurata</i>	9	44	48	39	36	176
<i>Halictus confusus confusus</i>	0	0	0	1	0	1
<i>Halictus ligatus</i>	0	2	1	16	0	19
<i>Lasioglossum admirandum</i>	0	1	1	0	0	2
<i>Lasioglossum albipenne</i>	0	0	0	1	0	1
<i>Lasioglossum anomalum</i>	1	0	0	0	0	1
<i>Lasioglossum bruneri</i>	3	1	2	3	1	10
<i>Lasioglossum cressonii</i>	1	1	0	0	0	2
<i>Lasioglossum ephialtum</i>	50	40	71	167	132	460
<i>Lasioglossum georgeickworti</i>	0	0	1	1	1	3
<i>Lasioglossum hitchensi</i>	0	1	0	0	0	1
<i>Lasioglossum leucocomum</i>	2	0	0	2	0	4
<i>Lasioglossum leucozonium</i>	0	0	0	4	0	4
<i>Lasioglossum marinum</i>	3	57	36	71	41	208
<i>Lasioglossum michiganense</i>	2	0	0	1	0	3
<i>Lasioglossum oceanicum</i>	0	0	0	0	1	1
<i>Lasioglossum oblongum</i>	13	8	30	63	27	141
<i>Lasioglossum pectorale</i>	0	0	1	1	0	2
<i>Lasioglossum pilosum</i>	10	3	15	27	12	67
<i>Lasioglossum smilacinae</i>	2	0	0	0	0	2

Appendix 4. Continued.

Species	April	May	June	July	August	Total
<i>Lasioglossum tegulare</i>	0	0	0	5	1	6
<i>Lasioglossum versatum</i>	5	3	1	5	0	14
<i>Lasioglossum viridatum</i>	0	1	0	0	4	5
<i>Lasioglossum (Dialictus) viridatum</i> group	0	0	2	6	8	16
<i>Lasioglossum (Dialictus) spp.</i>	0	0	5	5	2	12
<i>Sphecodes atlantis</i>	0	1	1	0	0	2
Family Megachilidae	79	18	13	1	1	112
<i>Anthidium oblongatum</i>	0	0	0	0	1	1
<i>Osmia cornifrons</i>	2	0	0	0	0	2
<i>Osmia lignaria lignaria</i>	2	0	0	0	0	2
<i>Osmia pumila</i>	75	18	13	1	0	107
Family Apidae	66	98	128	66	110	468
<i>Apis mellifera</i>	0	2	1	1	1	5
<i>Bombus griseocollis</i>	0	7	9	0	0	16
<i>Bombus impatiens</i>	0	1	11	10	28	50
<i>Ceratina calcarata</i>	1	7	6	1	5	20
<i>Ceratina dupla</i>	55	62	81	48	73	319
<i>Ceratina mikmaqi</i>	2	14	20	4	3	43
<i>Ceratina (Zadontomerus) spp.</i>	0	1	1	0	0	2
<i>Melissodes bimaculata</i>	0	0	0	1	0	1
<i>Melissodes (Eumelissodes) agilis/trinodis</i>	0	0	0	1	0	1
<i>Nomada bethunei</i>	0	2	0	0	0	2
<i>Nomada maculata</i>	2	0	0	0	0	2
<i>Nomada (Gnathias) sp. sensu Mitchell</i>	4	0	0	0	0	4
<i>Nomada sayi/illinoensis</i>	1	0	0	0	0	1
<i>Peponapis pruinosa</i>	0	0	0	1	0	1
<i>Xylocopa virginica virginica</i>	1	4	0	0	1	6
Total individuals per month	247	305	376	507	408	1843

Appendix 5. Bee species captured in 2012 and their abundance by month.

Species	April	May	June	July	August	September	Total
Family Colletidae	0	19	3	9	19	7	57
<i>Colletes thoracicus</i>	0	18	0	0	0	0	18
<i>Hylaeus illinoisensis</i>	0	0	0	0	1	0	1
<i>Hylaeus mesillae cressonii</i>	0	1	1	1	1	2	6
<i>Hylaeus modestus modestus</i>	0	0	0	3	8	0	11
<i>Hylaeus aff. nelumbonis</i>	0	0	0	3	1	1	5
<i>Hylaeus schwarzii</i>	0	0	2	1	3	2	8
<i>Hylaeus affinis/modestus</i>	0	0	0	1	5	2	8
Family Andrenidae	3	44	5	0	0	0	52
<i>Andrena barbara</i>	0	1	0	0	0	0	1
<i>Andrena carlini</i>	2	0	0	0	0	0	2
<i>Andrena commoda</i>	0	1	2	0	0	0	3
<i>Andrena crataegi</i>	0	13	1	0	0	0	14
<i>Andrena cressonii cressonii</i>	0	0	1	0	0	0	1
<i>Andrena forbesii</i>	0	4	0	0	0	0	4
<i>Andrena hippotes</i>	0	2	0	0	0	0	2
<i>Andrena mandibularis</i>	1	0	0	0	0	0	1
<i>Andrena nasonii</i>	0	10	1	0	0	0	11
<i>Andrena perplexa</i>	0	2	0	0	0	0	2
<i>Andrena pruni</i>	0	1	0	0	0	0	1
<i>Andrena vicina</i>	0	3	0	0	0	0	3
<i>Andrena violae</i>	0	5	0	0	0	0	5
<i>Andrena wheeleri</i>	0	2	0	0	0	0	2
Family Halictidae	56	358	132	482	357	112	1497
<i>Agapostemon virescens</i>	0	0	3	0	0	0	3
<i>Augochlorella aurata</i>	3	21	3	6	3	1	37
<i>Halictus ligatus</i>	0	1	0	0	0	0	1
<i>Lasioglossum admirandum</i>	0	1	0	1	0	0	2
<i>Lasioglossum bruneri</i>	2	3	2	6	0	0	13
<i>Lasioglossum cressonii</i>	0	0	2	0	0	0	2
<i>Lasioglossum ephialtum</i>	26	172	60	203	141	20	622
<i>Lasioglossum georgeickworti</i>	1	2	1	1	2	0	7
<i>Lasioglossum georgeickworti?</i>	0	0	0	1	0	0	1
<i>Lasioglossum leucomum</i>	0	0	0	1	1	0	2
<i>Lasioglossum leucozonium</i>	0	1	0	0	1	0	2
<i>Lasioglossum marinum</i>	1	79	38	102	123	48	391
<i>Lasioglossum michiganense</i>	0	0	0	0	0	1	1
<i>Lasioglossum oceanicum</i>	0	0	1	0	0	0	1

Appendix 5. Continued.

Species	April	May	June	July	August	September	Total
<i>Lasioglossum oblongum</i>	13	60	19	131	56	16	295
<i>Lasioglossum pilosum</i>	7	3	1	9	9	2	31
<i>Lasioglossum tegulare</i>	0	0	0	0	2	0	2
<i>Lasioglossum versatum</i>	0	2	1	1	1	0	5
<i>Lasioglossum (Dialictus) viridatum</i> group	1	4	0	11	15	18	49
<i>Lasioglossum (Dialictus) spp.</i>	2	7	1	9	2	6	27
<i>Sphecodes cressonii</i>	0	1	0	0	0	0	1
<i>Sphecodes sp.</i>	0	1	0	0	1	0	2
Family Megachilidae	32	70	8	0	0	1	111
<i>Megachile mendica</i>	0	0	0	0	0	1	1
<i>Osmia lignaria lignaria</i>	4	0	0	0	0	0	4
<i>Osmia pumila</i>	28	70	7	0	0	0	105
<i>Osmia sinillima</i>	0	0	1	0	0	0	1
Family Apidae	159	99	36	21	22	31	368
<i>Apis mellifera</i>	0	3	1	0	3	12	19
<i>Bombus bimaculatus</i>	0	4	2	0	0	0	6
<i>Bombus griseocollis</i>	0	7	9	1	0	3	20
<i>Bombus impatiens</i>	0	5	9	9	14	13	50
<i>Bombus perplexus</i>	0	2	0	0	0	0	2
<i>Bombus vagans</i>	0	1	0	0	0	0	1
<i>Ceratina calcarata</i>	7	4	2	0	1	0	14
<i>Ceratina dupla</i>	147	51	12	10	3	3	226
<i>Ceratina mikmaqi</i>	1	2	0	1	1	0	5
<i>Nomada articulata</i>	0	4	0	0	0	0	4
<i>Nomada australis</i>	0	1	0	0	0	0	1
<i>Nomada bethunei</i>	0	3	0	0	0	0	3
<i>Nomada cressonii</i>	0	1	0	0	0	0	1
<i>Nomada illinoensis</i>	0	1	0	0	0	0	1
<i>Nomada imbricata</i>	0	2	0	0	0	0	2
<i>Nomada maculata</i>	0	1	0	0	0	0	1
<i>Nomada pygmaea</i>	0	2	0	0	0	0	2
<i>Nomada (Gnathias) sp. sensu Mitchell</i>	0	1	0	0	0	0	1
<i>Nomada valida</i>	0	1	0	0	0	0	1
<i>Nomada spp.</i>	0	1	1	0	0	0	2
<i>Xylocopa virginica virginica</i>	4	2	0	0	0	0	6
Total individuals per month	250	590	184	512	398	151	2085



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A Journal of Bee Biology, Ecology, Evolution, & Systematics

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