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The Bee Fauna of Coastal Napatree Point and Two Inland Sites in Southern Rhode Island

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Abstract - We surveyed the bee fauna at Napatree Point, a coastal barrier beach in southwestern Rhode Island, using bee-bowl and netting samples, and compared results to bee-bowl samples at 2 inland sites. We collected a total of 53 species and morphospecies at Napatree Point, including 5 likely Rhode Island state records and several coastal dune and sand-nesting species that were not found inland. The comparative bee-bowl samples (colored bowls with soapy water placed at the sites to collect visiting bees) captured 35 species at Napatree Point and 66 at the inland sites (which included 6 likely state records, 2 shared with Napatree). The Napatree fauna shared numerous species with the inland sites, but overall species composition differed substantially. Both Napatree and inland sites showed greatest bee activity and species richness in spring. During spring, the most common bees at Napatree were twig- and cavity-nesting species such as *Ceratina dupla* and *Osmia simillima*, and the wood-nesting *Lasioglossum oblongum*, while the most abundant bees inland were the soil-nesting *Andrena nasonii* and *Augochlorella aurata*. Netting samples differed from bee-bowl samples in that they captured larger species and species foraging at flowers distant from the bee-bowl transects, but they missed several diminutive species that were captured by bee bowls. Use of 2 sampling methods, therefore, provided a broader view of the bee fauna than would have been possible with a single collection method.

Introduction

Declines of pollinator species and the lack of monitoring programs to track their status have engendered increasing concern (Allen-Wardell et al. 1998, National Research Council 2007, Tepedino and Ginsberg 2000, Winfree 2010). Coastal bees and their habitats, in particular, are not well studied. Coastal areas are considered to be particularly vulnerable by the National Park Service and other organizations because of the potential effects of storms and sea-level rise associated with climate change (Rykken et al. 2014).

Coastal dune habitats have distinctive floras and faunas (Ehrenfeld 1990), with many dune specialists including rare and endemic species (Howe et al. 2010, Rykken et al. 2014). Recently, Ascher et al. (2014) surveyed the bees at Gardiners Island and surrounding islands near Long Island, NY, and Goldstein and Ascher (2016) surveyed bees at Martha's Vineyard, MA. Bees have also been surveyed at inland dune sites in Maryland (Selfridge et al. 2017) and at coastal sand dunes in Wales (Howe et al. 2010).

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Napatree Point, a barrier beach in Westerly at the southwestern corner of Rhode Island, is managed as a conservation area, but the bee fauna of this site has never been surveyed. We studied the bee fauna of Napatree Point using standardized sampling protocols to create a baseline for future monitoring efforts there, and we collected comparative inland samples at 2 sites in southern Rhode Island. We conducted 6 bee-bowl samplings over the spring and summer of 2017, where we set up bee bowls along transects at 2 sites in Napatree and 2 sites inland (Francis C. Carter Preserve and Great Swamp Management Area). We also netted at flowering patches at Napatree Point throughout the field season to provide a more complete survey of the Napatree bee fauna.

Methods

Study sites

We conducted the fieldwork for this study at 3 sites in Rhode Island: Napatree Point Conservation Area, Francis C. Carter Memorial Preserve, and Great Swamp Management Area (Fig. 1).

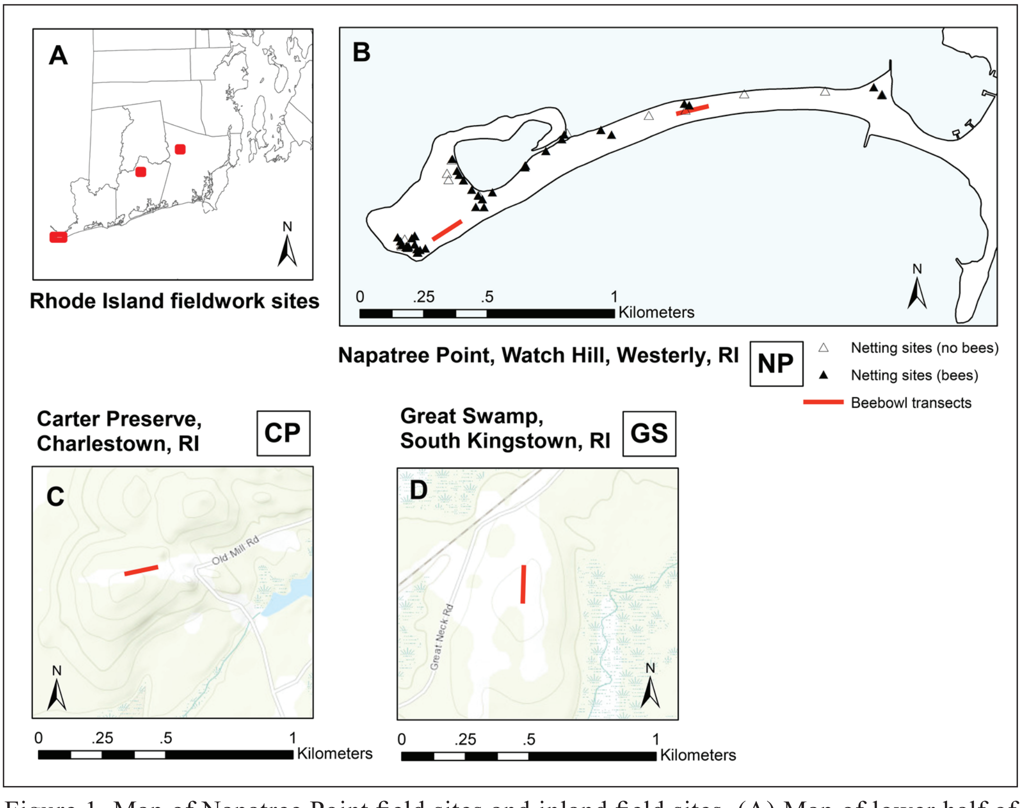

Figure 1. Map of Napatree Point field sites and inland field sites. (A) Map of lower half of Rhode Island showing sampling locations (as squares). (B) Map of Napatree Point showing bee-bowl transects and netting sites. (C) Bee-bowl transect location in Carter Preserve. (D) Bee-bowl transect location in Great Swamp. Maps created with ArcGIS using Esri World Topo Map.

Napatree Point Conservation Area, located in Westerly, RI, is a barrier beach habitat (sandy ocean beach, primary dune, secondary dune area, bay) on a moraine, with an abandoned fort and surrounding forested habitat at the west end. The area is bounded to the north by Little Narragansett Bay and to the south by the Atlantic Ocean (Mayo et al. 2015). Napatree Point is managed by the Watch Hill Conservancy and the Watch Hill Fire District. One bee-bowl transect was located in central Napatree Point (41°18'39.1"N, 71°52'19.5"W to 41°18'40.1"N, 71°52'14.0"W) in an area of secondary dunes dominated by *Ammophila breviligulata* Fernald (Beach Grass) meadows with patches of barrier-island shrubs (Ehrenfeld 1990); high winds are frequent. The other bee-bowl transect was located on the western end of Napatree (41°18'22.9"N, 71°53'00.6"W to 41°18'25.3"N, 71°52'55.7"W), closer to trees (including coastal shrub thickets and planted non-native species such as *Pinus thunbergii* (Parlatore) (Japanese Black Pine), a small lagoon, and the abandoned military fort (Fig. 1B). Additional information on Napatree Point is available from the Napatree Point Conservation Area (http://portal.napatreepoint.info/).

We collected comparative samples at 2 inland sites. One was at the Francis C. Carter Memorial Preserve in Charlestown, RI (Fig. 1C). The field site was located in a power line right-of-way (41°25'54.5"N, 71°40'16.1"W to 41°25'55.4"N, 71°40'10.4"W). The site is an open, dry area with trees on either side; the dominant vegetation consists of *Kalmia angustifolia* L. (Sheep Laurel), *Gaylussacia baccata* (Wangenh.) K. Koch (Black Huckleberry), and *Solidago* spp. (goldenrods). Carter Preserve is managed by the Nature Conservancy. Carter Preserve is 2.7 km inland and 21 km from Napatree Point.

The second inland site was in the Great Swamp Management Area in South Kingston, RI (Fig. 1D). The field was located on a walking trail in an old field surrounded by trees (41°28'23.2"N, 71°34'19.1"W to 41°28'28.1"N, 71°34'18.9"W). This site is a dense meadow of numerous herbaceous species, including *Potentilla* spp. (cinquefoils), *Trifolium repens* L. (White Clover), *Euthamia graminifolia* L. (Nuttall) (Grass-leaved Goldenrod), and *S. rugosa* Miller (Rough-stemmed Goldenrod). Great Swamp is managed by the RI Department of Environmental Management. Great Swamp is 3.4 km inland and 31 km from Napatree Point.

Sampling methods

Variations of pan or bowl traps have been widely used to sample bees (Cane et al. 2000, Droege et al. 2010, Westphal et al. 2008, Williams et al 2001). Bowl traps have some advantages over traditional capture by aerial netting in that they avoid investigator bias and can catch small bees that may be missed by netting (Droege et al. 2010, Selfridge et al. 2017, Westphal et al. 2008). However, the technique does not provide information on floral associations, and large bees may escape from bowls more easily (Westphal et al. 2008; A. Rothwell, pers. observ.). Though collecting bees with aerial nets can be influenced by collector bias, it readily captures larger bees, and so pairing the 2 methods can sample a broader range of bees than either alone (Cane et al. 2000).

We used the 2010 National Park Service Native Bee/Climate Change Study sampling protocol for bee-bowl sampling (Rykken et al. 2014). This sampling procedure compares bees found in vulnerable habitats to bees found in common inland habitats sampled using standardized bee-bowl transects. We set and collected bee bowls 6 times over the summer in 2017 (Fig. 2) on 16 May, 7 June, 27 June, 19 July, 23 August, and 10 September. (Great Swamp was re-sampled on 22 July, after a truck drove through the site and destroyed the 19 July samples). We placed bee bowls at coastal and inland sites on the same day.

The sampling transects were 150 m long, with 30 bee bowls spaced 5 m apart. The bee bowls consisted of plastic cups (7.5 cm diameter, 3.5 cm height), alternating white (unpainted) or painted blue or yellow (fluorescent colors, Guerra Paint and Pigment, New York, NY), in a pattern of blue, white, yellow. We filled the bowls 7/8 full with a solution of store-bought spring or distilled water mixed with blue Dawn dish detergent and left them out in the field for 24 h. While setting up and collecting the bee bowls, we wore lab gloves to avoid any effects of odor contamination (e.g., sweat bees lick human sweat). Insects collected from the bowls were placed into whirlpack bags with 70% ethanol, processed, and pinned prior to identification by S. Droege (Patuxent Wildlife Research Center, Laurel, MD), who also identified many of the netted specimens. We based bee sizes, for comparisons of bees captured in bee bowl vs. netting samples, on length measurements in Mitchell (1960, 1962) and Discover Life (www.discoverlife.org).

We surveyed flowering vegetation within 1 m on either side of each bee-bowl transect and tallied the number of 5-m transect sections (between bowls) with flowering vegetation. We recorded the occurrence of each flowering species within 1 m on either side of each transect.

For netting samples (taken only at Napatree Point), we monitored flowering plants and netted bees at flowering patches through the summer as flower species of interest (mostly common species in the barrier beach environment) entered peak anthesis. During the summer of 2017, we conducted netting on 10 days: 2 June, 14 June, 29 June, 5 July, 31 July, 10 August, 22 August, 5 September, 25 September, and 13 October (Fig. 2). A. Rothwell obtained all netting samples by collecting bees at each flowering patch for 30 min, and limited collections to 15 individuals per sample to avoid over-collecting. We transferred netted bees to labeled containers, and the specimens were held in a freezer at least overnight before being pinned and labeled. We identified the netted bees to species under

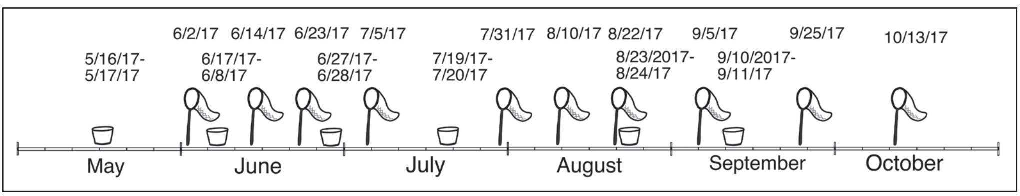

Figure 2. Dates for bee-bowl sampling and netting sampling. The bowl graphic symbolizes bee-bowl events and the net graphic symbolizes netting-sampling events. Netting only took place at Napatree Point. Bee bowls were placed at coastal and inland sites on the same day.

a dissecting microscope, using standard keys (Discoverlife.com; Mitchell 1960, 1962), with additional identifications and confirmations by S. Droege and J. Gibbs (University of Manitoba, Winnepeg, MN, Canada). We assessed apparent new records for Rhode Island by comparing our records to those listed as occurring in Rhode Island as per John Ascher's list of species records for the state on the Discover Life web site. We placed voucher specimens of most species in the University of Rhode Island Insect Collection, with additional specimens placed in the US National Collection (Smithsonian Institution, Washington, DC). We identified most flowering plants at the sample sites; difficult identifications were later verified by botanists (see Acknowledgments).

Data analysis

We compared the bee-bowl data from the 2 Napatree coastal sites and 2 inland sites for species diversity, species richness, and evenness. We collected bee-bowl samples in exactly the same way at each site; thus, we quantified species richness simply by totaling the number of species collected at each site. We also estimated the total numbers of species present at each bee-bowl transect using the online estimation program SPECRICH (www.mbr-pwrc.usgs.gov/software/specrich.html, accessed 20 July 2018), written by J.E. Hines (Patuxent Wildlife Research Center, Laurel, MD) based on the method of Burnham and Overton (1979). We employed the Shannon–Weiner diversity index (H') to quantify diversity (Peet 1974, Shannon and Weaver 1949, Southwood and Henderson 2000). We calculated evenness as 1 minus the Berger–Parker dominance index, or the proportion of the sample that consisted of species other than the dominant species (Southwood and Henderson 2000).

We compared species compositions of the 4 sample sites using canonical correspondence analysis (CCA) in the PAST package (paleontological statistics software package; Hammer et al. 2001). The samples were from the bee bowls at 4 transects, each sampled 6 times over the season (Fig. 2) for a total of 24 samples. The environmental variables included soil type (proportion of sand in soil types), forest cover, and distance from the coast. To assess these variables, we used ArcGIS to create a 200-m circular buffer from each bee-bowl transect. We analyzed soils data and the Rhode Island ecological communities classification data from the Rhode Island GIS database system (RIGIS, http://www.rigis.org/).

We compared taxonomic composition between the Napatree and inland sites by chi-square (SAS, version 9.3, FREQ procedure; SAS Institute, Inc., Cary, NC) using 10 taxonomic categories (Colletidae, Andrenidae, green Halictidae, *Halictus*, *Lasioglossum*, *Sphecodes*, Megachilidae, *Ceratina*, corbiculate Apidae, other Apidae). We combined the genera *Halictus*, *Lasioglossum*, and *Sphecodes* into 1 category (because of small sample sizes of some groups) for the comparison of netting vs. bee-bowl samples at Napatree Point.

To examine the phenology at each site, we plotted both bee abundance and numbers of species in each sample over the season. We tested these patterns for differences by comparing numbers at Napatree vs. inland sites during each of the 6 samples with chi-square tests, using SAS, version 9.3, FREQ procedure. We also compared differences in captures of bees in different size categories using chi-square tests.

Results

At Napatree, we caught 654 individual bees at the combined bee-bowl sites and 176 individual bees through netted samples, for a total of 830 individuals. These collections represented 35 species and morphospecies at the bee-bowl sites and 33 species and morphospecies in the netted samples, totaling 53 species (Table 1). In the bee-bowl samples at the inland sites, we caught 448 individual bees at the Great Swamp and 262 individual bees at the Carter Preserve, for a total of 710 individuals. There were 46 species and morphospecies in the Great Swamp samples and 45 species and morphospecies at the Carter Preserve, totaling 66 species at the inland sites (Table 2). There is no official list of the bees of Rhode Island, but based on currently available compilations, our samples collected 9 species that are likely new records for the state (S. Droege, pers. comm., based on current records in Discover

Table 1. Species and number of individuals from netting sampling and bee-bowl sampling at Napatree. An asterisk (*) denotes possible Rhode Island State record, † denotes native pollen-specialist bees (oligolectic). Plant species: AB = *Ampelopsis brevipedunculata* (Porcelainberry), CE = *Cakile edentula* (Bigelow) Hook (Sea Rocket), CV = *Cirsium vulgare* (Bull Thistle), DC = *Daucus carota* L. (Queen Anne's Lace), HM = *Heracleum maximum* Bartram (Cow-parsnip), LaJ = *Lathyrus japonicus* (Beach Pea), LC = *Limonium carolinianum* (Sea-lavender), LoJ = *Lonicera japonica* Thunberg (Japanese Honeysuckle), RaR = *Raphanus raphanistrum* (Wild Radish), RoR = *Rosa rugosa* (Rugosa Rose), SC = *Solidago canadensis/altissima* (Canada Goldenrod/Tall Goldenrod), SS = *Solidago sempirvirens* (Seaside Goldenrod), TC = *Teucrium canadense* L. (American Germander). ‡ = Bee was near plant; not on flower. **14 males from netting samples were identified by J. Gibbs as possibly *L. atwoodi* Gibbs, *L. viridatum* Lovell or *L. oblongum* Lovell. These were included in with *L. oblongum*. ***4 males, tentatively identified by J. Gibbs as *L. hitchensii/subviridatum* (Cockerell), were included in *L.* sp. **** Possible *B. sandersoni* Franklin? *Augochlora pura* Say was collected at Napatree Point in additional samples in 2018. [Table continued on following page.]

Family/species	Napatree bee bowls	Napatree netted bees	Plant species on which netted bees were collected
Colletidae			
Colletes compactus Cresson	0	1	SS
Colletes kincaidii Cockerell*	0	3	SS
Colletes simulans Cresson†	0	3	SS
Hylaeus affinis (Smith)/modestus Say	2	3	RaR, SC
Hylaeus mesillae Cockerell	1	0	
Hylaeus schwarzii (Cockerell)	1	0	
Andrenidae			
Andrena alleghaniensis Viereck*	1	0	
Andrena asteris Robertson†	0	5	SS
Andrena commoda Smith	3	0	
Andrena hirticincta Provancher†	0	3	SS
Andrena nasonii Robertson	2	0	
Andrena perplexa Smith	1	0	
Andrena pruni Robertson	4	0	
Andrena thaspii Graenicher	0	1	HM‡
Perdita octomaculata Say†	0	24	SS

Life: www.discoverlife.org; Scott et al. 2016). According to a recent compilation of northeastern native pollen-specialist or oligolectic bees (Fowler 2016), there were 4 native specialist bees in our Napatree Point samples (Table 1) and 1 at the Great Swamp (Table 2). We collected the specialist species during the expected time of the season, based on the flower taxa upon which they specialize.

Table 1, continued.

Family/species	Napatree bee bowls	Napatree netted bees	Plant species on which netted bees were collected
Halictidae			
Agapostemon sericeus Forster	1	1	SS
Agapostemon virescens Fabricius	5	1	CV
Augochlorella aurata Smith	6	1	SC
Halictus confusus Smith	2	1	RaR
Halictus ligatus Say	1	1	AB
Lasioglossum coriaceum Smith	4	0	
Lasioglossum ephialtum Gibbs*	0	9	LC, SC
Lasioglossum georgeickworti Gibbs*	27	0	
Lasioglossum leucozonium Schrank	1	0	
Lasioglossum marinum Crawford	53	19	CE, LaJ, LC, RaR
Lasioglossum oblongum Lovell	97	14**	LC
Lasioglossum tegulare Robertson	5	1	DC
Lasioglossum versatum Robertson	4	0	
Lasioglossum zephyrum Smith	0	1	
Lasioglossum sp.	2	14***	LC
Sphecodes sp.	0	1	AB
Megachilidae			
Hoplitis pilosifrons Cresson	3	0	
Hoplitis producta Cresson	0	1	
Megachile melanophaea Smith	0	1	LaJ
Osmia atriventris Cresson	1	0	
Osmia bucephala Cresson*	1	0	
Osmia pumila Cresson	1	0	
Osmia simillima Smith	104	7	LaJ, RaR
Apidae			
Apis mellifera L.	0	6	RaR, SS
Bombus griseocollis De Geer	0	1	RaR
Bombus impatiens Cresson	0	24	AB, CV, LaJ, RaR, RoR, SC, SS
Bombus vagans Smith****	1	11	AB, LaJ, LC, LoJ, RaR, SC, TC
Ceratina calcarata Robertson	48	2	CV, SS
Ceratina dupla Say	243	7	LC, RaR, SC
Ceratina mikmaqi Rehan and Sheffield	5	2	RaR, CV
Ceratina sp.	16	2	LC, SC
Melissodes druriellus Latreille	0	3	SS
Nomada articulata Smith	1	0	
Nomada sp. (bidentate group)	2	0	
Nomada luteolodies Robertson	1	0	
Nomada maculata Cresson	4	0	
Xylocopa virginica L.	0	2	SS
Total individuals	654	176	
Total species	35	33	

Table 2. Species and number of individuals from bee bowls at inland sites. An asterisk (*) denotes possible Rhode Island State record, † denotes native pollen-specialist bees (oligolectic), and ** indicates that some specimens may be *H. poeyi* Lepeletier. [Table continued on following page.]

Family/species	Great Swamp bee bowls	Carter Preserve bee bowls
Colletidae		
Hylaeus affinis (Smith)/*modestus* Say	14	2
Andrenidae		
Andrena bradleyi Viereck†	1	0
Andrena carlini Cockerell	4	9
Andrena nasonii Robertson	67	87
Andrena perplexa Smith	1	0
Calliopsis andreniformis Smith	0	2
Halictidae		
Agapostemon sericeus Forster	0	3
Agapostemon texanus Cresson	1	6
Agapostemon virescens Fabricius	28	5
Augochlora pura Say	0	2
Augochlorella aurata Smith	92	32
Augochlorella persimilis (Viereck)*	1	2
Augochloropsis metallica (Fabricius)	1	0
Halictus confusus Smith	3	1
Halictus ligatus Say	13**	8**
Halictus parallelus Say	1	2
Halictus rubicundus (Christ)	0	3
Lasioglossum abanci (Crawford)	1	0
Lasioglossum acuminatum McGinley	0	3
Lasioglossum bruneri (Crawford)	0	1
Lasioglossum coeruleum (Robertson)*	1	0
Lasioglossum coreopsis (Robertson)*	0	1
Lasioglossum coriaceum Smith	11	3
Lasioglossum cressonii (Robertson)	28	0
Lasioglossum ephialtum Gibbs*	1	0
Lasioglossum leucocomum (Lovell)	0	3
Lasioglossum leucozonium Schrank	6	2
Lasioglossum oblongum Lovell	1	0
Lasioglossum oceanicum (Cockerell)	2	3
Lasioglossum pectorale (Smith)	0	6
Lasioglossum smilacinae (Robertson)	1	0
Lasioglossum tegulare Robertson	6	14
Lasioglossum timothyi Gibbs	0	1
Lasioglossum versatum Robertson	38	10
Lasioglossum sp.	0	1
Sphecodes coronus Mitchell	1	0
Sphecodes mandibularis Cresson	1	0
Sphecodes ranunculi Robertson	0	1
Sphecodes sp.	0	1
Megachilidae		
Hoplitis producta Cresson	1	0
Hoplitis spoliata (Provancher)	0	1
Megachile brevis Say	0	1
Osmia atriventris Cresson	5	4
Osmia bucephala Cresson*	0	1

The most common flowering species near each transect are listed below. Napatree 1: *Lathyrus japonicus* Willdenow (Beach Pea), *Rosa rugosa* Thunberg (Rugosa Rose), *Raphanus raphanistrum* L. (Wild Radish), *Oenothera biennis* L. (Common Evening Primrose), and *Erigeron canadensis* L. (Horseweed). Napatree 2: Rugosa Rose, *Toxicodendron radicans* (L.) Kuntze (Eastern Poison Ivy), and *Lepidium virginicum* L. (Virginia Pepperweed); Great Swamp: *Taraxacum offiniale* Weber ex Wiggers (Dandelion), *Potentilla* spp. (cinquefoils), *Rosa multiflora* Thunberg (Multiflora Rose), *Rubus* spp. (brambles), *Stellaria graminea* L. (Lesser Stitchwort), White Clover, *Achillea millefolium* L. (Yarrow), *Vicia* sp. (a vetch), *Hypericum perforatum* L. (St. Johnswort), *Spiranthes vernalis* Engelmann & Gray (Spring Lady's Tresses), abundant *Solidago* (especially *S. juncea* Aiton [Early Goldenrod] and Rough-stemmed Goldenrod), Grass-leaved Goldenrod, and *Symphyotrichum racemosum* (Elliott) Nesom (Small White Aster). Carter Preserve: *Kalmia* spp. (laurels), Black Huckleberry, *Lysimachia quadrifolia* L. (Whorled Loosestrife), *Rubus hispidus* L. (Swamp Dewberry), goldenrods (especially *S. odora* Aiton [Sweet Goldenrod]), and Small White Aster.

We collected a total of 56 netting samples from 24 flowering species, with most bees collected at *Solidago sempervirens* L. (Seaside Goldenrod) and other golden-

Table 2, continued.

Family/species	Great Swamp bee bowls	Carter Preserve bee bowls
Osmia collinsiae Robertson	1	0
Osmia inspergens Lovell and Cockerell	0	1
Osmia pumila Cresson	11	2
Apidae		
Apis mellifera L.	2	0
Bombus fervidus Fabricius	0	1
Bombus griseocollis De Geer	3	0
Bombus impatiens Cresson	5	2
Bombus vagans Smith	2	0
Ceratina calcarata Robertson	43	4
Ceratina dupla Say	19	6
Ceratina mikmaqi Rehan and Sheffield	9	6
Ceratina sp.	7	3
Melissodes bimaculatus (Lepeletier)	0	1
Nomada articulata Smith	1	5
Nomada sp. (bidentate group)	1	0
Nomada cressonii Robertson	3	0
Nomada imbricata Scopoli*	1	0
Nomada maculata Cresson	2	0
Nomada pygmaea Cresson	3	1
Nomada sayi/illinoensis Robertson	3	0
Nomada sp.	0	7
Peponapis pruinosa (Say)	1	2
Total individuals	448	262
Total species	46	45

rods, *Limonium carolinianum* (Walter) Britton (Sea-lavender), Wild Radish, Beach Pea, *Ampelopsis brevipedunculata* (Maximovich) Trautvetter (Porcelain Vine), and *Cirsium vulgare* (Savi) Tenore (Bull Thistle).

The bee fauna collected in bee bowls at Napatree differed substantially in taxonomic composition from that at the inland sites ($\chi^2 = 530.3$, df = 9, $P < 0.0001$). Estimates of species diversity, richness, and evenness tended to be higher at inland than at Napatree transects (Table 3). A CCA shows Napatree samples distinctly clumped toward the left along the first (horizontal) axis, with inland samples to the right (Fig. 3). Inland samples were scattered far more broadly along the second

Table 3. Species diversity, richness, and evenness at the bee-bowl transects. Total number of species at each bee-bowl transect estimated using SPECRICH (https://www.mbr-pwrc.usgs.gov/software/specrich.html).

	Napatree Site 1	Napatree Site 2	Great Swamp	Carter Preserve
Diversity (Shannon–Weiner index)	0.82	0.75	1.23	1.23
Species richness (total species collected)	22	26	46	45
Estimate of total number of species (± SE)	49.8 (± 10.37)	34.0 (± 4.00)	111.4 (± 22.15)	59.0 (± 5.29)
Evenness (1 - Berger–Parker index)	0.62	0.51	0.79	0.67

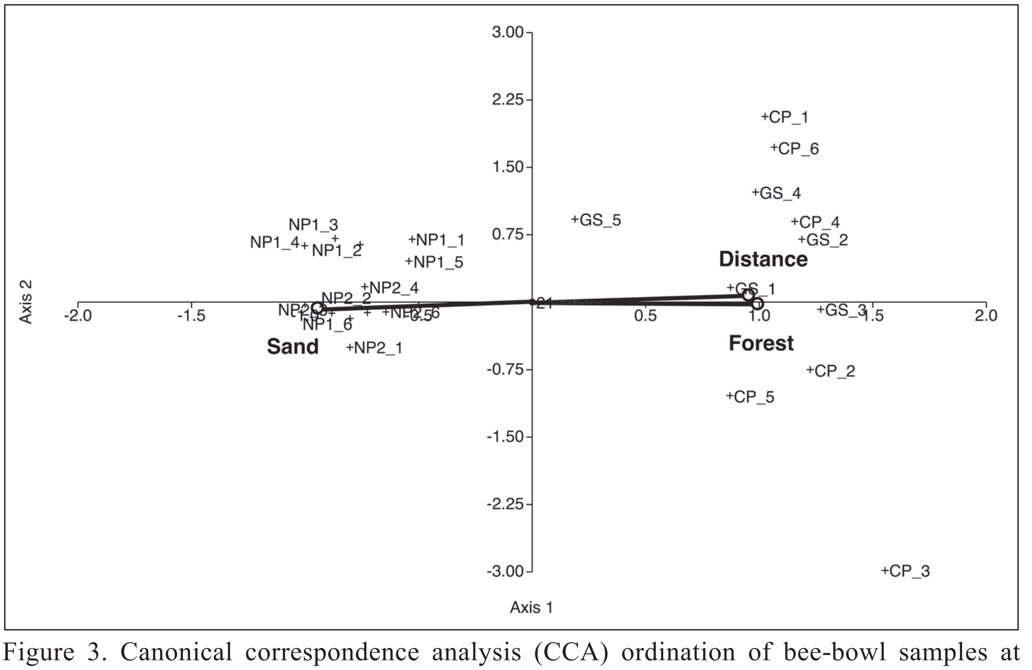

Figure 3. Canonical correspondence analysis (CCA) ordination of bee-bowl samples at Napatree sites and inland sites. "Sand" indicates the percent of sandy soil composition, "Distance" indicates the distance to the coast, "Forest" indicates the percent of forest cover. NP1 indicates Napatree Site 1, NP2 indicates Napatree Site 2, GS indicates Great Swamp and CP indicates Carter Preserve. A number indicating the sampling date session follows each site.

(vertical) axis than the Napatree samples. Each data point in Figure 3 represents a sample for a single site on a single day (except that no bees were caught at Napatree Site 2 on 23 August). The vectors for all of the environmental variables (soil type, forest cover, and distance from the coast) fell along the horizontal axis, suggesting that these environmental factors were associated with the difference in bee communities between coastal and inland sites.

Bee phenologies at Napatree Point and at inland sites displayed the greatest numbers of individuals and species in the spring (Fig. 4), but they differed in several details (individuals: $\chi^2 = 187.9$, df = 5, $P < 0.0001$; species: $\chi^2 = 16.5$, df = 5, $P = 0.0056$). Bee numbers apparently declined through the season, but by early June, individual numbers decreased sharply at Napatree but more gradually at the inland

Figure 4. Phenology of bee-bowl samples at Napatree sites compared to inland sites.

sites. Late in the season, individual numbers dropped inland but rose at Napatree Point. Species numbers displayed similar patterns at Napatree Point and inland sites (with inland species numbers being higher). However, the number of species at Napatree increased in the September samples.

Common species (those with greater than 45 individuals collected) were most often collected early in the season at Napatree Point (Fig. 5). *Ceratina dupla*, a twig-nesting species, was the most abundant species at Napatree early in the season, and numbers again increased slightly at the end of the season. The most

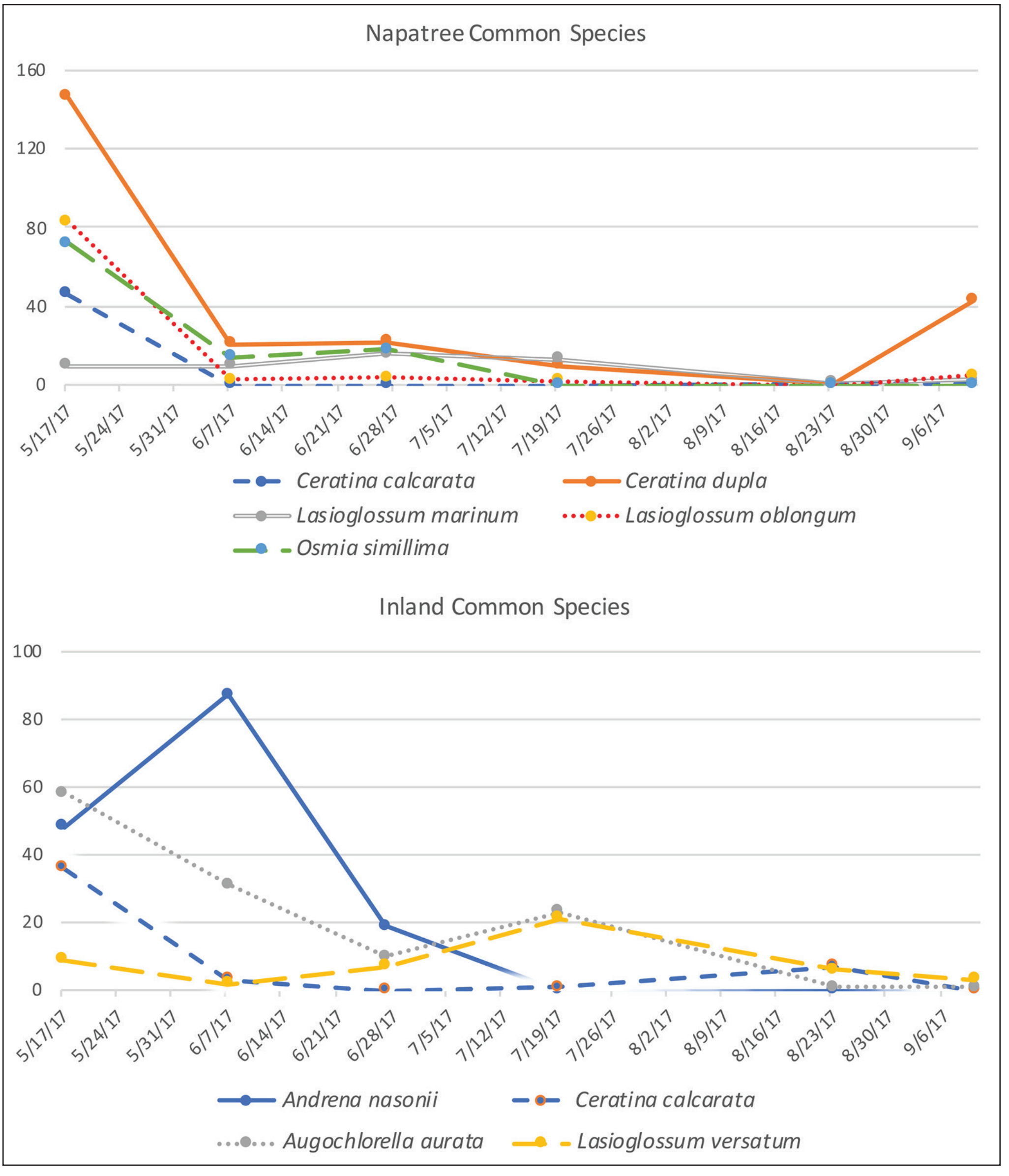

Figure 5. Total number of individuals of common species captured in bee bowls at Napatree Point and at inland sites.

commonly collected species at the inland sites was the soil-nesting *Andrena nasonii*, which peaked in early June. There was also a small July increase in numbers of the social, soil-nesting halictids *Augochlorella aurata* and *Lasioglossum versatum* at the inland sites.

The bee taxa detected by netted samples differed substantially from those from bee-bowl samples at Napatree Point ($\chi^2 = 338.2$, df = 7, $P < 0.0001$). Bee-bowl samples were biased toward smaller bees (Fig. 6), capturing a significantly lower proportion of large bees than did netting samples ($\chi^2 = 36.6$, df = 1, $P < 0.0001$). The most commonly netted species included bees that were not found in bee-bowl samples at Napatree, including *Perdita octomaculata* and larger bees such as *Bombus impatiens* and *B. vagans*, as well as some species that were also common in bee-bowl samples, such as the coastal dune species *Lasioglossum marinum* (Fig. 5). We collected no netting samples in May 2017 because there were no flowering species at anthesis in the open secondary dune habitat where we placed the bee-bowl transects. However, site visits in May 2018 revealed several flowering herbs in the woods and thicket habitats surrounding the fort at the western end of Napatree Point, including *Cardamine parviflora* L. (Sand Bittercress), *Arabidopsis thaliana* (L.) Heynhold (Thale Cress), *Barbarea vulgaris* Aiton (Bittercress), *Galium aparine* L. (Cleavers), and Dandelion. In netted samples at Napatree, the Shannon–Weiner index value was 1.27, species richness was 33, and evenness was 0.86. For comparison, the combined bee-bowl samples at Napatree had a Shannon–Weiner index value of 0.916, species richness of 35, and evenness of 0.63.

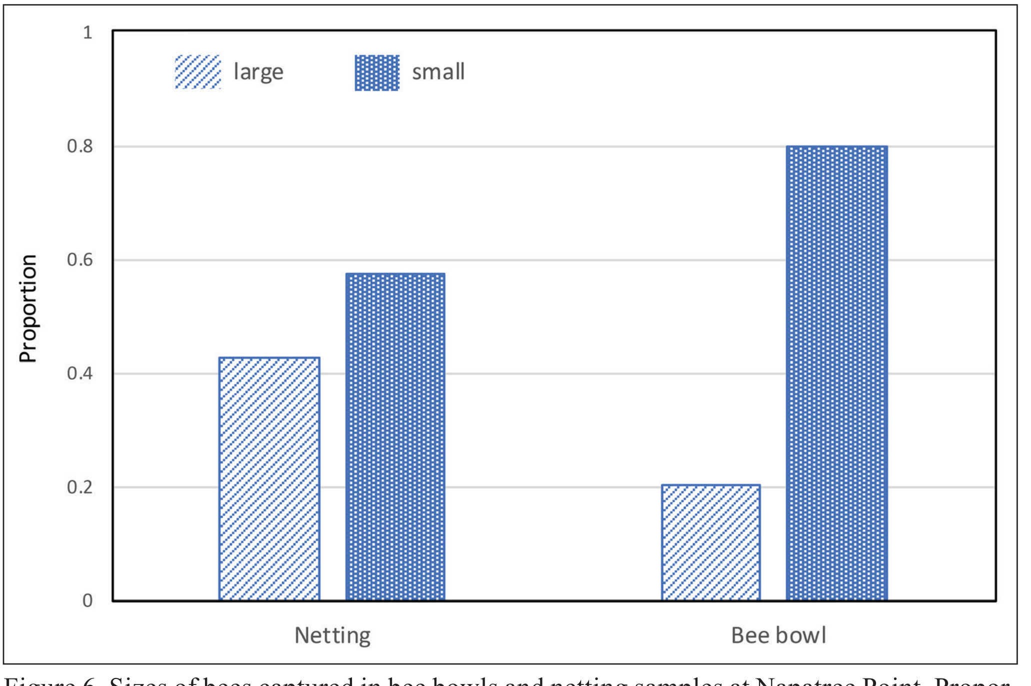

Figure 6. Sizes of bees captured in bee bowls and netting samples at Napatree Point. Proportion of all captures that were large (≥10 mm length) vs. small (<10 mm length) collected by the 2 sampling methods.

Discussion

Based on our samples, the bee fauna at Napatree differred from that of the 2 inland sites in several ways. Many species were shared between Napatree Point and the 2 inland sites (Tables 1, 2), but species composition of the Napatree bee fauna was clearly distinct from those of the 2 inland sites (Fig. 3). The horizontal axis of the CCA, which reflects similarities of species composition among samples, is essentially an axis of distance from the coast, which is characterized by sandier soils and less forest cover at Napatree than inland, with associated differences in the bee faunas.

Species diversity (as measured by the Shannon–Weiner index), species richness, and evenness, tended to be lower at Napatree than at the inland sites, but there were more novel species at Napatree, including 4 oligolectic native bee species—*Colletes simulans, Andrena asteris, Andrena hirticincta, Perdita octomaculata*—that were not present at the inland sites (Tables 1, 2). *Lasioglossum marinum* and *L. oblongum*, though both considered uncommon bees (Gibbs 2011), were abundant at Napatree Point. Both species are also abundant on Grass Island, CT, another coastal site (Zarillo and Stoner, in press).

Previous bee collections at Great Gull Island and Fishers Island, RI (coastal habitats within 5–23 km [3–14 mi] of Napatree Point) did not yield *L. oblongum* (Ascher et al. 2014). However, some of those surveys were conducted before the name *L. oblongum* was in standard usage, starting ca. 1960 (Gibbs 2010, Mitchell 1960); thus, *L. oblongum* might have been present but not recognized taxonomically in early records. The most recent survey at those islands was in 1976 (Ascher et al. 2014). Pan-trapping became a popular bee-sampling method starting in the 1990s (Cane et al. 2000), and the earlier surveys at Great Gull Island and Fishers Island presumably used netting to sample bees and might have under-sampled smaller-sized bees such as *L. oblongum*. More recent samples from coastal northeastern sites used bee bowls and collected *L. oblongum* (Goldstein and Ascher 2016; Rykken and Farrell 2013; Zarillo and Stoner, in press).

Bee phenology was similar at Napatree and inland sites in general form, with some interesting differences. At Napatree, the numbers of individuals and species captured increased during the last bee-bowl sampling in September, whereas the inland sites showed a decline in numbers on the same date. The number of *Ceratina dupla* captured on Napatree increased in September, possibly because *C. dupla* can be bivoltine at some sites, creating a second brood in later summer (Vickruck et al. 2011). Foraging by late season females and males before overwintering might also be possible.

The most common coastal and inland bee species differed in nest-site associations. Abundant species at Napatree Point included *L. marinum*, which is a coastal dune species, and *L. oblongum*, which nests in rotting logs (Sakagami and Michener 1962) and has been collected from under the bark of fallen logs (Gibbs 2011). This species has been found in forests (Gibbs 2010, 2011; Ulyshen et al. 2010) as well as coastal areas (Zarillo and Stoner, in press), including Gardiners Island, in New York, about 29 km (18 miles) from Napatree Point (Ascher et al. 2014), and on Martha's Vineyard, MA (Goldstein and Ascher 2016). *Osmia simillima*, another common spring bee at Napatree, nests in twigs and cavities, and could presumably find appropriate nesting sites in the woods and possibly in the crumbling walls of the fort. Interestingly, other samples at coastal sites collected relatively few individuals of this species (Ascher et al. 2014; Goldstein and Ascher 2016; Rykken and Farrell 2013; Stage 2009; Zarillo and Stoner, in press). This species has been reported to nest in *Quercus* (oak) apple-galls (Cane et al. 2007) and wood buried in a dune area (Scott 2017). We did not see oaks on Napatree, but driftwood and pine wood are common. In general, *Osmia* are cavity nesters and can use a wide variety of substrates (Bosch 2001). *Bombus* spp. typically nest in larger hollows, including cavities under rock piles (Hatfield et al. 2012). On Napatree, *O. simillima* and the *Bombus* species may have utilized crevices and hollows at the abandoned fort structure located at the west end of Napatree. Alternatively, these strong-flying species could have flown in from nearby mainland nesting sites. *Osmia* species can fly up to 500 m (Biddinger et al. 2013) and *Bombus* species can fly up to several kilometers (Rao and Strange 2012). The sand-nesting species *Perdita octomaculata* was also common at Napatree but not inland, although this species can occur at inland sites with sandy soil (Eickwort 1977).

Abundant inland species included *Andrena nasonii, Augochlorella aurata,* and *Lasioglossum versatum*, which are all ground-nesting bees (Michener 1966, Renauld et al. 2016, Richards et al. 2011, Selfridge et al. 2017). *Ceratina calcarata* was among the common bees found both at coastal Napatree and inland sites. This species is a twig nester that uses brambles, *Rhus* (sumac), and other plants with soft pith for nesting (Ginsberg 1983, Vickruck et al. 2011); these are common plants at the inland sites. *Rhus copallinum* L. (Poison Sumac) has been reported to grow on the west and east end of Napatree (H. Leeson, Rhode Island Natural History Survey, Kingston, RI, pers. comm.), and we observed apparent *Ceratina* nests in twigs of other shrub species that had been clipped or had been broken or browsed by deer.

Bee species collected in netting samples differed substantially from bee-bowl samples at Napatree Point. The differences in phenology may partly have resulted from the relatively late start of netting sampling (about 2 weeks after bee-bowl samples) because we did not detect any flowering activity in the open dune habitats when we took the first bee-bowl sample in May. Site visits in 2018 revealed several herbaceous species flowering in the woods around the fort, where we had not sampled in 2017. The end of the season showed a difference in phenology as well, in that *Bombus* captures increased through the season in netting samples, as is typical for bumble bees (Plowright and Laverty 1984), but they were not captured in the bee bowls. *Bombus* can thermoregulate (Heinrich 1972), and thus can forage at lower fall temperatures than other bees. Many of these late-summer *Bombus* specimens were males or gynes.

Bee size is another factor in sampling effectiveness (Fig. 6). The most common species collected in bee bowls at Napatree included the diminutive *Lasioglossum* and *Ceratina* bees. Netting samples caught high numbers of *L. marinum* but did not catch other bees commonly collected in bee bowls (Table 1). In general, bee bowls catch smaller bees that can be missed by netting (Droege et al. 2010, Selfridge et al. 2017, Westphal et al. 2008). We captured numerous *B. impatiens* and *B. vagans* and smaller numbers of *B. griseocollis* and *Xylocopa virginica* in netting samples, but captured none of these species in bee bowls, likely because these larger bees could climb out of the bee bowls (A. Rothwell, pers. observ.; Westphal et al. 2008).

We captured several *Perdita octomaculata* by netting, while our bee-bowl samples never included this species (Table 1). *Perdita octomaculata* is a small bee which would presumably be effectively sampled by bee bowls. This species emerges and forages on goldenrods late in the summer (Eickwort 1977, Ginsberg 1983), and we netted this bee on 25 September. The last bee-bowl sample was on 10 September, which may have been too early to catch the species. Furthermore, the 2 locations where *P. octomaculata* were caught were at least 44 m from the closest bee-bowl transect (Napatree Site 2), and *P. octomaculata* might have foraged for its preferred host plants, goldenrods, at sites distant from the bee-bowl transect. *Perdita octomaculata* specifically nests in sandy slopes, which is the area where they were netted, and the bees may not have foraged in more distant areas.

Some investigators have reported that results from bee bowls and bee netting were highly correlated (Richards et al. 2011), but there were marked differences in our study. Richards et al. (2011) conducted timed walking samples using sweep nets in a figure-eight motion to collect insects from vegetation, flowers, etc., which differs substantially from our more traditional method of focusing on a single flowering patch for a period of time. The different results between our bee bowl and netting samples suggest that the focused netting method we used helped capture a distinct subset of the bee fauna that bee-bowl sampling missed. We limited our netting collections at flower patches to 15 individuals per sample, which undoubtedly affected the numbers of selected species captured. Netting samples were taken through all open areas of Napatree and thus were not restricted to just 2 transect sites, as were the bee-bowl samples. Therefore, our results suggest that, while repeated samples using objective methods such as bee bowls have great value for comparative samples and monitoring programs, multiple sampling methods provide a more complete view of a local bee fauna for survey purposes.

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