

Taxonomic and Behavioral Composition of an Island Fauna: A Survey of Bees (Hymenoptera: Apoidea: Anthophila) on Martha's Vineyard, Massachusetts

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**TAXONOMIC AND BEHAVIORAL COMPOSITION OF AN ISLAND
FAUNA: A SURVEY OF BEES (HYMENOPTERA: APOIDEA:
ANTHOPHILA) ON MARTHA'S VINEYARD, MASSACHUSETTS**

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Abstract.—An intensive survey of bees (Hymenoptera: Apoidea: Anthophila) on Martha's Vineyard, the largest offshore island in Massachusetts, USA, was conducted mostly from 2010–2011 at over 60 sites across the island's six towns. From over 14,500 specimens collected, processed and databased, we document 182 bee species in 31 genera. Historical records of an additional four species were identified from museum collections. Most bee specimens were collected from trap lines of bee bowls deployed to maximize coverage of habitats, and many others by direct collection targeting known host plants of pollen specialists (oligoleges) and their cleptoparasites. The island's fauna is more species-rich and includes a diverse assemblage of sand-nesting specialists (psammophiles) and pollen specialists with broader botanical associations than the recorded faunas of other regional islands. Notable finds include the first records of *Anthophora walshii* Cresson from the northeastern USA since the 1970s; two oligoleges of Maleberry *Lyonia ligustrina* (L.), *Colletes productus* Robertson and *Melitta melittoides* (Viereck); the parasitic *Nomada rodecki* Mitchell, newly associated with *M. melittoides* and newly placed within the *Nomada basalis* species group (previously associated with *Melitta* in Europe); and two species (in addition to *N. rodecki*) newly recorded from Massachusetts: *Andrena neonana* Viereck and *Nomada xanthura* Cockerell. We note 23 species not recorded from other Massachusetts offshore islands, of which 19 were unrecorded from southeastern Massachusetts. Two bumble bee species in the nominate subgenus *Bombus*, *B. affinis* Cresson and *B. terricola* Kirby, that have undergone regional declines were recorded historically from Martha's Vineyard and nearby islands but not found in this survey. Tables and figures are provided to summarize the phenology, taxonomic and behavioral composition of the island's bee fauna, which are discussed with reference to the faunas of Massachusetts, New York, and comparable mainland and island sites. As with other studies employing extensive bee bowl-trapping we found the most numerous species caught to be eusocial halictines. Our results underscore the role of maritime habitats underlain by sandy soils in sustaining regional diversity of bees in addition to Lepidoptera and other well-documented insect groups. Collection of a large proportion of pollen specialists and cleptoparasitic species from one but not both sampling years reinforces the need for multi-year studies of bee faunas.

Key Words: native bees, sandplain, Martha's Vineyard, sandplain grassland, pitch pine-scrub oak barrens, invertebrate conservation, pollinator communities, *Nomada rodecki*

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Our understanding of the more than 3500 described bee species found in America North of Mexico (Hurd 1979; Ascher and Pickering 2015) has improved following recent taxonomic revisions (e.g., Droege et al. 2010; Gibbs 2010; 2011; Gibbs et al. 2013) and regional inventory efforts, the latter inspired in part by the recognized need to evaluate the status of pollinating insects (National Research Council 2007). Georeferenced specimen records and images of living and pinned bees and their diagnostic characters are increasingly disseminated through biodiversity portals such as Discover Life (www.discoverlife.org) and are being used to both to explore declines of bees, notably bumblebees and their social parasites (Cameron et al. 2011), and to evaluate the persistence of bee faunas (Colla et al. 2012a; Bartomeus et al. 2013) and their response to climate change (Bartomeus et al. 2011). The limited evidence for taxonomically pervasive declines or phenological mismatches between hosts and pollinators may alleviate concerns about a general pollinator crisis (Potts et al. 2010; Tylianakis 2013) and dampen some of the more alarming reports of local bee "extinctions" (Burkle et al. 2013). However, assessments of compositional change in bee faunas (e.g., Gixti and Packer 2006; Burkle et al. 2013, cf. Marlin and LaBerge 2001; Gardner and Spivak 2014) necessarily vary with scale and availability of historical data, and few endeavors adequate to the task of sampling and identifying oligolectic bees and associated bee cleptoparasites have been undertaken.

Since available baseline data are often insufficient to evaluate putative declines of bees specifically or of pollinators in general (National Research Council 2007), faunal surveys of islands and other discrete areas known to serve as refugia for invertebrates are particularly relevant.

The offshore islands of Massachusetts—Martha's Vineyard, Nantucket, and the Elizabeth Islands—belong to the terminal moraine archipelagic region known as the Outer Lands which also includes Long Island, New York (NY) and Block Island, Rhode Island (RI). Entomological studies of the Outer Lands have included bees as part of more general faunistic inventories (Leonard 1928; Johnson 1930), as did Proctor's (1946) study further north on Mount Desert Island, Maine. Johnson (1930) and Jones and Kimball (1943), respectively, published treatments of the Nantucket insect fauna and of the lepidopteran fauna of both Nantucket and Martha's Vineyard (MV). Subsequent and ongoing work on the Massachusetts offshore islands has included treatments of ground beetles (Carabidae) and ants (Formicidae) on Nantucket (Purinton 1996; Ellison 2012), aquatic macroinvertebrates on Martha's Vineyard (Whitmore 2008), scarab beetles (Scarabaeidae) (Goldstein and Simmons 2002), lepidopteran faunas and assessments of faunal change (Goldstein et al. 2015 and unpubl.; Mello, unpubl.). For entomologists, the Massachusetts offshore islands are of interest due to their increasingly well-documented insect diversity, with recent studies (e.g. Ellison

2012) reinforcing earlier observations of unusually high diversity (e.g. Jones and Kimball 1943) and suggestions that the islands have served as refugia for threatened insects and natural communities otherwise in decline regionally (Dean 2000; Goldstein 1997). Such observations have further spawned both autecological and genetic studies (Goldstein 2010; Goldstein and DeSalle 2003) of moths and beetles extirpated from mainland New England. Martha's Vineyard supports the highest documented concentration of regionally threatened invertebrates in New England (Massachusetts Natural Heritage and Endangered Species Program database; Goldstein et al., in prep.), variously attributed to the persistence of species that are either biogeographically relictual species or lost elsewhere to anthropogenic habitat alteration and other systemic impacts such as the establishment of introduced parasitoids (Goldstein et al. 2015). Although the islands have served to buffer against certain threats, significant landscape-level changes (Dunwiddie 1994; Foster and Motzkin 1999; Motzkin and Foster 2002) and concomitant faunal turnover during the last century have been documented on both Martha's Vineyard and Nantucket islands (Goldstein, unpub. data; Mello, unpub. data), so these areas serve as natural laboratories for exploring recent faunal change.

The present study complements other ongoing studies of insects associated with New England sandplains, and of bees from these and other habitats elsewhere in New England, New York, New Jersey and Maritime Canada. Its primary goals include: (1) documenting and characterizing the bee fauna of Massachusetts' largest offshore island; (2) comparing the fauna of Martha's Vineyard with data available for other sites in the context of regional data (e.g. for Massachusetts) and;

(3) supplementing information on life histories, floral host-parasite associations, and habitat preferences of regional bees. Georeferenced specimen records assembled for this study contribute to an ongoing collaborative database of bee pollinators that is mapped by Discover Life (www.discoverlife.org) and displayed on the Encyclopedia of Life (www.eol.org). These data have recently been further shared with www.idigbio.org and will soon be publicly available there. They are intended in part to inform sustainable local agriculture and have served regional status assessments of bees and their response to climate change (Bartomeus et al. 2011; 2013). A secondary goal of this study is to expand our understanding of the coastal aculeate Hymenoptera (Goldstein et al. in prep.) by processing and determining wasps captured incidentally in the course of bee trapping efforts.

STUDY SITE

Situated approximately 3.5 miles off Cape Cod and 15 miles landward of Nantucket, Martha's Vineyard is the largest of 16 named islands off Massachusetts' southeastern coast and the third largest on the East Coast of the United States following Long Island (New York) and Mount Desert Island (Maine). Including its brackish and freshwater ponds, the island is approximately 100 square miles in area (~64,000 acres, 25,900 ha), with a land area of approximately 87.48 square miles (226.6 sq. km). Martha's Vineyard comprises six towns, in part: Vineyard Haven (a.k.a. Tisbury), Oak Bluffs, Edgartown, West Tisbury, Chilmark, and Aquinnah, formerly Gay Head. The uninhabited neighboring island of Noman's Land to the south falls within the town of Chilmark, whereas the island of Chappaquiddick—periodically separated from Martha's Vineyard—is

formally included within Edgartown. Together with the town of Gosnold, which is made up of the Elizabeth Islands (from the west: Cuttyhunk, Penikese, Nashawena, Pasque, Naushon, Uncatena, Vechatimest, Nonamesset and the small Weepecket Islands), these municipalities comprise the County of Dukes County (Fig. 1).

Martha's Vineyard and its neighboring islands are above-water remnants of an extensive coastal plain. Its morainal backbone was deposited at the junction of two glacial lobes intersecting during the glacial maximum of the Laurentide Ice sheet approximately 18,000 years ago: the Cape Cod Bay lobe to the east and the Buzzards Bay lobe to the west (Chamberlain 1964; Oldale 2001). The spring sapping of meltwater streams generated outwash sediments that comprise the central and southeastern portion of the island (Fig. 2). Terminologically, we emphasize the distinction between coastal plain, sandplain, and outwash plain. Strictly speaking, geologically, "coastal plain" refers to a geo-regional feature that is now largely submerged, and whose only above-water remnants in the region are formations on the western end of Martha's Vineyard (Aquinnah). "Sandplain" refers to a narrow range of edaphic conditions characterized by sandy, well-drained soils, including but not necessarily limited to coastal soils of glacial origins underlying any of a range of specific, overlapping plant communities. These include sandplain grasslands, coastal heathlands, and pitch pine/scrub oak barrens and shrublands. "Outwash plain" refers to a geological class of sandplain overlain by sediments derived from glacial outwash (Fig. 2), as opposed to dry lake beds, for example. None of these terms are mutually exclusive. Ecologically, more than 40 terrestrial, palustrine, and estuarine communities are represented on Martha's Vineyard (Swain and

Kearsley 2000). The island's terminal moraine supports an array of kettle ponds, bogs, fens, highbush blueberry thickets, woodland vernal pools and other wetlands, some with characteristic assemblages of Lepidoptera. Palustrine habitats include shrub swamps and coastal interdunal marsh communities, sea-level fens; estuarine communities such as salt and brackish flats, marshes, and tidal swamps may be among those less likely to support diverse bee communities.

Among the more conspicuous terrestrial communities are dry sandplain habitats located on the Island's central outwash plain. In addition to northeastern pitch pine-scrub oak barrens, of which Martha's Vineyard supports one of the most extensive and intact concentrations in New England, this area supports a mosaic of natural communities, some considered globally rare: sandplain and cultural grasslands, coastal heathlands, sandplain maritime and scrub oak shrublands, and mixed oak and oak-hickory forest. The land use history of Martha's Vineyard, like that of Nantucket and the Elizabeth Islands, is complex, involving conversion to agriculture followed by shrinkage of grass-dominated habitat and, most recently, limited restoration of grasslands and related habitats. Several authors (e.g. Motzkin and Foster 2002; Foster and Motzkin 2003) have been careful to avoid oversimplifying sandplain habitats as products of linear succession or in static terms heavily focused on grasslands. Following Motzkin et al. (2002), we stress the dynamic, disturbance-dependent nature of sandplain communities and the fact that some of this mosaic appears to have been climatically or abiotically mediated, through extensive fire histories, wind-borne salt spray, and localized cold pockets. Such "frost bottoms"—dry former meltwater channels that undergo summer freezes—support

high concentrations of threatened plants and animals (Massachusetts Natural Heritage and Endangered Species Program database, Westborough, MA) and have been identified as refugia for regionally rare Lepidoptera whose occurrences pre-dated the isolation of the islands (Goldstein 1997).

Aside from pollen hosts, the most conspicuous resource upon which bees specialize is nesting substrate. Sandy soils and in particular those associated with barrens and other sandplain communities dominating the large Martha's Vineyard outwash plain, support a number of soil specialist insects. Bried and Dillon (2012) report diverse bees from scrub oak patches in the Albany Pine Bush Preserve, including sand specialists and other species with narrow distributions. Although many other studies point to specific associations of bees with sandy substrates (e.g. Pearson 1933; Wilson et al. 2008; Droege et al. 2009; Arduser 2010; Hall and Ascher 2010; Orr, 2010; Grundel et al. 2011), our understanding of the precise edaphic requirements of these bees is limited.

Biogeographically, Martha's Vineyard has been characterized as occupying a transitional zone between northern and southern biotas (Whitmore 2008, citing Jones and Kimball 1943). Both Johnson (1930) and Jones and Kimball (1943) discuss the insect fauna's austral component, and emphasized the cohort of lepidopteran species whose northern limits coincide approximately with the southernmost extent of the Laurentide ice sheet. Many such species are regionally restricted to pitch pine-scrub oak barrens. More recent work has revealed species with western as well as southern affinities, some of which are in turn affiliated with open, grassy shrublands, grasslands and heathlands. Metzler et al. (2005) characterize a number of prairie Lepidoptera as having

distributions consistent with a post-glacial colonization trajectory northward along the unsubmerged coastal plain terminus, and several moths exhibit disjunct eastern distributions confined to the coast from Florida northward to southern New Jersey, Long Island, and Massachusetts.

MATERIALS AND METHODS

Sampling.—Sampling in this study was conducted by hand-netting and bowl-trapping to maximize ecological and botanical coverage of the island. Efforts were concentrated in intact natural areas representing a range of soil and habitat types and botanical communities. A majority of sampling locations were characterized by carver soils overlaying the eastern moraine and much of the eastern outwash plain. Bees were collected by net on an ad hoc and opportunistic basis, targeting individual flower genera with known or suspected bee associates such as *Ame-lanchier*, *Aster*, *Baptisia*, *Ilex*, *Lyonia*, *Lysimachia*, *Malus*, *Prunus*, *Rhus*, *Salix*, *Solidago* sensu lato (including *Euthamia*), *Tephrosia*, and *Vaccinium*.

The protocol for “bee-bowling” involved 3.25 oz plastic soufflé or cole slaw cups, unpainted (white) and painted with two coats of either fluorescent blue or yellow, and filled with soapy water (water and liquid Blue Dawn™ dish soap). Cups were painted by hand using the pigments provided by Guerra Paints (New York, NY) as formulated by Droege et al. (2012). From the end of Season 1 (2010) onwards, additional painted and unpainted cups were purchased from New Horizons Supported Services, Upper Marlboro, Maryland. Trap-lines of 25–30 individual cups were laid out in the early morning, at ~5m intervals with colors alternating. These were initially deployed for 12–18 hours, but quickly modified to 48 hours to ensure diel

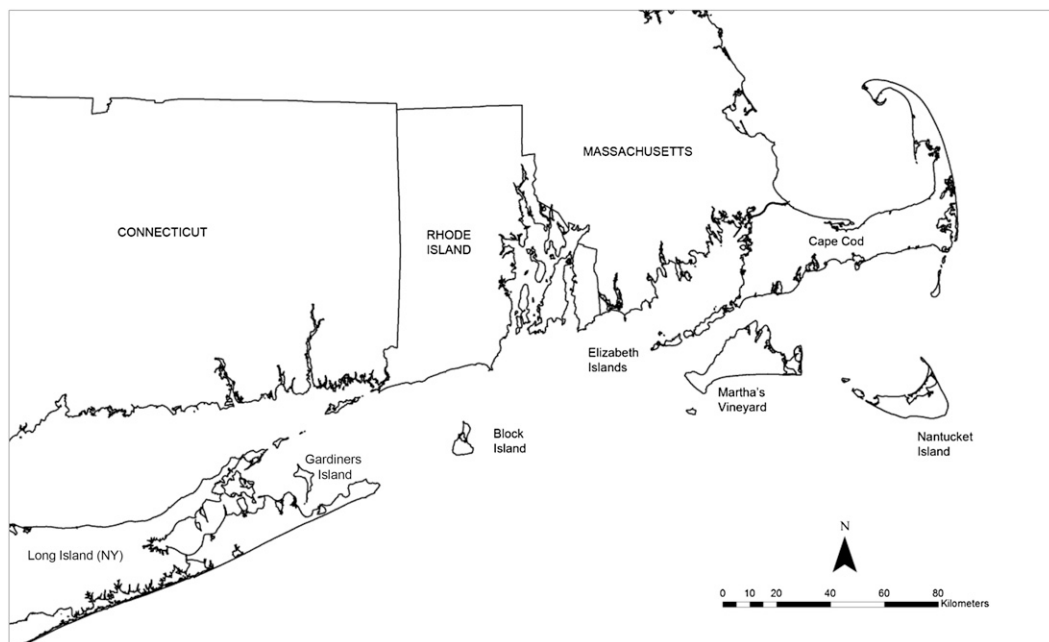


Fig. 1. Cape Cod, the Massachusetts offshore islands and the remaining Outer Lands, in part, including Block Island, RI, and Long Island, NY.

coverage, and following the observation that 48 hours seemed to be the maximum duration of exposure to avoid excessive evaporation without resorting to propylene glycol (Droege et al. 2012). Bees and by-catch were retrieved via hand-held strainers and stored in 70% ethanol in whirl-paks under refrigeration.

The bee-bowling regime involved over 300 trap-lines (~7,500 bee bowls): 145 trap-lines were deployed between 24 April and 23 September 2010 and 156 trap-lines between 8 April and 24 October 2011, spanning the entire bee flight season and distributed at 70 sites across the eastern and western moraines and outwash plain, across the primary soil types, and in all six towns on Martha's Vineyard (Fig. 3; Table 1). Limited additional collecting was undertaken in 2012. Hand-netting and approximately 85% of the trap-lines from 2010 and 80% of those from 2011 were undertaken by PZG, the trapping greatly supplemented by SRB,

TSH, LSR and other volunteer collaborators (see acknowledgments). Collecting efforts in 2012 were much more limited in scope and intensity, confined to 14 collecting days between April and September.

Specimen processing and databasing.—Netted specimens were processed fresh. Those from bowl traps, by far the majority of the material handled, were first rinsed and sorted into vials of 70% ethanol, then rinsed in water and 70% ethanol, followed by a spin (10 minutes) in 95% ethanol prior to being blow-dried for 5 minutes in a ball jar lidded with a wire mesh insert, following the procedures outlined in Droege et al. (2012). Depending on their size, specimens were allowed to air dry for anywhere from 1 hour (smaller specimens) to 24 hours or more in the case of the larger bees such as *Bombus* species. All specimen sorting, preparation, and labeling was performed by PZG. With few exceptions (e.g. many *Lasioglossom*), determinations of prepared specimens were made by JSA;

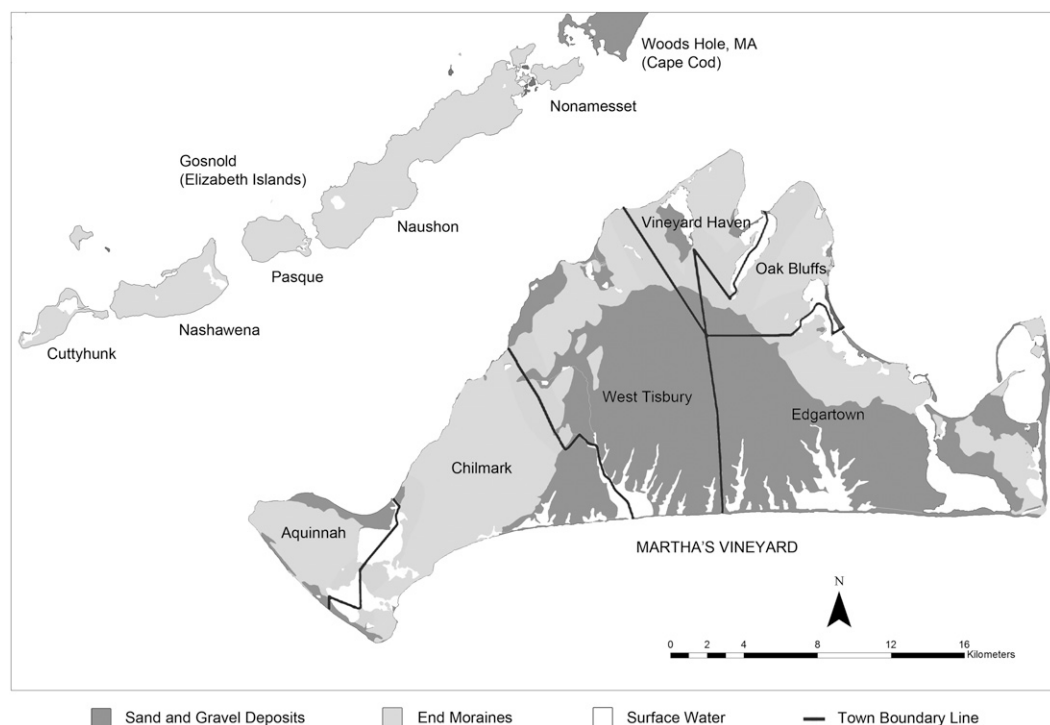


Fig. 2. Dukes County (excluding Nomans Land) in relation to the nearest point on Cape Cod at Woods Hole, MA: Martha's Vineyard and Gosnold (Elizabeth Islands) with indication of town boundary lines, sand and gravel deposits, end moraines, and surface water.

representative *Lasioglossum* (*Dialictus*) determined by J. Gibbs were used as reference. Most specimens were prepared and databased and no specimens were discarded. However, due to resource limitations a subset of specimens of the most abundant and readily identified species were left unprepared, including *Agapostemon* spp., *Augochlorella aurata* (Smith), *Bombus impatiens* Cresson, *Halictus ligatus* Say, and *Lasioglossum leucozonium* Schrank, and these unprepared specimens were not databased. Undetermined series were retained in fluid. Likewise, some prepared specimens of the more distinctive *Lasioglossum* species *L. versatum* (Robertson) and *L. leucomum* (Lovell) were not databased. These limitations in the dataset preclude rigorous quantitative assessment of bee abundance, but we nevertheless attempt to identify the most abundant species, recognizing that for

these the reported totals of specimen records in the database are in some cases lower than the actual numbers of specimens collected. Specimens were deposited in the collection of the American Museum of Natural History (AMNH), with the exception of a synoptic reference collection of databased material deposited at the Islands Regional Office of The Trustees of Reservations (TTOR) in Vineyard Haven, MA, as a resource available to biologists and land stewards. Most specimens were entered in the AMNH Division of Invertebrate Zoology Database (Schuh et al., 2010) using Arthropod Easy Capture software (2013, available as a downloadable file from the URL: <http://sourceforge.net/p/arthropodeasy> Version: 1.34) and an archival label affixed with matrix-encoded unique specimen identifiers. Specimens of wasps, i.e. aculeate Hymenoptera other

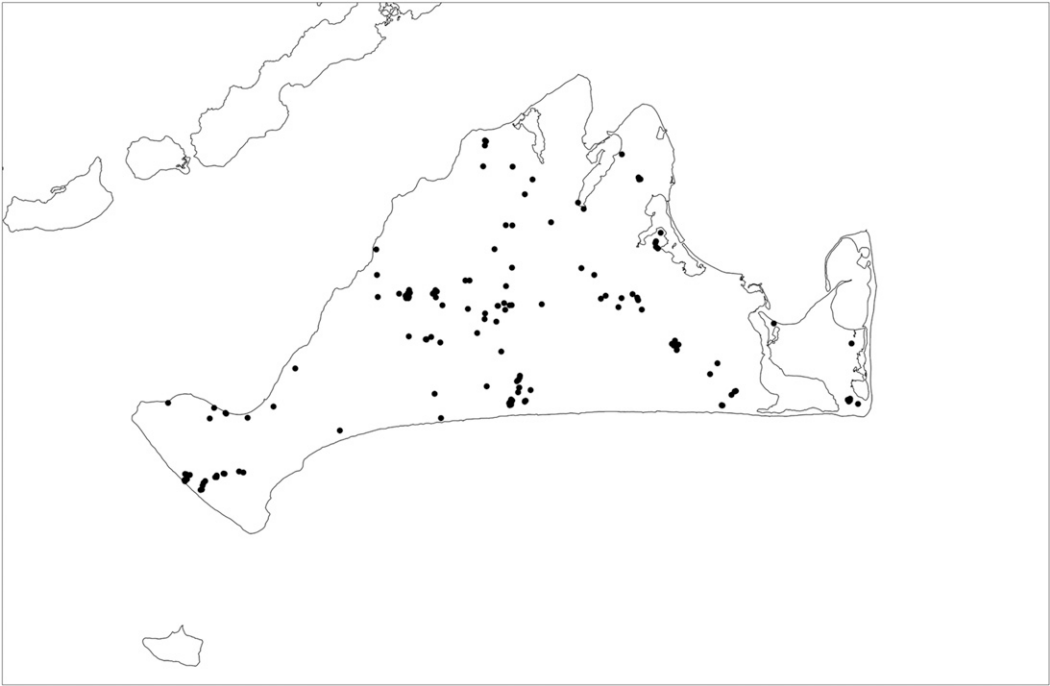


Fig. 3. Primary bee sampling locations on Martha's Vineyard based on georeferenced specimen records.

than bees, were also prepared in anticipation of generating a more expansive checklist, and relevant specialist-collaborators consulted for determinations.

Analysis and Summary Statistics.—A figure (Fig. 4) summarizing the flight seasons (span from earliest and latest collection events) of males and females of each bee species was generated from databased MV specimen records by S. Kornbluth (see Acknowledgments). Life history information and behaviors associated with sociality, nesting substrate, and hostplant choice are summarized by genus, and reflect available knowledge of North American bees (Hurd 1979; cf. Giles and Ascher 2006; Ascher et al. 2014). For reference, we evaluate the taxonomic and behavioral composition of the Martha's Vineyard fauna in comparison with recently published data from Black Rock Forest and Gardiners

Island, NY updated from the latter two studies and additional unpublished data compiled for Massachusetts by Ascher, Milam, Veit, and Goldstein (in prep.). These include the mainland southeastern Massachusetts (SEMA) counties of Barnstable (BA; = Cape Cod), Plymouth (PL), and Bristol (BR), and for Nantucket (NA; Goldstein et al. unpubl.) and the Elizabeth Islands (Stage 2009; Kent et al. 2013 and unpubl.; see Wagner and Ascher, 2014), which occupy Dukes County (DU) along with Martha's Vineyard. The recent study of Gardiners Island (Ascher et al. 2014) is referenced repeatedly due to its proximity, geological similarity of the island to MV, and consequent overlap in bee species. Noteworthy occurrences of species considered regionally rare, in decline, at or near the periphery of their ranges, or exhibiting unknown or poorly documented life histories were identified as such with

Table 1. Summary of bee trapping effort by town and numbers of trapping events per week on Martha's Vineyard from April – September 2010 and April – October 2011. Numbers in colored boxes (blue for 2010, red for 2011) indicate the number of trapping events (setting and retrieval of trap lines of 25 bee cups set out for 48 hours) per week. Sites, more than 50 in all, are grouped by town.: AQ = Aquinnah; CH = Chilmark; ED = Edgartown; OB = Oak Bluffs; VH = Vineyard Haven; WT = West Tisbury. This table illustrates only the coverage as reflected in the trapping schedule, and does not reflect additional ad hoc hand-netting efforts.

| Month: | April | | | May | | | June | | | July | | | August | | | Sept | | | Oct | | | Σ | Σ | | | |
|---------|-------|---|---|-----|----|---|------|----|---|------|----|---|--------|---|---|------|----|---|-----|----|---|---|---|----|------|------|
| Week: | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 2010 | 2011 |
| AQ 2010 | | | | | 5 | 2 | 2 | 4 | 3 | 3 | 3 | 3 | 5 | 2 | | | | | | | | | | | 29 | |
| AQ 2011 | | | | 4 | | 3 | 4 | | 3 | | | | 1 | | | | | | | | | | | | | 15 |
| CH 2010 | | | | | 1 | | 1 | 1 | | 3 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | | | | | | | 17 | |
| CH 2011 | 2 | | | 2 | | | 2 | | 1 | 2 | 4 | | | 2 | | 1 | | 2 | | 2 | 2 | | | | 22 | |
| ED 2010 | | | | 1 | 4 | 1 | 4 | 2 | 2 | 2 | 2 | 2 | 1 | 4 | 2 | 3 | 5 | 1 | 2 | 2 | | | | | 38 | |
| ED 2011 | | | | 3 | 1 | 5 | 6 | | 3 | 1 | 5 | 1 | 2 | 1 | 2 | | 1 | 2 | | | | | | | 33 | |
| OB 2010 | | | | | | | | 2 | 1 | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | 1 | | | | | | 8 | |
| OB 2011 | | | | | 1 | 2 | 1 | 2 | | 1 | | 1 | | 1 | | 2 | | 1 | | | | | | | 11 | |
| VH 2010 | | | | | 1 | | | 2 | 1 | 1 | | 1 | 1 | 1 | 1 | 1 | 1 | | 1 | | | | | 11 | | |
| VH 2011 | | | | 2 | 1 | | | | | | | | 1 | | | | | | | | | | | | 4 | |
| WT 2010 | | | | 3 | 3 | 1 | 4 | 4 | 1 | 2 | 3 | 2 | 2 | 1 | 3 | 1 | 4 | 4 | 1 | 3 | | | | | 42 | |
| WT 2011 | 2 | | | 6 | 3 | 1 | 4 | 4 | | 4 | | 9 | 3 | 7 | 3 | 5 | 2 | 7 | 4 | 1 | 3 | 4 | 1 | 2 | 71 | |
| Σ2010 | | | | 4 | 13 | 1 | 8 | 12 | 3 | 10 | 7 | 8 | 3 | 6 | 8 | 10 | 8 | 9 | 1 | 18 | 3 | 5 | 5 | 3 | 145 | |
| Σ2011 | 4 | | | 17 | 6 | 2 | 10 | 18 | 4 | 1 | 18 | 8 | 12 | 4 | 9 | 3 | 13 | 6 | 1 | 5 | 8 | | 3 | 4 | 156 | |

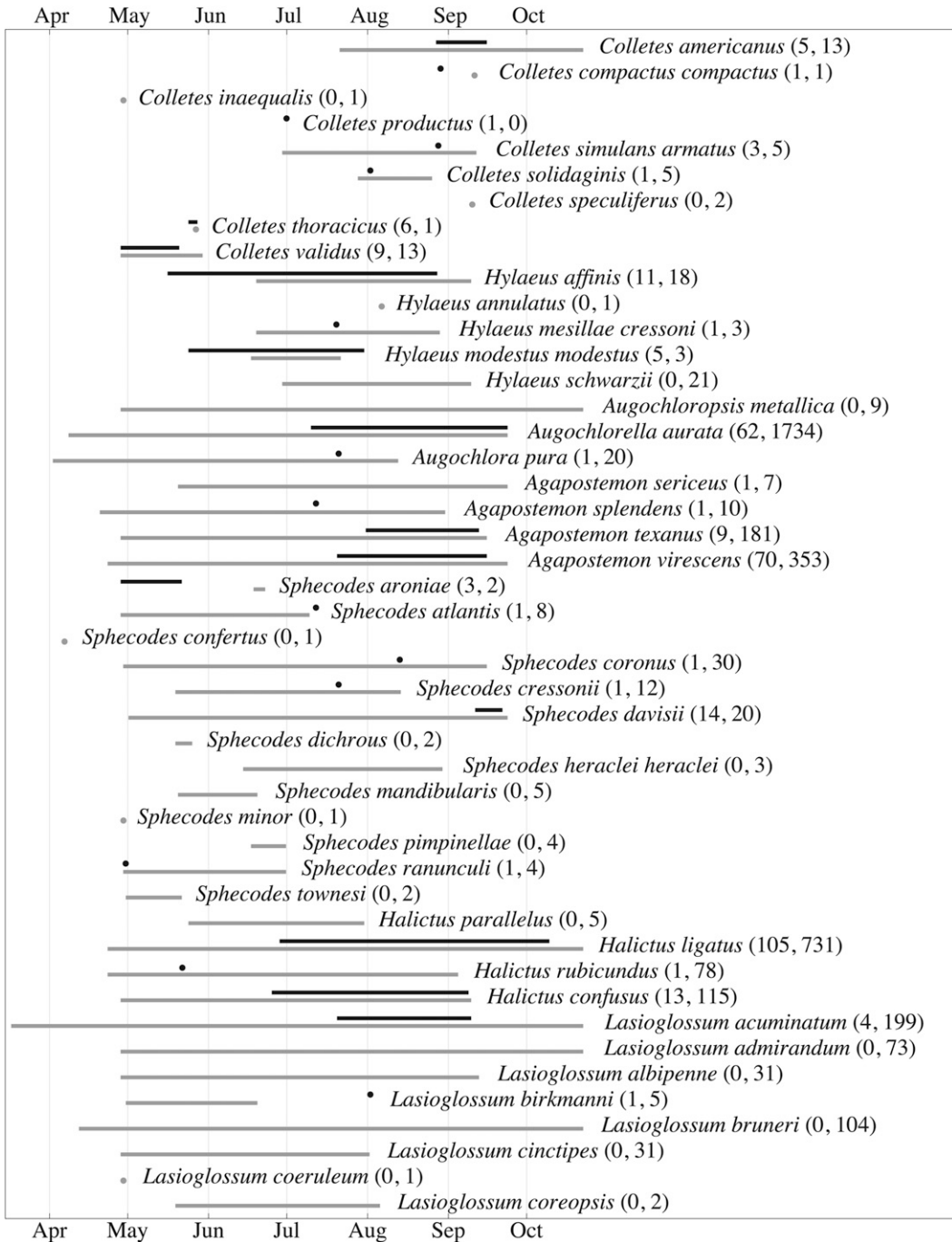


Fig. 4. Phenologies of 183 bee species inferred from databased specimens from Martha's Vineyard; does not include 3 of the 4 species known only from historical records as they were not databased or had incomplete collection data. Flight season span from earliest collection event to latest are given for males in black (above) and females in gray (below). Note that males of many solitary species (e.g., *Andrena*) are protandrous and have brief flight seasons, whereas in eusocial species only females are present in early spring and males fly only during summer-fall.

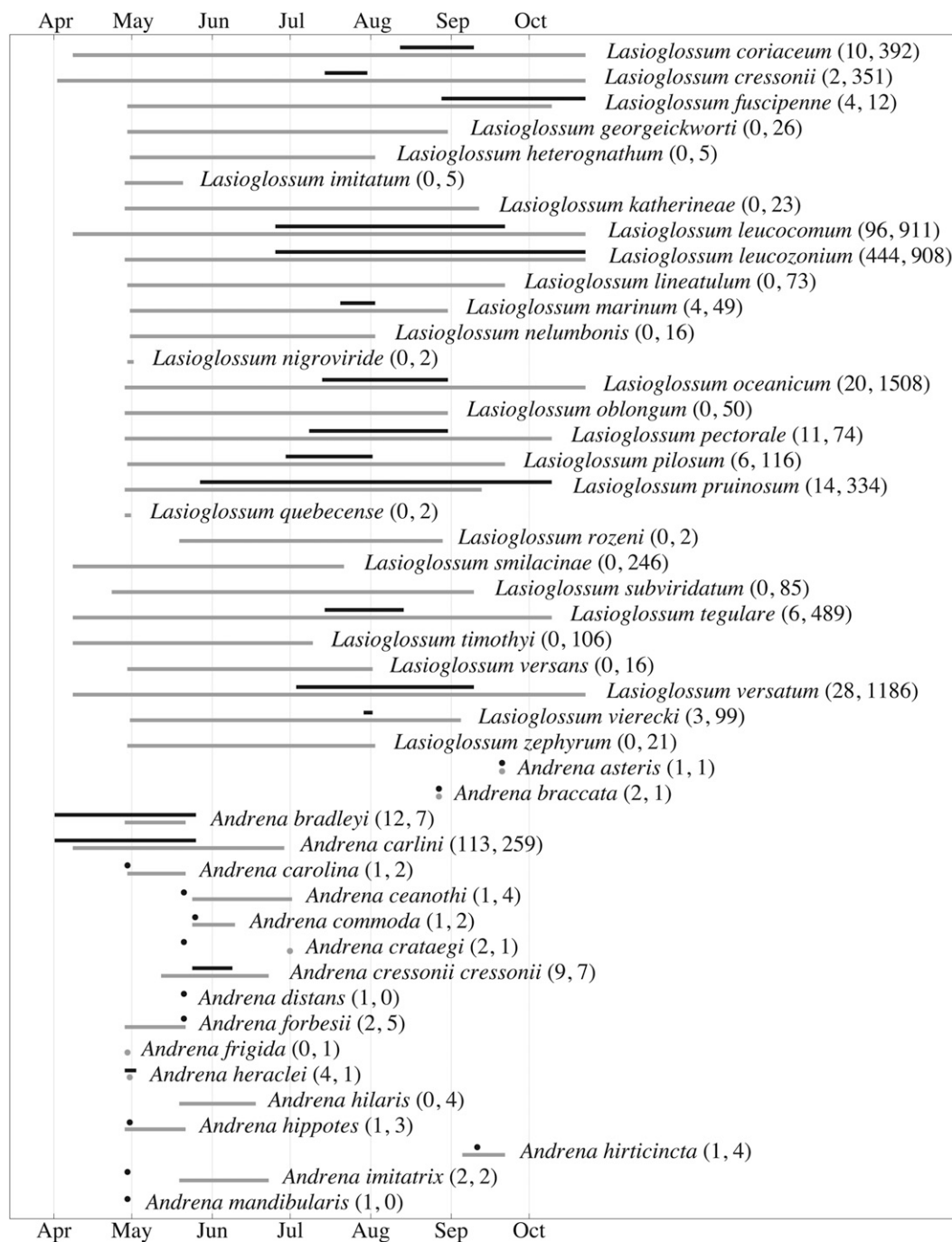


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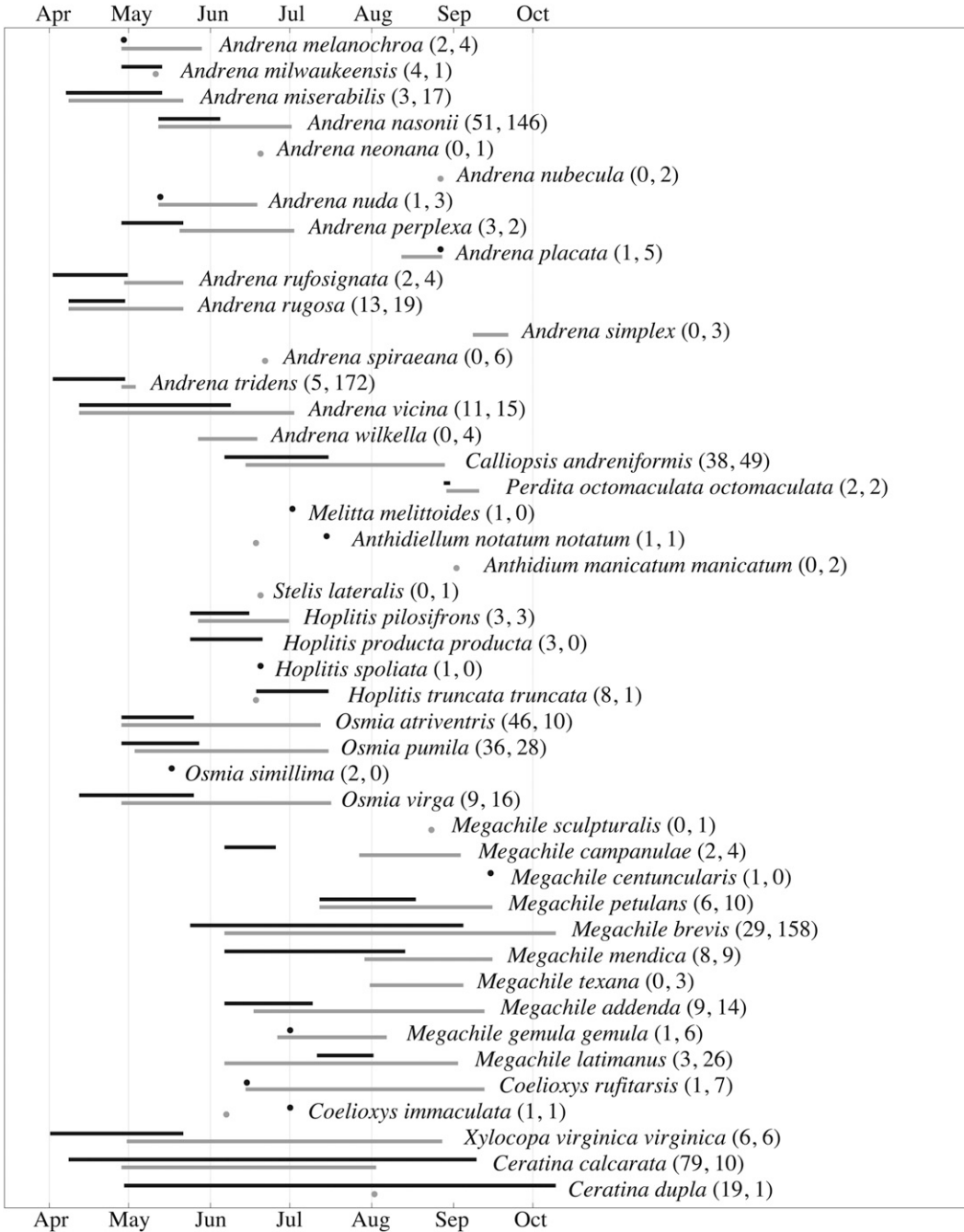


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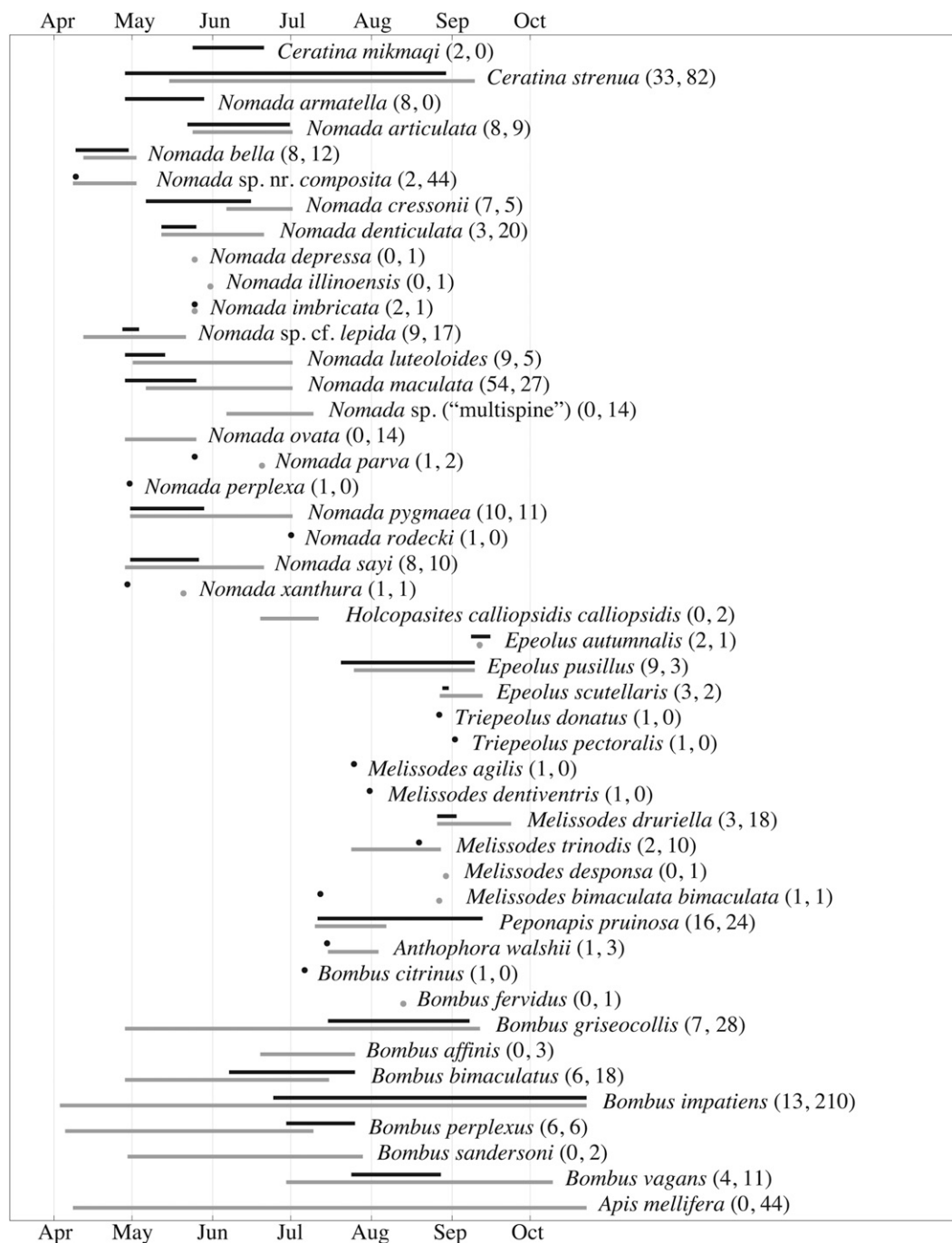


Fig. 4. Continued.

reference to literature, the Digital Bee Collections Network (DBCN) database, and discussions with relevant experts. We examine the distribution of behavioural traits including sociality and parasitism and the prevalence of oligolecty among (1) the most abundant species; (2) those species recorded only as singletons; and (3) species recorded from single and multiple island towns, as a coarse assessment of prevalence. Summary statistics, numerical data and graphics were compiled and generated by PZG.

RESULTS

Over 14,500 bee specimens were collected, mounted, determined, and databased. From these samples we document 182 species in all six New World bee families, comprising slightly less than half of the approximately 377 bees known to occur to have occurred in Massachusetts (Ascher, Milam, Veit, and Goldstein, in prep.); Table 2, Appendix). We located historical records in museum collections for an additional four species we did not encounter in the field: *Sphecodes autumnalis* Mitchell, *Sphecodes illinoensis* (Robertson) (Museum of Comparative Zoology), *Bombus* (*Bombus*) *affinis* (American Museum of Natural History), and *B. (B.) terricola* (USDA-ARS Bee Biology and Systematics Laboratory). The total of 186 MV species includes representatives of 31/41 (76%) of genera known from Massachusetts; at least 50 species previously unrecorded from Dukes County; 23 species not recorded from any of the other Massachusetts offshore islands (MAI; Dukes County + Nantucket County), 16 of which are also unrecorded from Gardiners Island, NY; and 19 species previously unrecorded from southeastern Massachusetts, including both the islands and the three mainland counties of Barnstable, Bristol, and Plymouth. Five species are considered

exotic or adventive, including the European Honey Bee *Apis mellifera* Linnaeus (Appendix). Calendar spans of adult flight activity are shown spanning the first and last recorded capture dates for databased male and female specimens of 183 species with databased MV records (Fig. 4), including the relatively recent specimens of *B. affinis* but none of the other 3 species known only from records prior to this work. Records are presented taxonomically by family below (and see Fig. 5) and in comparison with other data sets (Table 2; Fig. 6). Bee families are represented in the same rank order of species diversity as in bee data compiled from Massachusetts as a whole, New York State, the eastern United States as a whole, and at least two other recently studied sites in New York state (Black Rock Forest; Giles and Ascher 2006; and Gardiners Island; Ascher et al. 2014): Melittidae < Colletidae < Megachilidae < Andrenidae < Apidae < Halictidae (Figs 5–6). A study from southeastern Connecticut (Wagner et al. 2014) also recapitulated this order although the number of apids (41) was only slightly higher than that of andrenids (39).

Below, a presentation of our findings by family and a summary of exotic bee occurrences are followed by a summary of sampling overlap, and species recorded from the immediate region that were not documented here (Table 3). We then present the fauna's behavioral composition with respect to nesting substrate (Table 4), sociality and oligolecty (Table 5). Lastly, we present the behavioral features of the most widespread and abundant species within our sample.

Family-level Treatments

Colletidae.—The 14 species of colletids in two genera of solitary bees represent less than 8% of the total bee species recorded.

Table 2. Summary of bee species totals by genus (and subgenus for selected genera) documented from Massachusetts (MA), Martha's Vineyard (MV; cf. Figs. 5–6), all the MA offshore islands (both Nantucket and Dukes Counties, including MV), Gardiners Island (GI) and Black Rock Forest (BRF), NY, with updated taxonomy and identifications.

| | | MA | MV | MAI | GI | BRF |
|-------------------|---|----|----|-----|----|-----|
| COLLETIDAE | | | | | | |
| | <u>Colletinae</u> | | | | | |
| | <i>Colletes</i> | 13 | 9 | 10 | 8 | 2 |
| | <u>Hylaeinae</u> | | | | | |
| | <i>Hylaeus (Hylaeus)</i> | 5 | 2 | 2 | 1 | 1 |
| | <i>Hylaeus (Prosopis)</i> | 5 | 3 | 3 | 3 | 1 |
| | <i>Hylaeus (Cephalylaeus)</i> | 1 | | | | |
| HALICTIDAE | | | | | | |
| | <u>Halictinae</u> | | | | | |
| | Rophitini | | | | | |
| | <i>Dufourea</i> | 2 | | | | |
| | Augochlorini | | | | | |
| | <i>Augochloropsis (Paraugochloropsis)</i> | 1 | 1 | 1 | 1 | 1 |
| | <i>Augochlorella</i> | 1 | 1 | 1 | 1 | 1 |
| | <i>Augochlora (Augochlora)</i> | 1 | 1 | 1 | 1 | 1 |
| | <i>Agapostemon (Agapostemon)</i> | 4 | 4 | 4 | 4 | 2 |
| | Halictini | | | | | |
| | <i>Sphecodes</i> | 22 | 15 | 17 | 10 | 4 |
| | <i>Halictus</i> | 4 | 4 | 4 | 4 | 3 |
| | <i>Lasioglossum (Lasioglossum)</i> | 4 | 3 | 3 | 2 | 3 |
| | <i>Lasioglossum (Leuchalictus)</i> | 1 | 1 | 1 | 1 | 1 |
| | <i>Lasioglossum (Evyllaeus)</i> | 1 | 1 | 1 | | 1 |
| | <i>Lasioglossum (Dialictus)</i> | 54 | 27 | 31 | 15 | 29 |
| | <i>Lasioglossum (Hemihalictus)</i> | 7 | 3 | 5 | 4 | 4 |
| | <i>Lasioglossum (Sphecodogastra)</i> | 3 | 1 | 2 | 1 | 2 |
| ANDRENIDAE | | | | | | |
| | <u>Andreninae</u> | | | | | |
| | <i>Andrena (Andrena)</i> | 9 | 6 | 7 | 4 | 7 |
| | <i>Andrena (Callandrena s.l.)</i> | 7 | 4 | 4 | 4 | 2 |
| | <i>Andrena (Cnemidandrena)</i> | 4 | 2 | 3 | 3 | 2 |
| | <i>Andrena (Conandrena)</i> | 1 | 1 | 1 | 1 | 1 |
| | <i>Andrena (Derandrena)</i> | 2 | | | | 1 |
| | <i>Andrena (Euandrena)</i> | 3 | | | | 1 |
| | <i>Andrena (Gonandrena)</i> | 4 | | | | 1 |
| | <i>Andrena (Holandrena)</i> | 1 | 1 | 1 | 1 | 1 |
| | <i>Andrena (Iomelissa)</i> | 1 | | | | 1 |
| | <i>Andrena (Larandrena)</i> | 1 | 1 | 1 | 1 | 1 |
| | <i>Andrena (Leucandrena)</i> | 2 | | | | |
| | <i>Andrena (Melandrena)</i> | 9 | 4 | 5 | 4 | 7 |
| | <i>Andrena (Micrandrena)</i> | 4 | 2 | 2 | 1 | |
| | <i>Andrena (Parandrena)</i> | 1 | | | | |
| | <i>Andrena (Plastandrena)</i> | 1 | 1 | 1 | 1 | 1 |
| | <i>Andrena (Ptilandrena)</i> | 2 | 1 | 1 | | |
| | <i>Andrena (Rhacandrena)</i> | 2 | | 1 | 1 | 1 |
| | <i>Andrena (Scaphandrena)</i> | 1 | | | | 1 |
| | <i>Andrena (Scapteropsis)</i> | 7 | 1 | 3 | 3 | 2 |
| | <i>Andrena (Simandrena)</i> | 2 | 1 | 1 | 1 | 1 |
| | * <i>Andrena (Taeniandrena)</i> | 1 | 1 | 1 | 1 | 1 |

Table 2. Continued.

| | | MA | MV | MAI | GI | BRF |
|---------------------|--------------------------------------|----|----|-----|----|-----|
| | <i>Andrena (Thysandrena)</i> | 2 | | | | 1 |
| | <i>Andrena (Trachandrena)</i> | 11 | 7 | 7 | 5 | 6 |
| | <i>Andrena (Tylandrena)</i> | 2 | 1 | 1 | 1 | 1 |
| Panurginae | | | | | | |
| Calliopsini | <i>Calliopsis (Calliopsis)</i> | 1 | 1 | 1 | 1 | 1 |
| Protandrenini | <i>Pseudopanurgus</i> | 3 | | | 1 | 1 |
| Panurgini | <i>Panurginus</i> | 1 | | | | |
| | <i>Perdita</i> | 3 | 1 | 1 | 2 | |
| MELITTIDAE | | | | | | |
| Melittinae | | | | | | |
| Macropidini | <i>Macropis (Macropis)</i> | 3 | | | | |
| Melittini | <i>Melitta (Cilissa)</i> | 2 | 1 | 2 | | |
| MEGACHILIDAE | | | | | | |
| Megachilinae | | | | | | |
| Anthidiini | <i>Anthidiellum (Loyolanthidium)</i> | 1 | 1 | 1 | | |
| | * <i>Anthidium</i> | 2 | 1 | 1 | | 1 |
| | <i>Stelis</i> | 5 | 1 | 1 | 1 | 2 |
| | * <i>Pseudoanthidium</i> | 1 | | | | |
| Osmiini | <i>Heriades (Neotrypetes)</i> | 3 | | | | 1 |
| | * <i>Chelostoma (Gyrodromella)</i> | 1 | | | | |
| | <i>Hoplitis (Alcidamea)</i> | 4 | 4 | 4 | 2 | 2 |
| | <i>Osmia (Helicosmia)</i> | 2 | | | 1 | |
| | <i>Osmia (Melanosmia)</i> | 12 | 4 | 5 | 3 | 9 |
| | <i>Osmia (Osmia)</i> | 3 | | | | 2 |
| Megachilini | * <i>Megachile (Callomegachile)</i> | 1 | 1 | 1 | 1 | 1 |
| | <i>Megachile (Chelostomoides)</i> | 1 | 1 | 1 | 1 | 1 |
| | * <i>Megachile (Eutricharaea)</i> | 1 | | | | |
| | <i>Megachile (Leptorachis)</i> | 1 | 1 | 1 | 1 | |
| | <i>Megachile (Litomegachile)</i> | 3 | 3 | 3 | 2 | 1 |
| | <i>Megachile (Megachile)</i> | 4 | 1 | 2 | 2 | 2 |
| | <i>Megachile (Sayapis)</i> | 3 | | | 1 | 1 |
| | <i>Megachile (Xanthosarus)</i> | 6 | 3 | 4 | 3 | 1 |
| | <i>Coelioxys (Boreocoelioxys)</i> | 6 | 1 | 3 | 3 | 2 |
| | <i>Coelioxys (Coelioxys)</i> | 2 | 1 | 1 | | |
| | <i>Coelioxys (Glyptocoelioxys)</i> | | | | 1 | |
| | <i>Coelioxys (Cyrtoceelioxys)</i> | 1 | | | | |
| | <i>Coelioxys (Synocoelioxys)</i> | 1 | | | | |
| APIDAE | | | | | | |
| Xylocopinae | | | | | | |
| Xylocopini | <i>Xylocopa (Xylocopoides)</i> | 1 | 1 | 1 | 1 | 1 |
| Ceratinini | <i>Ceratina (Zadontomerus)</i> | 4 | 4 | 4 | 2 | 2 |

Table 2. Continued.

| | | MA | MV | MAI | GI | BRF |
|-------------------------|---|-----|------|------|-----|-----|
| <u>Nomadinae</u> | | | | | | |
| | Nomadini | | | | | |
| | <i>Nomada</i> | 37 | 20 | 24 | 12 | 19 |
| | Ammobatoidini | | | | | |
| | <i>Holcopasites</i> | 2 | 1 | 1 | | |
| | Epeolini | | | | | |
| | <i>Epeolus</i> | 6 | 3 | 4 | 4 | |
| | <i>Triepeolus</i> | 5 | 2 | 3 | 1 | |
| <u>Apinae</u> | | | | | | |
| | Osirini | | | | | |
| | <i>Epeoloides</i> | 1 | | | | |
| | Eucerini | | | | | |
| | <i>Eucera</i> (<i>Synhalonia</i>) | 1 | | | | |
| | <i>Ptilothrix</i> | | | | 1 | |
| | <i>Melissodes</i> (<i>Apomelissodes</i>) | 1 | | | | |
| | <i>Melissodes</i> (<i>Eumelissodes</i>) | 7 | 4 | 4 | 2 | 2 |
| | <i>Melissodes</i> (<i>Helimelissodes</i>) | 1 | 1 | 1 | 1 | |
| | <i>Melissodes</i> (<i>Melissodes</i>) | 1 | 1 | 1 | | |
| | <i>Peponapis</i> (<i>Peponapis</i>) | 1 | 1 | 1 | 1 | |
| | Anthophorini | | | | | |
| | <i>Anthophora</i> | 3 | 1 | 1 | 1 | 1 |
| | <i>Habropoda</i> | 1 | | 1 | 1 | |
| | Bombini | | | | | |
| | <i>Bombus</i> (<i>Bombias</i>) | 1 | | | | |
| | <i>B.</i> (<i>Subterraneobombus</i>) | 1 | | | | |
| | <i>Bombus</i> (<i>Psithyrus</i>) | 4 | 1 | 2 | 1 | 1 |
| | <i>Bombus</i> (<i>Thoracobombus</i>) | 2 | 1 | 2 | 2 | |
| | <i>Bombus</i> (<i>Cullumanobombus</i>) | 2 | 1 | 1 | 2 | 1 |
| | <i>Bombus</i> (<i>Bombus</i>) | 2 | 2(H) | 2(H) | | |
| | <i>Bombus</i> (<i>Pyrobombus</i>) | 6 | 5 | 5 | 4 | 6 |
| | Apini | | | | | |
| | <i>Apis</i> | 1 | 1 | 1 | 1 | 1 |
| | TOTAL | 377 | 186 | 217 | 151 | 158 |

*Refers to genera and subgenera represented in Massachusetts only by exotic species.

H refers to *Bombus* species known only from historical specimens.

The five species of *Hylaeus* account for over 20% of all cavity nesters; the remaining nine *Colletes* species (64% of the 14 known from Massachusetts) nest in the ground. *Colletes* appear to be abundant at coastal sites throughout the Northeast, perhaps reflecting the availability of appropriate sandy substrates and of asteraeous host plants for specialists such as *Colletes solidaginis* Swenk and *C. speculiferus* Cockerell (= *mittelli* Stephen; see Kuhlmann and Ascher 2011). In July

2011, *Colletes productus* Robertson and *Melitta melittoides* were collected in association with Maleberry *Lyonia ligustrina* (L.), a plant targeted specifically as a known host of these and other pollen specialists including *Perdita novaeangliae* Viereck, which we did not record. We documented only 5 of the 10 *Hylaeus* species known from Massachusetts, including *Hylaeus schwarzii* (Cockerell), recorded on 30 June and 29 August 2010 at Black Point, Chilmark. This species has

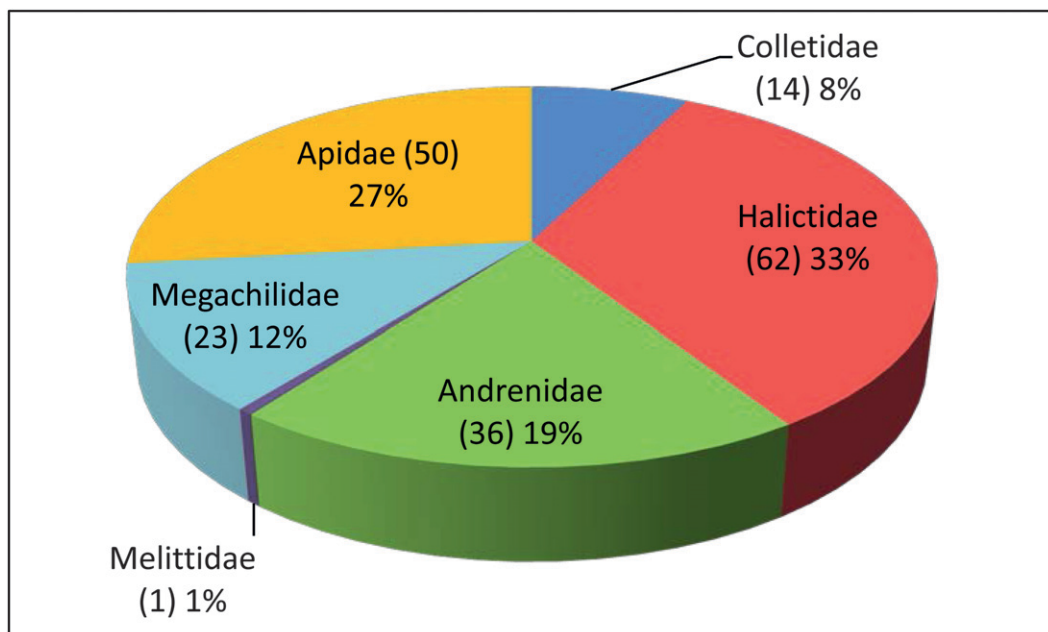


Fig. 5. Taxonomic distribution by family of 186 bee species recorded from Martha's Vineyard, including four known only from historical records ($n=186$).

a limited, coastal distribution in the region: it is also known from both Penikese and Cuttyhunk Islands (Dukes County; Stage 2009) and from the eastern Massachusetts mainland (Plymouth, Essex, and Suffolk Counties), but not from Gardiners Island, New York, where a similar species occurs that may be a dark form of *H. nelumbonis* (Robertson) (Ascher et al. 2014). Of the 14 colletids documented, a majority, including 5 of 9 *Colletes*, were found in only one of the six island towns, and none found in more than 4 towns, although this is almost certainly an artifact of low sampling effort in the Spring.

The blister beetle *Tricrania sanguinipennis* Say (Meloidae), which has been observed in West Tisbury (Lambert's Cove, Cedar Tree Neck, Manuel Correllus State Forest; pers. obs. and T. Simmons and M. Pelikan, pers. comm.) is an inquiline associated with spring-flying *Colletes* in the *inaequalis* species group (Stephen, 1954) and late-spring/early

summer-flying *C. thoracicus* Smith (= *rufithorax*, Parker and Böving 1925; Erickson et al. 1976; Cline and Huether 2011). A reported association with the more distantly related autumnal species *C. compactus* Cresson (Frost, 1912) is anomalous. Both *C. thoracicus* and *C. validus* Cresson might seem as likely as potential hosts as *C. inaequalis* on Martha's Vineyard given their relative abundance (Fig. 4) in our samples from early May. Our sampling, however, was not intensive in early Spring when *T. sanguinipennis* has been recorded and when *C. inaequalis* is likely to emerge. We note that while many late-season *Colletes* species in the Northeast USA host *Epeolus* cleptoparasites, these spring-active *Colletes* in the *inaequalis* group do not.

Halictidae.—The 62 species in seven genera of Halictidae, all Halictinae, account for more than a third of all species recorded, a majority (33 of 43) of eusocial bee species, most of the individuals

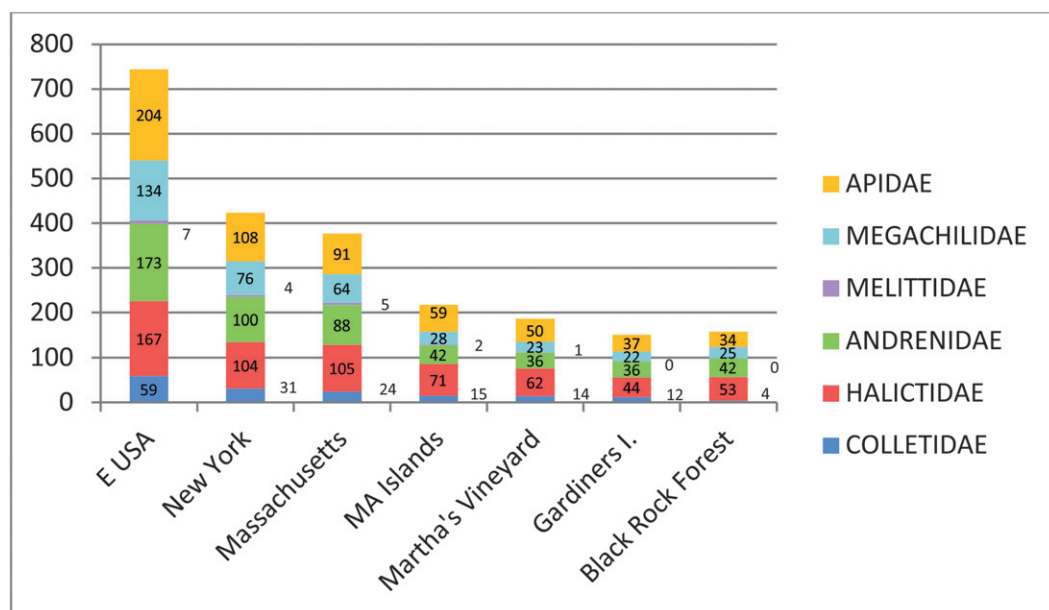


Fig. 6. Taxonomic composition of bee species by family recorded from Martha's Vineyard and other eastern US sites.

recovered from traps, and over one-third (16 of 46) of the parasitic bee species documented from the island. Most halictids (56 of 62) are known or inferred to excavate nests in soil or, in the case of parasites, to occupy the nests of soil-nesting hosts, whereas at least 5 excavate nest burrows in wood (Table 4). Of the pollen-collecting halictids we recorded, more than half (33 of 62) are known or inferred to be eusocial whereas 14 are solitary or communal (Table 5).

As on Gardiners Island, all 3 augochlorine species regularly encountered north of New Jersey were recorded on Martha's Vineyard, with the soil-nesting *Augochlorella aurata* by far the most abundant species in its tribe and possibly the most abundant bee on the island. As is typical in the northeastern United States, *Augochloropsis metallica* Fabricius was relatively scarce. All specimens of this species were referable to the form *fulgida* (Smith), which has been treated as specifically distinct (Arduser, 2010).

Of the four northeastern *Agapostemon* species, all were recorded from Martha's Vineyard, with *A. virescens* (Fabricius) and *A. texanus* Cresson most prevalent, followed by *A. sericeus* (Förster). *Agapostemon splendens* (Lepeletier) was more localized, being strongly associated with sandy nesting substrates, but still appeared in four of six island towns.

We documented all four *Halictus* known from the region, and as expected (cf. Ascher et al. 2012) *H. ligatus* was one of the most abundant species encountered, whereas *H. parallelus* Say was relatively scarce, and *H. rubicundus* (Christ) and *H. confusus* Smith were intermediate in numbers.

Individual *Lasioglossum* sensu lato were abundant, especially the widely distributed *L. (Leuchalictus) leucozonium*, now known to be an exotic member of a European subgenus (see Giles and Ascher 2006; Zayed et al. 2007), and the native *L. (Lasioglossum) coriaceum* (Smith) and *L. (L.) acuminatum* McGinley

Table 3. Bee species not recorded in this study but “expected” to occur on MV based on their occurrences from nearby islands or adjacent mainland counties. DU=Dukes County; NA=Nantucket County; BA=Barnstable County; BR=Bristol County; PL=Plymouth County; ml=southeastern Massachusetts mainland, i.e. any of the latter three counties). OLI denotes oligolectic or mesolectic species associated with particular plant families, abbreviated as follows: AST=Asteraceae; ERI=Ericaceae; MYR=Myrsinaceae (=Primulaceae); PON=Pontederiaceae; SAL=Salicaceae; COR=Cornaceae; LIL=Liliaceae. We note that an early record of *L. cephalotes* from the Elizabeth Islands, made prior to the description of *L. rozeni*, likely represents a mis-determination of the latter.

| | DU | NA | BA | BR | PL | ml | OLI |
|-------------------|----|----|----|----|----|----|-----|
| COLLETIDAE | | | | | | | |
| <u>Colletinae</u> | | | | | | | |
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Table 3. Continued.

| | | DU | NA | BA | BR | PL | ml | OLI |
|---------------------|---|-----|----|----|----|----|----|-----|
| MELITTIDAE | | | | | | | | |
| | <u>Melittinae</u> | | | | | | | |
| | Macropidini | | | | | | | |
| | <i>Macropis (Macropis) ciliata</i> Patton, 1880 | | | BA | | | + | MYR |
| | <i>Macropis (Macropis) nuda</i> (Provancher, 1882) | | | BA | | PL | + | MYR |
| | <i>Macropis (Macropis) patellata</i> Patton, 1880 | | | BA | | | + | MYR |
| | <i>Melitta (Cilissa) americana</i> (Smith, 1853) | | NA | BA | BR | PL | + | ERI |
| MEGACHILIDAE | | | | | | | | |
| | <u>Megachilinae</u> | | | | | | | |
| | Anthidiini | | | | | | | |
| | <i>Stelis (Dolichostelis) louisae</i> Cockerell, 1911 | | | | | PL | + | |
| | <i>Stelis (Stelis) labiata</i> (Provancher, 1888) | | | | | PL | + | |
| | Osmiini | | | | | | | |
| | <i>Heriades (Neotrypetes) carinata</i> Cresson, 1864 | | | | | PL | + | |
| | <i>Osmia (Melanosmia) albiventris</i> Cresson, 1864 | DU | | | | PL | + | |
| | <i>Osmia (Melanosmia) bucephala</i> Cresson, 1864 | | | | | PL | + | |
| | <i>Osmia (Melanosmia) felti</i> Cockerell, 1911 | | | | | PL | + | |
| | <i>Osmia (Melanosmia) inspergens</i> Lovell and Cockerell, 1907 | | | | | PL | + | |
| | <i>Osmia (Osmia) lignaria lignaria</i> Say, 1837 | | | BA | | PL | + | |
| | Megachilini | | | | | | | |
| | <i>Megachile (Eutricharaea) rotundata</i> (Fabricius, 1793) | | | | | PL | + | |
| | <i>Megachile (Megachile) inermis</i> Provancher, 1888 | DU | | BA | | | + | |
| | <i>Megachile (Megachile) montivaga</i> Cresson, 1878 | | | | | PL | + | |
| | <i>Megachile (Megachile) relativa</i> Cresson, 1878 | | | BA | | PL | + | |
| | <i>Megachile (Sayapis) frugalis</i> Cresson, 1872 | | | BA | | PL | + | |
| | <i>Megachile (Sayapis) inimica sayi</i> Cresson, 1878 | | | | BR | PL | + | |
| | <i>Megachile (Sayapis) pugnata</i> Say, 1837 | | | | | PL | + | AST |
| | <i>Megachile (Xanthosarus) f. frigida</i> Smith, 1853 | | | BA | | | + | |
| | <i>Megachile (Xanthosarus) m. melanophaea</i> Smith, 1853 | DU | | | | PL | | |
| | <i>Coelioxys (Boreocoelioxys) octodentata</i> Say, 1824 | DU? | NA | BA | | PL | + | |
| | <i>Coelioxys (Boreocoelioxys) sayi</i> Robertson, 1897 | DU | | BA | | PL | + | |
| | <i>Coelioxys (Coelioxys) sodalis</i> Cresson, 1878 | | | BA | | | | |
| | <i>Coelioxys (Cyrtocoelioxys) modesta</i> Smith, 1854 | | | BA | | | + | |
| APIDAE | | | | | | | | |
| | <u>Nomadinae</u> | | | | | | | |
| | Nomadini | | | | | | | |
| | <i>Nomada australis</i> Mitchell, 1962 | | | BA | | | + | |
| | <i>Nomada bethunei</i> Cockerell, 1903 | DU | | | | PL | + | |
| | <i>Nomada composita</i> Mitchell, 1962 | DU | | | | PL | + | |
| | <i>Nomada cuneata</i> (Robertson, 1903) | | | | BR | | + | |
| | <i>Nomada electa</i> Cresson, 1863 | DU | NA | BA | | | + | |
| | <i>Nomada vicina</i> Cresson, 1863 | DU | NA | | | PL | + | |
| | Ammobatoidini | | | | | | | |
| | <i>Holcopasites illinoiensis</i> (Robertson, 1891) | | | | | PL | + | |
| | Epeolini | | | | | | | |
| | <i>Epeolus ilicis</i> Mitchell, 1962 | | | BA | | | + | |
| | <i>Epeolus lectoides</i> Robertson, 1901 | DU | | BA | | | + | |
| | <i>Triepeolus lunatus</i> (Say, 1824) | DU | | | | | | |
| | <i>Triepeolus pectoralis</i> (Robertson, 1897) | DU | | | | PL | + | |

Table 3. Continued.

| | | DU | NA | BA | BR | PL | ml | OLI |
|--------------|--|----|----|-----|----|----|----|-----|
| Apinae | | | | | | | | |
| Eucerini | | | | | | | | |
| | <i>Melissodes (Apomelissodes) apicata</i> Lovell and Cockerell, 1906 | | | | BR | PL | + | PON |
| | <i>Melissodes (Eumelissodes) illata</i> Lovell and Cockerell, 1906 | | | BA | | PL | + | AST |
| Anthophorini | | | | | | | | |
| | <i>Anthophora (Clisodon) terminalis</i> Cresson, 1869 | | | | | PL | + | |
| | <i>Habropoda laboriosa</i> (Fabricius, 1804) | DU | | BA | | | + | |
| Bombini | | | | | | | | |
| | <i>Bombus (Psithyrus) ashtoni</i> (Cresson, 1864) | DU | | BA | | PL | + | |
| | <i>Bombus (Thoracobombus) pensylvanicus</i> (DeGeer, 1773) | DU | | BA | | PL | + | |
| | <i>Bombus (Cullumanobombus) rufocinctus</i> Cresson, 1863 | | | BA? | | | + | |
| | <i>Bombus (Pyrobombus) ternarius</i> Say, 1837 | | | BA | | | + | |
| TOTAL | 77 | 26 | 8 | 35 | 14 | 44 | 63 | 14 |

(1986). This last species is apparently localized regionally, e.g., unrecorded from Gardiners Island, but abundant where it does occur. We encountered *Lasioglossum fuscipenne* (Smith), close to its northeastern range limits (McGinley 1986), in small numbers.

The 27 species of metallic *Lasioglossum* (*Dialictus*) we recorded include four *Lasioglossum* (*Dialictus*) species described recently by Gibbs (2010; 2011): the eusocial *L. georgeickworti* Gibbs, *L. katherineae* Gibbs, and *L. timothyi* Gibbs, and the social parasite *L. rozeni* Gibbs. Of these, only the last was recorded from Gardiners Island (Ascher et al. 2014). The most ubiquitous *Dialictus* were the relatively large ground-nesting species *Lasioglossum oceanicum* (Cockerell) (= *nymphaearum* auct.; following Gibbs 2010, not 2011, based on apparent validity of the lectotype designation by Cresson, 1928) and true *L. versatum* (= *Halictus subconnexus rohweri* Ellis, not *Dialictus versatus* sensu Mitchell, 1960; see Gibbs 2010, 2011). Other common species included *L. bruneri* (Crawford), *L. cressonii* (Robertson), *L. smilacinae* (Robertson) (= *Dialictus*

laevissimus (Smith), in part, of Mitchell, 1960; see Gibbs, 2011), and *L. subviridatum* (Cockerell) [= *Dialictus lineatulum* (Crawford), in part, of Mitchell, 1960, and commonly misidentified prior to Gibbs, 2010, 2011, as *L. oblongum* (Lovell)]. *Lasioglossum pruinosum* (Robertson), recorded primarily from sandplain grassland sites, appears to be generally scarce in the region and is better known from prairies of the central and western states (Gibbs 2010). The psammophilic species *L. vierecki* (Crawford) occurred at several open, sandy sites, and the apparent sand specialist *L. pilosum* (Smith) and its cryptic sister species *L. leucocomum* (treated as a synonym of the former prior to Gibbs 2010, 2011) were widespread (5 of 6 towns). By contrast, these sand specialists were scarce on Gardiners Island or altogether absent (*L. vierecki*). Potential habitat specialists among *Dialictus* also include *L. katherineae* Gibbs, described in part from material collected by J. Milam (pers. comm.) from the inland sandplains at Montague, Franklin County, MA; and *L. marinum* (Crawford), an associate of Atlantic coastal dunes, which was encountered in close

Table 4. Continued.

| FAMILY Subfamily Tribe Genus | Massachusetts (377) | | | | | | | Martha's Vineyard (186) | | | | | | | Offshore Islands (217) | | | | | | | Gardiners Island (151) | | | | | | | Black Rock Forest (158) | | | | | | | |
|--|---------------------|-----|----|-----|-----|-----|---|-------------------------|-----|----|-----|-----|-----|---|------------------------|-----|----|-----|-----|-----|---|------------------------|-----|----|-----|-----|-----|-----|-------------------------|-----|----|-----|-----|-----|---|--|
| | Soil | Cav | Wo | Stm | Hiv | Oth | ? | Soil | Cav | Wo | Stm | Hiv | Oth | ? | Soil | Cav | Wo | Stm | Hiv | Oth | ? | Soil | Cav | Wo | Stm | Hiv | Oth | ? | Soil | Cav | Wo | Stm | Hiv | Oth | ? | |
| <i>(Heliomelissodes)</i> <i>(Melissodes)</i> <i>Peponapis</i> Anthophorini <i>Anthophora</i> <i>Habropoda</i> | 1 | | | | | | | 1 | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | |
| | 1 | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| | 1 | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| | 2 | | 1 | | | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| | 1 | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| Bombini | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Bombus</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>(Bombias)</i> | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>(Subterraneobombus)</i> | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>(Psithyrus)</i> | | | | | 4 | | | | | | | | 1 | | | | | | | | | | | | | | 1 | | | | | | | | 1 | |
| <i>(Thoracobombus)</i> | | | | | 2 | | | | | | | 1 | | | | | | | | | | | | | | 2 | | | | | | | | | | |
| <i>(Cullumanobombus)</i> | | | | | 2 | | | | | | | 1 | | | | | | | | | | | | | | 2 | | | | | | | | | 1 | |
| <i>(Bombus)</i> | | | | | 2 | | | | | | | 2 | | | | | | | | | | | | | | 2 | | | | | | | | | | |
| <i>(Pyrobombus)</i> | | | | | 6 | | | | | | | 5 | | | | | | | | | | | | | | 4 | | | | | | | | | 6 | |
| Apini | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Apis</i> | | | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | 1 | | | | | | | | 1 | |
| TOTAL | 268 | 69 | 9 | 8 | 19 | 1 | 3 | 137 | 22 | 6 | 8 | 11 | 1 | 1 | 161 | 27 | 7 | 8 | 13 | 1 | | 110 | 20 | 7 | 4 | 10 | | 113 | 24 | 8 | 4 | | | 9 | | |

Table 5. Summary of behavioral syndromes and pollen specialization of bees reported in this study, arranged by genus (cf. Figs 8–10) and presented alongside analogous data for comparison sites as in Tables 2, 4. Five behavioral columns are presented for each location, the middle column (PAR=Parasitic) bracketed by two columns on the left summarizing social structure (SOL=Solitary communal and SOC=Social, including subsocial, primitively eusocial, eusocial) and two columns on the right summarizing habits of pollen collecting bees (OLI-Oligolectic or mesolectic and POL=Polylectic). For a given row, the sum of the two [SOL+SOC] cells equals the sum of the [OLI+POL] cells, since each of these reflect the non-parasitic bees. Summing the first three or the last three of the five cells for a given row (family, genus, subgenus, etc.) gives the total number of species treated for that taxon. Cf. Goldstein and Scott (2015). Emboldened rows reflect totals for each family and seven genera for which subgenera are differentiated (*LasioGLOSSUM*, *Andrena*, *Osmia*, *Megachile*, *Coelioxys*, *Melissodes*, and *Bombus*).

| FAMILY Subfamily Tribe Genus | Massachusetts (377) | | | | | Martha's Vineyard (186) | | | | | Offshore Islands (217) | | | | | Gardiners Island (151) | | | | | Black Rock Forest (158) | | | | |
|---------------------------------|---------------------|-----------|-----------|----------|-----------|-------------------------|-----------|-----------|----------|-----------|------------------------|-----------|-----------|----------|-----------|------------------------|-----------|-----------|----------|-----------|-------------------------|-----------|----------|----------|-----------|
| | SOL | SOC | PAR | OLI | POL | SOL | SOC | PAR | OLI | POL | SOL | SOC | PAR | OLI | POL | SOL | SOC | PAR | OLI | POL | SOL | SOC | PAR | OLI | POL |
| COLLETIDAE | 24 | 0 | 0 | 5 | 19 | 14 | 0 | 0 | 3 | 11 | 15 | 0 | 0 | 3 | 12 | 12 | 0 | 0 | 2 | 10 | 4 | 0 | 0 | 2 | 2 |
| Colletinae | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Colletes</i> | 13 | 0 | 0 | 4 | 9 | 9 | 0 | 0 | 3 | 6 | 10 | 0 | 0 | 3 | 7 | 8 | 0 | 0 | 2 | 6 | 2 | 0 | 0 | 2 | 0 |
| Hylaeinae | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Hylaeus</i> | 11 | 0 | 0 | 1 | 10 | 5 | 0 | 0 | 0 | 5 | 5 | 0 | 0 | 0 | 5 | 4 | 0 | 0 | 0 | 4 | 2 | 0 | 0 | 0 | 2 |
| HALICTIDAE | 23 | 58 | 24 | 3 | 78 | 14 | 32 | 16 | 1 | 45 | 13 | 40 | 18 | 1 | 52 | 13 | 20 | 11 | 0 | 33 | 13 | 33 | 6 | 2 | 44 |
| Rophitinae | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Rophitini</i> | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Dufourea</i> | | | | | | | | | | | | | | | | | | | | | | | | | |
| Halictinae | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Augochlorini</i> | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| <i>Augochlorella</i> | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| <i>Augochloropsis</i> | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| <i>Augochlora</i> | | | | | | | | | | | | | | | | | | | | | | | | | |
| Halictini: Caenohalictina | 4 | 0 | 0 | 0 | 4 | 4 | 0 | 0 | 0 | 4 | 4 | 0 | 0 | 0 | 4 | 4 | 0 | 0 | 0 | 4 | 2 | 0 | 0 | 0 | 2 |
| <i>Agapostemon</i> | | | | | | | | | | | | | | | | | | | | | | | | | |
| Halictini: Halictina | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Sphecodes</i> | 0 | 0 | 22 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 17 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 4 | 0 | 0 |
| <i>Halictus</i> | 0 | 4 | 0 | 0 | 4 | 0 | 4 | 0 | 0 | 4 | 0 | 4 | 0 | 0 | 4 | 0 | 4 | 0 | 0 | 4 | 0 | 3 | 0 | 0 | 3 |
| LasioGLOSSUM | 15 | 52 | 2 | 2 | 65 | 8 | 27 | 1 | 1 | 34 | 7 | 35 | 1 | 1 | 41 | 7 | 15 | 1 | 0 | 22 | 9 | 29 | 2 | 2 | 36 |
| (<i>LasioGLOSSUM</i>) | 4 | 0 | 0 | 0 | 4 | 3 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 2 | 3 | 0 | 0 | 0 | 3 |
| (<i>Leuchalictus</i>) | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| (<i>Evytaeus</i>) | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| (<i>Dialictus</i>) | 2 | 50 | 2 | 0 | 52 | 0 | 26 | 1 | 0 | 26 | 0 | 32 | 1 | 0 | 32 | 0 | 15 | 1 | 0 | 15 | 1 | 28 | 2 | 0 | 29 |
| (<i>Hemihalictus</i>) | 6 | 1 | 0 | 1 | 6 | 3 | 0 | 0 | 1 | 2 | 3 | 0 | 0 | 1 | 2 | 3 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 1 | 1 |
| (<i>Sphecodogastra</i>) | 2 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 1 |

Table 5. Continued.

| FAMILY Subfamily Tribe Genus | Massachusetts (377) | | | | | | Martha's Vineyard (186) | | | | | | Offshore Islands (217) | | | | | | Gardiners Island (151) | | | | | | Black Rock Forest (158) | | | | | |
|---------------------------------|---------------------|-----|-----|-----|-----|----|-------------------------|-----|-----|-----|-----|----|------------------------|-----|-----|-----|-----|---|------------------------|-----|-----|-----|-----|----|-------------------------|-----|-----|-----|-----|--|
| | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | |
| ANDRENIDAE | 88 | 0 | 0 | 0 | 37 | 51 | 36 | 0 | 0 | 14 | 22 | 42 | 0 | 0 | 16 | 26 | 36 | 0 | 0 | 13 | 23 | 42 | 0 | 0 | 14 | 28 | | | | |
| Andreninae | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Andrenini | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Andrena | 80 | 0 | 0 | 30 | 50 | 34 | 0 | 0 | 12 | 22 | 40 | 0 | 0 | 14 | 26 | 32 | 0 | 0 | 10 | 22 | 40 | 0 | 0 | 12 | 28 | | | | | |
| (Andrena) | 9 | 0 | 0 | 4 | 5 | 6 | 0 | 0 | 2 | 4 | 7 | 0 | 0 | 2 | 5 | 4 | 0 | 0 | 2 | 2 | 7 | 0 | 0 | 3 | 4 | | | | | |
| (Callandrena) | 7 | 0 | 0 | 5 | 2 | 4 | 0 | 0 | 4 | 0 | 4 | 0 | 0 | 4 | 0 | 4 | 0 | 0 | 4 | 0 | 2 | 0 | 0 | 2 | 0 | | | | | |
| (Cnemidandrena) | 4 | 0 | 0 | 4 | 0 | 2 | 0 | 0 | 2 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 2 | 0 | | | | | |
| (Conandrena) | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | | | | | |
| (Derandrena) | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | | | | | | |
| (Euandrena) | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | | | | | | |
| (Gonandrena) | 4 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | | | | | | |
| (Holandrena) | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | |
| (Iomelissa) | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | | | | | | |
| (Larandrena) | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | | | | | | |
| (Leucandrena) | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | | |
| (Melandrena) | 9 | 0 | 0 | 0 | 9 | 4 | 0 | 0 | 0 | 4 | 5 | 0 | 0 | 0 | 5 | 4 | 0 | 0 | 0 | 4 | 7 | 0 | 0 | 7 | | | | | | |
| (Micrandrena) | 4 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | | | | | | |
| (Parandrena) | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | | |
| (Plastandrena) | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | |
| (Prilandrena) | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | | |
| (Rhacandrena) | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | | | | | | |
| (Scaphandrena) | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | | | | | | |
| (Scrapterosis) | 7 | 0 | 0 | 1 | 6 | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 2 | 3 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 2 | | | | | | |
| (Simandrena) | 2 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | | | | | | |
| (Taenidandrena) | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | | | | | | |
| (Thysandrena) | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | | | | | | | |
| (Trachandrena) | 11 | 0 | 0 | 2 | 9 | 7 | 0 | 0 | 1 | 6 | 7 | 0 | 0 | 1 | 6 | 5 | 0 | 0 | 0 | 5 | 6 | 0 | 0 | 1 | | | | | | |
| (Tylandrena) | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | | | | | | |
| Panurginae | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Calliopsis | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | | | | | |
| Pseudopanurgus | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | | | | | | |

Table 5. Continued.

| FAMILY Subfamily Tribe Genus | Massachusetts (377) | | | | | | Martha's Vineyard (186) | | | | | | Offshore Islands (217) | | | | | | Gardiners Island (151) | | | | | | Black Rock Forest (158) | | | | | | | |
|--|---------------------|----------|-----------|----------|-----------|-----------|-------------------------|----------|----------|-----------|-----------|----------|------------------------|----------|-----------|-----------|----------|----------|------------------------|-----------|-----------|----------|----------|----------|-------------------------|----------|----------|----------|----------|----------|---|---|
| | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | | | |
| <i>Panurginus</i> <i>Perdita</i> MELITTIDAE | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 3 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 5 | 0 | 0 | 5 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| <i>Melittinae</i> Macropidini <i>Macropis</i> Melitini <i>Melitta</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| MEGACHILIDAE Megachilinae Anthidiini <i>Anthidiellum</i> <i>Anthidium</i> <i>Stelis</i> <i>Pseudoanthidium</i> Osmiini | 49 | 0 | 15 | 3 | 46 | 20 | 0 | 3 | 1 | 19 | 23 | 0 | 5 | 1 | 22 | 17 | 0 | 5 | 0 | 17 | 22 | 0 | 4 | 2 | 20 | | | | | | | |
| | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 2 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>Chelostoma</i> <i>Heriades</i> <i>Hoplitis</i> <i>Osmia</i> (<i>Helicosmia</i>) (<i>Melanosmia</i>) (<i>Osmia</i>) Megachilini | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | | | | | | | |
| | 4 | 0 | 0 | 0 | 4 | 4 | 0 | 0 | 0 | 4 | 4 | 0 | 0 | 0 | 0 | 4 | 2 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 2 | | | | | | |
| | 17 | 0 | 0 | 1 | 16 | 4 | 0 | 0 | 1 | 3 | 5 | 0 | 0 | 1 | 4 | 4 | 0 | 0 | 0 | 4 | 11 | 0 | 0 | 1 | 10 | | | | | | | |
| | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 12 | 0 | 0 | 1 | 11 | 4 | 0 | 0 | 1 | 3 | 5 | 0 | 0 | 1 | 4 | 3 | 0 | 0 | 0 | 3 | 9 | 0 | 0 | 1 | 8 | | | | | | | |
| | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | | | | | | | |
| <i>Megachile</i> (<i>Callomegachile</i>) (<i>Chelostomoides</i>) (<i>Eutricharaea</i>) (<i>Leptorachis</i>) (<i>Litomegachile</i>) | 20 | 0 | 0 | 1 | 19 | 10 | 0 | 0 | 0 | 10 | 12 | 0 | 0 | 0 | 12 | 11 | 0 | 0 | 11 | 8 | 0 | 0 | 1 | 7 | | | | | | | | |
| | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | | | | | | | | |
| | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | | | | | | | |
| | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | | | | | | | |
| | 3 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | | | | | | | | |

Table 5. Continued.

| FAMILY Subfamily Tribe Genus | Massachusetts (377) | | | | | | Martha's Vineyard (186) | | | | | | Offshore Islands (217) | | | | | | Gardiners Island (151) | | | | | | Black Rock Forest (158) | | | | | |
|--|---------------------|-----|-----|-----|-----|----|-------------------------|-----|-----|-----|-----|----|------------------------|-----|-----|-----|-----|----|------------------------|-----|-----|-----|-----|----|-------------------------|-----|-----|-----|-----|---|
| | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | | SOL | SOC | PAR | OLI | POL | |
| <i>Melissodes</i> (<i>Apomelissodes</i>) (<i>Eumelissodes</i>) (<i>Helimelissodes</i>) (<i>Melissodes</i>) <i>Peponapis</i> <i>Anthophorini</i> <i>Anthophora</i> <i>Habropoda</i> <i>Bombini</i> <i>Bombus</i> (<i>Bombias</i>) (<i>Subterraneanobombus</i>) (<i>Psithyrus</i>) (<i>Thoracobombus</i>) (<i>Cullumanobombus</i>) (<i>Bombus</i>) (<i>Pyrobombus</i>) <i>Apini</i> <i>Apis</i> | 11 | 0 | 0 | 10 | 1 | 7 | 0 | 0 | 0 | 6 | 1 | 7 | 0 | 0 | 0 | 6 | 1 | 4 | 0 | 0 | 0 | 4 | 0 | 2 | 0 | 2 | 0 | 0 | 2 | 0 |
| | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 7 | 0 | 0 | 7 | 0 | 4 | 0 | 4 | 0 | 4 | 0 | 4 | 0 | 4 | 0 | 4 | 0 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | 0 | 2 | 0 | 0 |
| | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0 | 14 | 4 | 0 | 14 | 0 | 9 | 1 | 0 | 0 | 9 | 0 | 10 | 2 | 0 | 10 | 0 | 0 | 8 | 1 | 0 | 8 | 1 | 0 | 7 | 1 | 0 | 0 | 7 | 7 |
| | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| | 0 | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0 | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| | 0 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0 | 6 | 0 | 0 | 6 | 0 | 5 | 0 | 5 | 0 | 5 | 0 | 5 | 0 | 5 | 0 | 5 | 0 | 4 | 0 | 4 | 0 | 4 | 0 | 6 | 0 | 0 | 0 | 6 | 6 |
| | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| TOTAL | 205 | 77 | 94 | 64 | 219 | 93 | 47 | 46 | 26 | 114 | 104 | 56 | 57 | 30 | 130 | 85 | 32 | 34 | 20 | 97 | 84 | 44 | 30 | 22 | 106 | | | | | |

proximity to such habitats on the western end of the island.

Lasioglossum albipenne (Robertson), a species of northern and western-montane affinities and uncommon in the northeast was found in small numbers. This species was also recorded from tiny Great Gull Island, New York, but not from nearby Gardiners Island (Ascher et al. 2014). *Lasioglossum coreopsis* (Robertson), a species near its northeastern range limits, is unknown from other offshore islands but has been recorded locally from mainland southeastern Massachusetts and also from coastal Connecticut (T. Zarrillo, pers. com.).

The island's 15 *Sphecodes* species (including two known from historical specimens) represent two-thirds of the 22 known from Massachusetts species and include *S. aroniae* Mitchell, probably near its northern range limits and under-recorded in regional collections due to confusion with the closely related and more northern *S. ranunculi* Robertson (both were found on Martha's Vineyard). *Sphecodes townesi* Mitchell, may also have been under-recorded due to its similarity to the more common *S. levis* Lovell and Cockerell (not found on MV). The absence of *Sphecodes johnsonii* Lovell was surprising given its occurrence on the nearby mainland and its abundance on the Elizabeth Islands and Gardiners Island.

Andrenidae.—Andrenids, of which the genus *Andrena* accounts for 34 of the 36 species we documented, are solitary soil nesters. This family may be under-sampled, even after a targeted effort in the spring of 2011 that added 13 species of *Andrena* to the 21 found in 2010, a higher percent increase than for any other genus. *Andrena* (*Micrandrena*) *neonana* Viereck, a small species of southern affinities, was previously unrecorded from Massachusetts. *Andrena* species in general were detected less uniformly than those of other genera,

with 24 of 34 species recorded from only one or two of the islands six towns. Andrenids also account for more than half of the pollen specialist (oligolectic) species we encountered (Table 5, Appendix), including the blueberry specialists *Andrena bradleyi* Viereck and *A. carolina* Viereck. Willows (*Salix* spp.) are among the first trees to flower in spring and represent important hosts for several of early-emerging *Andrena* species, but are not a dominant component of plant communities in many coastal sandplain areas. Variability in temperatures from 2010 to 2011 combined with intermittently inclement weather also impeded our sampling at flowering willows. Relatively few willow specialists have been recorded from the offshore islands (MAI) or southeastern Massachusetts (SEMA) generally, whereas autumnal composite specialists are well represented by four species of subgenus *Callandrena* and two of subgenus *Cnemidandrena*. *Andrena* (*Trachandrena*) *ceanothi* Viereck seems to have an association with sandplain habitats both on Martha's Vineyard and the mainland, where it has been found at sites such as Montague Plains, MA (J. Milam, pers. comm.) and the Albany Pine Bush, NY (J.S. Ascher and T. McCabe, unpublished; not reported by Bried and Dillon, 2012).

Melittidae.—*Melitta melittoides*, the only melittid recorded during this study, was collected on its pollen host Malberry (*Lyonia ligustrina*) along with its potential cleptoparasite *Nomada rodecki* (see discussion below regarding this new association).

Megachilidae.—The 23 megachilid species (13% of all bee species recorded) from seven genera are either solitary (20) or cleptoparasitic (3) and account for 17 of the 22 cavity nesting species we encountered. Megachilids and in particular *Megachile* and *Osmia* may be collectively under-represented on Martha's

Vineyard (14 species in both genera combined) and other nearby islands relative to the adjacent mainland of SEMA (27 species). Collections from three of the Elizabeth Islands contribute only four additional megachilid species to the total known from the other offshore islands. One species we encountered, *Osmia similima* Smith, is of northern affinities but has been found recently from other coastal sites in Massachusetts (S. Kent, pers. comm.) and historically from Gardiners Island. *Osmia virga* Sandhouse has likely been under-recorded due to confusion with *O. felti* Cockerell (Giles and Ascher 2006), but has recently been collected in large numbers from various sandplain sites in New England, New York, and New Jersey and should be a locally important pollinator of blueberry (*Vaccinium* spp.).

Megachile addenda Cresson, a potentially important pollinator of cranberries (Cane et al. 1996), was found on Martha's Vineyard along with its cleptoparasite *Coelioxys immaculata* Cockerell. We also recorded *Megachile petulans* Cresson, a species of southern affinities, but not its likely cleptoparasite *Coelioxys germana* Cresson (see Ascher et al. 2014).

Apidae.—The 50 apid species (27.5% of the total) represent 11 genera comprising solitary (8), subsocial (5) or eusocial (10), and parasitic (27) species (Table 5) scattered among nine tribes in three subfamilies. Our non-corbiculate Apidae (i.e. all except *Bombus* and *Apis*) comprise 39 species in 9 genera, all of which are ground-nesters except the five species of Xylocopinae: four *Ceratina*, which use pithy stems, and the Carpenter Bee *Xylocopa virginica* (Linnaeus).

In 2010 one female *Anthophora walshii* was recovered from bee bowls set along a fire lane in the vicinity of Willow Tree Bottom on the West Tisbury side of the Manuel F. Correllus

State Forest, the ~5,100 acre core of island sandplain, predominantly pitch pine/scrub oak barrens crisscrossed by fire lanes and known for many years for its concentration of regionally rare insects. Intensive searches the following season (2011) resulted in collections of additional male and female specimens from flowers of the wild indigo *Baptisia tinctoria* (L.) R.Br. ex Ait.f. to the immediate north and east of the original trapping site, and trapping efforts yielded an additional female specimen further to the east, on the Edgartown side of the Forest along a fire-lane that supports significant concentrations of *Tephrosia virginiana* (L.) Pers. as well as *B. tinctoria*. That year (2011) an unusually heavy flowering of *B. tinctoria* covered large swaths along fire lanes, a previously unfamiliar phenomenon that was observed again in 2015. The range of *Anthophora walshii* is disjunct, with isolated populations in Virginia, southern New England and historically on Long Island, New York, where it was collected at Montauk Point in 1937 (Giles and Ascher 2006), separated from larger populations in the midwestern and central United States. In Massachusetts, it was recorded historically from Woods Hole, Barnstable County, and more recently from Cuttyhunk Island in the 1970s by Stage (2009), but we are not aware of other subsequent New England records.

Melissodes dentiventris Smith is at the northeastern limits of its range in Massachusetts where it was recorded in a taxonomic revision (LaBerge, 1961) from Woods Hole and Truro on Cape Cod. This composite specialist, sometimes associated with *Pityopsis* and with sandy soils (S. Droege, pers. comm.), is rare in recent collections from the northeastern United States. It appears commonly in the tallgrass prairie region and Ozarks in association with *Aster* species and other late

season composites far from sandy sites or *Pityopsis* (M. Arduser, pers. comm.).

The Apidae include 27 of the 46 parasitic bee species recorded from the island: 20 *Nomada*, 6 related cleptoparasitic nomadines in the Epeolini (5 species of *Epeolus* and *Triepeolus*) and Ammobatoidini (*Holcopasites calliopsidis* (Linsley); and the social parasite *Bombus* (*Psithyrus*) *citrinus* (Smith). With the exception of *N. articulata* Smith, which is associated with the halictid genus *Agapostemon*, and *N. rodecki*, which is newly associated with *Melitta* (see below), these *Nomada* are known or suspected to parasitize various, primarily vernal *Andrena* (Fig. 4). *Epeolus* and *Triepeolus* are mostly autumnal associated with *Colletes* and *Melissodes*, respectively, while *Holcopasites* is aestival and associated with *Calliopsis*. The recorded diversity of *Nomada* on Martha's Vineyard is moderate, roughly half the described species known from Massachusetts.

Noteworthy among our *Nomada* are *N. xanthura* Cockerell, a new state record, and three distinct morphospecies that appear to be undescribed. The first of these, referred to as *Nomada* sp. near *composita* Mitchell, differs from true *composita* in the extent of its pseudopygidial hairs and is also recorded from Gardiners Island other regional sites (Ascher et al. 2014; S. Droege, pers. comm.). We encountered this morphospecies in association with andrenids visiting *Salix humilis* Marsh., among them *Andrena tridens* Robertson and *A. imitatrix* Cresson, and may be a parasite of one or both of these (more likely the former). During the same series of collecting events, *Nomada luteoloides* Robertson was collected alongside its likely host *Andrena carlini* Cockerell. The second conspicuous morphospecies, belonging to *Gnathias* sensu Mitchell (1962), has been nicknamed "multi-spine" (S. Droege, pers. comm.) based

on exceptionally numerous and dense spines at the apex of the hind tibia. Both males and females of a third potentially undescribed *Nomada* species near *lepida* Cresson were collected at several sites in 2011.

The collection of *Nomada rodecki* together with *Melitta melittoides* suggests a new host-parasite association consistent with placement of this enigmatic cleptoparasite in the *basalis* species group of Alexander (1994), which includes European species associated with *Melitta* (Maximilian Schwarz, pers. comm.). *Nomada rodecki* has also been collected together with *Melitta americana* (Smith) on the mainland, in pine barrens at Plymouth, Massachusetts (M. Veit, unpubl.) and southern New Jersey (D. Cariveau, unpubl.). Presence of this enigmatic species so far north of the type locality of Southern Pines, North Carolina (Mitchell 1962) is noteworthy, as it represents a range extension (and new state and regional record), but consistent with disjunct occurrence of many other southern species at coastal New England sandplain sites (Jones and Kimball 1943; Goldstein et al., unpubl.).

Exotic Species

Only five exotic bee species were recorded, fewer than are routinely found at urban sites in the northeastern USA (Matteson et al. 2008). Two of these, the deliberately introduced European Honey Bee *Apis mellifera* and the adventive *Lasioglossum leucozonium* were among the most abundant and widespread species on the island (see below). The other adventive species recorded were *Andrena wilkella* (Kirby), *Anthidium manicatum* (Linnaeus), and *Megachile sculpturalis* Smith, all now very widely distributed and abundant in New England. The latter is a recent arrival to the U.S. and is known to occupy and even usurp tunnels

excavated by the Eastern Carpenter Bee *Xylocopa v. virginica*. Carpenter bees have themselves increased in abundance in the northeastern USA (cf. Leonard 1928), and are abundant on Nantucket where they were unrecorded historically (Johnson 1930). We treat *Megachile centuncularis* (L.) as native in this study, but its status in the Nearctic (native versus adventive) remains unresolved (Giles & Ascher 2006).

“Missing” Species

As our initial efforts in 2010 relied heavily on bee cups supplemented with hand-netting, we understood that at least a small but significant component of the bee fauna remained undocumented. We therefore evaluated our findings after the first year of sampling (2010) and targeted gaps in seasonal and taxonomic coverage by expanding the list of host flowers we targeted and directing more efforts towards early season (spring) and late season (fall) sampling. This included targeting *Andrena* and other bee visitors to spring-flowering willow (*Salix* spp.) and the late-season oligoleges or mesoleges (Cane and Sipes 2006) of Asteraceae including several *Colletes*, *Andrena*, and *Pseudopanurgus*. These efforts expanded the sampling of several genera, notably *Andrena* associated with willow, but failed to record any known bee specialists of *Ilex* spp.; *Prunus maritima* Marshall 1785 not Wangenh. 1787; *Lysimachia* spp., the host of *Macropis*; and *Hibiscus moscheutos* Welw. ex Hiern., the host of *Ptilothrix bombiformis* (Cresson).

Species occurring commonly in the region but not found on Martha’s Vineyard included four *Andrena* (*Gonandrena*) associated with *Cornus* and the *Andrena* subgenera *Leucandrena* and *Thysandrena*. The absence of *Osmia chalybea* Smith is noteworthy, given its occurrence on

Gardiners Island and the abundance on MV of an appropriate host plant *Cirsium horridulum* Michaux (S. Droege, pers. comm.). We regard the occurrence of this species in New England proper as in need of verification. Although, Mitchell (1962) reports it from Connecticut, and a Connecticut record is depicted in Rust (1974, Fig. 26), no details or voucher specimens are available, and confusion is possible with its close relative *O. texana* Cresson, a species with a more northern distribution.

Two pollen-collecting bumble bee species in subgenus *Bombus*, *B. affinis* and *B. terricola* are well documented to have declined regionally (Cameron et al. 2011; Bartomeus et al. 2013). Both were recorded from Martha’s Vineyard as recently as 1992 and 1956, respectively, but were not encountered in this study despite extensive and targeted effort. A 2009 report of *B. affinis* from nearby Cape Cod (Rich Hatfield, pers. comm.) represents its only recent record from the region. *Bombus terricola* may be rebounding in numbers in its core range to the north but remains absent or scarce at the southern edge of its historical range, including coastal southern New England. These two species as well as *Sphecodes autumnalis* and *S. illinoensis* (the latter recorded recently from the Elizabeth Islands) are the only species known historically from Martha’s Vineyard that our efforts did not recover.

Ecological and Behavioral Composition

Despite diverse study designs and methods, certain patterns emerge when comparing the ecological and behavioral composition of the Martha’s Vineyard bee fauna with that of other sites surveyed in the region.

Substrate.—Nearly three-quarters (73%) of the documented Martha’s

Vineyard bee species are soil nesters (Fig. 7; Table 4), and compared with other sites no nesting substrate appears conspicuously over- or under-represented among species recorded from Martha's Vineyard (cf. Massachusetts 71%; Black Rock Forest, 71%; Gardiners Island, 71%). We attribute the slightly higher percentage of soil-nesting species on Martha's Vineyard in part to relatively more effective sampling of halictids via bee cups (cf. Goldstein and Scott, 2015).

Behavior and sociality.—The proportion of bee species exhibiting different behavioral syndromes (Solitary: 50%; Subsocial: 2%; Eusocial: 23%; Parasitic: 25%) is typical for the region, with solitary species dominant (Fig. 8, Table 5). Parasitic species comprise 25% of the island fauna, comparable to that of Massachusetts as a whole. In contrast to the many parasitic species represented in our sampling by few individuals, the more abundant and widespread species tended to be eusocial, soil-nesting polylectic Halictinae, especially in late summer and fall when both workers and males are common (Fig. 4; cf. Ginsberg 1983; Giles & Ascher 2006; see 'Abundance and Distribution', below).

Oligolectic species.—The 26 pollen specialists we recorded from Martha's Vineyard comprise 14% of the island fauna (Fig. 9) and, although fewer than half of the 59 known Massachusetts oligoleges (Fig. 10), most (90%) of the 29 known oligoleges currently known from the Massachusetts offshore islands; the recorded diversity of flower specialists recorded from Nantucket and Cuttyhunk (12 species each) is much lower. The diversity of oligoleges on Martha's Vineyard relative to other offshore islands parallels the island's documented botanical diversity of more than 700 native plant species (Swanson and Knapp 1999; Cullina et al. 2011).

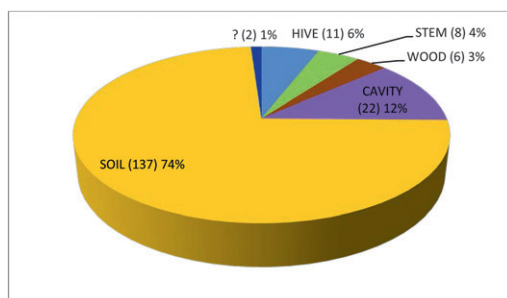


Fig. 7. Nesting substrates of 186 Martha's Vineyard bee species.

Martha's Vineyard's known oligoleges and mesoleges (treated together with oligoleges in our analyses) are associated with 8 plant families (Fig. 10, Appendix), with Asteraceae (14 species) and Ericaceae (6 species) the hosts for the greatest numbers of bees. Specialists of willows (*Salix*) may be under-sampled on the island (see above), given that species such as *A. wellesleyana* Robertson known from mainland sandplains were not recorded on MV. The relatively diverse bee fauna associated with late-season Asteraceae seems typical for the region including its islands (Table 5). Among the four plant families represented by the hosts of specialist bees recorded from Gardiners Island (Ascher et al. 2014), 13 of 17 of these oligoleges or mesoleges were associated with Asteraceae, of which only *Andrena canadensis* Dalla Torre was not recorded from Martha's Vineyard but which is known from the Elizabeth Islands. Salicaceae (1), Cucurbitaceae (1), and Ericaceae (2) account for the remaining four Gardiners Island oligolectic bee species.

Ericaceae specialists, accounting for 6 of 26 oligolectic bee species, include several associates of blueberry/cranberry (*Vaccinium*): *Colletes validus*, *Andrena bradleyi*, *A. carolina*, *Osmia virga*, and *Megachile addenda*. Blueberry and cranberry are important hosts for many regionally rare Lepidoptera that persist on Martha's

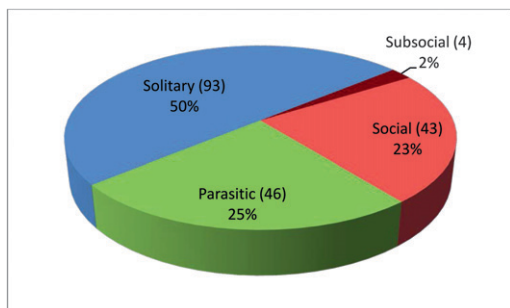


Fig. 8. Behavioral composition of 186 Martha's Vineyard bee species with respect to sociality and parasitic status.

Vineyard. The presence of *Vaccinium*-associated bees may reflect the apparency of ericads in various coastal grassland, heathland, and shrubland types (Dunwiddie et al. 1996), and along with the very abundant *Andrena carlini*, these bees represent important unmanaged pollinators. *Habropoda laboriosa* (Fabricius), a well known visitor of blueberries, was not found, but has recently been recorded from Gardiners Island (Ascher et al. 2014), the Elizabeth Islands (S. Kent, pers. comm.), southern Connecticut, mainland Massachusetts, and New Hampshire (a new state record based on a specimen examined in the University of New Hampshire collection) where it reaches its northeastern limit.

Other noteworthy ericad specialists were recorded in association with Maleberry (*Lyonia ligustrina*): *Melitta melittoides*, its presumed cleptoparasite *N. rodecki* (see above), and *Colletes productus*, a regional specialist on Maleberry known from other ericads elsewhere in its range (e.g. *Vaccinium arboreum* in the Ozarks and Ouichitas; M. Arduser, pers. comm.). We did not record *Perdita novaeangliae* Viereck, another *Lyonia*-specialist known from the southern New England mainland. Maleberry was actively sampled by net and with bee cups during its late/June early July flowering

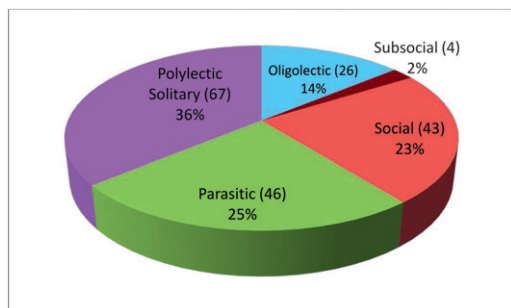


Fig. 9. Behavioral composition of 186 bee species recorded from Martha's Vineyard showing proportion of oligolectic (solitary), polylectic solitary, subsocial (polylectic), eusocial (polylectic), parasitic bee species (n=186).

season at three sites in West Tisbury where significant Maleberry had been identified: Long Point Wildlife Refuge, Polly Hill Arboretum, and the Frances Newhall Woods preserve. Two of these were unproductive, but the Long Point site, a wetland extension of Middle Point Cove, yielded *Colletes productus*, *Melitta melittoides* and its cleptoparasite *Nomada rodecki*. *Melitta melittoides*, the only species of Melittidae recorded from Martha's Vineyard, is the first *Melitta* and the only recent record of any melittid from the offshore islands. Although Johnson (1930) recorded the *Lysimachia* specialist *Macropis nuda* Provancher from Nantucket, the only specimen among Johnson's extant collections is from New Hampshire, and no *Macropis* have been observed at *Lysimachia* despite its being targeted during our work. The newly proposed association of *Nomada rodecki* with *M. melittoides* is unique among North American *Nomada* species, which usually parasitize *Andrena* or, less commonly *Agapostemon* or *Eucera* (*Synhalonia*).

Abundance and Distribution

Based on over 14,500 specimens databased, eusocial halictine sweat bees

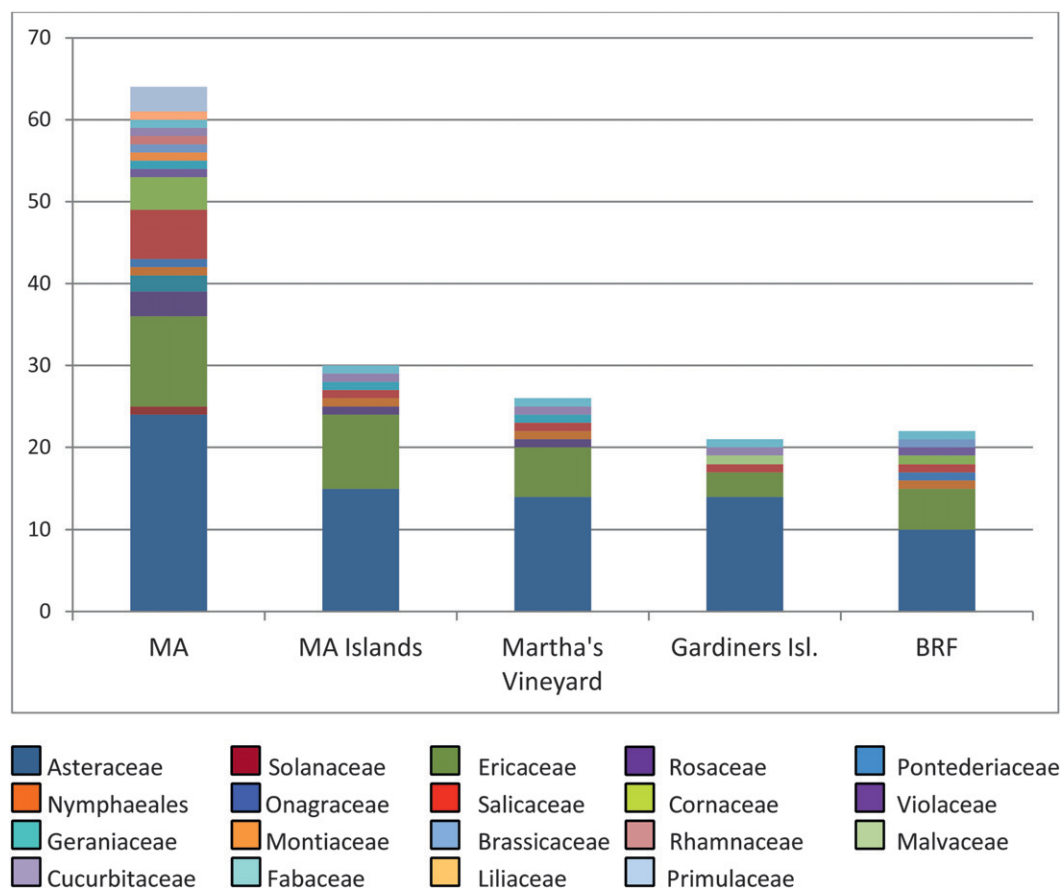


Fig. 10. Representation of plant families among host plants of oligolectic (and mesolectic) bees on Martha's Vineyard compared with other eastern sites.

account for the 9 most abundant species (comprising 9061 specimen records; Fig. 11), all of which were recorded from every town. This underrepresents the true dominance of these species because the only specimen material left unprocessed consisted of these 9 species (see Methods, above). Among the 15 most abundant species recorded, the only two non-halictids were the solitary mining bee *Andrena* (*Melandrena*) *carlini* (10th most abundant) and the eusocial bumble bee *Bombus impatiens* (14th most abundant). These are among the most conspicuous and presumably important pollinators on Martha's Vineyard; *A. carlini* of spring-blooming apples and

blueberries; *B. impatiens* of buzz-pollinated Solanaceae and other crops in summer, when workers become numerous, into late fall. In contrast to the most commonly encountered species, most of which are primitively eusocial species, only 2 of the 26 species recorded as singleton records are eusocial, *Bombus fervidus* (Fabricius) and *Lasioglossum coeruleum* (Robertson), the latter a wood nester and the only non-parasitic halictid in this "rare" cohort. Of the remaining 24 species represented by singleton records in our efforts, 10 are parasitic (4 *Nomada*, 2 each of *Sphecodes* and *Triepeolus*, *Stelis lateralis* Cresson and *Bombus citrinus*) and 13 solitary pollen-collectors (4 *Andrena*,

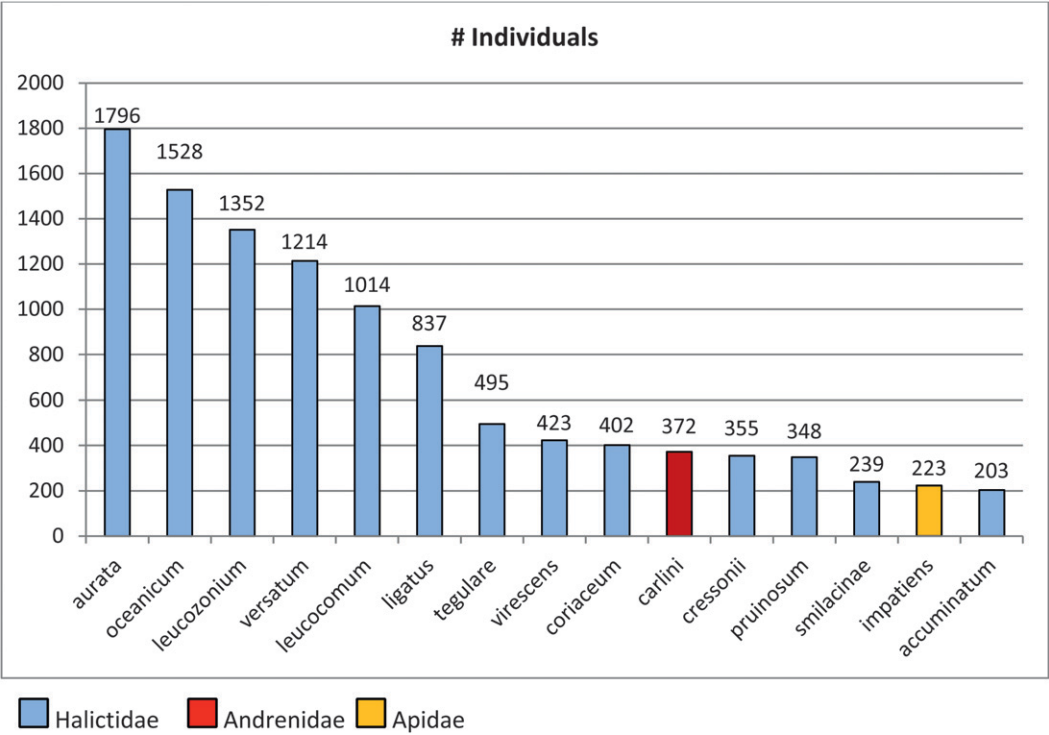


Fig. 11. The ten most numerically abundant bee species recorded in this study with number of individuals databased indicated.

3 *Melissodes*, 2 *Colletes*, 2 *Megachile*, and 1 each of *Hoplitis*, *Hylaeus*, and *Melitta*).

The distribution of bees across Martha’s Vineyard’s six towns provides a measure of how widely bees were documented. Of the 182 species recorded (i.e. not including the four species known only from historical records), 26 occurred in all 6 towns (cf. Fig. 2). An additional 16 species are recorded from five of the six towns, and in 9 of these cases the “missing” town was one of the two least intensively sampled (Oak Bluffs and Tisbury/Vineyard Haven). Nearly 25% of species, 45 of the 182 documented, were recorded from only a single town, and more than half (24) of these were represented by singleton specimens; another 50 species were recorded from two towns. This combined cohort of 95

narrowly distributed bees is dominated by 49 species of solitary bees (52.58%) and 31 parasitic bees (32.63%). By comparison, parasitic species are represented by only 7 (15.56% of species) occurring in 3–4 towns and 6 (8.33%) among the most widespread cohort, those occurring in 5–6 towns (Fig. 12). Looked at another way, 49 of 92 (52.63%) solitary species and 30 of 44 (73.17%) parasitic species were retrieved from only 1 or 2 of the 6 towns, as opposed to 32.61% (15 of 46) of the more widespread, more wide-ranging, or simply more numerous eusocial bees.

Of the 26 most widespread species, i.e. those occurring in all six towns, 13 (50%) (50%) are polylectic solitary species, 11 (42.31%) eusocial, 6 (23.1%) parasitic, and 1 subsocial (*Ceratina calcarata* Robertson). Among the widespread bees are two non-native species, *Lasioglossum*

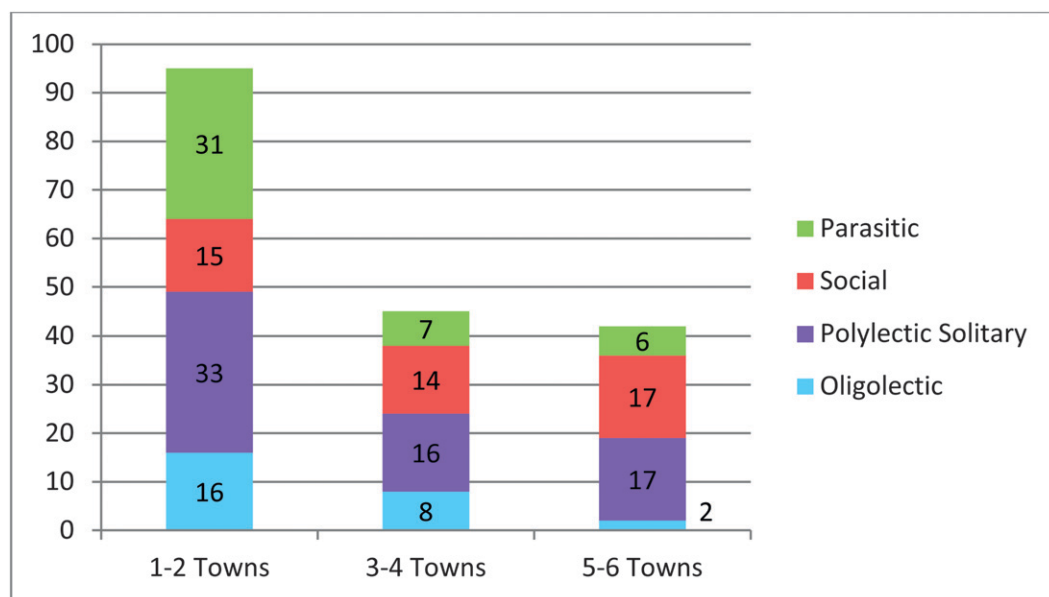


Fig. 12. Cohorts of bees collected from 1–2 towns (95 species), 3–4 towns (45 species), and 5–6 towns (42 species) according to behavioural syndrome. Four species known only from historical records are not included (n=182).

leucozonium and *Apis mellifera*. A majority of the more widespread oligoletes (6 of 8 occurring in 3 or more towns and 3 of 5 recorded from 4 or more towns) are associated with Asteraceae or *Vaccinium* (Ericaceae). Two Ericaceae specialists regionally associated with *Vaccinium*, *Andrena bradleyi* and *Osmia virga*, were each recorded from four towns, and another, *A. carolina*, was recorded from two. *Calliopsis andreniformis* Smith, often but not exclusively associated with Fabaceae, was recorded from five of the six island towns.

Complementarity Across Samples

An examination of the overlap in species composition across the primary sampling years (2010–2011) suggests an additional disparity in the degree to which eusocial bees are sampled relative to oligolectic and parasitic bees

(Figs. 13–14). Seventy-one species were collected in only a single year, with eusocial and subsocial bees accounting for only 6 of these (8.45%). In contrast, 39 of 47 social and subsocial bees encountered (82.98%) were sampled in both years, representing over a third of the 110 species persistent across samples. None of the other behavioral cohorts exhibits this degree of asymmetry: Parasitic bee species were evenly distributed, at least numerically, between year-specific and persistent species cohorts (23 and 21 species, respectively); oligolectic bees were the least persistent, with only 10 of 26 species recorded in both years; and 40 of 66 polylectic solitary bees were recovered in both years.

DISCUSSION

Declines and extirpations of native bees are of concern in their own right, but have drawn more general attention as a function

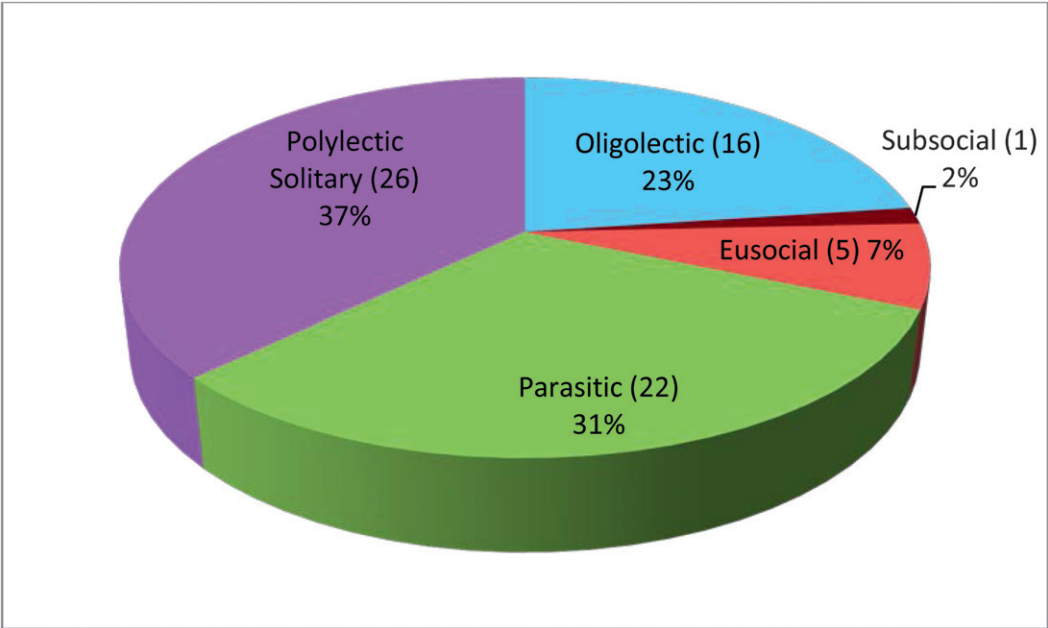


Fig. 13. Behavioral composition with respect to sociality, parasitic status, and pollen specialization of 71 bee species collected in only one of the two comparable sampling years, either 2010 (n=25) or 2011 (n=46) but not both. Five species collected from incomparable sample in subsequent years (*Andrena spiraeana*) or known only from historical records are excluded.

of their interactions with flowering plants, and their presumptive roles in sustaining biological diversity in the broad sense (Potts et al. 2010). An understanding of local bee faunas, including those of islands, may help not only to identify patterns of decline among different taxonomic groups or behavioral cohorts of bees, but also to identify and understand potential refugia, if they exist. This work reinforces that of earlier authors (e.g. Jones and Kimball 1943; Ellison 2012) who commented to the effect that Massachusetts’ offshore islands support surprisingly diverse insect communities. Although many bees may be less likely thwarted by water barriers than many moths, the role of Martha’s Vineyard in supporting disjunct and remnant populations of bees parallels patterns in other insect groups, especially Lepidoptera. As has been seen in such groups, bee species such as *Anthophora walshii* have persisted

on Martha’s Vineyard despite a lack of recent records from the northeastern USA. Isolation does not appear to have buffered populations of *Bombus* from apparently systemic threats. *Bombus affinis* and *B. terricola* (both in subgenus *Bombus*) have disappeared in parallel with mainland declines, suggesting that the factors involved were not impeded by a water boundary.

Bombus (Thoracobombus) pensylvanicus (DeGeer), well known historically from the northeastern USA but now scarce regionally was, like *B. affinis* and *B. terricola*, found on two of the Elizabeth Islands in the 1970s by Stage but not in subsequent re-surveys (Stage 2009). *Bombus terricola* was recorded historically from Nantucket (Johnson 1930). The socially parasitic species *B. ashtoni* (Cresson) seems likely to have occurred on Martha’s Vineyard in association

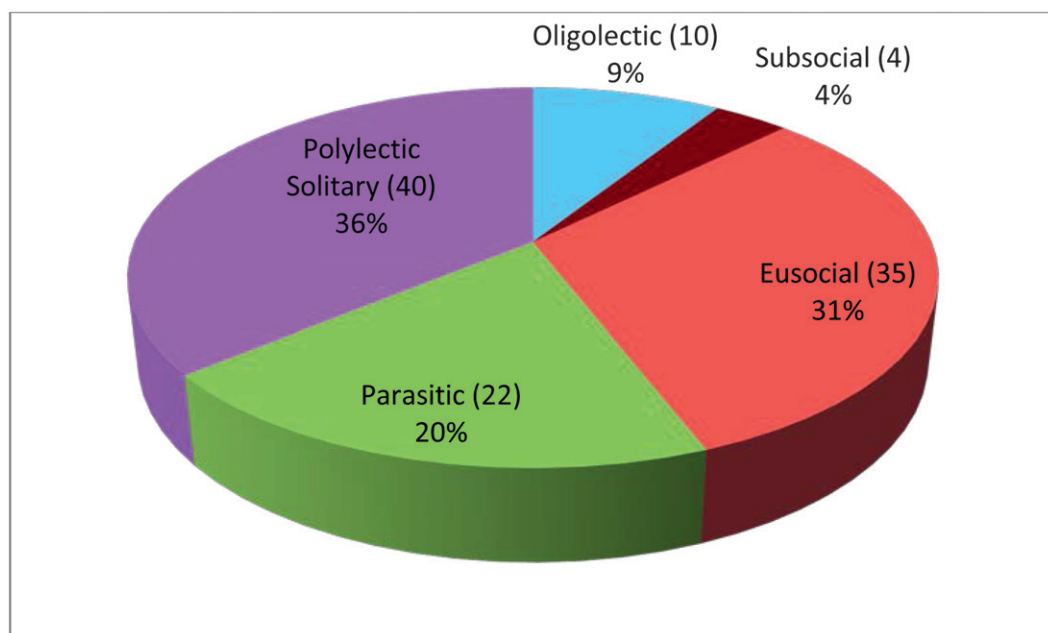


Fig. 14. Behavioral composition of 110 species persistent across 2010 and 2011 samples, i.e. recorded both years. Note higher persistence across samples of eusocial polylectic bees relative to oligolectic solitary species.

with its host species *B. affinis* and *B. terricola*. The absence of all four of these *Bombus* species from our collections on Martha's Vineyard and other islands is consistent with strong evidence of regional declines (Cameron et al. 2011; Bartomeus et al. 2013, 2014) more plausibly attributed to pathogens spread through use of bumble bees for greenhouse pollination rather than to systemic declines in floral resources or habitat. As bumblebees have been brought to Martha's Vineyard for greenhouse pollination, it is unsurprising that island bumblebees share vulnerability to exposure with mainland populations.

Bombus (*Pyrobombus*) *sandersoni* Franklin, newly recorded from Martha's Vineyard, may be generally under-reported because its color pattern is nearly identical to that of *B. vagans* Smith and to a lesser extent *B. perplexus* Cresson. As identification criteria for these species are better

understood, records are increasing, especially in samples from bogs and forest sites (Giles and Ascher 2006; C. T. Maier, pers. comm.). Assessments of this species as threatened in a recent assessment of historical specimens (Colla et al. 2012b) may be untenable, as identification problems contributed to under-recording of *B. sandersoni* in specimen databases then available (relevant specimens were on loan at the time the data were used) and prevent its routine identification from images, leading to lack of representation in citizen science databases, e.g., www.bugguide.net. Regular recent collections of *B. fervidus* (e.g., from Nantucket; Goldstein unpubl.) and routine appearance of identifiable images in online databases may contradict assessment of this species as threatened (Colla et al. 2012b). Truly declining species, in contrast, tend to be reported rarely and locally (*B. affinis*) or not at all (*B. ashtoni*) in available recent data sources.

Species-specific conservation efforts, such as captive rearing and threatened species regulation are unlikely to be undertaken on a widespread basis and are not likely to prove effective either in stemming systemic bee declines or addressing their causes. Notwithstanding the controversial role of pesticides and the impacts of introduced parasites on *Bombus* spp., the most conspicuous systemic threat to most bees, other pollinators, and herbivorous insects in general is the degradation of plant communities and their associated soils. A number of lepidopteran and coleopteran open-habitat specialists (e.g. *Speyeria idalia* (Drury), Nymphalidae; *Grammia arge* (Drury), Erebididae; *Pyrrhia aurantiago* (Guenée), Noctuidae; *Nicrophorus americanus* (Olivier), Silphidae; *Strategus antaeus* (Drury), Scarabaeidae) were extirpated from Martha's Vineyard during the 20th century, and many others associated with coastal sandplain communities in particular face severe pressure. In addition to unregulated development and inadequate natural areas management, an increasing threat is that of deer browsing, which threatens understory plants regionally (Rawinski 2008; Urbanek et al. 2012). Since being hunted to extirpation from the island over a century ago, deer have recolonized and their numbers are now estimated at 45–53 per square mile. (T. Simmons pers. comm.). Although there are not enough available data to characterize specific impacts of deer browse on Martha's Vineyard, it has been supposed that deer contributed to a reduction of available floral hosts and their bee specialists on smaller islands (Ascher et al. 2014), and we suspect that some important bee host plants such as *Helianthus divaricatus* L. recorded historically from Martha's Vineyard have been extirpated.

Although the dozens of small farms on Martha's Vineyard comprise only a fraction

of the extensive area that was historically farmed or grazed, avocational beekeeping has surged in recent years. *Apis mellifera* numbers among the 24 most widespread species in our samples. It remains to be seen to what extent the more than 100 colonies currently in operation (R. Baird, pers. comm.) will impact native pollinators and their host plants.

IMPLICATIONS FOR SAMPLING AND MONITORING PROGRAMS

Although the numbers of species recorded in consecutive years were compatible (130 in 2010 versus 140 in 2011), only 111 of 182 species were common to both years' efforts. This limited overlap highlights the limits of even an intensive single year survey, suggesting high variance in bee populations and/or in the reliability with which they can be sampled. Based on recorded bee occurrences from the Elizabeth Islands (Stage 2009; Kent et al., unpubl.) and Nantucket (Johnson 1930; Goldstein et al. unpubl.), and from the adjacent mainland counties of Plymouth, Bristol, and Barnstable on Cape Cod, we compiled a list of 77 species potentially occurring on Martha's Vineyard but not yet recorded, including 14 oligolectic associates of Asteraceae (3), Ericaceae (3), Myrsinaceae (=Primulaceae sensu lato; 3), Pontederiaceae (2), Salicaceae (1), Cornaceae (1), and Liliaceae (1) (Table 3). Adding these to the 186 species documented thus far yields 263 species as an upper limit for potential occurrences of described native species on the island. Using SPECRICH (Burnham and Overton 1979; <http://www.mbr-pwrc.usgs.gov/software/specrich.html>) calculated upon just the species observed in the course of this work, we obtain a more plausible interpolated estimate of 208 species (std. err.=7.4833). Regardless, we do not consider it likely that more than 65% of the bee fauna was documented in either year of intensive sampling.

The idea that intrinsic behaviors influence either bee distributions or the reliability with which they are sampled bears directly on the design of monitoring efforts. The behavioral composition of bee assemblages is trophically complex, and parasitic species that rely on the provisioned nests of other bees may afford an indirect gauge of the stability of bee communities which in turn reflects available pollen resources (Sheffield 2013). One might anticipate oligolectic and cleptoparasitic bees to have more limited flight seasons (Fig. 5) and to be more localized and less readily encountered than polylectic eusocial halictines, although Jauker et al. (2013) found small-bodied eusocial bees to be more sensitive to habitat loss and fragmentation. In our study, oligolectic and parasitic species are indeed better represented within the cohort of localized bees than among more frequently encountered and widespread species, which are dominated by eusocial polylectic halictids (Fig. 12). Whether overlap between the 2010 and 2011 sampling years (Figs. 13–14) speaks to abundance, persistence, or vulnerability to sampling, the behavioral composition of the species that persisted across samples, versus those that were unique to either year's efforts, seem to echo that of the species most widespread geographically. The result that over half the collective fauna of parasitic and oligolectic bees could be missed in a given year, versus less than 15% of the eusocial bee fauna, should raise concerns about the reliability of short-term sampling efforts. The limited sampling overlap across consecutive years and the predominance of rarely sampled species also underscores a need for caution when inferring declines or reporting extirpations ("extinctions") of bees or bee-plant associations after short-term sampling effort (cf. Burkle et al. 2013).

Bee surveys and calls for pollinator monitoring initiatives are on the rise, including ambitious estimates for detecting minuscule faunal shifts both quickly and economically (LeBuhn et al. 2012). In part, it has been our aim to illustrate the necessity of applying taxonomic and behavioral information to obtaining and interpreting faunal data. In our view, both the year-to-year variability in bee samples and the potential for sampling bias against behaviorally relevant cohorts of bees such as pollen specialists and parasitic species (Goldstein and Scott 2015), highlight the need for intensive and repeated quantitative sampling. But this goal seems unrealistic if undertaken at the expense of detailed and time-consuming taxonomic evaluation required to obtain and interpret samples properly. As others have noted both on general principles and with specific regard to sampling bees (Gagic et al. 2014), the risks of interpreting raw species numbers as a surrogate for community integrity or some other emergent property for ecological risk assessment is significant, and as we examined the findings of this intensive but relatively small survey, we found suggestions such as LeBuhn et al.'s (2012) increasingly unrealistic. Although we do not purport to assess community integrity or identify faunal decline in this study, we have presented compositional aspects of our samples that we suspect reflect more general limitations of common sampling techniques in ways that could either mask or be mistaken for actual patterns. The idea that anything less than the most prohibitively intensive sampling can be standardized, particularly across years, is in our view questionable, and its limitations amplified when taxonomically mediated behavioural variables are not accommodated. Such variables potentially introduce "concealed trait interference" (Jauker

et al. 2013) and may be necessary to account for potential bias against species that represent sensitive and relevant gauges of environmental change (cf. Sheffield et al. 2013). We hasten to acknowledge that although taxon-specific declines have been identified, as in *Bombus* (Cameron et al. 2011), neither collection data-mining (Bartomeus et al. 2013) nor *in situ* research (Jauker et al., 2013) have detected generalized or systemic declines associated with parasitic behaviors or oligolecty. In fact, Jauker et al. (2013) describe the counter-intuitive finding that eusocial bees as a cohort appeared more vulnerable to habitat loss and fragmentation than solitary or parasitic bees, but were able to attribute this phenomenon to acute vulnerabilities of bumble bees. Regardless of whether parasitic and oligolectic bees show evidence of imminent threat or systemic decline, the basis for their relevance to assessing the stability of pollinator assemblages lies in the same biological reasons underlying their potential vulnerability—pollen specialization and dependence on pollinating bees as hosts—reasons exclusive (but not independent) of the small population sizes we suspect render them susceptible to under-sampling regardless of decline. Even in long-studied areas such as coastal New England many species remain to be described and adequately diagnosed, and essential ecological data such as floral, edaphic, and host-parasite associations have yet to be documented. The example of *Nomada rodecki* represents a host-cleptoparasite relationship potentially novel to the New World at the family level and the addition of a new species group, equivalent to a subgenus in other bee taxa, to the New World fauna. At the very least, our growing understanding of the north-eastern offshore islands fauna should help us refine our understanding of

faunal persistence and of how readily bees move among islands and other isolated areas.

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APPENDIX. BEE SPECIES RECORDED FROM MARTHA'S VINEYARD, DUKES COUNTY, MASSACHUSETTS. THE "NEST" COLUMN RECORDS BROADLY DEFINED NESTING PREFERENCES IDENTIFIED AS FOLLOWS: C=CAVITY; H=HIVE; S=SOIL; P=PITHY STEMS; R=RESIN CELL; W=WOOD. DETAILS OF NESTING PREFERENCES ARE ANNOTATED WITH SUPERScript NUMBERS AS FOLLOWS:

¹Cells of cellophane-like material

²Variable clumps of cells dug in rotting wood

³E.g., rotting logs

⁴On rocks, twigs, etc.; isolated single cells made of resin

⁵Lined with woolly substance such as trichome hairs (carder bees)

⁶Lined with resin

⁷Lined with leaves or other plant material

⁸Burrows excavated by bees in hard wood such as beams and other solid timber

Brackets [] refer to the known or inferred nest substrate of the host bee in cases of parasitic species.

The "status" column records broad behavioral traits as follows: B=subsocial; E=eusocial; P=parasitic; S=solitary (including communal species, e.g., of *Agapostemon* and *Lasioglossum* sensu stricto). The "host" column records host plant families for pollen-specialist bees including oligolectic (and mesolectic) species, abbreviated as follows: Ast=Asteraceae; Eri=Ericaceae; Nym=Nymphaeales; Sal=Salicaceae; Ros=Rosaceae; Ger=Geraniaceae; Fab=Fabaceae; Cuc=Cucurbitaceae. The "SE MA" column identifies species newly documented from southeastern Massachusetts, i.e. Barnstable, Bristol, Dukes, Nantucket, and Plymouth counties.

* Species accepted or suspected to be exotic.

† Recorded from Martha's Vineyard historically but not by us.

APPENDIX.

| | NEST | BEHAV | HOST | SE MA |
|--|----------------|-------|------|-------|
| COLLETIDAE | | | | |
| <u>Colletinae</u> | | | | |
| <i>Colletes americanus</i> Cresson, 1868 | S ¹ | S | | |
| <i>Colletes compactus</i> Cresson, 1868 | S ¹ | S | Ast | |
| <i>Colletes inaequalis</i> Say, 1837 | S ¹ | S | | |
| <i>Colletes productus</i> Robertson, 1891 | S ¹ | S | Eri | + |
| <i>Colletes simulans armatus</i> Patton, 1879 | S ¹ | S | Ast | |
| <i>Colletes solidaginis</i> Swenk, 1906 | S ¹ | S | | |
| <i>Colletes speculiferus</i> Cockerell, 1927 | S ¹ | S | | + |
| <i>Colletes thoracicus</i> Smith, 1853 | S ¹ | S | | |
| <i>Colletes validus</i> Cresson, 1868 | S ¹ | S | | |
| <u>Hylaeinae</u> | | | | |
| <i>Hylaeus (Prosopis) affinis</i> (Smith, 1853) | C ¹ | S | | |
| <i>Hylaeus (Hylaeus) annulatus</i> (Linnaeus, 1758) | C ¹ | S | | + |
| <i>Hylaeus (Hylaeus) mesillae cressoni</i> (Cockerell, 1907) | C ¹ | S | | |
| <i>Hylaeus (Prosopis) modestus modestus</i> Say, 1837 | C ¹ | S | | |
| <i>Hylaeus (Prosopis) schwarzii</i> (Cockerell, 1896) | C ¹ | S | | |
| HALICTIDAE | | | | |
| <u>Halictinae</u> | | | | |
| <u>Augochlorini</u> | | | | |
| <i>Augochloropsis (Paraugochloropsis) metallica</i> (F., 1793) | S | S | | |
| <i>Augochlorella aurata</i> (Smith, 1853) | S | E | | |
| <i>Augochlora (Augochlora) pura</i> (Say, 1837) | W ² | S | | |
| <u>Halictini</u> | | | | |
| <i>Agapostemon (Agapostemon) sericeus</i> (Förster, 1771) | S | S | | |
| <i>Agapostemon (Agapostemon) splendens</i> (Lepeletier, 1841) | S | S | | |
| <i>Agapostemon (Agapostemon) texanus</i> Cresson, 1872 | S | S | | |
| <i>Agapostemon (Agapostemon) virescens</i> (Fabricius, 1775) | S | S | | |
| <i>Sphecodes aroniae</i> Mitchell, 1960 | [S] | P | | + |
| <i>Sphecodes atlantis</i> Mitchell, 1956 | [S] | P | | + |
| † <i>Sphecodes autumnalis</i> Mitchell, 1956 | [S] | P | | |
| <i>Sphecodes confertus</i> Say, 1837 | [S] | P | | |
| <i>Sphecodes coronus</i> Mitchell, 1956 | [S] | P | | |
| <i>Sphecodes cressonii</i> (Robertson, 1903) | [S] | P | | |
| <i>Sphecodes davisii</i> Robertson, 1897 | [S] | P | | |
| <i>Sphecodes dichrous</i> Smith, 1853 | [S] | P | | |
| <i>Sphecodes heraclei</i> Robertson, 1897 | [S] | P | | |
| † <i>Sphecodes illinoensis</i> (Robertson, 1903) | [S] | P | | |
| <i>Sphecodes mandibularis</i> Cresson, 1872 | [S] | P | | |
| <i>Sphecodes minor</i> Robertson, 1898 | [S] | P | | |
| <i>Sphecodes pimpinellae</i> Robertson, 1900 | [S] | P | | |
| <i>Sphecodes ranunculi</i> Robertson, 1897 | [S] | P | | |
| <i>Sphecodes townesi</i> Mitchell, 1956 | [S] | P | | + |
| <i>Halictus (Nealictus) parallelus</i> Say, 1837 | S | E | | |
| <i>Halictus (Odontalictus) ligatus</i> Say, 1837 | S | E | | |
| <i>Halictus (Protohalictus) rubicundus</i> (Christ, 1791) | S | E | | |
| <i>Halictus (Seladonia) confusus confusus</i> Smith, 1853 | S | E | | |
| <i>Lasioglossum (Lasioglossum) acuminatum</i> McGinley, 1986 | S | S | | |
| <i>Lasioglossum (Lasioglossum) coriaceum</i> (Smith, 1853) | S | S | | |

APPENDIX. Continued.

| | NEST | BEHAV | HOST | SE MA |
|--|----------------|-------|------|-------|
| <i>Lasioglossum (Lasioglossum) fuscipenne</i> (Smith, 1853) | S | S | | |
| * <i>Lasioglossum (Leuchalictus) leucozonium</i> (Schränk, 1781) | S | S | | |
| <i>Lasioglossum (Evyllaes) cinctipes</i> (Provancher, 1888) | S | E | | |
| <i>Lasioglossum (Dialictus) admirandum</i> (Sandhouse, 1924) | S | E | | |
| <i>Lasioglossum (Dialictus) albipenne</i> (Robertson, 1890) | S | E | | + |
| <i>Lasioglossum (Dialictus) bruneri</i> (Crawford, 1902) | S | E | | |
| <i>Lasioglossum (Dialictus) coeruleum</i> (Robertson, 1893) | W ³ | E | | |
| <i>Lasioglossum (Dialictus) coreopsis</i> (Robertson, 1902) | S | E | | |
| <i>Lasioglossum (Dialictus) cressonii</i> (Robertson, 1890) | W ³ | E | | |
| <i>Lasioglossum (Dialictus) georgeickworti</i> Gibbs, 2011 | S | E | | |
| <i>Lasioglossum (Dialictus) heterognathum</i> (Mitchell, 1960) | S | E | | |
| <i>Lasioglossum (Dialictus) imitatum</i> (Smith, 1853) | S | E | | |
| <i>Lasioglossum (Dialictus) katherinae</i> (Gibbs, 2011) | S | E | | + |
| <i>Lasioglossum (Dialictus) leucocomum</i> (Lovell, 1908) | S | E | | |
| <i>Lasioglossum (Dialictus) lineatulum</i> (Crawford, 1906) | S | E | | |
| <i>Lasioglossum (Dialictus) marinum</i> (Crawford, 1904) | S | E | | |
| <i>Lasioglossum (Dialictus) nigroviride</i> (Graenicher, 1911) | S | E | | |
| <i>Lasioglossum (Dialictus) oceanicum</i> (Cockerell, 1916) | S | E | | |
| <i>Lasioglossum (Dialictus) oblongum</i> (Lovell, 1905) | W ³ | E | | |
| <i>Lasioglossum (Dialictus) pilosum</i> (Smith, 1853) | S | E | | |
| <i>Lasioglossum (Dialictus) pruinosum</i> (Robertson, 1892) | S | E | | |
| <i>Lasioglossum (Dialictus) rozeni</i> Gibbs, 2011 | [S?] | P | | |
| <i>Lasioglossum (Dialictus) smilacinae</i> (Robertson, 1899) | S | E | | |
| <i>Lasioglossum (Dialictus) subviridatum</i> (Cockerell, 1938) | W ³ | E | | |
| <i>Lasioglossum (Dialictus) tegulare</i> (Robertson, 1890) | S | E | | |
| <i>Lasioglossum (Dialictus) timothyi</i> (Gibbs, 2010) | S? | E | | |
| <i>Lasioglossum (Dialictus) versans</i> (Lovell, 1905) | S | E | | |
| <i>Lasioglossum (Dialictus) versatum</i> (Robertson, 1902) | S | E | | |
| <i>Lasioglossum (Dialictus) vierecki</i> (Crawford, 1904) | S | E | | |
| <i>Lasioglossum (Dialictus) zephyrium</i> (Smith, 1853) | S | E | | |
| <i>Lasioglossum (Hemihalictus) birkmanni</i> (Crawford, 1906) | S | S | | |
| <i>Lasioglossum (Hemihalictus) nelumbonis</i> (Robertson, 1890) | S | S | Nym? | + |
| <i>Lasioglossum (Hemihalictus) pectorale</i> (Smith, 1853) | S | S | | |
| <i>Lasioglossum (Sphecodogastra) quebecense</i> (Crawford, 1907) | S | S | | |

ANDRENIDAE

Andreninae

Andrenini

| | | | | |
|---|---|---|-----|---|
| <i>Andrena (Andrena) carolina</i> Viereck, 1909 | S | S | Eri | |
| <i>Andrena (Andrena) frigida</i> Smith, 1853 | S | S | Sal | + |
| <i>Andrena (Andrena) mandibularis</i> Robertson, 1892 | S | S | | |
| <i>Andrena (Andrena) milwaukeeensis</i> Graenicher, 1903 | S | S | | + |
| <i>Andrena (Andrena) rufosignata</i> Cockerell, 1902 | S | S | | |
| <i>Andrena (Andrena) tridens</i> Robertson, 1902 | S | S | | |
| <i>Andrena (Callandrena s.l.) asteris</i> Robertson, 1891 | S | S | Ast | |
| <i>Andrena (Callandrena s.l.) braccata</i> Viereck, 1907 | S | S | Ast | |
| <i>Andrena (Callandrena s.l.) placata</i> Mitchell, 1960 | S | S | Ast | |
| <i>Andrena (Callandrena s.l.) simplex</i> Smith, 1853 | S | S | Ast | |
| <i>Andrena (Cnemidandrena) hirticincta</i> Provancher, 1888 | S | S | Ast | |
| <i>Andrena (Cnemidandrena) nubecula</i> Smith, 1853 | S | S | Ast | |

APPENDIX. Continued.

| | NEST | BEHAV | HOST | SE MA |
|--|----------------|-------|-------------|-------|
| <i>Andrena</i> (<i>Conandrena</i>) <i>bradleyi</i> Viereck, 1907 | S | S | Eri | |
| <i>Andrena</i> (<i>Holandrena</i>) <i>cressonii</i> <i>cressonii</i> Robertson, 1891 | S | S | | |
| <i>Andrena</i> (<i>Larandrena</i>) <i>miserabilis</i> Cresson, 1872 | S | S | | |
| <i>Andrena</i> (<i>Melandrena</i>) <i>carlini</i> Cockerell, 1901 | S | S | | |
| <i>Andrena</i> (<i>Melandrena</i>) <i>commoda</i> Smith, 1879 | S | S | | |
| <i>Andrena</i> (<i>Melandrena</i>) <i>hilaris</i> Smith, 1853 | S | S | | + |
| <i>Andrena</i> (<i>Melandrena</i>) <i>vicina</i> Smith, 1853 | S | S | | |
| <i>Andrena</i> (<i>Micrandrena</i>) <i>melanochroa</i> Cockerell, 1898 | S | S | Ros | + |
| <i>Andrena</i> (<i>Micrandrena</i>) <i>neonana</i> Viereck, 1917 | S | S | | + |
| <i>Andrena</i> (<i>Plastandrena</i>) <i>crataegi</i> Robertson, 1893 | S | S | | |
| <i>Andrena</i> (<i>Ptilandrena</i>) <i>distans</i> Provancher, 1888 | S | S | Ger | |
| <i>Andrena</i> (<i>Scrapteropsis</i>) <i>imitatrix</i> Cresson, 1872 | S | S | | |
| <i>Andrena</i> (<i>Simandrena</i>) <i>nasonii</i> Robertson, 1895 | S | S | | |
| * <i>Andrena</i> (<i>Taeniandrena</i>) <i>wilkella</i> (Kirby, 1802) | S | S | | + |
| <i>Andrena</i> (<i>Trachandrena</i>) <i>ceanothi</i> Viereck, 1917 | S | S | Eri | |
| <i>Andrena</i> (<i>Trachandrena</i>) <i>forbesii</i> Robertson, 1891 | S | S | | |
| <i>Andrena</i> (<i>Trachandrena</i>) <i>heraclei</i> (Robertson, 1897) | | | | |
| <i>Andrena</i> (<i>Trachandrena</i>) <i>hippotes</i> Robertson, 1895 | S | S | | + |
| <i>Andrena</i> (<i>Trachandrena</i>) <i>nuda</i> Robertson, 1891 | S | S | | |
| <i>Andrena</i> (<i>Trachandrena</i>) <i>rugosa</i> Robertson, 1891 | S | S | | |
| <i>Andrena</i> (<i>Trachandrena</i>) <i>spiraean</i> Robertson, 1895 | S | S | | |
| <i>Andrena</i> (<i>Tylandrena</i>) <i>perplexa</i> Smith, 1853 | S | S | | |
| <u>Panurginae</u> | | | | |
| <u>Calliopsini</u> | | | | |
| <i>Calliopsis</i> (<i>Calliopsis</i>) <i>andreniformis</i> Smith, 1853 | S | S | Fab? | |
| <u>Panurgini</u> | | | | |
| <i>Perdita</i> (<i>Perdita</i>) <i>o. octomaculata</i> (Say, 1824) | S | S | Ast | |
| MELITTIDAE | | | | |
| <u>Melittinae</u> | | | | |
| <u>Melittini</u> | | | | |
| <i>Melitta</i> (<i>Cilissa</i>) <i>melittoides</i> (Viereck, 1909) | S | S | Eri | + |
| MEGACHILIDAE | | | | |
| <u>Megachilinae</u> | | | | |
| <u>Anthidiini</u> | | | | |
| <i>Anthidiellum</i> (<i>Loyolanthidium</i>) <i>n. notatum</i> (Latreille, 1809) | R ⁴ | S | | |
| * <i>Anthidium</i> (<i>Anthidium</i>) <i>m. manicatum</i> (Linnaeus, 1758) | C ⁵ | S | | |
| <i>Stelis</i> (<i>Stelis</i>) <i>lateralis</i> Cresson, 1864 | [C] | P | | |
| <u>Osmiini</u> | | | | |
| <i>Hoplitis</i> (<i>Alcidamea</i>) <i>pilosifrons</i> (Cresson, 1864) | P | S | | |
| <i>Hoplitis</i> (<i>Alcidamea</i>) <i>producta producta</i> (Cresson, 1864) | P | S | | |
| <i>Hoplitis</i> (<i>Alcidamea</i>) <i>spoliata</i> (Provancher, 1888) | P | S | | |
| <i>Hoplitis</i> (<i>Alcidamea</i>) <i>truncata</i> (Cresson, 1878) | P | S | | |
| <i>Osmia</i> (<i>Melanosmia</i>) <i>atriventris</i> Cresson, 1864 | C | S | | |
| <i>Osmia</i> (<i>Melanosmia</i>) <i>pumila</i> Cresson, 1864 | C | S | | |
| <i>Osmia</i> (<i>Melanosmia</i>) <i>simillima</i> Smith, 1853 | C | S | | |
| <i>Osmia</i> (<i>Melanosmia</i>) <i>virga</i> Sandhouse, 1939 | C | S | Eri | |
| <u>Megachilini</u> | | | | |
| * <i>Megachile</i> (<i>Callomegachile</i>) <i>sculpturalis</i> Smith, 1853 | C ⁶ | S | | |

APPENDIX. Continued.

| | NEST | BEHAV | HOST | SE MA |
|--|----------------|-------|------|-------|
| <i>Megachile (Chelostomoides) campanulae</i> (Robertson, 1903) | C ⁶ | S | | |
| <i>Megachile (Leptorachis) petulans</i> Cresson, 1878 | C ⁷ | S | | + |
| <i>Megachile (Litomegachile) brevis</i> Say, 1837 | C ⁷ | S | | |
| <i>Megachile (Litomegachile) mendica</i> Cresson, 1878 | C ⁷ | S | | |
| <i>Megachile (Litomegachile) texana</i> Cresson, 1878 | C ⁷ | S | | |
| <i>Megachile (Megachile) centuncularis</i> (Linnaeus, 1758) | C ⁷ | S | | |
| <i>Megachile (Xanthosarus) addenda</i> Cresson, 1878 | S ⁷ | S | | |
| <i>Megachile (Xanthosarus) gemula gemula</i> Cresson, 1878 | C ⁷ | S | | |
| <i>Megachile (Xanthosarus) latimanus</i> Say, 1823 | C ⁷ | S | | |
| <i>Coelioxys (Boreocoelioxys) rufitarsis</i> Smith, 1854 | [C] | P | | |
| <i>Coelioxys (Coelioxys) immaculata</i> Cockerell, 1912 | [C] | P | | |
| APIDAE | | | | |
| <u>Xylocopinae</u> | | | | |
| <u>Xylocopini</u> | | | | |
| <i>Xylocopa (Xylocopoides) v. virginica</i> (Linnaeus, 1771) | W ⁸ | B | | |
| <u>Ceratinini</u> | | | | |
| <i>Ceratina (Zadontomerus) calcarata</i> Robertson, 1900 | P | B | | |
| <i>Ceratina (Zadontomerus) dupla</i> Say, 1837 | P | B | | |
| <i>Ceratina (Zadontomerus) mikmaqi</i> Rehan & Sheffield, 2011 | P | B | | |
| <i>Ceratina (Zadontomerus) strenua</i> Smith, 1879 | P | B | | |
| <u>Nomadinae</u> | | | | |
| <u>Nomadini</u> | | | | |
| <i>Nomada armatella</i> Cockerell, 1903 | [S] | P | | + |
| <i>Nomada articulata</i> Smith, 1854 | [S] | P | | |
| <i>Nomada bella</i> Cresson, 1863 | [S] | P | | |
| <i>Nomada</i> sp. nr. <i>composita</i> | [S] | P | | + |
| <i>Nomada cressonii</i> Robertson, 1893 | [S] | P | | |
| <i>Nomada denticulata</i> Robertson, 1902 | [S] | P | | |
| <i>Nomada depressa</i> Cresson, 1863 | [S] | P | | + |
| <i>Nomada illinoensis</i> Robertson, 1900 | [S] | P | | + |
| <i>Nomada imbricata</i> Smith, 1854 | [S] | P | | |
| <i>Nomada</i> sp. cf. <i>lepida</i> Cresson, 1863 | [S] | P | | |
| <i>Nomada luteoloides</i> Robertson, 1895 | [S] | P | | |
| <i>Nomada maculata</i> Cresson, 1863 | [S] | P | | |
| <i>Nomada</i> [<i>Gnathias</i>] sp. ["multispine"] | [S] | P | | + |
| <i>Nomada ovata</i> (Robertson, 1903) | [S] | P | | |
| <i>Nomada parva</i> Robertson, 1900 | [S] | P | | + |
| <i>Nomada perplexa</i> Cresson, 1863 | [S] | P | | |
| <i>Nomada pygmaea</i> Cresson, 1863 | [S] | P | | |
| <i>Nomada rodecki</i> Mitchell, 1962 | [S] | P | | |
| <i>Nomada sayi</i> Robertson, 1893 | [S] | P | | + |
| <i>Nomada xanthura</i> Cockerell, 1908 | [S] | P | | + |
| <u>Ammobatoidini</u> | | | | |
| <i>Holcopasites calliopsidis</i> (Linsley, 1943) | [S] | P | | + |
| <u>Epeolini</u> | | | | |
| <i>Epeolus autumnalis</i> Robertson, 1902 | [S] | P | | |
| <i>Epeolus pusillus</i> Cresson, 1864 | [S] | P | | |
| <i>Epeolus scutellaris</i> Say, 1824 | [S] | P | | |
| <i>Triepeolus donatus</i> (Smith, 1854) | [S] | P | | + |
| <i>Triepeolus pectoralis</i> (Robertson, 1897) | [S] | P | | |

APPENDIX. Continued.

| | NEST | BEHAV | HOST | SE MA |
|---|------|-------|------------|-------|
| Apinae | | | | |
| Eucerini | | | | |
| <i>Melissodes (Eumelissodes) agilis</i> Cresson, 1878 | S | S | Ast | |
| <i>Melissodes (Eumelissodes) dentiventris</i> Smith, 1854 | S | S | Ast | |
| <i>Melissodes (Eumelissodes) druriella</i> (Kirby, 1802) | S | S | Ast | |
| <i>Melissodes (Eumelissodes) trinodis</i> Robertson, 1901 | S | S | Ast | + |
| <i>Melissodes (Heliomelissodes) desponsa</i> Smith, 1854 | S | S | Ast | |
| <i>Melissodes (Melissodes) b. bimaculata</i> (Lep., 1825) | S | S | | |
| <i>Peponapis (Peponapis) pruinosa</i> (Say, 1837) | S | S | Cuc | |
| Anthophorini | | | | |
| <i>Anthophora (Mystacanthophora) walshii</i> Cresson, 1869 | S | S | | |
| Bombini | | | | |
| <i>Bombus (Psithyrus) citrinus</i> (Smith, 1854) | [H] | P | | |
| <i>Bombus (Thoracobombus) fervidus</i> (Fabricius, 1798) | H | E | | |
| <i>Bombus (Cullumanobombus) griseocollis</i> (DeGeer, 1773) | H | E | | |
| † <i>Bombus (Bombus) affinis</i> Cresson, 1863 | H | E | | |
| <i>Bombus (Pyrobombus) bimaculatus</i> Cresson, 1863 | H | E | | |
| <i>Bombus (Pyrobombus) impatiens</i> Cresson, 1863 | H | E | | |
| <i>Bombus (Pyrobombus) perplexus</i> Cresson, 1863 | H | E | | |
| <i>Bombus (Pyrobombus) sandersoni</i> Franklin, 1913 | H | E | | |
| † <i>Bombus (Bombus) terricola</i> Kirby, 1837 | H | E | | |
| <i>Bombus (Pyrobombus) vagans vagans</i> Smith, 1854 | H | E | | |
| Apini | | | | |
| * <i>Apis (Apis) mellifera</i> Linnaeus, 1758 | H | E | | |