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An unusually large nesting aggregation of the digger bee *Anthophora bomboides* Kirby, 1838 (Hymenoptera: Apidae) in the San Juan Islands, Washington State

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Abstract. Large aggregations of solitary bees have been reported from natural and managed landscapes where abundant nesting habitat and floral resources co-occur. Here we describe an unusually large aggregation of the bee *Anthophora* (*Melea*) *bomboides* Kirby, 1838 (Hymenoptera: Apidae) nesting in a coastal bluff in San Juan County, Washington State. Nest densities as high as 630/m^2 were recorded along a steep sandy embankment measuring 1.0 km long with a mean height of 9.3 m. The population estimate of 133,492 nesting females exceeds previously reported occurrences for this species by two orders of magnitude. Floral resources supporting this aggregation over three years of observation included dense flowering shrubs covering 16 ha of abandoned farmland immediately adjacent to the bluff. We also report an additional 31 species of bees and wasps collected at the site and discuss recently adopted conservation measures to protect the site's floral resources from conifer encroachment.

Key Words. Digger bees, Batesian mimicry, nesting aggregations, conservation, island bees.

INTRODUCTION

The behaviors and habitat requirements associated with nesting play a critical role in determining bee distribution and abundance (Westrich 1996, Potts et al. 2005). Many solitary bees nest in dense aggregations, either as a result of convergence upon limited nesting habitat or when successive generations continue returning to the site of their emergence (Michener 2007). This behavior may also arise from some unknown trigger, such as an instinctive gregarious response to the visual or chemical signals given off by conspecific nest holes (Michener 2007). Where nesting habitat is plentiful, floral resources have been identified as the most significant factor limiting bee abundance (Roulston & Goodell 2011). In landscapes with ample nest sites and flowers, large aggregations of tens or hundreds of thousands of nests have been reported for a number of bee taxa (Malyshev 1936), including sweat bees (McKinley et al. 1994) and managed alkali bees (Cane 2008). The exceptional pollination potential provided by such occurrences has been demonstrated for alfalfa (Cane 2008) and is expected for other crops and native plants. In addition, large, persistent aggregations can also anchor diverse communities of other insects, including other solitary bees, cuckoo bees (Rozen & Özbek 2005), parasitic wasps, and more (Westrich 1990).

Recent declines in managed honey bees have led to increased interest in the natural history and population dynamics of wild species, with particular emphasis on their role as pollinators (Cane 2008, Winfree et al. 2007). Understanding nesting requirements is critical for predicting the distribution and persistence of bees, and for managing land to maintain or enhance their diversity and abundance. In addition, bees capable of nesting in large aggregations are of particular interest as potential managed pollinators in agricultural settings (Cane 1997, 2008). Notably, two *Anthophora* species have been used or proposed for such a purpose: the Asian shaggy digger, *A.* (*Anthophora*) *villosula* Smith, 1854, native to East Asia and deliberately introduced to the Mid-Atlantic United States (Batra 1994) [*A. villosula* was recently reinstated as a species distinct from *A. plumipes* (Pallas, 1772) of Europe (Černá et al., 2017)], and the abrupt digger, *A.* (*Melea*) *abrupta* Say, 1838 (Graham et al. 2015), native to eastern North America. Here we add to the literature on wild bee nesting habits by describing an unusually large aggregation of the American bumble bee digger, *A.* (*Melea*) *bomboides* Kirby, 1838. Results of density assessments are reported, as well as accounts of nearby flower resources and other bees and wasps inhabiting the site. Threats to the site's nesting habitat are also discussed, and we report on recently adopted conservation measures to protect the site's floral resources from encroaching conifers.

Methods

Study species. The American bumble bee digger, *A.* (*Melea*) *bomboides* (Apidae: Apinae: Anthophorini), is a robust North American digger bee found across the continent, but particularly common from the Rocky Mountains westward to the Pacific Coast (Brooks 1983). Five subspecies have been recognized along with intergrades (Brooks 1983), although recent authors have often treated these as synonyms (Brooks 1988). The putative subspecies differ in setae color, with coat patterns that vary geographically in parallel with bumble bee (genus *Bombus* Latreille, 1802) coat patterns (Williams et al. 2014). Images of all four of the widespread forms (subspecies sensu Brooks 1983) are available at BugGuide (2017a), but none are available for the additional all-black form *A. b. aterrima* Cockerell, 1924, reported only from Plumas County, California. Whereas many bees and other Hymenoptera are involved in Müllerian mimicry complexes, species of *Anthophora* (*Melea*) are considered Batesian mimics of syntopic bumble bees (*Bombus*), because they closely parallel the coat pattern of local bumble bees, and, unusual for apid bees, have reduced stings that are short and ineffective (Brooks 1983, 1988).

Brooks (1983) noted *A. b. solitaria* Ritsema, 1880 [a replacement name for *A. insularis* Smith, 1879, from Vancouver Island, a junior primary homonym of *A. insularis* Smith, 1857, from Sarawak] as the subspecies from the region of our study site, listing historical records from nearby Victoria, British Columbia, and Friday Harbor, San Juan Island, Washington. Recent citizen science records show *A. b. solitaria* nesting in a similar coastal setting in British Columbia (http://bugguide.net/node/view/1436791). Bees from our site are indeed referable to this form, usually matching the description by Brooks (1983). However, we note considerable variability among bees collected for this study, especially males. Whereas males of *A. b. solitaria* are described as having metasomal terga (T) 2–3 with pale orange setae, in our samples we find individuals with T3 black or with a few pale setae distally and T2 with orange tones weak or absent, reducing or eliminating the contrast of T1 with pale setae. These individuals are close in appearance to the nominate form in eastern and northern North America. Other individuals have conspicuous orange setae on T2 and T3 but the latter with many black setae interspersed. Females were less variable in color, but some were notably darker with black setae present on the corners of T3. Molecular markers will be needed to rigorously interpret the genetic basis of observed variability within our study population and more generally among formerly recognized subspecies in the subgenus.

Anthophora (*Melea*) *bomboides* nests in sandy banks, coastal bluffs, or other areas of steep, exposed soil, often in aggregations of dozens to several thousand individuals (Brooks 1983). Although the aggregation reported herein was in a natural bluff, this species has also been induced to nest in a cob structure in Oregon (BugGuide 2017b), and other members of the subgenus are known to inhabit adobe, mud-bricks, mortar, and other manmade substrates, e.g., the abrupt digger, *A*. (*Melea*) *abrupta* (Norden

Figure 1. The distinctive down-curved turret covering the entrance to a typical *Anthophora* (*Melea*) *bomboides* nest. (Photo: T. Hanson, Cowlitz Bay Preserve, Waldron Island, Washington, 2017.)

1984), and the Palearctic bumble bee digger, *A*. (*Melea*) *plagiata* (Illiger, 1806) (Steinmann 1986, Westrich 1990). Females dig or re-use tunnels measuring 10–70 cm in length and provision an average of 4.6 cells in the first tunnel of the season (Brooks 1983). Many individuals also dig a second, late-season tunnel containing an average of 3.2 cells (Brooks 1983). Distinctive, down-curved turrets mark the tunnel entrances during the nesting season (Fig. 1), and some of this material is later recycled to close the nest with a solid plug. The bees overwinter as prepupae (i.e., post-defecating larvae), emerging for a flight period lasting 8–10 weeks in the late spring and early summer. Their natural history is described in detail by Brooks (1983), who studied populations in northern California.

Study Site. The Cowlitz Bay Preserve ("the site") is a natural area on Waldron Island, Washington, owned and managed by the San Juan Preservation Trust, a local nonprofit organization. The site includes 109 ha of coniferous forest, wetlands, and regenerating farmland on the southwestern shoreline of the island (Fig. 2). It provides a "complete habitat" (Westrich 1996) for *Anthophora*, offering nesting substrate in close proximity to floral resources and a source of fresh water used in nest construction (Brooks 1983). The land rises steeply from the beach in a bluff comprised of sand, small cobbles, and other marine sorted glacial outwash. The bluff measures 1.0 km in length, with a mean height of 9.3 m. *Anthophora bomboides* nest across the surface of this bluff, forming exceptionally dense aggregations in places. Floral resources occur

Figure 2. Aerial view of the Cowlitz Bay Preserve on Waldron Island, Washington, showing a complete habitat for *Anthophora* – the sandy bluff for nesting (above beach), wetlands for fresh water (center), and extensive floral resources in the regenerating pastures (center, above beach and bluff). Encroaching coniferous forest is also visible surrounding the wetland and shrub thickets. (Photo: T. Hanson, Cowlitz Bay Preserve, Waldron Island, Washington, 2017.)

along the beach fringe and toe of the bluff, but particularly in dense shrubs that occupy approximately 16 ha of abandoned pastures on top of the bluff. Cleared of original forest in the late 19th century, these pastures were grazed through the 1960s (Sprenger et al. 2005) but have been undisturbed since the Cowlitz Bay Preserve was established in 1971. They have since grown up in dense shrub thickets dominated by Nootka rose, *Rosa nutkana* C. Presl. (Rosaceae), an important pollen source for *Anthophora* and other resident bees. Other notable floral resources include common snowberry, *Symphoricarpos albus* (L.) S. F. Blake (Caprifoliaceae), Himalayan blackberry, *Rubus armeniacus* Focke (Rosaceae), and large patches of a clonal domestic cherry, *Prunus* sp. (Rosaceae). In total, botanical surveys have documented 182 plant species on the site, including over 100 angiosperms known to provide nectar and/or pollen to bees (Habegger 1996 a, b). Coniferous forest communities less favorable as bee forage surround the shrub thickets and have begun encroaching steadily upon them.

Surveys and Population Estimate. Data for population estimates were collected during site visits by TH in 2015 and 2017. The length of the bluff was measured by meter tape stretched along the beach at its base, with height determined by clinometer at 15 m intervals. The proportion of habitable slope (steep, non-vegetated) was estimated at each 15-m interval to determine the total potential nesting habitat. Within that total, locations with exceptionally high nest density were singled out for more specific measurement, using a meter tape to gauge their length and a clinometer for their height. Overall nest density was measured by counting nest holes within 68 20-cm × 50-cm plot frames located at 15-m intervals along the bluff. High-density areas were subsampled with counts from an additional 35 20-cm × 50-cm plots. Since the placement of plot frames was limited to accessible parts of the slope, many steep and highly populated areas could not be sampled directly. Each plot frame measurement was therefore rated on an ordinal scale from 1 (under-representation of nearby density) to 5 (over-representation of nearby density) to gain a general sense of sampling accuracy. Occupancy was gauged at the end of the season by an ad hoc survey of 133 nest holes, counting the proportion that had been capped. All nest density counts were conducted in June during the early and mid points of the flight period to minimize counting second nests constructed by some females late in the flight period. Among the various hymenopterans observed nesting at the site, *Anthophora* (*Melea*) nests were identified by the presence of completed or partial turrets, a distinct feature of the subgenus. Net surveys were conducted throughout the site in 2015 and 2016, with particular attention paid to nesting habitat along the bluff. Net surveys occurred during and immediately after the flight period of *Anthophora* to collect voucher specimens of the target species, as well as to document the presence of other bees and wasps, especially those potentially nesting in the bluff and the potential local *Bombus* models of *Anthophora* mimicry. Floral resources were documented by recording plant species blooming throughout the site during the flight periods in 2015, 2016, and 2017, including along the bluff, the beach fringe, and trails through the shrub thickets and surrounding forest.

RESULTS

The bluff measured 1,005 m long and varied in height from 2.0 m to 14.8 m with a mean height of 9.3 m. The mean proportion of habitable, non-vegetated surface area was estimated at 36%, putting the estimated total potential nesting surface at 3,783 m^2.

Table 1. Bees and wasps collected in 2015 and 2016 at Cowlitz Bay Preserve, Waldron Island, Washington State, site of a large *Anthophora* (*Melea*) *bomboides* aggregation. Common names follow those employed at www.bugguide.net and www.inaturalist.org, reformatted per journal guidelines.

BEES:	Common Name:
Colletidae:	
Colletes aff. *kincaidii* Cockerell, 1898[b]	Kincaid's cellophane bee
Colletes fulgidus Swenk, 1904[b]	Glittering cellophane bee
Andrenidae:	
Andrena (*Melandrena*) *nivalis* Smith, 1853[c]	Snowy miner
Andrena (*Plastandrena*) *prunorum* Cockerell, 1896[c]	Prunus miner
Halictidae:	
Halictus (*Protohalictus*) *rubicundus* (Christ, 1791)[b,c]	Orange-legged furrow bee
Lasioglossum (*Dialictus*) sp.[c]	Undet. metallic sweat bee
Lasioglossum (*Hemihalictus*) *ovaliceps* (Cockerell, 1898)[c]	Oval-headed sweat bee
Sphecodes aff. *prosphorus* Lovell & Cockerell, 1907[d]	Undet. cuckoo-sweat bee
Sphecodes sp.[d]	Undet. cuckoo-sweat bee
Megachilidae:	
Coelioxys (*Boreocoelioxys*) *rufitarsis* Smith, 1854[d]	Red-footed sharptail
Megachile (*Xanthosarus*) *perihirta* Cockerell, 1898[c]	Western leafcutter
Osmia (*Melanosmia*) sp.[b]	Undetermined mason bee
Apidae:	
Anthophora (*Melea*) *bomboides* Kirby, 1838 [former subspecies *solitaria* Ritsema, 1880][a],	American bumble bee digger ["Vancouver" form]
Bombus (*Pyrobombus*) *bifarius* Cresson, 1878	Black-notched bumble bee
Bombus (*Pyrobombus*) *melanopygus* Nylander, 1848	Black-tailed bumble bee
Bombus (*Pyrobombus*) *mixtus* Cresson, 1878	Fuzzy-horned bumble bee
Bombus (*Pyrobombus*) *sitkensis* Nylander, 1848	Sitka bumble bee
Ceratina (*Zadontomerus*) sp.	Undet. small carpenter
Epeolus olympiellus Cockerell, 1904[d,f]	Olympic cellophane-cuckoo
Eucera (*Synhalonia*) *frater lata* (Provancher, 1888)[b,c]	Monk longhorn ["Vancouver" form]
Melissodes sp.[c]	Undet. longhorn
Nomada (≥ 4 spp.)[d]	Undet. nomads
Trieopeolus sp.[d]	Undet. longhorn-cuckoo

WASPS:	Common name:
Chrysididae:	
Chrysidinae[e]	Undet. cuckoo wasp
Crabronidae:	
Aphilanthops subfrigidus Dunning[b,c]	Western ant-queen kidnapper
Crabro[b,c]	Undet. shield-handed squarehead
Crossocerus[b,c]	Undet. equilateral squarehead
Oxybelus[c]	Undet. prong-backed flyhunter

Table 1. Continued.

BEES:	Common Name:
Vespidae:	
Eumeninae (likely *Ancistrocerus*)	Undet. potter wasp

[a]Known bluff nester
[b]Potential bluff nester
[c]Ground nester
[d]cleptoparasite
[e]Includes known parasitoids and cleptoparasites of bees
[f]det. with reference to Onuferko 2017

Within that area, exceptionally dense aggregations occupied 493 m^2. Outside of those high-density areas, nest counts of clearly turreted holes ranged from $0/m^2$ to $72/m^2$ with a mean of $5.3/m^2$. Within the high-density aggregations, nest counts ranged from $70/m^2$ to $630/m^2$ with a mean of $261/m^2$ (Fig. 3). Nest occupancy was measured at 88%, putting the adjusted total population estimate for the bluff at 133,492 nesting females. The mean sampling accuracy measure for all nest counts was 2.9, near the midpoint on an ordinal scale of 1 (under-estimate) to 5 (over-estimate). Twenty-six other bee species and six wasp species were collected on the Preserve (Table 1). Notable among these are two *Bombus* (*Pyrobombus*) Dalla Torre, 1880, species with orange (black-tailed bumble bee, *B. melanopygus* Nylander, 1848) or partly orange (black-notched bumble bee, *B. bifarius* Cresson, 1878) setae on T2–T3 that are the apparent models for the *Anthophora* at this site. The list of observed aculeate Hymenoptera also includes at least six other known or potential bluff nesters and nine species of cuckoo bees that are also likely to be using the bluff habitat. For example, the Western leafcutter, *Megachile* (*Xanthosarus*) *perihirta* Cockerell, 1898, is known to nest in embankments (Hobbs 1957), and its presumed cuckoo, the red-footed sharptail, *Coelioxys* (*Boreocoelioxys*) *rufitarsis* Smith, 1854, was also captured on site. Similar inferred host/cuckoo associations observed at the site include miners in the genus *Andrena* with nomads in the genus *Nomada*, cellophane bees in the genus *Colletes* with the Olympic cellophane-cuckoo *Epeolus olympiellus* Cockerell, 1904, and a longhorn in the genus *Melissodes* with a longhorn cuckoo in the genus *Trieopeolus*.

Floral resources blooming during the flight period of *A. bomboides* included 53 plant species as summarized in Table 2. Among these, *R. nutkana* reached peak bloom during the flight period and stood out as the site's most prolific and important source for pollen. Other important pollen and/or nectar sources included the American searocket, *Cakile edentula* (Bigelow) Hook. (Brassicaceae), winter vetch, *Vicia villosa* Roth (Fabaceae), and the aforementioned *S. albus*, *R. armeniacus*, and *Prunus* sp.

DISCUSSION

Previous population estimates for *A.* (*Melea*) *bomboides* aggregations have reached as high as 2,000–5,000 nesting females (Brooks 1983), making the aggregation described here the largest known occurrence by two orders of magnitude. Published aggregation estimates for related digger bees are also much smaller, including 900 nesting females for the closely-related abrupt digger, *A.* (*Melea*) *abrupta* (Norden 1984), 1,000 for Edward's digger, *A.* (*Pyganthophora*) *edwardsii* Cresson, 1878 (Thorp 1969), and 200–300 for the hairy-footed digger, *A.* (*Anthophora*) *plumipes* Pallas, 1772

Figure 3. View of bee activity in a dense area of an *Anthophora* (*Melea*) *bomboides* aggregation, where nest concentrations of up to 630/m2 were observed. (Photo: T. Hanson, Cowlitz Bay Preserve, Waldron Island, Washington, 2015).

(Stone 1994). An unpublished report of 180,000 nests for *A. edwardsii* has been noted elsewhere (Cane 2008), however, suggesting that digger bee aggregations of multiple *Anthophora* subgenera have the potential to become very large. Nest sites of similar magnitude have also been described for other wild solitary bees, including 155,000 for the prairie nomia, *Dieunomia* (*Epinoma*) *triangulifera* (Vachal, 1897) (Halictidae)

Table 2. Plants observed blooming during the flight period of *Anthophora* (*Melea*) in 2015, 2016, and 2017 at Cowlitz Bay Preserve, Waldron Island, Washington State. Bold type indicates the most prolific and important floral resources. Taxonomy and common names follow USDA PLANTS database (https://plants.usda.gov/).

Species (Family)	Common Name
Achillea millefolium L. (Asteraceae)	Common yarrow
Arbutus menziesii Pursh (Ericaceae)	Pacific madrone
Artemisia suksdorfii Piper (Asteraceae)	Coastal wormwood
Atriplex patula L. (Chenopodiaceae)	Spear saltbush
Cakile edentula (Bigel.) Hook. (Brassicaceae)*	American searocket
Cerastium arvense L. (Caryophyllaceae)	Field chickweed
Chamerion angustifolium (L.) Holub. (Onagraceae)	Fireweed
Cirsium arvense (L.) Scop. (Asteraceae)*	Canada thistle
Cirsium vulgare (Savi) Tenore (Asteraceae)*	Bull thistle
Collinsia parviflora Lindl. (Scrophulariaceae)	Maiden blue-eyed Mary
Crataegus monogyna Jacq. (Rosaceae)*	Oneseed hawthorn
Daucus carota L. (Apiaceae)*	Queen Anne's lace
Erodium cicutarium (L.) L'Her ex Aiton (Geraniaceae)*	Redstem storksbill
Fragaria vesca L. (Rosaceae)	Woodland strawberry
Galium aparine L. (Rubiaceae)*	Stickywilly
Galium trifidum L. (Rubiaceae)	Threepetal bedstraw
Galium triflorum Michx. (Rubiaceae)	Fragrant bedstraw
Gaultheria shallon Pursh (Ericaceae)	Salal
Geranium molle L. (Geraniaceae)*	Dovefoot geranium
Grindelia integrifolia DC. (Asteraceae)	Puget Sound gumweed
Hypochoeris radicata L. (Asteraceae)*	Hairy cat's ear
Lathyrus japonicus Willd. (Fabaceae)	Beach pea
Lonicera hispidula (Lindl.) Douglas (Caprifoliaceae)	Pink honeysuckle
Lupinus bicolor Lindl. (Fabaceae)	Miniature lupine
Mahonia aquifolium (Pursh) Nutt. (Berberidaceae)	Hollyleaved barberry
Mahonia nervosa (Pursh) Nutt. (Berberidaceae)	Cascade barberry
Malus fusca (Raf.) C. K. Schneid. (Rosaceae)	Oregon crab apple
Myosotis discolor Pers. (Boraginaceae)*	Changing forget-me-not
Prunella vulgaris L. (Lamiaceae)	Common selfheal
Prunus sp.* (Rosaceae)	Domestic cherry
Ranunculus occidentalis Nutt. (Ranunculaceae)	Western buttercup
Ribes divaricatum Dougl. (Grossulariaceae)	Spreading gooseberry
Rosa gymnocarpa Nutt. (Rosaceae)	Dwarf rose
Rosa nutkana C. Presl. (Rosaceae)	Nootka rose
Rubus armeniacus Weihe & Nees (Rosaceae)*	Himalayan blackberry
Rubus spectabilis Pursh (Rosaceae)	Salmonberry
Rubus ursinus Cham. & Schlect. (Rosaceae)	California blackberry
Sambucus racemosa L. (Caprifoliaceae)	Red elderberry
Sanicula crassicaulis Poepp. (Apiaceae)	Pacific blacksnakeroot
Sonchus asper (L.) Hill. (Asteraceae)*	Spiny sowthistle
Spergularia macrotheca Heynh. (Caryophyllaceae)	Sticky sandspurry
Spiraea douglasii Hook. (Rosaceae)	Rose spirea
Symphoricarpos albus (L.) Blake (Caprifoliaceae)	Common snowberry
Taraxacum officinale F. H. Wigg (Asteraceae)*	Common dandelion
Tellima grandiflora (Pursh) Dougl. (Saxifragaceae)	Bigflower tellima
Trifolium dubium Sibth. (Fabaceae)*	Suckling clover
Trifolium repens L. (Fabaceae)*	White clover
Urtica dioica L. (Urticaceae)	Stinging nettle

Table 2. Continued.

Species (Family)	Common Name
Vicia americana Muhl. ex Willd. (Fabaceae)	American vetch
Vicia hirsuta (L.) Gray (Fabaceae)*	Tiny vetch
Vicia nigricans Hook. & Arn. (Fabaceae)	Black vetch
Vicia sativa L. (Fabaceae)*	Garden vetch
Vicia villosa Roth (Fabaceae)*	Winter vetch

*Non-native

(Minckley et al. 1994) and 423,000 for the Caesalpinia digger, *Centris* (*Paracentris*) *caesalpiniae* Cockereall, 1897 (Rozen and Buchmann 1990; this immense aggregation was remarkably ephemeral). In agricultural settings, managed populations of the cavity-nesting alfalfa leafcutter, *Megachile* (*Eutricharaea*) *rotundata* Fabricius, 1787 (Megachilidae), often exceed 100,000 females in a single structure (Stephen 1981), while artificial nesting beds of the alkali bee, *Nomia* (*Acunomia*) *melanderi* Cockerell, 1906 (Halictidae), regularly contain from hundreds of thousands to 5.3 million females (Cane 2008). Aggregations of comparable or even larger size can also form naturally, with the famous example being the ca. 7.6 million nests of the pantaloon bee *Dasypoda* (Melittidae) reported at a ca. 36 ha site by Malyshev (1936).

The unusual size of the *A. bomboides* aggregation described here is apparently made possible by a serendipitous co-occurrence of abundant nesting habitat and abundant floral resources. Pastures adjacent to the bluff were abandoned in the 1970s and became overgrown with flowering shrubs and small trees that bloom throughout the *A. bomboides* flight period. Among these, Nootka rose and a clonal domestic cherry are particularly prolific and important. While coastal bluffs with similar nesting habitat occur nearby and on neighboring islands, they are bordered by coniferous forest, the typical climax vegetation community of the region. Such forest offers comparatively limited floral resources (Regal 1982), and fresh water sources are often scarce, creating a classic "partial habitat" for *Anthophora*. Visits to several of these bluffs found nesting *A. bomboides* routinely present, but only in numbers of a few dozen to several hundred.

The dynamics of large nesting aggregations are poorly understood, but several factors may limit their size. Stored provisions accumulated by females, as well as concentrations of larvae and pupae, typically attract parasites and other natural enemies (Wcislo & Cane 1996). Common wasps at this site included cuckoo wasps of the subfamily Chrysidinae, many of which are parasitoids or cleptoparasites that attack bees. Additionally, northern flickers, *Colaptes auratus* (Linnaeus, 1758) (Picidae), a native woodpecker, were frequently observed perching vertically on the face of the bluff, excavating nests with their bills and presumably feeding on immature bees. The accumulation of fungi and other pathogens in soil or nesting materials can also be detrimental and is known to limit the longevity of managed *M. rotundata* populations (Pitts-Singer & Cane 2011). The impacts of parasites and pathogens were not assessed in this study, and they may well limit or cause temporal variation in the size of the population. Photographs taken of the bluff in 1978, however, show that the aggregation has been active and large for at least 40 years, an age comparable to the oldest managed bee beds of *N. melanderi* (Cane 2008). Similarly persistent nesting bluffs with nests of the closely related (consubgeneric) *A.* (*Melea*) *plagiata* and associates are known in eastern Turkey (Rozen & Özbek 2005).

Threats to the site's nesting habitat include coastal erosion in the form of wave action during winter storms, which can remove large sections of the bluff. Over the course of this study, several areas containing thousands of bee nests were lost in this way. While the process does expose pristine nesting habitat that can be re-colonized, it carries the risk of catastrophic mortality in a large storm event. Should the entire aggregation be eliminated in this way, re-colonization would have to occur from a population of several hundred nests located 3.5 km away on the opposite shore of the island or from populations on neighboring islands (>5 km distant). All known aggregations of this species in the San Juan archipelago are located in similar shoreline habitats, and risk of erosion from major storm events is expected to increase with the rising sea levels predicted by regional climate change models (Mote et al. 2008).

A second threat to the site comes from the encroachment of coniferous forest into the flowering shrub thickets, i.e., "coniferization." Vegetation surveys in 1996 estimated the shrub cover at 29 ha (Habegger 1996b), while recent estimates put the total at 16 ha (R. R. McGregor, personal communication), a reduction of nearly 50%. The replacement of flowering shrubs with cone-bearing trees has obvious negative implications for bees, and the coniferization of heathland in Yorkshire, England has been associated with steep declines in bee abundance and diversity (Archer 1989). If this encroachment process continues at the Cowlitz Bay site, floral resources will dwindle and the bee population will diminish. On a positive note, land managers for the Cowlitz Bay Preserve are now aware of the significance of the *A. bomboides* aggregation in their care (D. Dougherty & R. R. McGregor, personal communication). They plan to protect the flowering shrublands through removal of conifers or other encroaching vegetation, a form of active management that has been shown to improve conditions for bees in a variety of settings (e.g., Romey et al. 2007, Hanula & Horn 2011). This is in stark contrast to earlier management recommendations for the site, which identified the rose-dominated thickets as invasive and with little conservation value (Sprenger et al. 2005). It underscores the importance of not only identifying and studying significant bee aggregations, but also working with landowners and managers towards the preservation of complete habitats for bees.

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