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INTERACTIONS AMONG THE BEE AND PLANT COMMUNITIES IN COASTAL DUNES AND THE IMPLICATIONS FOR CONSERVATION BIOLOGY.

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Abstract. *While bees are considered important pollinators, they also make other contributions to plant and animal communities that have not been fully appreciated. The nests of the ground-nesting leafcutter bee* Megachile wheeleri *Mitchell were studied in a coastal dunes preserve to examine links between plants, bees and animals. Nesting is restricted to the* Poa-Lathyrus *plant community in semi-stabilized dunes. Nest material including leaves, cocoons, pollen and feces probably make important localized contributions to soil nutrients, and brood may be an important food resource for mammals.*

Some introduced plant species probably displace nesting habitat and foraging resources, but others may enhance nest habitat without impacting forage plants. Nesting habitat is currently expanding in the Preserve. These studies characterized conditions within the least disturbed dunes system and can be used to assess the impact of disturbances at other sites. One of the bee's host plants is a dominant component of the plant community, and maintaining pollinator populations should be a conservation goal. Considerations for native pollinator populations should be included in native plant restoration programs.

Key Words: leafcutter bees, coastal dunes, nutrient cycling, mortality, rodents

Introduction

Bees are important pollinators (reviewed by Proctor and Yeo 1972, Kevan and Baker 1983, Barth 1985). There is growing concern for the need to conserve native bee populations to pollinate native plants (Harper 1979, Tepedino 1979, Kevan 1986, Armbruster and Guinn 1989, Roubik 1989, Bawa 1990, Thorp 1990, Osborne et al. 1991, Thorp and Gordon 1992, Frankie et al. 1988). The visitation frequency and behavior of bees are important determinants of the number and quality of seeds and fruits for many flowering plants (see reviews in McGregor 1976, Handel 1983, Kevan and Baker 1983, Rathcke 1983, Lee 1988, Roubik 1989). The rate of successful reproduction of plants in a population determines whether that population increases, remains stable or decreases. Recent evidence indicates that maintaining native bee populations for pollination is critical for the reproduction and survival of some native plant populations (Loope et al. 1988, Tepedino et al. 1990). While we are concerned about maintaining stable populations of endangered plant species, we must also keep in mind that seeds and fruits produced by many plants are important food resources for a wide variety of organisms, and that many of these require pollination by bees (Kevan and Baker 1983). Although pollination is a very important contribution that native bees make to native plant and animal communities, it is not the only one. Bees may be an important food resource for wildlife, and nesting activities may substantially increase the nutrients available in the nesting substrate.

The objective of this paper is to increase interest in conserving native bees through a discussion of the interactions among bee nests, plants and mammals in coastal dunes. I will draw from studies on the bee community (Gordon 1984), the nest distribution, mortality, and resource utilization of a solitary bee (Chapter 1, 2, 3), and my field experience in the Preserve over the last 15 years.

Study Site.

The studies were conducted on The Nature Conservancy's Lanphere-Christensen Dunes Preserve, located on the North Spit of Humboldt Bay in Arcata, California (Fig. 1). The best preserved example of coastal dunes in the Pacific Border Region is contained within the the original Preserve's boundaries (Fig. 1, 2), and the Preserve has been designated a National Landmark (Sweet 1981, Pickart 1987a). While the Preserve contains some of the least altered dunes in the state (Barbour and Johnson 1977), it should be noted that introduced species comprise 29% of the flora (Barker 1976). The study site was described by Barbour and Johnson (1977), Wiedemann (1984), and Gordon (1984, 1992). Coastal dune ecology is treated in general by Wiedemann et al. (1974), Chapman (1976), Barbour et al. (1985), Carter (1988) and Nordstrom and Psuty (1990).

Study Organism.

Megachile wheeleri Mitchell (Fig. 3) is a ground-nesting solitary bee in the leafcutter bee family Megachilidae. Each female independently constructs and provisions a series of nests, one at a time. After excavating a shallow tunnel in the sand, she constructs a single brood cell from leaf pieces, provisions it with pollen and nectar, lays an egg, and seals the cell (Figs. 4, 5). After completing the brood cell she collapses the tunnel, abandons the nest, and begins another. Nectar and pollen are collected primarily from *Achillea borealis* Bong. ssp. *arenicola* (Heller) Keck., *Erigeron glaucus* Ker. and *Solidago spathulata* D.C. Leaf cuttings are taken primarily from *S. spathulata*, but *E. glaucus* is used to a minor extent and a few other species are used rarely. After the larva consumes its provisions, it defecates, spins a cocoon, hibernates as a prepupa, and pupates in the spring. Adults are active from mid-June to mid-September and a single generation is produced each year (Gordon 1984).

Figure 1. *Aerial view of north spit looking south into Humboldt Bay in June, 1976. The study site is left of the middle of the beachline, where the spit is approximately 1 km. wide.*

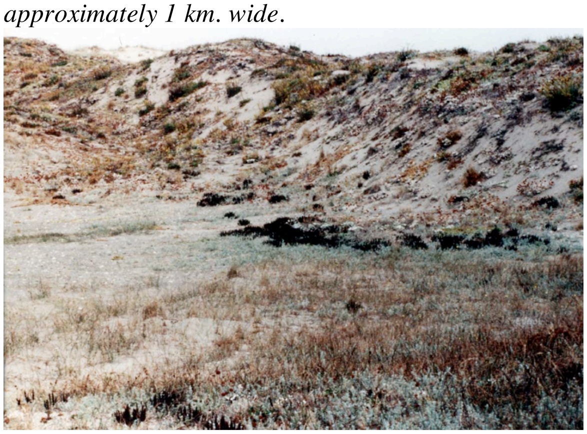

Figure 2. Megachile wheeleri *nesting habitat within foredunes (1989). A dense nest aggregation was found in the herbaceous vegetation in the center of the photograph, below the dark plants. Smaller aggregations with lower densities were found in the higher ground of the foredunes and inland dunes.*

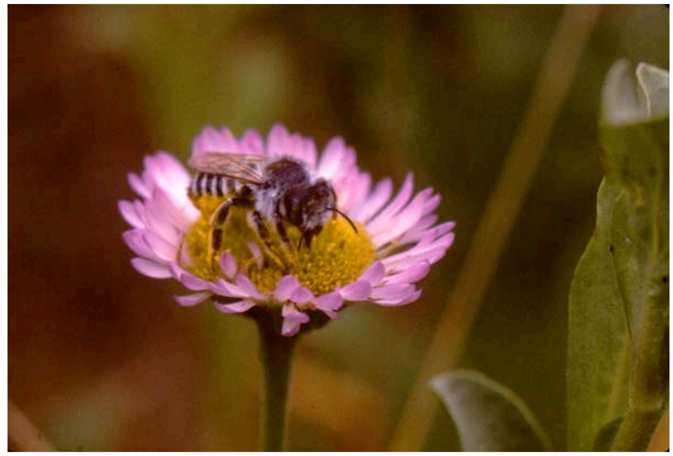

Figure 3. Megachile wheeleri *female foraging on Seaside daisy (Erigeron glaucus).*

Figure 4. *Excavated nest showing tunnel and brood cell constructed from leaf cuttings at end of tunnel (arrow).*

Figure 5. *Brood provision and egg (mm. scale). Most of the leaf pieces have been removed.*

Megachile wheeleri is one of the most abundant bee species in the Preserve fauna (Gordon 1984, Thorp and Gordon 1992). Within the "natural" plant communities (the least disturbed dunes) in the Preserve (Fig. 2), sparse to dense (Fig. 6) nest aggregations are found throughout the *Poa-Lathyrus* plant community type (Chapter 1), as broadly defined in Barbour and Johnson (1977). The plants that provide nest construction material and brood provisions also occur within this community, but these host plants generally do not occur in nest aggregation sites (Chapter 1). The lowest elevations do not contain nests, but dense nest aggregations can be found in the transitional zone between these lowlands and *Poa-Lathyrus* community. In fact, it appears that the largest and most dense aggregations are within this transitional zone. Vernal ponds form in the lowlands that may submerge nest sites during years with moderate to heavy rainfall (Fig. 7).

Figure 6. *The 83 nests piled in the center were excavated from this 1 sq. m. area, illustrating density in nest aggregation sites (1989). Tape indicates 50 cm.*

Figure. 7. *Vernal pond during a wet year (1980). Dense nest aggregations occurred at the edges of this pond.*

Random sampling throughout the nesting habitat (Gordon 1992) and within 13 nest aggregation sites yielded a maximum of 49 brood cells per 0.1 $m.^2$ sample unit, but mean densities in nesting sites were 5.1 ±0.7 (±SEM, n=130). The completed brood cell is provisioned with 0.267 ±.014 g. of nectar and pollen (dry weight $\bar{x}$ ±SEM, n=30), packaged within 0.2 g. leaf material. Pollen contains lipids, proteins, and minerals (Stanley and Linskens 1974) and, together with nectar, provides all the nutrients required for a bee to develop.

Nest Construction and Nutrient Cycling.

Nutrients are generally limited in dunes. Input is mainly from salt spray off the ocean and the poor water holding capacity of sand results in rapid leaching of nutrients (reviewed in Barbour et al. 1985, Carter 1988). Nitrogen is the most important factor limiting growth in dunes, but potassium is also critical (Willis 1963, Boorman and Fuller 1982, reviewed in Carter 1988) and pollen is a good source of both (Stanley and Linskens 1974). Based on the nest densities and provision weights above it is worth considering the potential contribution that nests make to soil nutrients. The provision mass of *M. rotundata* (Panzer), which is similar in consistency to that of *M. wheeleri*, contains 36% pollen and 64% nectar by weight (Klostermeyer et al. 1973). If a similar relationship holds for *M. wheeleri*, the average nest cell would contain 0.096 g. pollen and 0.171 g. nectar. The amount of nitrogen in pollen varies depending upon the species (Stanley and Linskens 1974). Based on Roubik's (1989) estimate of 3.5 % N, the average *M. wheeleri* provision contains 0.004 g. nitrogen. Extrapolating from that estimate, an average density of 5 cells per 0.1 $m.^2$ sample unit would contain 0.02 g. N, and the most dense sample contained 0.17 g. N.

Species diversity in dunes is apparently related to the low nutrient status of the soils, and adding N lowers diversity (Willis 1963, review in Carter 1988). Boorman and Fuller (1982) found that adding major nutrients depressed growth of most annuals, lowered plant species diversity and led to dominance of perennials. Applying N at a rate equivalent to 0.08 g. per 0.1 $m.^2$ produced this effect, but the amount of N presumed to be available at the average nest density of *M. wheeleri* is $^1/_4$ this value, and much of it is converted into bee biomass, unless the larva dies. Leaf material, fecal pellets and cocoons do remain in the sand. Because organic matter retains soluble ions for exchange in the soil solution this contribution may be as important as the nutrients contributed. It appears that *M. wheeleri* nests develop concentrations of critical nutrients that are not rapidly leached away, in amounts that do not decrease plant species diversity. Because *M. wheeleri* tends not to nest in the immediate proximity of its host plants, these benefits accrue to other species at the expense of those host plants. Dense nest aggregations border the edges lowlands so nutrients may also leach into vernal ponds (Fig. 7), and contribute to the aquatic food chain. The potential contribution of nests to soil nutrients would be worth investigating further.

Because most *Megachile* species do not nest in the ground (Stephen et al. 1969) it might be argued that this is an atypical situation and that the contribution of bee nests to soil nutrients has no application beyond the present situation. However, *M. wheeleri* was also reported to be the most abundant leafcutter bee in the the mixed prairie region of Alberta (Hobbs and Lilly 1954). Although nothing is known about the biology of many species in the large subgenus *Xeromegachile*, all appear to be ground-nesters in sandy soils (Mitchell 1937). This suggests that other sandy environments besides coastal dunes are similarly effected by other species. Cavity nesting *Megachile* species leave nest residues in wood and hollow twigs that must provide nutrients for wood decay fungi, perhaps accelerating decay. Indeed, upon consideration, it would seem that many bee species may be important agents for nutrient cycling.

Highly social bee species clean their nests regularly and Roubik (1989) suggested that fecal material and waste distributed around colonies are important nitrogen sources in tropical forests. In general, solitary bee species should contribute nutrients to their immediate nesting environment through fecal material. Leaf pieces and other foreign materials are not used for nest construction by all bee species (Stephen et al. 1969), so the contribution of organic matter is variable. The amount of nutrients contributed would depend upon the size of the bee (amount of fecal residue), nest architecture (leaf material, wax secretion, cocoon) and the density of the nest cells. The availability of these nutrients to plants and soil micro-organisms would depend upon the substrate, depth of the brood cells, amount of plant cover, depth of plant roots, et cetera.

Bee Brood as a Food Resource.

The primary source of nest cell mortality is small mammals, which decimated some nest aggregations (Gordon 1984, Gordon 1992). Skunks are known to predate ground-nesting bees (Stephen et al. 1969), and *Mephitis mephitis* consumed *M. wheeleri* brood in the Preserve during the summer months. Rodent predation occurred throughout the nesting habitats, but was lowest in open, sparsely vegetated sites, and highest near some mid-succession woody sites (Gordon 1992). Other small mammals may also utilize bee brood, which is very nutritious (Hocking and Matsumura 1960), appears to be an important food resource for some rodent populations through the winter. Excavation of bee nests by mammals resulted in severe disturbance in some nest sites (Fig. 8). The potential impact of such disturbance on plant community composition raises some interesting questions. Does it retard succession, open sites to invasion by weedy species, or have minor impact on vegetation?

Figure 8. *Disturbance in* M. wheeleri *nest site resulting from mammal digging.*

Bee Nests, Disturbance, and Plant Succession.

It is interesting to note that two species of introduced hairgrass, *Aira praecox* and *A. caryophyllea* appear to improve nesting substrate conditions for *M. wheeleri*. These species are common in the Preserve, and can be used as cues to locate nesting habitat (Chapter 1). Dunes adjacent to the Preserve have been severely disturbed, reducing the native plant populations (Gordon 1984, Pickart 1987a) and probably the populations of several bee species as well. Displacement of the native flora by invasive weeds such as European beach grass (*Ammophila arenaria*) and bush lupine (*Lupinus arboreus*) (Miller 1987, 1988, Gordon 1984, Sweet 1981) probably reduces *M. wheeleri* populations by reducing foraging resources and nesting habitat (compare Figs. 2 and 9). Dunes near the Preserve that were covered with thickets of these plants were not systematically sampled, but the results from the nest habitat study on the Preserve (Chapter 1) suggest that *M. wheeleri* probably does not nest in such habitats. *Ammophila arenaria* has been shown to reduce abundance of sand-dwelling beetles (Slobodchikoff and Doyen 1977) that inhabit *Megachile wheeleri* nest sites (Gordon 1992) which also suggests *M. wheeleri* nest habitat is displaced.

This opinion is also supported by impressions received while searching for brood cells to bait field experiments. *Megachile wheeleri* nests were found in patches of native vegetation that remain in the foredunes and at the edges of forested hollows, but not within the *A. arenaria* or *L. arboreus* thickets. Some nest sites were found in non-native vegetation. It appears that *M. wheeleri* nests in grassy areas in disturbed sites, and that different plant species associations may be used to identify nest habitats.

Figure 9. *Dense* M. wheeleri *nest aggregations were found along the edges of this off-road vehicle trail through bush lupine thickets in the foredunes north of the study site (1989).*

Off-road vehicles also probably destroy both foraging resources and nesting habitats. Because *M. wheeleri* constructs shallow nests, adults and larvae may also be crushed or injured, although cocoons may be tough enough to withstand some trampling. Interestingly, within the bush lupine scrub north of the Preserve, nesting sites were found along edges of ORV roads indicating that some ORV damage to that plant community may facilitate the survival of *M. wheeleri* populations by creating nesting habitat (Figs. 9, 10).

Figure 10. *Closer view of the nest sites (white stakes) in Fig. 9.*

Within the Preserve *M. wheeleri* nesting habitat is currently expanding. In the the southern portion of the study area, sites that were barren sand ten years ago have been colonized by plants and succession has proceeded to the stage which contains favorable nesting habitat (Fig. 11) *Megachile wheeleri* is colonizing these sites and the population may have been increasing over the last few years because of the expanding nesting habitat and the drought. Mortality is lower in these sites (Gordon 1992) and there has not been extensive flooding of the lowlands for several years. In a wet year portions of these areas may be submerged for several months, and possibly cause mortality. However, populations seem to have survived in the past (Gordon 1984) (Fig. 7), so it is not clear how much mortality actually results from flooding.

Figure 11. *Successional advance in lower areas is expanding* M. wheeleri *nesting habitat in the preserve (1981).*

Implications for Conservation Biology.

Since these studies were conducted in the least disturbed dunes habitats, they represent the closest approximation to conditions in the natural system and can be used as a standard for comparison with disturbed sites nearby, and to monitor changes within the study site. It is interesting to note that while some introduced plant species (lupine, European beach grass) are probably displacing bee nesting habitat and host plants, others (hairgrass) may actually be enhance nest habitat and have no effect on host plants. On a more theoretical note it should also be apparent that, in the long term, until the next major episode of sand deposition occurs on the beach, woody plant communities will expand over the dunes (Wiedemann 1984) and natural succession will reduce nesting habitat for several bee species, and probably reduce species diversity in the bee and plant communities.

Solidago spathulata is a dominant component of the native *Poa-Lathyrus* community (Pickart 1987b) and, because of its abundance, is probably also the predominant food resource for *M. wheeleri*. *Solidago spathulata* is visited by a diverse array of insects, including several bee and wasp species that probably contribute to its pollination, but the amount of pollen in each *M. wheeleri* brood provision is equivalent to the total production of 1,400 *S. spathulata* flower heads. The native bee community contains several bee species that are abundant and are probably important pollinators of other native plants in the dunes (Gordon 1984, Thorp and Gordon 1992). Compared to other Pacific Northwest coastal dunes, the Lanphere-Christensen Dunes Preserve is unique with respect to the abundance of spring and summer insect populations (Wiedemann pers comm., pers. obs.). The relationships between the abundance and diversity of native plant and insect species in this Preserve deserve greater scrutiny. The importance of maintaining adequate pollinator and natural enemy populations to sustain high growth and reproductive capacity of plants is well understood in agriculture (Estes et al. 1983, Liss et al. 1986). While conservation biologists may not want to maximize plant reproductive capacity, the goal of maintaining a balanced natural system is desirable.

Long-term success for returning a highly disturbed system to a more natural condition may require more than establishing plant populations. Restoration of native dune plants has been successful on disturbed sites (Pickart 1988, Guinon 1988), but may still benefit from restoration of native pollinators as well. *Megachile wheeleri* is particularly well suited for restoration programs because of its abundance, the ease with which brood can be collected and the fact that brood cells are strong enough to withstand transplanting. Restoration of other bee species on the Preserve may be more difficult. The key to successfully conserving and restoring native plant populations is understanding their reproductive biology, and this must also include pollination requirements. Conserving or augmenting the necessary populations of pollinators requires an understanding of their life history, resource requirements, and demography.

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