

Abstract

The study was conducted within what is now the Lanphere Unit of the Humboldt Bay National Wildlife Refuge Complex on the North Spit of Humboldt Bay near Arcata, California between June 1989 and May 1990. The study site included the least disturbed coastal dune system in the Northern Pacific Border Region.

Megachile (Xeromegachile) wheeleri Mitchell is a ground-nesting solitary bee that constructs a single, distinctive brood cell. Adults fly from mid-June to mid-September, producing one generation per year. The bee overwinters as a prepupa in a tough cocoon buried 2-5 cm. below the surface. It was one of most abundant bees in the Preserve during the study.

Overwintering mortality was examined with multiple decrement life tables. Marked brood cells were baited for two treatments that allowed or eliminated surface access. Five replicates included two early successional sites, one in mid-successional site, one site adjacent to a young shore pine forest and one site in a large clearing within the same forest.

Overall mortality was 56%, caused mainly by mammal predation (39%). A cleptoparasitic bee, *Coelioxys rufitarsus* (Smith), caused the least mortality (4%). Herbivorous soil arthropods and "other causes" generated low mortality (8% each). Several sealed cocoons with dead bees contained numerous dead *Tyrophagus* sp. mites (Astigmata: Acaridae). Eliminating mammal predation was predicted to reduce overall mortality to 34%. Total mortality varied among habitats. It was lowest (11-19%) in sparsely-vegetated pioneer succession, resulting mainly from "other causes." It was highest (100%) in some mid-successional forested sites, where rodents were the main cause. The variation in mortality among sites and the impact of combinations of mortality agents is discussed.

Introduction

The objective of this study was to assess the overwintering mortality of the brood of *Megachile (Xeromegachile) wheeleri* Mitchell with particular interest in nest parasites and the impact of predation by rodents. Previous studies suggested that cleptoparasitic bees and flies, fungal infections and small mammals (particularly rodents and possibly gophers) would be the main mortality agents (Gordon 1984, 1992, 2000).

Materials and Methods

Study Organism. *Megachile wheeleri* is a ground-nesting solitary bee that constructs a single brood cell per nest in burrows 2-5 centimeters deep. Distinctive brood cells are formed from leaf pieces, provisioned with pollen and nectar and then sealed after an egg is laid. After the larva consumes the provision, it spins a tough cocoon and overwinters as a prepupa. Pupation begins in April and adults begin to emerge in June. Nest construction begins in mid-June and continues into mid-September. There is a single generation per year. *Coelioxys rufitarsus* Smith, a cleptoparasitic megachilid bee (Baker 1975) was known to parasitize *M. wheeleri* nests (Gordon 1984).

Study Site. The study was conducted within the boundaries of the original Lanphere-Christensen Dunes Preserve on the North Spit of Humboldt Bay near Arcata, California between June 1989 and May 1990. The site has since been incorporated into the Humboldt Bay National Wildlife Refuge Complex. Descriptions of the study site are provided by Barbour and Johnson (1977), Gordon (1992, 2000) and Wiedemann (1984). Elevation ranged from approximately 0.25 m below sea level to 80 m.

Mortality Assessment. Mortality of overwintering brood nests was examined between mid-September 1989 and late May 1990, after nest construction ceased and before the adults began to emerge. The study evaluated mortality by baiting known numbers of brood cells in *M. wheeleri* nesting areas after the bees had ceased nesting activity. At each site, 0.1 m² plots were baited with five marked brood cells buried 3 cm deep. Surface access was either allowed or excluded by 0.6 mm mesh screen. A 10 m² area was divided into 100 plots and the treatments were randomly assigned to 25 plots. Five of these experimental sites were established within the preserve.

Survivorship of brood cells was evaluated by excavating brood cells prior to emergence in April and examining them with x-ray radiographs. Dead cells were opened to determine causes of mortality. Mortality in brood cells containing dead larvae in pollen and leaves or dead larvae in cocoons was classified as "other" causes.

Background mortality for disappearing brood was determined because brood cells missing from the experimentally baited plots were to be classified as mortality caused by mammal predation. To do this, three replicates of 0.6 mm mesh cages each containing 20 brood cells were buried in barren sand habitats at three elevations (0.3 m, 1 m, and 3 m) during the study period. At the end of the study they were excavated and the proportion of missing cells was determined to estimate the amount of "background disappearance."

Analysis of Mortality. Multiple decrement life tables (Carey 1989) were used to partition the mortality caused by several agents acting together and to predict the mortality that would result from various combinations of agents by eliminating specific causes-of-death. Data from the five treatments were pooled into two: surface access allowed or not allowed.

Results

Background Mortality. There were no significant differences in mortality for brood in the buried cages among the three elevations (DF=2, Chi square=0.824, P=0.6624). The cages buried in open sand yielded a rate of 1.7% disappearing brood cells. Because missing brood was attributed to removal by mammals, mammal predation may be slightly overestimated and "other" mortality slightly underestimated.

Parasite. Based on radiographs, dissections of dead brood cells, and emergence records from other studies, the only parasite was the cuckoo bee *Coelioxys (Boreocoelioxys) rufitarsus* (Smith). *C. rufitarsus* emerged during the summer of 1989 and the spring of 1990 from *M. wheeleri* brood cells constructed in 1989.

Other. Most cocoons that were dissected to determine the cause of death contained fungal hyphae and/ or fruiting bodies, with no obvious remains of the bee larva and no obvious cause of death. No chalkbrood "mummies" were found. Several sealed cocoons contained numerous dead *Tyrophagus* sp. mites (Astigmata: Acaridae). Mites were also found in a few uncompleted brood cells containing pollen. All these types of dead cells were categorized as death due to "other" causes.

Mammal Predation. Evidence that mammals had been digging in natural nest sites was found throughout the summer and fall. Rodent predation could be identified by the presence of excavated holes that often had cocoons with holes in them nearby. During a visit to the study site in October it was evident that mammal predation had occurred at all three baited experimental sites near forested hollows (A, C, and E), and that rodents had penetrated some exclosures at site C by digging below the screen, even though it extended 3 cm below the surface. Although gophers were active in many places in the study area and near some experimental sites, there was no evidence of gopher tunneling within any of the experimental sites. There was no evidence of small mammal predation (skunk or fox) in the experimental sites.

Soil Arthropods. Damage to cells from soil arthropods was as high as 24-32% at three sites (Table 1). Some brood cells excavated for other studies between July and September exhibited minor damage from herbivorous insects. Some agents causing leaf damage were unable to penetrate the cocoon, but other agents were capable of chewing through the tough cocoon. Cocoons with larger portions chewed away were found during the January and May excavations.

Three beetle species were recovered in the leaf pieces of brood cells: adults and larvae of *Coelus ciliatus* Eschscholtz (Tenebrionidae), larvae of *Cardiophorus* sp. (Elateridae), and larvae that are possibly a *Colops* species (Malachiidae). Unidentified cutworm (Noctuidae), other lepidopterous larvae, adult weevils and hispter (Histeridae) beetles were also recovered during excavations.

Variation in Mortality. Variation in mortality among habitats is evident in Table 1. In the treatment exposed to mammals, two sites (C and E) suffered 100% mortality; one site (A) had 52% overall mortality, and the remaining two sites (B and D) had 19 and 11% mortality. Mammal predation was the major cause at two sites (93% at C and 88% at E), soil arthropods were the main cause of mortality at one site (A), and "other" was the main cause at two sites that had the lowest mortality (B and D).

The effect of eliminating mammal predation can be seen by comparing the two treatments (Table 1). When mammals were excluded the total mortality dropped nearly 40% at two sites (C and E) but increased slightly (around 3%) in the other three sites. Eliminating mammals changed the mortality from soil arthropods, but not the same way at each site. At site C it decreased to zero, and in site E it increased four-fold. The overall mortality and the major causes remained essentially the same at the other three sites (A, B, and D).

Predicted Changes in Mortality by Removing Agents. The expected mortality for combinations of causes can be calculated from the predicted mortality for each cause acting individually (Carey 1989). Figure 1 shows the predicted effects if various mortality agents are eliminated and potential combinations are examined. If brood cells were exposed to only one agent, mammal predation would cause the greatest mortality, and parasite would cause the least. When two or three agents act in combination, it is obvious that mammal predation has the greatest impact on mortality.

Discussion

Parasite. Considering that *Megachile wheeleri* nests are very abundant in the dunes, it is surprising that the only parasite is a cleptoparasitic bee, and that the rate of parasitism is so low.

"Other." Soil fungi or other micro-organisms were probably responsible for most "other" mortality. Mites found in *M. wheeleri* cocoons probably fed on fungus and facultatively fed on the bee carcass after it died of other causes (G. C. Eickwort, pers. comm.). *Tyrophagus* mites are common omnivorous soil mites that are found in bumble bee nests and moldy pollen in honey bee hives (DeJong et al. 1982, Eickwort 1990).

Much of the brood that is not encased within cocoons by the time the first rain falls is probably killed by soil micro-organisms. It usually rains in mid-September, and radiographs of brood cells collected on September 11, 1989 revealed that 16% had not formed cocoons, including 7% that contained eggs or first instar larvae (n=495). The amount of "other" mortality in the various studies on the Preserve ranged from 4-22%. These rates are consistent with the proportion of the population at risk when the first rains arrive, and with the rates reported for other solitary bees (reviewed in Roubik 1989).

Mammal Predation. Rodents are probably responsible for the mammal predation observed during this study. There was no indication that mammals other than rodents were excavating in the experimental plots during the study period (mid September to late May). Rodent predation was first observed during a previous study (Gordon 1984) in the forest clearing where the greatest mortality occurred during the present study (site C). During subsequent years, rodent predation was observed to spread into other sites within the Preserve. A survey of *M. wheeleri* nesting did verify that rodent predation occurred at very low levels throughout the entire study area (Gordon 2000).

Although mammal predation was the main cause of mortality near two forested areas, it was very low or nonexistent in early successional sites. Mammal predation was most intense in a clearing within a young forest (site C), where rodents even dug beneath several exclosures.

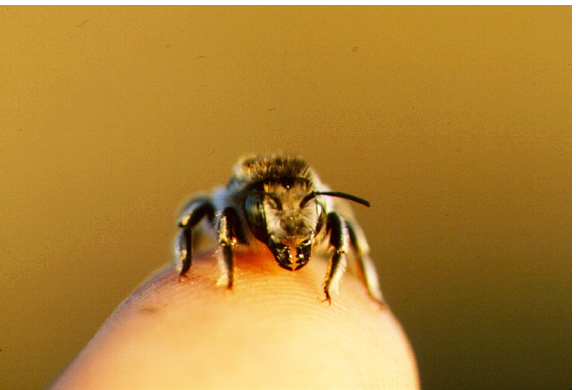
Skunks are known to predate ground-nesting bees (Stephen et al. 1969) and *Mephitis mephitis* consumed *M. wheeleri* brood in the preserve during the summer months. One was trapped during a previous study in the summer of 1978 using brood cells as bait (Gordon 1984). It appears that skunks are attracted to the brood cells when they contain pollen because skunk predation was no longer observed after the bees pupated in September. Other mammals in that may also eat bee brood include grey foxes, raccoons, two other species of rodents, and shrews. Gopher tunnels were observed near and within some *M. wheeleri* nesting habitats, but it is not clear if they do or do not eat bee brood since there was no gopher activity in the experimental plots.

Overwintering Mortality of Brood of *Megachile wheeleri* Mitchell (Hymenoptera: Megachilidae) a Ground-Nesting Leafcutter Bee in Coastal Dunes of Northern California.

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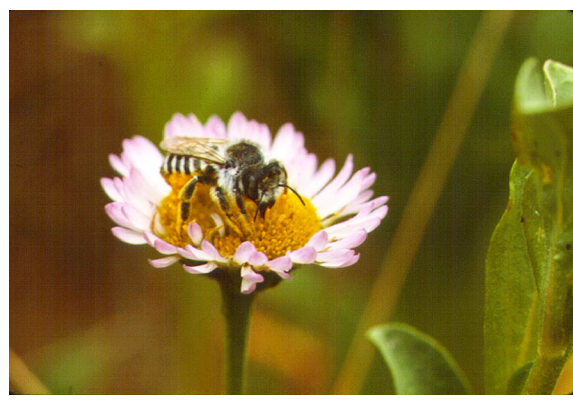
Female *Megachile wheeleri*.



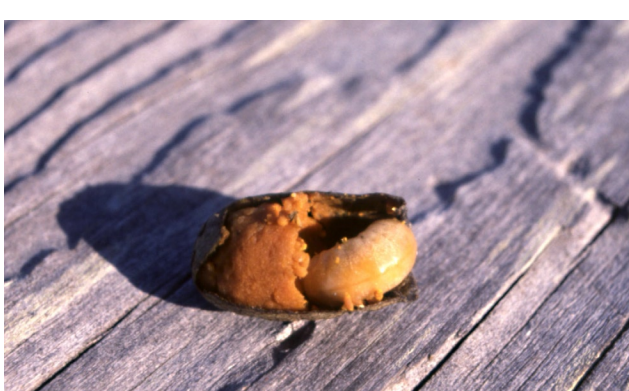
Provisioned brood cell with egg.



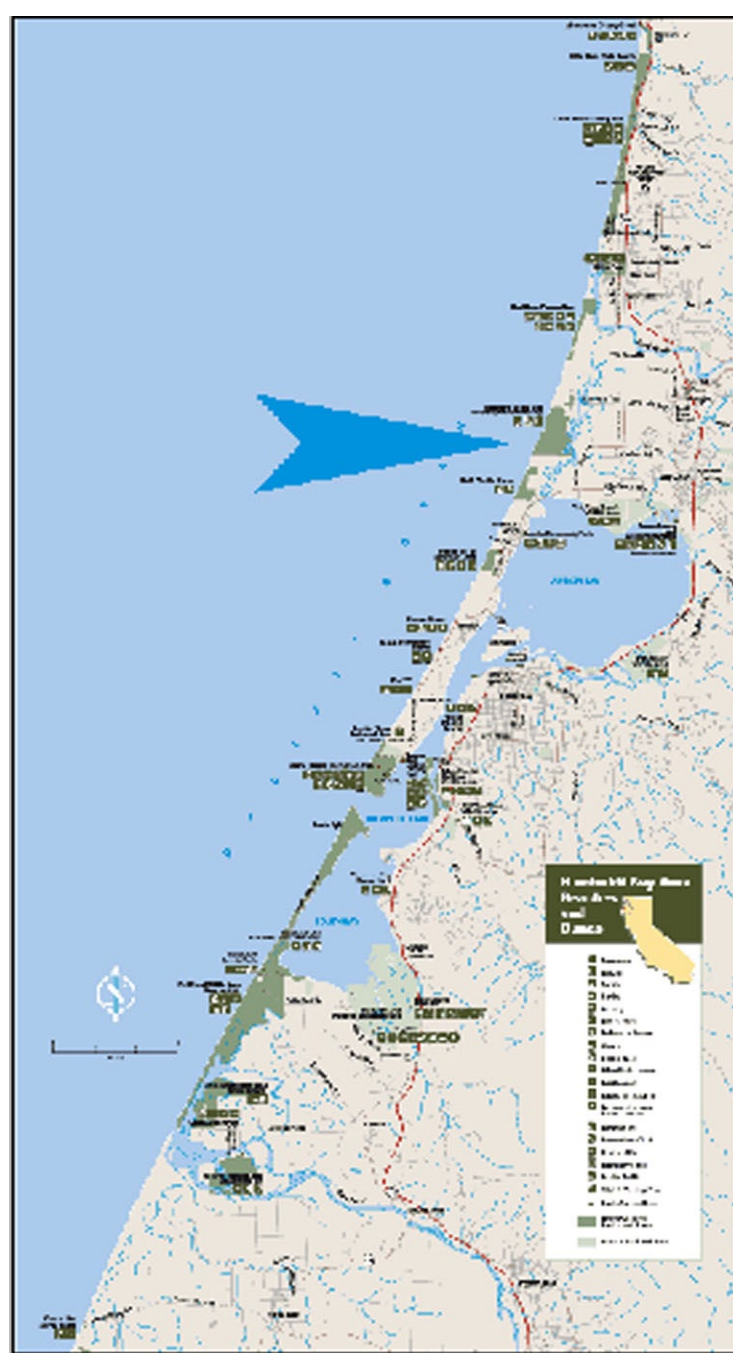
Aerial view of study site with Humboldt Bay in background.



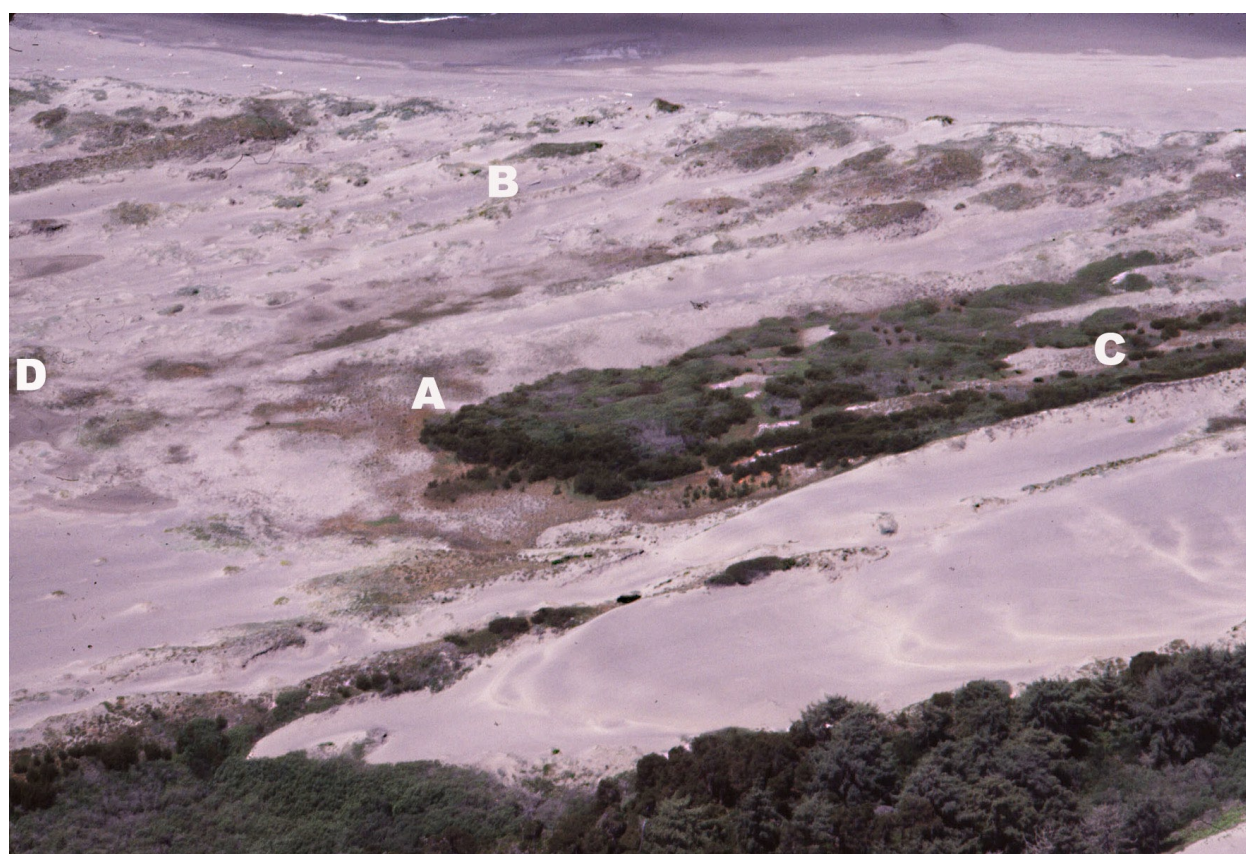
Female foraging on *Erigeron glaucus*.



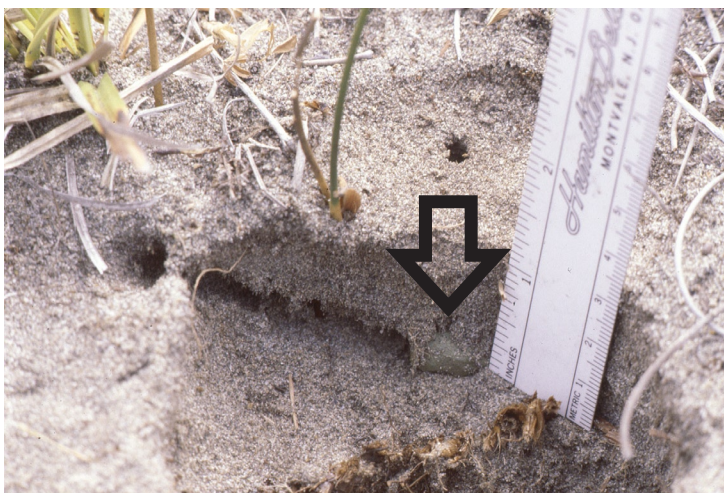
Larva feeding in brood cell.



Location of the study site in Northern California. The Lanphere Unit of the Humboldt Bay National Wildlife Refuge Complex.



Aerial view of study site showing locations of four of the five experimentally baited nesting sites.



Nest of *Megachile wheeleri* exposing the single brood cell constructed of leaf pieces.



Nest site with surface soil removed to expose brood cells.

Soil Arthropods. The big surprise was the amount of mortality inflicted by soil arthropods that are probably feeding on buried vegetation and roots and not damaging the bee larvae directly. Adults and larvae of *Coelus ciliatus* feed on buried leaf material (Doyen 1976, J. T. Doyen, pers. comm.) and were found in *M. wheeleri* brood cells. These beetles appear to inflict a minor amount of mortality on brood by feeding on leaves used to construct brood cells. Larvae of other beetle species probably also damage brood cells, but I did not find positive evidence. Many root feeders such as noctuid moth and scarab beetle larvae probably chew through cocoons. This type of mortality was highest at site A, which had a dense mat of fibrous roots and probably contains many root feeding insects. *Megachile wheeleri* cocoons in these habitats are typically enmeshed within dense masses of roots. Because several bee larvae were found alive in recently damaged cocoons excavated in May, it appears that root feeders simply damage cocoons and do not kill the larvae. Chewing through the cocoon probably allows micro-organisms to enter which kill the bee later. Herbivorous soil arthropods probably impact a variety of other insects which nest and pupate in root zones of soils.

Other Potential Predators and Parasites. Mutilid and chrysidid wasps have been collected in the dunes and bombyliid flies are often seen in nest sites, but *Coelioxys rufitarsus* was the only parasite recorded from radiographs or emergence in petri dishes from over 1,000 *Megachile wheeleri* brood cells. Several other bee and wasp species also nest in these sites that are potential hosts for these parasites.

Summary and Conclusions. This study focused on the mortality in the overwintering brood. Rodent predation is the major cause of mortality in overwintering brood in some dunes habitats, but minor or nonexistent in others. Even when mammal predation was eliminated, there was substantial mortality in the brood population from herbivorous soil arthropods and micro-organisms. Mortality caused by a cleptoparasitic bee is minor. Brood mortality was lowest in sparsely-vegetated pioneer-succession habitats, and highest in some mid-successional forested areas where it was 100%, mainly caused by rodents. Bee larvae are available all winter, are very nutritious (Hocking and Matsumura 1960), and are probably an important food resource for some rodent populations.

Acknowledgement

Lanphere-Christensen Dunes Preserve manager and the Preserve's Humboldt State University Research Advisory Committee granted permission to work on Preserve. John Doyen identified beetle larvae and adult Tenebrionidae, Phil Ward identified ants, and George Eickwort identified mites. John Neves took radiographs of bee cocoons. This study was submitted in partial fulfillment of the requirements of the Ph.D. at the University of California, Davis.

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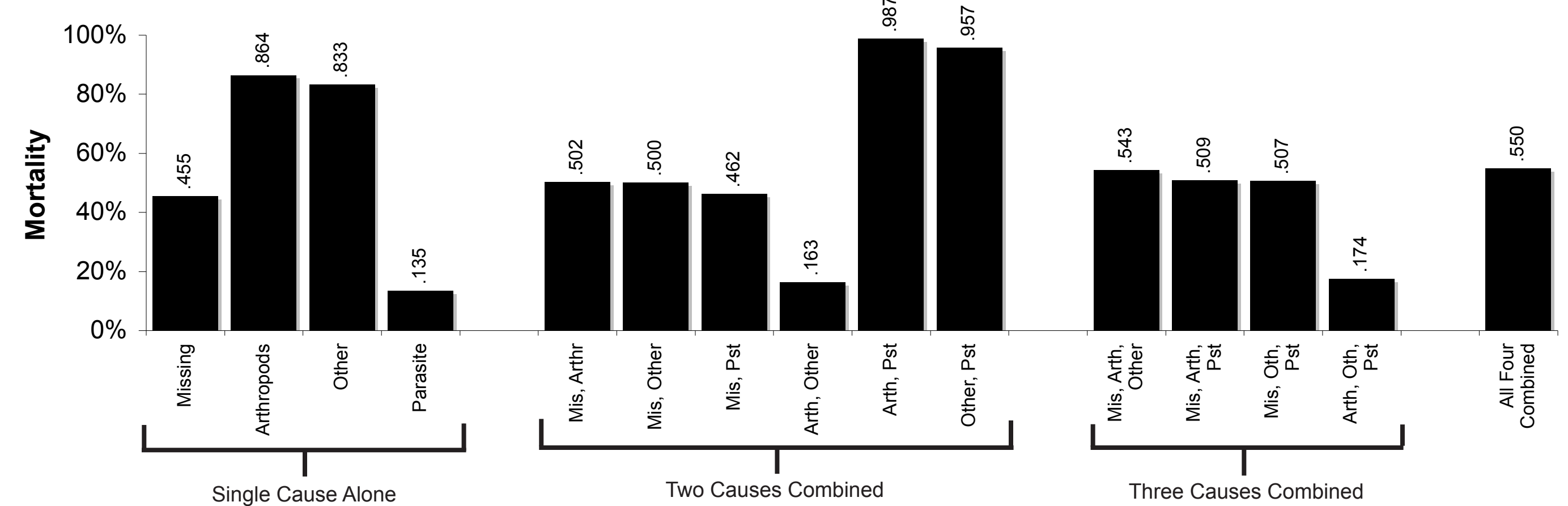


Figure 1. Impact of potential combinations of mortality in overwintering *Megachile wheeleri* brood cells for five experimental sites baited with known numbers of brood cells. Missing brood cells were attributed to mammal predation. Multiple decrement life tables allow specific combinations of causes to be estimated by factoring out all other causes and predicting the effects of specific causes alone or in various combinations. Differences in mortality when brood is exposed to a single cause, combinations of two causes, three causes or all four causes are estimated. It is clear that if brood cells were exposed to only one mortality agent, mammal predation would have the greatest impact and parasite would have the least. If two or three agents act in combination, it is obvious that mammal predation still has the greatest impact on mortality.

Table 1. Cause-specific probabilities of death in the presence of all other causes within two experimental treatments that allowed or excluded predation by mammals. Five different sites compared by treatment (with or without mammal predation). Multiple decrement life tables for overwintering *Megachile wheeleri* brood cells. Missing brood cells were classified as mammal predation. Because there was a 0.017 disappearance rate for caged cells, the amount of mammal predation is probably overestimated slightly.

Experimental Treatment	Number Beginning	Fraction Dying	Mortality by Cause			
			Parasite	Soil		Mammal Predation
				Arthropods	Other	
Kx	adx	ad1x	ad2x	ad3x	ad4x	
Mammals Allowed Access to Nests (Surface Exposed)						
A (Near Young Forest)	75	.520	.040	.240	.147	.093
C (In Clearing in Young Forest)	75	1.000		.067		.933
E (Near Brush)	75	1.000	.013	.080	.027	.880
B (Early Successional Flatland)	75	.187	.013	.013	.120	.040
D (Early Successional Flatland)	75	.107			.093	.013
Mammals Excluded (No Surface Access Allowed to Nests)						
A (Near Young Forest)	50	.560	.020	.260	.160	.120
C (In Clearing in Young Forest)	50	.580		.320		.260 a
E (Near Brush)	50	.220			.120	.100
B (Early Successional Flatland)	50	.200		.040	.100	.060
D (Early Successional Flatland)	50	.120			.080	.040

a. Rodents dug under some surface exclosures and excavated brood cells.



Location of baited experimental site A.



Location of site B showing exclosure screens.



Exclosure site C. This site had 100% mortality. 93% caused by mammal predation.



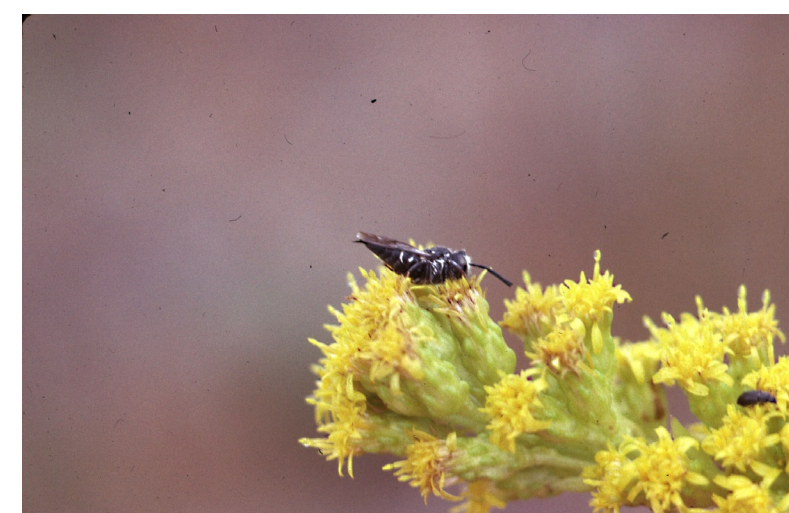
Mammal digging within an experimental site. Gopher mounds are visible. Gophers were expected to consume bee larvae, but no gophers penetrated the experimental plots.



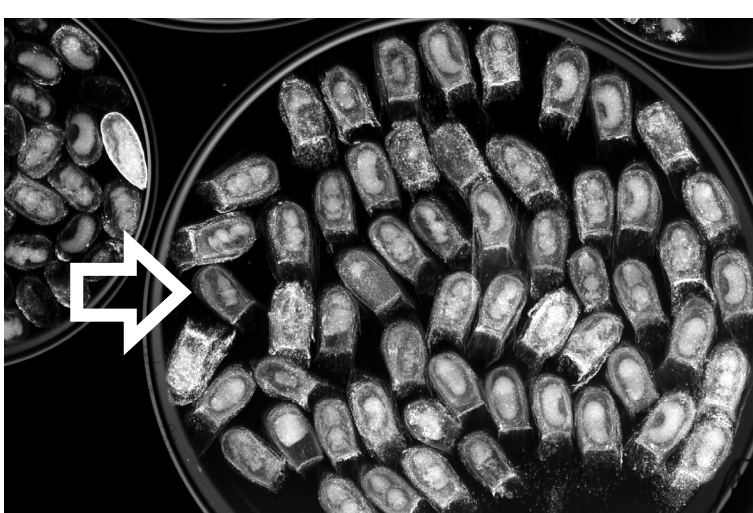
Evidence of rodent predation on ground-nesting bees and wasps.



Small mammal and rodent digging within the study area. Skunks are major predators during the summer when bee cells contain pollen, but appear to stop when the bee population spins cocoons.



Female *Coelioxys rufitarsus* a cleptoparasite of *Megachile wheeleri*.



X-ray radiograph of *Megachile wheeleri* brood cells. A *Coelioxys* pupa is indicated.



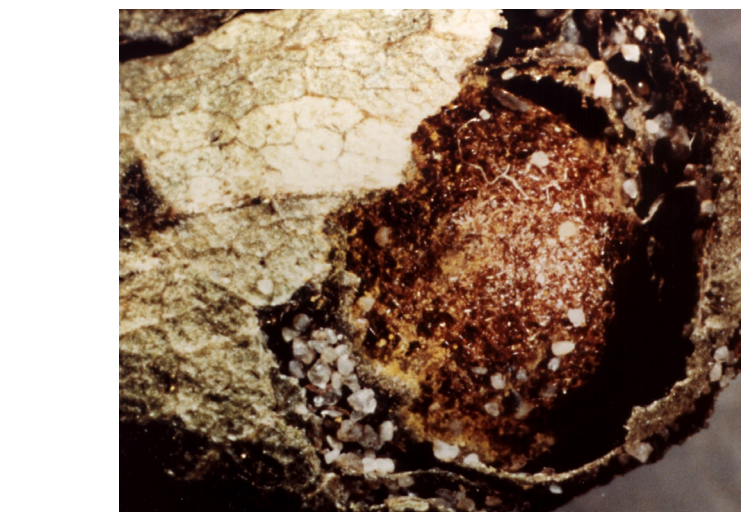
Nest site excavated to illustrate density of roots within some habitats.



Megachile wheeleri brood cell that has been penetrated by an herbivorous larva. The bee larva probably died from micro-organisms.



Brood cell damaged by an herbivorous arthropod that consumed dead leaves and pollen. The bee larva probably died from micro-organisms.



An herbivorous larva has consumed leaf material but did not penetrate the cocoon.



An adult *Coelus ciliatus* beetle (Tenebrionidae) found eating dead leaves of the brood cell. Larvae were also collected with brood cells.



Insect larvae and adults excavated from the sand in the area in the photo. *Coelus ciliatus* and *Hister* beetle adults.



Megachile wheeleri cocoons excavated in May. Note the dense wad of roots encasing the cocoons.



Rodent predators excavate the brood cells, husk the leaves, chew a hole in the cocoon and eat the prepupa.



Cocoons from rodent predation are often found in piles. Note the fecal pollen coating the cocoon. This is probably why roots grow tightly around cocoons in some habitats.



Digging typical of rodent predation on ground nesting bees in the study area.