EFFECTS OF RESOURCE AVAILABILITY ON FORAGING TRIP DURATION
IN THE SILVER BEE, HABROPoda MISERABILIS

HUMBOLDT STATE UNIVERSITY

by

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ABSTRACT

Effects of resource availability on foraging trip duration in the silver bee, *Habropoda miserabilis*

Jane V. Monroe

Habitat fragmentation can have negative effects throughout an ecosystem, but its impact is dependent on the spatial scale at which community members respond to the environment. Because solitary bees are central-place foragers, their access to floral resources is constrained by their nest location. Therefore, if habitat fragmentation causes the distance between nest and resource patches to be larger than the spatial scale at which a bee species interacts with its environment, bee fitness may suffer. I used foraging trip duration as a measure of bee response to differences in levels of resource availability at various spatial scales to determine the foraging range of the silver bee, *Habropoda miserabilis*. I timed 260 foraging trips and mapped pollen availability in the silver bee’s habitat. The results suggest that the silver bee responds to its environment at a broad spatial scale. Several factors, including weather conditions and individual foraging ability, contribute to the complexity of the relationship between foraging trip duration and resource availability, but the silver bee seems to be unaffected by small-scale habitat variation. Because the silver bee can easily fly the width of its dune habitat, this bee may act as a “pollination bridge” between scattered patches of dune-mat vegetation, and is therefore critically important to the ecosystem’s health, especially in light of increased habitat fragmentation inflicted on the dunes by invasive plant species.
ACKNOWLEDGMENTS

Many people helped with this project. Thanks to my advisor, Michael Mesler, for his support, guidance, and enthusiasm, and for introducing me to the silver bee. To my committee members, Mike Camann, Matthew Johnson, and Sharyn Marks, much appreciation for their assistance. Thanks to Mike Camann and Pete Haggard for sharing their vast knowledge of insects. Janée Mason, Maricela Escalante, Cherie Cornelison, Pete Haggard, Michael Mesler, Laurie Maxwell-Chamberlain, Gisela Rohde, and Mary-Kate Durkee helped me time bees in all sorts of weather. Tom Mendenhall provided computer assistance and generously donated a GPS unit for my fieldwork. Thanks also to Kristine Brenneman and Kim McFarland for their support and encouragement.
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INTRODUCTION

Habitat fragmentation is an ongoing concern among conservation biologists because of its effects on biodiversity, ecosystem function, and ecosystem services. Disruption of landscape connectivity can have cascading effects throughout an ecosystem (Carvalheiro et al. 2008). Negative impacts may include species loss (Rathcke and Jules 1993), changes to community composition (Stoner and Joern 2004), alteration of food webs (Stoner and Joern 2004), loss of biotic interactions (Tscharntke et al. 2002), and loss of ecosystem or community stability (Steffan-Dewenter and Tscharntke 1999). However, responses to habitat fragmentation are dependent upon the spatial scale at which community members respond to their environment. A landscape that appears fragmented to one species may not seem so to another. For example, a habitat may be perceived as a matrix containing isolated patches of resources, or as one large patch containing intermixed resources (Williams and Kremen 2007). Determining the spatial scale at which a species perceives the attributes of its environment is therefore critical to assessing the effects of habitat degradation on a given community.

Bees (Hymenoptera: Apoidea) are mainly central-place foragers (see Orians and Pearson 1979) who are adapted to naturally patchy environments. Nesting resources (substrate and/or construction materials) are often spatially separated from the pollen and nectar resources that are required for food and nest provisions. For example, the leafcutter bee *Megachile wheeleri* nests along the edges of cryptogamic mats (soil crusts of moss and lichen), but relies on various plant species for pollen and nectar (Gordon
In the same dune habitat, the wool-carder bee *Anthidium palliventre* requires “wool” from beach buckwheat (*Eriogonum latifolium*) for nest cell construction but digs its nests in cryptogamic mats (Nyoka 2004). Because it is a central-place forager, a bee’s access to floral resources is constrained by its nest location. Its foraging range must encompass both appropriate nesting substrate and sufficient floral resources for successful reproduction.

Recent studies have used various methods to determine the foraging ranges for several solitary bee and bumblebee species (see Gathmann and Tscharntke 2002, Steffan-Dewenter et al. 2002, Kremen et al. 2004, Westphal et al. 2006b, Winfree et al. 2007, Beil et al. 2008, Osborne et al. 2008, Guédot et al. 2009). Here, following others (Steffan-Dewenter et al. 2002, Westphal et al. 2006b, Osborne et al. 2008), I consider foraging range to be equivalent to the spatial scale at which a bee responds to its environment (or “spatial scale of response”), since the latter will not extend beyond the former in a central-place forager. Foraging range can be affected by resource distribution in the ecosystem (López-Uribe et al. 2008) but is ultimately limited by flight capacity.

The Humboldt Bay dune system in northern California is home to over 40 bee species (Thorp and Gordon 1992), many of which are restricted to the dunes. Habitat quality varies: Lanphere Dunes Reserve is relatively pristine, while areas to the north and south of it are highly degraded by human activities (such as off-road vehicle use) and invasive plant species. The dune ecosystem naturally contains high spatial variability: open sand alternates with patches of dune-mat vegetation, cryptogamic mats, Hooker’s willow (*Salix hookeriana*), and beach pine (*Pinus contorta* ssp. *contorta*). Adding to this
natural heterogeneity is further fragmentation caused by massive incursions of European beachgrass (*Ammophila arenaria*), other non-native grasses, yellow bush lupine (*Lupinus arboreus*), and iceplant (*Carpobrotus* spp.), all of which grow in patches of monocultures. The grasses provide neither food resources nor nesting substrate for native bees. A previous study (Nyoka 2004) has shown that invasive plants have negative effects on native solitary dune bees.

Plants that depend on native bees for pollination services may also be impacted by habitat fragmentation (Kearns and Inouye 1997), particularly when the spatial scale at which the bee responds to its environment is smaller than the distance between plant patches (Harris and Johnson 2004). Seed set may depend on the ability of wild bees to transport pollen between flower patches, but bee abundance and species richness decline with increasing patch isolation (Steffan-Dewenter and Tscharntke 1999). Wild bees’ success in reproduction may suffer if their foraging range does not include adequate supplies of nectar and pollen. Thus, if a bee species’ foraging range limits its ability to visit widely scattered or isolated plant patches, plant-pollinator mutualisms may be disrupted (Steffan-Dewenter and Tscharntke 1999). A bee functioning on a sufficiently large spatial scale should be able to ameliorate some of the negative effects of habitat fragmentation on plant reproduction (Lennartsson 2002) while preserving its own fitness. In the case of the Humboldt Bay dunes, the persistence of the overall pollination web, in the face of increasing habitat fragmentation, most likely depends partly on generalist pollinators (Pauw 2007) native to the dunes, especially those with bigger foraging ranges (Harris and Johnson 2004).
The silver bee, *Habropoda miserabilis* (Cresson), is a rather large (15-21 mm body length) solitary bee in the family Apidae. It nests in aggregations in the coastal sand dunes of northern California and southern Oregon, and is abundant seasonally in the Humboldt Bay dune system. During nesting season (generally April to early July for the populations considered in this study), female silver bees make foraging trips from their nests, which they dig in the sand, to flower patches to collect nectar and pollen. The silver bee is a polylectic bee whose plant resources include beach pea (*Lathyrus littoralis*), the invasive yellow bush lupine, yellow sand-verbena (*Abronia latifolia*), Hooker’s willow, and other dune plants, though floral resources on the dunes are somewhat limited and constantly changing during the early spring (Gordon 1984). The silver bee pupates in late summer, and adults overwinter in their natal cells to emerge the following spring (Stephen and Torchio 1961). The silver bee is accustomed to a certain degree of patchiness, since it nests mainly in open sand (see Appendix I) and forages in dune-mat and other flower patches.

The silver bee’s short flight season (a few weeks) limits the amount of time it has to dig cells and provision its offspring. A bee that can complete more foraging trips per unit time should be able to provision more eggs over her lifetime (provided she does not run out of eggs) (Goodell 2003, Williams and Kremen 2007). Time has a greater effect on foraging success than does energetic cost (Westphal et al. 2006a). Thus, foraging trip duration may be a good indicator of fitness, since a bee that can make quicker trips will presumably be able to provision more cells. Gathmann and Tscharntke (2002) found that foraging trip duration in the bee *Osmia rufa* decreased with increasing flower cover.
Osmia lignaria nesting on conventional farms far from natural habitat produced fewer offspring than those nesting on organic farms or in riparian areas, apparently because of the extra time and energy the former spent foraging far from the nest (Williams and Kremen 2007). The amount of time it takes to provision one cell depends on foraging trip duration, pollen unloading time, transport capacity (how much pollen and nectar a bee can carry), and the quantity of resources required by the offspring (Neff 2008). For solitary bee species with low rates of reproduction, even a slight alteration in the number of offspring can have great consequences for fitness (Williams and Kremen 2007). Foraging trip duration may therefore have a strong effect on the silver bee’s success in reproduction.

Foraging trip duration is partially dependent on resource availability at the bee’s spatial scale of response. Westphal et al. (2006a) found that the bumblebee species Bombus terrestris took less time to forage when living in areas of abundant resources than when living in areas of sparser resources, as measured at a spatial scale of 3000 m radius around the colony site. The same study determined that bumblebee colonies making briefer foraging trips in areas of abundant resources gained significantly more weight, and produced more brood, than colonies making longer foraging trips in sparser habitat.

Given that foraging trip duration is strongly affected by resource availability, and that a central-place forager’s access to pollen and nectar is restricted by nest location, foraging trip duration should be a useful variable for determining the spatial scale at which a bee interacts with its environment. If the silver bee perceives floral resource
availability at a particular spatial scale, its foraging trip duration should vary predictably at that scale; that is, abundant floral resources at the bee’s spatial scale of response should result in shorter foraging trip durations, and sparser floral resources at the same scale should result in longer foraging trip durations.

Determining the spatial scale at which the silver bee responds to its environment will reveal details about how the massive fragmentation occurring on the Humboldt Bay dunes may affect native bees and the plants dependent on them for pollination services. I hypothesized that the silver bee’s spatial scale of response, as gauged by foraging trip duration, will be large, since it is a big bee accustomed to a habitat where appropriate nesting substrate is often spatially separated from floral resources.
METHODS

This study involved silver bee nest aggregations that were located along a 27 km stretch of northern California’s Humboldt Bay Dunes, from the southern tip of the North Spit up to Clam Beach on the north. At their widest point, the dunes span about 1300 m (Pickart and Sawyer 1998), but for the most part they are less than 500 m wide. On the west they are bounded by the Pacific Ocean, and on the east by Humboldt Bay, agricultural land (in which no crops flower during the silver bee’s flight season), dune forest, and human habitation. My study aggregations were located at the Eureka Protected Area, Samoa Dunes, Manila Dunes, Ma-le’l Dunes, Lanphere Dunes Reserve, Mad River Beach, and Clam Beach (Figure 1).

To test my hypothesis, I timed foraging trips at 25 aggregations. I chose 7 spatial scales—250, 500, 750, 1000, 1500, 2000, and 3000 m—and used ArcGIS to map them as buffers around each aggregation. Resource availability was measured as the percentage of each buffer’s area that contained pollen-providing flowers. I chose to focus on pollen rather than nectar because it is not possible to tell whether a silver bee arriving at her nest has acquired nectar during her foraging trip, but pollen packed on her scopae is readily apparent.

I found nest aggregations by searching likely areas of the North Spit on foot in the early spring for telltale nest holes, for males scouting for emerging females, and for the conspicuous pollen-laden females. I utilized each active aggregation that I located; there are several long stretches of the dunes that contain no nest sites, probably because of a
lack of suitable nesting substrate. Aggregation sites were marked as waypoints in a Garmin GPS III Plus. The average minimum distance between aggregations was 686 m, with minimum distances ranging from 60-5250 m. Three pairs of aggregations were within 100 m of one another, so from each pair, the aggregation with the fewest trip timings was removed. Excluding these three sites from the dataset increased the average minimum distance to 770 m.

I used ArcGIS 9.2 to map the distribution of pollen resources, using a combination of the National Agriculture Imagery Program (NAIP) 2005 aerial photos and ground-truthing. I divided the landscape into two categories: pollen-providing territory (higher resource availability) and low/no-pollen territory (low or no resource availability), and established zones of each category by drawing polygons around different blocks. For example, zones dominated by beach pine or open stretches of sand were assigned to the low/no-pollen category. Pollen-providing zones included stands of yellow bush lupine, patches of beach pea-phase dune-mat, and other pollen resources such as blackberry brambles (*Rubus* sp.). Because of the nature of the plants (yellow bush lupine is a large shrub with many flower spikes per plant, while beach pea is a low-growing dune-mat plant), as well as differences in plant density, polygons marked as pollen-providing zones varied in resource availability; however, all had considerably greater pollen resources than did the polygons in the low/no-pollen category. In this way, the entire North Spit, as well as the landscape extending to 3000 m beyond it, was mapped into one of two pollen categories. Because large portions of the landscape were not part of the dunes, this task was simplified for much of the territory involved: ground-
truthing was obviously not necessary to confidently label ocean and bay as low/no-pollen zones.

ArcGIS 9.2 was also employed to determine the level of pollen availability surrounding every nest aggregation at various spatial scales. Following Steffan-Dewenter et al. (2002), I calculated the amount of pollen-providing territory in each buffer around each nest aggregation as a percent of the total territory within that buffer (i.e., that scale) (Figure 2). Pearson correlation coefficients were calculated to determine if the percentage of pollen-providing territory at one spatial scale predicted that at another (for example, if percent of pollen-providing territory at 250 m predicted percent of pollen-providing territory at 500 m).

I recorded foraging trips to the nearest second using a stopwatch. If a bee returned without pollen, her trip was not recorded. Trips were considered complete the moment the bee landed at her nest entrance, except on particularly windy days, when the bees often had trouble locating and then entering their nests. In such cases, once it was obvious that a bee had successfully located her nest but was being blown away from it, I stopped the stopwatch but continued to observe the bee to ensure that she eventually entered the correct nest. On a very windy day, it sometimes took a bee several additional minutes to enter her nest.

At each aggregation, I timed as many bees as possible (2-34 bees per site), though individual bees were timed only once each. Wind speed and temperature were recorded approximately once per hour during timing rounds. I randomly chose which site(s) to visit each day, and visited sites nearly every day from May 12 to June 27, 2008, skipping
days that were very drizzly or below 11.7°C (53°F), in which conditions the bees are not likely to be active (Nyoka 2004). After June 27 only a couple of aggregations were still active. All timing rounds were completed between 10:00am and 16:45pm.

All foraging times measured at a given nest aggregation were pooled across dates and averaged. I spent 1-5 days at each aggregation. Individual foraging trip durations could not be considered independent because, although these bees are solitary and do not communicate information about food resources to one another, all bees at one aggregation are responding to the same environment. I calculated two average foraging times for some of the aggregations, since one of the silver bee’s main pollen and nectar sources, beach pea, finishes flowering relatively abruptly partway through the bee’s flight season, which leaves yellow bush lupine as the bees’ major pollen source. The loss of beach pea greatly altered the percentage of pollen-providing territory in many buffers, since it is a common dune-mat plant. I chose June 10 as the end of the beach pea flowering period because after that date, most (approximately 80-85%) of the beach pea that I observed was fruiting, and I saw no bees of any species on it. Aggregations at which timing rounds were conducted both before and after June 10 therefore have two average foraging trip durations to go along with the two different levels of pollen availability that were measured. Foraging trips were timed at 18 aggregations during beach pea’s flowering period, and at 7 aggregations after beach pea had ceased flowering, with 3 aggregations being in both sets. According to Anderson-Darling tests, both sets of data were normally distributed.
Mean foraging trip duration was regressed against percentage of pollen-providing territory using Minitab 15. If the silver bee responds to its environment at a certain spatial scale, the linear regression for that buffer should have a higher adjusted $r^2$ value than the others (Steffan-Dewenter et al. 2002), since more variation in foraging trip durations would be explained by changes in resource availability at that scale (for example, longer trips would occur predictably with lower pollen availability). Likewise, if the silver bee’s foraging trip durations are not affected by changes in percentage of pollen-providing territory at a particular spatial scale (for example, longer trips would not necessarily occur in conjunction with lower pollen availability), that buffer is not the silver bee’s spatial scale of response, and its adjusted $r^2$ will be low.

To determine if foraging trip durations were spatially autocorrelated, I used the “ape” package in R to calculate Moran’s $I$. This test would reveal if foraging times at different sites were related to each other based on distribution of aggregations across the dunes.

Because weather conditions and other factors unrelated to pollen availability may have affected foraging trip duration, I regressed wind speed, time of departure, and temperature against individual unaveraged foraging trip durations (since these additional variables could not themselves be averaged). Similarly, I ran an ANOVA on nest site versus individual foraging trip times. To determine if date affected foraging trip duration, I ran a linear regression using foraging trip duration averaged by aggregation and separated by date.
To obtain a separate assessment of the silver bee’s spatial scale of response, I estimated foraging range based on body size (as indexed by intertegular span), using equations developed by Greenleaf et al. (2007). I measured the distance across the thorax, from wing base to wing base, on 29 adult female silver bees collected from their overwintering cells during the fall and winter of 2008-09. I then plugged these measurements into the Greenleaf et al. (2007) equations, to obtain estimates of the silver bee’s maximum homing distance (in homing tests, defined as the distance from which 50% of individual bees return home after release), typical homing distance (defined as the distance from which 90% of bees return home), and maximum feeder training distance (defined as the greatest distance from home from which an individual bee finds it energetically profitable to forage at an artificial feeder).
Figure 1. Selected silver bee aggregations at the northern Humboldt Bay dunes.
Figure 2. Distribution of pollen resources around two nest aggregations, overlaid with buffers from 250 m to 3000 m. The top aggregation has greater pollen availability within 1000 m. Stippled = pollen-providing territory; light grey = low/no pollen; dark grey = ocean, bay, and river.
RESULTS

A total of 260 foraging trips were timed. Individual foraging trip durations lasted 8.4-90.3 min, with an overall mean of 34.5 min; mean foraging trip duration during beach pea’s flowering period was 30.5 min, increasing to 42.7 min after beach pea ceased blooming. Averaged by aggregation, foraging trip durations ranged from 15.4-54.0 min.

The percentage of pollen-providing territory in each buffer size varied widely between aggregations. The 250 m scale had the widest range of percentage of pollen-providing territory, from 0.0% at one aggregation to 68.1% at another, while the 3000 m scale had the least variation, ranging from 0.3-2.7% during beach pea’s flowering period (Figure 3). Percentage of pollen-providing territory at each spatial scale was strongly correlated only with spatial scales of a similar radius (Figure 4); for example, the percentage of pollen-providing territory at the 250 m radius was not strongly predicted by that at 3000 m.

Comparing the periods during and after beach pea season, the reduction in percent of pollen-providing territory varied from aggregation to aggregation. For example, one of the three aggregations timed both during and after beach pea season experienced no change in the amount of pollen-providing territory within 250 m, while another dropped from 39.2% to 0.0%. For the same three aggregations, the amount of pollen-providing territory at 3000 m decreased by one-quarter (during: 2.0%; after: 1.5%) to two-thirds (during: 2.0%; after: 0.7%). After beach pea season, the distance from a given
aggregation to the nearest patch of pollen-providing territory increased by as much as
1400 m.

Foraging trip duration did not respond to resource availability except at spatial
scales ≥ 2000 m, and then only after beach pea had ceased flowering (Table 1). For the
period while beach pea was still in bloom, no relationship was evident between foraging
trip duration and resource availability at any spatial scale tested. The relationship after
beach pea had ceased flowering was strongest at 3000 m (linear regression: $P=0.011$,
adjusted $r^2=0.705$, $T=3.92$) (Figure 5), but was also significant at 2000 m (linear
regression: $P=0.031$, adjusted $r^2=0.566$, $T=2.97$).

Foraging trip duration differed significantly between nest sites (ANOVA:
$P<0.001$, adjusted $r^2=0.255$, $F=4.69$). The longest mean foraging trips, both during and
after beach pea’s flowering period, occurred at aggregations at Lanphere Dunes Reserve
(during: 54.0 min; after: 50.8 min), and the quickest foraging trips were at an
aggregation located near the Eureka Protected Area (during: 15.4 min; no longer active
after beach pea season). Both during and after beach pea’s flowering period, the nest
sites’ average foraging trip durations were weakly spatially autocorrelated with each
other (during: Moran’s $I=0.207$, $P=0.054$; after: Moran’s $I=0.413$, $P=0.088$).

Wind speed and time of departure had no effect on foraging trip duration (both $P$
values $>0.25$). In contrast, foraging trip duration decreased with increasing temperature
($P<0.05$). There was also a temporal pattern: foraging trip duration increased as the
silver bee’s flight season progressed (linear regression: $P=0.007$, adjusted $r^2=0.133$,
$T=2.84$) (Figure 6).
Finally, the sampled silver bees’ average intertegular span was 4.29 mm. Inserted into the Greenleaf et al. (2007) equations, this measurement returned a maximum homing distance of 5872 m, a typical homing distance of 2572 m, and a maximum feeder training distance of 5069 m.
Figure 3. At each spatial scale, the range of percent of pollen-providing territory during beach pea’s flowering season (a) and after (b). Pollen-providing territory decreases beyond the limits of the dunes. Each point on the graphs represents a silver bee aggregation.
Figure 4. Pearson correlation coefficients for the percentage of pollen-providing territory at each spatial scale, for the period during beach pea’s flowering season (a) and after (b). Percent of pollen-providing territory at each spatial scale is strongly predicted only by that at spatial scales of a similar radius.
Table 1. Results of linear regression analyses for foraging trip duration and percentage of pollen-providing territory at each spatial scale. “Bloom” indicates flowering season of beach pea.

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**Figure 5.** At 3000 m, the influence of pollen-providing territory on foraging trip duration during beach pea’s flowering period (a) and after (b).
Figure 6. Effects of date on foraging trip duration. Earlier in the flight season, silver bees completed each foraging trip in a shorter amount of time. Points on scatterplot represent averages of datapoints collected at each aggregation. On some occasions, more than one aggregation was timed per day.
DISCUSSION

Silver bee aggregations exist in a landscape with great variation in resource availability across both space and time. Even though foraging trip duration varied across sites and became longer as the season progressed, average trip time was not related to level of resource availability in most cases. The inability to detect such a relationship during beach pea’s flowering period suggests that the silver bee has a broad spatial scale of response and is unaffected by small-scale changes in resource availability. After beach pea’s flowering period, foraging trip duration was affected by percentage of pollen-providing territory at a spatial scale of 3000 m, which also implies that the silver bee routinely forages at a broad spatial scale. The silver bee, like some lepidopterans (Stoner and Joern 2004), may not perceive its habitat as fragmented, partly because it is a flower generalist that can fly easily between patches (Tscharntke et al. 2002).

The spatial scale at which the silver bee responds to its environment may be difficult to detect during beach pea’s flowering period because of complicating factors that obscure the relationship between foraging trip duration and resource availability. Factors such as relative locations of nectar and pollen sources, weather conditions, habitat patchiness, and individual foraging ability may all affect bee behavior and, consequently, foraging trip duration (Neff 2008). Because these factors may increase or decrease trip times, they may also mask the silver bee’s spatial scale of response.

The first issue that may add variability to trip times is that pollen-foraging trips may or may not include nectar collection. For example, yellow bush lupine provides
copious pollen but no nectar; a bee foraging on lupine has to find a nectar source during her pollen-foraging trip or make a separate nectar trip altogether. It may or may not be more energy- and time-efficient for a bee to combine nectar and pollen trips, depending on the locations of nectar and pollen sources relative to each other and to the nest site. Therefore, the choices that individual bees make regarding nectar collection may contribute to variation in foraging trip duration.

Second, trip times may be affected by bee exposure and thoracic heat dissipation (see Bergman et al. 1996). In the early spring, the coastal dunes are often windy, cloudy, and drizzly. The silver bee can fly in light drizzle and winds upwards of 24 kph, as long as the ambient temperature is at least 11.7°C (53°F), but bee flight speed is slowed by cooler temperatures (Danforth 1990). Because thoracic heat dissipates quickly in the cold, wind, and damp, the silver bee’s strong flight capabilities are important not only for the distances it needs to fly, but also for the inhospitable weather conditions it regularly encounters. These conditions may lengthen travel times if an individual bee adjusts her foraging behavior to minimize the effects of wind and exposure. For example, options such as flying downwind, flying circuitous routes, sticking to less-windy hollows and avoiding hills, basking (Klein et al. 2004), and/or resting before returning to the nest site may all result in longer foraging trip durations.

Next, differences in individual foraging ability and habits, combined with the patchy nature of the dunes, may affect the trip times of different bees in various ways. Whether a bee locates a given flower patch depends in part on her individual searching ability, which direction she flies upon leaving the nest, her ability to accurately memorize
and relocate a rewarding patch, the distance to the patch, and the visibility of various
flower patches (Osborne et al. 2008). Patch constancy (a bee’s “loyalty” to rewarding
patches) may also affect foraging trip duration, since a bee who displays constancy will
reduce her search times (Westphal et al. 2006a), though she may also incur longer travel
times if her chosen patch is quite distant compared to others. Furthermore, a particular
patch may or may not contain sufficient pollen for a full load (Williams and Tepedino
2003); the silver bee, like many other bees (Roulston and Cane 2002), frequently collects
more than one pollen species per foraging trip (see Appendix I), suggesting that it visits
multiple patches per trip. Also, flower handling time may be longer for a bee who has
not learned how to efficiently harvest pollen from hard-to-work legumes like beach pea
and yellow bush lupine, and may vary between bees who are working different flower
types (Neff 2008). A bee may or may not engage in multiple activities during one
foraging trip (collecting pollen, collecting nectar, searching for new patches, handling
different flower species, resting and/or flying circuitous routes, etc.), and her choices
seem likely to affect trip times.

The silver bee may show a response to resource distribution only when beach pea
has ceased flowering because bees may employ a smaller foraging range when resource
availability is high, then switch to a bigger foraging range to account for reductions in
resource distribution as the season progresses (Minckley et al. 1994, López-UrIBE et al.
2008). Because the distance to the nearest resource patch varied between silver bee
aggregations, each aggregation may have had a different “beach pea foraging range” than
the others. In other words, the aggregations were not all responding to the environment
at the same scale while beach pea was in bloom. Bee species may often have more than one foraging range in different locations, dependent on resource availability and distribution (Knight et al. 2009); it stands to reason that bees at the same site may have multiple foraging ranges across time as well. The significance of date in statistical analysis implies that temporal changes in floral resources and in bee condition (age and wing tatter, for example) have strong effects on foraging trip duration. Changes in resource availability (reduced density, greater distances between patches), whether from day to day or over the course of one day, necessitate longer search and travel times. Once beach pea finished flowering, aggregations experienced decreases of up to 100% in the amount of pollen-providing territory within 250 m, and the distance to the nearest pollen-providing patch increased by up to 1400 m.

The bees may have been travelling long distances even during beach pea’s flowering period in order to collect yellow bush lupine pollen, which would have further obscured the relationship between foraging trip duration and resource availability. Since yellow bush lupine has much more pollen per unit area than does beach pea or any other dune-mat plant, searching and travelling long distances for lupine may be an energetically profitable strategy in such a patchy, low-resource-density environment, even while beach pea is in full bloom, especially if competition further reduces beach pea pollen quantities (Osborne et al. 1999). A preference for lupine pollen may help to explain the finding that, counter to expectations, bees nesting in “pristine” habitat had longer foraging trip durations than bees nesting in degraded areas. Yellow bush lupine has been eradicated from Lanphere Dunes Reserve (“LDR”), so the LDR bees, which had
the longest mean foraging trip durations both during and after beach pea season, had some of the lowest amounts of pollen-providing territory available nearby (during: 1.7-2.3% within 1500 m; after: 0.0-0.2% within 1500 m). On the other hand, the quickest foraging trips occurred at an aggregation near the Eureka Protected Area that had 32.2% yellow bush lupine cover within 250 m. Silver bees at nearly every aggregation—including two of the four LDR sites—routinely brought yellow bush lupine pollen back to their nests throughout the flight season. For the LDR bees, this meant travelling at least 1100 m to a small patch of lupine; if the bees did not discover this patch during their searches, the next closest source of yellow bush lupine pollen was over 1200 m farther on, meaning that some of the LDR bees must have been regularly travelling over 2300 m to acquire lupine pollen, even before beach pea ceased flowering.

Such willingness to travel long distances suggests that yellow bush lupine pollen is energetically and nutritionally worth the effort, and that the bees are unaffected by small-scale habitat variation. Osborne et al. (2008) found that *Bombus terrestris* colony weights and numbers of workers did not change with distance to forage, and the authors surmised that this lack of difference occurred because, although forage availability differed within 500 m, it did not within 3000 m, allowing all colonies access to the same amount of floral resources. Because the silver bee is solitary, the increased search and travel times incurred either as floral resources become even more patchily distributed, or as a result of complicating factors like weather conditions, could lead to fewer offspring (Williams and Kremen 2007). However, like *B. terrestris* (Westphal et al. 2006b), the silver bee seems to routinely forage at broad scales—at least 3000 m. The Greenleaf et
al. (2007) equations predict a silver bee maximum feeder training distance of 5069 m and a maximum homing distance of 5872 m; homing distance is thought to be a good indicator of maximum foraging range and habitat size (Guédot et al. 2009). Other large bees respond to their environment at broad spatial scales: a model for central-place foragers predicts a spatial scale of response of over 4000 m for various bumblebees (Bombus sp.) (Cresswell et al. 2000), and the carpenter bee Xylocopa flavorufa forages up to 6000 m from its nest (Pasquet et al. 2008). Finally, Euplasia surinamensis, a euglossine bee that is adapted to foraging on plants with a highly patchy, low-density distribution, has a homing distance of 23 km (Janzen 1971). It should not be surprising, then, that the silver bee, also accustomed to a highly patchy distribution of resources, would have a foraging range of 3000 m or more (though it is not known if, like E. surinamensis, the silver bee follows traplines). The silver bee should easily be able to fly the width of the dunes (usually around 500 m, with a maximum of 1300 m), and resource availability beyond the dunes may not be important; specific habitat restrictions are common among solitary wild bees (Steffan-Dewenter et al. 2002). For example, bees in a sandy ecosystem in Germany did not forage to a meaningful extent in the surrounding agricultural landscape (Beil et al. 2008).

The silver bee’s flight capabilities and spatial scale of response make it an important member of the Humboldt Bay dune ecosystem. As a large bee with a broad foraging range and polylectic behavior, it may be envisioned as a “connector bee” for patches of dune-mat vegetation. If, as seems likely, it is often visiting multiple patches per foraging trip, the silver bee may act as a bridge to facilitate reproduction between
plants in spatially separated fragments. Such plants can be pollinator-limited, leading to inbreeding depression (Lennartsson 2002) and declines in seed set (Steffan-Dewenter and Tscharntke 1999). Because disturbed and fragmented habitats tend to have larger bee species (Gathmann and Tscharntke 2002), and larger bees have disproportionately bigger foraging ranges than smaller bees (Greenleaf et al. 2007), isolated dune plant populations may rely on the silver bee’s pollination services. In turn, the silver bee may indirectly affect smaller bee species and oligolectic bees, by ensuring that the necessary plants maintain viable populations.

The silver bee has a potentially complicated role in dune ecology because it forages heavily on yellow bush lupine, possibly contributing to the invasive plant’s spread. Tepedino et al. (2008) surmise that invasive plants may increase native bee population sizes in some habitats, and yellow bush lupine’s copious pollen output may allow the silver bee to extend its range (spatially and/or temporally) or maintain healthy population levels in the face of dune destruction by European beachgrass. Yellow bush lupine acts as a magnet species in central Chile (where it is also an invasive), drawing pollinators to nearby less-attractive flower species and increasing their seed output significantly (Molina-Montenegro et al. 2008). It is yet to be determined if the small, scattered dune-mat plants (including the endangered Humboldt wallflower [Erysimum menziesii ssp. eurekense]) receive more pollinator visits in the presence of yellow bush lupine. However, lupine does contribute to the loss of open-sand and dune-mat zones by forming monocultures that replace them, and by enriching the substrate (Cipra 2006); lupine therefore facilitates the growth of other invasive plants and prevents ground-
nesting bees from establishing nests (Nyoka 2004). Nyoka (2004) suggests that native plants in this dune system are receiving sufficient pollination despite the habitat disturbance; it may be that the silver bee and bumblebees, with their large foraging ranges, strong flight capabilities, and abundance (at least for a short time), are largely responsible for maintaining pollination levels of certain plant species.

Like yellow bush lupine, European beachgrass contributes to the loss of open-sand and dune-mat zones, reduces available forage resources, fragments the habitat, and obliterates nesting substrate. Extensive stands of European beachgrass and other non-native grasses cover large portions of the dunes. European beachgrass’s tendency to hold sand in place alters the general structure of the dunes (Pickart and Sawyer 1998) and creates hummocks that silver bees sometimes use as aggregation sites, but European beachgrass’s profuse root system may hinder nest-digging and often entangles the bees. Mats of roots erode from the sides of hummocks and overlay nest entrances in a network that the bees must climb through when entering or leaving their nests.

Conservation of the silver bee should be a priority. As a wide-ranging pollinator of early-spring dune-mat plants, it may hold a vital position in maintaining the community’s health while contending with invasive plant species and the recreational popularity of the dunes. Aggregations are regularly subject to human disturbance, partly because the silver bee readily nests in or at the edges of trails (because these areas provide open sand). Many trails are heavily used by people, dogs, and horses, which contributes not only to surface nest damage but also to erosion and compaction of sand. While this study was under way, one of the active nest sites was destroyed when a
Another aggregation, in a European beachgrass hummock, later appeared to have been disturbed by people climbing on it, gouging out the sand to a depth great enough to unearth pre-emergent silver bees overwintering in their cells (K. McFarland, pers. comm.). Because availability of nesting substrate seems to be an increasingly limiting factor for the silver bee, and because of the bee’s importance to the dune community, its own needs must be considered by dune conservationists. Its relationships with yellow bush lupine and European beachgrass must be taken into account, as well as its need for both open (or sparsely vegetated) sand and sufficient floral resources within or close to the dunes. As a big bee with a large spatial scale of response, but inhabiting a relatively small zone, the silver bee plays a critical role throughout the Humboldt Bay coastal dunes.
REFERENCES


While timing the silver bee’s foraging trips, I was also able to observe and consider some of its behaviors regarding navigation, nesting, and nest sites:

**Navigation**

A silver bee female makes use of landmarks to find her way to and from her nest. She normally exits her nest hole very quickly, flying directly from just inside its mouth. She then often turns and hovers in front of it, and zips back and forth in widening arcs to orient herself to the nest’s appearance and location. She also seems to make note of any useful landmarks, such as large and small plants, twigs, pebbles, detritus, people observing the bees, and so forth. Often she will hover for a few moments in front of chosen landmarks as if memorizing their appearance and their distance and direction from her nest hole. Once satisfied, she flies away to forage. These “landmark checks” are done upon most exit instances, possibly to account for short-term landscape changes, which are not infrequent in the sandy, windy dunes.

Upon returning from her trip, a bee nearly always approaches her nest more slowly, and often has to spend a few seconds or more searching for her nest hole before landing at its mouth. She will also sometimes land just outside her nest hole and walk in.

A bee’s ability to relocate her nest may be affected by changes in her chosen landmarks or by windblown sand obscuring her nest hole. Wind or another bee digging a nearby nest may cover the returning bee’s nest hole with sand, and small landmarks such
as twigs may be moved, blown away, or covered by windblown sand. In poor conditions such as those caused by high winds, a bee may spend over twenty minutes searching the immediate area for her nest. She also has to contend with gusts of wind blowing her away from her intended destination. Once she finally locates and reaches her nest, if it has been obscured by sand she may have to spend another twenty to thirty minutes digging out the opening again, while bearing a full load of pollen on her scopae. In particularly poor conditions, it is not unusual for a bee to try to dig out the wrong place; when the expected nest opening is not quickly revealed, she often becomes confused and makes short re-orientation flights, often with several brief attempts at digging in spots very close to each other as she attempts to locate her nest entrance. Occasionally a bee who is searching for her nest will enter other bees’ nest holes, but she always walks back out when she realizes her mistake. A bee sometimes seems unable to relocate her nest, even after extensive searching, which is not surprising since early spring is a period of much wind-driven sand movement.

Windblown sand is not the only problem for a silver bee trying to locate her nest upon returning from a foraging trip. Sudden changes to her chosen landmarks may throw her off as well, though individual bees had varying responses to such problems. An anecdotal example: While timing foraging trips at one of the aggregations, my helpers and I had set up a lawn chair at the edge of the site. While observing bees, we noticed a couple of them making orienting flights and landmark checks around the lawn chair and its occupant before flying away to forage—it was not uncommon for bees to choose stationary human observers as landmarks. Since we were not timing these particular
bees, it was not a concern when we moved the lawn chair to the opposite side of the aggregation site. Later we noticed a pollen-laden bee who appeared to be lost; she kept flying over the site, hovering here and there, and repeatedly flying over the place where the lawn chair had originally been, then flying over the aggregation again, unable to locate her nest hole. During the approximately twenty minutes she spent searching, other bees returned from their own foraging trips and easily located their nests. Finally, we moved the lawn chair back to its original location. Almost immediately, the confused bee flew to the lawn chair, oriented herself, then turned and flew directly to her nest hole. It was a very obvious demonstration of the bees’ dependence on visual landmarks to orient themselves in the landscape. Of course, not all the bees displayed such confusion when one landmark failed them. Usually they seemed to be able to use supplemental landmarks to aid in nest-finding.

Nesting and Nest Sites

When digging a nest, a silver bee takes occasional breaks, probably to feed on nectar. These nectaring breaks usually last ten to fifteen minutes; as soon as the bee returns, she continues with nest excavation.

Female silver bees carrying full pollen loads frequently have more than one species of pollen packed on their scopae (observable as several colors swirled together). Upon return from a nest-provisioning trip, a bee generally spends four to eleven minutes in the nest, unloading the pollen she collected, before leaving again for the next foraging
trip. Towards the end of the season, a bee may take much longer to exit her nest again (often more than twenty minutes).

There are two general types of preferred aggregation sites. The first is a slightly sloped zone of open sand, either with or without scattered, sparse dune-mat plants such as beach strawberry (*Fragaria chiloensis*). This type of site is most frequent from Samoa south (but also occurs north); here the bees often dig their nests at the base of small plants or beside stones or twigs that serve as orienting landmarks. The second type of nesting site is the “cliffside” aggregation, of which there are several at Ma-l’el Dunes and in the Mad River Beach area. These aggregations are located on vertical or near-vertical faces, where the sand has either hardened and compacted into layered “shelves,” or is held together by European beachgrass roots. The bees dig nest holes straight into the face so that it resembles a miniature Anasazi cliff dwelling. This type of aggregation gives the illusion of being the busiest, because the bees tend to dig their holes close together in relatively compact areas, compared to the usually more-scattered layout of the other aggregation type.

Early in the season, all aggregations are inhabited only by silver bees. As the season wears on, the male silver bees die off. Later, other insect species arrive to patrol the aggregation sites, including parasitic Hymenoptera (*Sphecoides* sp. and others). Many of the aggregations eventually have large populations of *Bembix* wasps adjacent to them, in open, sloping sand. The wasps do not interact much with the bees, except for instances when they accidentally interrupt each other’s flight paths.
The silver bee itself appears to have a somewhat staggered flight season in the Humboldt Bay dune system; the aggregations are not all on the same schedule. In general, activity at the aggregations further south begins and ends earlier in the spring than at the aggregations to the north, but there are exceptions, possibly having to do with microclimatic differences, substrate temperature differences, or the orientation of the aggregation site relative to the sun.