

# Subalpine Bumble Bee Foraging Distances and Densities in Relation to Flower Availability

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**ABSTRACT** Bees feed almost exclusively on nectar and pollen from flowers. However, little is known about how food availability limits bee populations, especially in high elevation areas. Foraging distances and relationships between forager densities and resource availability can provide insights into the potential for food limitation in mobile consumer populations. For example, if floral resources are limited, bee consumers should fly farther to forage, and they should be more abundant in areas with more flowers. I estimated subalpine bumble bee foraging distances by calculating forager recapture probabilities at increasing distances from eight marking locations. I measured forager and flower densities over the flowering season in six half-hectare plots. Because subalpine bumble bees have little time to build their colonies, they may forage over short distances and forager density may not be constrained by flower density. However, late in the season, when floral resources dwindle, foraging distances may increase, and there may be stronger relationships between forager and flower densities. Throughout the flowering season, marked bees were primarily found within 100 m (and never >1,000 m) from their original marking location, suggesting that they typically did not fly far to forage. Although the density of early season foraging queens increased with early-season flower density, the density of mid- and late-season workers and males did not vary with flower density. Short foraging distances and no relationships between mid- and late-season forager and flower densities suggest that high elevation bumble bees may have ample floral resources for colony growth reproduction.

**KEY WORDS** bumble bee, flower density, food availability, foraging distance, subalpine

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Food availability often affects consumer behavior and population growth (Rogers 1987, Guyer 1988, Kreiter and Wise 2001), which may subsequently feed back to affect species interactions (Wise 2006, Pitelka and Batzli 2007). Although it is difficult to experimentally test whether populations of highly mobile consumers are food limited, examining consumer behaviors and patterns of abundance can provide insights into whether consumers have food shortages or surpluses (Petersen et al. 2006, Wirsing and Murray 2007). If food is scarce, mobile consumers should have to spend more time foraging and may travel farther to collect sufficient resources when resources are exhausted near the nest (Suzuki et al. 2007). If food is scarce and if foraging is energetically costly, consumers might also produce fewer offspring or have lower survival rates, leading to lower population densities (Schulz et al. 1998, Mduma et al. 1999, Vet 2001). Alternatively, if food is abundant, consumers could forage near their nests, and their densities might be determined by factors other than food availability (Hairston et al. 1960, Nie and Liu 2005). In this study, to understand whether highly mobile consumers might be food limited, I measured bumble bee consumer foraging dis-

tances and the relationships between forager and flower densities.

Bee foraging distances are governed by physiological and ecological constraints. Body size determines the possible foraging ranges of bee pollinators (Gathman and Tschardtke 2002, Greenleaf et al. 2007), and larger colonial bees may also build larger colonies that require more food (Wright et al. 2000, Westphal et al. 2006). Thus, it is often difficult to differentiate between the importance of resource demand and body size in driving differences in foraging distances among bee species. However, within a species, if nearby resources are scarce, bees should travel farther to collect sufficient resources to feed themselves and provision their offspring (Cresswell et al. 2000). Instead, if bees have ample resources and if resource quality is constant at near and far sites (but see Batra 1993, Osborne et al. 1999, Heithaus et al. 2005), they could minimize foraging time and energy use by feeding closer to their nest (Heinrich 1979b). Estimates of average bumble bee foraging distances vary from 100 to 2,750 m, with differences found within and among species (Walther-Hellwig and Frankl 2000, Darvill et al. 2004, Knight et al. 2005). Theoretically, to maximize energy loss while foraging and in flight, bumble bees should forage within 1,000 m from their nest unless (1) nectar

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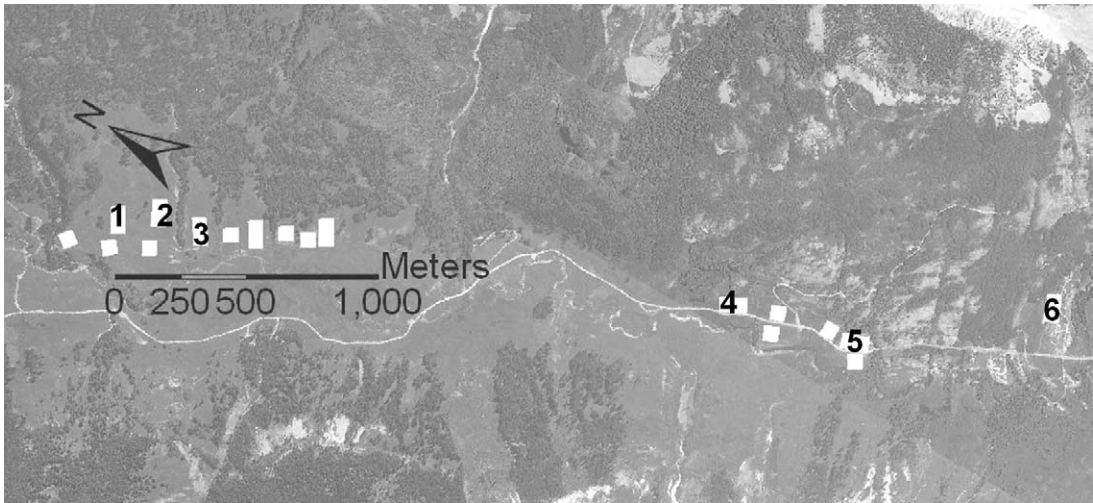


Fig. 1. Study area in the East River Valley, CO, showing plots used for mark-recapture study (bees marked in eight rectangular 50 by 100-m plots and recaptured in those plots plus the 10 additional square 50 by 50-m plots) and for measuring forager and flower densities (50 by 100-m plots labeled 1–6).

availability per flower drops below  $1 \mu\text{l}$  per flower near the nest and (2) nectar per flower is greater farther away (Cresswell et al. 2000). Despite the potential for food availability to influence foraging distances, few studies have assessed how temporal or spatial variability in resources affects bee foraging distances (but see Osborne et al. 2008).

Bumble bees may only exhaust local resources when forager density is high and flower density is low. Because bumble bee density increases over the season as colonies grow (Heinrich 1979a, Pleasants 1981), flower availability per bee may be lowest, and therefore most limiting to colony growth, late in the season (Pyke 1982). For example, in montane areas, bumble bees are more abundant in meadows that are wetter and produce more late-season flowers than in drier meadows that have more early-season flowers (Hatfield and LeBuhn 2007). Similarly, in subalpine meadows, flower composition only influences bumble bee composition near the end of the flowering season (Bowers 1985).

To provide insight into whether subalpine bumble bees might have ample or scarce floral resources, (1) I measured bumble bee foraging distances by calculating recapture probabilities at increasing distances from marking locations, and (2) I tested natural relationships between forager densities and flower densities within their foraging areas. Because subalpine bumble bees have little time to build their colonies (e.g., 9–11 wk; Pyke 1982), subalpine bumble bees may generally forage over short distances (e.g.,  $<1,000$  m), and forager density may not be correlated with flower density within their foraging areas. However, late in the season, when floral resources may be more limiting, foraging distances may increase, and there may be stronger relationships between forager and flower densities.

## Materials and Methods

I studied bumble bee foraging distances and forager and flower densities for 11 wk (6 June to 28 August 2004), spanning most of the flowering period, in Gunnison National Forest near the Rocky Mountain Biological Laboratory (RMBL), Gothic, CO (2,879- to 2,957-m elevation; Fig. 1; Table S1). Twelve bumble bee species and two social nest parasite species are found around the RMBL (Beattie et al. 1973, Pyke 1982). I identified bumble bees (*Bombus* spp., Apidae) to species based on pile color patterns (Stephen 1957). The nest parasites (*Psithyrus* spp., Apidae) could have been either of two species (*P. insularis* or *P. suckleyi*), which are difficult to distinguish in the field, so I identified them to genus only. Bumble bees around the RMBL visit a variety of perennial wildflower species, partitioning their resources according to proboscis length and corolla depth or nectar spur lengths (Inouye 1978, Pyke 1982). The three most common bumble bee species in this study, *B. appositus*, *B. flavifrons*, and *B. bifarius*, have long, intermediate, and short proboscises, respectively (Pyke 1982).

Around the RMBL, queen bumble bees emerge from their winter diapause in May or June (S.E.E., unpublished data). Each founding queen searches for an underground nest site in which to establish her colony. After producing female workers, the founding queen produces new queens (i.e., gynes) and males. At the end of the season, in late August to early September, gynes and males mate, and only the gynes overwinter. As in most temperate areas, bumble bees around the RMBL produce only one generation per season.

To estimate foraging distances, I marked and recaptured foragers to determine the spatial scale at which individuals returned to forage. I marked bees on their thorax with a paint pen (Marvy Uchida, Tor-

rance, CA) in eight 0.5-ha plots, using a unique color for each plot. I also recaptured bees in 10 additional 0.25-ha plots (Fig. 1; Table S1) in July when bee density was low and required additional search effort. I also marked each bee encountered in the 0.25-ha plots to standardize search effort time. I caught and marked bees in the study plots for  $\approx 4$  h/wk per plot. Because new bees hatch and old bees die every 2–4 wk, I marked and recaptured bees continuously throughout the entire season. To avoid recapturing recently marked bees (i.e., those that may not have returned to the nest after marking), I did not catch bees with fresh paint.

I estimated foraging distances by calculating recapture rates at increasing distances from the marking locations. With 8 marking plots and 18 recapture plots, there were 144 plot pairs, representing unique distances over which marked bees could fly and be recaptured, including the possibility for no movement (i.e., recapture in their original marking plot). For each pair of plots, I calculated a recapture rate by dividing the number of bees recaptured in the recipient plot by the number of bees marked in the marking plot and by dividing this proportion by the search effort (in hours) in the recipient plot. I assumed that bees did not radiate out from the linear strip of study meadows. For example, no marked bees were observed on the southwest side of the river or in the dense spruce forest, which bordered the marking plot (Fig. 1), both of which have far fewer flowers than in the open south-facing study meadows (S.E.E., unpublished data). Also, I assumed that bees recaptured in their marking meadow were flying no farther than the distance between marking meadows (200–300 m) to nest or forage between captures.

To determine recapture rates at increasing distances from the marking locations, I divided the 144 plot pairs into categories according to the distance between plot centers. The first category, 0 m, represented recaptures in the same plot where the bees were marked. The categories grouped plot pairs into 100-m intervals up to the maximum distance of 3,766 m. The relative recapture rate for each distance category was calculated by dividing the average recapture rate (or the single rate for the 901–1,000 m category because there was only one plot pair in this distance category) by the sum of all average recapture rates from each category. Therefore, the recapture probability in each distance category represents the probability that a bee (if recaptured) would be found in that distance interval. To compare relative recapture rates among species, I calculated separate relative recapture probabilities for the three most common species: *B. appositus*, *B. flavifrons*, and *B. bifarius*. To compare relative recapture rates across the season for all species combined, I calculated separate relative recapture probabilities for early (weeks 1–4), midway (weeks 5–8), and late (weeks 9–11) seasons. Recapture rates were too low to test for species-specific recapture rates within each time period.

To assess whether meadows with more flowers had more bumble bee foragers, I measured natural forager

**Table 1.** Bumble bee (*Bombus* spp.) and bumble bee social nest parasite (*Psithyrus* spp.) capture rate (no. of bees caught per hour, averaged over 11 wk), range, and averages ( $\pm$ SE) for six subalpine meadows in Colorado

Species	Range	Mean $\pm$ SE
<i>Bombus appositus</i>	11.9–47.8	28.2 $\pm$ 5.2
<i>Bombus bifarius</i>	14.7–48.0	33.0 $\pm$ 5.6
<i>Bombus californicus</i>	0.2–2.6	1.0 $\pm$ 0.4
<i>Bombus flavifrons</i>	10.1–49.9	29.4 $\pm$ 7.2
<i>Bombus frigidus</i>	0.9–20.7	6.3 $\pm$ 3.0
<i>Bombus nevadensis</i>	0–0.3	0.1 $\pm$ 0.1
<i>Bombus occidentalis</i>	2.7–18.5	8.6 $\pm$ 2.6
<i>Bombus sylvicola</i>	0–0.6	0.2 $\pm$ 0.1
<i>Psithyrus</i> spp.	2.4–8.8	6.1 $\pm$ 1.1

and flower densities over the 11 study weeks in six 0.5-ha plots, each separated by  $\geq 288$  m (Fig. 1). I quantified forager density by recording the rate at which bumble bees were caught in each plot. Each week, I caught bees in each plot for  $\approx 4$  h of measured observation time ( $\approx 1$  h, twice between 0900 and 1200 hours and twice between 1230 and 1530 hours). I restricted catching periods to times when there were no storms to avoid storm-related shifts in foraging rates (Peat and Goulson 2005).

During each catching period, I systematically walked the entire plot and captured, marked, and released each bee I encountered. Recaptured bees were not excluded because I was not trying to determine the total number of unique bees in the meadows but rather the number of active foraging bouts observed per hour of observation time in each plot. Because I did not recapture recently marked bees, any recaptured bees probably represent two separate foraging bouts from the colony. For each bee, I recorded its species, caste (founding queen, worker, male, or gyne) and the flower species it were visiting. I excluded bees that were caught while they were grooming on leaves, flying, or crawling on the ground from forager density estimates. I included the social nest parasites, *Psithyrus* spp., because they also deplete nectar resources. However, because of their low abundance (Table 1), including or excluding *Psithyrus* did not affect the results. I calculated forager density as the average number of bees caught per hour per 0.5-ha plot (averaged within weeks across the entire season).

I sampled flower density in 16 quadrats (0.25 by 25 m) per plot (four randomly placed quadrats in each of four 25 by 50-m subplots per plot; Fig. 1). In each quadrat, I recorded the number of open flowers of all flower species, and later, I excluded flower species that were not visited by bumble bees during this study. For species that consistently had  $>10$  open flowers per inflorescence, I counted the number of inflorescences in each quadrat, and 20 inflorescences were subsampled to calculate the average number of flowers per inflorescence (or florets per capitulum in the Asteraceae). I multiplied the average number of flowers per inflorescence by the number of inflorescences to calculate total flower number. Although, ideally, I would have standardized flower number to total pollen and nectar availability, per-flower pollen and nec-

tar production estimates were not available for most species (Tepedino and Stanton 1982). However, flower density was dominated by a few species, so flower composition was similar among meadows. To calculate total flower density, I summed average flower density over the 11 sampling wk in each plot.

I used Pearson's correlation coefficients to assess the relationships between forager density (capture rate per 0.5-ha plot, all bee species combined) and flower density (flowers per m<sup>2</sup>, all bumble bee-visited flower species combined). I combined all bumble bee species because they overlap in flower species use (Table S2). To determine whether the density of different bumble bee castes increased with flower density, I tested the relationship between forager density and total flower density, separating analyses by caste. To determine whether forager-flower density relationships varied over the season, I tested the relationship between forager density (all castes combined) and flower density, separating analyses by early (weeks 1–4), mid (weeks 5–8), and late (weeks 9–11) seasons. To determine whether meadows with more early, mid-, or late season flowers also had more total flowers (all weeks combined), I quantified correlations between total flower density and early, mid-, and late season flower densities.

Because it takes ≈4 wk to provision, develop, and hatch a new cohort of bumble bee offspring (Heinrich 1979a), time lags in the relationships between forager and flower densities were also examined. Forager density could be a function of (1) previous flower availability (i.e., food to provision new offspring) and/or (2) previous colony size (i.e., workers available to provision and care for new offspring). Therefore, I used correlations to test whether meadows with more early season flowers or foragers had more mid-season flowers and whether meadows with more mid-season flowers or foragers had more late season flowers. I performed all analyses with JMP 4.04 (SAS Institute 2001).

## Results

I observed eight *Bombus* species and the bumble bee nest usurper, *Psithyrus* spp., in the study meadows (Table 1). The three most common species, *B. appositus*, *B. flavifrons*, and *B. bifarius*, collectively accounted for 80 ± 4% of all bees captured (mean ± SE,  $n = 6$  plots), and each species individually accounted for ≈30% of all bees captured (Table 1). In all plots, I observed bumble bees on 47 flower species from 18 plant families (Table S3). Foragers primarily visited flower species that were among the top 25% of species based on floral abundance, but uncommon bee species and *B. appositus* workers also frequently visited two patchy uncommon Gentianaceae species: *Fraseria speciosa* and *Pneumomanthe parryii* (Table S2). Flower density was dominated by a few species; only four species contributed to >5% of all flowers: *Potentilla pulcherrima* (41.8 ± 8.8%, Rosaceae), *Delphinium barbeyi* (14.0 ± 4.4%, Ranunculaceae), *Heliomeris multiflora* (9.8 ± 3.5%, Asteraceae), and *Erigeron speciosus*

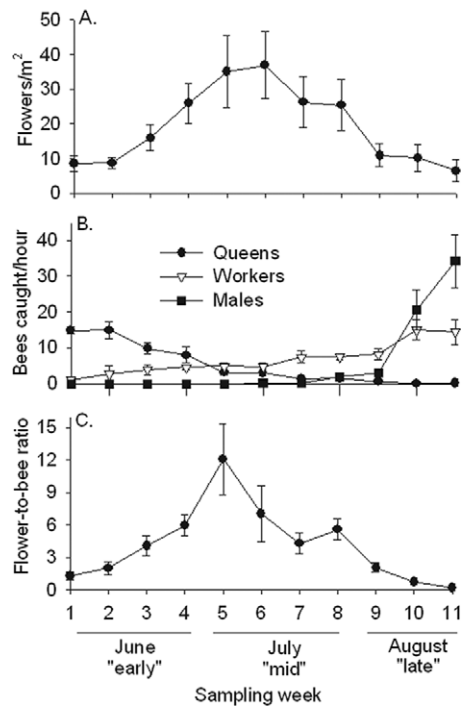


Fig. 2. Mean ( $\pm$ SE) (A) flower density (all flower species combined per m<sup>2</sup>), (B) forager density (bees caught per hour per 0.5-ha plot, separated by caste: queens, workers, and males), and (C) flower-to-bee ratio among six subalpine meadows.

(6.7 ± 2.9%, Asteraceae). Total flower density varied four-fold among meadows (Table S3). Because flower density peaked midway through the season when bee density was at its lowest, flower availability per bee was lowest early and late in the season (Fig. 2).

I primarily recaptured bees in the same plot in which they were marked. Of the 3,258 individual bees marked, 637 were recaptures (19.6%). Of the 637 recaptured individuals, 590 (92.6%) were recaptured in their marking plot. After correcting for sampling effort, there was an 82.3% chance that, if a marked bee was recaptured, it would be recaptured in its marking plot (Fig. 3). The remaining bees were recaptured within 1,000 m of their marking plot; no bees were recaptured at distances between 1,000 and 3,766 m from the marking plot. The high likelihood of recaptures in the marking plot was constant across *Bombus* species (Fig. 3A) and across the season (Fig. 3B).

Meadows with more flowers harbored more founding queen foragers ( $r = 0.83$ ,  $P = 0.04$ ; Fig. 4A), but this trend disappeared for workers, males, and gynes ( $r < 0.36$ ,  $P > 0.4$ ). Similarly, meadows with more early-blooming flowers had more early season foragers ( $r = 0.85$ ,  $P = 0.03$ ; Fig. 4B), but meadows with more mid- or late season flowers did not have more mid- or late season foragers ( $r < 0.11$ ,  $P > 0.8$ ). Because only flower densities from the middle of the season were significantly correlated with total flower densities (late:  $r = 0.49$ ,  $P = 0.3$ ; mid:  $r = 0.99$ ,  $P = 0.0001$ ; early:

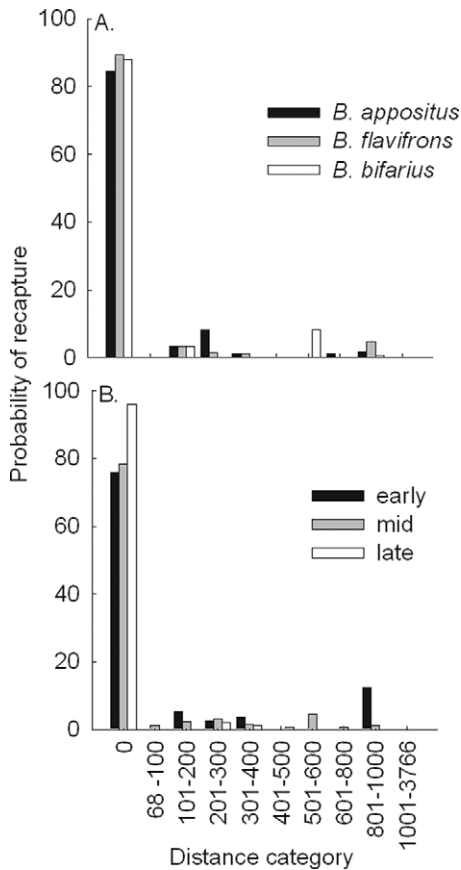


Fig. 3. The probability that if a marked bumble bee was recaptured it would be recaptured at increasing distances from where it was marked (Fig. 1) for the three most common *Bombus* species (A) and all *Bombus* species divided into early, mid-, and late season (B). Recapture probabilities at each distance are corrected for sampling effort (see Materials and Methods section).

$r = 0.57$ ,  $P = 0.2$ ), early season flower densities were not an indicator of future flower availability. Meadows with more flowers or foragers early in the season did not have more foragers midway through the season, nor did meadows with more flowers or foragers midway through the season have more foragers late in the season ( $r < 0.51$ ,  $P > 0.2$ ).

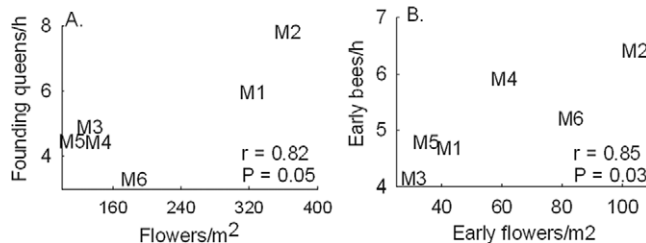


Fig. 4. Relationships between *Bombus* forager density (average number of bees caught per hour per 0.5-ha plot; labeled 1–6, as in Fig. 1) and total flower density (flowers per  $m^2$  over the 11-wk study) for founding queens over the entire season (A) and for early-season bees (all casts combined) and flowers (B).

## Discussion

Food availability is an important component of consumer behavior, population growth, and species interactions (Rogers 1987, Guyer 1988, Kreiter and Wise 2001, Pitelka and Batzli 2007). As in many consumer–resource mutualisms (Holland et al. 2005), little is known about whether bee pollinator consumers are limited by floral nectar and pollen resources. Because bumble bees often fly long distances to forage and because their densities are often closely related to flower availability, it is often assumed that bumble bees exhaust local floral resources (Saville et al. 1997, Kremen et al. 2002, Westphal et al. 2003, Knight et al. 2005, Carvell et al. 2007, Heard et al. 2007, Osborne et al. 2008). However, the subalpine bumble bees in this study foraged over relatively short distances ( $< 100$  m), and meadows with naturally more flowers only harbored more foragers early in the season. These results suggest that (1) bumble bees did not exhaust local resources; (2) flower density did not adequately represent resource availability; or (3) bee density was limited by factors other than floral resources (e.g., nest sites or parasites).

Although previous studies have shown that bee densities are positively correlated with flower densities at large spatial scales (Kremen et al. 2002, Westphal et al. 2003, Heard et al. 2007), such observational studies (including this study) are difficult to interpret. For example, if forager density is not correlated with flower density at a specific spatial scale, this could suggest that the bees are not using the resources at that spatial scale (Steffan-Dewenter et al. 2002). Alternatively, bees could be using the resources at that spatial scale, but their densities could be controlled by nest site availability or parasitism (Potts et al. 2005, Carvell et al. 2008). Therefore, to understand whether correlations between forager and flower densities (or lack thereof) indicate that bees are (or are not) limited by floral resources, studies should also measure bee reproduction and population density in response to natural or experimental variation in floral resource availability (Goulson et al. 2002, Pelletier and McNeil 2003, Thomson 2004, Greenleaf 2005, Carvell et al. 2008).

Because nectar and pollen production per flower may vary among species or among habitats within species, flower number may not adequately represent resource availability (Tepedino and Stanton 1982,

Cartar 2004, Goulson et al. 2007). Although testing all species-specific correlations would have required numerous tests (with inflated type I error probability), in post hoc analyses, we tested correlations between forager densities and the most frequently used flower species, and these results supported our overall conclusions. Specifically, founding queens were positively correlated with their most frequently used flower species and other casts were not (Table S3). Some exceptions to this pattern occurred with rare bee species or rare and patchy plant Gentianaceae species. Because some very rare plant species were commonly used by some bee species, this also supports the hypothesis that, if flowers influence forager density, it is not flower quantity, but flower quality, which may limit bee density (Suzuki et al. 2007).

Bumble bee foragers in this study were recaptured over shorter distances than bumble bees in lower elevation areas. At lower elevations, direct forager observations and inferences based on correlations at different spatial scales suggest that bumble bees typically use floral resources that are located >1,000 m from their nests (Saville et al. 1997, Steffan-Dewenter et al. 2002, Darvill et al. 2004, Knight et al. 2005, Westphal et al. 2006). Assuming constant flower densities in near and far sites, energetic calculations predict that bumble bees should only fly farther than 1,000 m to forage (1) if nectar availability per flower drops below  $1 \mu\text{l}$  per flower near the nest and (2) if nectar per flower is greater farther away (Cresswell et al. 2000). In agricultural areas in the United Kingdom, marked *B. terrestris* individuals flew farther than 1,000 m to forage, although there were flowers nearby (Osborne et al. 1997, 2008), but no studies have measured per-flower resource availability in relation to foraging distance. In addition to these low-elevation studies, in a higher alpine site in northern Sweden, low *B. alpinus* abundance, coupled with a high number of unique individuals captured in a 1-ha site, suggested that queens flew farther than 100 m to forage (Stenstrom and Bergman 1998). However, in this study and in another study in a subalpine habitat in Utah, marked bumble bees were primarily recaptured within a 100-m radius (Bowers 1985). Therefore, it is possible that factors specific to subalpine habitats (e.g., elevation, solar radiation, season length, flower species composition, or pollinator composition) may influence floral rewards and bee foraging distances.

In this study, meadows with more flowers did not harbor more workers, gynes, or males. In contrast, bumble bee forager densities at low elevations (<200 m) increase in areas with more flowers or more available natural habitat (Kremen et al. 2002, Steffan-Dewenter et al. 2002, Westphal et al. 2003, Darvill et al. 2004, Knight et al. 2005, Carvell et al. 2007, Heard et al. 2007), and in this study, more founding queens were found in meadows with more flowers. Because most of these queens were recaptured within a 100-m radius, if they were parsing themselves out in proportion to resource availability (Dreisig 1995), more queens may have overwintered in meadows with more flowers. Alternatively, the queens may have made a

small number of long distance flights before dispersing into the meadow in which they would nest and forage. Because founding queens were the only caste that increased with flower densities, floral resource availability might only determine colony establishment and not colony growth. However, in another subalpine study, in the beginning of the season, meadow size and elevation were better predictors of bumble bee presence or absence than flower species composition and abundance (Bowers 1985).

The subalpine environment (e.g., 2,879- to 2,957-m elevation in this study), in contrast to lower elevations, may allow less time for colonies to grow large and exhaust local resources. For bumble bee queens to reproduce, they need at least 1–2 wk to establish a nest, 3–4 wk to produce the minimum of one worker brood, and another 3–4 wk to hatch a reproductive cohort (Alford 1975, Heinrich 1979a). In 1974, bumble bee surveys located near this study site found no gynes or males, suggesting that reproduction was low or did not occur in this area (Pyke 1982). In general, Pyke (1982) found that gynes and males were only produced in areas where the flowering season was >11 wk. In 2006 and 2007 in this study area, >50% of *B. appositus* colonies did not produce any gynes or males (Elliott 2008). Because colony growth increases over time, flower requirements per colony may also increase across elevational, latitudinal, or other climatic gradients that influence the length of the flowering period (e.g., snow melt and precipitation patterns, Inouye et al. 2002). At high latitudes, it is possible that the increased day lengths might help ameliorate short flowering seasons at high elevations, which could help explain the different results between this study and Sweden study of Stenstrom and Bergman (1998).

Similarly, within an area, interannual variation in floral resources, queen densities, nest-site availability, parasitism, etc., could alter the relationship (or lack thereof) between forager and flower densities. However, in 2 subsequent yr (2005 and 2007), forager densities were not correlated with floral resources at the patch or whole meadow scales (Elliott 2008). The RMBL site may be particularly flower rich (e.g., the adjacent town of Crested Butte is the official “Wild-flower Capital” of Colorado) and therefore an important location to preserve to maintain healthy bumble bee pollinator populations with ample resources. In addition to studies that compare across habitat types (e.g., elevation), studies such as this one should also be replicated within habitat types (e.g., subalpine meadows).

The relationship between flower and forager densities could have been masked or simply not have existed if nest parasitism increased in areas with more flowers or if density was limited by factors besides flower availability. Nest parasites are more common in captive *B. terrestris* colonies in areas with rich agricultural floral resources than in colonies in agricultural areas with few floral resources (Carvell et al. 2008). If more nest parasites were present in the meadows with the most flowers and queens at the beginning of the season, more colonies in those meadows may have

been attacked, cancelling the positive effect of flower density on bee density. Bee density could have also been limited by nest sites (Alford 1975). If there were more nest sites in the meadows with more flowers, that could also explain the initial correlations between queen and flower densities. Nest density may depend on the availability of suitable nesting substrates (Potts et al. 2003). Because bumble bees are ground nesting, soil conditions and vegetation type (e.g., root structure and surface density) should influence nest and forager densities (Alford 1975).

Because bumble bee nests are inherently very difficult to locate, information on nest densities is scarce (Heinrich 1979a). The nesting locations in this study were also inferred instead of directly measured. Specifically, bees were mostly recaptured in the meadows in which they were marked, and this pattern was found in a series of adjacent meadows. It seems unlikely that bees nesting in one meadow would fly a long distance from their nest (e.g., >1,000 m) to forage in a second meadow where other bees were nesting and flying long distances to forage in the first meadow. This pattern suggests that the bees were nesting in or near the meadows in which they were marked. However, although most bumble bee nests found around the RMBL have been found in meadow clearings (S.E.E., unpublished data), it is still not impossible that the bees were flying longer distances from nests in forest or riparian habitats to repeatedly forage in certain meadows. Knowing precisely where bees nest relative to floral resources is important for predicting the energetic costs of different foraging distances (Cresswell et al. 2000). Therefore, future studies of natural nest site availabilities and nest densities will be crucial to understanding the limits (including but not limited to the relative role of floral resources) to bee population densities.

In conclusion, bumble bees in this study had short foraging distances compared with other large-bodied bumble bees (Greenleaf et al. 2007), and forager densities were only correlated with flower densities early in the season. Short foraging distances could suggest that bees had ample floral resources near their nests or that the costs of long-distance flights outweighed the benefits of increased resource acquisition (Cresswell et al. 2000). Forager densities may not have increased in meadows with more flowers midway and late in the season because (1) resources did not limit colony growth and/or (2) parallel increases in flower density and parasitism rates masked any relationship between flower densities and the densities of workers, males, and gynes. A subsequent 2-yr study in this system supported the first explanation that colony growth and reproduction was not limited by food availability (Elliott 2008). To understand the role of food availability in driving subalpine bumble bee consumer behavior, population growth, and interactions with their mutualistic plant partners, future work should experimentally test whether bumble bees are food limited and whether and why food limitation varies among habitats.

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## References Cited

- Alford, D. V. 1975. *Bumblebees*. Davis-Poynter, London, United Kingdom.
- Batra, S.W.T. 1993. Opportunistic bumble bees congregate to feed at rare, distant alpine honeydew bonanzas. *J. Kansas Entomol. Soc.* 66: 125–127.
- Beattie, A. J., D. Breedlove, and P. Ehrlich. 1973. The ecology of pollinators and predators of *Frasera speciosa*. *Ecology* 54: 81–91.
- Bowers, M. A. 1985. Bumble bee colonization, extinction, and reproduction in subalpine meadows in northeastern Utah. *Ecology* 66: 914–927.
- Cartar, R. V. 2004. Resource tracking by bumble bees: responses to plant-level differences in quality. *Ecology* 85: 2764–2771.
- Carvell, C., P. Rothery, R. F. Pywell, and M. S. Heard. 2008. Effects of resource availability and social parasite invasion on field colonies of *Bombus terrestris*. *Ecol. Entomol.* 33: 321–327.
- Carvell, C., W. R. Meek, R. F. Pywell, D. Goulson, and M. Nowakowski. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J. Appl. Ecol.* 44: 29–40.
- Cresswell, J. E., J. L. Osborne, and D. Goulson. 2000. An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Ecol. Entomol.* 25: 249–255.
- Darvill, B., M. E. Knight, and D. Goulson. 2004. Use of genetic markers to quantify bumblebee foraging range and nest density. *Oikos* 107: 471–478.
- Dreisig, H. 1995. Ideal free distributions of nectar foraging bumblebees. *Oikos* 72: 161–172.
- Elliott, S. E. 2008. Reciprocal benefits in a plant-pollinator mutualism. PhD dissertation, Dartmouth College, Hanover, NH.
- Gathman, A., and T. Tschardt. 2002. Foraging ranges of solitary bees. *J. Anim. Ecol.* 71: 757–764.
- Goulson, D., W.O.H. Hughes, L. C. Derwent, and J. C. Stout. 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia (Berl.)* 130: 267–273.
- Goulson, D., J. L. Cruise, K. R. Sparrow, A. J. Harris, K. J. Park, M. C. Tinsley, and A. S. Gilburn. 2007. Choosing rewarding flowers; perceptual limitations and innate preferences influence decision making in bumblebees and honeybees. *Behav. Ecol. Sociobiol.* 61: 1523–1529.
- Greenleaf, S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia (Berl.)* 153: 589–596.
- Greenleaf, S. S. 2005. Local-scale and foraging-scale habitats affect bee community abundance, species richness, and pollination services in Northern California. Princeton University, Princeton, NJ.

- Guyer, C. 1988. Food supplementation in a tropical anole, *Norops humilis*, demographic effects. *Ecology* 69: 350–361.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *Am. Nat.* 94: 421–425.
- Hatfield, R. G., and G. LeBuhn. 2007. Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera: Apidae), in montane meadows. *Biol. Conserv.* 139: 150–158.
- Heard, M. S., C. Carvell, N. L. Carreck, P. Rothery, J. L. Osborne, and A.F.G. Bourke. 2007. Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. *Biol. Lett.* 3: 638–641.
- Heinrich, B. 1979a. Bumblebee economics. Harvard University Press, Cambridge, MA.
- Heinrich, B. 1979b. Resource heterogeneity and patterns of movement in foraging bumblebees. *Oecologia (Berl.)* 40: 235–245.
- Heithaus, E. R., P. A. Heithaus, and S. Y. Liu. 2005. Satiation in collection of myrmecochorous diaspores by colonies of *Aphaenogaster rudis* (Formicidae: Myrmicinae) in central Ohio, USA. *J. Insect Behav.* 18: 827–846.
- Holland, J., B. A. Ness, and J. L. Bronstein. 2005. Mutualisms as consumer-resource interactions, pp. 17–33. In P. Barbosa and I. Castellanos (eds.), *Ecology of predator-prey interactions*. Oxford University Press, New York.
- Inouye, D. W. 1978. Resource partitioning in bumblebees—experimental studies of foraging behavior. *Ecology* 59: 672–678.
- Inouye, D. W., M. A. Morales, and G. J. Dodge. 2002. Variation in timing and abundance of flowering by *Delphinium barbeji* Huth (Ranunculaceae): the roles of snowpack, frost, and La Nina, in the context of climate change. *Oecologia (Berl.)* 130: 543–550.
- Knight, M. E., A. P. Martin, S. Bishop, J. L. Osborne, R. J. Hale, A. Sanderson, and D. Goulson. 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molec. Ecol.* 14: 1811–1820.
- Kreiter, N. A., and D. H. Wise. 2001. Prey availability limits fecundity and influences the movement pattern of female fishing spiders. *Oecologia (Berl.)* 127: 417–424.
- Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci.* 99: 16812–16816.
- Mduma, S.A.R., A.R.E. Sinclair, and R. Hilborn. 1999. Food regulates the Serengeti wildebeest: a 40-year record. *J. Anim. Ecol.* 68: 1101–1122.
- Nie, H., and J. Liu. 2005. Regulation of root vole population dynamics by food supply and predation: a two-factor experiment. *Oikos* 109: 387–395.
- Osborne, J., I. Williams, J. Riley, and A. Smith. 1997. Harmonic radar: a new technique for investigating bumblebee and honeybee foraging flight. *Proc. Int. Symp. Pollination* 437: 159–163.
- Osborne, J. L., S. J. Clark, R. J. Morris, I. H. Williams, J. R. Riley, A. D. Smith, D. R. Reynolds, and A. S. Edwards. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *J. Appl. Ecol.* 36: 519–533.
- Osborne, J. L., A. P. Martin, N. L. Carreck, J. L. Swain, M. E. Knight, D. Goulson, R. J. Hale, and R. A. Sanderson. 2008. Bumblebee flight distances in relation to the forage landscape. *J. Anim. Ecol.* 77: 406–415.
- Peat, J., and D. Goulson. 2005. Effects of experience and weather on foraging rate and pollen versus nectar collection in the bumblebee, *Bombus terrestris*. *Behav. Ecol. Sociobiol.* 58: 152–156.
- Pelletier, L., and J. N. McNeil. 2003. The effect of food supplementation on reproductive success in bumblebee field colonies. *Oikos* 103: 688–694.
- Petersen, S. L., P. G. Ryan, and D. Gremillet. 2006. Is food availability limiting African penguins *Spheniscus demersus* at Boulders? A comparison of foraging effort at mainland and island colonies. *Ibis* 148: 14–26.
- Pitelka, F. A., and G. O. Batzli. 2007. Population cycles of lemmings near Barrow, Alaska: a historical review. *Acta Theriol.* 52: 323–336.
- Pleasants, J. M. 1981. Bumblebee response to variation in nectar availability. *Ecology* 62: 1648–1661.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* 84: 2628–2642.
- Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecol. Entomol.* 30: 78–85.
- Pyke, G. H. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. *Ecology* 63: 555–573.
- Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in Northeastern Minnesota. *Wildlife Monogr.* 97: 1–72.
- SAS Institute. 2001. JMP 4.04 computer program. SAS Institute, Cary, NC.
- Saville, N., W. Dramstad, G. Fry, and S. Corbet. 1997. Bumblebee movement in a fragmented agricultural landscape. *Agric. Ecosyst. Environ.* 61: 145–154.
- Schulz, D. J., Z. Y. Huang, and G. E. Robinson. 1998. Effects of colony food shortage on behavioral development in honey bees. *Behav. Ecol. Sociobiol.* 42: 295–303.
- Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tschardtke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83: 1421–1432.
- Stenstrom, M., and P. Bergman. 1998. Bumblebees at an alpine site in northern Sweden: temporal development, population size, and plant utilization. *Ecography* 21: 306–316.
- Stephen, W. 1957. Bumble bees of western America. Technical Bulletin, Oregon State College, Agricultural Experimental Station.
- Suzuki, Y., L. G. Kawaguchi, and Y. Toquenaga. 2007. Estimating nest locations of bumblebee *Bombus ardens* from flower quality and distribution. *Ecol. Res.* 22: 220–227.
- Tepedino, V. J., and N. L. Stanton. 1982. Estimating floral resources and flower visitors in studies of pollinator-plant communities. *Oikos* 38: 384–386.
- Thomson, D. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology* 85: 458–470.
- Vet, L.E.M. 2001. Parasitoid searching efficiency links behaviour to population processes. *Appl. Entomol. Zool.* 36: 399–408.
- Walther-Hellwig, K., and R. Frankl. 2000. Foraging habits and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *J. Appl. Entomol. Zeitschrift Angewandte Entomol.* 124: 299–306.
- Westphal, C., I. Steffan-Dewenter, and T. Tschardtke. 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* 6: 961–965.



- Westphal, C., I. Steffan-Dewenter, and T. Tschardtke. 2006. Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia (Berl.)* 149: 289–300.
- Wirsing, A. J., and D. L. Murray. 2007. Food supplementation experiments revisited: verifying that supplemental food is used by its intended recipients. *Can. J. Zool.* 85: 679–685.
- Wise, D. H. 2006. Cannibalism, food limitation, intraspecific competition and the regulation of spider populations. *Annu. Rev. Entomol.* 51: 441–465.
- Wright, P. J., R. Bonser, and U. O. Chukwu. 2000. The size-distance relationship in the wood ant *Formica rufa*. *Ecol. Entomol.* 25: 226–233.

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