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Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area?

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Abstract

We investigated how habitat fragmentation affects the movement of marked bumblebees between plant patches in a temperate conservation area in metropolitan Boston, Massachusetts. Our study was conducted on populations of sweet pepperbush (*Clethra alnifolia* L. f.) separated by a road and natural woodland, and buttonbush (*Cephalanthus occidentalis* L.) separated by a railroad. Bumblebees showed high site fidelity and only rarely crossed roads or railroads. When bees captured at one sweet pepperbush population were moved across a road to a new sweet pepperbush population and released, they returned to their original site, some within 20 min of their capture. When all inflorescences were removed from one sweet pepperbush patch, most bees moved to another sweet pepperbush population on the same side of the road. The results show that while bumblebees have the ability to cross a road and railroad, these human structures may restrict bumblebee movement and act to fragment plant populations because of the innate site fidelity displayed by foraging bees. Moreover, marked bees were almost never observed to move between populations unless they were displaced, or forced to seek additional forage sites. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Habitat fragmentation; Bumblebees; *Bombus*; *Clethra alnifolia*; Anthropogenic barriers; Pollination

1. Introduction

Animal movement is important for the pollination and seed dispersal of plants. Fragmentation of habitats by roads, railroads, fields, buildings and other human activities can restrict animal movement (Mader, 1984; Didham et al., 1996; Forman and Alexander, 1998). If animals are unable to cross such barriers, they may not obtain sufficient nectar, pollen, and fruit resources to survive. Flowers may remain unvisited and fruits undispersed, leading to declines in gene flow (Oostermeijer et al., 1994; Westerbergh and Saura, 1994) and seed production and the eventual decline of plant populations (Jennersten, 1988; Lamont et al., 1993; Noderhaug, 1995; Steffan-Dewenter and Tscharntke, 1999).

Habitat fragmentation is becoming more of a danger to the persistence of plant populations due to an ever-increasing human population, and an increasing alteration of the natural environment (Saunders et al., 1991). Despite the recognized impact of habitat fragmentation on plant–pollinator interactions (Aizen and Feinsinger, 1994a,b; Steffan-Dewenter and Tscharntke, 1999), few field studies have been conducted on how artificial barriers affect pollinator movement. Evidence from fragmented forests in Brazil suggests that some understory butterflies (Lovejoy et al., 1986) and euglossine bees (Powell and Powell, 1987) may not readily cross pastures. Yet it is generally unknown how roads constructed across a landscape affects pollinator movement.

Bumblebees in the genus *Bombus* and related genera are important pollinators of numerous temperate plant species (Heinrich, 1976, 1979a). Therefore, it is valuable to document how habitat fragmentation affects bumblebee movement and thus, plant gene flow. Bumblebees are known to be strong fliers, and are able to travel considerable distances (Heinrich, 1979a; Osborne et al., 1999); they are certainly capable of crossing a human-dominated landscape interwoven with barriers such as roads and railroads. But do landscape elements such roads or railroads restrict bumblebee movement in their normal foraging activities, or will bumblebees cross such features as they would any other intervening

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space of natural habitat? If captured in one plant patch and released in another patch of the same species, will bumblebees cross a roadway or natural barrier to return to their original site or adopt the new patch as a foraging site? Will bumblebees forced to move from a site where all flowers have been removed, seek out replacement forage sites located across a road, or will they tend to relocate to new sites on the same side of the road as their original forage site? Such questions are critical to understanding the ability of pollinator and plant populations to persist in a fragmented landscape.

Bumblebees show high vagility and are known to display flower constancy and high site fidelity (Heinrich, 1976; Osborne and Williams, 2001). Therefore, it would be important to discern how habitat fragmentation superimposed on this behavior affects their foraging activity. We hypothesized that bees would be more likely to move between sites separated by natural habitat than sites separated by a road. To test this hypothesis we conducted a series of experiments using marked bumblebees in a suburban forest habitat.

2. Methods

2.1. Study location, plant species and bumblebee species

The study was conducted at the Webster conservation area (N 42° 19′ 33.1″, W 71° 10′ 31.9″), a deciduous temperate woodland, located in Newton, Massachusetts. The study focused on a small (~1225 m^2) wetland population of buttonbush (*Cephalanthus occidentalis* L., Rubiaceae) divided into two fragments (sites A and B) by a raised 14 m wide railroad bed, and scattered moist woodland populations of sweet pepperbush (*Clethra alnifolia* L. f, Clethraceae; Fig. 1) on either side of a 4-lane, 14 m wide road, the Hammond Pond Parkway. The four sweet pepperbush study populations are referred to as sites I, II, III and IV, with site I located on one side of the road and the remaining three sites on the other side of it (Fig. 1).

Buttonbush is a deciduous shrub that ranges in height from 1 to 4 m, and bears small white tubular flowers clustered on ball shaped inflorescences. Sweet pepperbush is a tall deciduous shrub that ranges in height from 1 to 3 m or more, with small white fragrant flowers borne on terminal racemes 5–15 cm long. Both shrub species are frequently visited by bumblebees, which are the primary pollinators of sweet pepperbush (Hemingson, 1986). In buttonbush, cross-pollination is known to enhance fruit set greatly compared to self-pollination (Imbert and Richards, 1993). The term 'bees' or 'bumblebees' referred to in this paper are worker bees of *Bombus impatiens* and *B. affinis*, and also include several (3–15%, depending on site and year) carpenter bees (*Xylocopa* species). For all observations and experiments, counts of bumblebees reported include only those bees whose tag numbers could be read.

2.2. Mark and recapture of bees

In July 1997, 93 bees were captured on the buttonbush plants in both fragments (Table 1), cooled to make them passive and marked with Opalithplättchen or numbered plastic tags (Kearns and Inouye, 1993) glued to their thorax. Marked bees were returned to the shrub where they were originally captured within 10–20 min of capture. The area was surveyed for marked bees for 1–2 h on 6 days over a 2-week period.

In August of 1997, 137 bumblebees were marked at four sweet pepperbush sites designated "site I", "site II", "site III" and "site IV" (Fig. 1), with most bees captured from site I and site II (Table 1). Sites were separated from each other by a road or by intervening forest. The sites were observed for 0.5–1.5 h for 5–6 days over a 7–9 day period. In late July and early August of 1998, 137 bees were marked but only at sites I and II that are separated by the Hammond Pond road.

2.3. Bee displacement experiments

In late July of 1998 and early August of 1999, we captured bumblebees at the site I sweet pepperbush population, marked them, and then released them at site II located across the road. In 1999, we conducted a similar displacement of bees from site II to site I. Reciprocal displacements were also carried out between site II and site III located within the woods and separated by trees and shrubs (Table 2). After the displacement of bees, the original capture sites were monitored for a total time range of 205–570 min (depending on site) over a 4-day period to determine how many bees returned to their capture site. A Chi-Square test was performed to determine whether fewer bees returned to their original site when separated from it by a road than when separated by natural, woodland habitat.

2.4. Experiment where bees are forced to seek new forage sites

In mid August 2000, we marked 102 bees at the sweet pepperbush site II. After marking the bees, we removed all flowers from the plants at that site in order to force bees to seek additional forage sites. We hypothesized that bees would be more likely to move to replacement populations separated from site II by natural woods rather than seek populations located across a road. Nearby sweet pepperbush sites (I, III and IV) and a field with flowering purple loosestrife (*Lythrum salicaria* L., Lythraceae)—a major weed of wetlands in temperate North America—were monitored on 6 days over a 9 day

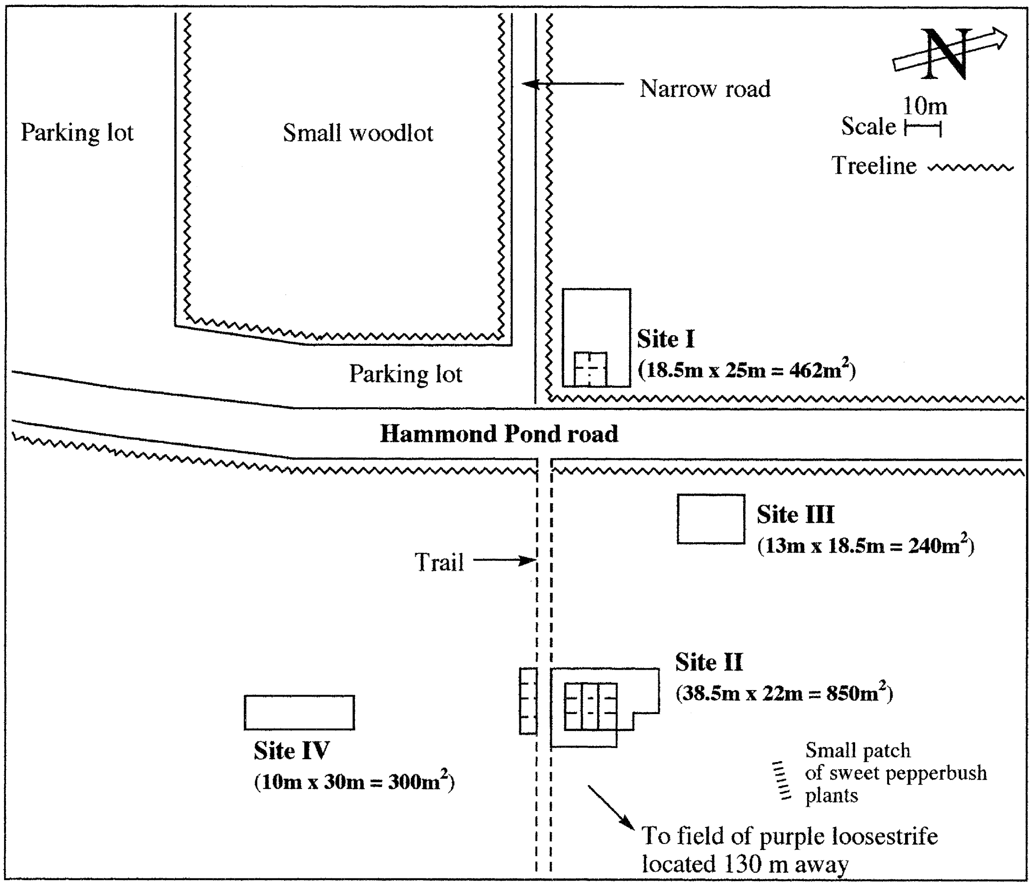

Fig. 1. Location and approximate area of sweet pepperbush populations (sites I–IV) in wetland patches in the Webster conservation reserve. Hatched areas at sites I and II show observation quadrats.

period for a total time range of 15–500 min (depending on site) for marked bees.

2.5. Site differences between sites I and II

Most of our experiments centered on the two bigger sweet pepperbush sites (I and II) separated by a road. Therefore, we decided to examine if these sites differed in aspects of inflorescence density that might determine bee visitation rates. Although fruit/seed set provide direct assessment of successful pollinator visits, we did not measure this, as fruit set is very high in sweet pepperbush (Jordan and Hartman, 1995). Since pollinator visitation is a function of plant density (Kunin, 1997), in 1998 we demarcated four quadrats (25 m^2 each) at site I and 11 quadrats of similar size at site II to census bees and record visitation rates of pollinating bees per quadrat at these sweet pepperbush sites (Fig. 1). Fewer quadrats were demarcated at site I because thick growth of the thorny greenbrier vine, (*Smilax rotundifolia* L., Liliaceae) hindered movement outside the marked quadrats. At site II, 11 quadrats were demarcated at the center of the population and to one side of the trail as fewer bees were seen at the peripheral plants of the population. Bees were censused on 8 days over a 12-day period from late July to early August. Observation sessions lasted 5 min per quadrat. Inflorescence density (number of inflorescences present per quadrat) was also determined at both sites. A Mann–Whitney *U* test was conducted to compare both sites on inflorescence density per quadrat.

In 2000, we counted the number of inflorescences on randomly selected plants at sites I and II. Sweet pepperbush plants primarily propagate vegetatively through the regeneration of clonal sprouts (Jordan and Hartman, 1995); therefore in a given area several ramets could belong to the same genet. To avoid picking stems belonging to the same genet, we randomly selected 20 single stems separated by a distance of 2 m or more in the general area of the demarcated quadrats at sites I and II to represent single plants (Fig. 1). This was done prior to the flower removal experiment. A *t*-test (two tailed) for independent samples was performed to determine if the two sites differed for mean inflorescence count per plant. We also determined if the two sites differed in bee visitation rates. On each of these plants we further selected one inflorescence (of similar size and number of open flowers) and counted the number of bumblebee visits to it during a 5-min observation session. Bumblebee visits per inflorescence per 5-min observation session were monitored between 13:30–16:50 on 4

Table 1
Number of bees (*Bombus* and *Xylocopa*) marked and observed later at study sites (excludes bees from the displacement and flower removal experiments)

Site	Number of bees marked		Number of marked bees observed		Fraction of marked bees observed	
	1997	1998	1997	1998	1997	1998
Buttonbush						
A (north)	80	–	18	–	0.23	–
B (south)	13	–	0	–	0.00	–
Total	93		18		0.19	
Sweet pepperbush						
I	55	82	19	37	0.35	0.45
II	59	55	18	18	0.31	0.33
III	12	–	4	–	0.33	–
IV	11	–	1	–	0.09	–
Total	137	137	42	55	0.40	0.40

August and 9:50–13:05 on 5 August 2000 for site II, and between 13:45–17:05 on 5 August and 9:00–13:30 on 8 August 2000 for site I.

3. Results

3.1. Observation and movement of marked bees across barriers

Of the 367 bees marked at all sites in 1997 and 1998, 31% were observed again on subsequent days (Table 1). These recapture rates conform to other studies of marked bees (Kwak et al., 1991; Dramstad, 1996; Osborne and Williams, 2001).

Marked bees were almost exclusively observed at the patches where they were originally captured, marked and released. Only three bees were observed at sites other than where they were marked (Table 2). In 1997 at the buttonbush sites, two of the 80 bees marked on the north side of the railroad tracks (site A) were subsequently observed on the south side of the tracks (site B) foraging on purple loosestrife. Bees marked on the sweet pepperbush plants that year were only observed at the original sites where they had been marked over the course of several weeks. In 1998, the 137 bees marked at the sweet pepperbush sites also showed the same site fidelity with one exception. A single bee (W9) marked at site II was observed 130 m away at a large patch of purple loosestrife, separated by intervening forest (Fig. 1).

3.2. Bee displacement experiments

Twelve (48%) of the 25 bees caught at site I in 1998, marked, and released 20 min later at site II, were observed again (Table 2). One of these bees was later observed foraging at site II. The remaining 11 bees were observed again only at site I, one of which was observed there only 20 minutes after being moved to site II.

In the 1999 experiments involving reciprocal displacement of bees between sites separated by a road (sites I and II) versus sites separated by natural forest (sites II and III), 36–59% of the displaced bees were observed again. Only two bees, one each from sites I and II were observed foraging at their site of release. The remaining 31 bees observed had crossed back to their original capture site. The reciprocal displacement between sites II and III showed a slightly greater tendency of bees to forage at the new site. One bee from site II continued to visit site III, while three bees from site III continued to visit site II. Of these three bees displaced from site III to site II, one bee (B37) was observed on subsequent days to forage at both its release and capture sites.

There was no significant difference between the effect of a road (separating site I and site II) or natural woodland (separating site II and site III) on bee movement between site of release and site of capture ($\chi^2 = 1.92$, df $= 1$, P-value > 0.05). However, the power of the test was low ($1-\beta = 0.28$). Contrary to our prediction, our results show a trend, albeit non-significant, for fewer bees to travel back to their original site when the sites were separated by forest than when separated by a road.

3.3. Response of bees forced to seek new forage sites

Of the 102 bees marked at site II from where all flowers were subsequently removed, 12 bees were observed again (Table 2). Eleven of the 12 bees observed were seen on sweet pepperbush plants located at sites on the same side of the road as site II (Fig. 1). Of these, seven were seen at site IV, which is located 35 m away from site II. One bee was seen at site III where not more

Table 2
Bumblebee movements across anthropogenic barriers at the Webster conservation area (the number of bees marked at each site are denoted in parentheses)

Direction of bee movement		Year	Number of marked bees observed across barrier	Barrier (width m)	Fraction of recoveries to marked bees observed across barrier	Number of marked bees displaced to release site
From site:	To site:					
Buttonbush						
A (80)	B (13)	1997	2	Railroad (14 m)	0.11	–
Sweet pepperbush						
Site II (55)	Field (0)	1998	1	Natural forest (130 m)	0.02	–
Bee displacement experiment						
Capture site	*Release site*					
Site I (25)	Site II	1998	11	Road and Natural forest (14 + 70 m)	0.92[a]	1
Site I (46)	Site II	1999	20	Road and Natural forest (14 + 70 m)	0.95	1
Site II (46)	Site I	1999	26	Road and Natural forest (14 + 70 m)	0.96	1
Site III (35)	Site II	1999	17	Natural forest (40 m)	0.85	3
Site II (33)	Site III	1999	11	Road and Natural forest (14 + 70 m)	0.92	1
Flower removal experiment						
Capture and release site	*Observation site*					
Site II (102)	Site I	2000	1	Natural forest (40 m)	0.08	–
Site II (102)	Site III	2000	1	Natural forest (40 m)	0.08	–
Site II (102)	Site IV	2000	7	Natural forest (35 m)	0.58[b]	–
Site II (102)	Patch near site II	2000	1	Natural forest (20 m)	0.08	–
Site II (102)	Site II	2000	2	–	–	–

[a] At this site, 11 of 12 (92%) marked bees observed had moved back to their original site.

[b] Of the 12 marked bees observed from those tagged at site II, seven (58%) were observed at site IV after flower removal at site II.

than 2% of the plants were flowering that year, and one bee was seen at a small patch of plants adjacent to the flowerless site II. Only a single bee was observed across the road at site I (located 84m from site II), which was flowering strongly. Two of the marked bees were seen to return to site II where we had missed removing flowers from one plant.

3.4. *Differences between site I and site II*

Sweet pepperbush sites I and II did not differ significantly in the density of inflorescences, but site I had higher bee visitation rates compared to site II. In 1998, mean inflorescence density per quadrat between sweet pepperbush site I and site II (Table 3) did not differ significantly ($U=16$, $P=0.47$). However, site I had on average almost double the number of bee visits per quadrat compared to site II. Similarly, in 2000, mean inflorescence count per plant between sites I and II did not vary significantly ($t_{\mathrm{stat}}=0.70$, df = 29, P-value = 0.49). However, overall bee visitation rates to inflorescences from morning to late afternoon over the course of 2 days in 2000, were significantly higher at site I compared to site II (Table 3).

4. Discussion

4.1. *Artificial and natural barriers*

Regardless of the distances (35–110 m) that separate sweet pepperbush patches, or the presence of a natural or artificial barrier between them, none of the bees marked at any of the sweet pepperbush sites were observed to move on their own among patches. The high site fidelity of foraging bees was particularly unexpected at site III, which had very few inflorescences in 1997, and is located only 37 and 40 m from the larger sites I and II, respectively (Fig. 1). These observations match similar reports, where no bees were observed to cross a gap of 4–8 m separating two forage sectors within a patch (Comba, 1999). Rasmussen and Brødsgaard (1992), report 2.6% of bumblebees moved between patches separated by distances of 10–40 m, while Osborne and Williams (2001) report a slightly higher percentage of bumblebee movement (12–14%) between patch groups in an experimental area. We failed to observe inter-patch movement possibly because of the greater distances separating our study patches.

Bumblebees appear to be reluctant to cross barriers unless floral resources at their forage sites are declining or have been removed. We observed no instances of bee movement from one population of plants to another of the same species. The two bees that moved from buttonbush site A to site B were leaving an area with declining floral resources and moving to an area with abundant purple loosestrife flowers. A bumblebee (W9), which moved from the sweet pepperbush site II to an open field, was also observed to be visiting purple loosestrife flowers (Table 2). These instances of bee movement to purple loosestrife may reflect the need for bees to seek new floral resources as their current forage plants finish flowering and they shift their "majoring" to other flowering plants (Heinrich, 1979b). The response of bees forced to seek replacement sites when flowers at their foraging site were removed, shows bees tend to move to new flower patches of the same species available nearby. They likely expend less energy in moving to nearby familiar forage flowers, compared to looking for new species of flowers and learning to work them. We observed fewer marked bees in this experiment (~12%), perhaps due to survey constraints spread over a much wider area. Since the flowers at site II were removed during the peak of flowering, the bees probably did not make the gradual transition from declining floral resources to a new species of flowering plants, and preferred to switch to nearby sweet pepperbush patches instead. Only one bee was observed at site I located across the road on one day, which shows bees are capable of crossing barriers to look for familiar forage plants.

Table 3
Mean (±1 S.D.) visitation rates of marked and unmarked bumblebees on sweet pepperbush plants, and inflorescence counts per quadrat at sites I and II in 1998, and mean (±1 S.D.) visitation rates of bumblebees and inflorescence count per plant in 2000

Sweet pepperbush sites	1998					2000			
	N^a	Bumblebee visitor		N^b	Inflorescence count per quadrat	N^a	Bumblebee visits per inflorescence	N^c	Inflorescence count per plant
		Unmarked	Marked						
I	156	4.52±2.85*	1.77±0.96*	4	403.75±230.85	93	2.68±2.58*	20	22.65±3.90
II	28	2.21±1.62*	0.43±0.57*	11	316.91±237.27	80	0.90±1.13*	20	28.55±7.49

[a] Number of 5 min observation sessions.
[b] Number of quadrats observed per site.
[c] Number of plants per site.
* $P<0.01$, t-test for independent samples.

4.2. Bumblebee displacement

The fact that bees return to their original site after being experimentally transported between sites show that roads and railroads are not insurmountable barriers to bumblebee movement. However, the very low numbers of bees that crossed these barriers without being experimentally transported (Table 2), underscores the high site fidelity of foraging bees (Heinrich, 1976; Bowers, 1985; Dramstad, 1996; Saville et al., 1997; Comba, 1999; Wesselingh et al., 2000; Osborne and Williams, 2001). Our observations confirm those of other studies where bumblebee pollinators mostly remain site constant regardless of the availability of equally rewarding (Osborne and Williams, 2001) or even richer forage patches nearby (Comba, 1999), and tend to visit closest neighboring plants within patches (Rasmussen and Brødsgaard, 1992; Comba, 1999). We did not measure wind direction or wind speed during bee displacement, although wind is known to influence bumblebee flights with longer flights downwind than upwind (Comba, 1999). However, as part of a current study conducted by the authors, bees displaced 100–500 m from their foraging site in winds of 4–8 mph from all directions were eventually able to find their way back to their forage sites, some within 10–15 min. Therefore, in our displacement experiments it is unlikely that bees were influenced significantly by winds.

Our observations suggests that although a railroad and a road are not impassable barriers to bumblebee movement, they may constrain or discourage bee movement by contributing to spatial cues that determine bee site-specific foraging behavior. This may explain the trend observed for higher numbers of displaced bees to remain at the release site to which they were moved, when capture and release sites were separated by a more homogeneous natural habitat (Table 2). In uniform habitats, bumblebees react with longer interplant flights and fewer backward turns, and can perceive environmental landmarks that break the uniformity of their forage patches (Plowright and Galen, 1985). When bees reach the edge of a patch most bees turn back and continue to forage (Rasmussen and Brødsgaard, 1992). Thus, a road or railroad that bisects a plant population may be a strong landmark possibly acts as a barrier, as site-specific bees may turn back from the road and restrict their foraging to only one fragment of the divided population.

Site fidelity was also underscored by the rapid return of displaced bees to their original sites. Feeding site fidelity was strong enough to propel these bees across a road back to their original forage site. Bees are known to follow a fixed flight path to return to their original forage sites (Heinrich, 1976; Thomson et al., 1987; Thomson, 1995; Wesselingh et al., 2000). Studies by Manning (1956) and Kunin (1997) show bees use spatial cues to return to individual plants and flowers, often where they have obtained higher nectar rewards (Dreisig, 1995; Wesselingh et al., 2000). This suggests that bees are sensitive to site characteristics. However, the rapid return of bees to their capture site when released on the same species of plants at a different site, suggests site fidelity is a stronger cue in foraging behavior than flower constancy. Nevertheless, the few bees that did not return to their original site indicate that bees can adopt new patches as foraging sites. Perhaps these bees were young foragers with the flexibility of changing their traplines to adopt a new or richer forage site. The fraction (0.08–0.15) of displaced bees for sites II and III sweet pepperbush patches separated by forest was almost double that for sites I and II separated by a road (0.04–0.08; Table 2). Site quality—determined by size of forage area or inflorescence density—may play a role as suggested by the adoption of the larger site II by three bees displaced from the smaller site III to the larger site II. In contrast one displaced bee from site II adopted site III.

Although inflorescence density per quadrat or the number of inflorescence per plant did not significantly differ between the smaller site I and the larger site II, the rate of marked and unmarked bumblebee visits appear to be much higher at site I compared to site II (Table 3). We did not qualitatively or quantitatively measure nectar or pollen resources at the different sweet pepperbush sites. However, with fewer bees visiting inflorescences at site II compared to site I, flowers at site II were expected to have more nectar and pollen available. Therefore, bees displaced from site I to site II were expected to encounter less competition by exploitation or nectar removal, which should have facilitated their displacement to the more profitable site, and vice versa. This proved not to be the case. Thus patch size or profitability may not be the only qualities affecting bee displacement. For instance, the road could be a major landmark for "traplining" bees that facilitates in orientation and recognition of original forage sites.

4.3. Response of bumblebees forced to seek new forage sites

Bees can traverse roads in their quest for new forage plants but rarely do so when forage is available owing to their high site fidelity. This is demonstrated by the observation of a single marked bee at site I after being forced to move from site II. However, of the 12 marked bees observed after flowers were cut at site II, 11 were seen at sweet pepperbush patches occurring on the same side of the road as site II and separated from it by natural woods. The close proximity of site IV to site II may explain why seven of the 11 bees were seen at site IV, which is 35 m away from site II. In comparison, site I is located at 84 m from site II in addition to being separated from it by a road (Fig. 1). Yet site I is larger than site IV and appeared to have more bee visitors (personal observation) compared to it. However, it has been suggested patch size may not have as strong an effect on pollinator visitation rate as does flower density (Kunin, 1997) or plant density (Comba, 1999). Although we didn't compare inflorescence or plant densities and bee visitation rates between sites I and IV, the number of bees visiting site I were much higher compared to site IV (personal observation). Indeed, site I continued to attract a higher number of bees compared to site IV, although it was near the end of its flowering. This could be due to the sunnier location of site I near the road or due to the higher production of nectar by the remaining flowers, either of which were not quantified in our study. Within site IV, marked bees from site II were invariably observed within the same forage area of the population over a number of days. This conforms to similar observations by Comba (1999). Indeed a section of the plants at site IV were flowering strongly but had very few bees perhaps because the plants were under constant shade. Our observations suggest that bees are more likely to remain on one side of a barrier if continuing resources are available there, and will seek new food sources when the original supply begins to decline.

While bumblebee movement may not be impeded by habitat fragmentation, habitat loss through activities such as road construction can definitely result in loss of potential nest sites for bees—an important issue that needs to be addressed in future studies on habitat fragmentation (Cane, 2001). Further studies on spatial distribution and variation in plant population genetic structure at the landscape level, along with detailed investigations of bumblebee flights and the sources of origin of pollen carried by bumblebees will help to clarify the effects of habitat fragmentation on pollinator movement.

5. Conclusions

Bumblebee pollinators are not restricted by barriers such as roads and railroads at the landscape level, where normal plant patchiness is comparable to habitat fragmentation by artificial barriers. High site fidelity displayed by bumblebees may further restrict their movement more than previously suspected because of this aspect of their foraging behavior. Although bumblebees are occasionally long-distance pollinators (Heinrich, 1979a), especially where flowers are sparse, they do not appear to travel between patches frequently where sizable patches of flowers are available. This applies even when patches are separated by natural habitat and the intervening distance is fairly short (30–40 m). When a natural population is divided into two sections by a road, field, or railroad, individual bumblebees may tend to treat it as two separate populations and not readily cross the intervening area. This is particularly true where each smaller plant population is large enough to meet their foraging needs. Thus, division of plant patches by roads and other structures may further reduce the naturally low frequency of bumblebee movement between plant patches, leading to lower rates of visitation in small isolated populations. The result may have implications for decline in gene flow in fragmented populations of plant species that depend on bumblebee visitation.

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