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Do Bumblebees (Hymenoptera: Apidae) Really Forage Close to Their Nests?

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This paper questions whether bumblebees really forage as close to their nests as has commonly been assumed in the bumblebee literature. Three experiments are described that involved marking and reobservation bumblebees. None of these experiments showed any tendency for bumblebees to concentrate their foraging close to (e.g., within 50 m from) the nest. Rather, the results suggested that bumblebees may prefer to forage at some distance from their nest. Further, a closer review of the bumblebee literature showed that similar findings were quite common. Some possible explanations to the observed behavior patterns are given as outlines for further research.

KEY WORDS: bumblebees (*Bombus*); flight distances; foraging behavior.

INTRODUCTION

Securing the existence of thriving and successful pollinator populations is an important conservation goal (Kevan, 1975; Senft, 1990). From a bumblebee's perspective, the spatial arrangement of forage resources is likely to be an important factor in colony success. In addition, the spatial scale of bumblebee foraging is of particular importance because of the pollination services bumblebees provide to both crops and wild flowers (Corbet *et al.*, 1991; Free, 1970b; Procter and Yeo, 1973). With plant populations facing fragmentation in many agricultural landscapes (Opdam, 1990), flight patterns of pollinators may determine whether a plant population is likely to suffer from isolation effects (see Rathcke and Jules, 1993). Knowledge of bumblebee foraging behavior, including flight

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patterns and foraging ranges, would make it possible to predict whether isolation is a likely threat to bumblebee-pollinated plant species in any given landscape.

A commonly used technique in studies of bumblebee behavior is mark-reobservation. Usually bumblebee foragers have been caught and marked at some selected location(s), followed by tracking the movement of individuals within a study plot or sampling a study area for marked individuals (Jennersten *et al.*, 1988; Kwak, 1978; Kwak *et al.*, 1991; Teräs, 1979; Thomson *et al.*, 1987). This method has provided important results related to questions concerning bumblebee movement on an influorescence, within a forage patch, or between a few well-defined patches. However, to address questions about bumblebee movement at a landscape scale, it is essential also to know their total foraging range.

Optimal foraging models predict that, within given constraints, an animal will forage in such a manner as to maximize fitness (Eickwort and Ginsberg, 1980). When optimal foraging is applied to bees, fitness is usually measured in terms of net energy return: energy which bumblebees obtain from nectar. Bumblebees are central-place foragers (Plowright and Laverty, 1984), and individual foragers bring nectar and pollen back to the nest. Since flying is energetically costly, one prediction following optimal foraging models is that bumblebees should minimize their travel distances to maximize energetic gain. Indeed, Heinrich (1975, p. 150) states, "Foraging profits by social insects depend markedly on the distance of the food source from the hive."

A search of the bumblebee literature reveals the general conclusion that bumblebees prefer to forage in close proximity to their nests (see, e.g., Bowers, 1985; Heinrich, 1976a; Kevan and Baker, 1983; Mosquin, 1971; Rotenberry, 1990; Teräs, 1976, 1983). The rationale supporting this conclusion is the energy cost of flying, although others believe time to be even more important; e.g., Heinrich (1975) calculated that a foraging distance of 1 km from the hive costs a bumblebee 6.7 min of foraging time, equivalent to the time used to collect the nectar of 267 clover blossoms. Similar arguments are used for honeybees, e.g., by Beutler (1951) and Nuñez (1982), yet empirical data on bumblebee foraging ranges from their nests are scarce (but see Butler, 1951; Saville, 1993).

Locating bumblebee nests in the field is difficult. Bergwall (1970), for example, did not succeed in his attempts to follow bumblebee workers back to their nest. Several authors report similar experiences [Coville, 1890 (quoted by Alford, 1975); Saville, 1993; Harder, 1986; Svensson, 1991]. Often nests are found more or less by chance (Alford, 1975; Harder, 1986; Sladen, 1912).

The expression "foraging area" also needs to be clearly defined. When "foraging area" is used as the entire area workers from a specific colony use for gathering nectar and pollen, the location of the nest is essential. If "foraging area" is used as a synonym for "forage patch," the situation is somewhat different. Most data seem to indicate that bumblebees concentrate their foraging in patches. This does not imply that bumblebees do not include several patches in their foraging area. In addition, foraging areas have a temporal aspect as pointed to by Visscher and Seeley (1982), who found the total geographic range visited by honeybees from a hive during a summer to be a circle about 8 km in radius; only small sections received visitors *at any one time.* Should bumblebees be expected to behave differently?

This paper reports the results of three mark-reobservation studies of bumblebee foraging from known nest locations. In all three studies, the numbers of reobservations of bumblebees marked at their nests were surprisingly low and, in general, much lower than when bumblebees were marked on forage patches. A close search of the literature revealed that other authors have reported a similar phenomenon. In total, the findings led to the conclusion that bumblebees are seldom observed to forage close to their nest, i.e., that this is adaptive behavior. Some possible hypotheses concerning this are presented.

METHODS AND STUDY SITES

A mark-reobservation technique was used to establish bumblebee flight distances. All bumblebees were marked with site- or nest-specific color (Kwak, 1987; McDonald and Levin, 1965), using a marking tube and colored Tipp-Ex correction fluid or honeybee queen marker colors (HonningCentralen A.L.). No anesthetic was needed. Reobservations were conducted along standard bee walk transects (see, e.g., Banaszak, 1980; Pollard, 1977). Bumblebee identification follows Prys-Jones and Corbet (1991) and Løken (1985). In general, *B. lucorum* and *B. terrestris* were grouped, since these two species are too difficult to differentiate in the field (Kwak, 1987; Schmid-Hempel and Schmid-Hempel, 1988).

Study 1: The Meadow with Commercially Produced Colonies of *Bombus lucorum/terrestris*

This site was an abandoned meadow (59°40'N, 10°48'E) of approximately 4500 m^2, in an early successional stage. The vegetation within the meadow was dominated by perennial herbs and grasses, with raspberry (*Rubus idaeus*) (Rosaceae) as an important species. Raspberry is reported by von Hagen (1986) to be a good nectar producer and is known to be attractive to bumblebees (Liu *et al.*, 1975; Teräs, 1976). The meadow appeared as a clearing surrounded by spruce and birch forest.

During late May 1993 the meadow was divided into a 36 $\times$ 5 grid of 5$\times$5-m squares, marked in the field by numbered wooden poles. Five bumblebee nests were brought from a local producer (PollineringService a/s), and on 27

May, bumblebee nest boxes were set in cages (for protection) and placed along the edges of the meadow (all between-nest distances >25 m). Cages were raised approximately 25 cm above ground level with the aid of wooden poles, to prevent entrance by small mammals. Nests were shaded against direct sunlight to prevent overheating. For the first few days, each nest was provided with a sucrose solution in bird feeders (as recommended by the nest producer).

Bumblebees were caught and marked as they were entering or leaving the nests (Table I). Reobservation walks started 10 days after setting out the nests. Reobservations were made on warm, dry, and still days. One reobservation walk included walking slowly through the middle of each square of the grid, 925 m in total. Twenty-four reobservation walks were conducted between 8 June and 2 July. When it was realized that the marked bumblebees foraged outside the meadow, probable forage patches (in nonforested areas) within a radius of approximately 1 km from the meadow were searched for marked bumblebees.

Nest traffic was recorded by an observer sitting in front of the nest, being careful not to disturb bumblebees going in or out. Observers recorded the exact time of all nest exits and entries, whether a returning bumblebee had a pollen load, and the color of mark on all arriving and departing bumblebees. Although it was not possible to record nest traffic simultaneously with the transect walks, a total of 39.3 h was used to record nest traffic on the different nests between 9 and 30 June.

Study 2: The Farmland Site

This site was a gently sloping area dominated by intensive agriculture (59°40′N, 10°48′E); the main crops were wheat and barley. Rocky outcrops with remnant seminatural vegetation exist within the fields. The flora of these habitat islands comprised mainly herbaceous perennials (for a more detailed description, see Saville, 1993).

To arrange reobservation walks in this area, three selected islands and a grass bank (160 m long) were gridded into 5×5-m squares marked in the field with red ribbon. The size of the islands included in this study were 175, 1500, and 4000 m^2. The crop was also monitored for bumblebees; 20 5×5-m squares were located in the crop. One reobservation walk included walking at a slow and even pace through all 306 5×5-m squares (1530-m length). Eight reobservation walks were conducted during a period of nine dates. Walks were conducted only between 0900 and 1700 on warm (ambient temperatures ranging from 16.3 to 21.4°C) days, and never in rain.

During spring and early summer, two *B. pascuorum* nests, one *B. lapidarius* nest, one *B. lucorum/terrestris* nest, and one *B. wurfleini* nest were

Table I. Number of Bumblebees Marked, Number of Reobservation Walks, Number of Marked and Unmarked Bumblebees per Walk, and Percentage of Marked Bumblebees Reobserved per Walk on Different Dates in the Meadow with Commercially Produced Colonies of *B. terrestris/lucorum* (Study 1).

	Date									
	8 June	9 June	10 June	11 June	15 June	16 June	17 June	28 June	29 June	2 July
No. of bees marked to date	106	118	118	118	129	159	159	162	162	162
No. of transect walks	3	4	2	2	1	1	1	5	3	2
Marked bees/walk	1	0.25	0	0	1	0	3	0.2	0	0
% marked bees/walk	0.94	0.21	0	0	0.78	0	1.89	0.12	0	0
Unmarked bees/walk	5.67	9	7.5	20	14	15	20	13	17	21

Table II. Number of Bumblebees Marked and Reobserved on Different Dates on the Farmland Site (Study 2), Number of Walks, and Percentage of Marked Bumblebees Reobserved on the Different Walks[a]

	Date							
	5 Aug.	6 Aug.	6 Aug.	10 Aug.	11 Aug.	13 Aug.	13 Aug.	13 Aug.
Walk No.	1	2	3	4	5	6	7	8
Nest-marked to date	117	117	117	117	128	128	128	128
Reobservations	21	12	23	4	9	8	11	13
% marked bees	17.95	10.26	19.66	3.42	7.03	6.25	8.59	10.16
Forage-marked to date	41	41	41	41	41	41	41	41
Reobservations	9	22	21	12	10	5	16	10
% marked bees	21.95	53.66	51.22	29.27	24.39	12.20	39.02	24.39
No. of unmarked bees	119							86

[a]Number of unmarked bumblebees is given for the two walks when it was recorded.

detected by observing a bumblebee disappear into a hole in the ground or into the vegetation. Unfortunately, the *B. lucorum/terrestris* nest was destroyed before the start of this study. Marking was carried out during a period of 3 days before the first reobservation walk. All workers detected when entering or leaving the active nests were marked (Table II). In addition, within two selected squares which were rich in bumblebees and forage, all bumblebees foraging were caught and marked with a site-specific color (Table II).

In addition to bumblebee species, we also recorded caste, color of mark and location within the grid, bumblebee activity, flower species visited, and presence/absence of pollen load. On two reobservation walks (5 and 13 August) all unmarked bumblebees were also recorded.

Study 3: The Larger-Scale Farmland Study

This study was conducted in a larger area which included the farmland site described above. The areas and methods used are described in detail by Saville (1993). Bumblebees were marked while foraging in six spatially separated (30 to 365 m apart) forage patches and from a *B. lucorum/terrestris* nest detected along a forest edge (Table III). The reobservation transect was 1850 m long, marked out as 25-m sections. Monitoring was done as a "dawn-to-dusk" study, where different observers walked parts of the transect approximately every 1.5 h from dawn to dusk on 1 day. Ambient temperatures ranged from 10 to 22°C. Simultaneously one observer was recording all exits and entries to the nest. The reobservation transect included a spruce forest edge, a deciduous forest edge, a crop interface, a grass bank, a roadside verge, and edge and interior habitat of habitat islands with and without a tree cover.

Table III. Number of Bumblebees Marked and Reobserved from Nests and Forage Patches During the "Dawn-to-Dusk" Study (Study 3)

		Number	
		Marked	Reobserved
Nest		82	37
Forage patch	1	13	24
	2	42	73
	3	24	33
	4	40	48
	5	29	26
	6	18	20
Sum		248	261

RESULTS

Study 1: The Meadow with Commercially Produced Colonies of *B. lucorum/terrestris*

In total, 162 bumblebees from five nests were marked (Table I). The total number of reobservations of marked bumblebees was only nine. The percentage of marked bumblebees reobserved per walk ranged from 0 to 1.89 on the different dates (Table I). During the same 24 reobservation walks a total of 315 unmarked bumblebees was recorded, making the overall proportion of marked bumblebees 0.03. Of the unmarked bumblebees observed foraging in the meadow, 77 (24.4%) were *B. lucorum/terrestris*. The main bumblebee forage plant in the meadow was raspberry.

The total number of unmarked bumblebees recorded along the transect was greater than the number of marked bumblebees on all dates (Table I). While reobservation of marked bumblebees varied from 0 to 3 per walk, observations of unmarked bumblebees per walk ranged from 5.7 to 21. During the 39.3 h of nest survey, a total of 466 nest entries was recorded; 76.2% of the recorded nest entries were of marked bumblebees.

For 2 days, two observers tried to locate the marked bumblebees that foraged outside the meadow by searching attractive forage patches in the surrounding area, including a clear-cut area with a dense flowering of *Geum rivale* (Rosaceae). Only three marked bumblebees were found, foraging in a garden approximately 300 m from the nests. Suspecting pollen to be a limited resource in the meadow, we attempted to attract pollen foragers by placing lupine flower stalks in baskets with water 30 cm from the nest entrances. No bumblebees were seen to pay any attention to these flowers. Also, during the hours of nest survey, only 36.1% of foragers returning to their nests had pollen in their corbiculae (pollen baskets), indicating that pollen collection was not their main occupation.

Study 2: The Farmland Site

In total, 206 reobservations were made of marked bumblebees (Table II). On the 2 days when all bumblebees were counted, 119 and 86 unmarked bumblebees were recorded, respectively. The proportions of marked and unmarked bumblebees along the transect on these two dates were 0.201 and 0.211. Pooling all reobservations, 51% were of bumblebees marked from forage patches, yet these represented only 25% of all marked bumblebees (Fig. 1). On all walks forage patch-marked bumblebees had a higher percentage of reobservation than bumblebees marked from nests. The hypothesis that the proportion of reobservations of nest-marked versus forage patch-marked bumblebees would equal the

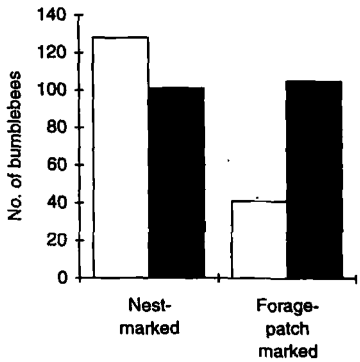

Fig. 1. Number of nest- versus forage patch-marked bumblebees marked (□) and reobserved (■) (all data pooled) at the farmland site.

proportion of bumblebees marked from nests versus forage patches was rejected on a $P = 0.01$ level ($\chi^2 = 42.1$).

Marked bumblebees that were not detected in the study needed to fly a minimum of 75 m to reach the nearest unmonitored site of seminatural, noncrop area or forage on weeds growing in the cereal fields. On the 100 m of transect located within the crop, only four bumblebees were recorded during the entire study. None of these were marked. The maximum reobservation distance recorded was a marked *B. lapidarius* discovered by chance on a habitat island outside our survey area >300 m from the nest.

Study 3: The Larger-Scale Farmland Study

A total of 248 bumblebees was marked before the "dawn-to-dusk" study: 166 (66.9%) were marked while foraging and 82 (33.1%) were marked at the *B. lucorum/terrestris* nest (Table III). Of the 261 reobservations recorded during this day of intensive survey, 224 (85.8%) were of the forage patch-marked bumblebees and 37 (14.2%) were of the nest-marked bumblebees (Fig. 2). The hypothesis that the proportion of reobservations of nest-marked versus forage patch-marked bumblebees would equal the proportion of bees marked from nests versus forage patches was rejected on a $P = 0.01$ level ($\chi^2 = 80.0$).

In addition to the low number of reobservations of the nest-marked bumblebees in the surveyed forage patches, it is worth noting that none of the 77 *B. lucorum/terrestris* workers marked in these forage patches were recorded entering the nest. A total of 169 unmarked *B. lucorum/terrestris* workers, and 35 unmarked males, was recorded foraging in the study area. It is interesting that while only 22.2% of the reobservations of forage patch-marked bumblebees were males, 51.4% of the reobservations of nest-marked bumblebees were males.

All groups of bumblebees marked from forage patches had much larger reobservation values (3 to 4×) than those marked from the nest.

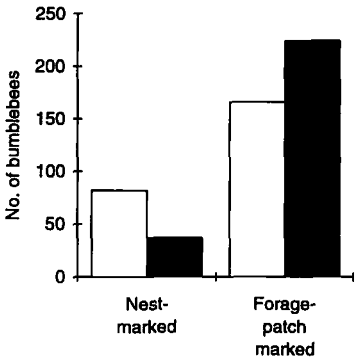

Fig. 2. Number of nest- versus forage patch-marked bumblebees marked (□) and reobserved (■) (all data pooled) during the 1992 "dawn-to-dusk" study.

Nest traffic recordings showed the nest to be quite active during the study period, with 272 recorded exits and 333 recorded entries; 36% of these nest traffic recordings were of marked bumblebees.

Distances from point of marking to farthest point of reobservation along the transect varied, but for all groups single individuals were reobserved at a maximum distance of 175–300 m from the location of marking. However, during the dawn-to-dusk study 80–100% of the bumblebees marked on different forage patches were reobserved within 50 m from the point of marking. Five days later, a nest-marked *B. lucorum/terrestris* worker was reobserved, 300–325 m from her nest.

DISCUSSION

Forage Patch Fidelity

Reobservations of bumblebees marked while foraging indicate that they tend to stay loyal to their forage patch. This is shown clearly in the larger-scale farmland study, with 80–100% of reobservations in the original marking section or the neighboring 25-m section during the day of survey. On the farmland site in 1993 a similar pattern emerged. This supports results reported by several other authors; bumblebees return to the same patch of forage, their foraging bouts/traplines (Brian, 1965; Inouye, 1978; Teräs, 1979, 1985; Thomson *et al.*, 1982). Jennersten *et al.* (1988) provide a good example of high numbers of reobservation when bumblebees are marked on forage patches. In their experiment, 86 forage patch-marked queens made 485 appearances in a studied patch of sticky catchfly (*Lychnis viscaria*) (*Caryophyllaceae*), and 51 forage patch-marked bumblebees made 227 appearances to a surveyed patch during three "dawn-to-dusk" studies (Jennersten *et al.*, 1988).

Movement from the Nest

In the few studies involving marking from known nests, the majority of the marked bumblebees have tended to "disappear," as they did in our studies. In contrast to the findings by Jennersten *et al.* (1988) on forage patch-marked bumblebees, Saville (1993) had, in one study, a total of almost 200 bumblebees belonging to three nests marked. Surveying nearby forage patches gave a grand total of seven reobservations of marked bumblebees. Saville (1993) also reports other studies with similar results.

Heinrich (1979a) had a nest box containing a *B. vagans* colony (or parts of one) within an enclosure of 5×5×2 m. The enclosure contained at least 1500 open and nonwilted flowers or influorescences of at least eight species of plants at any one time. In spite of this nest being surrounded by such a rich flower patch, Heinrich (1979a, p. 246) reports, "During all 26 observed first nest exits the bees typically flew very rapidly from one end of the enclosure to another and (on sunny days) spent the first 20 sec to 30 min out of the hive bouncing against the ceiling and walls. Eight of the 26 bees visited no flowers before returning to the hive." Later Heinrich removed the enclosure, and after 1–2 days all the bumblebees visited flowers outside the area. The author was unable to locate most of the bumblebees, according to him probably because they had established their "new foraging areas at great distance from their hive" (Heinrich, 1979a, p. 250).

Bergwall (1970, p. 11) describes how bumblebees from a detected nest were foraging at a distance from the nest too great for the author to be able to determine their flower choices. Thomson *et al.* (1987) had a captive *B. affinis* colony. The authors do not say how many foragers from this colony were marked, but the one individual they followed closely consistently flew to the far end of the grid (35 m) to begin foraging on *Aralia hispida* (*Araliaceae*). Pollen loads taken from other returning foragers showed them to be foraging on the same plant species, outside the study area (ca. 900 m^2). Hobbs *et al.* (1961) had bumblebee colonies in artificial nests next to plots of different clover species. Workers from natural nests on the prairie foraged in the plots, whereas many of the workers from the artificial nests were going elsewhere for food, even though "the plots were only a few yards from their nests" (p. 414).

Movement of Nest-Marked Versus Forage Patch-Marked Bumblebees

When reobservation rates in forage patches of nest-marked and forage patch-marked bumblebees are compared, it is evident that bumblebees marked from forage patches yield higher numbers (or percentages) of reobservations than bumblebees marked from known nests. Since bumblebee foragers are known to return to their forage patches, this finding seems to be as expected. But why do marked workers from known nests within the area, close to forage, fail to show up in larger numbers in any of the surveys, or forage patch-marked workers fail to show up as nest entries? In the larger-scale farmland study, the number of reobservations of nest-marked bumblebees during the dawn-to-dusk study was only 37, of which 19 were males. Since 272 exits and 333 entries were recorded at the nest, obviously most nest-marked foragers were not detected. The one nest-marked *B. lucorum/terrestris* observed 5 days after the dawn-to-dusk study had traveled more than 300 m. It is interesting that more than 200 other *B. lucorum/terrestris* workers were recorded foraging at shorter distances from this nest during the dawn-to-dusk study. It is also worth noting that none of the 77 workers marked at nearby forage patches showed up as nest entries.

Predicting where bumblebee workers from known nest sites will forage is clearly difficult. It seems reasonable to assume, however, that the presence of other foragers of the same species, caste, and sex proves that attractive forage is present. In study 1, the abandoned meadow experiment, workers from the set-out nests were expected to forage in the meadow, but only nine observations were recorded. The three marked bumblebees recorded outside the meadow were found foraging at distances of more than 300 m from their nests. The low percentages of reobservations of nest-marked bumblebees compared to bumblebees marked while foraging at the farmland site in 1993 show a similar tendency. And in the larger-scale farmland study, bumblebees from the *B. lucorum/terrestris* nest "disappeared," while the forage patch-marked bumblebees were frequently reobserved. In both these studies, marked individuals were observed by chance outside the study area. Several authors have reported similar observations; in most mark-reobservation studies with forage patch-marked bumblebees, a few reobservations are recorded at distances of 150 m to 2 km from the location of marking (Heinrich, 1979b; Kwak, 1979; Kwak *et al.*, 1991; Teräs, 1979). In the studies reported here, marked individuals were always seen near the farthest point of recording. There is no evidence that they did not fly even farther. Rather, short flight distances may be a sampling artifact, in that no observations can be recorded outside the sampling domain. Alford (1975, p. 88) states that "bumblebee foragers do not collect food indiscriminately in the area surrounding their nests." The author assumes, though, that "most foragers probably forage within a few hundred meters from their nest, even if they may venture further afield" (p. 88).

Bumblebees are capable of flying distances in the range of kilometers (Rau, 1924). Morgan and Percival (1967) emphasize that if a bumblebee colony is moved to a location within 1 km of the original site, some of the foragers may return to the old site for a day or so. Brian (1954) refers to results given by Schröder (1912) when she states that bumblebees are strong fliers, with a speed of flight of 3–5 m/s. Cartar and Dill (1990) estimated that a foraging bumblebee would usually spend no more than 2 min in transit between forage patch and colony. Together, this information indicates that bumblebees may usually fly

360 to 600 m to get from the hive to their forage patch. Heinrich (1979b, p. 141) states that bumblebees may forage "miles away from their nest," as honeybees do. Honeybees (*Apis mellifera*) sometimes forage in the range of kilometers from their hive (Beutler, 1951; Eckert, 1955; Eickwort and Ginsberg, 1980; Visscher and Seeley, 1982). Beekeepers have expressed that honeybees tend not to forage "on their own doorstep." Maybe a similar behavior is found in bumblebees. Maybe bumblebee foraging is not always under such strict energetic constraints on flight distances as has been commonly assumed, or there may be costs not yet fully understood influencing the spatial pattern of bumblebee foraging.

Foraging Areas

Some confusion seems to exist in the literature when it comes to bumblebee foraging areas, in addition to a common use of relative terms such as large and small. Free (1970a), for example, states that bumblebees are reputed to have larger foraging areas than they actually do, without giving a definition of large. A commonly cited foraging distance is that reported by Butler (1951) of 18.3 m. This being a note in the annual report of the Bee Department, Rothampstead Experimental Station, no exact information is given about the experiment, methodology, or results. Heinrich (1979b) estimates a foraging area of 500 m^2. Assuming that this area is a circle surrounding the nest, 500 m^2 is equivalent to a radius of 12.6 m, which is very different from our results with nest-marked bumblebees. For comparison, a circle with a radius of, e.g., 300 m will cover an area of 282 743.33 m^2, or 28.27 ha.

Comparison of foraging areas of honeybees with bumblebees or other wild bee species presents some confusion in the literature. Osborne *et al.* (1991) assume many wild bee species to have a smaller foraging range than honeybees, while Levin (1981) quotes Heinrich (1975) and Free (1970b) when he states that honeybees have considerably smaller foraging areas than other bees and lepidopterans. Free (1968) points to how it has often been assumed that bumblebees have larger foraging areas than honeybees, although no direct comparison has been made. Levin and Kerster (1974) point to the fact that little information is available concerning the foraging areas of bumblebees, although their foraging areas on herbs appear to be similar to those of honeybees. According to Procter and Yeo (1973, p. 353), a single honeybee colony may forage over an area of 48.6 ha (0.486 km^2), while Visscher and Seeley (1982) found their honeybee colony to forage over an area of 113 km^2.

Pollen Transport

While bumblebees are foraging in a patch the majority of movements are to the next flower (Ott *et al.*, 1985; Rasmussen and Brødsgaard, 1992; Stoltz, 1986; Zimmerman, 1982). Indeed, Procter and Yeo (1973, p. 181) state, "the frequent concentration of social bees on very limited foraging areas means that, considering the number of flower visits made, they contribute rather meagerly to outbreeding among plants." The results presented here indicate, however, that when bumblebees leave a forage patch, they may travel distances in the range of, e.g., 300 m. These long "leaving-patch" flights may result in pollen from the last flowers visited in one forage patch being deposited on a flower at a distance hundreds of meters from the parental plant. The amount of pollen transported such distances may be a minor proportion of the total amount of pollen transported by bumblebees, yet it could still have an important influence on gene dispersal within a particular plant species (Levin, 1981). The now well-documented pollen carryover effect (see references in Broyles and Wyatt, 1991) will increase the number of plants that could have their pollen transported long distances. And indeed, Broyles and Wyatt (1991) refer to several studies employing genetic markers to measure pollen-mediated gene dispersal which indicate that gene flow is extensive and probably exceeds beyond the boundaries of local populations. These studies conclude that pollen dispersal distances may be much greater than those inferred from observations on pollinator foraging behavior.

Nest Location

The data reported here also indicate that conclusions concerning the location of a bumblebee nest based solely on observations of bumblebee foraging should be interpreted with caution. A high number of bumblebee foragers in a flower patch does not necessarily indicate that these bumblebees have their nest within a distance of, e.g., 100 m, or "nearby" as has occasionally been assumed (e.g., Teräs, 1976; but see findings of Bond and Pope, 1974).

Why Do Nest-Marked Bumblebees "Disappear"?

There are some possible explanations why nest-marked bumblebees are reobserved in such low numbers near their nest. Some of these can be discarded based on existing data, while others need further investigations. For example, the high number of reobservations of forage patch-marked bumblebees discards the claim that marked bumblebees do not forage. The possibility that marked bumblebees tend to stay inside the nest was not supported in the "dawn to dusk" study, where nest traffic was recorded. Also the possibility of there being no forage available within the study area can be discarded. In all studies other individuals have been seen foraging within the area. It remains a possibility that the forage outside the sampling area may have been of a higher quality in all cases, since in none of these studies was forage resource quality assessed. The fact that other individuals found the existing forage resources attractive may be taken as an indication that this explanation is inadequate, but it cannot be eliminated based on the presented data.

Could this Behavior Be Adaptive?

Nest Predation

Bumblebee nests are attacked by predators and parasites of various kinds (Alford, 1975; Free, 1982; Holm, 1966; Morgan and Percival, 1967; Prys-Jones and Corbet, 1991; Sladen, 1912). In addition, bumblebee queens can try to take over already established nests (see review by Alford, 1975). Free (1970b) points out that colonies in nest boxes seem more susceptible to attack than naturally occurring colonies, probably because such colonies are more easily discovered. Maybe foraging at high densities in close proximity to the nest attracts predators to the nest or makes the nest more easily discovered.

Cuckoo-bees (*Psithyrus* spp.) can take over an already established bumblebee colony and are likely to be an important factor in bumblebee adaptation and survival. No bumblebee reproductives are produced in these colonies; instead bumblebee workers feed and rear the *Psithyrus* reproductives. Sladen (1912) estimated *Psithyrus* spp. to have taken over approximately 20–40% of the *B. lapidarius* colonies he observed. Awram (1970; quoted by Alford, 1975) noted that more than half the nests of *B. pratorum* obtained by him were parasitized by *P. sylvestris*. To my knowledge, no published study has shown how *Psithyrus* spp. locate bumblebee nests. *Psithyrus* can be observed nest-searching in late spring, and scent has been suggested to be an important aid in nest location (Morgan and Percival, 1967; Sladen, 1912), a hypothesis which has been questioned by other authors (Free and Butler, 1959). Perhaps vision is important at longer distances, and scent a close-in orientation guide, in the same way that Alford (1975) believes that a bumblebee forager returning to her nest relies more on visual memory and acuity than colony odor.

If bumblebees scent-mark visited flowers (see discussion by Corbet *et al.* 1984), one could hypothesize that foraging close to the nest could create a "scent magnet," guiding a searching cuckoo-bee to the nest location. Carefully planned studies on nest-search behavior of *Psithyrus* queens could clarify this.

Predation of Foragers

With a high proportion of the working force of a colony foraging in the vicinity of the nest, the probability of a predator seriously diminishing the number of workers at any one time may be a significant risk. By using several dispersed forage patches, this risk will be reduced (Tinbergen *et al.*, 1967). Gentry (1978) (quoted by Handel, 1983) found that in cases where a large number of pollinators accumulated on tropical trees, bee-eating birds congregated and drove bees away.

The literature is divided concerning the predation risk faced by bumblebee foragers. Some authors have pointed to predation as a potentially significant factor (Cartar and Dill, 1990; Morgan and Percival, 1967; Rodd *et al.*, 1980), while others believe workers of bees and wasps to be fairly immune to predation Brian (1965) or to show no behavioral changes influenced by predation risk (Morse, 1986). Goldblatt and Fell (1987) suggest fluctuation in predation pressure to be a factor influencing life expectancy in bumblebee colonies. In other species increased predation risk can cause shifts in foraging behavior (Heggenes *et al.*, 1993; Suhonen, 1993; see also references in Morse, 1986). In studies of bumblebee foraging behavior, however, predation has rarely been considered of importance (Hodges, 1985; Pyke, 1978; Zimmerman, 1982).

Competition/Depletion of Resources

Bumblebees have been found to be outcompeted by honeybees on particular flowers (Brian, 1965; Eickwort and Ginsberg, 1980; Holmes, 1964; Pleasants, 1981), and different bumblebee species may compete on particular flower species (Inouye, 1978; Pleasants, 1981). It is also likely that a strong bumblebee colony could deplete resources in smaller areas; e.g., Heinrich (1976b) found bumblebees to be capable of removing 94% of the standing crop of nectar within an area. It could then be argued that the resources available near the nest might be depleted below a threshold level, beyond which attempts by bumblebees to locate and extract the remaining nectar would be less profitable than flying to more distant resources (assuming that less depleted resources could be found). Maybe the traplining behavior often observed in bumblebee studies is the most advantageous from an energetic point of view even if the location of the trapline sequence is at a distance of, e.g., 3–500 m from the nest.

From an energetic point of view, the best strategy is to fly the longest distance before starting to load when increased load increases flight costs (Heinrich, 1979b). Individual workers would then be expected to fly out to the farther end of the trapline, or the farthest foraging patch, and start working their way homeward. When workers depart from a nest, they would be expected to head off rapidly in what could be described as a "transit flight mode," in clear contrast to the "foraging flight mode" from flower to flower. This is the observed behavior in all our studies.

In general, the assumption has been that bumblebees aim only to maximize net energy gain. Waddington (1983) pointed to the need to verify this assumption, suggesting that other factors may be involved in determining optimal foraging behavior (see review by Schoener, 1971; Eickwort and Ginsberg, 1980), but to my knowledge this has not been done.

Conclusion

Bumblebees have been observed to fly distances of several hundred meters between forage patches, indicating the use of foraging areas in the range of hectares rather than square meters. The data presented here also show how bumblebees apparently choose not to forage on available resources close (e.g., less than 50 m) to the nest. Conclusions concerning the location of bumblebee nests based on the observation of foragers, therefore, should be viewed with caution. The different patterns that emerge from mark-reobservation studies involving bumblebees marked from known nests and those marked in forage patches imply that the importance of bumblebees in pollen dispersal on the landscape level could be far greater than has been hitherto assumed.

If it turns out to be common bumblebee behavior not to forage as close to the nest as possible, this behavior may have several possible explanations, e.g., predator avoidance and intracolony competition. If bumblebees are to be useful in crop pollination, these processes warrant further study. To avoid future misunderstandings concerning distances and areas in studies of bumblebee foraging behavior, the use of clearly defined, nonrelative terms is needed.

There is a great need for experimental studies of bumblebee foraging behavior in relation to known nest sites. Preferably such studies should also look at nest success in terms of reproductive output. Only by studying nest success, and relating this to available forage plants and their spatial patterns and distribution, can we develop successfuly management strategies.

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