Bumblebee movement in a fragmented agricultural landscape

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Abstract

This paper presents the results of a bumblebee mark-reobservation study conducted in a fragmented agricultural landscape, where bumblebee resources (forage, and probably also nest sites) exist mainly on scattered remnants of semi-natural habitat. The results show that reobservations of bumblebees marked while foraging were numerous and in general at short distances (less than 50 m) from where they were marked. In contrast, when bumblebees were marked at the nest, the numbers of reobservations were very low, even though monitoring of nest traffic showed the nest to be very active during reobservation walks. The results indicate that bumblebees do not necessarily forage close to their nest, and that caution is needed if foraging area and nest location are based solely on the observation of foragers.

1. Introduction

Because of agricultural intensification, remnant habitats in many agricultural areas have become increasingly fragmented. Bumblebees depend on resources in these remnants for suitable nest sites and forage. To maintain bumblebee populations in a way that allows them to perform effective pollination services for wild flowers and arable crops, it is necessary to understand the spatial scale of bumblebee movements. If bumblebee flight distances are addressed in terms of a hierarchy of scales (Allen

and Hoekstra, 1992; Forman and Godron, 1986; Gulinck, 1986; O'Neill et al., 1986), interflower movement, interpatch movement and forage area at a broader landscape scale emerge as identifiable steps in the hierarchy.

Until now, the majority of studies on bumblebee movement have focused on smaller scale movements, e.g. within inflorescence (e.g. Galen and Plowright, 1985; Pyke, 1979) and between flowers within a patch (e.g. Hodges and Miller, 1981; Manning, 1956; Pyke, 1978). However, to understand how bumblebees use remnant habitats on farmland, and their potential for pollinating crops in large fields, knowledge of interpatch movement is essential. For remnants to be beneficial in terms of pollination services for the farmer, bumblebees must fly

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across areas of crop with little or no reward, to reach flowering entomophilous crops (e.g. field bean (*Vicia faba* L.) or red clover (*Trifolium pratense* L.)), and must reach the center of these fields. In studies of seed yield, pollinator-limitation has been found towards the center of fields of field bean exceeding about 12 ha. This corresponds to an edge-to-center distance of 173 m (Bond and Pope, 1974; Free and Williams, 1976), and it has been suggested that this is the critical field size for bumblebees to penetrate to the middle of a field. In mark-recapture studies, however, single individuals have been reobserved at distances of 250–600 m from the point of marking (Dramstad, 1995; Kwak et al., 1991; Teräs, 1979).

Several studies have looked at nest traffic (Brian, 1952, 1954b; Free, 1955a,b; Shelly et al., 1991), particularly in relation to weather (e.g. A.C. Baker, Cambridge University, 1992, unpublished work; Corbet et al., 1993; M. Fussell, 1991, unpublished work), but few have tried to relate nest activity to the spatial distribution of foragers in the landscape. Of the few studies that have quantified the forage distances of bumblebees from known nests there seems to be general agreement that bumblebees often forage within a few hundred meters of the nest (Alford, 1975; Banaszak, 1983; Bowers, 1985), though some individuals travel further. From the perspective of maximizing net energy gain, bumblebees should prefer to forage as close to their nest as possible (Heinrich, 1975b).

In addition to nest location, the distribution of foraging bumblebees in a fragmented landscape with patchy floral resources is likely to be influenced by forage preference and in particular by flower constancy (Free, 1970; Teräs, 1976; Thomson, 1981) or "majoring" and "minoring" (Heinrich, 1976, 1979a,b; Oster and Heinrich, 1976; Ranta, 1981). The tendency of bumblebees to establish predictable foraging areas or routes (e.g. Brian, 1952, 1954a; Corbet et al., 1984; Free and Butler, 1959; Heinrich, 1975a, 1976, 1979a; Manning, 1956; Plowright and Galen, 1985) will also affect rates of reobservation in a mark-reobservation study.

This study investigates bumblebee movement at the upper scale in the hierarchy of bumblebee foraging, that is between isolated habitat patches of semi-natural vegetation in an agricultural landscape within a matrix of cereal crops and forest.

2. Methods

2.1. Study area

The study was conducted in Akershus county, southeastern Norway, in arable farmland with gently undulating topography (less than 5°) and largely moraine soils. The main crops are cereals. Despite agricultural intensification, remnants of semi-natural habitat remain scattered throughout the landscape, some because they are difficult to remove and others because they constitute traditional ownership boundaries. These remnants comprise uncultivated habitat islands associated with glacial rock outcrops (variously covered with trees, herbs and areas of bare rock), cereal crop interfaces (including ditches and grassy banks), farm tracks and roadsides. These semi-natural habitats are separated by relatively small distances (less than 300 m).

2.2. Marking and reobservation of bumblebees on forage patches

Bee walk transects (e.g. Banaszak, 1980; Pollard, 1977; Pollard et al., 1975; Teräs, 1983) were marked out in 25 m sections within a 1 km × 1.5 km region (Fig. 1a and Fig. 1b), divided into Area 1 and Area 2. The transects were set out to cover as many forage patches as possible within the study area. The first transect (Area 1, Fig. 1a) covered a linear distance of 1850 m, including six habitat islands, two forest edges, a grass bank, a crop interface and a road verge. The second transect (Area 2, Fig. 1b) covered a linear distance of 1625 m, including a forest edge, a dirt road, two crop interfaces and eight habitat islands, including the surroundings of a farm pond. Habitat islands or transect sections, containing high densities of bumblebees and forage plants (arrows on Fig. 1a and Fig. 1b), were allocated different marking colours.

Bumblebees were caught while foraging and marked on the thorax with an area-specific colour mark. Marking was carried out using a specially designed, 2.5 cm diameter "piston marking tube", similar to that described by McDonald and Levin (1965) and Kwak (1987). White or coloured typists' correction fluid (Tipp-Ex®) was used in Area 1 (six different colours), and red and green honeybee queen

marking paints were used in Area 2. Identification and nomenclature of the *Bombus* species follows Prys-Jones and Corbet (1991) and Løken (1985). Because of the difficulties involved in separating *B. terrestris* (L.) and *B. lucorum* (L.) (Prys-Jones and Corbet, 1991) they were grouped together. They are denoted as *B. lucorum* because of the doubt concerning the status of *B. terrestris* in the study area (Løken, 1960, 1985).

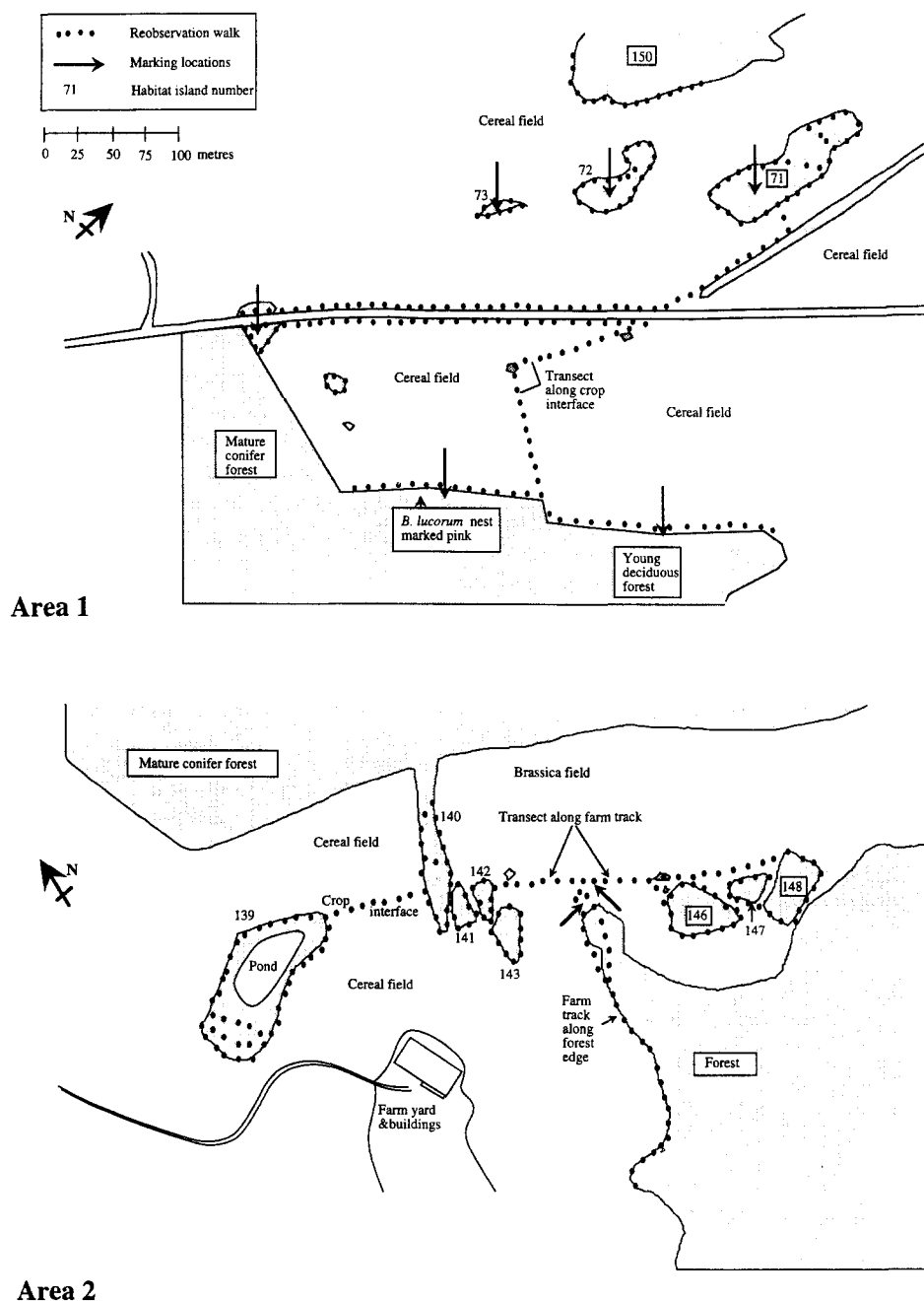Bumblebees were marked over a period of eight

Fig. 1. Map showing reobservation walk, land use and marking sites in Areas 1 and 2.

Table 1
Number of bumblebees marked and reobserved from nest and from forage patches in the two areas of survey

Area	From forage patches	From nest
Marked in Area 1 by 27 July	166	82
Marked in Area 1 by 31 July	166	119
Marked in Area 2 by 31 July	182	0
Total number of reobservations in Area 1	233	36
Total number of reobservations in Area 2	194	0

days (22–29 July 1992) in Area 1 and on one day (31 July 1992) in Area 2 (Table 1). For the purpose of this paper, all bumblebee species (listed in Table 2) are considered together, except for the nest-marking experiment which used a *B. lucorum* nest in Area 1.

Reobservations were made systematically on standardized bee walks, and by observers during the simultaneous marking procedures on different areas. On the bee walks bumblebee visits to flowers within 1.5 m each side of the observer (or 3 m to one side) were recorded. Bumblebee species, caste, sex, flower being used, type of behaviour, presence or absence and colour of mark, time and section of the walk, were recorded for each bumblebee observed. Flower identification followed Lid (1985).

In Area 2, two reobservation transects were walked on 31 July (1600 to 1824 hours) and three on 1 August (1100 to 1853 hours). In Area 1, marked bumblebees were monitored during repeated transect walks as a "dawn-to-dusk study" from 0500 to 1938 hours (when activity ceased because of a heavy

Table 2
Number of observations of different bumblebee species in the two areas

Bumblebee spp.	Area 1	Area 2
B. hortorum	6	1
B. wurfleini	4	39
B. hypnorum	79	14
B. lapidarius	30	76
B. lucorum	372	1225
B. pascuorum	122	510
B. pratorum	25	140
Sum	638	2005

thunderstorm) on 27 July. During this study, different observers monitored specific transect lengths for the entire monitoring period, so that simultaneous measurements of activity could be taken. Area 2 was also monitored on 7 August, one week after the last marking had been carried out.

2.3. Marking and monitoring bumblebees from the nest

A total of 119 bumblebees from a *B. lucorum* nest in Area 1 were marked between 22 and 29 July. Eighty-two of these had been marked by the time of the dawn-to-dusk study (Table 1).

All exits and entries were recorded at the nest during the dawn-to-dusk study. To gain an indication of movement from the nest in all directions, the area close to the nest was sampled more intensively by nine parallel 30m × 2 m sections. Sections three and four followed the forest edge, two sections were at increasing distance into the crop, and similarly five sections were spaced further into the forest. The nest was situated on the third of these parallel transects.

3. Results

3.1. Vegetation

Appendix A lists all available forage plants for the entire length of transects surveyed. Larger, wooded habitat islands (e.g. numbers 150, 71 and 139, Fig. 1) generally supported more species than smaller ones (e.g. 73, 141, 142 and 143, Fig. 1). The species-poor habitat islands tended to be dry and treeless, dominated by areas of bare rock. A further description of flower species and their use by bumblebees in the two areas is given by Saville (1993).

3.2. Spatial distribution of bumblebees across the agricultural landscape

3.2.1. Bumblebee occurrence in Areas 1 and 2

All bumblebee species recorded were present in both areas (Table 2). There were, however, some differences in castes, i.e. *B. hypnorum* (L.) males were recorded only in Area 1 and *B. lapidarius* (L.) males only in Area 2. *B. hortorum* (L.) was the only

species with no workers recorded at all. Because of differences in sampling effort, however, the numbers of bumblebees observed cannot be directly compared between areas.

3.2.2. Reobservation of bumblebees marked while foraging

Of the 166 bumblebees marked while foraging in Area 1, 233 reobservations were made during the dawn-to-dusk study (Table 1). In Area 2, 182 bumblebees were marked whilst foraging and 194 reobservations were made over the three monitoring days (Table 1). The total proportion of reobservation is 1.40 in Area 1 and 1.07 in Area 2, indicating that in both areas each marked bumblebee was seen, on average, more than once.

3.2.3. Area 1

In Area 1, reobservations of bumblebees marked while foraging along the forest edges were limited to the edge where they were marked. Bumblebees marked on the different habitat islands were also reobserved on the habitat islands where they were marked, except for 12 individuals (5.2% of reobservations) which were reobserved on another habitat island or field boundary, 75–250 m away. The maximum distance of any reobservation of a bumblebee marked while foraging from the marking point was approximately 350 m.

On the two parallel 30m × 2 m sections in the crop next to the nest, there were no reobservations of marked bumblebees on any of the 50 walk replicates during the dawn-to-dusk study. In fact, no bumblebees at all were observed on these sections. On the sections in the forest, four bumblebees were recorded. These were all *B. pascuorum* (Scop.) workers, one of which had been marked on the same edge.

3.2.4. Area 2

In Area 2, most of the marked bumblebees (more than 80%) were reobserved on the patches of *Cirsium arvense* (L.) and *Lamium purpureum* (L.) where they were marked. During all three days of reobservation, only 12 bumblebees (6.18%) were reobserved more than 50 m from the section where they were marked. The maximum movement distance recorded during the bee walks was one reobservation made about 300 m from the location of marking (Fig. 2).

Because only 12 reobservations were made on the last day of recording, it is impossible to draw any conclusions as to whether or not the marked bumblebees had spread out with time.

In addition to reobservations made during standard bee walks, occasional reobservations were made during the marking procedures. Maximum distances were all within the range of 100–250 m. Several of these individuals had apparently flown across cereal fields to reach flowers.

3.2.5. Activity of foragers at the nest

Eighty-two individuals were marked at the *B. lucorum* nest before 27 July. Nest traffic data showed that they were very active during the dawn-to-dusk study (Fig. 3). Although the sun did not reach the coniferous forest edge where the nest was located until around 1030 hours, foragers emerged from the nest in small numbers from 0520 hours onwards. The most intensive periods of nest entering, with a decreased frequency of exits, coincide with periods of rain, or with the few minutes preceding them (Fig. 3).

3.2.6. Distribution of foraging bumblebees in relation to the nest

A total of 272 exits from and 333 entries to the nest were recorded during the dawn-to-dusk study in Area 1. Of these, 91 of the departures, and 133 of the entries involved marked bumblebees. Yet only a total of 36 reobservations of nest-marked *B. lucorum* were recorded at foraging sites, and 17 of these
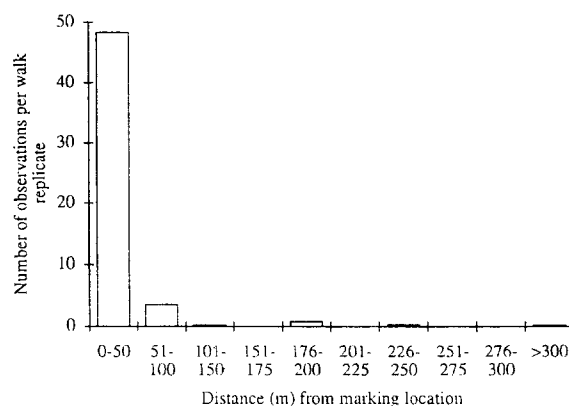

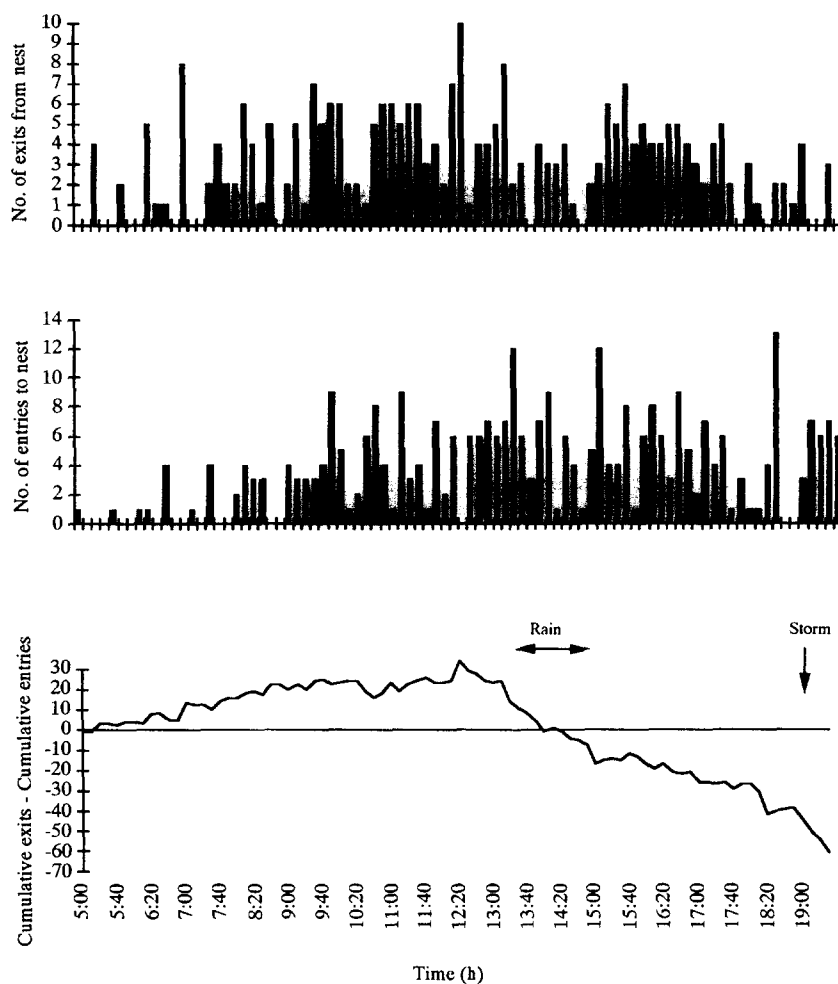Fig. 2. Number of reobservations of marked bumblebees at different distances from the marking locatons.

Fig. 3. Activity of foragers at the entrance of the *B. lucorum* nest on 27 July.

reobservations were males, of which not more than five were marked. Assuming all marked bumblebees entering the nest had been foraging, and excluding the males from the calculations, the total proportion of nest-marked workers reobserved during forager counts was 0.1428.

One marked *B. lucorum* was reobserved in Area 2 five days later, about 350 m from the nest. All 36 reobservations made during the dawn-to-dusk study were on the conifer forest edge where they were marked, or along the adjacent deciduous forest edge. The remaining bumblebees from the nest were not reobserved on the study transects. Of the 72 *B. lucorum* marked while foraging on other patches in the study area, none were recorded entering the nest.

Unless they were foraging on weeds within the cereal fields or within the forest, the nest-marked bumblebees seen leaving the nest must have travelled at least 250–350 m to reach forage patches outside the study area.

4. Discussion

4.1. Reobservations of bumblebees marked at forage patches

Single individual bumblebees were recorded flying distances of 150–350 m between patches of forage, but bumblebees marked at a forage patch were

most often reobserved within the 25 m section of marking. This is consistent with findings by other authors, and knowledge about the patch fidelity of bumblebee foragers. Because the total number of reobservations on the last day of monitoring in Area 2 was low, it was not possible to identify any trend towards a weakening of this patch fidelity with time.

The degree of discontinuity in the forage resource where the bumblebees were marked may affect the extent to which they disperse. Bumblebees marked along linear stretches of flowers, namely the row of *Angelica sylvestris* (L.) heads at the forest edge in Area 1 and the *Lamium purpureum* dominated "track" between fields in Area 2, were mainly reobserved on the same linear feature, though not necessarily at exactly the same point along that feature. This concentration of reobservations near the marking points is not the result of greater sampling effort in the vicinity.

Bumblebees marked on isolated patches of forage, e.g. on small habitat islands, appeared to disperse more widely, across discontinuities in the landscape (e.g. cereal fields).

The nest location of the forage-patch marked bumblebees was not known. Without knowledge of the nest location of marked bees, conclusions drawn from reobservations are limited in terms of foraging ranges or defining what constitutes a patch. This study indicates, however, that the spatial scale of bumblebee foraging ranges is larger than has hitherto commonly been assumed.

4.2. The B. lucorum nest

To understand the processes determining the distribution of bumblebees in the agricultural landscape requires knowledge of how far from the nest bumblebees fly to forage, and how the spatial pattern of their resources affects their foraging behaviour. Although a total of 82 bumblebees from a *B. lucorum* nest on the conifer forest edge were marked before an intensive dawn-to-dusk reobservation, which monitored all forage within 0–250 m of the nest, the main forage patches of these bumblebees were not found. In addition, none of the 72 *B. lucorum* workers marked on other forage patches in the study area was recorded entering or departing from the nest, indicating that these workers belonged to other nests.

In general, however, bumblebee numbers were small on the west-facing forest edge where the nest was located, probably because it was densely shaded, cool and damp for much of the day. Ranking the different sections of the transect in Area 1 according to their total bumblebees, the conifer forest edge comes out among the lower half. Also, *Angelica sylvestris*, which was the dominant species in flower during the study, was past its peak of flowering. It was still the plant species receiving the highest number of visits in this area, however. Further, bumblebees marked while foraging along this edge showed the same reobservation pattern of patch fidelity as bumblebees marked while foraging in the other locations.

These results demonstrate that bumblebees do not always forage close to the nest. Observers at the nest found that most bumblebees seemed to fly up and head off rapidly, high above the adjacent cereal field or over the forest. The reobservation of a nest-marked *B. lucorum* in Area 2, on the other side of the forest, shows that bumblebees may fly over (or around) barriers such as conifer forest, in order to reach forage patches.

Other studies (Alford, 1975; Banaszak, 1983; A. K. Hagstrom, Cambridge University, 1992, unpublished work) suggest that where appropriate forage is available, microclimatic conditions are favourable, and competition is not too intense, bumblebees will forage close to the nest, or within "a few hundred metres of it". The authors do not know which of these factors, if any, caused the numbers of reobservations of nest-marked bumblebees in this study to be so small.

Interestingly, the first records of nest activity in the morning were returning foragers, although there were no observations of foraging bumblebees in the study area at this time. These early morning arrivals may have spent the night outside, or they may represent return of the earliest departing bumblebees which were not detected leaving the nest or on flowers. Sixty-one more entries to the nest were observed than exits.

4.3. Limitations of the data

The authors have attempted to monitor, as comprehensively as possible, areas of forage within 0–

250 m of the points where bumblebees were marked. However, with limited time and resources available, it was impossible to sample comprehensively all the areas into which bumblebees may have dispersed, up to the maximum distance a bumblebee may be expected to fly. To reduce the sampling effort, it was assumed that bees have a negligible probability of being reobserved in areas where no forage is available (such as cereal crops), and these areas were not monitored systematically. This assumption was supported by the records from the crop and forest sections.

As reobservation efficiency decreases with distance from the marking point, this calls for some caution when interpreting the results. In addition, to construct an accurate map of available resources (Zimmerman and Pleasants, 1982), flower counts should be supplemented with quantification of nectar and pollen resources and their diurnal variability. However, this seems to be an impossible task at the landscape scale.

5. Conclusions

When bumblebees were marked while foraging on flower patches, reobservations were numerous, and mainly in the same 25 m section where they were marked or in the neighbouring one. This supports findings by other authors, that bumblebees have a high forage patch fidelity. As has also been found by several authors, a small percentage of marked individuals were reobserved at larger distances, up to 350 m from the marking location, showing that bumblebees sometimes fly farther. In contrast, when bumblebees were marked at the nest, the number of reobservations was very small. These bumblebees probably foraged outside the study area, indicating that bumblebees do not always forage close to the nest. This study also shows that forage site fidelity does not necessarily mean that the nest is close by.

Acknowledgements

Appendix A. Species flowering in Areas 1 and 2, July / August 1992. % values are percentage of 25 m sample sections with flowers of species

Visited species	% in Area 1	% in Area 2
Matricaria perforata	72.7	81.8
Achillea millefolium	63.6	72.7
Chamomilla suaveolens	72.7	63.6
Galeopsis tetrahit / bifida	72.7	54.5
Linaria vulgaris	72.7	45.5
Cirsium arvense	72.7	36.4
Achillea ptarmica	63.6	45.5
Vicia cracca	90.9	9.1
Solidago virgaurea	54.5	27.3
Angelica sylvestris	72.7	0.0
Hypericum maculatum	45.5	27.3
Leontodon autumnalis	45.5	18.2
Trifolium pratense	36.4	27.3
Trifolium hybridum	27.3	36.4
Fumaria officinalis	36.4	18.2
Lamium purpureum	9.1	36.4
Lotus corniculatus	27.3	18.2
Sedum telephium	45.5	0.0
Viola tricolor	27.3	18.2
Hieracium umbellatum	45.5	0.0
Campanula rotundifolia	45.5	0.0
Trifolium repens	36.4	0.0
Lathyrus pratensis	36.4	0.0
Centaurea jacea	27.3	0.0
Stachys palustris	18.2	9.1
Melampyrum pratense	27.3	0.0
Cirsium palustre	18.2	0.0
Cirsium vulgare	0.0	18.2
Succisa pratensis	18.2	0.0
Epilobium angustifolium	9.1	9.1

Rhinanthus minor	18.2	0.0
Arctium lappa	0.0	9.1
Melampyrum sylvaticum	9.1	0.0
Knautia arvensis	9.1	9.1
Total number of species	32	22

Unvisited species in flower	% in Area 1	% in Area 2
Sonchus asper	90.9	18.2
Polygonum aviculare	27.3	54.5
Lapsana communis	72.7	9.1
Spergula arvensis	36.4	27.3
Myosotis arvensis	45.5	9.1
Ranunculus acris	36.4	18.2
Leucanthemum vulgare	18.2	36.4
Galium boreale	45.5	0.0
Senecio vulgaris	18.2	27.3
Stellaria media	27.3	18.2
Polygonum lapathifolium	9.1	27.3
Stellaria graminea	0.0	36.4
Ranunculus repens	18.2	18.2
Galium album	27.3	0.0
Erysimum cheiranthoides	9.1	18.2
Bidens tripartita	0.0	27.3
Potentilla argentea	9.1	18.2
Brassica rapa	9.1	9.1
Polygonum persicaria	0.0	18.2
Epilobium ciliatum	9.1	9.1
Verbascum sp.	0.0	18.2
Trifolium arvense	9.1	0.0
Galium verum	9.1	0.0
Potentilla reptans	0.0	9.1
Epilobium montanum	0.0	9.1
Veronica chamaedrys	9.1	0.0
Potentilla erecta	9.1	0.0
Mentha arvensis	0.0	9.1
Cerastium fontanum	0.0	9.1
Lysimachia vulgaris	9.1	0.0
Total number of species	22	23

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