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Site constancy of bumble bees in an experimentally patchy habitat

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Abstract

Habitat fragmentation alters the spatial and temporal distribution of floral resources in farmland. This will affect the foraging behaviour of bees utilising these resources and consequently pollen flow within and between patches of flowering plants. One element of bees' foraging behaviour, which is likely to be affected, is the degree to which individual bees remain constant to a particular site or patch, both within and between foraging trips. Mark-re-observation was used to investigate whether foraging bumble bees showed site constancy over several days to regular patches of forage, even when those patches contained qualitatively and quantitatively similar resources. The authors also investigated whether site constancy was affected by the arrangement of patches within the area. The experimental arena was a field of barley containing patches of a grass/herb mixture, including *Centaurea nigra* L. (black knapweed) which provided nectar and pollen for bumble bees, particularly *Bombus lapidarius* L. Patches were either contiguous or non-contiguous in patch groups. Twenty to 28% of marked *B. lapidarius* were re-observed in the experimental arena during the week following marking. The number of re-observations of bees decreased over time probably because floral density decreased, the bees sought alternative forage elsewhere or they died from natural causes. The bees showed striking site constancy: 86–88% of re-observations were constant to patch group ($27 \times 27 \text{ m}^2$ or $45 \times 45 \text{ m}^2$) and fewer re-observations were constant to small patches ($9 \times 9 \text{ m}^2$) within a patch group. Most observed moves were to patches or patch groups adjacent to those on which the bumble bees were marked. There was limited evidence that bumble bees were more constant to $9 \times 9 \text{ m}^2$ patches surrounded by barley (70–73% of re-observations were patch constant) than to $9 \times 9 \text{ m}^2$ patches that were contiguous (20–50% of re-observations were patch constant). The implications of the observed bumble bee site constancy for plant gene flow in the arable ecosystem are discussed. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Bumble bees; Site constancy; Habitat fragmentation; Floral resources

1. Introduction

Species diversity and population densities of bumble bees have declined markedly in Europe in recent decades (e.g. Belgium and France, Rasmont, 1988;

Germany, Donath, 1985; and the UK, Williams, 1986). Decline has been greatest in intensively cultivated arable landscapes. Habitat fragmentation and the resultant loss of essential forage and nesting sites are thought to be major contributory factors. The arable landscape consists of a mosaic of cultivated areas, often providing no forage, and patches of semi-natural vegetation which differ in their suitability as forage sources. These fragments differ in size and may be

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isolated from one another, or may be connected by a network of hedges, banks and waysides. A reduction in the availability and distribution of resources is likely to affect insect behaviour and populations. There is a growing literature on the effects of habitat fragmentation on insect populations and metapopulations (Opdam, 1989; Hanski and Gilpin, 1991) in farmland (Samways, 1989; Wratten and Thomas, 1990; Woiwod and Thomas, 1992; Kinnunen and Tiainen, 1994; Woiwod and Wynne, 1994), but there is a need for further information on behavioural responses of insects to landscape-scale changes in the spatial and temporal configuration of resources caused by fragmentation (Bronstein, 1995; Lima and Zollner, 1996). This study examines one aspect of bee behaviour at a landscape scale: site constancy and movement of foraging bumble bees in relation to the patchiness of floral resources.

Bumble bees are vital pollinators, not only for the crops which require bees to improve seed or fruit set and yield, but also for a large number of wild flower species growing in uncropped areas of arable ecosystems (Corbet et al., 1991). If the latter are to survive in the fragments of semi-natural vegetation, they will require bees to transfer pollen between the plants and often between different patches of plants (Neal, 1998). The influence of resource patchiness and forager site constancy on pollen flow between plants is discussed.

1.1. Site constancy: costs and benefits to bees

Bees, foraging for nectar and pollen, have long been known to show constancy, not only to flower species (Bennett, 1883; Christy, 1883), but also to forage area (Free and Butler, 1959). A *flower constant* forager has been defined as one that “restricts its visits to one flower type, even when other rewarding types are accessible” (Waser, 1986). Similarly, a *site constant* (or area constant) forager could be defined as one that restricts its visits to one area of forage, even when other rewarding areas are accessible. Bumble bees have been shown to revisit the same patches of forage day after day (Heinrich, 1976; Bowers, 1985; Dramstad, 1996; Saville et al., 1997; Osborne et al., 1999) and even to use specific plant-to-plant routes, or traplines (Manning, 1956; Thomson et al., 1982, 1987), although these behaviours are plastic and

subject to changes in the environment and relearning (Heinrich, 1976; Chittka et al., 1997).

A bee might remain constant to one foraging site, or patch, during one foraging trip because that site provides adequate resources for the bee to collect in that trip. If the site does not provide sufficient resources then the bee will have to move to another patch. But why should a bee show site constancy over several trips or follow a previously learned route between plants and patches? There must be important advantages to the complex and detailed learning behaviour and navigation which results in bees following the same routes from their colony to a forage patch time after time (Menzel et al., 1996; Osborne et al., 1999). The simplest explanation is that site fidelity results from one area being more profitable in terms of pollen or nectar than other accessible areas. However, one aim of this study was to ask whether bees show site constancy in a situation where resources are evenly distributed. If so, it may be that the benefits of memorising the landmarks and location of a forage patch in terms of the time and energy saved in relocating that patch, outweigh the risks and costs associated with searching for a new patch. The costs involve extra energy and time spent searching for rewards, and the risks include the possibility of getting lost, finding no forage alternatives or being eaten. The relative importance of these costs and risks will depend on the degree of spatial separation between resource patches.

1.2. Site constancy: costs and benefits to plants

Foraging constancy by bees also has implications for plant reproduction. Although flower constancy may be beneficial to a plant species if it increases pollen transfer to compatible stigmas, it is difficult to see how site constancy could benefit plant reproductive success. If a bee is more constant to area than to plant, then site constancy by bees in a fragmented landscape, within each foraging trip, will lead to restricted pollen and gene flow between patches. Even site constancy between trips may limit gene flow, because the bee may still carry viable pollen on her body from the previous trip. This “constant” behaviour acts as an environmental barrier effectively turning the patches of plants into partially isolated subpopulations (Rasmussen and Brødsgaard, 1992;

Dobrowolski et al., 1993; Goodell et al., 1997). The ratio of selfing to crossing between the subpopulations will increase, affecting genetic diversity and fitness. This has implications for the conservation of wild plants in fragmented arable landscapes (Kwak et al., 1991).

1.3. Measuring site constancy

The main objective was to examine whether bees show site constancy over different trips given a choice of equally rewarding patches separated only by a few metres (whole arena was $200 \times 200 \text{ m}^2$). Also, the proportion of bees exhibiting site constancy to one large area of forage (a group of contiguous patches) was compared with the proportion exhibiting site constancy to a group of non-contiguous forage patches. The total area of forage available is similar for each group of patches although it might be expected that increased patchiness would reduce site constancy. If the patches are joined together into one large area, with no visible boundaries, the bee may be more likely to continue from one patch to another without having to fly up out of the patch and locate a new foraging site. For the non-contiguous patches, if a bee has to visit more than one patch in one trip, then the bee may just as easily leave the patch group and forage elsewhere as fly to another patch within the group.

The patch layout was such that, by individually numbering bees on two patch groups, data could also be gathered on movement between continuous and discontinuous forage areas. Although this data set was limited, it allows speculation on the potential consequences for pollen flow between plants in patchy habitats.

Site constancy cannot be investigated fully at an inter-flower or inter-plant scale. Previous mark-re-observation experiments on bee foraging at a landscape scale have been performed in complicated, irregular arenas where resource patch sizes varied (Leong et al., 1995) and the quality and quantity of forage within those patches was mixed (Dramstad, 1996; Schaffer, 1996; Saville et al., 1997; Osborne et al., 1999). Although there was only one experimental array in this study, it allowed data collection at a realistic field scale, and forage quality and quantity were evenly distributed between patches, aiding the interpretation of the re-observation data.

2. Methods

2.1. Experimental arena

Mark-re-observation was employed to investigate the degree of bumble bee (*Bombus lapidarius* L.) site constancy and movement on an experimental array of forage patches planted within a field of winter barley. As replication in space was not possible, the same experiment was repeated over 2 years. The experiments were performed on the habitat fragmentation experiment at Rothamsted (HFE: formerly known as the farmland ecology experiment, Marshall et al., 1992) which was set up in 1989 to investigate the movement and population dynamics of selected predators and parasitoids in a patchy environment. It consists of a 4 ha field of winter barley, into which was sown a regular array of patches of a seed mixture containing four species of grass and four species of broad-leaved perennials, including black knapweed (*Centaurea nigra* L.) which flowers in July and is visited by bumble bees, particularly *B. lapidarius* L. Flower and bee density were recorded at the beginning and end of the first experiment. The $9 \times 9 \text{ m}^2$ patches were arranged in groups of nine (Fig. 1). In each patch group, the patches were either separated from one another (non-contiguous) by 9 m strips of barley, or placed next to each other (contiguous). The experiment is situated next to a double hedge, providing a source of plants and insects which could colonise the patches. The patches are mown each year in late August.

2.2. Marking bees

B. lapidarius workers, foraging for nectar and pollen from knapweed on the patches, were caught and marked on two occasions: 17 July 1995 and 15 July 1996. Each bee was caught in a honey bee queen marking cage as she foraged on a flower head, and immediately given a paint mark or a numbered disk on the dorsal surface of the thorax while held against the plastic mesh at one end of the cage. To determine movement between patch groups, the colour of the paint was chosen according to the patch group on which the bee was caught (Table 1). To investigate movement within patch groups, bees on patch groups 7 and 8 were tagged with individually identifiable coloured, numbered disks (Opalithplättchen,

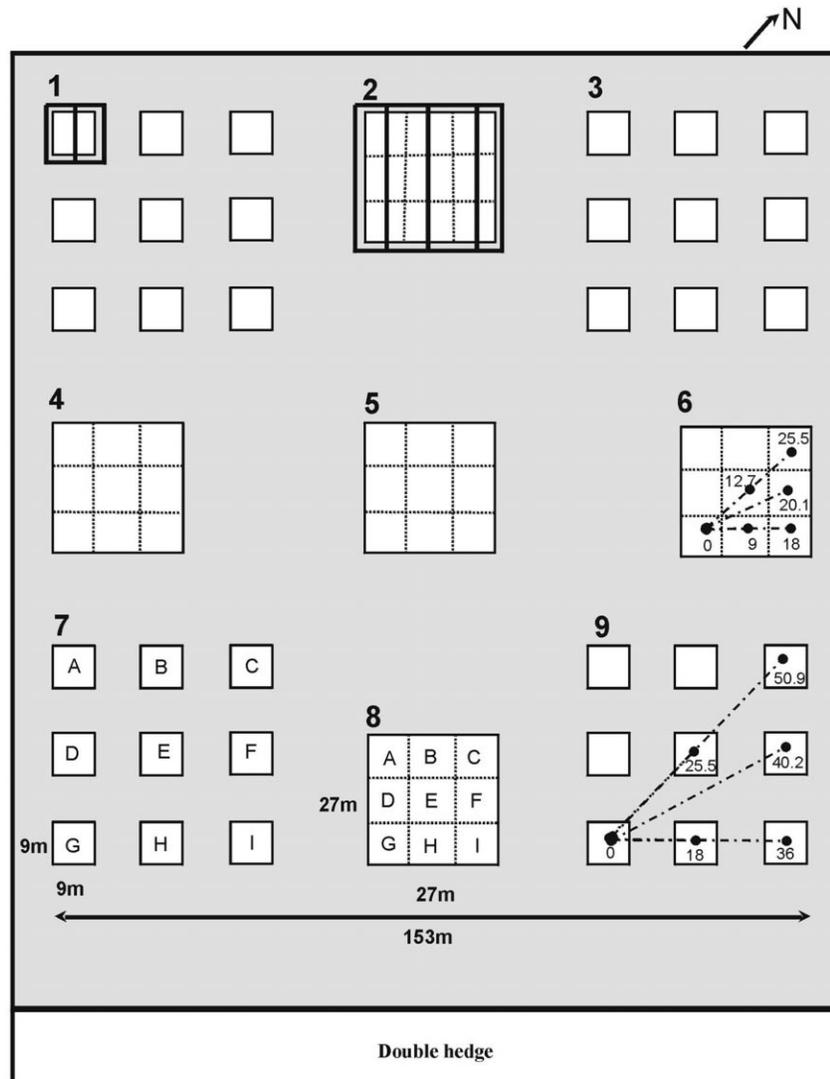


Fig. 1. Plan of the HFE at Rothamsted, consisting of a field of barley (■) into which have been sown patches (□) of a grass/herb mixture containing *Alopecurus pratensis* L., *Cynosurus cristatus* L., *Festuca rubra* L., *Trisetum flavescens* L. Beauv., *T. dubium* Sibth., *Leucanthemum vulgare* Lam., *C. nigra* L., *Plantago lanceolata* L. Patch groups are denoted by numbers (1–9). Each patch group consists of nine smaller patches ($9 \times 9 \text{ m}^2$), either contiguous or separated by barley. Small patches within groups, where bees were tagged with disks, are denoted by letters (A–I). All patches were surveyed for re-observed bees along a standard route (□). Dashed lines and associated numbers on patch groups 6 and 9 show mean distances (m) of possible moves between patches within a group. These distances are used in Fig. 5.

from EH Thorne, Lincoln, UK). This procedure took longer than painting so could not be performed for all bees in the experiment. After marking, each bee was released on the patch of capture. A similar length of time was spent collecting and marking bees on

each patch group, but different numbers of bees were marked (Table 1) because bee densities differed with patch group (J.L. Osborne, unpublished data). A total of 377 workers were marked in 1995 and 727 were marked in 1996 (Table 1).

Table 1

Number of bees marked with different colours and subsequently re-observed. Number of re-observations are greater than number of bees re-observed because some bees were seen twice or three times

Year	Patch group	Colour	Number of bees marked	Number of bees re-observed	Number of re-observations
1995	1	Pale blue	71	17	20
	2	White	30	8	9
	3	Red	20	3	3
	4	Yellow	23	3	3
	5	Green	30	6	6
	6	Pink	25	4	4
	7	Red disk	90	29	39
	8	Green disk	26	8	8
	9	Dark blue	62	28	37
Total			377	106	129
1996	1	Pale blue	90	25	27
	2	White	75	15	18
	3	Dark blue	88	25	27
	4	Yellow	80	16	17
	5	Green	75	26	28
	6	Pink	75	11	12
	7	Red disk	90	6	11
	8	Green disk	64	11	15
	9	Red	90	23	32
Total			727	158	187

2.3. Re-observation of bees

During the week following marking (on 3 days in 1995 and 5 days in 1996), the patches were surveyed for marked bees foraging on knapweed (Table 2) when the weather was warm and dry. A standard walk was made around the edge and through the centre of each

patch (as demonstrated for patch groups 1 and 2 in Fig. 1), examining as much knapweed to left and right of the observer as possible. The path taken was limited to minimise trampling. Each standard walk of the experiment took ca. 2 h and the patch groups were surveyed in a different order each day. When a marked forager was seen, the mark colour or disk identity and location were noted. If possible, the bee was captured and given a second paint mark in 1995 or a numbered disk in 1996 so that the number of sightings of individual bees could be monitored.

Table 2

Survey periods

Year	M/R ^a	Days after marking	Date	Survey period (h)
1995	M		17 July	10:00–17:05
	R	1	18 July	10:30–16:00
	R	3	20 July	13:00–16:08
	R	8	25 July	10:36–12:03
1996	M		15 July	09:56–17:45
	R	1 (a.m.)	16 July	09:55–12:03
	R	1 (p.m.)	16 July	14:25–16:30
	R	2	17 July	10:30–12:40
	R	3	18 July	10:30–12:18
	R	4	19 July	09:45–11:22
	R	7	22 July	09:55–11:10

^a M: marking day, R: re-observation period.

2.4. Statistical analyses

One-tailed goodness of fit tests (Siegel and Castellan, 1988) were used to test whether or not the bees re-observed on the HFE were constant to the patch group on which they were marked (Table 3a). The observed proportion of re-observations on the patch groups where they were marked was compared with the expected proportion assuming random return to patch group irrespective of marking location, for which the expected probability was 0.111 (i.e. given

Table 3

See text for explanation of tests: (a) one-tailed goodness of fit tests (Siegel and Castellan, 1988) to assess whether bees revisited the same patch group as where they were marked (using all re-observations); (b) one-tailed binomial tests to assess whether bees revisited the same patch within the patch group where they were marked, using re-observations of bees disk-marked (disked) on patch group (PG) 7 and patch group (PG) 8 (Fig. 1)^a

Year	Bees	<i>k</i>	<i>n</i>	<i>p</i>	<i>np</i>	<i>npq</i>	<i>z</i>	One tailed significance value	
								Normal test	Binomial test
<i>(a) One-tailed goodness of fit tests</i>									
1995	All	114	129	0.111	14.33	12.74	5.47	<i>P</i> < 0.0001	
1996	All	161	187	0.111	20.78	18.47	6.27	<i>P</i> < 0.0001	
<i>(b) One-tailed binomial tests</i>									
1995	Disked, PG 7	24	33	0.098 ^b	3.24			<i>P</i> < 0.0001	
	Disked, PG 8	1	5	0.098 ^b	0.49			<i>P</i> = 0.404	
1996	Disked, PG 7	7	10	0.096 ^b	0.96			<i>P</i> < 0.0001	
	Disked, PG 8	6	11	0.096 ^b	1.05			<i>P</i> = 0.0002	

^a *k*: observed number of re-observations on same patch or group; *n*: total number of re-observations; *p*: expected proportion of re-observations on same patch or group; *np*: expected number of re-observations on same patch or group; *q* = 1 – *p*; *npq*: variance for approximation to normal distribution; *z*: approximation to normal distribution: $((k - 0.5) - np) / \sqrt{npq}$; *P*: probability of observed result.

^b Calculated from all re-observations in that year ($k/n \times 1/9$).

that they return to the HFE, they have a one in nine chance of returning to the same patch group). Re-observations from different days were combined as results were similar over days. Although the data were binomial, they were tested against a normal distribution because $n > 35$ and $npq > 9$.

To compare site constancy between contiguous and non-contiguous patch groups, a logistic regression was performed on the proportion of total re-observations made by bees returning to the patch group where they were marked (or seen previously). Each patch group in each year was treated as a sample unit ($n_{\text{non-contig}} = 8$; $n_{\text{contig}} = 10$), and the regression assumed that the number of constant bees on a patch group followed a binomial distribution. The data for both years were used because initial analysis showed no overall difference in the proportion of constant bees between years.

One-tailed binomial tests (since $n < 35$ and $npq < 35$) were used to test whether bees were constant to the patch where they were marked, within patch group (Table 3b). The observed proportion of re-observations on the patch where the bees were disk-marked (patch groups 7 and 8) was compared with the expected proportion assuming random return to patch within a patch group irrespective of marking location within a patch group, for which the expected probability was 0.098 in 1995 and 0.096 in 1996. These expected probabilities were calculated from the observed proportion

of bees returning to the same patch group divided by nine (i.e. given the proportion of bees that returned to the same patch group, they have a one in nine chance of returning to the same patch).

3. Results

The marking and re-observation days were generally warm (18–25°C), although windspeeds varied (1.1–3.4 m s⁻¹). Bees foraged on all days, though densities declined as the density of flowers decreased over time. In 1995, there were 1.4 ± 0.2 foraging bees per 9 m² on the day when bees were marked and 0.9 ± 0.2 foraging bees per 9 m² at the end of the experiment. Flowering knapweed decreased from 165 ± 19 inflorescences per 9 m² when bees were marked to 67 ± 7 inflorescences per 9 m² at the end of the experiment. Inflorescence density was similar in all the patches and the soil type varied little across the experimental arena (C. Peters, pers. comm.) so it was assumed that nectar and pollen resources were comparable in each patch. In 1995, 6% of marked bees $n = 377$ had pollen loads. In 1996, 49% of marked bees had pollen loads $n = 727$, of which 67% were cream, the colour of knapweed pollen. The remaining third had loads of different colours indicating that they had also visited other plant species, probably in the same experimental

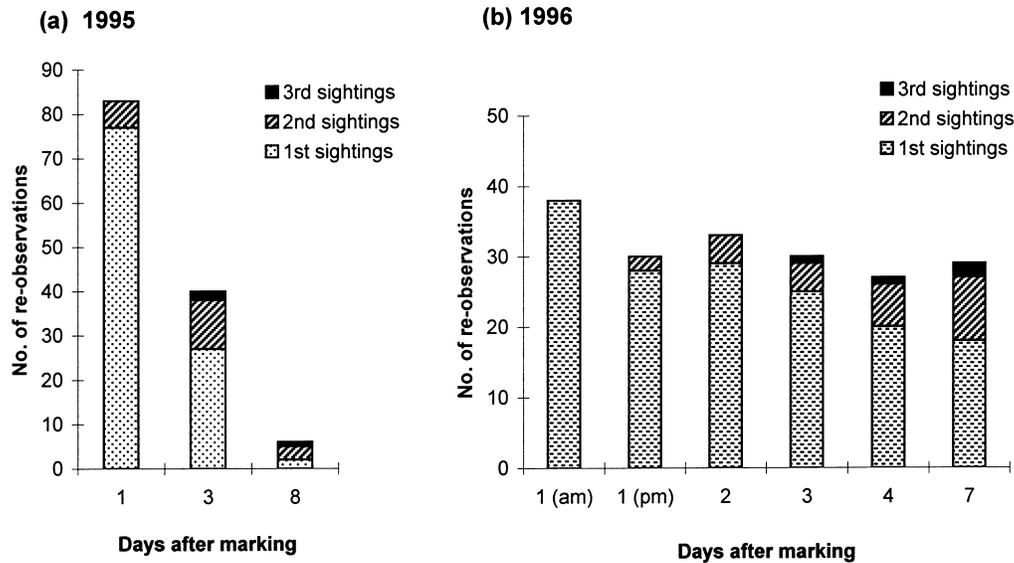


Fig. 2. Number of re-observations of marked bees in (a) 1995 and (b) 1996 which had returned to the HFE, categorised according to whether the bee had been seen before. Note different axis scales.

area (e.g. *Papaver rhoeas* L., *Trifolium dubium* Sibth.) on the same foraging trip.

3.1. Constancy to habitat fragmentation experiment

Twenty-eight per cent of bees marked in 1995 and 22% of those marked in 1996 were re-observed on the HFE during the week following marking (Table 1). Later in July and in early August of 1996, there were six re-observations of marked bees foraging on other plants on the Rothamsted Estate: one on *Lupinus albus* L. ca. 210 m from the HFE, two on *Phacelia tanacetifolia* Benth and *Borago officinalis* L. ca. 350 m away and one disk-marked bee seen three times on *Calendula officinalis* L. 920 m from the HFE. Of the bees re-observed on the HFE, the numbers seen on different patch groups varied but were in proportion to the number marked. The number of re-observations per period decreased over time in 1995, and to a lesser extent in 1996 (Fig. 2).

In 1995, 86 bees were seen only once, 17 were seen twice and three were seen three times. In 1996, 133 were re-observed only once, 21 were re-observed only twice and four were seen three times. No bees were seen more than three times. The proportion of multiple re-observations of the individual bees increased

over time, particularly in 1995 (Fig. 2). However, capture of marked bees was difficult without disturbing them or trampling the patches. In 1995 only 66% of re-observed bees were given a second paint mark and, in 1996, only 56% of re-observed bees were tagged with a disk, so the numbers of double and triple sightings were probably greater than recorded.

3.2. Constancy to patch group

The majority of re-observations (88% in 1995, $n = 129$ and 86% in 1996, $n = 187$) were on the patch group where the bee had been marked (for first sightings) or had been previously seen (for second and third sightings) (Fig. 3). The percentages varied little over time (Fig. 3). Results were similar when only first sightings were considered, with 86% being constant to patch group in 1995 ($n = 106$) and 85% in 1996 ($n = 158$). Of the bees seen twice or three times, most were constant to their marking patch group: 100% ($n = 20$) in 1995 and 92% ($n = 25$) in 1996. One-tailed tests showed that the proportion of bees re-observed on the same patch group as where they were marked was significantly greater than expected if the bees had chosen a patch group at random (Table 3a). These foragers exhibited strong site fidelity over days.

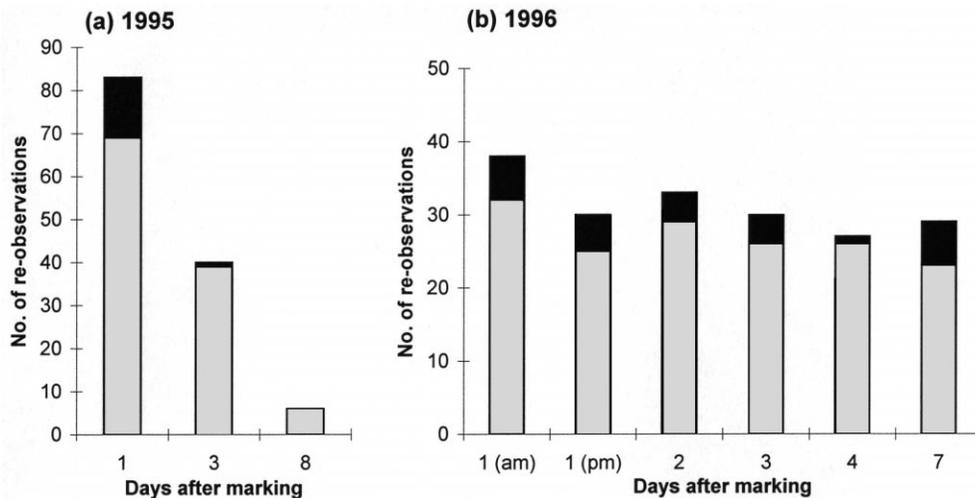


Fig. 3. Number of re-observations of marked bees in (a) 1995 and (b) 1996 which had returned to the same patch group as before (■) or had moved to a different patch group (■). Note different axis scales.

In the logistic regression comparing types of patch group ($\chi^2 = 33.11$, d.f. = 16, $P < 0.01$), overdispersion was present and accounted for. All proportions were >0.5 and 44% were >0.9 . The regression showed no significant difference ($F_{1,16} = 3.96$; $P > 0.05$) in the proportion of constant bees between the contiguous ($p = 0.80$, $n = 120$) and non-contiguous patch groups ($p = 0.91$, $n = 196$).

3.3. Moves between patch groups

Of the bees that were not constant to patch group, most moved to adjacent groups. Moves between patch groups were categorised according to whether they were to adjacent neighbouring groups or to diagonally adjacent groups or groups further afield, although comparisons were limited by the design of the experimental arena with patch groups having different numbers of neighbouring groups at different distances (Fig. 1). For example, the central patch group (5) has four adjacent neighbouring groups and four diagonally adjacent groups, whereas a corner patch group (1, 3, 7 or 9) has two adjacent neighbouring groups and one diagonally adjacent group. In 1995, there were 15 moves between patch groups (14 first sightings; one on second sighting), six to adjacent patch groups, four to diagonally adjacent patch groups and five to

the next group but one. In 1996 there were 26 moves. Of the bees seen once, 16 moves were to adjacent patch groups, two to diagonally adjacent groups and the other four were not to adjacent patch groups. Two bees were seen twice and both moved to an adjacent patch and then back again.

3.4. Constancy to patch

Although data could only be collected for bees marked on patch groups 7 and 8 (PG 7 and PG 8), many of these bees were constant to the patch on which they were marked within patch group (Fig. 4). Of the bees disk-marked on the non-contiguous patches (PG 7), 73% ($n = 33$) of re-observations in 1995 and 70% ($n = 10$) in 1996 were on the same patch as that on which they had been marked or seen previously. On the contiguous patches (PG 8), 20% ($n = 5$) of re-observations in 1995 and 55% ($n = 11$) in 1996 were on the same patch as that on which they had been marked or seen previously (Fig. 4). The number of observed returns to patches within patch groups was significantly greater than expected if the bees had chosen at random ($P < 0.001$ in three cases; Table 3b), except for bees seen on patch group 8 in 1995 ($P > 0.05$) for which the sample size was small.

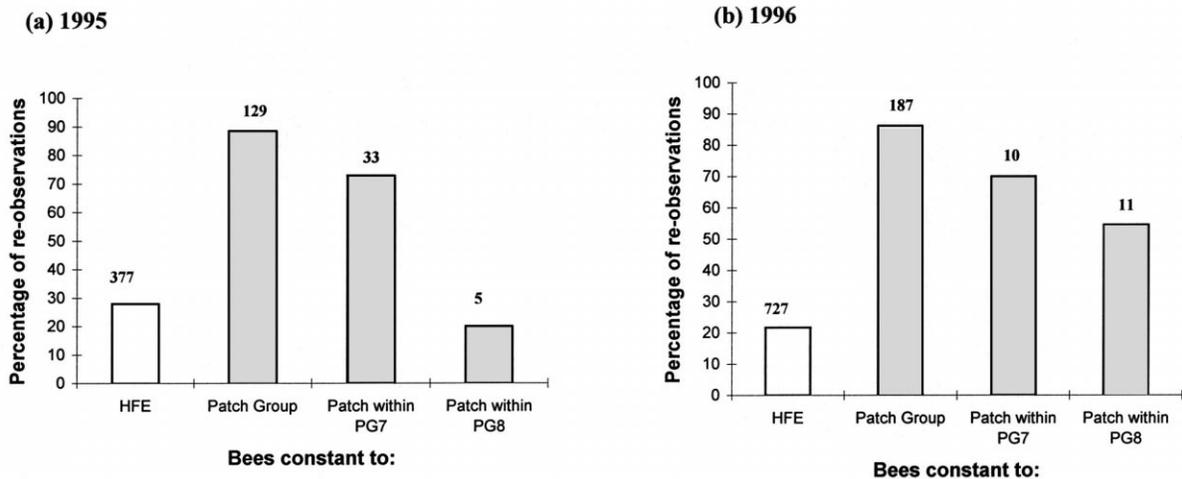


Fig. 4. Percentage of marked bees re-observed (□) or percentage of re-observations (■) where a bee was constant to a previous site in (a) 1995 and (b) 1996, compared across spatial scales: “HFE” = $200 \times 200 \text{ m}^2$; “patch group” = $45 \times 45 \text{ m}^2$ or $27 \times 27 \text{ m}^2$ (see Fig. 1); “patch within PG 7” = $9 \times 9 \text{ m}^2$ separated from others; “patch within PG 8” = $9 \times 9 \text{ m}^2$ joined to others. Numbers above columns indicate total number of marked bees (for □) or total number of re-observations (for ■).

3.5. Moves between patches within patch group

When considering distance moved by bees between patches, the two patch groups are not directly comparable: the intervening barley strips on PG 7 resulted in the patches being 9 m apart. Fig. 5 gives a summary of distances moved by bees within PG 7 and PG 8, although sample sizes are small for PG 8. Over both years, there were 41 observations of red-disk-marked bees returning to the non-contiguous PG 7, and 13 observations of green-disk-marked bees returning to the contiguous PG 8. As explained above, the majority of bees returned to the same patch in PG 7 (31 bees = 76%) and to a lesser extent in PG 8 (7 bees = 54%). Of the bees that did move, most moved to a directly adjacent patch. This was 9 m away in PG 8 and 18 m away on PG 7 (Figs. 1 and 5). A few bees moved to patches at further distances within the group. It is interesting to note (although sample size is small) that a lower proportion of bees moved the distance of 18 m when the patches were contiguous and the bees had the option of moving a shorter distance. Put another way, the proportion of bees re-observed at different distances from the marking site dropped more steeply for contiguous areas of forage than for forage patches separated by barley (Fig. 5).

3.6. Comparing constancy at different scales

Although limited to one field, the experimental design of the HFE allowed data resolution at different spatial scales, from the whole experimental area to the discrete patch group and the discrete patch. Fig. 4 demonstrates that the proportions of re-observed bees showing site constancy at each level of spatial resolution were remarkably similar for both years. Twenty-two to 28% of marked bees were re-observed in the 4 ha experimental area in the week following marking, 86–88% of re-observations were site-specific to patch group, 70–73% of bees were site-specific to a $9 \times 9 \text{ m}^2$ patch within a group if it was not contiguous with others (separated by barley) and 20–50% were site-specific to a $9 \times 9 \text{ m}^2$ patch which was contiguous with others in the group.

4. Discussion

4.1. Temporal pattern of re-observations

Mark-re-observation (recapture) techniques have certain limitations (Southwood, 1978) and, in common with other marking studies on bumble bees

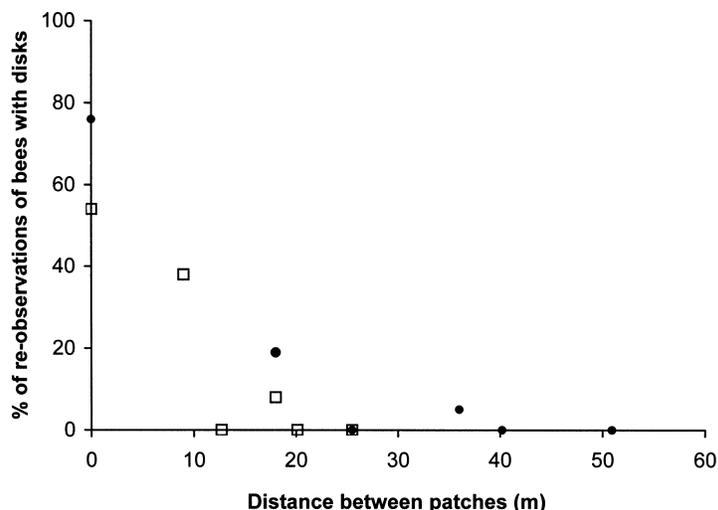


Fig. 5. Number of disk-marked bees re-observed at different distances from their marking patch as a percentage of the total number of disk-marked bees re-observed on the marking patch group (totals: $n = 13$ for PG 8; $n = 41$ for PG 7), combining data for 1995 and 1996. (□) green disked bees on PG 8, (●) red disked bees on PG 7. For example, in PG 7, 19% (8 out of 41) red disked bees were seen on an adjacent patch to where they were marked: they had moved 18 m on average. Distances are calculated as the average between two patches. Because of the different spatial structure of the two patch groups, moves of different lengths are possible (Fig. 1). Where a move is possible, a symbol is present, even if no bees were re-observed at this distance (percentage = 0).

(Dramstad, 1996; Schaffer, 1996; Saville et al., 1997), most of the marked bees (70–80%) were not observed again. The reasons for this probably include natural mortality, declining profitability of the patches, and failure to re-observe some bees that returned to the HFE because of survey constraints. Natural longevity of foragers can be short in midsummer; Brian (1952) found that 50% of *Bombus pascuorum* L. workers in a colony were dead within 3 weeks of emergence. Although nearly twice as many bees were marked in 1996, the percentage re-observed was smaller than in 1995. It is unlikely that the paint and glue used for marking caused mortality. No toxic side-effects have been observed in experiments where foragers at a colony have been similarly marked and observed for 3–4 weeks (e.g. Osborne et al., 1999), and the glue and numbered disks are used regularly by beekeepers to identify honey bee queens which live several years.

As the density of knapweed heads was decreasing, the decrease in the number of re-observations over time (particularly in 1995) may also have been the result of a gradual switch of foragers to other profitable nectar and pollen sources outside the HFE. Four bees were seen foraging 300–900 m from the experiment in

1996. While the rewards in an area remain profitable it “pays” to be constant to it and avoid the risks of foraging elsewhere, but when those rewards diminish (Heinrich, 1976; Visscher and Seeley, 1982) the bee must take risks and seek more rewarding resources. The influence of temporal changes in resource availability on area constancy have not been fully examined, although Dukas and Real (1993) and Thomson et al. (1982) showed that, as rewards diminished, interplant flight distance increased, and site constancy decreased. Interestingly, Thomson et al. (1987) showed that bumble bees with fixed foraging routes, or “traplines”, actually increased the area included on those routes when competition from other bees was removed.

Other marked bees that did return to forage on the HFE were probably missed because observation time per patch was limited and some bumble bees would have made few trips per day, spending long periods in the nest (Free, 1955; Osborne, unpublished).

4.2. Spatial pattern of site constancy

When bumble bees foraged in a habitat with an array of patches containing qualitatively and quantita-

tively similar resources, separated by short distances, they showed site constancy to groups of patches, and even to individual $9 \times 9 \text{ m}^2$ patches, over several days. Despite other similar neighbouring patches of forage being easily accessible, the bees still chose to avoid the risks associated with finding a new forage patch once they had learnt to return to a particular area.

The area over which a bee forages in one trip, and the consequent scale at which site constancy is observed will depend on many factors, including density of resources and isolation of that site. Meentemeyer and Box (1987) note that movement patterns are more easily observed on a small scale, where conditions are controllable, than on a landscape scale where they are not, but they point out that by observing behaviour at a fine scale, patterns that exist on a larger scale may be overlooked. The degree of observed site constancy varied depending on the scale of resolution of the data (Fig. 4). The reasons for low constancy at the HFE level are explained above. Within the experiment, site constancy was not as strong at patch level as it was at patch group level and this may reflect the spatial scale at which a bee forages. Individual bees possibly need to visit the flowers in more than one $9 \times 9 \text{ m}^2$ patch to fill their crops and/or pollen baskets on one trip. They will therefore move between patches, spending less than 100% of their time on one patch. Whereas a patch group (nine patches) may contain enough forage for a bee to fill her crop so she will spend 100% of her time foraging on different patches in a group and constancy will appear higher than for an individual patch. Further studies quantifying resources at different spatial scales and the relative constancy of individual bees would indicate “viable forage areas” and these areas will expand and contract as floral resources alter over time.

4.3. Consequences of patch separation

Site constancy was not increased in a group of contiguous patches over a group of non-contiguous patches (both groups containing the same area of forage plants). Reasons for this may be found by looking more closely at patterns of constancy to individual patches, although conclusions are tentative because of sample sizes. Bees were more constant to a patch if it was surrounded by barley than if it was contiguous with other patches in its patch group. The

9 m wide strips of barley were not an “actual barrier” (Fry, 1989) to bee movement because bees readily flew across them. More probably they were a “perceived barrier” causing some foraging bees, on reaching the barley, to change direction and thus remain in the patch (Plowright and Galen, 1985; Wood and Samways, 1991; Cresswell, 2000). For bees arriving at the HFE at the start of a foraging trip, the patches provided visual cues by which the bees could more accurately define the original foraging areas increasing the chance of them returning to exactly the same patch (Gary et al., 1977; Cartwright and Collett, 1982).

Whether the barley affected the trajectory of the foraging flight by acting as a perceived barrier during foraging, or acted as an aid to location for the bees at the start of a foraging trip, the resultant increase in site constancy may restrict plant gene flow in fragmented habitats (Rasmussen and Brødsgaard, 1992; Kwak et al., 1998; Osborne et al., 2000). On the other hand, considering only the distance of bee movement from one patch to another, which is of relevance to pollen flow models (Morris, 1993; Cresswell, 1997), the barley barrier actually served to increase the distance over which bees travel, and consequently the range over which pollen could potentially be transferred.

Standard models of pollen flow away from an insect-pollinated plant predict smooth curves where the proportion of cross-pollinations declines as a function of distance (see Handel, 1983). These are suitable where the recipient plants are spread in a regular manner, although the steepness of the curve will still depend on the plant density. But at the other extreme, if plants are distributed in small irregular patches at different distances from the pollen donor plant, then the curve may be more complicated and result in a series of steps because the bees have to fly over areas without plants (Handel, 1983). Further experiments with different patch arrays, such as those described by Richards et al. (1999), would be required to quantify such pollen movement.

What are the implications of habitat fragmentation for bumble bee populations? Bees are robust flyers, able to fly across large areas before finding suitable food (Visscher and Seeley, 1982; Osborne et al., 1999). However, increased spatial and temporal isolation of resource patches might reduce the profitability of individual foraging trips if the bee cannot fill her crop

at one site and has to visit several sites within one trip. This may affect the energetics of the colony and consequently its efficiency.

5. Conclusion

The main finding of this study was that bumble bees showed striking forage site constancy, even though the patches were separated by only 0–9 m and contained similar flowers. The observed site constancy varied with spatial resolution. Although habitat fragmentation may lead to increased site constancy, those bees that do move will have to move further between forage sites. Overall pollen flow between patches may be well restricted by the increased bee site constancy demonstrated here for patches surrounded by barley, but the distance between cross-pollinations may increase because foraging bees have to fly further between patches of plants. The relationship between bee behaviour, patch characteristics and actual pollen flow in bee-pollinated plants deserves further detailed investigation, particularly using designed plant arrays.

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