

# A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar

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## Summary

1. Bumble bees play a vital role in the pollination of many crops and wild flowers, and plans for their conservation require a knowledge of the dynamics and spatial scale of their foraging flights, which are, at present, poorly understood.

2. We investigated the foraging range and constancy of two colonies of bumble bees *Bombus terrestris* L. on a mixed arable farm using harmonic radar, which has a unique capability to record the trajectories of insects flying at low altitude in the field.

3. Foraging bees were fitted with lightweight radar transponders and tracked as they flew to and from the nest to forage. The resulting tracks gave information on length, direction and straightness of foraging routes. Superimposition onto a map of the foraging landscape allowed interpretation of the bees' destinations in relation to the spatial distribution of forage.

4. Outward tracks had a mean length of  $275.3 \pm 18.5$  m ( $n = 65$ ) and a range of 70–631 m, and were often to forage destinations beyond the nearest available forage. Most bees were constant to compass bearing and destination over successive trips, although one bee was tracked apparently switching between forage patches. Both outward and return tracks had a mean straightness ratio of  $0.93 \pm 0.01$  ( $n = 99$ ). The bees' ground speeds ranged from  $3.0 \text{ m s}^{-1}$  to  $15.7 \text{ m s}^{-1}$  ( $n = 100$ ) in a variety of wind conditions.

5. The results support the hypothesis that bumble bees do not necessarily forage close to their nest, and illustrate that studies on a landscape scale are required if we are to evaluate bee foraging ranges fully with respect to resource availability. Such evaluations are required to underpin assessments of gene flow in bee-pollinated crops and wild flowers. They are also required when making decisions about the management of bees as pollinators and the conservation of bee and plant biodiversity.

**Key-words:** bee movement, flight trajectory, foraging constancy, fragmented habitat, radar tracking.

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## Introduction

Wild bees are under threat from intensified agriculture (Williams 1989) and there has been a contraction in the ranges of several bumble bee species in Europe (Donath 1985; Williams 1986; Rasmont 1988), which has serious implications for the polli-

nation of crops and wild flowers (Corbet, Williams & Osborne 1991; Allen-Wardell *et al.* 1998). To develop rational strategies to conserve and increase the populations and diversity of bees, we need to understand not only their requirements in terms of nesting sites and food plants (Fussell & Corbet 1991; Fussell & Corbet 1992a,b; Matheson *et al.* 1996), but also the most useful spatial and temporal configuration of those resources. As Bronstein (1995) aptly pointed out in relation to plant–pollina-

tor interactions: 'we do not yet have a solid grasp of the scale at which individuals perceive their resource environment' and, as the study of behavioural ecology is extended to the landscape scale (Wiens 1989), the need to observe insect movement over ranges of hundreds of metres becomes more pressing (Bronstein 1995; Lima & Zollner 1996). Referring to honey bee recruitment studies, Seeley (1985) pointed out that 'honey bees rarely forage within 500 meters of their nest, but in setting up experiments, bee researchers rarely work beyond 300 meters from their hives'. Most bee movement studies have concentrated on movement at a fine to medium scale: the scale of flowers and localized distributions of plants (Pyke 1978; Morris 1993; Cresswell 1997; Park & Chung 1997). Movements on a larger scale have received limited attention, and there is still a significant gap in our knowledge of how far bumble bees regularly fly to forage, and how they respond to spatial and temporal changes in resource configuration (Bronstein 1995). Foraging decisions made by bees at a landscape scale are likely to be subject to different constraints than decisions made on a plant-to-plant scale.

The objective of this study was to track the foraging flights of individual bumble bees *Bombus terrestris* L. from colonies placed in a fragmented arable ecosystem, using the newly developed technique of harmonic radar (Riley *et al.* 1996, 1998; Osborne *et al.* 1997). We investigated the direction, length and destination of individual flights, as well as their straightness and speed, and used these data to describe the bees' foraging ranges, their forage preferences and their constancy to foraging sites on a landscape scale.

#### FORAGING RANGE

It has been assumed, citing optimal foraging theory, that a bumble bee should minimize the distance she flies between nest and forage, and so minimize her flight time and the energy expended, while maximizing the energy gained from the food she collects (Heinrich 1979). So, until recently, the assumption has been that 'as long as food is locally abundant, it is probable that the bumble bees forage close to the hive' (Heinrich 1976; also see Free & Butler 1959; Teräs 1976; Bowers 1985; Free 1993), although they can undoubtedly fly very long distances when circumstances demand (Rau 1924; Heinrich 1979): for example, bumble bees have been seen flying 20 km from the nearest land over an 80-km stretch of water (Mikkola 1984).

Estimates of bumble bee foraging ranges can be made using homing experiments (Rau 1924; Free & Butler 1959), pollen analysis (Brian 1952; Edwards-Anderka & Pengelly 1970) and, in particular, mark-re-observation studies (Schaffer & Wratten 1994;

Dramstad 1996; Schaffer 1996; Saville *et al.* 1997). Marking experiments, if performed on uniform crops or forage, often indicate a leptokurtic distribution of flight distances from the nest (Saville 1993; Schaffer & Wratten 1994). A few studies have concentrated on studying bee movement in larger, fragmented habitats (Kwak *et al.* 1991; Dramstad 1996; Saville *et al.* 1997). In all these experiments, the percentage of marked bees re-observed was very low, and Dramstad (1996), reviewing previous studies, suggested that a re-evaluation of the evidence was needed. Schaffer (1996) argues that because of the difficulty of seeing marked bees, the leptokurtic distribution may be an artefact: as an observer moves away from the nest, the area of the annulus to be searched increases, so the bees will be spread more thinly and will be more difficult to find. Indeed Dukas & Edelstein-Keshet (1998) have developed spatially explicit models to predict the optimal distribution of food provisioners away from a colony, comparing three different foraging currencies; the resultant distributions are not necessarily leptokurtic.

Estimates of honey bee forage ranges are easier to obtain than those of bumble bees, because the 'waggle' dances of a returning honey bee forager can be observed in the hive and then interpreted in terms of distance (and direction) to the food source (von Frisch 1967; reviewed in Seeley 1985; but see Gould 1976; Wenner, Meade & Friesen 1991). Waggle dance studies (Visscher & Seeley 1982; Schneider & McNally 1992, 1993; Waddington *et al.* 1994) have indicated foraging ranges of 1–6 km, implying that honey bees from a single hive can exploit forage sources lying within an area of up to 100 km<sup>2</sup> (Waddington *et al.* 1994). These conclusions are consistent with other field studies of honey bee behaviour (Buchmann & Shipman 1991), and support the long-held view of beekeepers that honey bees do not forage 'on their own doorsteps'. Could bumble bees be similar? J. E. Cresswell (unpublished data) has hypothesized that, provided resource levels are meagre, long-distance travel may be economically viable because travel time is a small proportion of total foraging time. Dramstad (1996) suggests that foraging at some distance from the nest may be an adaptive behaviour in bumble bees to avoid parasitism and competition, while Dukas & Edelstein-Keshet (1998) discuss the risk of predation and how it would affect their predicted spatial distribution of foragers from the colony. We used the harmonic radar technique to determine whether bumble bees do regularly forage close to their nest.

#### FORAGER CONSTANCY

Waser (1986) defined a flower constant forager as one that 'restricts its visits to one flower type, even

when other rewarding types are accessible'. Bumble bees show constancy both to flower type (Heinrich 1976; Waser 1986) and forage site (Heinrich 1976; Bowers 1985; Waser 1986; Dramstad 1996; Saville *et al.* 1997) and even use specific plant-to-plant routes, or traplines (Manning 1956; Thomson, Maddison & Plowright 1982; Thomson, Peterson & Harder 1987). However, bumble bees are considered to be less constant than honey bees because they often return to the nest with mixed pollen loads (Brian 1952; Free 1970; Macior 1994), and Ranta & Lundberg (1981) found more than one species of pollen in nectar loads extracted from bees' crops. The relationship between flower constancy and site fidelity has not been explored fully. A bumble bee may return with mixed loads because she is constant to a foraging site, but visits several plant species within that area (Heinrich 1976), or she may be visiting many species over several sites. Likewise, a bee returning with pure pollen loads is constant to species but may be visiting several sites. Neither mark-re-observation nor pollen analysis alone can be used to examine fully bumble bees' plant or area constancy on a landscape scale because these methods focus solely on either specific sites (mark-re-observation) or on evidence at the nest (pollen analysis). Harmonic radar allowed us to combine an investigation of bumble bee constancy to specific sites with a study of pollen retrieved at the nest.

## Methods

### THE HARMONIC RADAR

Although radar has been used for over 30 years to study the flight behaviour of insects migrating at high altitude (Riley 1989), it has only recently been adapted to observe insects flying near to the ground (Riley *et al.* 1996, 1998; Osborne *et al.* 1997). In this 'harmonic' adaptation, the insect to be tracked carries a small transponder that captures some of the energy in the radar transmissions, and re-radiates part of it at double the transmitted frequency. This signal is readily distinguishable from echoes from ground features, and so the insect can be tracked using standard radar techniques. Our transponders consist of a vertical dipole aerial 16 mm long, with a small low-barrier Schottky diode (Hewlett Packard, California, USA) and an inductive loop at the centre. The robust versions used in these experiments had dipoles made of 135- $\mu$ m diameter, copper-plated spring steel wire, and weighed about 12 mg. They were 6–7% of the insects' typical body mass of 175–200 mg, and are much lighter than the bees' normal pollen and nectar loads (up to 90% of body weight: Heinrich 1979). These transponders could be detected within a circle of radius 700 m centred on the radar, provided that they remained above the radar's local horizon. The altitude cov-

ered in unobstructed flat terrain was from ground level up to about 6–7 m. The radar was a 3.2-cm wavelength, 25 kW peak power, azimuthally scanning, dual frequency system as described elsewhere (Riley *et al.* 1996).

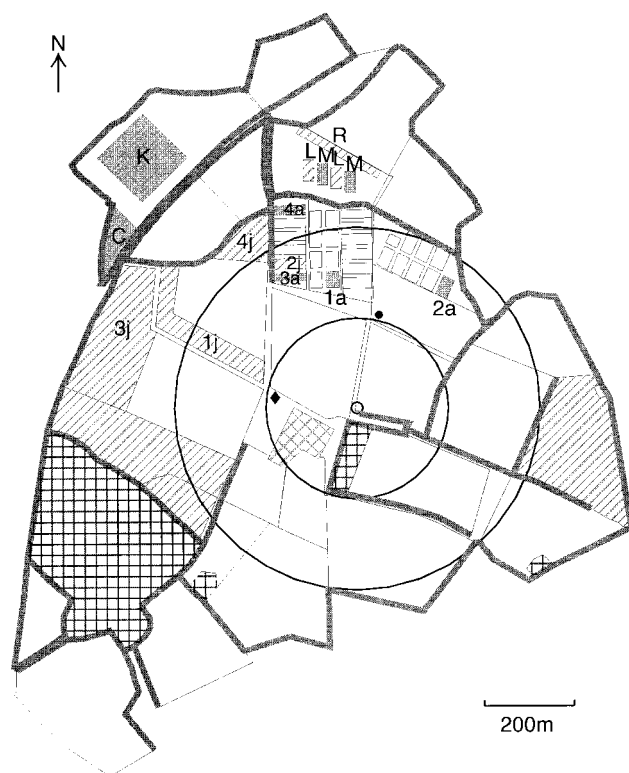
### THE EXPERIMENTAL ARENA

The experimental flight arena was a relatively flat area on Rothamsted Farm (Hertfordshire, UK) approximately 900 m in an east–west direction and 500 m north–south. It comprised arable farmland with flowering crops, hedges and wooded areas, providing mixed forage for bumble bees at different distances from the focal nests (Fig. 1). The radar was sited on the southern edge of the arena, and bees could be tracked until they flew beyond and below the radar's local horizon, which was formed by trees, buildings, hedges, tall crops and undulations in the terrain. Boundary hedges at approximately 610 m to the north-west, 460 m to the north and 410 m to the north-east formed the radar's horizon in the northern sector. Immediately to the south and south-west of the radar, and the June colony, visibility was truncated by tall buildings and trees.

The type and quantity of forage varied through June to August (Fig. 1). A patch of flowering plants was identified as being a potential forage area for bees with transponders if other *B. terrestris* workers were seen foraging on it for nectar and/or pollen. In June, bumble bees were foraging on *Brassica napus* L. (oilseed rape), winter and spring sown *Vicia faba* L. (field bean), *Lupinus albus* L. (lupin) and various flowers in the hedgerows. In August, they foraged on *L. albus*, *Helianthus annuus* L. (sunflower), on plots of bee 'forage mixture' containing *Phacelia tanacetifolia* Benth and *Borago officinalis* L. (borage) and, again, on flowers in the hedgerows. There were also several flowering plants, attractive to bees, along the edges of fields and paths [for example *Convolvulus arvensis* L. (bindweed) and *Triplospermum inodorum* (L.) Schultz Bip. (scentless mayweed) in August]. Gardens adjacent to the north-east farm boundary provided additional (but unidentified) bee forage during the trial periods.

### METEOROLOGICAL DATA

Experiments were performed in dry, bright conditions. Temperature, wind speed and direction were recorded at 1.9 m above the ground near the centre of the flight arena. Wind speed and direction were also recorded at four other stations, and at several altitudes, so that we could investigate the bees' air speeds and headings (Riley *et al.*, 1999).



**Fig. 1.** Plan of the experimental site on Rothamsted Farm showing positions of radar (○), 200 m and 400 m range rings, June colony (◆), August colony (●), field boundaries (thin line), forage in June (▨) and August (▩), hedges (thick line) and wooded areas (▧). Radar visibility was reduced by buildings (⊞) and hedges. Patches of potential bee forage are labelled with numbers used on the y-axis of Fig. 4. In June (▨), forage patches included rape (1j and 4j), spring field beans (2j) and winter field beans (3j). The hedges contained flowering hawthorn *Crataegus monogyna* Jacq. and bush vetch *Vicia sepium* L., and there were patches of lupins (L) and rape (R) over the north hedge. The woods contained bluebells *Hyacinthoides non-scripta* L. Chouard ex Rothm. and yellow archangel *Lamium galeopdolon* Ehrend. & Polatschek. In August (▩) forage included lupins (1a and 4a), a forage mixture containing phacelia and borage (2a) and sunflowers (3a). Hedges contained bramble *Rubus* spp. L., rosebay willowherb *Chamaenerion angustifolium* Scop., black knapweed *Centaurea nigra* L. and some white clover *Trifolium repens* L.. Beyond the hedges in August, there were patches of white clover (C), knapweed (K) and scentless mayweed (M). Gardens over the north-east hedges contained unknown forage throughout the season.

#### BUMBLE BEE COLONIES

Two colonies of *B. terrestris* (Koppert UK) were used, one for each of two 10-day trials conducted during 7–16 June and 31 July–9 August 1996. Each colony contained a queen, approximately 100 workers and their brood and food, housed in a plastic box (26 × 29 × 19 cm). In August, some males were produced, but these were removed as they emerged to avoid releasing sexuals onto the farm. Seven days before each trial a colony was placed in position, 57 cm above the ground on a stand, within a netting cage (2.7 × 2.7 × 1.8 m high) with one side open. The cage formed a wind-break and a landmark to aid orientation of foraging bees. The cotton wool, covering the nest, and the pollen and sugar syrup supplied with the colony were removed, the entrance opened and the bees allowed to fly to forage. Each forager was individually identified by gluing a coloured, numbered disk (Opalithplättchen, EH Thorne Ltd, Lincoln, UK) to her dorsal thorax after

her first foraging trip (e.g. B71 = bee with blue disk, number 71). A transparent perspex tunnel was attached to the entrance of the nest box to allow identification of individual foragers as they left and returned to the nest. The tunnel could be partitioned into sections so that bees could be temporarily trapped for examination or pollen sampling if necessary. The wax involucrum that the bees built over the comb was disrupted at intervals to allow free passage of bees fitted with transponders.

#### OBSERVATIONAL PROCEDURES

The frequency of foraging trips and the pollen sources visited were recorded for all foragers, including those tracked by radar. Each day from approximately 09.30 hours to 18.00 hours, the time and identity of each departing and returning bee, and the presence and colour of any pollen in the corbiculae were recorded. Each bee returning with pollen was captured and one of her pollen loads removed

for later microscopical examination to determine floral source. The bee was then released back into the entrance tunnel. In addition, during the August trials, bumble bees tracked by radar were captured on their return to the nest box and their thoracic body hair sampled for pollen. This was done by dabbing the bee's thorax (usually ventral, but when pollen was visibly present then also the dorsal) against a glass slide coated with glycerine jelly containing basic fuchsin stain. The bee was then released to return to the colony. A coverslip was placed over the jelly that was later examined microscopically to identify any pollen grains it contained.

#### TRACKING PROCEDURE

Each morning, after 60–90 min of observations at the colony entrance, a regular forager was selected, at random, for radar tracking. She was caught on departure from the colony, a transponder attached to her numbered disk (Riley *et al.* 1996; Osborne *et al.* 1997), and she was released at the nest box entrance. These bees flew away normally, showing no sign of being perturbed by the transponders. Co-ordination between the observers at the nest and at the radar was maintained by radio, and the bee's outward and return radar tracks were recorded, as were any further flights she made on that day. Some bees were tracked for 2 or 3 consecutive days: in these cases the transponder was usually removed from the bee at the end of the observation period for the day, and replaced the following day for further tracking. No more than three foraging bees were fitted with transponders concurrently to avoid confusion between tracks, which were not individually distinct. On the final day of the trials, the flight of one male bumble bee was tracked.

#### TRACK ANALYSIS

The radar tracks were recorded on time-lapse film of the radar screen and digitized, yielding position fixes at 3-s intervals along each flight path (examples in Fig. 2). The precision of the position fixes was limited to approximately  $\pm 7$  m in range and  $\pm 3$  m in azimuth (recent modifications to our signal capture system have improved the radar's range precision to  $\pm 3$  m). Outward and return trips were analysed separately. The tracks of some returning foragers showed that, atypically, they made several approach flights to the nest before eventually landing and returning to the colony. These tracks (13 in June and 22 in August) were not used in the analysis. Only the tracks of bees whose identity was confirmed by visual observation when arriving at, or departing from, the nest were subsequently plotted for analysis (Fig. 3). Where the time gap between two successive position fixes exceeded 60 s, a dotted

line was used to connect the points in Fig. 3 and calculations for distance and bearing were taken from the final end point of the track.

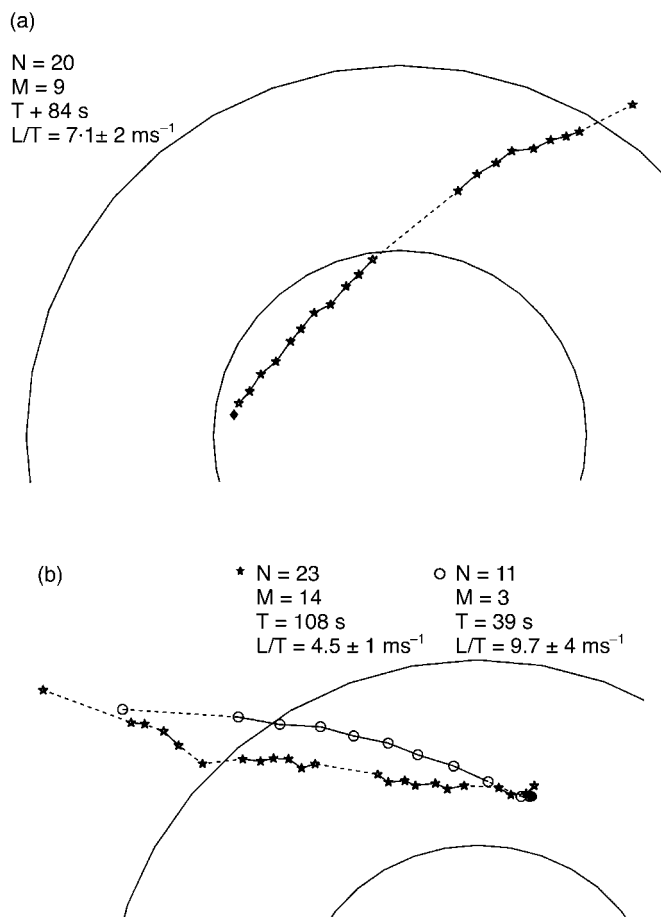
Each track was characterized by a set of parameters: the number of position fixes (N), the number of missing fixes (M), the track duration (T), the bearing of the track end point from the nest (B), the straight line distance (D) between the nest and the end point, the straight line distance (S) between the start point (which did not necessarily correspond exactly to the nest position) and the end point, and the length (L) along the track from start to end, found by summing the individual interfix segments. The ratio S/L provided a measure of the straightness of the track (Bell 1991) and L/T gave the average ground speed of the bee. Means are presented with ( $\pm$ ) their standard errors.

The radial distribution of forage from the nests was determined by measuring the distance from the nest to the nearest and most distant boundary points of identified forage plots. These distances are shown schematically in Fig. 4, together with the D-values of outward tracks. Since the end points of outward tracks did not necessarily correspond to the bee's destination (e.g. when bees flew beyond the radar horizon), whenever possible we inferred the foraging sites of tracked bees from the pollen they had collected.

## Results

#### EFFECTS OF TRANSPONDER ATTACHMENT

In May, before the full radar tracking trials began, we compared the flight performance of a few bumble bees before and after attachment of a transponder. Results from this preliminary study suggested that foraging was not adversely affected by the transponder, although sample sizes (number of bees) were too small to perform meaningful statistical tests. Three bees individually collected nectar loads weighing 110 mg, 86 mg and 129 mg before transponder attachment and the same three bees collected nectar loads weighing 84 mg, 99 mg and 120 mg, respectively, with the transponder attached, suggesting little difference in nectar collection. However, a total of 22 foraging trips by five bees with transponders lasted on average  $22.9 \pm 5.6$  min, while 27 trips made by the same bees before transponder attachment lasted on average  $12.8 \pm 2.5$  min, suggesting a difference in flight duration. In the full radar tracking experiment (excluding bees staying out overnight), 19 bees fitted with transponders spent 2.8–359.0 min (number of trips = 56) away from the nest, falling within the range of trip durations for all the bees foraging without transponders (1.2–416.1 min, number of trips = 722). The 56 trips made by these 19 bees whilst fitted with transponders lasted on average  $83.8 \pm 8.5$  min; 145 trips made by the



**Fig. 2.** Examples of bumble bee flights tracked by harmonic radar showing position fixes (★, ○), with dotted lines joining gaps caused by missing fixes (gaps all lasted < 60 s). (a) Bee Y18 headed north-east from the nest, on 8 June; (b) bee B23 headed north-west from the nest (★) on 31 July and returned (○) > 2 h later. See text for parameter description. Range rings are 200 m apart.

same bees before transponder attachment lasted an average of  $56.5 \pm 4.4$  min. For each bee the mean durations of forage trips before and after transponder attachment were calculated, although these were unavoidably based on varying numbers of trips. To compare flight durations with and without transponders, the resulting means were transformed [ $y = \log(x + 1)$ ] and analysed using a paired *t*-test:  $t = 3.41$ , d.f. = 18,  $P = 0.003$  (means on log scale: without transponder =  $1.62 \pm 0.04$ , with transponder =  $1.89 \pm 0.08$ ).

We scored the presence of pollen loads on 18 bees performing trips before and after transponder attachment: 10 did not collect pollen either before or after, four collected pollen before and after, and four collected pollen before but not after attachment of the transponder.

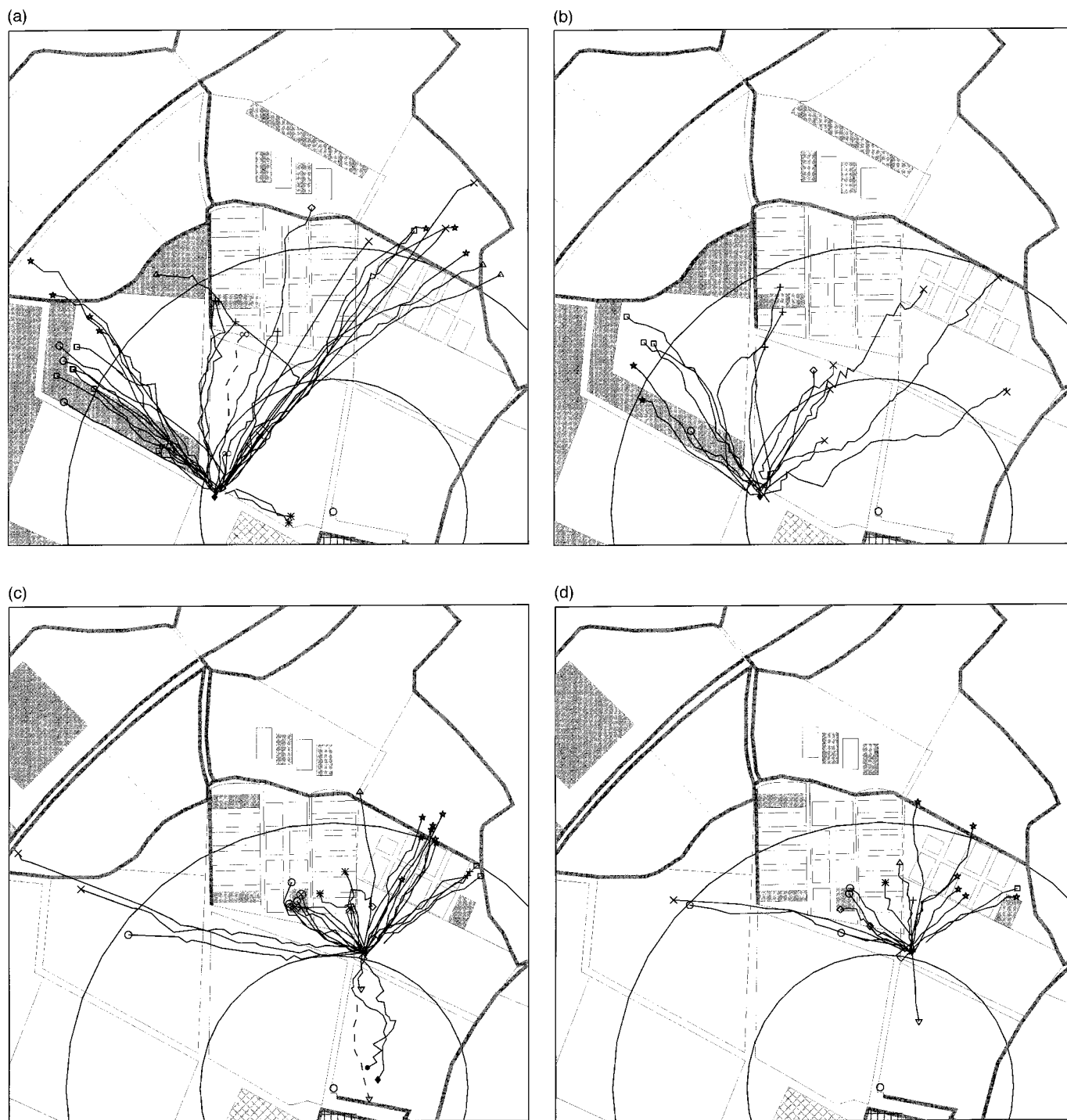
#### THE TRACKS

A total of 65 outward (35 in June and 30 in August) and 34 return (16 in June and 18 in August) tracks,

made by 21 different bees (nine in June and 12 in August) were plotted. Individual bees (denoted by different symbols in Fig. 3) produced from one to nine tracks (Table 1). Outward tracks ended when a bee landed in a patch of forage or flew over the radar's horizon (Fig. 3a,c). Return tracks were generally shorter than outward tracks (Fig. 3b,d), and some returning bees were not detected by the radar. The presence of hedges, combined with undulations in crop height and the terrain, meant that both outward and return tracks of individual foragers were not necessarily complete. Occasionally bees may have flown above the vertical coverage of the radar (about 6–7 m high).

#### DISTANCE

The mean *D* (maximum distance from the nest) of outward tracks was  $339 \pm 26.2$  m ( $n = 35$ ) with a range of 96–631 m in June (Fig. 3a), and  $201 \pm 18.7$  m ( $n = 30$ ) with a range of 70–556 m in August (Fig. 3c). Return tracks were shorter than



**Fig. 3.** Radar tracks of bees flying away from or returning to a colony. Shaded areas in the arena are described in Fig. 1. Range rings are at 200 and 400 m from the radar. Each symbol denotes an individual bee. Tracks have been joined where missing points occurred for less than 60 s. June: (a) 35 outward and (b) 16 return tracks; made by nine bees identified as follows: G30 (X), Y35 (○), R8 (+), R33 (☆), G22 (□), G20 (◇), Y18 (△), Y7 (▽), Y34 (\*). R8 (normally +) flew out on one trip (∞), stopped for 5 min 54 s and then continued. The continuation is plotted as - - - ∞ and is counted as one track. August: (c) 30 outward and (d) 18 return tracks; made by 12 bees identified as follows: B23 (X), B72 (○), B26 (+), G41 (☆), B60 (□), B71 (◇), B83 (△), B47 (▽), G37 (\*), G39 (⊗), G21 (◆), W30 (●). B47 flew out (▽), stopped for 18 min 36 s and then continued. The continuation is plotted as - - - ▽ and is counted as one track.

outward tracks, with a mean  $D$  of  $285 \pm 24.7$  m ( $n = 16$ ) and a range of 133–501 m in June (Fig. 3b) and  $163 \pm 19.8$  m ( $n = 18$ ) with a range of 75–376 m in August (Fig. 3d).

Outward tracks were often to points further than the nearest forage. In June, 28 out of 35 outward tracks ended over 250 m from the nest, despite the presence of flowering rape only 42 m away (Fig. 4a). In August, 15 out of 30 tracks ended over 200 m away despite a patch of flowering lupins at 108 m from the nest (Fig. 4b). Of the 12 tracks ending 200–250 m from the nest, 10 ended at the radar horizon formed by hedges, so the bees may have flown beyond this point, and the other two (to the south) were probably obscured from view by 'clutter' at the centre of the radar screen.

#### DESTINATIONS

Final fixes of outward tracks were categorized as positioned (a) on a forage patch, (b) less than 20 m from a forage patch, or (c) not on or near a forage patch (Fig. 4). In June (Fig. 4a), 13 out of 35 outward tracks ended at, or < 20 m from, a forage patch: either oilseed rape (42–396 m away) or spring beans (292–323 m away). No bees were tracked to the winter bean plot (303–473 m from the nest). Thirteen of the outward tracks ended at, over or < 20 m from a radar horizon formed by a hedge. Information from two of these bees, on their return, confirmed that they had foraged on or beyond the hedge: Y18 carried corbicular pollen from Rosaceae and lupins, and G30 returned after one trip with a red horse chestnut flower *Aesculus hippocastanum* L. draped over the transponder, indicating that she had probably visited the horse chestnut trees in the gardens beyond the north-east hedge. Two tracks were truncated because they were obscured from the radar by buildings. Seven tracks ended in no obvious forage patch. Three of these were by G30 which, on other trips, was tracked beyond the hedge. It is likely that the bee was flying over the hedge on all trips, but she flew out of vertical range on the three foreshortened tracks. R8 also made three tracks ending in no known forage. She may have flown to wild flowers on the field margins, although on one of these trips she departed from the colony carrying a dead larva and returned very quickly and was therefore not foraging on this occasion.

In August (Fig. 4b), seven of the 30 outward tracks ended at, or < 20 m from, the lupin patch closest to the nest (108–152 m away). A body hair swab from one of these bees (B71) contained two lupin grains. However, swabs from two other bees tracked to the lupins (B72 and G39) contained 1–5 sunflower pollen grains, while B71 and G37 (also tracked to lupins) returned from single trips with

unidentifiable cream-coloured pollen loads, suggesting that these bees may have flown beyond the lupins, untracked. No bees were tracked to the forage mixture (135–185 m from the nest), the sunflowers (179–256 m from the nest) or the more distant patch of lupins (278–343 m from the nest). Fourteen tracks ended at, over or < 20 m from a hedge. Of these tracked bees, one (B83) returned with bramble pollen loads and B23 had bramble grains on her body hair, also suggesting that they were foraging in a hedge. Three tracks went south towards the radar but were then obscured, and six ended in no obvious forage patch.

#### FLIGHT DIRECTION

Most bees tracked for more than one trip ( $n = 14$ ) were constant to direction on successive outward journeys (Table 1). The directional range was < 25° for nine bees on all trips. Four bees (G22 and Y18 in June and B71 and B72 in August) showed directional constancy on all but one trip. One bee (R33) made several trips in each of two different directions (Fig. 5): she made four outward trips to the north-west (range = 4.0°) and the last three trips were to the north-east (range = 7.6°). In between these different trip directions she was tracked, during one foraging trip, making an unusual flight from north-west of the nest to north-east (Fig. 5), possibly searching for a new foraging area.

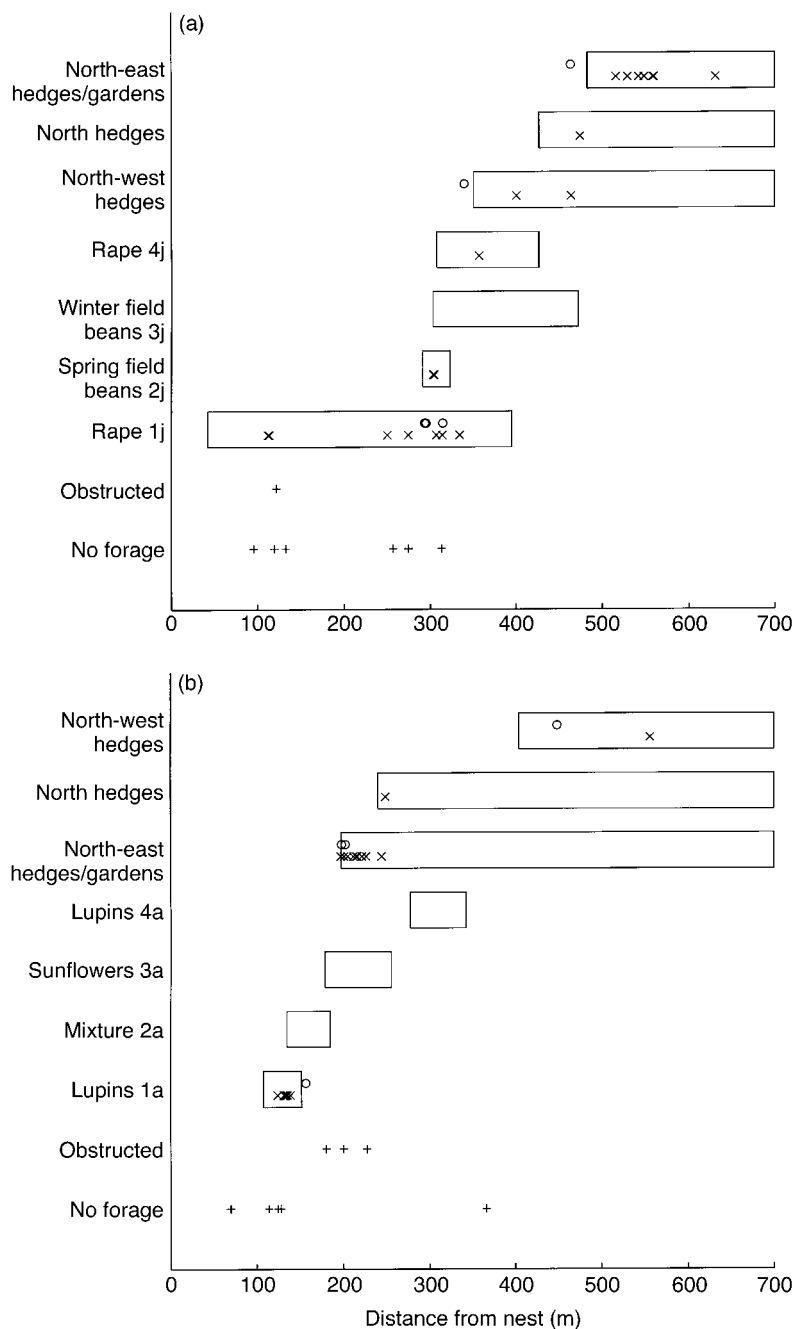
In June, when the radar coverage to the south of the nest was obstructed by buildings and hedges, only those bees seen to depart on foraging flights to the north of the nest were selected for transponder attachment and subsequent tracking, and 94% of the tracks ( $n = 35$ ) were to the north (Fig. 3a). In August, when a new site was chosen for the nest, radar coverage extended in all directions and bees were selected at random. Despite this, 90% of the outward tracks ( $n = 30$ ) were also directed to the north of the nest (Fig. 3c). The open side of the cage was towards the north in June and towards the south in August, and was observed not to influence departure bearings.

#### STRAIGHTNESS OF TRACKS

Most outward and return tracks were fairly straight (Fig. 6) and fast, with ground speeds ranging from  $3.0 \text{ m s}^{-1}$  to  $15.7 \text{ m s}^{-1}$  ( $n = 100$ ) in a variety of wind conditions. Outward tracks had a mean straightness ratio ( $S/L$ ) of  $0.95 \pm 0.01$  ( $n = 35$ ) for June and  $0.92 \pm 0.02$  ( $n = 30$ ) for August, with a range of 0.42–1.00. Return tracks had a mean ratio of  $0.92 \pm 0.01$  ( $n = 16$ ) in June and  $0.93 \pm 0.02$  ( $n = 18$ ) in August, with a range of 0.67–1.00.

Outward tracks in June (Fig. 6a) had an outlier with a straightness ratio of 0.69: Y18 ( $\Delta$ ) turned





**Fig. 4.** Collation of forage distribution and outward track end points in relation to the nest in (a) June and (b) August. Blocks define the range (from the nest) over which a particular forage type was available (see Fig. 1). Points denote the nest-to-end distance, D, and the end destination of each outward track (June:  $n = 35$ , August:  $n = 30$ ): tracks ended on a forage patch (X), less than 20 m from a forage patch (O), on no known forage patch or because of obstruction by the radar (+). Tracks ending on and beyond hedges are grouped together. Note that some points occur at the same position so are overlaid.

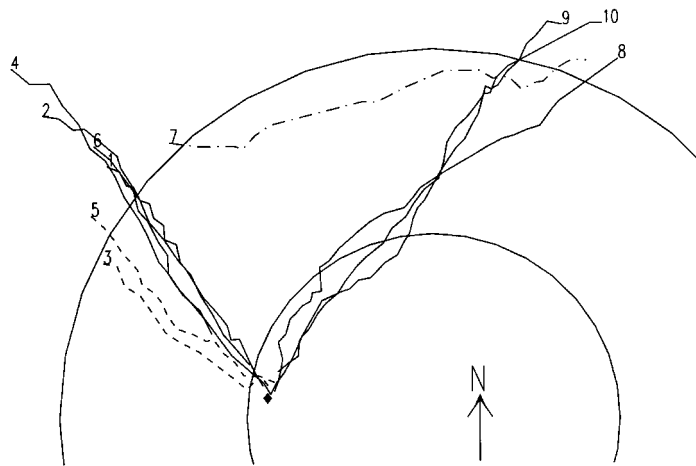
away from the usual route and veered in the direction of a rape plot to the north-west (Fig. 3a). Outward tracks in August (Fig. 6b) had two outliers: B71 ( $\diamond$ ) deviated from the usual route to lupins, making a looping track with a straightness ratio of 0.42, while W30 ( $\bullet$ ), the only male to be tracked, performed a zigzag track with a straightness ratio of 0.69 (Fig. 3b).

## Discussion

Bees fitted with transponders were seen to take off from the nest, to fly normally, and collect nectar weighing approximately 50% of their body weight. However, on average they spent more time away from the nest on foraging trips than those without transponders, perhaps because the transponder

**Table 1.** Summary information for individually tracked bees. Outward bearings are taken from the nest to the track end point. In most cases, all the tracks by one bee were less than 25° apart. Where one track was in a different direction, the angular difference between this track and a mean direction of the other tracks was calculated. Locations are marked on Fig. 1

Bee	Track dates	No. trips with transponder	No. of out tracks	No. of return tracks	Angular difference (°) between bearings of outward tracks < 25° part (no. tracks)	Angular separation of outward tracks > 25° from others (no. tracks)	Usual destination (no. outward tracks to that destination)
<b>Colony 1</b>							
Y35	11–12/6	3	3	1	11·9 (3)		Rape, 1j (3)
G22	14–16/6	7	7	3	9·8 (6)	88·6 (1)	Rape, 1j (6)
Y7	12/6	1	1	0	–		Rape, 1j (1)
R8	12–14/6	5	5	3	20·5 (5)		Beans, 2j (2) and small plots (3)
R33	12–16/6	7	7	2	7·6 (3) to north-west 4·0 (4) to north-east		North-west hedges (3) and north-east hedges (4)
G20	15/6	1	1	1	–		North hedge (1)
G30	9–12/6	9	6	6	9·6 (6)		North-east hedges (3)
Y18	8/6	3	3	0	3·1 (2)	66·4 (1)	North-east hedges (2)
Y34	14/6	2	2	0	5·1 (2)		South, out of view (2)
<b>Colony 2</b>							
B72	1–2/8	5	5	4	12·6 (4)	39·2 (1)	Lupins, 1a (4)
G39	5/8	1	1	0	–		Lupins, 1a (1)
B71	6/8	3	3	2	2·1 (2)	67·6 (1)	Lupins, 1a (2) and small plots (1)
G37	8/8	3	3	1	23·7 (3)		Small plots (3)
B23	31/7	2	2	1	3·5 (2)		North-west hedges (2)
B83	6/8	1	1	1	–		North hedges (1)
B26	3/8	3	2	1	0·7 (2)		North-east hedges (2)
G41	4–5/8	8	8	6	10·0 (8)		North-east hedges (7)
B60	4–5/8	2	2	1	4·5 (2)		North-east hedges (2)
B47	8/8	1	1	1	–		South, out of view (1)
G21	9/8	1	1	0	–		South, out of view (1)
W30	9/8	1	1	0	–		South, out of view (1)



**Fig. 5.** Series of tracks performed by bee R33 from 12 to 16 June. Range rings are 200 m apart. Outward tracks (—) and return tracks (---) are numbered chronologically. Track 7 (bee flying towards the north-east) was seen during a trip when the outward and return tracks were not recorded, on 15 June.

impeded the bees' access to certain flowers, slowing down their flower handling time and rate of pollen and/or nectar collection; one forager returned with a horse chestnut flower impaled on the transponder. However, it seems safe to assume that the actual foraging flight paths were not significantly perturbed by the transponders.

Because most bees flew close to the ground (*c.* 1–3 m in height) parts of their tracks sometimes fell below the local radar horizon that was created by tall crops, hedges and ground undulations, and when bees passed over hedges at the farm boundary their precise destinations often remained uncertain. Effects of this type may account for the relatively low number of return tracks quantified: the bees may have flown back at different altitudes to those used on their outward flights. In spite of incomplete coverage, our results provide a novel picture of the large-scale foraging strategies of two *B. terrestris* colonies operating in a patchy arable landscape.

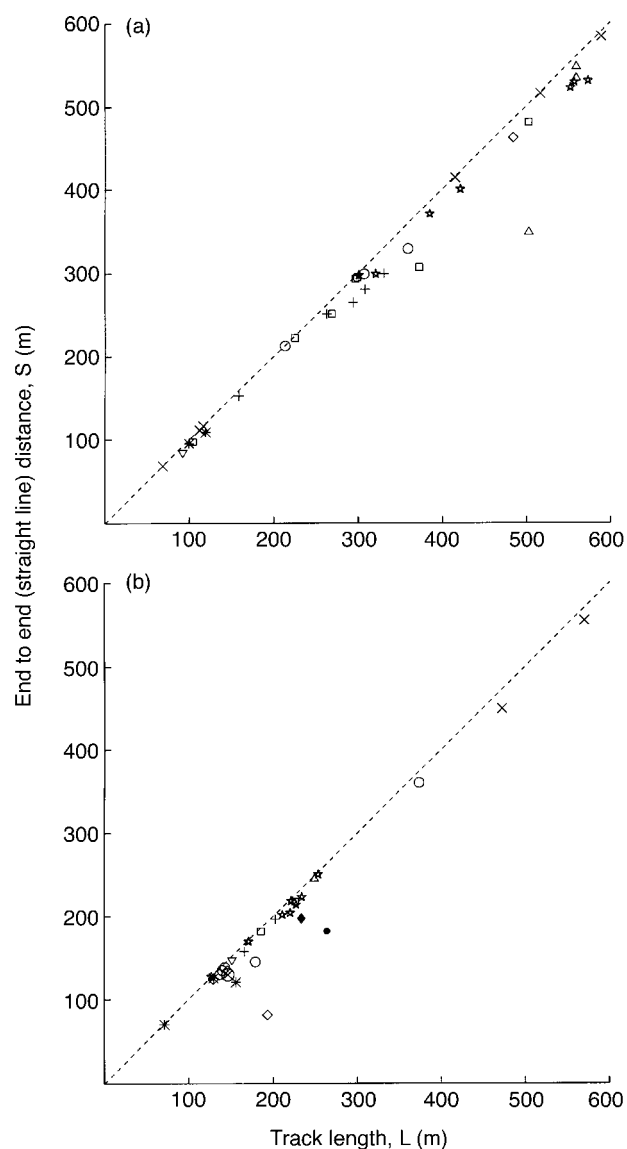
#### FORAGING RANGE

Most bees flew over 200 m from the nest to forage on a regular basis, a result which conflicts with the widely held view that bumble bees forage close to their nests. Although food resources were patchily distributed in our arable landscape, and reward levels were not quantified, there were nectar and pollen sources closer to the nest than 200 m, e.g. rape (in June), sunflowers and phacelia (in August), which were being visited by bumble bees. However, these were largely unvisited by the tracked bees. Many bees flew to hedges and pollen analysis suggested several flew beyond them to feed.

Arguments based on energetics and bumble bees' lack of organized recruitment are usually given to

support the hypothesis that bumble bees forage close to the nest (Heinrich 1979; Visscher & Seeley 1982). If a bee is foraging 'optimally' to maximize rates of energy return and the forage is evenly distributed, it has been assumed that she will forage close to the nest (although see Dukas & Edelstein-Keshet 1998). Heinrich (1979) stated that the extra energy consumed when bees fly long distances is likely to be negligible, and it is more likely that time is the constraining factor: bees flying shorter distances can spend more time collecting nectar and maximize energy returns to the nest. Visscher & Seeley (1982) suggest that bumble bees may have to compromise between energetically inexpensive short range searches in which they are not likely to find good forage patches, and costly, long searches in which good finds are more probable. This is not likely to be the case for honey bees, where long-range searches by a few bees may be energetically efficient for the hive as a whole, because many nest mates can be recruited to exploit any high-value finds (Visscher & Seeley 1982).

However, there is also a theoretical argument that suggests that when reward levels in the landscape are meagre, the net energy return to the nest may not be compromised if bumble bees forage further from the nest (J. E. Cresswell, unpublished data). If this is so, then because the area available to search increases with distance from the nest, the bees may also have more choice at larger distances. There may also be reasons for distant foraging that are quite unconnected with energy efficiency. Quality of food choice may be more important than quantity, for example the nutritional value of pollen is likely to vary between plant species (Schmidt *et al.* 1995). Also, distant foraging may reduce the incidence of predators and parasitoids close to the nest, and



**Fig. 6.** Relationship between overall track lengths,  $L$  (m), and the straight line distances between start and end point,  $S$  (m), for outward tracks made in (a) June and (b) August. Symbols denote different bees (see Fig. 3). Dotted line denotes  $L/S = 1$ .

reduce competition with nest mates for forage (Dramstad 1996; Dukas & Edelstein-Keshet 1998). Most of our bees flew further than expected given the distribution of forage patches. This result tends to support Dramstad's views, and implies that Cresswell's model and Dukas & Edelstein-Keshet's models need to be evaluated fully. Whether bumble bees regularly fly over distances of several kilometres, as honey bees do, remains to be determined.

The radius of the foraging area for honey bee colonies has been shown to change with respect to the distribution of resources (Waddington *et al.* 1994) and colony status (Schneider & McNally 1993). In our bumble bee study, the distribution of forage at different distances from the nest varied between the June and August trials. There were more patches of forage close to the nest in August

than in June (although nectar and pollen were not quantified) and, generally, track lengths were shorter. The difficulty of studying movement at a landscape scale is that conditions are not controllable, for example the forage patches in this study were irregularly spaced and sized, and so inferences had to be made with caution. More detailed measurements of forage quality and quantity on a landscape scale are required if the dynamics of foraging distance are to be investigated further.

#### FORAGER CONSTANCY

One advantage of radar tracking over pollen analysis or mark-re-observation is the ability to consider the bees' whole landscape in one study: the focal nest, the actual areas foraged and the relationship

between them. Individual bees were very constant to flight direction and distance over successive days, presumably avoiding the energetic costs and risks of searching for different sites when they had found a lucrative patch of forage. There was little evidence that patch preference on this scale was weakened overnight, as suggested by Keasar *et al.* (1996), who performed their experiments in a flight room. Changes did occur, however, and R33 provided an example of a bee switching from one foraging site to another over 3 days: having been constant to the north-west hedges, she then made a flight between forage areas (Fig. 5), and was subsequently constant to forage at or over the north-east hedges. To examine how bumble bees decide when to change foraging sites, particularly in a patchy landscape (Nonacs & Soriano 1998), quantification of the spatial and temporal changes in resource levels on a landscape scale is required.

The bees from the second colony showed a strong directional bias to the north. This is most likely due to the spatial distribution of forage patches (Fig. 1): there was no evidence that experienced foragers were affected by wind direction once they had found a foraging site.

The straightness of the tracks indicates that the bumble bees were not searching for food *en route*, and their directions of displacement showed that they were flying with a knowledge of their destinations. The navigational methods that they may use to do this are discussed elsewhere (Riley *et al.*, 1999), but the characteristic 'bee-lines' described here demonstrate route constancy and illustrate the clear difference between 'in transit' flight to and from forage patches and 'foraging flight' between plants (Dramstad 1996). The single drone track was less straight than a typical forager track, but as this drone was on his first flight from the nest he would not be expected to navigate competently and an exploratory, meandering path might be expected. We are currently investigating the 'learning' phase of flight in naive foragers (J. L. Osborne, unpublished data).

#### POLLINATION AND BEE CONSERVATION

Despite individual bees remaining constant to a profitable source of forage, bumble bees need to track the spatial and temporal changes in food resources over time. To accomplish this effectively, each colony must be familiar with a large area around the nest and each bee must be prepared to travel long distances for food. Understanding the spatial relationship between foraging areas and the nest sites of bees is important for the management of wild and domesticated bees as pollinators of both crops and wild flowers.

Farmers growing crops that require or benefit from bee pollination, such as field beans and orchard crops, need to consider whether their land is likely to support strong populations of appropriate bees. For example they may wish to know if there are appropriate uncultivated areas where bees can nest within flying distance of the crops, and what other forage in the area is likely to compete with the crop for bees. Also, if farmers intend to bring colonies of bees onto the crops to boost pollination, they will want to know where they should be sited to encourage the bees to visit their crops. Knowledge of the distances over which bees will travel from their colonies to forage would clearly help when making decisions of this sort.

Bee constancy and the dynamics of bee movement play a vital role in gene flow associated with hybrid seed production and the introduction of genetically modified crops. There is growing interest in modelling the potential spread of pollen from genetically modified crops into conventional crops and wild relatives (Raybould & Gray 1993; Scheffler, Parkinson & Dale 1993), and a basic understanding of bee movement patterns will underlie such models for bee-pollinated species.

Such movement patterns also affect gene flow and the survival of bee-pollinated wild flower species, particularly in fragmented landscapes (Westerbergh & Saura 1994; Kearns, Inouye & Waser 1998) where a plant population may become inviable if bees do not transport pollen between widely separated plants.

We also need studies of bee foraging ranges to predict the minimum required area to conserve pollinators (Bronstein 1995). For example, it may not be necessary to provide all the bees' requirements in one place as long as they are provided within commuting distance of each other (Westrich 1996). There is very little information on the population dynamics of bumble bees in the landscape and an understanding of foraging range could help us to design population studies on an appropriate scale.

The results of this study illustrate the importance of studying bee movement on a landscape scale, but further investigations specifically examining the spatial and temporal dynamics of forage quantity and quality would help us to understand when and how bumble bees make particular decisions with regard to large-scale foraging strategy.

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