Bumblebee flight distances in relation to the forage landscape

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Summary

1. Foraging range is a key aspect of the ecology of 'central place foragers'. Estimating how far bees fly under different circumstances is essential for predicting colony success, and for estimating bee-mediated gene flow between plant populations. It is likely to be strongly influenced by forage distribution, something that is hard to quantify in all but the simplest landscapes; and theories of foraging distance tend to assume a homogeneous forage distribution.

2. We quantified the distribution of bumblebee *Bombus terrestris* L. foragers away from experimentally positioned colonies, in an agricultural landscape, using two methods. We mass-marked foragers as they left the colony, and analysed pollen from foragers returning to the colonies. The data were set within the context of the 'forage landscape': a map of the spatial distribution of forage as determined from remote-sensed data. To our knowledge, this is the first time that empirical data on foraging distances and forage availability, at this resolution and scale, have been collected and combined for bumblebees.

3. The bees foraged at least 1·5 km from their colonies, and the proportion of foragers flying to one field declined, approximately linearly, with radial distance. In this landscape there was great variation in forage availability within 500 m of colonies but little variation beyond 1 km, regardless of colony location.

4. The scale of *B. terrestris* foraging was large enough to buffer against effects of forage patch and flowering crop heterogeneity, but bee species with shorter foraging ranges may experience highly variable colony success according to location.

Key-words: borage, foraging range, mass marking experiment, pollen analysis.

Introduction

Bumblebees have been widely used as model organisms for studying foraging economics and behavioural strategies (Heinrich 1979; Pyke 1984; Goulson 1999). However a key aspect of their foraging behaviour, their foraging range, remains poorly understood. Estimating how far bumblebees fly from their colonies to forage under different circumstances is essential for understanding the spatial dynamics of forage resource use (Bronstein 1995; Osborne *et al*. 1999; Walther-Hellwig & Frankl 2000) and the potential for pollen transport between patches or populations of plants (Schulke & Waser

2001). Resource usage is likely to affect the success of the colonies (Schmid-Hempel & Schmid-Hempel 1998; Goulson *et al*. 2002; Williams & Kremen 2007), so if we understand how bees respond to the spatial relationship between nest and food resources, we can make predictions about colony survival and distribution (Nakamura & Toquenaga 2002; Williams & Kremen 2007).

Theoretical models, predicting forager distributions for 'Central Place Foragers' (deVries & Biesmeijer 1998; Dukas & Edelstein-Keshet 1998; Cresswell, Osborne & Goulson 2000), differ between those for species considered 'social foragers', e.g. honeybees that communicate information about resource location to nest mates, and those relying on individual exploration to find resources, e.g. bumblebees. Testing the models for

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honeybees is feasible, because forager distributions can be documented by interpreting information from the dances performed by bees returning to the colony (Visscher & Seeley 1982; Steffan-Dewenter & Kuhn 2003). This technique cannot be used for bumblebees as they do not appear to communicate information relating to the location of forage to their nestmates (Dornhaus & Chittka 1999, 2004). Therefore, although models exist (Cresswell *et al.* 2000), there is limited empirical information on the distribution of bumblebee foragers away from colonies.

There are estimates of the range over which bumblebees fly to forage made using mark–reobservation techniques (Dramstad 1996; Walther-Hellwig & Frankl 2000), radar tracking (Osborne *et al.* 1999), genetic analysis (Darvill, Knight & Goulson 2004; Knight *et al.* 2005) or using statistical correlations (Westphal, Steffan-Dewenter & Tscharntke 2006). Greenleaf *et al.* (2007) provide a comprehensive review of foraging range studies for all bees, and predict a strong relationship between maximum foraging range and body size; but from all these studies it is not possible to determine the relationship between bee density (per unit area of forage) and radial distance from the colony because of the limited number of bees sampled, lack of quantification of the forage distribution, or differences in sampling effort with distance from the colonies. If the method for recording bee distributions relies on searching for bees at different distances from the nest (e.g. if they are marked), then the area of the annulus to be searched (area of a ring centred on the nest) increases with the square of the radial distance from the nest. So, even if the same number of bees fly to each distance from a colony, the density of bees foraging at each distance will decline with the reciprocal of the square of radial distance, i.e. the bees will be spread more thinly, and thus be more difficult to find (Schaffer 1996). To allow for this 'annulus effect', the area of forage at the different distances needs to be taken into account.

The aim of our experiment was to quantify the spatial distribution of *B. terrestris* nectar and pollen foragers away from experimental colonies in an arable landscape, using a novel mass-marking technique and pollen analysis (Martin *et al.* 2006); and relate this to the spatial distribution of habitats providing forage.

What shape would we expect the spatial distribution of bumblebee foragers away from a colony to take? Hypotheses based on energy and time budgets have been used to make predictions (Heinrich 1975, 1979; Goulson 2003) and to develop spatially explicit models (Dukas & Edelstein-Keshet 1998; Cresswell *et al.* 2000). Necessarily, such predictions are based on simplified assumptions of resource distribution and bee behaviour. If the distribution of forage patches (quantity and quality) is relatively homogeneous across the landscape, then optimal foraging theory predicts that bumblebees will have a higher probability of foraging close to the colony, thus reducing the energetic and time costs associated with travel (Heinrich 1979). In this scenario, we expect the absolute number of bees foraging in each annulus to decline with distance, and the density of bees on forage patches also to decline with distance in a steeply exponential fashion.

Field studies have shown that some bumblebee species (including *B. terrestris*) forage at least several hundred metres (Dramstad 1996; Osborne *et al.* 1999); and even kilometres from the nest (2·2 km in Kreyer *et al.* 2004). Walther-Hellwig & Frankl (2000) found 25% of resightings between 1500 and 1750 m from the colony. These studies do not necessarily conflict with the above prediction, because forage availability was not homogeneous at different distances from the colonies (although suitable forage was noted as being available near the colonies). One explanation for such long distance foraging is that the energy and time spent travelling to patches are not costly enough to restrict the distances travelled in proportion to the rewards gained during a foraging trip. *B. terrestris* fly at speeds of up to 15·7 km h^{-1} (Osborne *et al.* 1999; Riley *et al.* 1999), and flight uses approximately 1·2 kJ h^{-1} (Ellington, Machin & Casey 1990), so travelling considerable distances is possible within a few minutes and for little energetic cost. Dukas & Edelstein-Keshet (1998) have developed spatially explicit models to predict the optimal distribution of social food provisioners away from a colony, comparing three different foraging currencies (energy intake rate, efficiency and lifetime fitness) and they predict that the proportion of foragers going to different distances from the colony declines relatively slowly, regardless of currency in the model. Similarly, Cresswell *et al.* (2000) predict, using realistic parameters for time and energy expenditure, that if forage resources are meagre then bumblebees can forage profitably at rewarding flower patches > 4 km distant from their nest.

A different scenario would arise if worker behaviour results in an Ideal Free Distribution of foragers in the landscape (reviewed in Dukas & Edelstein-Keshet 1998; Goulson 2003). This predicts that foragers will distribute themselves evenly over the good forage available (assuming equivalent quantity and quality), regardless of distance from the colony. The result of such behaviour would be that the absolute number of foraging bees in each annulus actually increases with distance, as the density remains constant.

None of these scenarios take into account either the heterogeneity in the spatial distribution of forage (which is considered in our experiment) or behavioural parameters unrelated to energy/time budgets (but see Dukas & Edelstein-Keshet 1998). Such parameters include the likelihood that the bees will find patches of forage at some distance from the colony, the likelihood that they will stop to forage when they find a patch, the difference between nectar and pollen foragers (Peat & Goulson 2005), and the possibility that they may forage away from the colony to reduce competition, predation and parasitism pressure (Dramstad 1996; Dukas & Edelstein-Keshet 1998).

One difficulty in demonstrating the spatial distribution of bumblebees has been finding a technique to allow sufficient data collection at long distances from the colonies. We describe an experiment to examine the relationship between the distribution of *B. terrestris* and distance from the colony in an arable landscape using a mass-marking technique, and a novel forager trapping technique to analyse pollen being brought into the colony (Martin *et al.* 2006). The new equipment
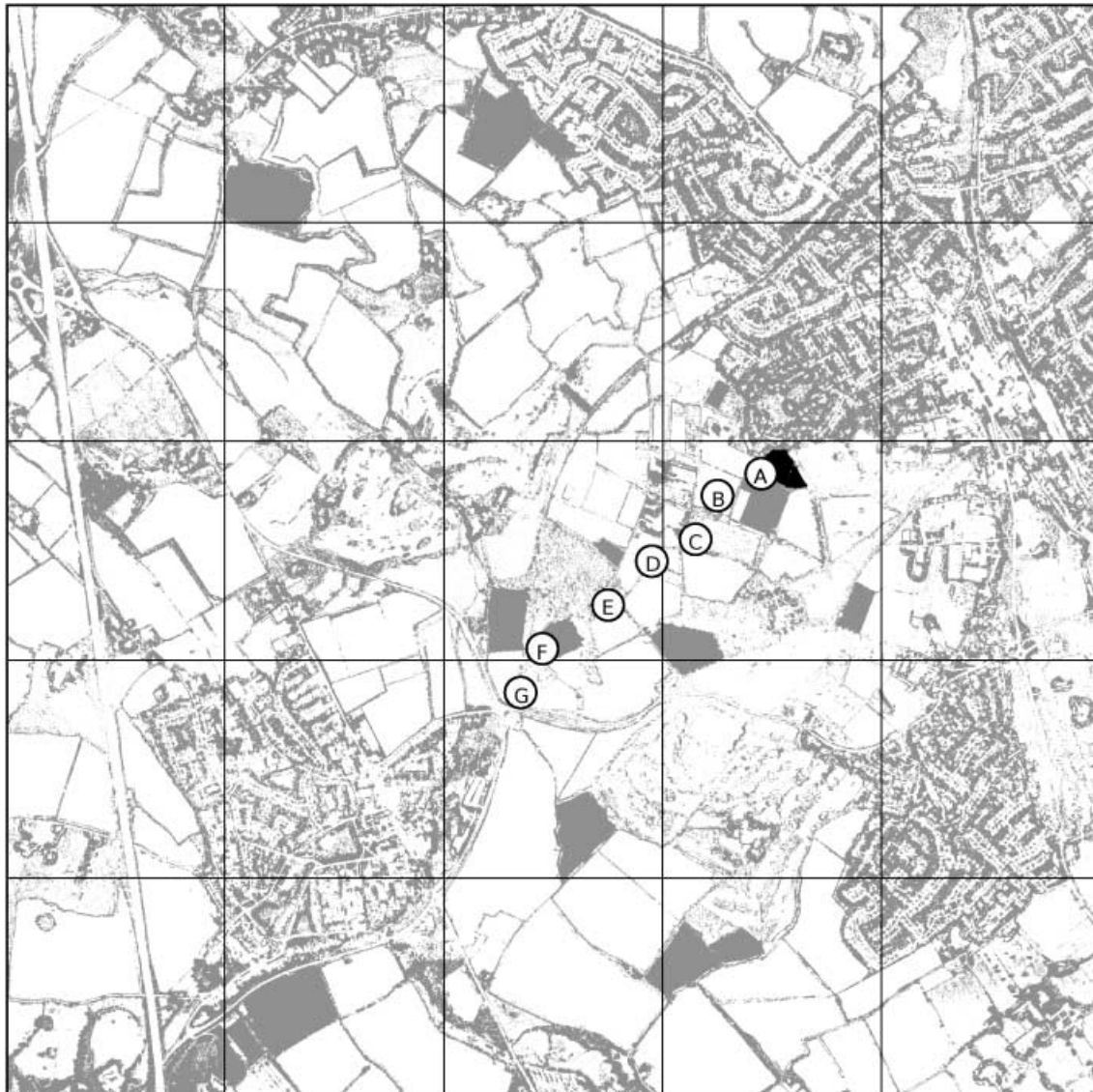
Fig. 1. Central 5 × 5 km area of classified landcover map (from satellite image) showing layout of experiment and forage available in surrounding landscape A–G = 7 sites on transect, each with four bumblebee colonies. Black area = field of borage. Grey pixels = habitat providing nectar and pollen during the experiment (spring-sown oilseed rape fields, field bean fields, hedgerows, gardens, ruderal and scrub). Gridlines = kilometre squares (UK National Grid reference of bottom left corner: TL1012). The classification, using ERDAS software, has not been smoothed, so features look 'speckled' which is a true reflection of the heterogeneity in the multispectral satellite image of the landscape.

allowed marking and re-observation of far more bees than have previously been examined, and collection of incoming pollen loads, giving two methods for estimating forager distribution for the same set of bumblebee colonies. We then set this within the context of all the forage available to the experimental colonies in the landscape.

Methods

STUDY AREA

The experiment was carried out on the Rothamsted estate (Hertfordshire, UK) comprising approximately 260 ha of arable farmland, and 60 ha of woodland. A 2-ha field of borage *Borago*

officinalis L. (cv Kings Gladiator) was sown on the north-east edge of the farm (Fig. 1), bordered on its northern edge by houses with gardens. Bumblebee colonies were arranged along a transect 1·5 km in length, originating at the borage field and running towards the south-west. A month earlier, Knight *et al*. (2005) used the same transect to estimate foraging range and nest density for four bumblebee species, including *B. terrestris*.

Borage was used as the target forage source because it provides copious nectar and pollen for bumblebees (Osborne 1994) and has a distinctive, cream coloured pollen grain, which is unlikely to be mistaken for another species. The habitat survey (Appendix S1) showed there was very little, if any, other borage growing in the surrounding landscape, except possibly a small number of plants in gardens, so it could be confidently assumed that foragers returning to the colony with borage pollen had been foraging on the sown field.

BUMBLEBEE COLONIES

Twenty-eight bumblebee *B. terrestris audax* colonies were reared (by Koppert BV, the Netherlands) using queens captured on and around Rothamsted Farm while they were searching for nest sites during Spring 2002. On 1 July, when the borage crop had begun to flower, four colonies (one small with < 50 workers, two medium with 50–100 workers and one large with > 100 workers) were placed at each of seven transect points, placed at approximately 250 m intervals along its length, and coinciding with field boundaries where wild bumblebee colonies could have established (Fig. 1). At each site the colonies (each in a small honeybee hive described in Martin *et al*. 2006) were placed 2 m apart, with their entrances facing into the field on whose boundary they were sited (Table 1). They were left in place for 10 days before beginning the experiment to allow the bees to settle and orientate.

Colonies were fitted with modular entrances (Martin *et al*. 2006), enabling us to trap foragers as they entered the hive, or automatically mark bees with coloured dye powder as they walked through the hive entrance. When not trapping or marking bees (i.e. most of the time), a standard entrance was fitted.

At the end of the experiment (2 August) colonies were collected after sunset and killed by freezing. The nest weight, nest volume and final number of workers were recorded.

TRAPPING OF INCOMING FORAGERS

On seven occasions (between 12 and 30 July) during borage flowering, foragers returning to the colonies were captured using the forager trap modules, so that pollen loads being brought into the colony could be sampled (Martin *et al*. 2006). The traps were placed in the hive entrances for 20 or 30 min, depending on forager activity, so that they caught about 20 foragers, and traps were placed on the colonies at all sites over a period of about 2 h. After narcotizing the bees in a trap with CO_2 for 30 s, the total number of bees, the number of bees carrying pollen loads and the colours of the pollen loads were recorded, and a sample of each colour load was taken for later microscopic identification. The foragers were then returned to their colony, within an hour of being caught.

OBSERVATION OF MARKED BEES

The dye dispenser modules allowed bees to be marked with site-specific colours as they left their colonies, and they were then observed foraging on the borage field. Seven different powder dye colours (Stirling Industrial Colours Ltd, Ciba Speciality Chemicals Ltd, London, UK) were used to distinguish between bees from the different sites. All four colonies at each site had the same colour dye, so marked bees could be identified to site but not to colony. Site A used violet, B red, C orange, D yellow, E green, F blue and G pink. The dispensers were fitted to the colonies for 2–3 days each week, during 4 weeks of flowering (normally starting on the day after the forager traps were used). They were fitted to the colonies the day before marked bee observations were to be made, so that all the foragers, including overnight absentees, were likely to be marked; and they were removed after 2–3 days.

While the dispensers were on the colony, observers searched for marked bees on the borage field by walking a 1 km 'strip' (20×50 m parallel lengths, each separated by *c*. 12 m) covering the whole field, at a speed of *c*. 10 m min^{-1}. Marked bees seen in a 1 m wide strip on one side of the observer were recorded. These walks were done over four 2-day periods when dispensers were in place (between 12 July

and 2 August), and the number of marked bees recorded was summed for all transects walked on each sampling occasion. Each sampling occasion was a morning or afternoon when two or three transect walks were carried out simultaneously (by different observers starting at different points). There were 11 sampling occasions, comprising a total of 31×1 km walks. All observations were performed in dry weather between 10.00 and 17.30 h when the temperature was above 15 °C.

THE 'FORAGE LANDSCAPE'

Remote-sensed data derived from the Ikonos satellite (Space Imaging Inc., Colorado, USA) and NERC compact airborne spectrographic imagery (CASI) air photography, both taken in June 2002, were used to create a high resolution map (1 pixel represents 2×2 m) of a 10×10 km area in Hertfordshire, centred on Rothamsted Research. Standard supervised classification of the georectified raw multispectral imagery was undertaken using Erdas Imagine (Erdas Software 2004, ERSI, UK). Ground truth data, for the training areas needed in the supervised classification, were collected using the NCC Phase 1 habitat survey technique (Nature Conservancy Council 1990), modified to make it relevant to bumblebee resource requirements by recording the species and number of flowering plants available to bees in each habitat. The methodology for the surveys and calculation of forage scores is described in Appendix S1. In summary, field surveys were undertaken in spring, early summer and late summer so that variation in the abundance of flowering plants could be monitored over time. The final classified map contained 25 land cover types and each was given a forage rank of 0–3 (Table S1) on the basis of flower density and the likely usage of the plant families present by *B. terrestri*s; summarized from comparative studies and reviews (Fussell & Corbet 1991; Fussell & Corbet 1992; Dramstad & Fry 1995; Carvell *et al*. 2001; Goulson *et al*. 2005; Benton 2006) (Table S2). The land cover types providing most forage during the experiment (forage rank = 2 or 3 equating to habitats with *at least* 250 flowers or flower spikes per 40 m^2 of good forage for bumblebee feeding, and usually substantially more: Appendix S1 in Supplementary material) were the borage field itself, spring oilseed rape *Brassica napus* L. fields, field bean *Vicia faba* L. fields, gardens, hedgerows, ruderal habitat and scrub. To put the results into the context of the overall 'forage landscape', the proportion of the classified landscape containing these land cover types, known to be particularly good for foraging bumblebees (grey in Fig. 1), was calculated by placing circles of increasing radii (by 250 m) centred on each colony site on to the map. This allowed us to build a picture of the 'forage landscape' available to each set of bumblebee colonies; and also to calculate the relative contribution of the borage field to the forage available in annuli at different distances from each colony.

ANALYSIS

Interpretation of the distribution of bees away from the colonies relies on the colonies at the different sites having similar foraging activity, and the efficiency of the dye dispensers being similar for all colonies (Martin *et al*. 2006). To confirm that foraging activity was similar, a two-way ANOVA was performed on the number of foragers caught in each trap ($\log_{10}(x + 1)$) to compare forager activity between sites and trapping occasion. To confirm whether colony performance at different sites could be assumed to be similar throughout the experiment, a one-way ANOVA was performed on the following $\log_{10}$ transformed variables: final number of workers collected in the colonies; final nest weight (g) and final estimated nest volume (cm^3).

Table 1. Details of colonies placed at each site on the transect (Fig. 1), with distance to centre of borage field, calculated borage%forage250 (covariate for percentage of 'forage landscape' occupied by the borage field) and average (± SE) parameters to compare nest activity. $n = 4$ for each site. Results of ANOVAS to compare colony performance between sites are presented (sampling occasion was included in the ANOVA for forager activity)

Site	Distance (m) to mid-borage field	Neighbouring boundary	borage%forage250 @ annular range	Average forager trap count/20 min^{-1}, $n = 28$	Average final no. workers collected	Average nest weight (g)	Average estimated nest vol (cm^3)
A	125	Fenceline, low vegetation, no hedge	24·8 @ 0–250 m	19·10 ± 2·69*	140·0 ± 32†	140·7 ± 28·4†	490 ± 227†
B	375	1–2 m hedge and trees	13·19 @ 250–500 m	16·11 ± 1·99	38·5 ± 11·4	115·5 ± 21·7	628 ± 156
C	625	Grass by cereal field, no hedge	6·85 @ 500–750 m	18·21 ± 1·71	82·3 ± 17·9	197·8 ± 18·4	787 ± 39
D	875	Fenceline with unmown grass	2·82 @ 750–1000 m	17·75 ± 2·09	34·8 ± 9·8	151·7 ± 21·0	649 ± 177
E	1125	Woodland edge	3·34 @ 1000–1250 m	8·25 ± 1·43	17·3 ± 1·5	105·8 ± 11·7	444 ± 82
F	1375	Woodland hedge	5·16 @ 1250–1500 m	14·21 ± 1·42	39·3 ± 12·8	129·5 ± 22·1	522 ± 98
G	1625	Tall hedge	3·83 @ 1500–1750 m	12·04 ± 1·64	28·8 ± 10·2	125·8 ± 16·6	646 ± 75
			F-values from ANOVA:	Occasion $F_{6,139} = 3·91$	$F_{6,25} = 4·80$	$F_{6,25} = 2·29$	$F_{6,25} = 1·12$
				Site $F_{6,139} = 3·90$	‡$F_{5,23} = 2·29$		
				O × S $F_{36,139} = 0·91$			
			Probability:	Occasion $P = 0·001$	$P = 0·004$	$P = 0·08$	$P = 0·39$
				Site $P = 0·001$	‡$P = 0·09$		
				O × S $P = 0·615$			

*$N = 20$ for site A because of vandalized colonies.

†$N = 2$ for site A because of vandalized colonies.

‡Without including site A where colonies were vandalized, and workers transferred to remaining colonies.

Generalized Linear Models (GLM), with binomial error structure and logit link (Genstat version 9, VSN, Hemel Hempstead), were used to test the effect of sampling occasion and distance (between borage field and colony site) on: (1) the number of pollen foragers as a proportion of total bees caught in forager traps, and (2) the number of pollen foragers returning with borage pollen loads as a proportion of the total number of pollen foragers caught in the forager traps (i.e. the proportion of pollen foragers reaching the target field).

A GLM, with Poisson error structure and log link, was used to explain the relationship between distance (between borage field and colony site) and the number of marked bees of each colour seen on the borage field on each sampling occasion. The number of marked bees leaving the colonies at each site (over a 10-min period) on each sampling occasion was included as a covariate, accounting for any differences in colony activity (including effects of vandalism at site A). With regard to dye dispenser efficiency, Martin *et al.* (2006) showed (for the same colonies) that the dye dispensers marked 87% of the bees leaving the nests, and there was no difference in their effectiveness between sites or sampling occasions. They showed there was a significant effect of colony position on the persistence of dye on the returning bees so 'persistence' (= average percentage of bees returning with a mark/average percentage of bees leaving with a mark per site per week) was used as a second covariate in the GLM, before adding distance. A variable describing the proportion of forage available that was borage at a given distance from the colony was also included to account for the fact that the colonies were placed at different sites, and therefore experienced the borage in different contexts, and the area available to search for forage increased with distance from the colony. This variable (borage%forage250) was calculated by estimating (from the classified landscape) the number of 2 m cells within a 250 m wide annulus, which contained habitat with good forage (borage, spring oilseed rape, field bean, hedgerows, gardens, scrub or ruderal vegetation) and the percentage of those that were borage. For each colony site, this variable was calculated for an annulus of the radius at which the borage field occurred, e.g. for site A it was calculated for a 0–250 m around this site, and for site B it was calculated for a 250–500 m annulus around site B (Table 1, Fig. 1).

Results

COLONY COMPARISONS

Bees from all colony sites along the transect foraged for both nectar and pollen on the borage field. Of the 28 colonies, two were vandalized at site A during the third week of the experiment, but many workers from these colonies joined the unvandalized colonies at this site (Table 1). The effect of this vandalism at site A on the marked bee counts (Fig. 2b) was taken into account by using colony activity as a covariate in the GLM (see below).

Counts of bees caught in the forager traps over different dates showed that the foraging activity levels were significantly different between sites (two-way ANOVA: effect of site: $F_{6,139} = 3.9$; $P = 0.001$) (Table 1; Fig. 2a). There were no significant differences between sites in the final number of workers collected in the colony ($F_{5,23} = 2.29$; $P = 0.09$ when site A removed), nest weight (g) after the colonies had been collected ($F_{6,25} = 2.29$; $P = 0.08$) or estimated nest volume (cm³; $F_{6,25} = 1.12$; $P = 0.39$) (Table 1).
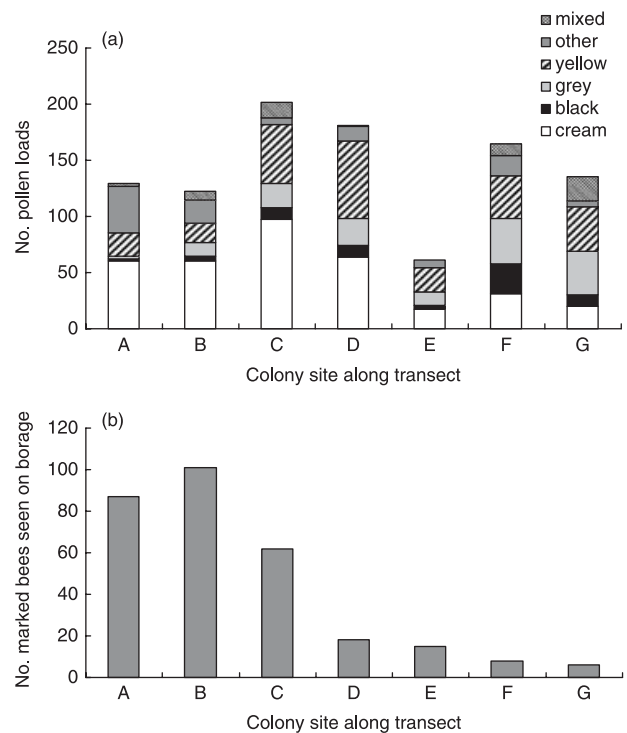

Fig. 2. Summary of samples over the whole experiment. (a) Total pollen loads collected at each colony site, separated by colour of load. Cream loads were 99% borage, yellow loads were primarily oilseed rape, *Brassica napus*; grey pollen was primarily bramble *Rubus* spp.; and black pollen was primarily poppy *Papaver rhoeas* L. (b) Total marked bees seen on borage, arriving from each colony site.

TRAPPING OF INCOMING FORAGERS

On all sampling occasions, bees returned to all colonies with pollen. The number of pollen collectors as a proportion of the number of bees caught did not vary with distance of the colony from the borage field ($F_{1,171} = 3.67$, $P > 0.05$), but varied significantly with sampling occasion ($F_{6,171} = 5.87$, $P < 0.001$).

Figure 2(a) shows the number of pollen foragers trapped at each site (all colonies) carrying different coloured pollen loads over the whole experiment. The cream coloured pollen was microscopically confirmed to be 99% borage. Bees at all sites returned with borage pollen. The nonborage pollen was a mixture of types: primarily oilseed rape and bramble *Rubus* spp. L. At site A, next to the borage field, an average of 62·9% of pollen foragers returned with borage pollen (represented as a proportion 0·63 on Fig. 3). At site G, 1·5 km from the borage field, an average of 16·9% of pollen foragers brought back borage pollen. The best fitting binomial GLM for the proportion of incoming pollen foragers with borage pollen loads per colony, included distance from the borage field ($F_{1,153} = 63.56$, $P < 0.001$, Fig. 3), and sampling occasion ($F_{6,153} = 7.56$, $P < 0.001$; the interaction was not significant; percentage deviance accounted for by this model was 41·6%). The average proportion of borage foragers returning to a colony was 14% for the first occasion, which was significantly
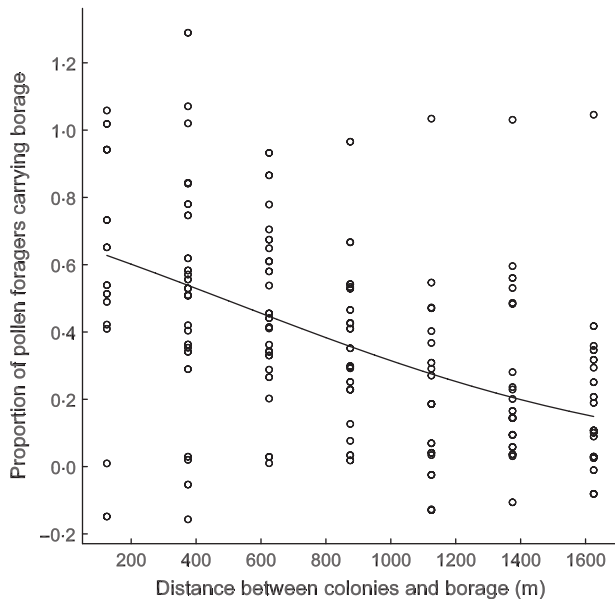
Fig. 3. Relationship between colony–borage distance and the proportion of pollen-foraging bees collecting borage pollen (converted to percentages in text). Fitted line is for the best GLM model (distance + sampling occasion). Points are back-transformed observed values, adjusted for the effect of sampling occasion.

Fig. 4. Relationship between colony–borage distance and the number of marked bees seen per sampling occasion on the borage field. Fitted line is for the best GLM model (distance + two covariates: colony activity level and borage%forage250). Points are back-transformed observed values, adjusted for the effect of the two covariates.
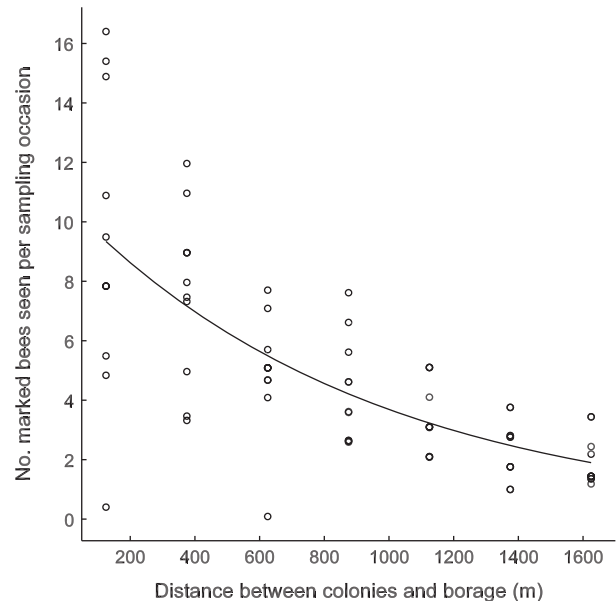
lower than for the other six occasions, when average proportions of borage foragers ranged from 31 to 46% (see Fig. 4 in Martin *et al.* 2006). At the range of distances tested, the negative relationship between distance and borage pollen foraging was approximately linear (Fig. 3).

OBSERVATION OF MARKED BEES

A total of 297 marked bees were seen foraging on the borage field on the 31 km walked over the 11 sampling occasions (Fig. 2b). The maximal GLM (Poisson, log link) for the number of marked bees found on the borage had terms fitted for three covariates (colony activity, dye persistence, borage%forage250) and distance, and interactions of the three covariates with distance. Dye persistence, and its interaction with distance, gave no significant change in deviance when dropped from the model. The other terms were all significant and retained in the model (percentage deviance accounted for by this model was 70·1%). So, having accounted for colony activity levels ($F_{1,71} = 12·85$, $P < 0·001$) and the relative area covered by the borage field compared with other forage (borage%forage250: $F_{1,71} = 93·93$, $P < 0·001$) there was still a significant negative effect of distance from the colony on the number of marked bees found on the borage ($F_{1,71} = 45·82$, $P < 0·001$: Fig. 4).

THE 'FORAGE LANDSCAPE'

The colonies at sites A–G experienced landscapes with differing proportions of suitable foraging habitat particularly close to the nests (Fig. 5). Bees at sites A and F had forage available on

most of the land within about 300 m of their nests; because site A was next to the borage field and site F was next to a field bean field. In contrast, bees at the other sites had forage available over 5–20% of the land within 300 m of their nests. Interestingly, Fig. 5 also shows that, if we consider the forage landscape available to bees within 1–3 km from their nest, colonies sited in different places all had similar prospects with 20–30% of land providing suitable forage within 1–3 km of each nest.

Discussion

The results of this experiment provide the first empirical demonstration of where bumblebees travel to forage, in the context of the spatial distribution of all the foraging habitats available to them in the landscape. *B. terrestris* travelled routinely to collect nectar and pollen from the field of borage at least 1·5 km away from their colonies, in a landscape providing forage resources at all distances (Fig. 5). Unfortunately, it was not possible to use a longer transect, to find the maximal foraging range. The model fitted to the results (Fig. 3) predicted that the percentage of borage pollen foragers would be close to zero (< 0·5%) for colonies positioned 4 km from the borage field.

One might have expected the colonies to perform differently from each other as they were placed in different locations but, although foraging activity differed between colonies (Table 1), the number of workers in the nonvandalized colonies at the end of the experiment and the weight of these colonies did not vary between sites (Table 1). This could be a reflection of the
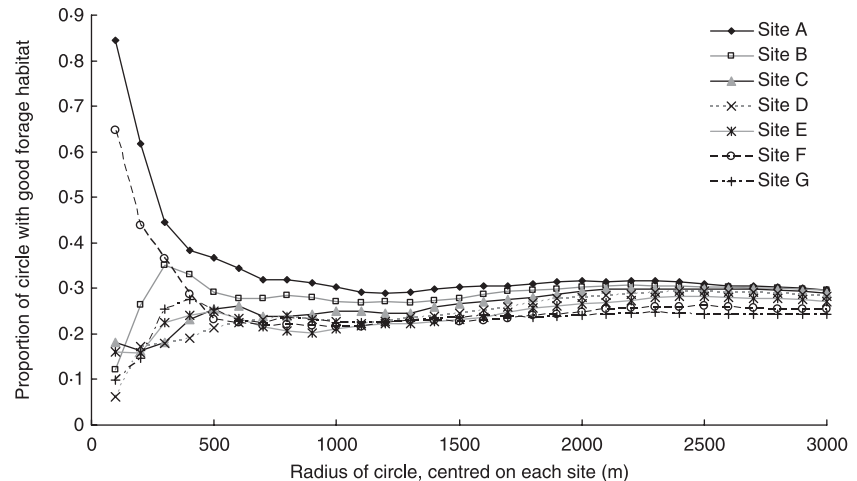
Fig. 5. Forage landscape for colonies at each site A–G, estimated by calculating the proportion of the landscape containing good forage habitats at different radial distances from each site (see text).

fact that each colony was able to provision from similar 'forage landscapes' (Fig. 5) at the scale of kilometres, although availability of forage habitats differed at the local scale. The borage field did represent a varying proportion of the forage available to each colony at the measured distances, and this was accounted for as a covariate in the marked bee analysis.

FORAGER DISTRIBUTIONS WITH DISTANCE

We used new equipment to gather two forms of data on forager distributions, and the results were mutually reinforcing. Trapping returning pollen foragers showed bees collected borage pollen at all distances, and the proportion declined with distance in an approximately linear fashion (Fig. 3). There was not a steep exponential decline, suggesting that the energetic or time costs of travelling over such distances were not prohibitive compared with the rewards gained (Heinrich 1979; Cresswell *et al.* 2000) for *B. terrestris* in this environment. Marked bees from all distances (0–1·5 km) were seen on the borage. Marked bees from all colony sites were seen on the borage and, for total numbers seen (Fig. 2b), the decline with distance was quite steep, but once colony activity, area surveyed and the contribution of borage to forage landscape were taken into account, the relationship between marked bee numbers and distance (Fig. 4) showed a shallow decline in forager density with radial distance. Both these relationships (Figs 3 and 4) are comparable with the prediction made by Dukas & Edelstein-Keshet (1998) for 'solitary' provisioners of a single nest site (i.e. not communicating with each other), when food parameters do not change with distance and direction from the nest, and rate of energy intake is maximized.

The distribution of foragers with distance may also be affected by the probability of bees finding the borage field in the first place, and the chances of stopping at it. If searching for food away from the nest, there is presumably a higher probability that they will find a patch close to the colony and stop there before exploring further afield. Reynolds *et al.* (2007) have mathematically characterized search strategies of individual honeybees, but there is little published information on the strategies used by bumblebees to search for food

resources in relation to their colony; and then which of those patches they choose to exploit.

THE EFFECT OF FORAGE LANDSCAPE ON FLIGHT DISTANCES

Borage is known to be highly rewarding because of its copious nectar and pollen, and it is highly visible so the field may have attracted more bees from longer distances than would have been the case for other large forage patches in the landscape. Colonies at site F had plentiful local forage (Fig. 5), but approximately 30% of the pollen foragers still travelled 1·4 km to forage on the borage (Fig. 3). However, in terms of area, the borage field only represented a very small proportion of the foraging landscape for colonies at the far end of the transect (column 3 in Table 1). The other major forage patches in this landscape were spring-sown flowering oilseed rape fields, field bean fields and gardens. When *B. terrestris* were given a choice of flowering crop plant species (growing in patches in a Latin Square design in a cage) the bees showed a strong preference for oilseed rape, followed by borage and then field bean (Osborne *et al.* unpublished). In terms of quantity and quality of resources, both these pieces of evidence suggest that it is unlikely that the borage field provided a foraging resource to over-ride the attractiveness of any other source. Nevertheless, the density–distance curves should be interpreted with caution, because the slope will vary depending on the relative quantity and quality of rewards available in different plant species (Cresswell *et al.* 2000). It is also likely that bees foraging on the borage were providing chemical cues to their fellow nest mates, signalling the presence of a good food source in the landscape (Dornhaus & Chittka 2001; Dornhaus & Chittka 2004), potentially increasing the chances of the bees finding the borage as a result of responding to olfactory cues learnt within the colony.

The experiment was performed in a landscape dominated by arable agriculture and some suburban areas. The results are therefore specific to this environment, although the proportions of different landcover types are not untypical of southern England. If classified maps of other areas were

available (created using a similar methodology to that described in Appendix S1) then estimates of spatial forage availability could be made (like Fig. 5) to establish the scale at which bumblebees are likely to experience resource variation in the landscape.

Within this arable landscape, the 'forage landscape' within 1–3 km of the colonies was similar, regardless of the position of those colonies within the landscape (Fig. 5). So, for *B. terrestris*, the location of the colonies may not limit their success in terms of forage availability because this species can clearly forage at the appropriate range. Our results support the conclusion of Westphal *et al.* (2006) that the scale at which landscape context affects bee populations will depend on the species' foraging range. In contrast to Westphal *et al.* (2006) our experiment shows the response of individual colonies to the landscape, rather than making statistical correlations between landscape elements and forager numbers from unknown colony locations. Walther-Hellwig & Frankl (2000) described *B. terrestris* as a spatial generalist, making the most of temporary large-scale resources. Species such as *B. terrestris*, with substantial foraging ranges (over thousands of metres), will be buffered from variation in forage habitat availability, which may be more evident and limiting at a smaller scale (over a few hundred metres). In this experiment, the colonies did not perform differently at the different sites (Table 1), and Fig. 5 shows that, as they foraged to the ranges measured, the amount of forage might not affect relative colony success in this landscape because all have similar 'forage landscapes'. This is not to say that forage availability does not limit colony success; *B. terrestris* colonies have been found to grow faster when placed in extensive suburban areas compared with agricultural landscapes, probably because more forage is available (Goulson *et al.* 2002). Our results suggest that, within this landscape, and for a species with a relatively long foraging range such as *B. terrestris*, there is little variance in the quality of nest site locations (Osborne *et al.* 2008) with regard to forage availability.

It would be interesting to perform the same experiment using species such as *Bombus pascuorum* Scopoli, *Bombus sylvarum* L. or *Bombus muscorum* L., which are believed to be 'doorstep foragers', only flying within a few hundred metres of the nest (Walther-Hellwig & Frankl 2000; Darvill *et al.* 2004; Knight *et al.* 2005). The positioning of colonies of these species, and the variability in availability of local forage between sites that we have demonstrated (Fig. 5), may potentially have more serious consequences on the foraging behaviour and ultimate success of their populations. It seems probable that differences in foraging range between bumblebee species may provide a partial explanation as to why a small number of species (including *B. terrestris*) remain common in arable landscapes while many other species have disappeared from intensively farmed areas.

The results presented here, linking the spatial availability of resources with bumblebee flight distances, will inform the current debate about whether distribution of food resources is the prime cause of rarity in bumblebee species (Goulson *et al.* 2005; Williams 2005). They can also be utilized to parameterize models of gene flow between fields of crops (Cresswell, Osborne & Bell 2002; Damgaard, Simonson & Osborne, in press), or populations of plants, which are based on a mechanistic understanding of how bees move across landscapes to utilize patches of plants providing nectar and pollen, while effecting pollination in the process.

Acknowledgements

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Supplementary material

The following material is available for this article.

Appendix S1. A habitat survey technique for quantifying bumblebee 'forage landscapes'.

Table S1. Landcover types recorded during the habitat survey, together with their overall rank as foraging sources.

Table S2. Plant families recorded during the habitat survey, and assigned 'family Forage Quality Values' (FQV).

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