

Bumblebee nest density and the scale of available forage in arable landscapes

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Abstract. 1. Combining the needs of agricultural production with enhancing biodiversity requires a landscape-scale approach since the geographic scale at which most non-farmed species operate is unconstrained by farm boundaries. Bumblebees are a key component of farmland biodiversity as pollinators of both crops and wild flora. However, the factors determining their densities in such landscapes remain poorly understood.

2. Using a combination of remote-sensed landscape data and molecular markers, we quantify the effects of land use (oilseed rape, field beans and non-cropped areas, all of which provide suitable bumblebee forage), at various spatial scales to find the best predictor of colony density for the bumblebee *Bombus pascuorum* Scopoli in an arable landscape.

3. Estimated colony density was positively correlated with the area of all habitat categories within 1000 m of the sample site. No significant relationships were found for greater or lesser distances. This concurs with earlier estimates of the foraging range of this species. We found no evidence that nest sizes increased with forage availability, although our data do not allow us to categorically exclude this possibility.

4. It has long been suspected that forage availability limits bee abundance in agricultural landscapes but there is little direct evidence for this. Here we report a direct relationship between floral abundance and bumblebee nest density within a notionally fixed area. Importantly, we suggest that the forage availability within the previously published estimated foraging distance for this species at this location is a good predictor of the scale of impact of forage provision on nesting density.

Key words. *Bombus pascuorum*, forage availability, foraging range, kinship, mass flowering crops, microsatellites, nest density.

Introduction

Intensification of farming systems in the last 60 years has led to general declines in farmland biodiversity but declines in pollinator abundance are of particular concern (Allen-Wardell *et al.*, 1998; Kremen *et al.*, 2002; Goulson *et al.*, 2005, 2006, 2008; Williams, 2005; Biesmeijer *et al.*, 2006). Pollination is an essential ecosystem service that provides direct economic

benefit (Kremen, 2005; Klein *et al.*, 2008). The area of entomophilous crops in Europe and the USA is increasing, and many researchers predict that we will soon be facing a serious shortage of both wild and managed bees (Borneck & Merle, 1989; Torchio, 1990; Buchmann & Nabhan, 1996; Steffan-Dewenter *et al.*, 2005; but see also Ghazoul, 2005 for a contrasting view).

Bumblebees (*Bombus* spp.) are a major group of pollinators in northern temperate climates, with at least 25 major crops grown within Europe being visited and pollinated by bumblebees, including field beans, red clover, alfalfa, oilseed rape and various hard and soft fruits (Corbet *et al.*, 1991). Some crops such as red

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clover (*Trifolium pratense*) are substantially dependent on pollination by long-tongued bumblebee species such as *B. pascuorum* and *B. hortorum* (Free, 1993). There is evidence that large crop monocultures may suffer from inadequate pollination, possibly because the flowers in nearby non-cropped areas are insufficiently abundant throughout the whole season to support a large enough resident bumblebee population to pollinate the whole crop (Ricketts *et al.*, 2008, and references therein). For example, in fields exceeding 12 ha in size, the yield of field beans was reduced through inadequate pollination by long-tongued bumblebees (Free & Williams, 1976). Similarly, Clifford & Anderson (1980) estimated that if field sizes exceeded 5 ha, then the yield of red clover in New Zealand declined due to a shortage of bumblebees. Bumblebees are not only important crop pollinators in agro-ecosystems, they also pollinate many associated wild flowers, many of which are currently either in national decline or threatened (e.g. UK BAP listed red hemp nettle *Galeopsis angustifolia*; Carvell *et al.*, 2006).

It is clear that appropriate management and conservation of bumblebee populations on arable farmlands is important both for ecological and economic reasons. However, as social insects with fairly large foraging ranges (Goulson & Stout, 2001; Chapman *et al.*, 2003; Darvill *et al.*, 2004; Knight *et al.*, 2005), their populations are likely to be determined by patterns of resource availability at a landscape scale. Thus, the current practice of promoting farmland biodiversity through individual farmers adopting various agri-environment schemes may not be maximising the benefit sought for a particular target species. Several authors have already highlighted the need for studies investigating the relationships between bumblebee populations and landscape scale and structure (e.g. Kremen & Ostfeld, 2005; Tscharrntke *et al.*, 2005; Osborne *et al.*, 2008a). Productive empirical research in this area has proved difficult due to the difficulties of tracking small, relatively abundant and highly mobile individual organisms over landscape scales (kilometres). Despite this, important in-roads have been made. Steffan-Dewenter *et al.* (2002) investigated relationships between forage availability in semi-natural habitats at incremental spatial scales (calcareous grasslands, extensive grasslands, fallows and ruderal areas, hedgerows, forest margins, vegetation along inshore waters & rock habitats) and pollinator visitation rates. They reported significant and important differences between the spatio-temporal scales at which three major pollinator guilds operate (solitary wild bees, honeybees and bumblebees) although they failed to find any significant relationships at all for the bumblebee pollinator guild. In a subsequent study, Westphal *et al.* (2003) focussed on the bumblebee guild specifically and reported the spatial scale of relevance for this guild to be 3 km. They found no significant relationship with the extent of semi-natural habitat available but their data suggested that mass flowering crops such as oilseed rape act as important early resources for bumblebee colony establishment in agro-ecosystems. A subsequent study by Herrmann *et al.* (2007) focussing on *B. pascuorum* demonstrated increased worker abundance in areas with more mass-flowering crops, but no increase in colony number, from which they inferred that colonies are larger in areas with more mass-flowering crops. However, they did not investigate the scale on which this effect operates, analysing data on land use within 1 km of their study sites.

These studies, among others (e.g. Kremen *et al.*, 2004), have allowed us to make very useful generalities about management practices for pollinator guilds; however, they also have their limitations. Key among these are the lack of empirical data on foraging ranges of pollinator species to inform their analyses, their grouping of data from all species together within guilds, and (with the exception of Herrmann *et al.*, 2007) their estimates of abundance for the eusocial hymenopteran species being based on densities of individual workers as opposed to nest densities. As the latter is a more accurate estimate of effective population size, it is expected to be far more revealing of population processes.

We here build upon these previously published studies and address some of their limitations. We examine the scale over which the availability of floral resources influences colony abundance of one common species, the long-tongued *B. pascuorum*, in an arable landscape, using individual genotypes of sampled individuals to estimate colony numbers at 10 independent sampling sites within a 10 × 10-km study area. This essentially combines the approach of Herrmann *et al.* (2007) (using molecular methods to study effects of land use on bumblebee colony density) with those of Westphal *et al.* (2003) in examining the spatial scale which best explains observed patterns. We discuss the results with reference to published estimates of foraging range for this species (Chapman *et al.*, 2003; Darvill *et al.*, 2004; Knight *et al.*, 2005).

Methods

Vegetation classification

The study area was a 10 × 10 km square centred on Rothamsted Research experimental farm, Hertfordshire, UK (UK Ordnance Survey National Grid coordinates 506000 West, 516000 East, 219000 North, 209000 South). Eighteen of the 100 1 × 1 km squares within this area were surveyed using a modified Nature Conservancy Council phase I survey methodology (NCC, 1990), adapted to allocate scores for both forage density and quality, and for nesting suitability of every landscape feature for *B. pascuorum* (described in Osborne *et al.*, 2008a, there scored for *B. terrestris*). To account for temporal changes in forage availability, three separate surveys were performed in spring (April/May), early summer (June/July) and late summer (August/September) 2002. Only survey data for the early summer period were used here, because *B. pascuorum* is a relatively late emerger in late April/early May (Edwards & Jenner, 2005) and because samples were collected at the end of this survey period in late July (see below). The surveyed squares were used to train a supervised classification using a maximum likelihood classifier of the entire 10 × 10-km landscape into 25 cover types. Two sources of remote-sensed data were available: first, Ikonos satellite data, at 4-m spatial resolution and 4 wavebands (red, green, blue and near-infrared), and second, compact airborne spectrographic imaging (CASI) data at 2-m resolution, and 15 wavebands. Post-classification testing against the field data gave an accuracy of 83% for the satellite and 91% for the aerial data (Kappa index). Once the two thematic maps

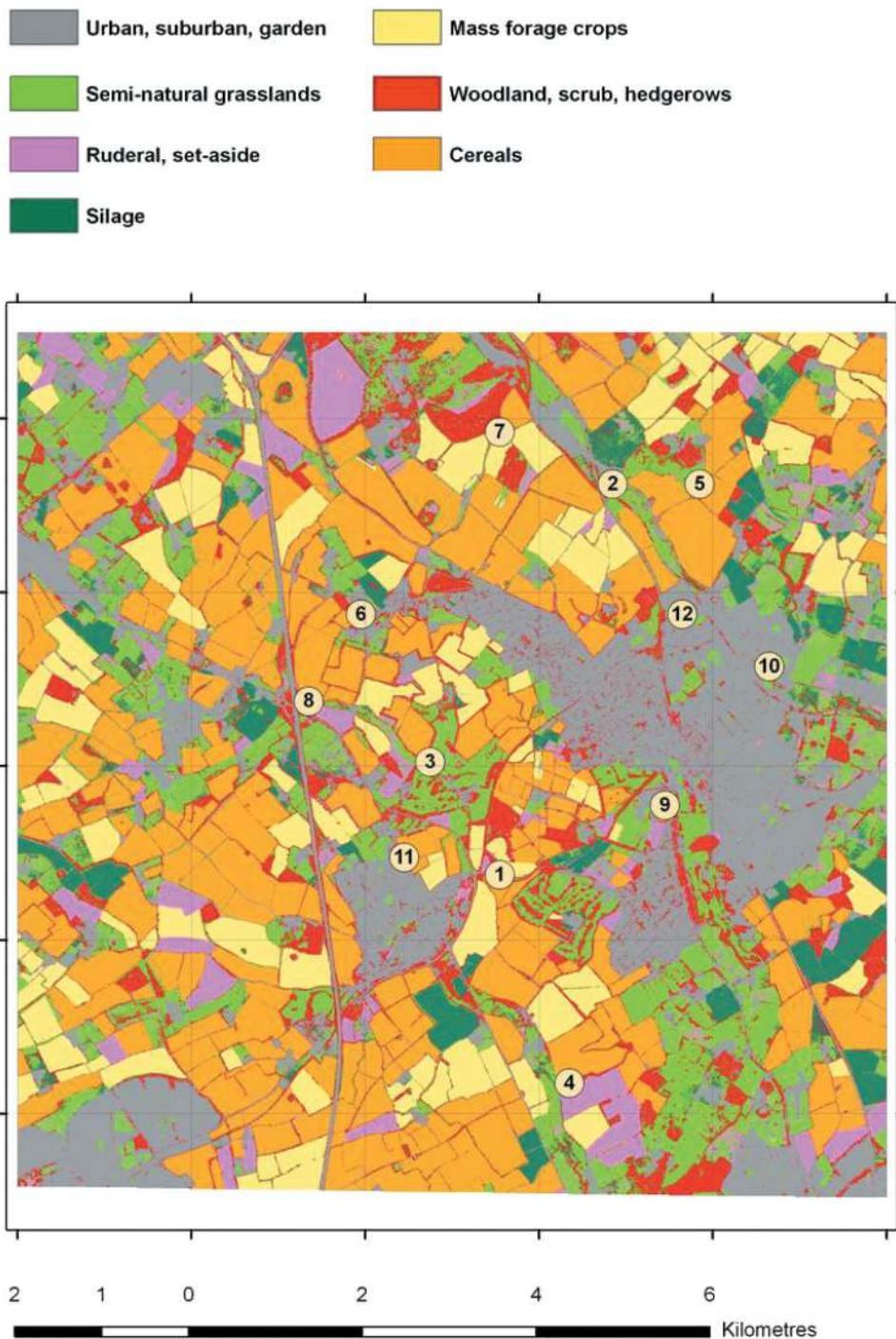


Fig. 1. Thematic map indicating distribution of habitat types for 10 × 10 km study area with sample sites 1–12 (see Table 1) indicated.

were created, they were fused together so that the CASI digital data formed the 5 × 5-km core, surrounded by the 10 × 10-km satellite data, in order to maximise the spatial and classification precision of the map in the centre of the study area (Fig. 1). Finally, a separate ‘garden’ category was created, by using a

moving-window search around urban areas for pixels of short or long grassland, ruderal, or scrub, as an individual garden can contain a wide variety of small-scale habitats, of value as both forage and nesting sites for bees. Surveys were also performed in 2003 and 2004 to update the map with respect to cropped

Table 1. Sampling summary and number of nests identified and estimated at each site using KINSHIP software. Note that the number of nests identified is based upon a standard sample size of 48 individuals (see main text). χ^2 and P columns refer to the goodness-of-fit of colony representative frequency data to a Poisson distribution. Figures given in brackets were not included in final data analysis due to unequal sample sizes and/or too few nests identified to fit a Poisson distribution. Nest density estimates assume a foraging range of 449 m (from Knight *et al.*, 2005) or 1 km (following Herrmann *et al.*, 2007).

Site number	Site name	OS grid reference	n	Effort (min)	Number of nests				Estimated nest density km ⁻² ($r = 0.449$ km)	Estimated nest density ($r = 1$ km)
					Identified	Estimated	χ^2	P		
1	Cutting	TL115127	60	40	38	149	0.02	0.888	235.3	47.4
2	Leeside Walk	TL128172	53	34	41	147	0.01	0.905	232.1	46.8
3	Golf Course	TL107140	51	66	26	66	0.05	0.817	104.2	21.0
4	Oryx	TL123103	52	35	39	162	0.01	0.928	255.8	51.6
5	Great Cutts	TL138172	34	69	(19)	(38)				
6	Turner's Hall	TL099157	51	39	28	62	0.19	0.661	97.9	19.7
7	Hillside	TL115178	54	25	34	109	0.03	0.851	172.1	34.7
8	M1	TL093147	56	52	31	62	0.27	0.606	97.9	19.7
9	Rothamsted	TL134135	59	28	40	140	0.03	0.862	221.0	44.6
10	Batford Mills	TL146151	48	62	36	105	0.02	0.875	165.8	33.4
11	John Fisher	TL104129	29	53	(20)	(47)				
12	Cemetery	TL136157	50	52	33	95	0.03	0.864	150.0	30.2

areas including mass-flowering crops. Non-cropped areas were assumed not to change.

Site locations and sample collection

Individual *B. pascuorum* workers were caught at 12 locations within the 10 × 10-km square area (Table 1) over a 3-day period in late July 2004 (26th–28th), when *B. pascuorum* colonies are at their peak of activity (Goulson, 2003). Sampling continued until approximately 50 individuals had been sampled at each site. Sampling effort at each site was measured by recording the time spent searching for bees. Sites were selected according to the following criteria:

- 1 A minimum of 1 km apart, based on results from a previous study (Knight *et al.*, 2005) that had estimated foraging range of this species to be approximately 450 m. Thus, at sample sites 1 km apart there is assumed to be little chance of sampling workers from the same nests.
- 2 Encompassing as much variation as possible in terms of forage availability in the surrounding area (i.e. to include sites we would expect to be both 'good' and 'bad' for bees according to the thematic map; Fig. 1) but not within or immediately adjacent to any bee-pollinated crop that was in flower at the time of sampling.
- 3 Including a suitable patch of forage to attract enough bees to allow a sample size of 50 workers to be caught within about an hour (Table 1).

All sampling was within a small area at each site (< 10 m²). At this time of year for this species, suitable forage largely consisted of white clover (*Trifolium repens* L.), comfrey (*Symphytum officinale* L.), bird's foot trefoil (*Lotus corniculatus* L.), teasel (*Dipsacus fullonum* L.), white dead nettle (*Lamium album* L.), red dead nettle (*Lamium purpureum* L.), and a variety of non-native ornamental plants in gardens, notably lavender (*Lavandula* spp. L.). Samples were immediately preserved in 100% ethanol for later DNA extraction.

Microsatellite genotyping

DNA was extracted from thoracic muscle tissue using the HotSHOT protocol (Truett *et al.*, 2000) and amplified at nine variable microsatellite loci (B118, B131, B132, B11, B10, B96, B126, B124, B121, Estoup *et al.*, 1995, 1996) using FAM-, HEX- or NED-labelled forward primers. Polymerase chain reaction (PCR) products were resolved on an ABI PRISM 377 automated sequencer (Applied Biosystems) with internal size standards (GeneScan ROX 350, Applied Biosystems). Identical sample controls were used throughout. Alleles were sized using GENESCAN and GENOTYPER software (Applied Biosystems). Any cases of scoring ambiguity or non-amplification were re-processed for confirmation of allele sizes.

Data analysis

Sister identification. Genotypes were checked for typographic errors using MSANALYSER (Dieringer & Schlötterer, 2002; <http://i122server.vu-wien.ac.at/People/Programme/M0001.01>). Current evidence suggests that *B. pascuorum* queens mate only once (Schmid-Hempel & Schmid-Hempel, 2000). In the absence of polyandry, any pair of bumblebee workers from the same nest has an expected relatedness of 0.75. Sister relationships among the individuals sampled were established within each species using the likelihood function of KINSHIP 1.3.1 (<http://www.gsoftnet.us/GSoft.html>; Goodnight & Queller, 1999) where $Rm(ateral) = 0.5$ and $Rp(ateral) = 1.0$. Confidence in sister pair assignment was calculated from 100 000 simulations, the number of iterations determined by repeating analysis runs using variable numbers of simulations and establishing the point after which results reached a plateau. To minimise type I errors, given the high number of pairwise comparisons within each data set, only sisters designated at $P \leq 0.001$ (the most stringent value that KINSHIP will return) were used in further analysis. KINSHIP

assumes linkage equilibrium and no inbreeding. This particular population had previously been extensively sampled and was known to conform to these assumptions (Knight *et al.*, 2005).

Estimating numbers of colonies represented at each site. Two related measures of colony number and density were available. First, the actual number of colonies represented in our sample at each sampling site was counted. Sisters were thus assigned to the same nest, non-sisters to separate nests, and the resultant number of nests simply counted. Since sample sizes varied and this would have a direct effect on the number of colonies counted, sample sizes were standardised to $n = 48$ by randomly removing the genotypes of the appropriate number of individuals from all sites where $n > 48$ (sites 5 and 11 were excluded from subsequent analyses because the sample sizes were too small, see Table 1).

Second, as inevitably some colonies that had workers present at the sampling site would by chance not be represented in the site sample, the number of colonies that were not sampled at each site were also estimated. This was achieved by plotting the number of colonies represented by lone individuals, two bees, three bees etc., and then fitting a Poisson distribution to these data to estimate the 'zero' category. Summing all categories including the estimated 'not sampled' then gave an estimate of the total number of colonies within foraging range of each site sampled (for full details of this approach see Darvill *et al.*, 2004; Knight *et al.*, 2005). Taking this approach does not require the sample size to be standardised, as the more individuals sampled the greater the accuracy of the fitted Poisson distribution, and hence of the zero category estimate.

Assessing relationship with available forage. Land cover types (Fig. 1) containing suitable forage were considered in three categories: winter and spring oilseed rape (OSR), winter and spring field beans (FB) and non-cropped areas (NCA; hedges, margins, set-aside, gardens etc. combined) which contained a range of flower species. Woodland and grassland were not included in this category since these habitats were not found to contain any significant forage during this time period for this species from the ground truthing exercise. The proportion of land covered by these habitats was estimated from the classified map (using 2004 crop data) at the following radii from the sample sites: 250, 500, 750, 1000, 1250, and 1500 m.

For each of the six radii, the relationship between the number of colonies estimated to be represented at the sampling point and the area of available forage split into the three categories (OSR, FB and NCA) calculated to be within that given radius was assessed using multiple regression. These tests were carried out separately for the two measures of colony density, first on the actual number of colonies represented by the sample at each site, and second on the estimated colony density at each site.

Results

Twelve sites were sampled that were a minimum of 1.15 km and a maximum of 7.40 km apart (Fig. 1). From these sites, 597 individual workers were sampled (Table 1). Two of the 12 original sample sites yielded considerably fewer than the targeted

Table 2. Distribution of sister relationships found between sites ($n = 15$) (upper half of matrix) with corresponding Euclidean distance (kilometres) between sites on lower half of matrix. See Table 1 for respective site names.

Site	1	2	3	4	6	7	8	9	10	12
1		2			2				1	
2	4.58				1	1			1	
3	1.50	3.68								
4	2.50	6.75	3.98						1	
6	3.28	3.20	1.80	5.78		3			2	
7	5.00	1.35	3.80	7.40	2.65				1	
8	2.78	4.25	1.58	5.22	1.15	3.80				
9	2.10	3.70	2.70	3.32	4.05	4.60	4.25			
10	3.90	2.80	4.02	5.25	4.70	4.02	5.32	2.02		
12	3.55	1.65	3.20	5.42	3.55	2.85	4.30	2.18	1.25	

50 individuals (sites 5, $n = 34$ and 11, $n = 29$) and so were excluded from the analysis. Note that this does not mean that there were no or few bees in these areas, simply that on the particular patch of forage that we searched we did not find enough adequate numbers to include these sites in our analysis. There was a low expected type II error from KINSHIP (0.015 with 100 000 simulated iterations where $P \leq 0.001$), thus falsely rejected sister pairs are unlikely to have had any significant effect on data trends, particularly since this very low frequency of falsely rejected sisters is expected to be distributed randomly with respect to sampling site. For 15 of the 373 sister pairs identified by KINSHIP (4.0%), each sister was caught at a different site. For all other sister pairs identified, the two individuals were caught at the same site. This suggests that some bees do travel further than 450 m from their nests although the numbers doing so is relatively small. There were no particular pairs of sites where the majority of these relationships were found (Table 2) although with such low numbers any existing patterns would be difficult to establish.

After standardising for a sample size of 48, a total of 346 independent nests were identified from the 10 sites (Table 1), of which 68 were represented by more than one sampled individual. Twelve 'non-circular nests' (cases where individual A is found to be a sister of individuals B and C but where individual B is not identified as a sister of individual C) were found. In these cases, data were re-examined and where individuals B and C would have been accepted as sisters at a less stringent significance level ($P \leq 0.01$), the group were accepted as true sisters (5/12 cases). Where no such relationship was evident between individuals B and C (7/12 cases), then the most parsimonious route was taken to gain circularity by omitting individuals from the family. While this may result in slightly overestimating the numbers of colonies sampled, these cases were randomly distributed among sites and given their small number are not expected to have had any significant effect on any observed trends in the data set as a whole.

Distributions of the number of workers sampled from each colony closely conformed to a Poisson distribution in all cases (Table 1). Estimated total numbers of colonies within foraging range of each site varied between 62 and 162 (mean 110). If we use Knight *et al.*'s (2005) estimate of foraging range of 449 m, calculated for the same study area, we obtain nest density estimates

Table 3. Regression analyses results for all foraging radii tested.

a:

Radius (m)	Overall		OSR only	FB only	NCA
	R^2	P	β , P	β , P	β , P
250	0.131	0.824	0.057, 0.929	0.355, 0.405	0.029, 0.964
500	0.251	0.601	0.069, 0.896	0.503, 0.278	0.012, 0.983
750	0.389	0.365	0.567, 0.295	0.743, 0.107	0.501, 0.376
1000	0.746	0.032	1.314, 0.011	1.019, 0.010	1.410, 0.014
1250	0.494	0.222	1.030, 0.065	0.674, 0.130	1.116, 0.086
1500	0.311	0.492	1.069, 0.151	0.615, 0.315	1.060, 0.214

b:

Radius (m)	Overall		OSR only	FB only	NCA
	R^2	P	β , P	β , P	β , P
250	0.055	0.947	-0.035, 0.958	0.234, 0.591	-0.025, 0.970
500	0.103	0.873	0.008, 0.989	0.318, 0.517	-0.005, 0.993
750	0.166	0.760	0.404, 0.511	0.488, 0.328	0.387, 0.550
1000	0.570	0.142	1.256, 0.037	0.771, 0.074	1.370, 0.042
1250	0.422	0.317	0.999, 0.087	0.401, 0.366	1.074, 0.114
1500	0.287	0.536	0.859, 0.242	0.214, 0.721	0.831, 0.326

'OSR', winter and spring oil seed rape; 'FB', winter and spring field beans; 'NCA', non-cropped areas; and β , standardised regression coefficient. Significant results are highlighted in bold. Table 3a for estimates, Table 3b for actual numbers of nests represented (standardised to $n = 48$).

ranging from 98 to 256 nests km^{-2} (mean 173). However, Herrmann *et al.* (2007) use a very similar approach to estimating *B. pascuorum* nest density in arable landscapes in Germany but using a 1 km radius. To enable direct comparison with their results, our nest density estimates calculated using a 1 km foraging range are 20–52 nests km^{-2} (mean 35) (Table 1).

The number of nests identified to be present at each site negatively correlated with our measure of effort (calculated as the number of minutes spent catching/the number of bees caught, Fig. 2a), Spearman Rank, $n = 10$, $r_s = -0.636$, $P = 0.048$) although the relationship was non-significant for the number of nests estimated (Fig. 2b) $n = 10$, $r_s = -0.559$, $P = 0.093$).

Significant positive relationships were found between estimated colony number and availability of cover containing forage at 1000 m only (Table 3). All three habitat categories (oilseed rape, field beans and non-cropped areas) contributed significantly to the model, suggesting that they all enhance colony survival. Availability of forage within lesser or greater distances poorly predicted the number of colonies present. Within 1000 m of each site, oilseed rape comprised 6.00% of the land cover (range 0–20.0%), field beans covered 4.28% (range 0–12.5%) and non-cropped areas covered 19.35% of land (range 8.1–34.1%).

Discussion

It has long been suspected that forage availability limits bee abundance in agricultural landscapes, and that declining availability

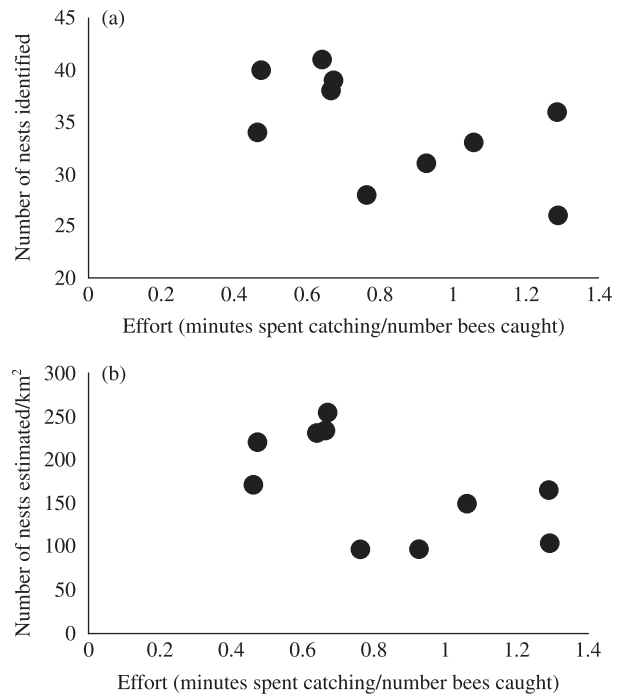


Fig. 2. Negative relationship between effort (measured for each site as the number of minutes spent catching/total number of bees caught) and the number of nests identified to be present at each site for both (a) counts and (b) estimated nesting density per km^2 .

of flowers has driven the declines of some bumblebee species, but there is little direct evidence for this (reviewed in Goulson, 2003; Goulson *et al.*, 2008). Here we demonstrate a direct link between floral abundance (provided by both mass flowering crops and non-crop areas) and the number of bumblebee colonies in an area. Whether this is because more queens choose to nest in the area (for example they may be more likely to nest in sites with a high proportion of non-farmed area), or because fewer nests survive until July (our sample period) in areas where there are fewer flowers, remains to be tested. While we cannot dismiss the possibility that this result simply represents bumblebees being attracted in from a much wider radius to the areas with better forage, there are some compelling arguments that would not support this. First, was this the case we might expect to find far more between-site sisters than we did. Second, although it is quite feasible that bumblebees are drawn from long distances to large patches of resources, here the patches of forage sampled were all small, and not either in nor immediately adjacent to any mass flowering resource. Finally, even if bumblebees are attracted to certain areas, this would not explain a relationship with the amount of forage within a radius of 1000 m.

Previous studies conducted in the same area estimated the foraging range of *B. pascuorum* to be 449 m (Knight *et al.*, 2005). Workers that were at the outer limit of their foraging range at our sample sites will be likely to have sisters that are foraging in the opposite direction from their nests, giving a predicted radius of influence of forage availability on total bee abundance at a given point in the landscape (i.e. including

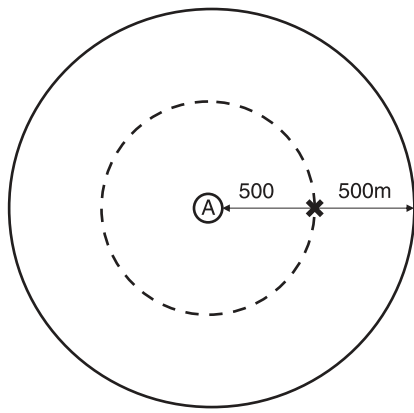


Fig. 3. Schematic explanation of the pattern of results, which are consistent with a *B. pascuorum* foraging range of ~500 m. The distance from the sampling point at which available forage predicts nest density is 1000 m. Sampling of individuals occurs at point A; these individuals will come from a number of different nests in the landscape, up to a maximum distance of 500 m from the sampling point A (dotted line circumference). Individuals that have travelled from the various nests at the maximum possible distance away from the sampling point A (e.g. the nest marked with a cross), will also be foraging 500 m in the opposite direction. Hence, for all the workers from many different nests, sampled at point A, the maximum radius of forage availability affecting their overall abundance is 1000 m.

unrelated workers from any nest) of twice the foraging range (~900 m) (see Fig. 3 for further explanation). This agrees closely with the results presented here, which suggest that the number of colonies from which workers are foraging at any particular site is best predicted by the availability of forage within 1000 m. Westphal *et al.* (2003) found that overall numbers of individual bumblebees (all species combined) were correlated most strongly with availability of oilseed rape within 3000 m of their focal plots, a considerably greater range than that found here. The difference in scale between these studies could be because Westphal *et al.* did not separate bumblebee species, and *B. pascuorum* has a shorter foraging range than some of the other common bumblebee species (Knight *et al.*, 2005). Most of their records were probably of *B. terrestris* and *B. lapidarius*, the two most common species on oilseed rape (D. Goulson, pers. obs.), which have longer foraging ranges (Knight *et al.*, 2005). Alternatively foraging ranges may well be different for the same species between these two study sites, driven by differences in forage availability and distribution. Westphal *et al.*'s study was conducted on a more intensively farmed system which likely presents a forage mosaic on a larger scale than that in the UK. That both inter- and intra-specific bumblebee foraging behaviour may vary according to the specific characteristics of the landscape (in particular the amount of arable land) is strongly supported by Heard *et al.* (2007)'s study of bumblebee visitation rates to experimental flower patches within difference landscape contexts.

Westphal *et al.*'s study also differs from ours in finding no significant effect of non-cropped areas. This difference may also be because they were largely looking at different species, and it seems likely that mass-flowering crops benefit most those species with

long foraging ranges, while those with shorter foraging ranges will be more dependent on small patches of resources available near the nest. Their most common study species were relatively short-tongued compared to *B. pascuorum*, thus with potentially different forage preferences. It may also be because they examined numbers of bees rather than numbers of nests; mass-flowering crops must provide a great boost to nests that have survived up until they flower, but in an intensive arable landscape with few non-cropped areas, most colonies may not survive until then. Thus in areas with a high proportion of oilseed rape they may have detected lots of workers from a small number of large nests. Clearly, further work is needed to resolve these differences, but overall these data as well as Westphal *et al.*'s support the conclusion that mass-flowering crops do enhance populations of the more common bumblebee species, but that, in agreement with Heard *et al.* (2007), here we find that non-cropped areas are also important for colony survival through the season.

Our results contrast markedly with those of Herrmann *et al.* (2007), who quantified the effects of mass flowering crops and non-cropped areas within a 1-km radius of study sites with both *B. pascuorum* worker abundance and estimated colony number. They describe a positive relationship between mass-flowering crop availability and worker abundance, but again no effect of non-cropped areas on worker abundance and specifically no effect of land use on colony number. This contrasts to the evidence presented here where the number of nests detected bore a negative relationship to sampling effort, suggesting that in sites where bees are very abundant, this abundance is not a result of larger nests, but of more nests. Their estimates of colony density are also much lower (mean ~8 nests km⁻²) than those presented here (mean ~35 nests km⁻² when using the same methods to calculate them), suggesting that there may be fundamental differences between the study sites that are influencing the population biology of *B. pascuorum*. One possibility, as discussed above, is that nest sites may be more limited in the German sites, so that fewer nests are founded, but those that grow to a large size in areas with a high density of mass-flowering crop. In comparison, if nest sites are more frequent at our lowland UK site, then many more nests may be founded but this would lead to intense competition for forage between nests and high nest mortality in areas with few flowers, resulting in the pattern we describe of nest density correlating positively with availability of all three sources of floral resources (oilseed rape, field beans and non-cropped areas). A comparison of the non-cropped areas present in the two studies supports this explanation: in the German study, just 6.1% of land was classed as semi-natural (which included hedgerows, fallows, field margins etc.) while our estimate of the mean area of non-cropped habitat within any 1000-m foraging radius of our sampling sites was much higher at 19.4%. Since bumblebees probably nest almost exclusively in non-cropped habitat, this would suggest that nest site availability is much lower at the German study site. This comparison may also shed light on why non-cropped areas were found to exert no significant effects on bumblebee populations in Germany but did have a significant effect in the UK; in Germany, non-cropped areas may simply be too scarce to be of much importance as floral resources. There is some anecdotal support of this suggestion: a high proportion of the non-cropped area in our UK study site was

made up of gardens, habitats known to support high bumblebee nest densities (Osborne *et al.*, 2008b).

Our results suggest that quantifying habitats with suitable forage is a good predictor of relative bumblebee colony density, but only if foraging range is known for the species in question. Once this is known, appropriate strategies to conserve particular bumblebee species and/or to improve crop pollination could be developed. For example, if a farmer wishes to conserve populations of the relatively long-tongued *B. pascuorum*, needed to pollinate crops with deep flowers such as field beans, then the farmer must provide adequate resources to support nests through the season within 1000 m of his crop. If the aim is to encourage nests of shorter-tongued and longer ranging species such as *B. terrestris* (an important pollinator of oilseed rape), then resources can be more widely dispersed. Forage ranges are not known for many bumblebee species, but have been estimated for four of the common bumblebee species that are important crop pollinators in the UK, *B. pascuorum*, *B. terrestris*, *B. lapidarius* and *B. pratorum* (Knight *et al.*, 2005). In order to develop conservation strategies for rarer species (which may differ markedly from common species), it would be valuable to quantify their foraging range or repeat the approach used here, to estimate the scale of habitat management needed to maximise colony numbers. An important caveat, as discussed, is that foraging ranges are not necessarily fixed for all habitats for any one species, and careful consideration of this should be taken with respect to the habitats and locations where published estimates were measured.

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