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The response of foraging bumblebees to successional change in newly created arable field margins

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Abstract

Agricultural intensification is likely to have been a major factor leading to serious declines in bumblebee abundance and diversity in the UK and elsewhere over recent decades. Opportunities to restore habitat for bumblebees on uncropped arable field margins are now available, although the methods by which this restoration can be achieved have not been fully investigated. We present the results of a three year study undertaken to investigate the response of foraging bumblebees to five different arable field margin treatments (sown and unsown), as part of a replicated field experiment on arable farmland in northern England (UK). Bumblebee abundance was closely linked to successional changes in availability of suitable forage plant species. Field margin treatments sown with a 'grass and wildflower' mixture had the highest bumblebee abundance, and provided a consistent supply of forage species, with different components of the seed mixture flowering in each year. The unsown natural regeneration treatment attracted foraging bumblebees in only the second year due to the local abundance of thistles, so we consider this option to be both inconsistent in terms of forage provision and agronomically unacceptable. Our results are discussed in terms of developing suitable measures to achieve the restoration of habitats for bumblebees on arable farmland.

Keywords: Bumblebees; Field margin; Foraging; Wildflower mixture; Succession

1. Introduction

Modern intensive farming is perceived to be the principal cause of declining biodiversity in the European countryside (Stoate et al., 2001), and this decline has been especially marked for bumblebees (*Bombus* spp.) (Williams, 1982; Rasmont, 1988; Banaszak, 1996). In the UK, many bumblebee species that were once widespread and common have shown serious reductions in density and contractions in range over recent decades (Alford, 1980; Williams, 1982; Edwards, 2001). This is thought to be largely due to the fragmentation and loss of foraging and nesting habitats (Osborne and Corbet, 1994), and in particular, declines in abundance of key forage plants such as *Centaurea nigra*, *Lotus corniculatus* and *Trifolium pratense* in the British countryside (Carvell et al., 2001). These declines have serious implications for the pollination of numerous crop and wild flower species, for which bumblebees are especially important (Corbet et al., 1991; Free, 1993). Their roles in enhancing the yields of many entomophilous crops (e.g. Holm, 1966; Willmer et al., 1994) and in maintaining small fragmented populations of wild plant species (Kwak et al., 1991; Steffan-Dewenter and Tscharntke, 1999) have been well documented, highlighting the need to prevent further bumblebee declines in agricultural and semi-natural ecosystems.

In recent years there have been attempts to restore and maintain habitats which enhance biodiversity in the agricultural landscape (Bignal, 1998). Policy developments within the UK agri-environment schemes (e.g. the Countryside Stewardship Scheme (DEFRA, 2003)) offer increased opportunities to achieve this restoration, particularly on arable field margins which are a key feature of British farmland (Marshall, 1998; Marshall and Moonen, 2002). Bumblebees are known to benefit

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from the presence of flowering perennial herb species, ideally in unfragmented species-rich grasslands (Carvell, 2002). However, they can also utilize forage resources in patches of established semi-natural vegetation such as field margins, green lanes (Croxton et al., 2002) and other habitat islands, due to their ability to fly considerable distances from the nest (Fussell and Corbet, 1991; Saville et al., 1997; Osborne et al., 1999; Bäckman and Tiainen, 2002). In addition to a season-long supply of suitable forage resources, bumblebees also require nesting sites, mating and hibernation areas, although there is little information describing the latter two requirements (Alford, 1969, 1975). Forage and nesting sites are currently more accessible targets for habitat restoration, and although in this paper we focus on foraging bumblebees, it is likely that, once established, suitable foraging habitats in non-cropped areas also have the potential to support nest sites (Svensson et al., 2000).

The addition of native perennial flower species (referred to here as 'wildflowers') to sown grass mixtures on arable field margins has become an increasingly attractive option, providing both conservation and agronomic benefits (e.g. Smith et al., 1993; Marshall, 1998; Miller and Lane, 1999; Thomas and Marshall, 1999; Meek et al., 2002). Such margins can enhance numbers of nectar- and pollen-feeding insects, including butterflies, bumblebees, honeybees and hoverflies during the flowering season, particularly if mixtures contain suitable forage species (Lagerlöf et al., 1992; Feber et al., 1996; Carreck et al., 1999). In addition, Feber et al. (1996) have highlighted the importance of subsequent management actions in maintaining suitable habitats for the different life-cycle stages of insect pollinators. Alternative options for arable field margins in the UK include the sowing of a mixture of tussocky grasses, or allowing natural regeneration on an 'uncropped wildlife strip', which may be allowed to establish, or be regularly cultivated to provide conditions for rare arable plants (Marshall, 1998; DEFRA, 2003).

Research to date suggests that many of these field margin habitat creation options are likely to contribute to the conservation of bumblebee populations on arable farmland, either through the provision of foraging or nesting sites. However there has been a lack of fully replicated field experiments to support this hypothesis. In particular, most studies have been conducted over limited time periods, such that the effects of successional changes in newly created habitats, and their potential longevity for bumblebees and other taxa in agricultural systems are unknown (e.g. Corbet, 1995). This is surprising given that many options for biodiversity enhancement in arable landscapes are intended to establish semi-permanent habitats. Agreements under the UK Countryside Stewardship Scheme, for example, are often expected to run for 10 years (DEFRA, 2003).

This study aims to address the following questions: can sown mixtures provide foraging habitats of greater value to bumblebees than unsown areas of natural regeneration on field margins, and which, if any, of these options are sustainable in the arable system over time? We present the results of a three year study undertaken to investigate the response of foraging bumblebees to five different arable field margin treatments, as part of a replicated field experiment on arable farmland in northern England (UK). Our results are discussed in terms of developing measures that are both agronomically acceptable and biologically suitable to achieve the restoration of habitats for bumblebees and other insect pollinators on arable farmland.

2. Methods

2.1. Site description and margin treatments

Three cereal field margins were selected on Manor Farm, Eddlethorpe, near Malton, North Yorkshire (Lat. 54°05′N, Long. 0°49′W), all situated along hedgerows on a variable sandy clay loam. In September 1999, each margin (or replicate) was divided into five contiguous plots, 72 m long and 6 m wide, and each plot was subject to one of five different treatments:

1. Natural regeneration, unsown, 6 m wide;
2. Sown 'tussocky' grass mixture, 6 m wide;
3. Sown 'grass and wildflower' mixture, 6 m wide (referred to as 'wildflower');
4. 'Split' treatment with 3 m sown 'tussocky' grass mixture adjacent to hedge and 3 m sown 'grass and wildflower' mixture adjacent to the crop; and
5. Cropped to the edge.

Details of the sown mixtures are given in Table 3. Plant species nomenclature follows Stace (1997). In April 2000, a selective graminicide was applied at 6.25 g ai/ha (=0.5 l/ha Fusilade-5) to the 'wildflower' treatments and the wildflower half of the 'split' margin treatments to control blackgrass, *Alopecurus myosuroides* and sterile brome, *Anisantha sterilis*. Following establishment, all plots (except those cropped to the edge) were cut and the herbage removed using a forage harvester in May 2000. In late August 2000 the two treatments containing wildflowers were cut to around 10 cm, with the cuttings removed. In late August 2001, the natural regeneration plots were cut as a means of controlling a developing thistle problem (see Section 4), with the cuttings left. Subsequent management was focused on the 'wildflower' treatments, and wildflower half of the 'split' plots, which received an annual cut during late August 2001 and 2002, with cuttings removed.

The 'cropped to the edge' treatment received conventional management as per the rest of the field concerned. During 2000 two of the margins were adjacent to winter wheat and one to winter barley, during 2001 two were adjacent to oil-seed rape and one to winter wheat, and in 2002 all were adjacent to winter wheat. It should be noted that the rape crops had finished flowering prior to sampling for this study.

2.2. Bumblebee monitoring

Bumblebee activity was recorded on transects along the central line of all three margin replicates, using an adapted form of the standard 'bee walk' methodology (Banaszak, 1980). In the establishment year (2000), walks were carried out 12 times throughout July. In 2001, 10 sampling visits were made from 25th June to 24th August, and in 2002, 11 visits were made from 27th May to 20th August. Walks were only carried out in dry conditions between the hours of 09.30 and 17.00, when the ambient temperature was above 15 °C. The direction in which each margin replicate was walked was varied with each visit. Foraging bumblebees were recorded to species level (following Prŷs-Jones and Corbet, 1991) but not separated to caste, within 3 m to each side of the observer to cover the entire margin strip. The flowering plant species which each bee was first seen to visit was also noted (i.e. if a bumblebee was seen flying to visit a second plant species that observation was not recorded). *Bombus terrestris* and *B. lucorum* workers cannot always be reliably distinguished in the field (Prŷs-Jones and Corbet, 1991), so these species were collectively recorded as *B. terrestris/lucorum* as in other studies (e.g. Fussell and Corbet, 1991). The cuckoo bumblebees (sub-genus *Psithyrus*) were also recorded, but only results for the social bumblebees are presented here.

2.3. Flower abundance scores

In order to gain a measure of forage availability, and to assess successional change in flowering on the different treatments, the number of flowers/inflorescences of each plant species that were present within each plot was estimated using a 5-point scale (modified from Feber et al., 1996), as follows:

0. No flowers present;
1. 1–25 flowers;
2. 26–200 flowers;
3. 201–1000 flowers;
4. 1001–5000 flowers;
5. Superabundant – more than 5000 flowers.

One flower 'unit' was counted as an umbel (e.g. *Daucus carota*), head (e.g. *Trifolium repens*), spike (e.g. *Rhinanthus minor*) or capitulum (e.g. *C. nigra*). Flower identification follows Stace (1997). Flower abundance scores were measured on every sampling date, immediately following bumblebee transects, during 2001 and 2002.

2.4. Data analysis

Bumblebee counts from each treatment in all three years were calculated and expressed as mean values per plot, per sampling date, and these data were normalized by log transformation. Differences in the abundance of bumblebees between the field margin treatments were tested by two-way Analysis of Variance (ANOVA), following the randomized block design, including replicates and treatments. Tukey's Honest Significant Difference test was also performed to assess pairwise comparisons between treatments. This analysis was carried out to detect differences within each year, and differences between years, in abundance of all bumblebees grouped. The same analysis was applied to individual *Bombus* species for 2001 and 2002 only, as the shorter sampling period during 2000 was less representative of the flight season for each species.

Differences in mean flower abundance scores between the margin treatments in 2001 and 2002 were also compared using ANOVA and Tukey's pairwise tests, as the data conformed to the normal distribution. Finally, changes in the number of bumblebees and availability of forage resources over the length of the experiment were examined, to detect any successional change in bee activity or flowering in the different treatments.

3. Results

3.1. Differences in bumblebee abundance between field margin treatments

Over the duration of this study, a total of 2241 foraging bumblebees were recorded, with the average number of individuals per plot on each sampling date remaining fairly consistent across the years (4.6 in 2000; 5.1 in 2001 and 4.0 in 2002). There were significant differences between field margin treatments in terms of mean total bumblebee numbers in each year, and across all years combined (Fig. 1: ANOVA, $F_{4,8} = 25.67$, $p < 0.001$ in 2000; $F_{4,8} = 10.07$, $p < 0.01$ in 2001; $F_{4,8} = 5.15$, $p < 0.05$ in 2002 and $F_{4,8} = 18.92$, $p < 0.001$ for all years). However, the preferred treatments were not the same each year, as confirmed by Tukey's pairwise comparisons. In 2000, significantly more bumblebees were recorded in the wildflower and 'split' tussocky grass and wildflower treatments than in all others ($p < 0.01$), but in 2001, the natural regeneration treatment was preferred, attracting significantly more bumblebees than the tussocky grass and cropped treatments ($p < 0.01$). The pattern in 2002 was similar to that of 2000, with highest numbers in the two treatments sown with the 'wildflower' mixture, although there were no significant pairwise comparisons ($p > 0.05$). When the mean number of bumblebees per plot was calculated across all

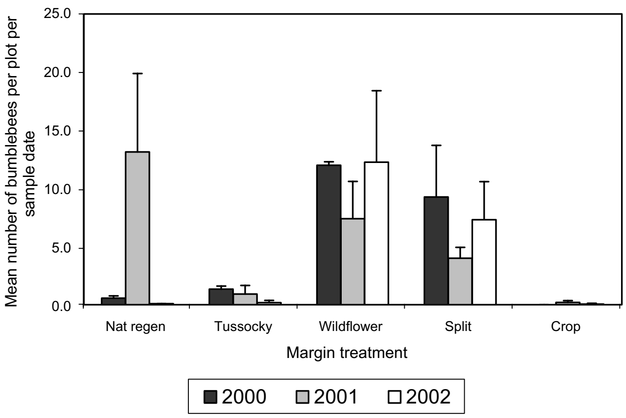

Fig. 1. Change in total bumblebee abundance on the different margin treatments over three years.

years, abundance was highest in the wildflower and 'split' plots, and significantly different in these compared to only the tussocky grass and cropped plots ($p < 0.01$).

Differences between years were tested for each margin treatment in turn. Significance was only detected for the natural regeneration treatment ($F_{2,4} = 20.06$, $p < 0.01$), where many more bees were recorded during 2001 (Fig. 1) in response to the increased thistle population (see Section 3.3). In all other treatments bumblebee numbers were relatively consistent over the three years. In general, no significant differences between the three replicates were apparent, although the high numbers in the natural regeneration treatment in 2001 were mainly biased towards two replicates.

3.2. Bumblebee species

Six social bumblebee species were recorded, all known to be fairly widespread across the UK (Williams, 1982). Table 1 shows differences in abundance of each species between the margin treatments in 2001 and 2002. *Bombus lapidarius* accounted for around 50% of observations in each year, followed by *B. pascuorum*. *B. terrestris/lucorum* and *B. hortorum* were observed less frequently, and *B. pratorum* was scarce, accounting for less than 1% of observations. Patterns of abundance across treatments were generally consistent between species, with the natural regeneration treatment being preferred in 2001 (though never significantly different to those sown with the 'wildflower' mixture $p < 0.05$), and the wildflower, followed by 'split', treatment preferred in 2002. Statistical significance between treatments was not always achieved for species recorded in lower numbers (Table 1).

3.3. Differences in flower abundance between field margin treatments

Both the mean flower abundance score for all species grouped and the species richness of plants in flower over the sampling period differed significantly between field margin treatments (Table 2). As expected, abundance and species richness were higher in plots featuring the sown 'wildflower' mixture than in all other treatments (Tukey's pairwise comparisons; $p < 0.01$). This response was consistent in 2001 and 2002.

Lists of sown and unsown flowering plant species recorded on the field margins in 2001 and 2002 are given in Table 4, with mean abundance scores shown to indicate relative flowering in each year. Species were grouped according to various characteristics (i.e. their life history, whether sown in the mixtures or visited by foraging bumblebees) in order to examine patterns of occurrence across the margin treatments (Table 2). As expected, sown species were significantly more abundant in the 'wildflower' and 'split' plots than in all others, and achieved notably higher mean abundance scores in 2002, the third year after establishment. This group consisted mostly of perennials, except *R. minor* which accounts for the flowering annuals occurring in the sown treatments. In contrast, flowers of unsown species were significantly more abundant in the natural regeneration treatment than in all others except the crop in 2001. This was due to patches of *Cirsium vulgare* (a biennial), flowering during 2001, but mainly absent during 2002 (Table 4) when there was no significant difference in unsown species between the treatments.

3.4. Forage plant preferences

The flowering plant species receiving the most foraging visits differed in each year of this study (Fig. 2), reflecting the relative abundance of those species flowering on the field margin treatments. In 2000, more than 90% of visits were to the annual species *Centaurea cyanus* (during the restricted July sampling period), whereas in 2001 and 2002 visits were more evenly spread across several species, with concentration on *C. vulgare* and *L. corniculatus* respectively. It is interesting to note that some species scoring highly in terms of flower abundance (e.g. *Leucanthemum vulgare*) received a low proportion of bumblebee visits. Fig. 3 shows the flower visits of three *Bombus* species in 2001 and 2002. Despite the dominance of *C. vulgare* in 2001 and *L. corniculatus* in 2002, some differences in other utilized forage species are apparent. For example, *B. lapidarius* (the shorter-tongued species here) visited *Senecio jacobaea* and *L. vulgare*, whereas the longer-tongued *B. pascuorum* and *B. hortorum* visited *R. minor* and *Prunella vulgaris* and in 2002, *Lathyrus pratensis*.

3.5. Temporal changes in bumblebee and flower abundance

Patterns of bumblebee activity throughout each season clearly reflected temporal changes in flower abundance on each margin treatment (Figs. 4a–d). During

Table 1
Bumblebee abundance by species on the different margin types

	Field margin type						ANOVA 2001	
	% of all records	Natural regeneration	Tussocky grass	Wildflower	Tussocky & wildflower	Cropped	$F_{4,8}$	Sig. level
(*a*) *Bombus* species 2001								
B. terrestris/lucorum	15.1	1.83 ± 0.62 b	0.10 ± 0.06 a	0.93 ± 0.41 ab	0.97 ± 0.35 ab	0 a	5.52	*
B. lapidarius	49.8	6.53 ± 3.51 c	0.27 ± 0.27 ab	4.20 ± 1.97 bc	1.50 ± 0.51 ac	0.17 ± 0.12 a	7.45	**
B. pratorum	0.5	0.07 ± 0.07	0.00	0.07 ± 0.03	0.00	0.00	1.02	ns
B. pascuorum	22.7	3.23 ± 1.99 b	0.30 ± 0.25 a	1.27 ± 0.47 ab	0.97 ± 0.30 ab	0.00 a	5.91	**
B. hortorum	11.9	1.37 ± 0.72	0.23 ± 0.19	0.87 ± 0.38	0.53 ± 0.26	0.03 ± 0.03	3.60	ns
							ANOVA 2002	
(*b*) *Bombus* species 2002								
B. terrestris/lucorum	7.5	0.00	0.03 ± 0.03	0.79 ± 0.42	0.67 ± 0.34	0.00	3.66	ns
B. lapidarius	54.2	0.00	0.03 ± 0.03	6.88 ± 3.44	3.76 ± 1.84	0.03 ± 0.03	4.65	*
B. pratorum	0.8	0.00	0.00	0.09 ± 0.05	0.06 ± 0.03	0.00	3.16	ns
B. pascuorum	29.2	0.09 ± 0.00	0.12 ± 0.12	3.45 ± 1.73	2.09 ± 0.77	0.00	4.87	*
B. hortorum	8.3	0.00	0.00	0.94 ± 0.69	0.67 ± 0.42	0.03 ± 0.03	2.47	ns

Numbers represent mean number of bumblebees per plot, per sampling date, with ± standard errors. Letters (a, b, c) indicate differences ($p < 0.05$) following Tukey's Honest Significant Difference tests.

ns, not significant.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

Table 2
Abundance of flowers, grouped by various ecological characteristics, on the different margin treatments

	Field margin type					ANOVA 2001	
	Natural regeneration	Tussocky grass	Wildflower	Tussocky & wildflower	Cropped	$F_{4,8}$	Sig. level
(a) Flower 'group' 2001							
Annuals	0.47 ± 0.33 ab	0.07 ± 0.03 a	2.93 ± 0.35 c	2.57 ± 0.18 bc	1.97 ± 0.78 ac	8.63	**
Perennials & Biennials	5.77 ± 1.18 b	2.03 ± 0.95 ab	11.10 ± 1.23 c	10.07 ± 1.30 c	1.37 ± 0.72 a	26.59	***
Sown species	0.57 ± 0.26 a	0.83 ± 0.39 a	12.57 ± 1.14 b	10.97 ± 0.94 b	0.10 ± 0.10 a	105.05	***
Unsown species	5.67 ± 1.42 b	1.27 ± 0.58 a	1.47 ± 0.34 a	1.67 ± 0.47 a	3.23 ± 1.16 ab	5.19	*
Bee forage species[A]	4.73 ± 0.94 a	1.60 ± 0.78 a	11.73 ± 1.58 b	10.40 ± 1.27 b	1.40 ± 0.68 a	32.25	***
Non-bee forage species	1.50 ± 0.61 ab	0.50 ± 0.29 a	2.30 ± 0.15 b	2.23 ± 0.09 b	1.93 ± 0.59 ab	4.81	*
Abundance score all flowers	6.23 ± 1.31 a	2.10 ± 0.97 a	14.03 ± 1.47 b	12.63 ± 1.24 b	3.33 ± 1.24 a	24.87	***
Species richness of plants in flower	3.80 ± 0.76 ab	1.83 ± 0.94 a	6.30 ± 0.35 b	5.90 ± 0.68 b	1.93 ± 0.47 a	10.99	**
						ANOVA 2002	
(b) Flower 'group' 2002							
Annuals	0.09 ± 0.05	0.03 ± 0.03	2.33 ± 0.90	2.52 ± 1.06	2.36 ± 1.45	2.88	ns
Perennials & Biennials	3.27 ± 0.52 a	1.97 ± 0.84 a	15.03 ± 2.52 b	13.00 ± 2.41 b	1.73 ± 0.93 a	19.60	***
Sown species	0.79 ± 0.36 a	1.18 ± 0.66 a	16.00 ± 3.14 b	14.00 ± 3.10 b	0.06 ± 0.06 a	25.73	***
Unsown species	2.58 ± 0.41	0.82 ± 0.19	1.36 ± 0.28	1.52 ± 0.31	4.03 ± 1.85	2.42	ns
Bee forage species	1.76 ± 0.53 a	1.39 ± 0.74 a	11.88 ± 3.68 b	10.97 ± 3.09 b	1.03 ± 0.37 a	10.49	**
Non-bee forage species	1.61 ± 0.08 ac	0.60 ± 0.12 a	5.48 ± 0.43 b	4.55 ± 0.33 bc	3.06 ± 1.43 ab	7.87	**
Abundance score all flowers	3.36 ± 0.55 a	2.00 ± 0.84 a	17.36 ± 3.41 b	15.55 ± 3.40 b	4.09 ± 1.79 a	14.34	***
Species richness of plants in flower	2.52 ± 0.44 a	1.61 ± 0.63 a	7.18 ± 0.82 b	6.61 ± 0.99 b	2.94 ± 1.16 a	13.32	***

Numbers represent the mean flower abundance score per plot, per sampling date, with ± standard errors. Letters (a, b, c) indicate differences ($p < 0.05$) following Tukey's Honest Significant Difference tests.

ns, not significant.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

[A] See Figs. 2 and 3 for list of bumblebee forage species visited in this study.

Table 3
Details of sown mixtures established on the replicated field margin experiment in 1999

Grass and wildflower mixture		Tussocky grass mixture	
Species	% of total	Species	% of total
Agrostis capillaris	10.0	*Dactylis glomerata*	37.5
Anthoxanthum odoratum	1.0	*Festuca pratensis*	35.0
Briza media	3.0	*Festuca rubra* spp. *commutatus*	25.0
Cynosurus cristatus	36.0	*Deschampsia caespitosa*	1.25
Festuca rubra spp. *commutatus*	10.0	*Phleum pratense*	1.25
Festuca rubra spp. *juncea*	12.0		
Hordeum secalinum	1.0		
Phleum bertolonii	5.0		
Trisetum flavescens	2.0		
Achillea millefolium	0.5		
Centaurea nigra	0.5		
Galium verum	1.5		
Geranium pratense	1.0		
Knautia arvensis	1.0		
Lathyrus pratensis	1.5		
Leontodon hispidus	0.5		
Leucanthemum vulgare	1.0		
Lotus corniculatus	0.5		
Malva moschata	1.0		
Plantago lanceolata	2.0		
Primula veris	1.5		
Prunella vulgaris	2.0		
Ranunculus acris	2.5		
Rhinanthus minor	2.0		
Rumex acetosa	1.0		
Centaurea cyanus	<0.1		
Total seed rate:	37.1 kg/ha		19.8 kg/ha

2001, the increase in bumblebees on the natural regeneration treatment towards the end of the season reflected the increase in flowering (mainly of *C. vulgare*) in that treatment, although the wildflower and split treatments provided a more continuous supply of forage plants (Figs. 4a and b). For 2002, the data demonstrate a continuous supply of flowers in the wildflower and split treatments, with little influence from the natural regeneration plots (Figs. 4c and d).

Significant associations were found between change in bumblebee numbers and temporal variation in flowering of forage plants, and this effect was strongest in 2002 (regression analysis on total bee numbers vs flower abundance of forage species per sampling date across all treatments: $R^2 = 16.5\%$, $p < 0.05$ in 2001; $R^2 = 81.3\%$, $p < 0.001$ in 2002).

4. Discussion

Effects of field margin habitat type on the abundance of foraging bumblebees can be explained to a large extent by the temporal availability of suitable flowers. Similar effects of flower abundance on numbers of bumblebees, butterflies and other pollinating insects have been demonstrated by several authors, in arable and semi-natural areas (e.g. Fussell and Corbet, 1991; Lagerlöf et al., 1992; Dramstad and Fry, 1995; Feber et al., 1996; Kells et al., 2001; Carvell, 2002; Bäckman and Tiainen, 2002). Our study adds valuable information to this debate, as it investigates both the biological and agronomic implications of different methods of habitat creation in arable systems over three years. It is also one of the few randomized, replicated studies comparing the value of different habitats included in the first tranche of the UK Countryside Stewardship Scheme (MAFF, 1999) for foraging bumblebees within intensively managed landscapes.

The two margin treatments containing the sown 'grass and wildflower' mixture were of value to bumblebees in all three years after establishment. Most of the seed mixture components flowered between May and late August, with a few exceptions (e.g. *Geranium pratense* and *Malva moschata*) which failed to establish well at this site. Despite the absence of flower abundance scores from 2000, the data on foraging preferences and from additional vegetation surveys (Meek et al., 2002), combined with these results from 2001 and 2002 show a clear pattern of succession on the sown treatments. The annual Cornflower (*C. cyanus*), thought to be an important pollen source (Engels et al., 1994), was the dominant forage species in year one, with the perennial sward developing and flowers such as *C. nigra*, *L. corniculatus* and *L. pratensis* increasing in abundance

Table 4
List of flowering plant species recorded on the field margins in 2001 and 2002

Sown species	Score 2001	Score 2002	Bee (b) or non-bee (n) forage species[a]	Unsown species	Score 2001	Score 2002	Bee (b) or non-bee (n) forage species[a]
Achillea millefolium	4.4	4.2	n	*Anthriscus sylvestris*		0.1	n
Centaurea cyanus	1.1	0.5	b	*Brassica napus*	0.1	0.0	n
Centaurea nigra	3.0	3.0	b	*Calystegia silvatica*	0.2	0.0	n
Galium verum	0.1	0.0	n	*Cerastium fontanum*		0.1	n
Knautia arvensis	0.3	0.3	n	*Chamerion angustifolium*	0.1	0.0	n
Lathyrus pratensis	1.7	5.3	b	*Cirsium arvense*	2.7	2.1	b
Leontodon hispidus	0.5	0.4	n	*Cirsium vulgare*	6.2	2.7	b
Leucanthemum vulgare	12.8	12.7	b	*Crepis capillaris*	1.1	0.3	b
Lotus corniculatus	11.5	14.1	b	*Daucus carota*	0.9	0.1	n
Malva moschata	0.2	0.7	n	*Epilobium ciliatum*	1.1	0.3	n
Plantago lanceolata		12.2	n	*Epilobium hirsutum*	2.5	0.8	b
Prunella vulgaris	4.3	5.3	b	*Epilobium obscurum*		1.0	n
Ranunculus acris	0.6	2.5	n	*Epilobium parviflorum*		0.3	n
Rhinanthus minor	9.7	9.2	b	*Epilobium tetragonum*		0.1	n
				Fallopia convolvulus		0.1	n
				Fodder radish		0.2	n
				Galium aparine		0.5	n
				Geranium dissectum	0.1	0.2	n
				Geum urbanum		0.1	n
				Heracleum sphondylium	0.3	0.5	n
				Hypochoeris radicata	1.0	2.3	n
				Lapsana communis	1.0	0.8	b
				Matricaria discoidea	0.5	0.1	n
				Matricaria recutita	1.7	0.9	n
				Myosotis arvensis	0.8	0.5	n
				Papaver rhoeas	0.3	0.8	n
				Persicaria maculosa		0.3	n
				Polygonum aviculare		0.5	n
				Pulicaria dysenterica	0.1	0.1	n
				Ranunculus repens	0.1	0.3	n
				Raphanus raphanistrum	0.3	0.7	b
				Rubus fruticosus	0.1	0.2	n
				Rumex crispus		0.1	n
				Rumex obtusifolius		2.0	n
				Senecio jacobaea	1.7	0.7	b
				Senecio vulgare		0.5	n
				Sonchus asper	0.3	0.2	n
				Taraxacum officinale		0.1	n
				Trifolium dubium	0.1	0.0	n
				Trifolium hybridum	0.9	0.0	b
				Trifolium pratense	0.9	0.1	b
				Trifolium repens	0.7	1.1	b
				Tripleurospermum inodorum	0.1	0.3	n
				Vicia tetrasperma	0.3	0.9	n
				Viola arvensis	0.4	0.0	n

Scores represent the mean flower abundance score per plot across all treatments.
[a] Refers to plant species visited by foraging bumblebees in this study.

over the second and third years. In addition to providing attractive forage species for bumblebees, it is likely that the sown wildflower treatments significantly reduced the cover of pernicious annual weeds as observed elsewhere (Marshall and Nowakowski, 1995; Meek et al., 2002).

The natural regeneration treatment, although less costly than the sown mixture option, was inconsistent both between years and across replicates in terms of flowering plant and bumblebee abundance. Patches of flowering thistles, *C. vulgare* and to a lesser extent *C. arvense*, were prominent in 2001 on two replicates and attracted foraging bumblebees of several species. Male bumblebees emerging towards the end of the season are particularly attracted to their flowers which appear at this time (e.g. Barrow, 1983). Whilst being attractive nectar sources (see also Feber et al., 1996), these thistles are pernicious weeds and are not considered agriculturally acceptable, requiring control under the UK In-

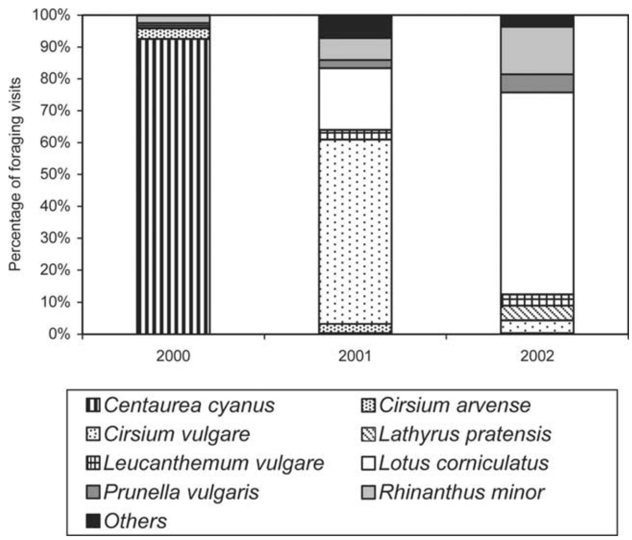

Fig. 2. Flower preferences of foraging bumblebees (all species) across all margin treatments in each year, for species receiving 30 or more visits in total.

jurious Weeds Act of 1959 (www.defra.gov.uk/environ/weedsact/default.htm). In our experiment, cutting at the end of August prevented *C. vulgare* from re-occurring the following year, as would be expected from this monocarpic biennial. Subsequently however, few other species in the developing perennial sward of the regeneration treatment produced flowers that were attractive to foraging bees. There is therefore no guarantee that field margins left to natural regeneration will provide a sustained supply of suitable forage for bumblebees, unless detailed knowledge of the seed or bud bank is available. Furthermore, natural regeneration may take at least five years to produce the equivalent diversity and density of perennial forage plants to sown swards, as suggested by Corbet (1995) when considering Schmidt's analysis of a 10-year succession (Schmidt, 1976 , as listed in Ellenberg, 1988).

The six *Bombus* species recorded during this study all belonged to the 'mainland ubiquitous group' (Williams, 1982), which is the usual assemblage found on arable farmland in the UK (Fussell and Corbet, 1991; Kells et al., 2001). *B. pratorum* accounted for a low proportion of records in both 2001 and 2002, but this is perhaps not surprising as the species tends to be observed more frequently in gardens (Prŷs-Jones and Corbet, 1991), possibly due to its agility in foraging at a range of flower depths and angles such as might be found in horticultural situations. *B. pratorum* is also known to establish its colonies early so worker numbers peak in advance of the other species. This highlights the importance of the sampling period which, in this study, could have been

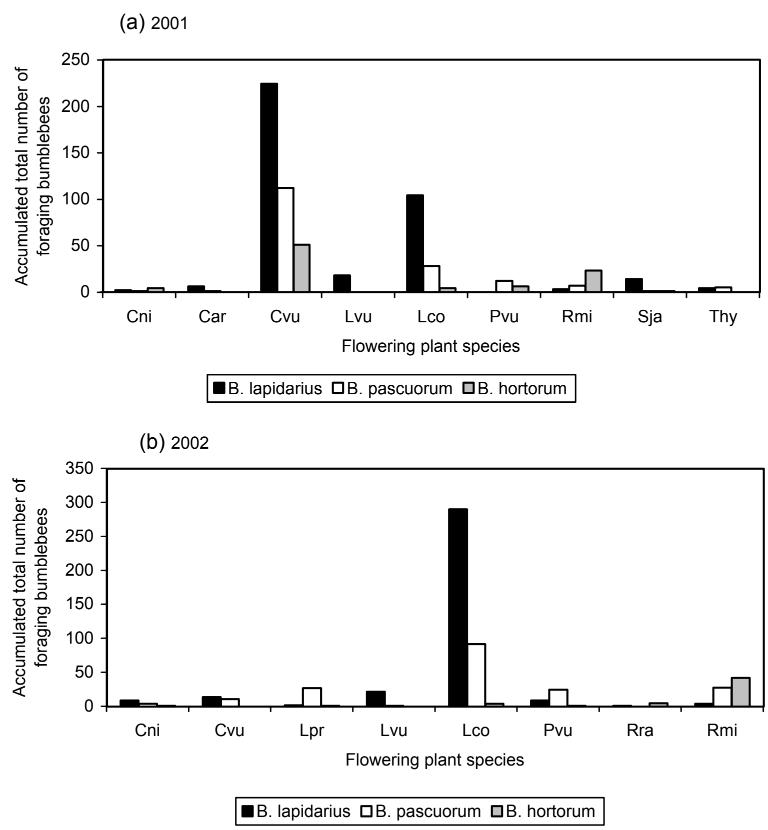

Fig. 3. Flower visits of three bumblebee species during (a) 2001 and (b) 2002. Key to plant species as follows: Cni, *Centaurea nigra*; Car, *Cirsium arvense*; Cvu, *Cirsium vulgare*; Lpr, *Lathyrus pratensis*; Lvu, *Leucanthemum vulgare*; Lco, *Lotus corniculatus*; Pvu, *Prunella vulgaris*; Rmi, *Rhinanthus minor*; Rra, *Raphanus raphanistrum*; Sja, *Senecio jacobaea*; Thy, *Trifolium hybridum*.

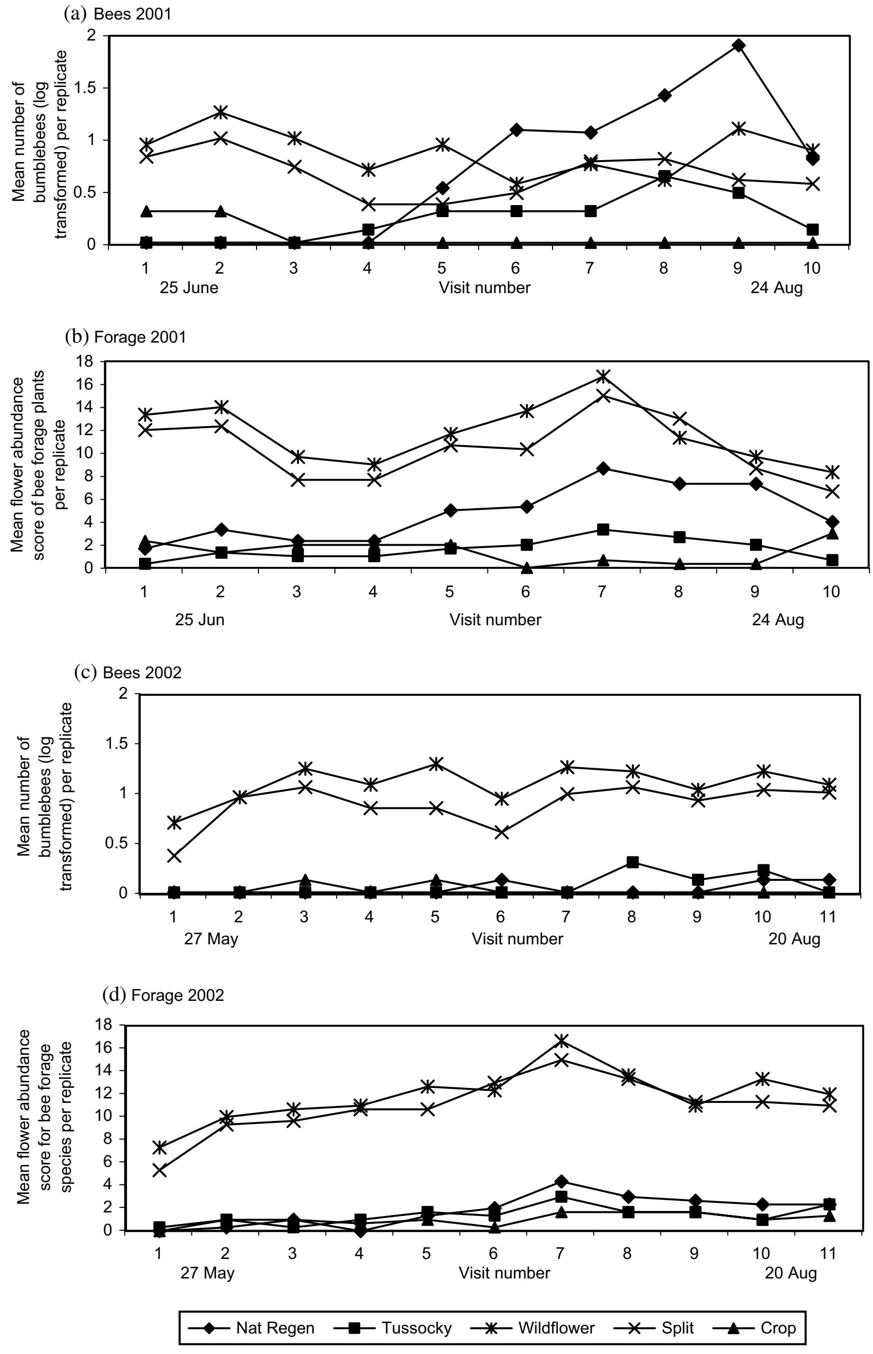

Fig. 4. Temporal changes in abundance of: (a) bumblebees in 2001; (b) flowers of bumblebee forage species in 2001; (c) bumblebees in 2002; (d) flowers of forage species in 2002, across the different field margin treatments.

brought forward to early May to assess whether the margin treatments provided resources for queens and early workers during colony initiation. The results suggest that this could be the case for the treatments containing sown wildflowers, but not for the natural regeneration, tussocky grass or cropped treatments.

In terms of forage plant visitation, the results of our study support the general hypothesis that bumblebees utilize flowers with corolla lengths most closely corresponding to their tongue lengths (Ranta and Lundberg, 1980). Further analysis of the flower visitation data might have included the calculation of preference indices, as defined by Murdoch (1969) and modified by Cowgill et al. (1993), which account for the relative numbers of flowers available from each species. This calculation was not compatible with the simplified flower abundance scores recorded here, and hence absolute preferences for particular species must be interpreted with caution. Nevertheless, the majority of visits were to perennials as would be expected for bumblebees requiring high nectar and pollen rewards per flower (Fussell and Corbet, 1992a). The potential for including additional such species (e.g. *T. pratense* or other legumes) in semi-permanent wildflower mixtures on farmland requires further investigation. Carreck and Williams (2002) have demonstrated that mixtures of certain nectar- and pollen-producing annuals can also attract a variety of insect pollinators, and may be more practical for farmers with short-term opportunities. In all cases, the requirements of the full assemblage of pollinator groups should be considered. Whilst there is substantial overlap between the key nectar source species of adult butterflies and those of bumblebees (e.g. flowers in the Fabaceae and Asteraceae families) (Feber et al., 1996), the hoverflies and solitary bees often visit more open-flowered composites or umbellifers (Apiaceae) (Cowgill et al., 1993) and might be excluded if only long-corolla flowers were sown.

The relative merits of different field margin management treatments, and conflicts between them, have been reviewed previously (e.g. Smith et al., 1993; Marshall and Moonen, 2002). As we have shown, newly created field margin treatments differ in their value as bumblebee foraging habitats but likewise, they may differ in terms of providing suitable nesting habitats. Nest-seeking queens have been shown to prefer patches of undisturbed tall grassland with a tussocky structure (Svensson et al., 2000). These tend to attract the small mammals whose disused nests or holes are often used by bumblebees (Fussell and Corbet, 1992b). The sown ‘tussocky grass’ treatment in this experiment, together with the grass half of the ‘split’ plots, had almost developed its intended structure by the third year having been left uncut since year one. With continued minimal intervention, we would expect this treatment to have much potential for the provision of bumblebee nesting sites, and propose the ‘split’ treatment as a means of restoring both foraging and nesting components together.

Conserving viable bumblebee populations in the agricultural landscape will undoubtedly involve a number of complex factors, and we do not attempt here to provide solutions to habitat provision for all life-cycle stages. It should be remembered that the abundance of workers (which contributed to the majority of records in this study) may in itself be a poor indication of population viability in the social Hymenoptera. These issues need to be addressed at the landscape scale, where measures of nest density and colony success may be the best means of evaluating different methods of habitat creation or enhancement (Goulson et al., 2002). Future research should also consider the spatial distribution of newly created habitats as their influence probably extends beyond individual farm boundaries, and the implications of their siting for any nearby semi-natural vegetation (Swash and Belding, 1999).

5. Conclusions

Our study highlights one of the key practical conflicts involved with enhancing biodiversity on uncropped arable field margins: the need to control agriculturally unacceptable weeds (e.g. *Cirsium* spp.) without compromising the long-term establishment of beneficial species. The recent Countryside Survey of the UK confirms that agricultural changes have favoured tall, competitive plants associated with fertile conditions, particularly on field boundaries, at the expense of herbaceous perennials such as *L. pratensis* and *T. pratense* (Haines-Young, 2000). Such perennials and their associated vegetation communities are favoured by the longer-tongued bumblebee species, most of which have shown serious declines and represent an essential pollinator compartment (Corbet, 2000). This reinforces the benefits of sowing carefully selected perennial mixtures on arable field margins where knowledge of the seed bank for natural regeneration is lacking. As we have demonstrated, these mixtures can be established and maintained to provide a continuity of forage resources for at least three years with minimal herbicide application under a simple cutting regime. It should now be possible to develop rapid and cost-effective indicators of field margin quality for bumblebees, which could be identified from this, and other research (e.g. Firbank et al., 2001; Kells et al., 2001). This approach to monitoring will be needed in order for measures that enhance bumblebee populations in arable landscapes to be applied across Britain and the rest of Europe.

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