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Providing foraging resources for bumblebees in intensively farmed landscapes

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Abstract

Habitat loss and the intensification of farming practices have caused severe declines in the range and abundance of many bumblebee species in the UK. This study examines the long-term effectiveness of four different management strategies to enhance and restore bumblebee foraging habitat on arable field margins in two regions with markedly contrasting landscape structure, farming systems and amount of semi-natural habitat. Bumblebees were monitored on 120 field margins in July and August, together with estimates of flower abundance and the vegetation composition. There were no differences in the abundance and diversity of the bumblebee assemblage between the two regions (East Anglia and the West Midlands), despite a greater abundance of flowers and flowering species on the lighter soils of the West Midlands. Very few bumblebees were recorded on intensively managed cereal field margins due to the lack of dicot species. Conservation headlands supported a significantly greater number of flowering dicots, but the majority of these were annuals which did not provide good forage for bumblebees. From an agronomic and ecological perspective, the removal of field margins from the cropping system was the best strategy for providing foraging habitat for bumblebees. Non-crop habitat resulting from natural regeneration provided good foraging habitat for bumblebee species, but most of the key forage species were pernicious weeds of agriculture (*Cirsium* spp.). Sowing non-crop field margins with wildlife seed mixtures had the potential for providing the best foraging habitat for bumblebees, so long as preferred forage species were introduced (e.g. *Trifolium pratense*). Further research is required to refine and target this management prescription for bumblebee conservation in the wider countryside.

Keywords: Habitat creation; Restoration; Field margins; Conservation headlands; Seed mixtures; Pollen and nectar resources

1. Introduction

In recent years many bumblebee (*Bombus*) species have shown serious declines in abundance and marked contractions in geographic range in both Europe and North America (e.g. Williams, 1982; Rasmont, 1995; Banaszak, 1996; Buchmann and Nabhan, 1996; Westrich, 1996). In the UK, three species have become extinct and a further five have become so restricted in their distribution that they have been placed on the UK Biodiversity Action Plan (UK BAP) (UK Biodiversity Steering Group, 1995) as priorities for conservation. The primary cause of these declines is thought to be the post-war intensification of agriculture (Osborne and Corbet, 1994). Traditional mixed livestock and arable farming has declined to be replaced with simplified cropping patterns which are applied to increasingly consolidated parcels of land. This has caused the loss and fragmentation of essential foraging and nesting habitats for bumblebees, such as species-rich hay meadows, field headlands and hedgerows. This is coupled with the increasingly intensive management of each land parcel, including the greater usage of fertilisers and insecticides, and shorter fallow periods. The net result has been the significant decline in abundance of a number of highly preferred bumblebee forage plants in the UK Countryside, especially members of the Fabaceae and Lamiaceae (Carvell et al., 2001).

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Bumblebees provide an essential pollination service for both semi-natural and agricultural ecosystems (Corbet et al., 1991; Kevan and Baker, 1983; Free, 1993). In order to maintain this service they require suitable sites for nesting and hibernation, and a continuous supply of pollen and nectar resources throughout the spring and summer months (Steffan-Dewenter and Tscharntke, 1999). Declines in the abundance and diversity of bumblebees may therefore have serious implications for plant community composition, the conservation of small, fragmented populations of native plant species (Kwak et al., 1991; Steffan-Dewenter and Tscharntke, 1999), and the yield of many entomophilous crops (Holm, 1966; Willmer et al., 1994). It is therefore essential to maintain and restore suitable habitats for bumblebees and other pollinators in agricultural landscapes. Indeed, this has been recently recognised as a globally important issue by the launch of the International Pollinator Initiative in 2000 (http://www.biodiv.org/doc/meetings/sbstta/sbstta-07/official/sbstta-07-09-add1-en.pdf).

Recent changes to European agri-environmental policy recognise the need to conserve and enhance biodiversity in intensively managed agricultural landscapes (Bignal, 1998). With this in mind, it is becoming increasingly important to develop practical, cost-effective prescriptions to manage farmland for the benefit of wildlife. In the UK, this policy is delivered nationwide through the Countryside Stewardship Scheme (Defra, 2002). The prescriptions available for habitat restoration and management on arable land were developed primarily from an experimental agri-environmental scheme (the Arable Stewardship Pilot Scheme (ASPS)) which was established in 1998 (MAFF, 1998). The scheme offered opportunities and financial incentives to maintain and restore wildlife habitats on intensively managed arable land by following a number of prescribed methods, including whole-field habitat enhancement (overwinter stubbles and spring fallow, undersown cereals and grass leys), and habitat creation at the edges of fields. The ASPS examined two contrasting field margin management philosophies: namely the enhancement of biodiversity within the crop through the reduction of herbicide and pesticide use at the field edge (conservation headlands), compared with the removal of the field margin from cropping followed by targeted habitat creation, either by sowing a seed mixture or allowing natural regeneration from the seed bank.

Conservation headlands encourage the survival of broad-leaved annuals and their associated insects (Critchley et al., 2004). However, annual plants, with some exceptions, do not generally provide a good supply of nectar and pollen. Nectar-rich perennial and biennial species are the favoured forage for bumblebees (Fussell and Corbet, 1992). The effectiveness of conservation headlands in providing bumblebee forage resources has been examined in the field, but the results have been inconclusive. Significantly higher numbers of bumblebees visited non-crop, naturally regenerated field margins compared with conservation headlands (Kells et al., 2001). However, a more recent study found no significant difference in the abundance of bumblebees between these habitat types (Meek et al., 2002a).

Non-crop field margins sown with tussocky grass species provide suitable habitat for animals for which a dense, sheltered vegetation structure is important, such as hibernating carabid and staphylinid beetles, spiders, small mammals, nesting bumblebees and certain breeding birds (Smith et al., 1999; Marshall and Moonen, 1998; Thomas et al., 1992; Svensson et al., 2000; Collins et al., 2003a,b; Kells and Goulson, 2003). Similarly, sowing non-crop field margins with perennial wildflowers can enhance the number of nectar- and pollen-feeding invertebrates, including butterflies, bumblebees, honeybees and hoverflies (e.g. Largerlöf et al., 1992; Feber et al., 1996; Carvell et al., 2004), especially if the margin occupies a sunny, sheltered position (e.g. Dover, 1996, Pywell et al., 2004). However, most of these studies have focused on a single location where geographic factors, such as the size of the local species pool and individual populations, may have a strong influence on the results. Furthermore, most studies have been conducted on newly created habitats in the early stages of succession.

In this study we examined the long-term effectiveness of both crop and non-crop ASPS field margin options in providing foraging habitat for bumblebees on a large number of sites situated in two contrasting landscape types. In order to achieve this we tested the following hypotheses:

- H1: *Regional effects on bumblebees*: the abundance and diversity of bumblebees are greater in the more enclosed, mixed farming region of the West Midlands, compared with the open, intensive arable region of East Anglia;
- H2: *Value of conservation headlands*: bumblebee species richness and abundance are significantly higher on conservation headlands compared with equivalent margins under conventional cereal production;
- H3: *Value of non-cropped habitats*: species richness and abundance of bumblebees are higher on non-cropped margin habitats compared with equivalent areas cropped with cereals;
- H4: *Value of sown non-crop habitats*: field margins sown with dicot seed mixtures provide better foraging habitat for bumblebees than naturally regenerated margins or conservation headlands.

The results are discussed in the context of (i) the ecological role of the different habitats in bumblebee conservation, and (ii) the implications for future agri-environment scheme policies aimed at the enhancement and creation of habitat for bumblebees on farmland.

2. Methods

2.1. Site selection

In 1998 the Arable Stewardship Pilot Scheme (ASPS) was established in two regions of the UK with markedly contrasting soil types, topography and farming systems (Fig. 1). The East Anglian Pilot Area was situated in the south-eastern lowlands of England on calcareous heavy soils and loams. The region is characterised by large, open fields supporting predominantly intensive arable farming. There is comparatively little remnant semi-natural habitat. In contrast, the West Midlands Pilot Area was situated in the central midlands of England on soils with a light to medium texture. This region is characterised by smaller, enclosed fields supporting more mixed and varied farming systems. More semi-natural habitat has survived in this region.

The sample comprised 19 farms in East Anglia and 17 farms in the West Midlands which had ASPS management agreements in place in 1999. In the summer of 2003 bumblebees were monitored on a number of field margins on each farm where ASPS options had been implemented. Sample field margins were selected using proportionate random sampling, such that the number of margins selected on a farm was in proportion to the number of margins of that type on the farm. This ensured that the sample was representative of the statistical population of margins under each management option. Three ASPS options were sampled for bumblebees (Table 1): conservation headland with no fertilisers (3b) (16 sites), naturally regenerated field margins (4c) (18 sites) and field margins sown with a wildlife seed mixture (5) (28 sites). These were selected on the basis of uptake and their potential value as foraging habitat for bumblebees. The non-crop margin options (4c and 5) remained static from 1999. However, the conservation headland option (3b) can move around the farm each year with the cereal crop rotation. Therefore, new samples of these were selected for the 2003 survey. A paired approach was adopted in which bumblebee numbers were estimated from both the targeted option and, at the same time, from a nearby, conventionally managed cereal field margin with similar aspect and boundary type. This acted as a control treatment. It was possible to pair a very high proportion (97%) of the ASPS options with a cereal control margin in this way. Bumblebees were recorded on a total of 75 crop and non-crop option margins in the East Anglia and 45 margins in the West Midlands.

Table 1
Sample size for the two Arable Stewardship Scheme Pilot Areas and options recorded in 2003

	East Anglia	West Midlands	Total
Conventional cereal field margin	36	22	58
3b (Conservation headland)	13	3	16
4c (Natural regeneration margin)	11	7	18
5 (Wildlife seed mixture margin)	15	13	28
Total	75	45	120

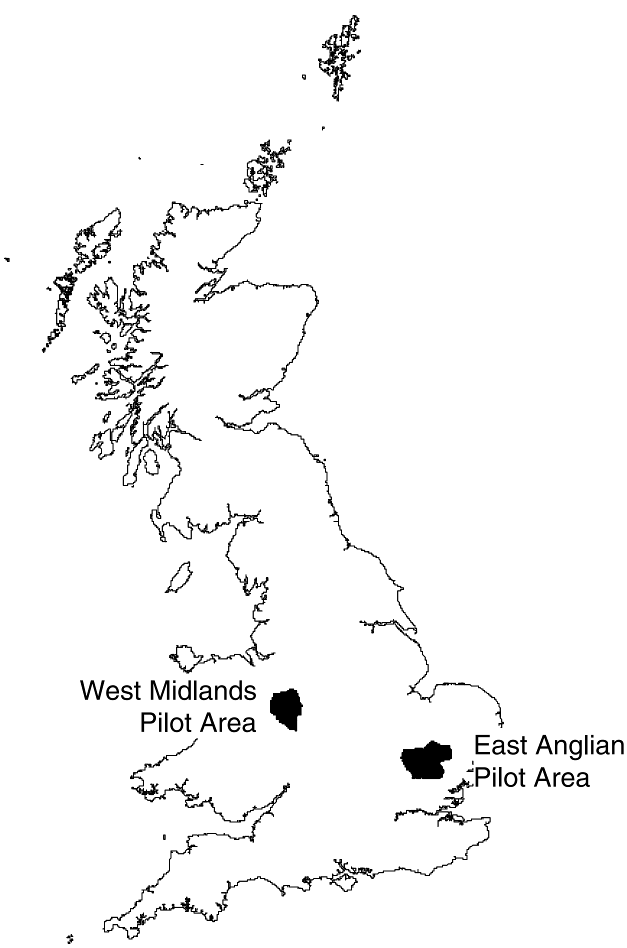

Fig. 1. A map showing the location of the two Arable Stewardship Scheme Pilot Areas.

2.2. Bumblebee monitoring

Bumblebees were recorded on the sample ASPS options in July and again in August. At each field margin site, a 100 m long sampling zone was randomly located, but not within 10 m of either end of the margin. On each visit, foraging bumblebees were counted along linear transects of 100×6 m sited along the centre line of options established in strips (Banaszak, 1980). For options established as blocks which were less than 100 m in length, bumblebees were counted along two parallel transects of 50×6 m. The crop edge and hedge base were avoided. A note was made of the plant species on which each bumblebee was foraging. *Bombus terrestris* and *B. lucorum* were collectively recorded, as workers of these species cannot be reliably distinguished in the field (Prŷs-Jones and Corbet, 1991). The cuckoo bumblebees (subgenus *Psithyrus* spp.), which are brood parasites of 'true' *Bombus* species, were counted together as a group for analysis, but honeybees and solitary species were not noted. Walks were carried out between 10.00 am and 17.00 pm when weather conformed to Butterfly Monitoring Scheme (BMS) rules (temperature above 13 °C with at least 60% clear sky, or 17 °C in any sky conditions; no count at all if raining) (Pollard and Yates, 1993). The shade (ambient) temperature, percentage sunshine and wind speed were recorded at the end of each transect walk.

2.3. Vegetation survey

Vegetation sampling was undertaken in the same sampling zone as that of the bumblebee counts, but encompassed the full width of the field margin (up to 12 m) rather than a 6 m width along the centre line. In the sampling zone, twenty 0.5×0.5 m quadrats were randomly positioned. The presence of all vascular plant species rooted in each quadrat was recorded, giving a frequency out of 20 for each species. This was converted to percentage frequency for analysis. Plant species nomenclature follows Stace (1997).

2.4. Flower survey

Following each bumblebee walk, the flowering dicotyledon component of the vegetation along each transect was recorded to give a measure of the forage resource availability. All flowering dicots were identified in the field (122 species) and the approximate abundance of single flowers and multi-flowered stems for groups such as umbellifers, labiates and vetches were scored using a simple floristic index (Carvell et al., 2004): (1) rare (approximately 1–25 flowers); (2) occasional (approximately 26–200 flowers); (3) frequent (approximately 201–1000 flowers); (4) abundant (approximately 1001 + flowers); (5) super-abundant (more than 5000 flowers). Flower abundance scores for the individual species were later combined into 18 broad groups to allow analysis following the approach described in Pywell et al. (2004): Convolvulaceae (bindweeds); Boraginaceae (borages); bramble/Rosaceae; Caryophyllaceae; Chenopodiaceae (fat hens); Asteraceae (thistles/daisies) red/purple; Asteraceae (thistles/daisies) yellow/white; Geraniaceae (cranesbills); Brassicaceae (crucifers); Onagraceae (epilobiums); Lamiaceae (dead nettles); Fabaceae (legumes) red/purple; Fabaceae (legumes) yellow/white; Polygonaceae; Scrophulariaceae; Apiaceae (umbellifers) and small-flowered annuals. In addition, scores for all flower groups were summed to give a comparative value for total flower abundance averaged across both visits.

2.5. Statistical analysis

A detrended correspondence analysis (DCA) (Hill, 1979) on plant frequency data was used to determine the variation in the plant communities between the 120 field margins. There was a unimodal response of species along the first axis, confirming that this was the appropriate method to use. DCA was undertaken using Canoco (version 4.5) software (ter Braak and Šmilauer, 1998).

Differences between field margin types were further investigated by comparing total species number of vascular plants (species richness), and species number of crops, dicotyledons, monocotyledons, annuals and perennials (excluding crops). In addition, the flower counts from each visit were combined to describe differences in forage resources between sites in terms of overall number of flowering plants (flower species richness) and total flower abundance.

Counts of individual bumblebee species from the July and August visits were summed for each margin. In addition, the summary groupings of total bumblebee abundance and species richness, and the functional grouping of short-tongued (*B. terrestris*/*lucorum*, *B. pratorum* and *B. lapidarius*) and long-tongued species (*B. pascuorum* and *B. hortorum*) (Prŷs-Jones and Corbet, 1991) were calculated for each site. Logarithmic transformation of all the count data was undertaken prior to analysis to normalise residual variation.

Overall differences in the plant groups, forage resources, and both individual and summary bumblebee variables between the two pilot areas were examined using two-sample *t*-tests. Differences between the individual field margin options and the paired conventional cereal field margin controls were examined using two-way analysis of variance (ANOVA) with site and treatment as factors. Finally, differences between the three field margin treatments (3b, 4c and 5) were examined using a one-way ANOVA with Tukey's Honest Significant difference test. Prior to this analysis, the effect of site was removed by subtracting the count or scores for the paired conventional cereal field margin control from that of the margin treatment.

The relationship between logarithmic bumblebee abundance and environmental factors, such as abundance scores for the different flower groups, was investigated using forward stepwise regression analysis. During the model-fitting process, Alpha- to-enter and Alpha-to-remove were set at 0.15, and only final models in which all variables were significant ($p \leqslant 0.05$) were accepted. All analyses were performed using Minitab 13 statistical software (Ryan et al., 2000).

3. Results

Across all 120 field margins a total of 1376 true bumblebees representing seven species were recorded. These included *B. ruderatus* recorded on one transect in East Anglia, which is a species not commonly seen on farmland in the UK. In addition, 58 individuals of the subgenus *Psithyrus* spp. were recorded.

3.1. Variation in plant communities between treatments

During the survey a total of 234 plant species (including crops) were recorded. The DCA indicated that the first two ordination axes accounted for 12.8% of the variation in the vegetation data between the sites. There was clear separation of the different field margin types (Fig. 2). The crop and non-crop field margin habitats clearly separated along axis 1 (Fig. 2a). The conventionally managed cereal field margin had the lowest axis 1 scores (0–3). There was considerable overlap with the ordination space occupied by the conservation headland sites (3b). The non-crop field margin options (4c and 5) were generally well separated from the crop and conservation headlands along axis 1, with scores of 2–4. The option 5 sites had the most extreme axis 1 scores. There was also some separation of the naturally regenerated margins (4c) and those sown with a wildlife seed mixture (5) along axis 2. The option 5 sites had a wider range of axis 2 scores (0–4) compared with option 4c (2–4).

Species with large weights in the DCA which were associated with the conventionally managed cereal field margins and conservation headlands were crop species, such as *Triticum aestivum* (Fig. 2b), together with the most frequent annual weed species of cereal fields: monocotyledons *Alopecurus myosuroides*, *Poa annua*, *Anisantha sterilis*; and dicotyledons *Galium aparine*, *Fallopia convolvulus*, *Veronica persica*, *Polygonum aviculare*, *Chenopodium album* and *Tripleurospermum inodorum*. Species associated with the naturally regenerated and sown field margins (4c and 5) were perennial monocots, such as *Dactylis glomerata*, *Holcus lanatus*, *Poa trivialis*, *Festuca rubra* and *Arrhenatherum elatius*, together with perennial dicots, *Cirsium arvense*, *C. vulgare*, *Carduus nutans*, *Urtica dioica*, *Rumex obtusifolius* and *Plantago major*.

The greatest number of preferred bumblebee forage plants from this study (shown in bold on Fig. 2b) were associated with the non-crop field margin options (4c and 5). Several of these species, such as *C. vulgare* and *C. nutans*, were associated with the cultivated natural regeneration margins (4c). Whereas others, such as *Trifoilum pratense*, *Lotus corniculatus* and *Phacelia tanacetifolia*, were introduced to sites in the wildlife seed mixtures (option 5).

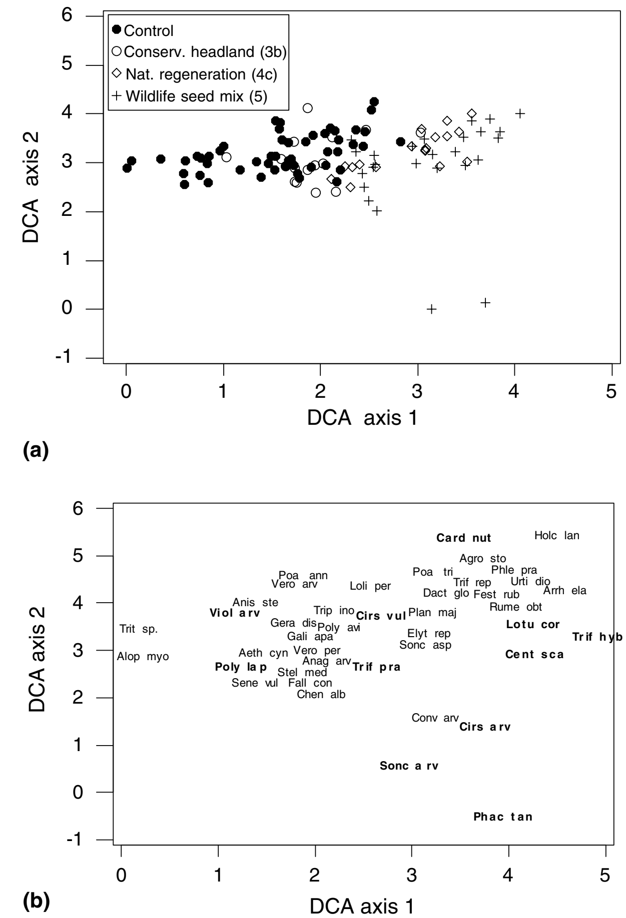

Fig. 2. Scatter plots of axes 1 and 2 from detrended correspondence analysis (DCA) of all field margin types. (a) sites; (b) species: only those with a minimum weight of >55 in the analysis are shown for clarity, together with the ten most preferred bumblebee forage plants from this study (in bold). Overlapping species labels have been moved slightly for clarity. Abbreviations of species names: **Monocots**: Agro sto = *Agrostis stolonifera, Alop myo = Alopecurus myosuroides, Anis ste = Anisantha sterilis, Arrh ela = Arrhenatherum elatius, Dact glo = Dactylis glomerata, Elyt rep = Elytrigia repens, Fest rub = Festuca rubra, Holc lan = Holcus lanatus, Loli per = Lolium perenne/multiflorum, Phle pra = Phleum pratense, Poa tri = Poa trivialis, Poa ann = Poa annua, Trit sp. = Triticum aestivum.* **Dicots**: *Aeth cyn = Aethusa cynapium, Anag arv = Anagallis arvensis, Card nut = Carduus nutans, Cent sca = Centaurea scabiosa, Chen alb = Chenopodium album, Cirs arv = Cirsium arvense, Cirs vul = Cirsium vulgare, Conv arv = Convolvulus arvensis, Fall con = Fallopia convolvulus, Gali apa = Galium aparine, Gera dis = Geranium dissectum, Lotu cor = Lotus corniculatus, Phac tan = Phacelia tanacetifolia, Plan maj = Plantago major, Poly avi = Polygonum aviculare, Poly lap = Polygonum lapathifolia, Rume obt = Rumex obtusifolius, Sene vul = Senecio vulgaris, Sonc arv = Sonchus arvensis, Sonc asp = Sonchus asper, Stel med = Stellaria media, Trif hyb = Trifolium hybridum, Trif pra = Trifolium pratense, Trif rep = Trifolium repens, Trip ino = Tripleurospermum inodorum, Urti dio = Urtica dioica, Vero arv = Veronica arvensis, Vero per = Veronica persica, Viol arv = Viola arvensis.*

3.2. Differences between the pilot areas

There were relatively few differences in the overall field margin vegetation composition, regardless of

Table 2
Differences in the mean species richness and abundance of vegetation, forage resources, and bumblebees per 100 m transect between the two Pilot Areas

	East Anglia ($n = 75$)	West Midlands ($n = 45$)	t-test	P-value
Vegetation species richness				
All species	14.4 ± 1.3	18.2 ± 1.5	−1.90	0.061ns
Crop	0.8 ± 0.1	0.9 ± 0.1	−1.09	0.279ns
Monocotyledons	3.2 ± 0.3	4.8 ± 0.4	**−3.09**	**0.003****
Dicotyledons	10.4 ± 1.1	12.5 ± 1.4	−1.19	0.236ns
Annuals	8.6 ± 0.8	8.5± 0.9	−0.08	0.934ns
Perennials	4.9 ± 0.7	8.8 ± 1.1	**−3.02**	**0.003****
Forage resources				
Total flower abundance	6.3 ± 0.8	10.8 ± 1.2	**−3.07**	**0.003****
Total flower species richness	6.4 ± 0.6	9.1 ± 0.90	**−2.41**	**0.018***
Bumblebees				
B. terrestris/lucorum	1.5 ± 0.4	3.6 ± 1.0	−1.79	0.055ns
B. lapidarius	8.0 ± 2.6	4.0 ± 1.4	0.47	0.637ns
B. pratorum	0.01 ± 0.01	0.3 ± 0.1	**−2.52**	**0.015***
B. pascuorum	1.7 ± 0.6	2.9 ± 1.1	−1.10	0.277ns
B. hortorum	0.5 ± 0.3	0.2 ± 0.1	0.65	0.515ns
Psithyrus spp.	0.6 ± 0.2	0.3 ± 0.2	1.44	0.152ns
Short-tongued species	9.5 ± 2.9	7.9 ± 2.1	−0.57	0.567ns
Long-tongued species	2.2± 0.9	3.1 ± 1.1	−0.92	0.360ns
Total bumblebees	12.4 ± 3.7	11.2 ± 2.9	−0.68	0.498ns
Species richness bumblebees	1.4 ± 0.2	2.0 ± 0.4	−1.30	0.199ns

Significant differences are given in bold. Bumblebee count data were log transformed prior to analysis; untransformed means (±SE) per 100 m are presented for clarity. NS = no significant difference.

* $p \leqslant 0.05$.

** $p \leqslant 0.01$.

treatment, between the two pilot areas (Table 2). Field margins in the West Midlands contained on average more species per 100 m (18.2 ± 1.5) compared with East Anglia (14.4 ± 1.3), but these differences were not quite significant ($p = 0.06$). However, margins in the West Midlands contained significantly more monocot species than East Anglia (4.8 ± 0.4 compared with 3.2 ± 0.3), and significantly more perennial species (8.8 ± 1.2 compared with 4.9 ± 0.7). Similarly, total abundance of dicot flowers and the number of flowering dicot species were both significantly greater in the West Midlands (10.8 ± 1.2 and 9.1 ± 0.9 respectively) compared with East Anglia (6.3 ± 0.8 and 6.4 ± 0.6) (Table 2). Despite these significant differences in the vegetation and forage resource, there were few differences in the abundance and species richness of bumblebees between the two pilot areas. Only *B. pratorum* was significantly more abundant in the West Midlands (0.3 ± 0.1 per 100 m) compared with East Anglia (0.01 ± 0.01).

3.3. Conservation headlands

There were a large number of significant differences in the vegetation composition of the conservation headlands (option 3b) compared with the conventionally managed cereal field margins (control) (Table 3). Conservation headlands contained on average more species per 100 m (15.4 ± 1.9) compared with the control (7.5 ± 1.0). This was primarily due to the significantly greater number of dicot species present on conservation headlands (12.2 ± 1.8) compared with the control (3.8 ± 0.7). The majority of these species were annuals. It follows that the conservation headlands also supported a significantly greater abundance of dicot flowers and species richness of flowering plants compared with the cereal control. However, there were no significant differences in the abundance of any bumblebee species, functional groupings, or overall species richness between the conservation headlands and the cereal field margin controls.

3.4. Habitat creation by natural regeneration

The non-crop, naturally regenerated field margin vegetation (option 4c) contained on average four times the number of plant species (29.7 ± 1.4) compared with the cereal field margin control (7.0 ± 1.0) (Table 4). Much of this difference was due to the greater number of dicot species on the 4c margins. There was an approximately equal split between annual and perennial species. The number of crop species was significantly higher on the control compared with the 4c margins. Flowering dicots were also significantly more abundant on the 4c margins in the July and August period compared with the controls (Table 4). The diversity of the forage resource was also significantly greater, with four times the

Table 3
Differences in the mean species richness and abundance of vegetation, forage resources, and bumblebees per 100 m transect between conventionally managed cereal field margins and conservation headlands (3b)

	Cereal field margin ($n = 13$)	Conservation headland (3b) ($n = 13$)	ANOVA $F_{1,12}$	P
Vegetation species richness				
All species	7.5 ± 1.0	15.4 ± 1.9	**14.30**	**0.003****
Crop	1.1 ± 0.1	1.0 ± 0.1	0.19	0.673ns
Monocotyledons	2.5 ± 0.5	2.1 ± 0.4	0.62	0.445ns
Dicotyledons	3.8 ± 0.7	12.2 ± 1.8	**22.15**	**0.001*****
Annuals	5.1 ± 0.8	10.9 ± 1.3	**11.55**	**0.005****
Perennials	1.3 ± 0.4	3.5 ± 0.9	**6.85**	**0.023***
Forage resources				
Total flower abundance	2.1 ± 0.6	7.2 ± 1.9	**7.43**	**0.018***
Total flower species richness	2.7 ± 0.5	6.6 ± 1.4	**7.26**	**0.020***
Bumblebees				
B. terrestris/lucorum	0.0 ± 0.0	0.1 ± 0.1	1.00	0.500ns
B. lapidarius	0.0 ± 0.0	1.3 ± 0.9	3.40	0.107ns
B. pascuorum	0.0 ± 0.0	0.1 ± 0.1	2.18	0.165ns
Short-tongued species	0.0 ± 0.0	1.5 ± 1.1	2.97	0.111ns
Long-tongued species	0.0 ± 0.0	0.1 ± 0.1	2.18	0.165ns
Total bumblebees	0.0 ± 0.0	1.6 ± 1.2	3.10	0.104ns
Species richness bumblebees	0.0 ± 0.0	0.5 ± 0.3	2.96	0.111ns

Significant differences are given in bold. Bumblebee count data were log transformed prior to analysis; untransformed means (±SE) per 100 m are presented for clarity. Ns = no significant difference.
* $p \leqslant 0.05$.
** $p \leqslant 0.01$.
*** $p \leqslant 0.001$.

Table 4
Differences in the mean species richness and abundance of vegetation, forage resources, and bumblebees per 100 m transect between conventionally managed cereal field margins and naturally regenerated field margins (4c)

	Cereal field margin ($n = 16$)	Nat. regeneration margin (4c) ($n = 16$)	ANOVA $F_{1,15}$	P
Vegetation species richness				
All species	7.0 ± 1.0	29.7 ± 1.4	**144.66**	**<0.001*****
Crop	1.0 ± 0.0	0.1 ± 0.1	**169.00**	**<0.001*****
Monocotyledons	3.2 ± 0.7	6.6 ± 0.7	**13.59**	**0.003****
Dicotyledons	2.8 ± 0.5	23.2 ± 1.3	**167.78**	**<0.001*****
Annuals	4.1 ± 0.6	15.6 ± 1.6	**34.06**	**<0.001*****
Perennials	1.8 ± 0.5	14.1 ± 1.4	**63.94**	**<0.001*****
Forage resources				
Total flower abundance	2.8 ± 0.9	15.1 ± 1.9	**36.07**	**<0.001*****
Total flower species richness	3.2 ± 0.8	12.7 ± 1.3	**39.53**	**<0.001*****
Bumblebees				
B. terrestris/lucorum	0.1 ± 0.1	4.0 ± 2.0	**16.82**	**0.001*****
B. lapidarius	0.0 ± 0.0	9.6 ± 4.6	**17.07**	**0.001*****
B. pratorum	0.0 ± 0.0	0.1 ± 0.1	1.00	0.333ns
B. pascuorum	0.1 ± 0.1	3.4 ± 1.3	**21.43**	**<0.001*****
B. hortorum	0.0 ± 0.0	0.3 ± 0.1	**4.69**	**0.047***
Psithyrus spp.	0.0 ± 0.0	1.0 ± 0.5	**5.50**	**0.033***
Short-tongued species	0.1 ± 0.1	13.6 ± 5.1	**28.23**	**<0.001*****
Long-tongued species	0.1 ± 0.1	3.7 ± 1.4	**22.37**	**<0.001*****
Total bumblebees	0.2 ± 0.1	18.3 ± 5.2	**73.18**	**<0.001*****
Species richness bumblebees	0.2 ± 0.1	2.7 ± 0.3	**60.76**	**<0.001*****

Significant differences are given in bold. Bumblebee count data were log transformed prior to analysis; untransformed means (±SE) per 100 m are presented for clarity. Ns = no significant difference.
* $p \leqslant 0.05$.
** $p \leqslant 0.01$.
*** $p \leqslant 0.001$.

number of flowering species on the 4c margins (12.7 ± 1.3) compared to the control (3.2 ± 0.8). With the exception of *B. pratorum*, all bumblebee species were significantly more abundant on the naturally regenerated margins compared with the conventional cereal field margins (Table 4). Overall, there was a mean of 18.3 (±5.2) bumblebees recorded per 100 m in July and August on the 4c margins compared with 0.2 (±0.1) on the control margins. Similarly, 2.7 (±0.3) bumblebee species were present on the 4c margins compared with 0.2 (±0.1) on the controls.

3.5. Habitat creation by sowing wildlife seed mixtures

The non-crop field margins sown with a wildlife seed mixture (option 5) contained more than twice the number of species (23.2 ± 1.9) than the conventionally managed cereal field margin (9.8 ± 1.3) (Table 5). Moreover, the option 5 margins contained a significantly greater number of monocots, dicots and perennials. There were no differences in the number of annuals between the two margin types. Flowering dicots were also significantly more abundant and diverse (12.0 ± 0.9) on the sown margins compared with the cereal controls (4.6 ± 0.8) (Table 5). With the exception of *B. hortorum*, all bumblebee species were significantly more abundant on the margins sown with the wildlife seed mixtures compared with the conventional cereal field margins (Table 5). Overall, there was a mean of 28.6 (±6.6) bumblebees recorded per 100 m in July and August on the option 5 margins compared with just 0.3 (±0.1) on the control margins. Similarly, 3.0 (±0.3) species were recorded on the option 5 margins compared with 0.2 (±0.1) on the controls.

3.6. Comparison of crop and non-crop habitat creation

Bumblebee abundance per 100 m (0.2 ± 0.1) and species richness (0.2 ± 0.1) were very low on the conventionally managed cereal field margin controls (Fig. 3). Similarly, few bumblebees were recorded on the conservation headlands (3b) (1.3 ± 0.9). In contrast, a comparatively large number (18.3 ± 4.9) and species richness (3.6 ± 0.5) of bumblebees were recorded on the non-crop, natural regeneration margins (4c). However, the greatest abundance (37.8 ± 8.6) and species richness (4.1 ± 0.5) of bumblebees were found on the non-crop field margins created by sowing a wildlife seed mixture (5).

After allowing for site effects, there were a large number of significant differences in the vegetation composition, forage resources, and bumblebee abun-

Table 5
Differences in the mean species richness and abundance of vegetation, forage resources, and bumblebees per 100 m transect between conventionally managed cereal field margins and field margins sown with wildlife seed mixtures (5)

	Cereal field margin ($n = 28$)	Wildlife seed mix margin (5) ($n = 28$)	ANOVA $F_{1,27}$	P
Vegetation species richness				
All species	9.8 ± 1.3	23.2 ± 1.9	**32.87**	**<0.001*****
Crop	1.0 ± 0.1	1.0 ± 0.2	0.03	0.874ns
Monocotyledons	2.5 ± 0.4	5.3 ± 0.6	**20.33**	**<0.001*****
Dicotyledons	6.4 ± 1.1	17.1 ± 1.7	**28.55**	**<0.001*****
Annuals	6.3 ± 0.8	10.1 ± 1.4	2.96	0.099ns
Perennials	2.5 ± 0.5	12.2 ± 1.3	**45.69**	**<0.001*****
Forage resources				
Total flower abundance	4.0 ± 0.8	14.3 ± 1.4	**54.06**	**<0.001*****
Total flower species richness	4.6 ± 0.8	12.0 ± 0.9	**45.21**	**<0.001*****
Bumblebees				
B. terrestris/lucorum	0.2 ± 0.1	7.0 ± 1.2	**49.97**	**<0.001*****
B. lapidarius	0.1 ± 0.1	21.2 ± 6.1	**63.22**	**<0.001*****
B. pratorum	0.0 ± 0.0	0.4 ± 0.18	**6.45**	**0.017***
B. pascuorum	0.04 ± 0.04	6.9 ± 2.0	**37.82**	**<0.001*****
B. hortorum	0.0 ± 0.0	1.4 ± 0.9	3.60	0.069ns
Psithyrus spp.	0.0 ± 0.0	0.9 ± 0.4	**8.98**	**0.006****
Short-tongued species	0.3 ± 0.1	28.6 ± 6.6	**93.27**	**<0.001*****
Long-tongued species	0.04 ± 0.04	8.3 ± 2.5	**36.08**	**<0.001*****
Total bumblebees	0.3 ± 0.1	37.8 ± 8.6	**106.24**	**<0.001*****
Species richness bumblebees	0.2 ± 0.1	3.0 ± 0.3	**90.39**	**<0.001*****

Significant differences are given in bold. Bumblebee count data were log transformed prior to analysis; untransformed means (±SE) per 100 m are presented for clarity. Ns = no significant difference.
* $p \leqslant 0.05$.
** $p \leqslant 0.01$.
*** $p \leqslant 0.001$.

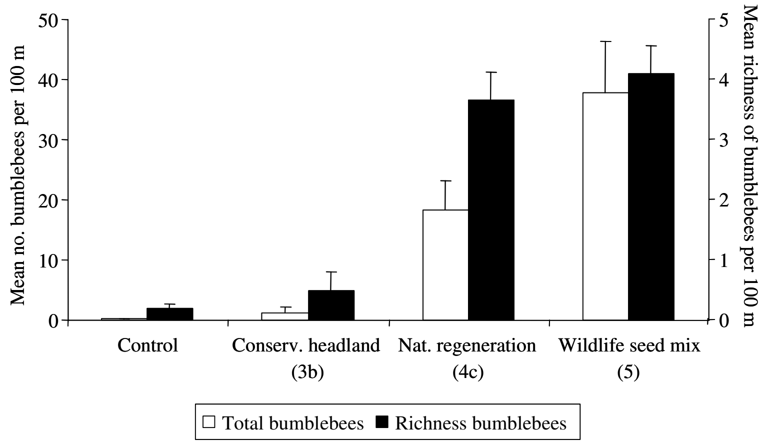

Fig. 3. Comparison of bumblebee abundance and species richness per 100 m on the different AS options and the cereal field margin control.

Table 6
Differences in the mean species richness and abundance of vegetation, forage resources, and bumblebees per 100 m transect between conservation headlands (3b), naturally regenerated field margins (4c) and field margins sown with wildlife seed mixtures (5)

	Conservation headland (3b) ($n = 13$)	Nat. regeneration margin (4c) ($n = 16$)	Wildlife seed mix margin ($n = 28$)	ANOVA $F_{2,54}$	P
Vegetation species richness					
All species	7.9a ± 2.1	22.30b ± 1.8	12.0a ± 2.1	**10.14**	**<0.001*****
Crop	−0.1ab ± 0.2	−0.9b ± 0.1	−0.04a ± 0.3	**4.22**	**0.021***
Monocotyledons	−0.4a ± 0.5	3.4b ± 0.9	3.0b ± 0.7	**6.89**	**0.002****
Dicotyledons	8.4a ± 1.8	19.9b ± 1.5	9.2a ± 1.7	**11.73**	**<0.001*****
Annuals	5.8ab ± 1.7	11.1b ± 1.9	2.3a ± 1.3	**7.77**	**0.001*****
Perennials	2.1a ± 0.8	12.1b ± 1.5	9.8b ± 1.4	**11.07**	**<0.001*****
Forage resources					
Total flower abundance	5.1a ± 1.9	12.3b ± 2.0	10.3ab ± 1.4	**3.52**	**0.036***
Total flower species richness	3.9a ± 1.5	9.5b ± 1.5	7.4ab ± 1.1	**3.37**	**0.042***
Bumblebees					
B. terrestris/lucorum	0.1a ± 0.1	3.9b ± 1.9	6.8b ± 1.2	**11.39**	**<0.001*****
B. lapidarius	1.3a ± 0.9	9.6ab ± 4.6	21.1b ± 6.1	**8.42**	**0.001*****
B. pratorum	0.0 ± 0.0	0.1 ± 0.1	0.4 ± 0.2	2.76	0.073ns
B. pascuorum	0.1a ± 0.1	3.3b ± 1.3	6.8b ± 2.0	**8.58**	**0.001*****
B. hortorum	0.0 ± 0.0	0.3 ± 0.1	1.4 ± 0.9	1.13	0.331ns
Psithyrus spp.	0.0 ± 0.0	1.0 ± 0.5	0.9 ± 0.4	2.10	0.133ns
Short-tongued species	1.5a ± 1.1	13.5b ± 5.1	28.3b ± 6.5	**13.08**	**<0.001*****
Long-tongued species	0.1a ± 0.1	3.6b ± 1.4	8.2b ± 2.5	**8.91**	**<0.001*****
Total bumblebees	1.6a ± 1.2	18.1b ± 5.2	37.5b ± 8.6	**16.75**	**<0.001*****
Species richness bumblebees	0.5a ± 0.3	2.6b ± 0.3	2.7b ± 0.3	**14.07**	**<0.001*****

Site effects were removed by subtracting the value from the paired conventionally managed cereal field margin prior to analysis. Bumblebee count data were log transformed prior to analysis. Untransformed means (±SE) per 100 m are presented for clarity. Significant differences are given in bold. Means with the same letter are not significantly different ($p \leqslant 0.05$) following Tukey's Honest Significant difference test. Ns = no significant difference.

* $p \leqslant 0.05$.

** $p \leqslant 0.01$.

*** $p \leqslant 0.001$.

dance and species richness between the different field margin types (Table 6). The naturally regenerated field margins (4c) contained significantly more plant species (22.3 ± 1.8) compared with either the field margins sown with a wildlife seed mixture (5) (12.0 ± 2.1) or the conservation headlands (3b) (7.9 ± 2.1). The non-crop margins (4c and 5) had a significantly greater number of monocot and perennials species than the conservation headlands. Furthermore, the natural regeneration margins contained a significantly higher number of dicot species than either the conservation headlands or the wildlife seed mixtures. Finally, the natural regeneration margins had a significantly greater number of annuals than the margins sown with wildlife seed mixtures.

There were also significant differences in bumblebee forage resources between the margin types (Table 6). The naturally regenerated margins contained a significantly greater abundance and species richness of dicot flowers in July and August than the conservation headland, but not the margins sown with wildlife seed mixtures.

Significantly greater numbers of *B. terrestris/lucorum* and *B. pascuorum* were recorded on the non-crop field margins (options 4c and 5) compared with the conservation headland (3b). Similarly, significantly higher numbers of *B. lapidarius* were recorded on the non-crop margins sown with wildlife seed mixtures compared with the conservation headlands. Total bumblebees were significantly greater on the wildlife seed mixture (37.5 ± 8.6) and natural regeneration margins (18.1 ± 5.2) compared with the conservation headlands (1.6 ± 1.2). There was a similar pattern for the richness of bumblebee species, with more than 2.5 species recorded on average on the non-crop margins compared with 0.5 species on the conservation headlands.

3.7. Forage plant preferences

During the study a total of 1434 foraging bumblebees (including *Psithyrus* spp.) were observed visiting 49 flowering plant species. The plant species receiving the most foraging visits varied between the different field margin types, reflecting the relative abundance of those species flowering on each margin treatment (Fig. 4). However, *C. arvense* and *C. vulgare* together accounted for a significant proportion of the foraging visits in all margins. The conventionally managed crop and conservation headlands provided the most limited range of forage plants. Annual dicot weeds, such as *Viola arvensis*, accounted for half of the foraging visits (6) in the crop. Over 80% of the foraging visits in the conservation headland were to *Cirsium* spp. Dicots of the Asteraceae family, such as *Cirsium* spp., *C. nutans* and *Sonchus arvensis*, accounted for over 70% of the foraging visits on the non-crop margins produced by natural regeneration. The non-crop margins sown with wildlife seed mixtures provided the greatest range of forage species. On these margins, sown forage species (*T. pratense*, *T. hybridum*, *L. corniculatus*, *P. tanacetifloia*) accounted for a significant proportion (28%) of foraging visits.

The short-tongued species group *B. terrestris/lucorum* showed a preference for foraging on *C. arvense* followed by *C. vulgare* and *P. tanacetifolia* (Fig. 5). These three species accounted for 56% of visits. *B. lapidarus* has an intermediate tongue length and showed a marked preference for foraging on *C. arvense* (37% of visits), followed by *T. hybridum*, *S. arvensis* and *C. vulgare*. The most abundant long-tongued species was *B. pascuorum*. This species showed a preference for foraging on *T. pratense* and *C. vulgare*, together accounting for 50% of the visits. The other long-tongued species, *B. hortorum*, also showed a strong preference for *T. pratense* (33%), followed by *C. vulgare*.

Stepwise multiple regression analyses allowed the above relationships to be examined in more detail (Table 7). All of the multiple regression models were highly significant, and with the exception of two species recorded in low numbers (*B. pratorum* and *B. hortorum*), most had a high degree of explanatory power, with R^2 values in excess of 65%. The results highlighted the importance of the red/purple- flowered legume group (Fabaceae) in explaining the abundance of most bumblebee species with the exception of *B. terrestris/lucorum* and *B. pratorum*. Similarly, the yellow/white-flowered legumes were positively associated with the abundance of all species except *B. terrestris/lucorum* and *Psithyrus* spp. Total flower abundance, red/purple legumes and Asteraceae (thistles/daisies) were the most important

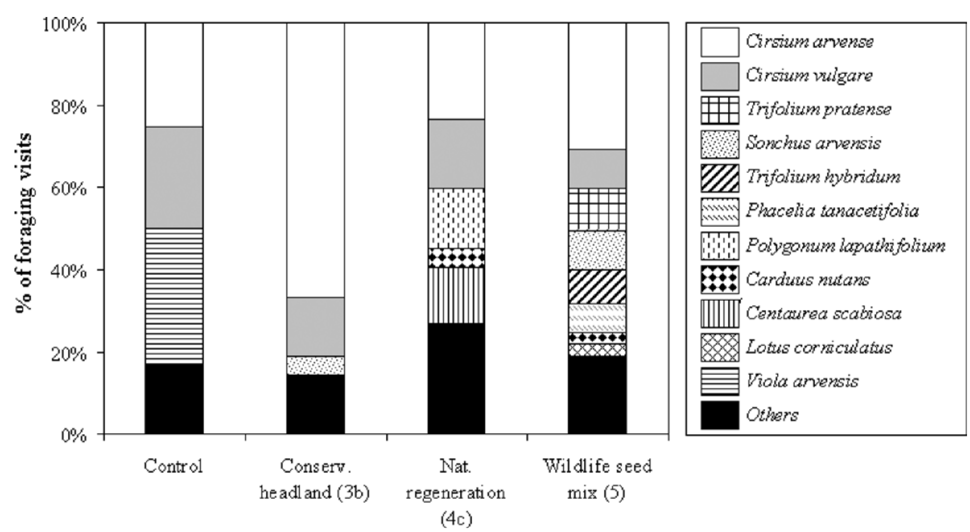

Fig. 4. Flower preferences of foraging bumblebees (all species) across the four field margin types sampled in this study.

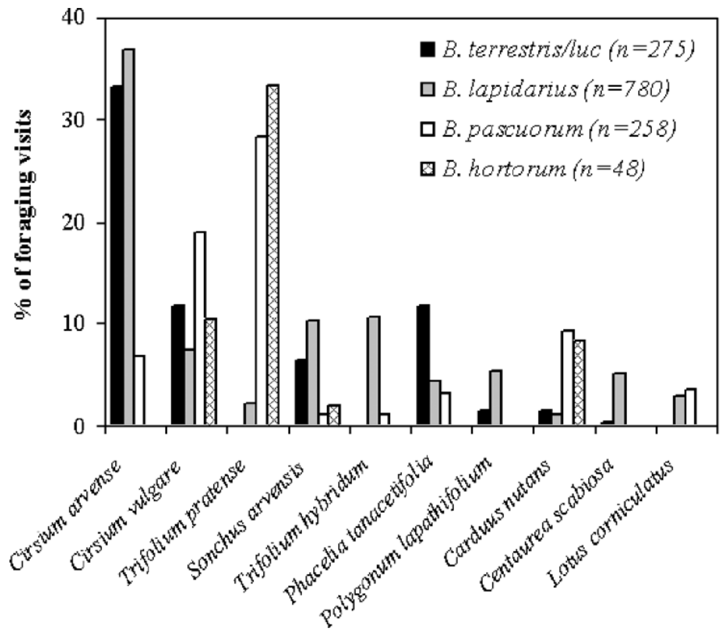

Fig. 5. Pattern of flower visitation of the four most abundant bumblebee species.

variables in explaining the total numbers of bumblebees. Small-flowered annuals had a strong negative effect. Red/purple thistles and daisies, yellow/white legumes, Convolvulaceae (bindweeds) and Boraginaceae (borages) were all important in explaining variation in bumblebee species richness between sites. There was a strong, positive association between borages and total flower abundance in explaining the numbers of the short-tongued generalists *B. terrestris/lucorum*. Similarly, both red/purple thistles and daisies, and legumes were important in explaining the abundance of *B. lapidarius*. Total flower abundance and yellow/white legumes were associated with large numbers of *B. pratorum*. Red/purple legumes, and thistles and daisies were significantly correlated with the abundance of *B. pascuorum*. Finally, legume flowers were important in explaining the abundance of *B. hortorum*.

4. Discussion

4.1. The bumblebee assemblage on farmland

This study confirmed the relatively impoverished nature of the bumblebee assemblage present within these two intensively farmed landscapes of lowland Britain. Six of the bumblebee species recorded belonged to the widespread lowland group defined by Williams (1982). Of these, 78% of the sample were classified as short-tongued, generalist species (*B. terrestris*, *B. lucorum*, *B. lapidarius*, *B. pratorum*) and the remaining 22% were long-tongued species (*B. pascuorum*, *B. hortorum*). Species within this latter group have undergone the most dramatic declines in geographic range and abundance in recent years. Indeed most of the threatened UK Biodiversity Action Plan (BAP) listed bumblebees are long-tongued species. Many of these species are associated with extensive areas of unimproved, flower-rich habitat supporting large numbers of flowers with long corollas, especially those belonging to the plant families Lamiaceae and Fabaceae (Falk, 1991). A recent analysis of change in the UK flora based on the Countryside Survey found that more than 70% of bumblebee forage plants declined, and nearly 30% had shown significant declines between 1978 and 1998 (Carvell et al., 2001). Amongst these were a number of preferred forage plants for long-tongued bumblebees (e.g. *T. pratense*, *L. corniculatus*).

However, in this study we recorded small numbers of the Nationally Scarce, long- tongued species *B. ruderatus* on one transect in East Anglia. Others were also noted close to transects in the same area. This species was formerly widespread in southern Britain, but has undergone dramatic declines such that there were fewer than 10 confirmed post-1980 sites. The BAP for this species requires the enhancement of existing populations and re-introduction at other suitable localities, so that by 2010 there are 20 viable populations within the historic range (UK Biodiversity Group, 1998). Our results suggest that habitat creation under the Arable Stewardship Pilot Scheme may be making an important contribution towards this policy objective.

4.2. Creation and enhancement of bumblebee foraging habitat on farmland

The observed effects of field margin type on the abundance of foraging bumblebees was largely explained by the availability of suitable flowers. In the last

Table 7
Summary of stepwise multiple regression models showing the habitat characteristics influencing bumblebee numbers on the different field margin options

	B. terrestris/lucorum	*B. lapidarius*	*B. pratorum*	*B. pascuorum*	*B. hortorum*	*Psithyrus* spp.	Short-tongued species	Long-tongued species	Total bumblebees	Richness bumblebees
Convolvulaceae (bindweeds)						0.147***				0.64***
Boraginaceae (borages)	0.122***			0.055*		0.050**	0.078*	0.055*	0.097*	0.36***
Caryophyllaceae									−0.193*	
Chenopodiaceae (fat hens)		0.120*								
Asteraceae (thistles/daisies) red/purple		0.137***		0.072***		0.038***	0.093**	0.076***	0.084**	0.348***
Asteraceae (thistles/daisies) yellow/white						−0.059***			−0.059*	
Geraniaceae (cranesbills)	−0.078*					−0.081*				
Brassicaceae (crucifers)						−0.119***				
Onagraceae (epilobiums)				0.083***				0.080***		0.261**
Lamiaceae (dead nettles)		−0.193**					0.123*			
Fabaceae (legumes) red/purple		0.279***		0.293***	0.074*	0.070**	0.257***	0.296***	0.275***	0.330*
Fabaceae (legumes) yellow/white		0.115**	0.074***	0.063*	0.059**			0.083**		0.332**
Small-flowered annuals	−0.092***						−0.109***		−0.013***	
Apiaceae (umbellifers)							−0.232*			
Others	−0.070*						−0.108**		−0.099*	
Total flower abundance	0.045***		0.062***				0.059***		0.078***	0.040*
Total flower species richness						0.021***				
F ratio	42.36	44.04	22.97	43.25	13.62	17.90	45.36	41.64	54.30	46.55
D.f.	5114	5114	2117	5114	2117	8111	8111	5114	8111	7112
Significance	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
R^2 (%)	65.0	65.9	28.0	65.5	18.9	56.3	76.6	64.6	79.6	74.4

Numbers presented are regression co-efficients.
$^{*}p \leqslant 0.05$.
$^{**}p \leqslant 0.01$.
$^{***}p \leqslant 0.001$.

40–50 years many plant species associated with lowland farmed landscapes have shown marked contractions in geographic range and severe declines in abundance (Wilson et al., 1999; Smart et al., 2000; Preston et al., 2002). The impoverished flora of arable land now typically comprises a small number of species which can tolerate modern, intensive farming practices, including autumn sowing, the frequent use of selective herbicides, high rates of fertiliser application and efficient seed cleaning (Robinson and Sutherland, 2002). The majority of these species, such as *Galium aparine*, *Polygonum aviculare* and *Alopecurus myosuroides*, do not provide suitable forage for bumblebees. Intensively managed cereal field margins have also been shown to provide poor habitat for other nectar-feeding invertebrates, such as butterflies (Pywell et al., 2004), as well as other groups, such as carabids, spiders and harvestmen (Meek et al., 2002b).

Restriction in the use of herbicide, and in some cases fertiliser, in conservation headlands has been shown to encourage the survival of annual dicots and their associated insects (Critchley et al., 2004). However, many arable plant communities have become impoverished following years of intensive management, and, with few exceptions (e.g. *Viola arvensis*), they do not provide good forage for bumblebees (Fussell and Corbet, 1992). These factors probably explained the lack of a positive effect of this management practice on bumblebee abundance.

There are good agronomic and ecological arguments for removing the edges of fields from arable cropping. These areas are typically less fertile, and more prone to drought and shading than other parts of the field. As such they typically produce lower yields (Boatman, 1992; Cook and Ingle, 1997), and often require greater inputs of pesticide and fertiliser for a lower economic return (de Snoo and Chaney, 1999). In addition, field edges often harbour populations of pernicious weeds (e.g. *Anisantha sterilis, G. aparine* and *Elytrigia repens*) which can spread into the crop and prove difficult to control (Marshall and Moonen, 2002). The vegetation community which develops on arable field margins by natural succession following removal from cropping will be dependant on the management history, the surrounding vegetation, and the composition and size of the seed bank (Firbank et al., 1993). The development of very diverse vegetation is likely to be constrained by the high residual soil fertility, the increasingly impoverished species pool in arable landscapes, together with evidence that the overall size of the seed bank in arable soils has declined markedly in recent years (Robinson and Sutherland, 2002).

Nevertheless, in this study relatively diverse plant communities with an average of 29.7 (±1.4) species per 100 m were recorded on the field margins following five years of natural regeneration. The management prescription for these margins required shallow (100–150 mm) cultivation in the spring or autumn of every year or every other year without the application of herbicide or fertilisers (MAFF, 1998). The aim of this management is to maintaining open vegetation for scarce arable plants. In the long term, this type of management encouraged the dominance of widespread perennial grasses and forbs which were originally present at the field edge and hedge bottom, and regenerate by vegetative means (e.g. *Cirsium arvense*, *Trifolium repens*, *E. repens*), or have a biennial life history (e.g. *C. vulgare*, *C. nutans*). Frequent cultivation prevented the plant communities from becoming dominated by grasses as was found for non-rotational setaside land (Firbank et al., 2003), and therefore maintained their value as bumblebee habitat. It was the abundance of perennial and biennial thistle species which primarily accounted for the greater numbers of foraging bumblebees found in this field margin type. However, the value of this habitat for foraging bees proved to be very variable, and most of the key forage plants it produced were pernicious weeds (*Cirsium* spp.) which require control under the Weeds Act (1959).

Introducing species to field margins by sowing a wildlife seed mixture offers the opportunity for directing vegetation succession and therefore achieving a more targeted habitat restoration for bumblebees. This type of field margin is only cultivated once to provide a seed bed for establishing the sown species, and is managed by cutting thereafter. Other studies have demonstrated that carefully designed wildflower seed mixtures can be very successful in supplying forage resources for a range of pollinating insects, including butterflies (Feber et al., 1996; Pywell et al., 2004) and bumblebees (Carreck et al., 1999; Bäckman and Tiainen, 2002; Carvell et al., 2004). The resultant dicot-rich vegetation is also good habitat for a wide range of other invertebrate groups (Meek et al., 2002b). Furthermore, sowing a field margin with perennial species will provide a barrier against the spread of pernicious weeds from the field edge into the crop (Marshall and Moonen, 2002). However, not all of the species sown in the wildlife seed mixture option were suitable forage plants for bumblebees, and some (e.g. *Zea mays*) may have had a negative impact by suppressing the abundance of unsown forage species.

The potential value of targeted habitat creation for bumblebees by sowing mixtures of preferred forage species has been recognised. In 2001 Defra announced revised prescriptions for wildlife enhancement on arable farmland which included a specific pollen and nectar seed mixture comprising legumes, such as *T. pratense* and *Lotus corniculatus* (option WM2, Defra, 2001). Further research is required to test the effectiveness of this prescription in providing forage for bumblebees. However, preliminary results suggest that this approach might be very effective, with an average of 323 (±125) bumblebees recorded per 100 m from two visits in July and August of 2003 on equivalent field margins managed under this prescription (B. Meek, personal communication).

4.3. Implications for bumblebee conservation in the wider countryside

The conservation measures required to sustain bumblebee populations within intensively managed landscapes are complex and poorly understood at present. They are likely to require the provision of suitable habitats for all life-cycle stages, including a season-long succession of nectar and pollen resources, together with mating, nesting and hibernation sites. This study has only focused on the effectiveness of management prescriptions in providing late-summer forage resources. More work is required to determine the importance of other factors, such as early season forage, and the quality of nesting and hibernation sites, for bumblebee population fitness. Indeed, most studies of bumblebees, including this one, make the assumption that an abundance of workers is positively correlated with the success of bumblebee colonies. Empirical measurements of colony density (Chapman et al., 2003) and fitness (Goulson et al., 2002) are now possible, and would be a more effective means of measuring the success of habitat restoration and enhancement. Finally, there have been very few studies of the responses of insect pollinators to habitat change at the landscape scale (Bronstein, 1995; Debinski and Holt, 2000; Steffan-Dewenter and Tscharntke, 2002a,b). These studies suggest that bumblebees may respond to spatial and temporal changes in resource supply at scales greater than a single farm, and that habitat restoration measures may need to be targeted at the regional, rather than the local level. Future research is therefore required to determine how the quantity and spatial distribution of habitats influences the fitness and dynamics of bumblebee populations in the whole landscape.

5. Conclusions

To return to the original hypotheses:

H1: *Regional effects on bumblebees*: despite a significantly greater abundance of dicot flowers and flowering species on the lighter soils of the West Midlands, there were no significant differences in the abundance or richness of bumblebee species recorded on the field margins between the two pilot areas;

H2: *Value of conservation headlands*: restrictions to herbicide and fertiliser application on conservation headlands resulted in a significantly greater number of non-crop plant species, especially dicots, together with a greater abundance and species richness of flowering dicots. However, the majority of these species were annuals which did not provide good forage for bumblebees. This resulted in no significant differences in bumblebee abundance or species richness between conservation headlands or conventional cereal field margins;

H3: *Value of non-cropped habitats*: removing the field margin from the cropping system and allowing vegetation to develop by natural regeneration provided good foraging habitat for bumblebee species compared with conventionally cropped margins. However, the value of this habitat proved to be very variable, and most of the key forage plants it produced were pernicious weeds (*Cirsium* spp.) which require control;

H4: *Value of sown non-crop habitats*: sowing non-crop field margins with wildlife seed mixtures had the potential for providing the best foraging habitat for bumblebees in intensively managed arable landscapes provided preferred forage species (e.g. *T. pratense*, *L. corniculatus*, *Borago officinalis*) are included in the mixture.

This study has demonstrated the value of different habitats in providing forage for bumblebee populations in the late summer. However, the provision of pollen and nectar in spring and early summer, together with suitable nesting and hibernation habitat, are required for the effective conservation of bumblebee populations in the wider countryside. Further work is required to define and test the effectiveness of agri-environment management prescriptions which will provide these essential habitats.

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