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The value of uncropped field margins for foraging bumblebees

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Synopsis

The intensification of agriculture has led to declines in species diversity and abundance within groups of certain flora and fauna. Bumblebees (*Bombus* spp.) are one group where a decline has been documented, and it is thought to be attributable to a decrease in forage resources and potential nest sites. As bumblebees play an important role in the pollination of many entomophilous crops, this decline could impact on agricultural productivity. We examined the role of naturally regenerated field margins in providing forage plants on land where nectar resources are otherwise impoverished. The following question was addressed – Are naturally regenerated unsprayed field margins more attractive to foraging bumblebees and honeybees than cropped field margins managed as conservation headlands? Significantly more bees visited naturally regenerated field margins than cropped field margins. Honeybees (*Apis mellifera*), *Bombus terrestris*, and *Bombus lapidarius* were the most commonly observed bee species. Different wildflower species within the naturally regenerated margins varied greatly in relative number of visits received, and bumblebee species were found to prefer different flower species to honeybees. The potential role that naturally regenerated field margins could play in the conservation of bumblebee species, and the implications for other species of flora and fauna, are discussed.

Introduction

In recent years there have been attempts to introduce conservation measures into arable systems (Firbank *et al.* 1991; Dennis & Fry 1992; Saunders *et al.* 1992; Dramstad & Fry 1995), and to reverse the detrimental effects of agricultural intensification on such species as rare arable weeds (Wilson 1999), chickfood insects (Aebischer 1991), beneficial insects (MAFF 1999), bumblebees and solitary bees (Williams 1982; O'Toole 1994), butterflies (Thomas 1995), songbirds (Fuller *et al.* 1995) and gamebirds (Potts 1986). As field edges produce lower yields than any other part of the field (Boatman & Sotherton 1988), often require increased effort for lower economic return (de Snoo & Chaney 1999), and generally contain the greatest floral diversity (Marshall 1989; de Snoo 1995; Wilson & Aebischer 1995), it is unsurprising that these are the areas which have become the focus of the conservation effort. The U.K. has seen the introduction of the Countryside Stewardship Scheme (CSS), and more recently the Arable Stewardship Scheme (ASS), both of which recognise the potential importance of field margins in agro-ecosystem conservation (MAFF 1998, 1999).

There are currently three main management regimes applied to land between the crop and the field boundary. Firstly, a narrow sterile strip immediately adjacent to the crop, created by ploughing or herbicide application (Fielder 1987), may act as a defence against weed ingress from the field boundary. Secondly, the outer strip of the crop may be maintained free from herbicide and pesticide application; such strips are known as conservation headlands. These encourage survival of certain broad-leaved annuals, and their associated insects. Thirdly, an uncropped strip, usually 6–12 m, wide, may be left around the edge of the field. Uncropped strips can be naturally regenerated, or sown with a seed mixture (Critchley 1996; MAFF 1999). Naturally regenerated, regularly cultivated, uncropped margins were primarily designed to conserve rare local arable flora and their associated fauna by providing an area free from both agrochemicals and competition from other species (Schumacher 1987; Boatman 1998). Sowing an uncropped margin with a grass or wildflower seed mixture can meet particular objectives, e.g. grass margins can provide winter cover for game birds, flowering plant margins can be used to enhance integrated pest management regimes (de Snoo & Chaney 1999).

The nature of vegetated margins makes them valuable habitats for invertebrates (Moreby & Southway 1999), birds (Rands 1985; Stoate 1999), and small mammals (Tew *et al.* 1994). Broad-spectrum insecticides used on crops to control aphids cause high mortality of the larval stages of other insects (Boatman & Sotherton 1988), many of which are parasitic on aphids; unsprayed margins offer a refuge for such beneficials (Chiverton & Sotherton 1991). Uncropped, unsprayed field margins have been found to be more attractive than conservation headlands for ground-dwelling invertebrates (Hawthorne & Hassell 1994; White & Hassell 1994). Both conservation headlands and uncropped margins can act as buffers to protect adjacent terrestrial and riparian habitats from agricultural pollution, for example by limiting pesticide drift and surface run-off (Boatman 1988; de Snoo 1995). Vegetated field margins, both cropped and uncropped, thus have a potentially valuable role to play in the implementation of conservation schemes on arable land (Smallshire & Cooke 1999). However, it is the subsequent management of these that has greatest impact on the resultant ecology, especially in the case of uncropped margins (Smith *et al.* 1993). Nature and frequency of cultivation, cutting, and spraying all have an effect, although in most field margin management schemes, spraying (other than spot treatments) is rare. Rare arable flora tend to benefit from annual ploughing (Critchley 1996).

Agricultural intensification is thought to be a major factor in the decline of bumblebees (*Bombus* spp.) within the U.K. in recent years (see Williams 1982; 1986). Bumblebees store only several days' worth of reserves (Corbet 1996), unlike honeybees (*Apis mellifera*), and therefore require a continuous supply of nectar and pollen throughout the period when colonies are active. Food sources, in terms of floral diversity and abundance, have become limited, both spatially and temporally, by the trend towards annually disturbed, anemophilous monocultures, application of herbicides (Torchio 1991) and other changes in land use (Williams 1982; Corbet *et al.* 1991). Removal of hedgerows and the levelling of other boundary features in the drive to increase field sizes and facilitate mechanisation have reduced the availability of potential nest sites (Osborne *et al.* 1991; Ortiz-Sánchez 1995).

The possession of certain morphological and physiological traits (Batra 1995 [pubescence]; Hippa *et al.* 1981 [thermo-regulatory ability]; King & Ferguson 1994 [ability to sonicate]; Free 1970 [comparatively long-tongued]) mean that bumblebees are the most effective pollinators of many plant species (Colbert & de Oliveira 1990; Corbet *et al.* 1991; Batra 1995), and, along with the other members of the family Apidae, they are necessary for the pollination of approximately 40 crop species grown in the U.K. (Osborne & Williams 1996). As such they are an integral component of agricultural landscapes, and their continued presence is important for safeguarding yields. Bumblebees also act as pollination vectors for numerous wildflower species, and have the ability to maintain small fragmented populations of rare plants (Kwak *et al.* 1991; Petanidou *et al.* 1991).

Little work has been done thus far on the possible contribution field margins may make to the conservation of bumblebee populations on arable land (although see Fussell & Corbet 1992; Lagerlof *et al.* 1992). Under the pilot ASS, a MAFF initiative (MAFF 1999), we undertook a preliminary study into the potential that naturally regenerated, unsprayed, field margins might have in providing forage resources to *Bombus* spp. in a landscape identified as being relatively impoverished in terms of nectar and pollen. We aimed to establish if naturally regenerated unsprayed field margins are more attractive to foraging bumblebees and honeybees than corresponding cropped field margins managed as conservation headlands. This was addressed by studying bee abundance and behaviour in an experimental field margin set-up in central England.

Methods

Study sites

This study was carried out on five arable farms centred around Newport, the west Midlands, from 29 June until

9 August 1999. All farms were located within a 12.5 km radius, at similar elevations, and had introduced field margins for the first time in 1999. Prior to that, these areas had been subject to the same treatment as the rest of the field.

Fields in which the experiments took place were planted with spring-sown cereals, and were matched for size as closely as possible. Two uncropped field margins, which had been allowed to undergo natural regeneration following spring cultivation, and a control margin managed as conservation headland were studied on each farm, each within a different field; controls were as similar in terms of height and density to the naturally regenerated field margins as possible. No management other than the spring cultivation was undertaken on these areas for the duration of the experiment. Both naturally regenerated margins and control margins were 4–6 m wide, and adjacent to the field boundary. Hedgerow nectar was not a factor in these experiments as adjacent boundaries were chosen to be relatively flower-free. Plant names follow Stace (1997).

Sampling methods

Observations of bee numbers, species, and chosen forage plant were made following an adaptation of Pollard's method of butterfly surveying (Pollard *et al.* 1975; Pollard 1977). Observations were made along a $0.5 \times 50\,\mathrm{m}^2$ transect through the centre of field margins and controls, parallel with the edge of the crop. All transects were conducted along the straight edges of fields; corners were not included. Three sets of observations, taken at 30 min intervals, were made at each site at 8–10 day intervals over a 40 day period, depending on ambient conditions. These were averaged for each site for each day. Individual sites were visited in a random order for each observation period. Transects were only walked on days when ambient temperature was 18°C or above, and it was not raining. All walks were completed between 09:30 and 18:00 h; all sites were visited within a 72 h period. Number of individual flowers of each species were counted for each flower species along the transects at each time observations were made, except in the case of e.g. *Matricaria* spp., where number of flowerheads were counted.

Flower preferences

An index was constructed to show preferences of individual *Bombus* species and *A. mellifera* for each flower species present.

$$\mathrm{PI} = (V_k/V_t)/(A_k/A_t),$$

where V_k is the number of foraging visits of that species to plant species k, V_t is the total number of visits of that species to all plant species, A_k is the total number of flowers of species k, and A_t is the total number of flowers of all species. Flower counts and average numbers of bee visits for each observation period were summed across all sites and all dates for the purposes of this index.

Analysis

Repeated measures ANOVA using SPSS9.0 for Windows (SPSS Inc., 1998) was used to determine if bee and flower numbers varied between experimental and control treatments. 'Timepoints' (i.e. dates) were treated as replicates as the gap between observations was enough to allow sufficient turnover of bees and flowers to justify this. Repeated measures ANOVA was also used to determine whether time had a significant effect on total bee numbers.

Results

Significantly more bees were recorded in uncropped field margins than in control margins ($F_{1,5} = 31.3$, $p = 0.003$) (Figure 1). Of the five sampling timepoints, most bees were recorded on timepoints 2–4, fewer at the beginning and the end (Figure 1). The response of bee numbers to time is best described as a quadratic relationship ($F_{1,5} = 51.5$, $p = 0.001$). This response occurred primarily in naturally regenerated margins, but not in controls, leading to a significant interaction between timepoint and treatment for bee numbers ($F_{1,5} = 34.8$, $p = 0.002$). Honeybees accounted for 87.5% of all observations on the control plots, and *Bombus lapidarius* accounted for the other 12.5%. No other *Bombus* species were observed foraging on the control plots.

Flower numbers through time

Many more open flowers were recorded on naturally regenerated field margins compared with controls ($F_{1,13} = 11.26$, $p < 0.005$) (Figure 2). There was a significant interaction between date and treatment for open flowers ($F_{4,52} = 2.74$, $p = 0.038$); this

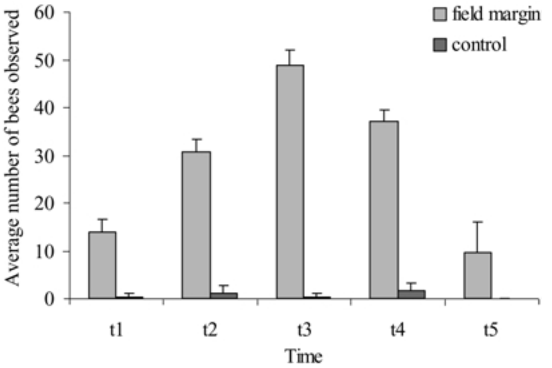

Figure 1. Average number of bees (*Bombus* + *Apis*) observed foraging on experimental and control plots across the duration of the experiment. Interval between timepoints was approximately 10 days $n = 10$ for experimental plots and $n = 5$ for controls. Error bars indicate SEM.

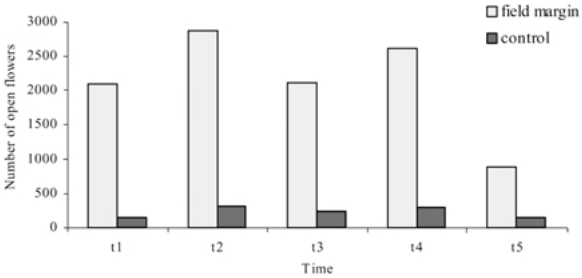

Figure 2. Total numbers of open flowers on control boundaries and uncropped field margins through time.

is expected due to the temporal nature of the flowering period. Differences between sites were not found to be significant ($F_{4,5} = 0.15$, $p = 0.957$). No significant association was found between numbers of foraging bees and temporal variation in floral density ($r = 0.64$, $p > 0.05$).

Bee species

Three species accounted for more than 98% of all observed visits across all timepoints (Table 1). These were *A. mellifera*, *B. terrestris/lucorum*, and *B. lapidarius*. *B. pascuorum*, *B. pratorum*, *B. hortorum*, and *Psithyrus sylvestris* accounted for the other 2% of recorded bee foragers. This pattern was apparent at all timepoints (Figure 3). Overall, *B. terrestris* was the most commonly observed bee species at all timepoints.

Flower preferences of foraging bees

There was great variation in the total number of open flowers of the different plant species (Figure 4A). Those species that were most numerous were not necessarily the species that received the highest proportion of foraging visits. Volunteer *Brassica* spp. were the most numerous inflorescences in the naturally regenerated margins, but did not score highly on the preference indices for honeybees and bumblebees when compared with species present at lower densities. *Matricaria* spp. and *Persicaria maculosa* were abundant, but were not visited at all by bumblebees, although honeybees were observed foraging on these (Figure 4B). Conversely, *Dipsacus fullonum* and *Phacelia tanacetifolia*, which were present in very small numbers at one site, received a disproportionately large number of bee visits.

The individual species preferences of *B. lapidarius* and *B. terrestris* were found to be quite different (Figure 4C), although both exhibited a high preference for *P. tanacetifolia*. *B. lapidarius* also exhibited a high preference for *Linum usitatissimum*, while *B. terrestris* preferentially foraged on *Cirsium* spp. and *D. fullonum*. *B. terrestris* was also recorded foraging on *Pentaglottis sempervivens* and *Lamium purpureum*;

Table 1. Total number of observations of each bee species across all timepoints, expressed as a percentage of the total number of observations of all species.

Species	Number of observations	Percentage of observations
A. mellifera	260	18.77
B. lapidarius	341	24.62
B. terrestris	758	54.73
B. pascuorum	19	1.37
B. pratorum	2	0.14
B. hortorum	3	0.23
P. sylvestris	2	0.14
Total	1385	100

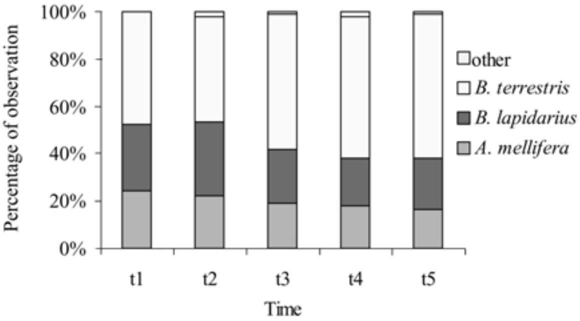

Figure 3. Numbers of each species observed on all uncropped field margins through time, as a percentage of the total number of bees observed. Other observed species were *B. pascuorum*, *B. hortorum*, and *P. sylvestris*.

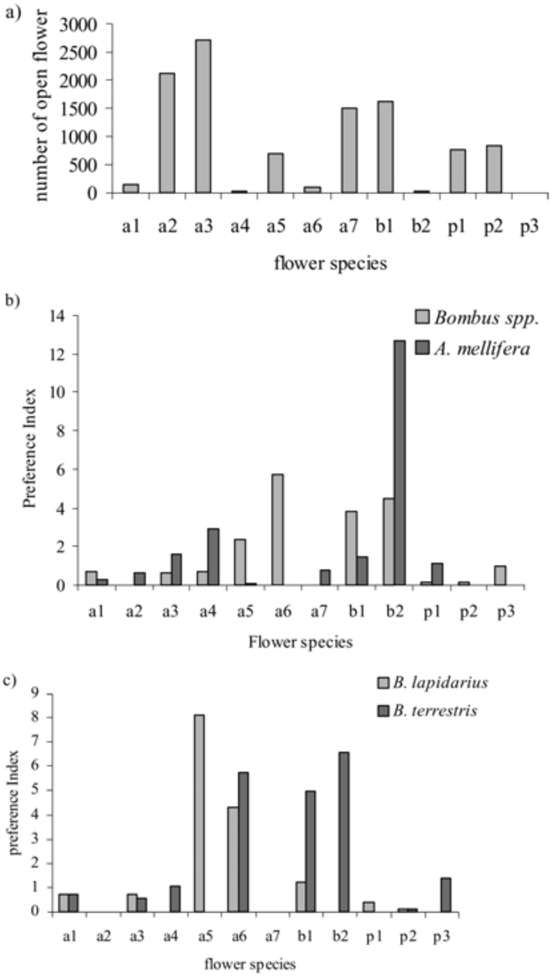

Figure 4. The preferences of bee species for each flower species. Flower species are the annuals (a1) *Viola arvensis*, (a2) *Matricaria* spp., (a3) *Brassica* spp., (a4) *Lamium purpureum*, (a5) *Linum usitatissimum*, (a6) *Phacelia tanacetifolia*, (a7) *Persicaria maculosa*; biennials (b1) *Cirsium* spp., (b2) *Dipsacus fullonum*; and perennials (p1) *Chamerion angustifolium*, (p2) *trifolium repens*, (p3) *Pentaglottis sempervivens*. (A) Total number of open flowers of each species summed across all timepoints; (B) relative preferences of *Bombus* spp. and *A. mellifera*; (C) relative preferences of *B. lapidarius* and *B. terrestris*. Data is taken from experimental margins only; for formula see text.

there were no recorded visits of *B. lapidarius* to either of these plant species.

Discussion

That naturally regenerated field margins provide an improved habitat for foraging bees when compared with cropped field boundaries was apparent across all field sites. The data revealed a significant difference between the average numbers of bees foraging on naturally regenerated margins and controls for the duration of this experiment, which covered a large part of the foraging period of most bee species. Similar results have been recorded for butterflies (Dover 1992; Sparks & Parish 1995; Feber *et al.* 1996). Temporal variation in numbers of foraging bees was found to be significant, with a peak in numbers mid-season; this is most likely a reflection of bumblebee population dynamics as these constituted the majority of observations at each timepoint (Figure 3).

The most commonly recorded bee species during this study were *A. mellifera*, *B. terrestris*, and *B. lapidarius*, and resource partitioning between these is evident. Some authors have suggested that *Bombus* spp. partition resources on the basis of proboscis length (Inouye 1976; 1978; Ranta & Lundberg 1980; Pyke 1982). However, *B. terrestris* and *B. lapidarius* have similar proboscis lengths (Prys-Jones & Corbet 1991), but exhibited different preferences for the flowers present; these generalists, along with *A. mellifera*, may act to exclude other *Bombus* species. The differential preferences of *A. mellifera* versus *Bombus* spp. may be explained by morphological differences between the species. *A. mellifera* have shorter proboscides (see Corbet *et al.* 1995), and preferentially visit smaller open flowers, compared to *Bombus* spp. The larger body size of *Bombus* spp. means these are energetically constrained to visiting flowers with higher nectar content. The presence of large acreages of crops such as oilseed rape in the locality of the study may have influenced observed visitation patterns; this could explain why *A. mellifera* was recorded in lower numbers than *B. terrestris*.

If field margins are left to regenerate naturally after cultivation, the resulting habitat diversity is probably influenced by years of intensive agriculture. The outcome of such natural regeneration will depend on species already present, either as plants along the field boundary, or in the seed or bud banks. Certain species in either of these may affect establishment of the successive vegetation (Egler 1954; Connell & Slayter 1977). The persistence of seeds in the seed bank varies between species (Feber *et al.* 1996), so seed bank age is potentially important. In this study similar wildflower species were found across all the naturally regenerated margins, most of which are common and widespread within the U.K. It was not therefore surprising to find that the dominant bumblebee fauna belonged to the mainland ubiquitous species group of Williams (1982), rather than habitat specialists or those with restricted ranges. Dramstad & Fry (1995) found a similar dominance of ubiquitous species on land subjected to intensive agricultural practices in Norway. However, along with *B. terrestris* (*B. lucorum*) and *B. lapidarius*, *B. pascuorum*, *B. pratorum*, and *B. hortorum* also belong to the ubiquitous species group, and yet there were few recorded sightings of any of these. It is known that *B. pascuorum* and *B. hortorum* preferentially visit flowers with deeper corollas than *B. lapidarius* and *B. terrestris* (Prys-Jones & Corbet 1991); it is disturbing that the two ubiquitous members (Williams 1986) of the longer-tongued species group should account for such a low proportion of observations here. Corbet (1995) has suggested that frequent disturbance has most affected the longer-tongued *Bombus* spp. as it has enabled shallower annual species to displace the deeper-flowered perennials that this sub-compartment of the pollination web preferentially feed on (Corbet 2000). The disappearance of this species group would have serious implications for flower species with deep corollas. However, diversity and density of perennials should increase in field margins with time, and with lack of disturbance; many perennials are highly attractive to all *Bombus* spp. (Fussell & Corbet 1992). This also has the advantage of causing failure of either germination or establishment of annual weeds (Greaves & Marshall 1987; Smith *et al.* 1993), most of which require an open sward for germination. Butterflies also prefer to forage on perennial species (Feber *et al.* 1996).

Control plots consistently contained lower densities of flowers than naturally regenerated margins (Figure 3). There was also lower floral diversity, with *Matricaria* spp. and *Chamerion angustifolium* the only entomophilous species present, compared with twelve entomophilous species on the naturally regenerated margins (see Figure 4). *A. mellifera* and *Bombus* spp. were shown to exhibit little or no foraging affinity in this case for either *Matricaria* spp. or *C. angustifolium*. Flowers that scored highly on the preference index (Figure 4) were absent from control plots, so the increase in number of foragers on naturally regenerated margins is not solely a function of increased flower density, but of the presence of more ‘attractive’ flower species. Floral species richness has been correlated with abundance of bees (Tscharntke *et al.* 1998), and butterflies (Sparks and Parish 1995). The increased floral diversity found on the naturally regenerated margins may result from an initial lack of competition during establishment.

The naturally regenerated margins used in this study were all in the initial year of establishment. Some contained volunteer crop species (for example *Brassica* spp. *P. tanacetifolia*), whilst others were comparatively bare. Edges produce lower yields than any other part of the field (Boatman and Sotherton 1988), and often require increased effort (de Snoo & Chaney 1999). Losses are therefore minimized by preferentially removing these areas from production (Rands 1985). Field edges are also likely to be the area of the field with the most diverse flora and fauna, although Fielder (1987) has noted that seedbed quality at the field edge is likely to be poor. Where there is a diverse local flora and weed populations are small then natural regeneration should be the preferred option. However, Smith *et al.* (1993; 1994) found that sowing a grass/wildflower mixture produced better control of annual grass weeds, and increased butterfly and overall invertebrate abundance. This should be considered in areas where the outcome of natural regeneration is likely to be unacceptable. However, although the sowing of a wildflower seed mixture may provide better cover, particularly during establishment, and a wider variety of nectar-producing plants, these can be expensive, and species from the local flora tend to be excluded from the resultant border (Smith *et al.* 1993). Management of either a naturally regenerated or a sown field margin should ensure that the herbaceous flora is not degraded through shading or herbicide application, and also that ploughing is limited to allow development of a mid-successional community, and its constituent deep-flowered perennials. Timing and depth of cultivations are also likely to influence the outcome of natural regeneration (Critchley *et al.* 1999). Naturally regenerated species in field margins have been maintained for at least three years in the absence of fertiliser application (Smith *et al.* 1993); the addition of fertiliser is likely to promote growth of a few of the most competitive species at the expense of all others (Wilson 1993; 1999).

Although the flight ranges of *Bombus* spp. remain to be quantified, observations suggest that bumblebees are not economically constrained to forage close to their nests (Dramstad & Fry 1995; Saville *et al.* 1997), and various models of bumblebee foraging have proposed that flight ranges in the order of kilometres can be economically viable (Dukas & Edelstein-Keshet 1998; Cresswell *et al.* 2000). This has implications for the spatial and temporal organisation of appropriate conservation measures.

That naturally regenerated margins benefit other species has already been noted (Hawthorne & Hassall 1994; Moreby & Southway, 1999; Stoate 1999; Tew *et al.* 1994). We would advocate from the results of this study that naturally regenerated field margins, with careful management, have the potential to supply a continuum of nectar and pollen to foraging bumblebees on agricultural land across the active period of colonies. With the development of a mid-successional community (here meaning open herbaceous vegetation that has been free from disturbance for at least 5 or 10 years), they should prove valuable in conserving the longer-tongued bumblebee species, which are most under threat (Corbet 2000). Also, as such margins become established, tussocks will form, which may be utilised as nest sites (Alford 1975). This should aid stabilization of bumblebee numbers on agricultural land, and safeguard the yields of certain crops. Management of naturally regenerated field margins for bumblebees should have a positive effect on other species traditionally associated with farmland, many of which are also in decline.

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References

Aebischer, N.J. (1991) Twenty years of monitoring invertebrates and weeds in cereal In *The Ecology of temperate cereal fields* (J.F. Darbyshire and G.R. Potts, eds), pp. 305–31. Oxford: Blackwell Science Publications.

Alford, D.V. (1975) *Bumblebees*. London: Davis-Poynter.

Batra, S.W.T. (1995) Bees and pollination in our changing environment. *Apidologie* **26**, 361–70.

Boatman, N.D. (1998) The value of buffer zones for the conservation of biodiversity. In *The 1998 Brighton Conference – Pests & Diseases*, pp. 939–950. Farnham, Surrey: British Crop Protection Council.

Boatman, N.D. and Sotherton, N.W. (1988) The agronomic consequences and costs of managing field margins for game and wildlife conservation. *Asp. Appl. Biol.* **17**, 47–56.

Chiverton, P.A. and Sotherton, N.W. (1991) The effects on beneficial arthropods of exclusion of herbicides from cereal crop edges. *J. Appl. Ecol.* **28**, 1027–39.

Colbert, S. and de Oliveira, D. (1990) Influence of pollen variety on raspberry (*Rubus idaeus* L.) development. *J. Hered.* **81**, 434–7.

Connell, J.H. and Slayter, R.O. (1977) Mechanisms of succession in natural communities and their in community stability and organization. *Am. Nat.* **111**, 1119–44.

Corbet, S.A. (1995) Insects, plants and succession: Advantages of long-term set-aside. *Agric. Ecosyst. Environ.* **53**, 201–17.

Corbet, S.A. (1996) Why bumblebees are special. In *Bumblebees for pleasure and profit* (A. Matheson, ed.), pp. 2–11. Cardiff: IBRA.

Corbet, S.A. (2000) Conserving compartments in pollination webs. *Conser. Biol.* **14**, 1229–31.

Corbet, S.A., Williams, I.H. and Osborne, J.L. (1991) Bees and the pollination of crops and wild flowers in the European Community. *Bee World* **72**, 47–59.

Corbet, S.A., Saville, N.M., Prys-Jones, O.E. and Unwin D.M. (1995) The competition box: A graphical aid to forecasting pollinator performance. *J. Appl. Ecol.* **32**, 707–19.

Cresswell, J.E., Osborne, J. and Goulson, D.G. (2000) An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Ecol. Entomol.* **25**, 249–55.

Critchley, C.N.R. (1996) Monitoring as a feedback mechanism for the conservation management of arable plant communities. In *Vegetation management in forestry, amenity and conservation areas* pp. 239–44. Aspects of Applied Biology 44. Warwick: Association of Applied Biologists.

Critchley, C.N.R. (1996) *Vegetation of Arable Field Margins in Breckland*. Ph.D. Thesis, Norwich: University of East Anglia.

Critchley, C.N.R., Fowbert, J.A., Diack, I.A. and Sherwood, A.J. (1999). Cultivation regimes to conserve annual plant communities in uncropped arable field boundary strips. In *Field margins and buffer zones; Ecology, management and policy* (N.D. Boatman, D.H.K. Davies, K. Chaney, R. Feber, G.R. de Snoo and T.H. Sparks, eds), pp. 139–46. Aspects of Applied Biology 54. Warwick: Association of Applied Biologists.

Dennis, P.D. and Fry, G.L.A. (1992) Field margins: Can they enhance natural enemy populations and general arthropod diversity on farmland? *Agric. Ecosyst. Environ.* **40**, 95–115.

Dover, J. 1992. The conservation of insects on arable farmland. In *The conservation of insects and their habitats* (N.W. Collins and J. Thomas, eds), pp. 294–318. London: Academic Press.

Dramstad, W. and Fry, G. (1995) Foraging activity of bumblebees (*Bombus*) in relation to flower resources on arable land. *Agric. Ecosyst. Environ.* **53**, 123–35.

Dukas, R. and Edelstein-Keshet L. (1998) The spatial distribution of colonial food provisioners. *J. Theor. Biol.* **190**, 121–34.

Egler, F. (1954) Vegetation science concepts I. Initial floristic composition – a factor in old-field vegetation development. *Vegetation* **4**, 412–17.

Feber, R.E., Smith, H. and MacDonald D.W. (1996) The effect on butterfly abundance of management of uncropped edges of arable fields. *J. Appl. Ecol.* **33**, 1191–205.

Fielder, A.G. (1987) Management options for field margins – an Agricultural Advisor's view. In *Field margins* (J.M. Way and P.W. Greig-Smith, eds), pp. 85–94. BCPC Monograph 35. Thornton Heath: British Crop Protection Council.

Firbank, L.G., Carter, N., Derbyshire, J.F. and Potts G.R. (eds) (1991) *The ecology of temperate cereal fields*. Oxford: Blackwell.

Free, J.B. (1970) *Insect pollination of crops*. London: Academic Press.

Free, J.B. and Butler, C.G. (1959) *Bumblebees*. London: Collins.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R. and Carter, N. (1995) Population declines and range contractions among lowland farm birds in Britain. *Conser. Biol.* **96**, 1425–41.

Fussell, M. and Corbet, S.A. (1992) Flower usage by bumblebees: A basis for forage plant management. *J. Appl. Ecol.* **29**, 451–65.

Greaves, M.P. and Marshall, E.J.P. (1987) Field margins: Definitions and statistics. In *Field margins* (J.M. Way and P.W. Greig-Smith, eds), pp. 3–9. BCPC Monograph 35. Thornton Heath: British Crop Protection Council.

Hawthorne, A. and Hassall, M. (1994) Effects of management techniques on carabid communities of cereal field margins. In *Field margins: Integrating agriculture and conservation* (N. Boatman, ed.), BCPC Monograph 58. Farnham, Surrey: British Crop Protection Council.

Hippa, H., Koponen, S. and Osmonen, O. (1981) Diurnal activity of flower visitors to the cloudberry (*Rubus chamaemorus* L.). *Rep. Kevo Subarctic Res. Stn.* **17**, 55–7.

Inouye, D. (1976) *Resource partitioning and community structure: A study of bumblebees in the Colorado Rocky mountains*. Doctoral Dissertation. North Carolina, USA: University of North Carolina, Chapel Hill.

Inouye, D. (1978) Response partitioning in bumblebees. Experimental studies in foraging behaviour. *Ecology* **59**, 672–8.

King, M.J. and Ferguson, A.M. (1994) Vibratory collection of *Actinidia deliciosa* (kiwifruit) pollen. *Ann. Botany* **74**, 479–82.

Kwak, M., van den Brand, C., Kramer, P. and Boerrigter, E. (1991) Visitation, flight distances and seed set in the rare species *Phyteuma nigrum* (Campanulaceae). *Acta Hort.* **288**, 303–7.

Lagerlof, J., Stark, J. and Svensson, B. (1992) Margins of agricultural fields as habitats for pollinating insects. *Agric. Ecosyst. Environ.* **40**, 117–24.

MAFF (1998) *The countryside stewardship scheme*. London: MAFF Publications.

MAFF (1999) *Arable stewardship*. London: MAFF Publications.

Marshall, E.J.P. (1989) Distribution patterns of plants associated with arable field edges. *J. Appl. Ecol.* **26**, 247–57.

Moreby, S.J. and Southway S. (1999) The importance of the crop edge compared to the mid-field, in providing invertebrate food for farmland birds. In *Field margins and buffer zones: Ecology, management and policy* (N.D. Boatman, D.H.K. Davies, K. Chaney, R. Feber, G.R. de Snoo and T.H. Sparks, eds), pp. 217–22. Aspects of Applied Biology 54. Warwick: Association of Applied Biologists.

O'Toole, C. (1994) Who cares for solitary bees? In *Forage for bees in an agricultural landscape* (A. Matheson, ed.), pp. 47–56. Cardiff: IBRA.

Ortiz-Sánchez, F.J. (1995) Diversity of bees (Hymenoptera: Apoidea) in several Spanish ecosystems. In *Changes in fauna of wild bees in Europe* (J. Banaszak, ed.), pp. 147–63. Bydgoszcz: Pedagogical University.

Osborne, J.L. and Williams, I.H. (1996) Bumblebees as pollinators of crops and wild-flowers. In *Bumblebees for pleasure and profit* (A. Matheson, ed.), pp. 24–32. Cardiff: IBRA.

Osborne, J., Williams I. and Corbet, S.A. (1991) Bees, pollination and habitat change in the European Community. *Bee World* **72**, 99–116.

Petanidou, T., den Nijs, H.C.M. and Ellis, A.C. (1991) Comparitive pollination of two rare Dutch *Gentiana* species, in relation to population size. *Acta Hort.* **288**, 308–17.

Pollard, E. (1977) A method for assessing changes in the abundance of butterflies. *Biol. Cons.* **12**, 115–34.

Pollard, E., Elias, D.O., Skelton, M.J. and Thomas, J.A. (1975) A method of assessing the abundance of butterflies in Monks Wood National Nature Reserve in 1973. *Entomologist's Gazette* **26**, 79–88.

Potts, G.R. (1986) *The partridge: Pesticides, predation and conservation*. London: Collins.

Prys-Jones, O.E. and Corbet, S.A. (1991) *Bumblebees: Naturalists' handbook 6.* Slough: Richmond Publishing Company.

Pyke, G.H. (1982) Local geographic distributions of bumblebees near Crested Bute, Colorado: Competition and community structure. *Ecology* **63**, 555–73.

Rands, M.R.W. (1985) Pesticide use on cereals and the survival of grey partridge chicks: A field experiment. *J. Appl. Ecol.* **22**, 49–54.

Ranta, E. and Lundberg, H. (1980) Resource partitioning in bumblebees: The significance of differences in proboscis length. *Oikos* **35**, 298–302.

Saunders, D., Hoobs, R. and Erhlich, P. (eds) (1992) *Reconstruction of fragmented ecosystems: Local and global perspectives*. Chipping Norton: Surrey Beatty.

Saville, N.M., Dramstad, W.E., Fry, G.L.A. and Corbet, S.A. (1997) Bumblebee movement in a fragmented agricultural landscape. *Agric. Ecosyst. Environ.* **61**, 145–54.

Schumacher, W. (1987) Methods taken to preserve arable weeds and their associated communities in central Europe. In *Field margins* (J.M. Way and P.W. Greig-Smith, eds), pp. 109–112. BCPC Monograph 35. Farnham, Surrey: British Crop Protection Council.

Smallshire, D. and Cooke, A.I. (1999) Field margins in UK agri-environment schemes. In *Field margins and buffer zones: Ecology, management and policy* (N.D. Boatman, D.H.K. Davies, K. Chaney, R. Feber, G.R. de Snoo and T.H. Sparks, eds), pp. 19–28. Aspects of Applied Biology 54. Warwick: Association of Applied Biologists.

Smith, H., Feber, R.E., Johnson, P.J., McCallum, K., Plesner Jensen, S., Younes, M. and MacDonald, D.W. (1993) *The Conservation and Management of Arable Field Margins.* Peterborough: English Nature.

Smith, H., Feber, R.E. and MacDonald, D.W. (1994) The role of wild flower seed mixtures in field margin restoration. In *Field margins: Integrating agriculture and conservation.* (N.D. Boatman, ed.), pp. 289–94. BCPC Monograph Number 58. Farnham, Surrey: British Crop Protection Council.

de Snoo, G.R. (1995) *Unsprayed field margins: Implications for environment, biodiversity and agricultural practice.* Ph.D. thesis. Holland: Leiden University.

de Snoo, G.R. and Chaney, K. (1999) Unsprayed field margins – what are we trying to achieve? In *Field margins and buffer zones: Ecology, management and policy* (N.D. Boatman, D.H.K. Davies, K. Chaney, R. Feber, G.R. de Snoo and T.H. Sparks, eds), pp. 1–12. Aspects of Applied Biology 54. Warwick: Association of Applied Biologists.

Sparks, T.H. and Parish, T. (1995) Factors affecting the abundance of butterflies in field boundaries in Swavesey fens, Cambridgeshire, U.K. . *Biol. Cons.* **73**, 221–7.

SPSS Inc. (1998) *SPSS for Windows: Advanced statistics*. Release 9.0. Chicago: SPSS Inc.

Stace, C.A. (1997) *New flora of the British Isles*. Cambridge: Cambridge University Press.

Stoate, C. (1999) The influence of filed boundary structure on breeding territory establishment of whitethroat *Sylvia communis* and yellowhammer *Emberiza citrinella*. In *Field margins and*

buffer Zones: Ecology, management and policy (N.D. Boatman, D.H.K. Davies, K. Chaney, R. Feber, G.R. de Snoo and T.H. Sparks, eds), pp. 125–30. Aspects of Applied Biology 54. Warwick: Association of Applied Biologists.

Tew, T.E., Todd, I.A. and MacDonald, D.W. (1994) Field margins and small mammals. In *Field margins: Integrating agriculture and conservation* (N.D. Boatman, ed.), pp. 85–94. BCPC Monograph 58. Farnham, Surrey: British Crop Protection Council.

Thomas, J.A. (1995) The conservation of declining butterfly populations in Britain and Europe: Priorities, problems and successes. *Biol. J. Linn. Soc.* **56**, 55–72.

Torchio, P.F. (1991) Bees as crop pollinators and the role of solitary species in changing environments. *Acta hort.* **288**, 49–61.

Tscharntke, T., Gathmann, A. and Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: Community structure and interactions. *J. Appl. Ecol.* **35**, 708–19.

White, P.C.L. and Hassall, M. (1994) Effects of management on spider communities of headlands in cereal fields. *Pedobiologia* **38**, 169–84.

Williams, P.H. (1982) The distribution and decline of British bumblebees (*Bombus* Latr.) *J. Apic. Res.* **21**, 236–45.

Williams, P.H. (1986) Environmental change and the distributions of British bumble bees (*Bombus* Latr.) *Bee World* **67**, 50–61.

Wilson, P.J. (1993) Conserving Britain's cornfield flowers. In *Brighton Crop Protection Conference – Weeds 1993*, pp. 411–16. Farnham, Surrey: British Crop Protection Council.

Wilson, P.J. and Aebischer N.J. (1995) The distribution of dicotyledonous arable weeds in relation to distance from the field edge. *J. Appl. Ecol.* **32**, 295–310.

Wilson, P.J. (1999) The effect of nitrogen on populations of rare arable plants in Britain. In *Field margins and buffer zones: Ecology, management and policy* (N.D. Boatman, D.H.K. Davies, K. Chaney, R. Feber, G.R. de Snoo and T.H. Sparks, eds), pp. 93–100. Aspects of Applied Biology 54. Warwick: Association of Applied Biologists.