UNIVERSITY OF SOUTHAMPTON

Faculty of Medicine, Health and Life Sciences
School of Biological Sciences

Bumblebee habitat restoration in the agricultural landscape

by

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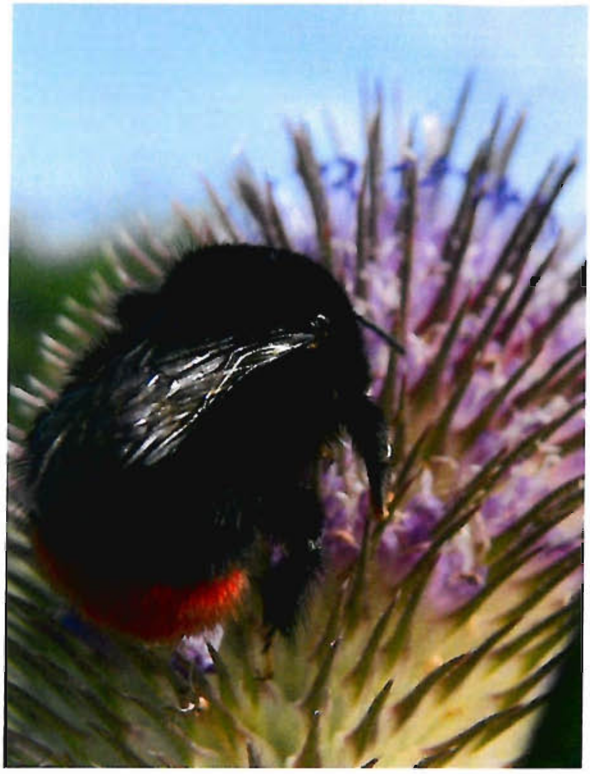
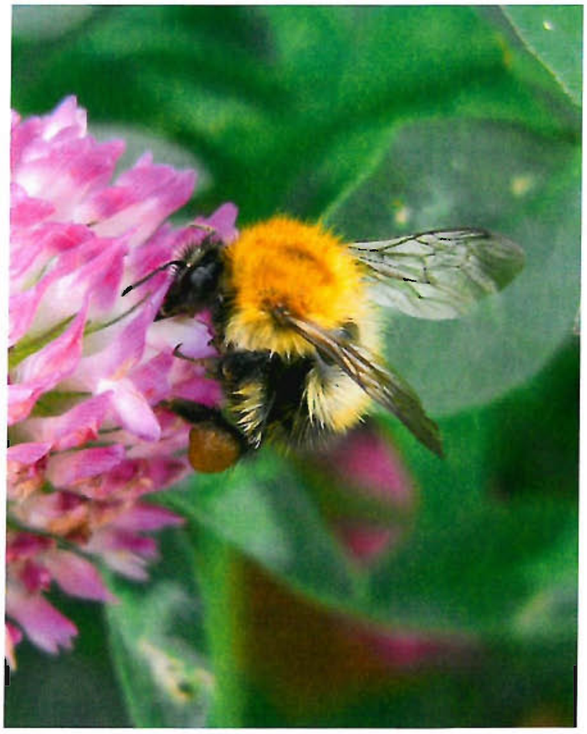


Bombus lapidarius queen visiting teasel, *Dipsacus fullonum*



Bombus pascuorum worker collecting pollen from red clover, *Trifolium pratense*

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ABSTRACT

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BUMBLEBEE HABITAT RESTORATION IN THE AGRICULTURAL LANDSCAPE

by Claire Carvell

Declines in abundance and diversity of bumblebees (*Bombus* spp.) have been linked to the loss and degradation of habitats as a result of agricultural intensification. This thesis aims to examine some of the causes of bumblebee declines in Britain, and to investigate methods of habitat restoration to reverse these declines within intensively managed agricultural landscapes. It provides the first comprehensive comparative studies of the value of different options within the agri-environment schemes (AES) for foraging bumblebees.

Twentieth century changes in bumblebee forage plants are assessed using two national plant species datasets. A large proportion of forage plants are found to have declined in both range (at the 10-km scale) and frequency (at the 1-km scale), reflecting serious reductions in the quality of foraging habitats for bumblebees across the agricultural landscape. Grass species associated with nesting habitats did not in general experience such declines, although the structural quality of vegetation for nesting is likely to have been degraded.

The response of foraging bumblebees to various restoration and management options for arable field margins is studied across a series of single and multi-site experiments. Bumblebee abundance is closely linked to flower abundance of suitable forage species, and to successional changes in availability of these both during the season and between years. Margins sown with a mixture of pollen and nectar-rich plants, such as *Trifolium pratense*, are shown to attract large numbers of bumblebees, including rare species. The analysis of pollen loads confirms contrasting forage plant preferences in *Bombus pascuorum* and *Bombus terrestris*, adding important information to that from transect counts on the functional value of introduced flower mixtures for local colonies. Widespread uptake of the Entry Level Environmental Stewardship scheme could therefore have rapid and positive effects on some species, but more diverse native plant communities may be required to provide a longer-lived forage supply to a greater range of *Bombus* species and other pollinators.

The thesis concludes that although the total area of suitably managed habitat required to sustain populations is large, current AES prescriptions providing a combination of widespread, low cost and more targeted, specialist options for habitat creation are likely to significantly enhance the quality of the agricultural landscape for bumblebees. Future success will require close links between policy makers and ecologists, between the management of farmed land and protected semi-natural grasslands across Britain, and regular monitoring of the effects of habitat restoration on rare and common bumblebees and their interactions with other components of agricultural ecosystems.

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List of tables, figures and appendices

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Definitions and abbreviations

The following abbreviations appear throughout the thesis but are always given in full on at least the first mention in the text.

AES	Agri-environment Schemes
BAP	Biodiversity Action Plan
CS	Countryside Survey
CSS	Countryside Stewardship Scheme
ES	Environmental Stewardship
ELS	Entry Level Stewardship
HLS	Higher Level Stewardship
New Atlas	The New Atlas of the British and Irish Flora (Preston et al., 2002)
PPI	Pollination Probability Index
SSSI	Site of Special Scientific Interest

Bumblebee nomenclature follows Prŷs-Jones and Corbet (1991) and vascular plant nomenclature follows Stace (1997).

1. Introduction

1.1 Bumblebee declines and conservation status in Britain

Many bumblebee species (Hymenoptera: Apidae) have shown serious declines in abundance and contractions in range over recent decades, across both Europe and North America (Alford, 1980; Williams, 1982; Rasmont, 1988; Buchmann and Nabhan, 1996). The British bumblebee fauna consists of 25 species, including six species of the subgenus *Psithyrus* which are brood parasites of the 'true' bumblebees known as cuckoo bees. The 19 'true' or social *Bombus* species, which will be the focus of this thesis, are listed in Table 1.1 along with a summary of their current conservation status. Relatively comprehensive records collated by Alford (1980) and Williams (1982) confirmed that by the 1980's only six species were still regularly found over their pre-1960 range. Two species are considered to have become extinct (Goulson, 2003), and in response to concerns over their population status, five species have been placed on the UK Biodiversity Action Plan (BAP) as priorities for conservation, one of which may itself now be extinct (Falk, 1991; Anon., 1995; Edwards, 1998; UK Biodiversity Group, 1998). A further three species have been proposed for inclusion on the UK BAP due to their apparent decline during the late 20th Century. At an international level, concern over these declines and those of other pollinator groups has resulted in the International Initiative for the Conservation and Sustainable Use of Pollinators (www.biodiv.org/programmes/areas/agro/pollinators). This recognises the urgent need for large-scale efforts to assess the magnitude, mechanisms and consequences of pollinator declines.

Several factors have been identified as possible contributors to the decline in bumblebee abundance and diversity in Britain. These include competition from the honeybee (*Apis mellifera*), changes in climate and the effects of predators and parasites (Williams, 1986). However, it is likely that agricultural intensification, changes in land use and farming practices resulting in the fragmentation, degradation and loss of semi-natural habitats, has been the single most important factor leading to bumblebee declines (Osborne and Corbet, 1994; Edwards, 1998; Goulson et al., 2005). For example the area of unimproved lowland grassland, an important habitat for bumblebees, declined in Britain by over 90% between 1932 and 1984 (Fuller, 1987). As a consequence, bumblebees are now largely confined to small remnants of semi-natural vegetation within the fragmented agricultural landscape (Saville et al., 1997), as well as urban gardens and parks which may have aided the survival of several still common species.

Declines in floral diversity across Britain have been well documented (Haines-Young, 2000; Preston et al., 2002). However, while a decrease in the abundance of suitable forage plants has been implicated as the major factor contributing to declines in bumblebee populations (Williams, 1986; Rasmont, 1988), no quantitative evidence of this decrease has been presented. Changes in abundance of food plants have been suggested as a direct cause for declining trends in abundance of both butterflies and farmland birds (Pollard et al. 1995; Fuller et al., 1995; Smart et al., 2000). A quantitative approach is taken in this thesis (Chapter 2), using data from the Countryside Surveys and *New Atlas of the British and Irish Flora* (Preston et al., 2002) in order to assess national scale changes in range and abundance of bumblebee forage plants and nesting habitats during the 20th Century.

The loss of bumblebees and other flower-visiting insects from our agricultural landscapes has potentially serious implications for the pollination services they provide (Allen-Wardell et al., 1998; Steffan-Dewenter et al., 2005). As such, wild pollinators can be considered as having economic, as well as intrinsic value. The yields of entomophilous fruit and field crops, such as beans, clovers and raspberries, are significantly enhanced by bumblebee visitation (Corbet et al., 1991; Free, 1993; Willmer et al., 1994). Furthermore, bees pollinate a large number of native plant species, many of which are already scarce and threatened by land use changes, and for which a reduction in pollinator abundance would be detrimental (Kwak et al., 1991; Steffan-Dewenter and Tscharntke, 1999). Whilst a diverse assemblage of pollinators is considered important to the maintenance of this ecological function (Fontaine et al., 2006), it has been suggested that bumblebees could compensate for the losses of other groups such as managed honeybees, especially with the recent decline of beekeeping due to diseases and loss of subsidies (Kremen et al., 2002).

Bumblebees forage under a wider range of temperatures and weather conditions than honeybees, can access a wider range of flower types and facilitate pollen transfer by their hairy bodies and 'buzz-foraging' behaviour. Corbet (2000) identifies the longer-tongued bumblebees (e.g. *B. hortorum*) as a particularly important yet vulnerable compartment in the pollination webs of agricultural landscapes. They perform a pollination service for deep-corolla perennial flowers that cannot be replaced by other bee species. For example, red clover (*Trifolium pratense*), which can be considered both a crop (with many cultivars) and an important component of semi-natural grassland, is entirely dependent on cross-pollination and almost exclusively pollinated by long-tongued bumblebees (Hawkins, 1961). It is therefore critical that habitat restoration measures are implemented in Britain and other regions to enhance bumblebee populations and conserve this integral component of agricultural and semi-natural ecosystems.

1.2 Bumblebee ecology and habitat requirements

In order to formulate methods for the restoration of habitats suitable for bumblebees, knowledge of their ecological requirements is essential. These have been well documented over the last century. Sladen (1912), Free and Butler (1959) and Alford (1975) describe in detail the biology of the

British species based on a combination of anecdotal observations and experimentation. More recently, the widespread decline in bumblebees and recognition of their ecological and economic importance have prompted new additions to the literature (Goulson, 2003; Benton, 2006). These publications serve as excellent summaries of recent scientific research as well as highlighting the argument for bumblebee conservation. However, there is still much to be discovered and the specific habitat requirements of many species, together with the habitat management techniques reauired to conserve their populations, have not been quantified in detail. Here I will briefly describe the annual life cycle of bumblebees in temperate regions and outline the resources and habitat components considered to be important during different stages of this cycle.

The colony is founded in spring by a single mated and overwintered queen. The timing of emergence varies from February to May depending on species and geographical location, but all queens require an almost immediate supply of pollen and nectar for development of their ovaries and to replace body fats lost during hibernation. The queen then searches for a suitable nest site, often selecting the abandoned nest of a small mammal, although it is not clear whether there are associations between bumblebee species and particular mammal species (Benton, 2006). Nests may be underground or on the surface in rough grassland, again depending on the species (Table 1), but must be suitably insulated and remain free from disturbance throughout the summer. Having selected a site, the queen provisions the nest with a wax pot in which she stores nectar, and a pollen lump into which she lays her eggs. Over about 4-5 weeks these hatch into larvae which are fed with pollen to aid their growth and development, then pupate and emerge as the first batch of workers. This period of nest founding is likely to be especially crucial to colony success. Therefore spring-flowering plants, such as white and red deadnettle (*Lamium* spp.) and willows (*Salix* spp.), must be available within the vicinity of nest sites to supply pollen and nectar for queens and early workers foraging when the weather allows.

As colony growth accelerates, additional batches of workers are produced and fed by their sisters while the queen remains in the nest laying eggs and incubating broods. The foraging range of workers again varies depending on species, and remains a subject of current research, but for most it is probably at least 300 metres and may extend to two kilometres or more in some situations (Dramstad, 1996; Osborne et al., 1999; Walther-Hellwig and Frankl, 2000; Knight et al., 2005). However, while foragers are able to exploit a relatively large habitat area within range of the nest, they are often restricted to a limited number of forage plants, usually perennials and biennials, which provide their preferred pollen and nectar sources and need to be available throughout the life of the colony (Heinrich, 1976; Fussell and Corbet, 1992; Goulson and Darvill, 2004). Any loss or interruption in these forage sources, such as by overgrazing or regular cutting, can have serious consequences, since colonies only store reserves of pollen and nectar to last several days.

Towards the end of the season, usually between June and late August when worker density has reached a peak, the colony switches to production of males and new queens. The males leave the nest to begin patrolling and scent-marking particular features on their route, in search of a mate (Goulson, 2003). Young queens leave the nest to forage and build up their fat reserves, occasionally returning to the nest for shelter. Eventually they mate and seek out suitable hibernation sites which may be north-facing banks, the base of old trees or underground in open grasslands. It appears that many colonies do not, however, succeed in producing new queens or males due to parasitism, predation or insufficient forage (e.g. Muller and Schmid-Hempel, 1992), and there is much yet to be discovered about the causes of colony failure and factors controlling fecundity.

In summary, for an area to support sustainable bumblebee populations, it must provide hibernation sites for queens, patrolling sites for males and, most importantly, undisturbed nesting sites and a seasonal succession of suitable forage resources. These have been described by Westrich (1996) as the four key ‘partial habitats’ required by most bee species. These habitats may be present within a localised site, or in the case of agricultural landscapes, distributed as small fragments of semi-natural vegetation amongst intensively managed fields. Where bumblebees are concerned, the challenge for ecologists is to determine the amount, spatial distribution and temporal availability of these habitats that are required in order to sustain populations of the different species.

1.3 The policy context: opportunities for habitat restoration under agri-environment schemes

The restoration or recreation of habitats and reassembly of ecological communities is a relatively new branch of ecology which has developed in response to habitat loss and landscape change (Jordan, Gilpin and Aber, 1987). Studies documenting different approaches to restoration have tended to focus on plant communities and the abiotic factors they require (e.g. Bakker and Berendse, 1999; Pywell et al., 2002). Only recently have interactions with other taxa, such as pollinators, in restored communities been considered (Neal, 1998; Dicks, 2002). From the policy perspective, however, the need to conserve rare and declining species has driven both national and international strategies for the protection and enhancement of biodiversity (UK Biodiversity Group, 1998; www.biodiv.org/convention/default).

Studies funded under the UK BAP initiative at first concentrated on mapping current distributions of the BAP bumblebees and further exploring their habitat requirements at the (mainly) protected sites where they had survived (Edwards, 1998; Carvell et al., 2002). More recently, attention has turned to the potential role of agricultural habitats in supporting rare species. This, coupled with recognition of the need to enhance populations of our common and widespread bumblebees, has coincided with recent changes in the European Common Agricultural Policy (CAP). An increasing emphasis has been placed on enhancing the environment while maintaining viable agricultural production, and provisions have been adopted for EU member states to operate agri-environment schemes (EEC regulation 2078/92). The schemes cover a range of objectives which differ depending on country or region, but all include measures whereby farmers are paid to manage their land for the benefit of particular habitats and species (Ovenden et al., 1998). In England, a new agri-environment scheme has recently been adopted which takes forward the two largest existing schemes, Environmentally Sensitive Areas (ESAs) and the Countryside Stewardship Scheme (CSS) (Defra, 2005a, b). Environmental Stewardship (ES) represents a commitment of increased funds towards environmental protection, with greater rewards for farmers participating at higher levels. It is particularly important that management options within the scheme are both based on sound scientific evidence and subject to scientific evaluation such that they are successful in attracting the desired species onto farmland (Kleijn and Sutherland, 2003).

These developments within the UK agri-environment schemes have brought considerable opportunities for the restoration of areas of semi-natural habitat on farmland, and these have potential to benefit bumblebees. At present, populations of the rarer *Bombus* species are mostly confined to large areas of extensively managed herb-rich grasslands, such as Salisbury Plain in Wiltshire, and coastal areas where the impacts of agriculture have been relatively marginal (Edwards, 1998). However, as bumblebees are mobile species which appear to operate at a landscape scale (Osborne et al., 1999), it is likely that suitable habitat restoration measures applied within the farmed landscape could be effective in enhancing populations of both the rarer and more widespread species.

To date, the plant species composition, density and spatial distribution of habitats required by the full bumblebee assemblage are not fully understood. Despite the option of sowing perennial wildflower mixtures along field margins being available within preliminary agri-environment schemes such as Arable Stewardship, within the CSS (Defra, 2001), these were not specifically designed to include a range of suitable bee forage plants. In practice, their uptake has been minimal due to the costs and difficulties associated with their management. Uptake by farmers has tended to be greatest for grass margins or 'beetlebanks' and annual seed mixtures targeted at farmland birds, containing seed-bearing crops to provide over-winter food sources and cover during the breeding season (Vickery et al., 2002). As part of this thesis, differences in the use by bumblebees of annual and perennial field margin options which are relevant to current agri-environment policy will be tested, using single- and multi-site experiments (Chapters 3, 4 and 6), in order to contribute to a research-based policy for targeted habitat restoration.

1.4 Aims and objectives

The overall aim of this research is to examine some of the causes of bumblebee declines in Britain, and investigate methods of habitat restoration to reverse these declines within intensively managed agricultural landscapes.
Specifically, the PhD will address the following objectives:

1. Assess and quantify 20th Century changes in range and abundance of bumblebee forage plants and nesting habitats at a national scale in Britain (Chapter 2);

2. Investigate the response of foraging bumblebees to successional change in newly created field margin habitats, using a replicated experiment on arable farmland in northern England (Chapter 3);

3. Assess the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis, using a replicated field margin experiment on arable farmland in northern England (Chapter 4);

4. Investigate the utilisation of pollen resources by bumblebees across an enhanced arable landscape (Chapter 5);

5. Compare the efficacy of agri-environment schemes to enhance bumblebee abundance and diversity on arable field margins, using a multi-site experiment conducted over three years (Chapter 6);

6. Discuss the potential role of habitat restoration and enhancement for the conservation of bumblebee species in Britain (Chapter 7).

Each chapter is presented in the format of a manuscript either published or in press, with the exception of Chapters 5 and 7.

1.5 Rationale for field methods used

This section gives a brief rationale for the two main field study methods (transect walks and pollen load analysis) used to estimate bumblebee abundance and assess foraging activity in the studies presented in Chapters 3 to 6. Detailed accounts of the methods used and statistics applied in data analysis are given within individual chapters.

1.5.1 Transects

The transect method was chosen to estimate abundance of foraging bumblebees at different times during each season on the various experimental field margins. It involves walking at a steady pace along a linear route (such as a field margin) of fixed length, recording all bees foraging within a fixed distance of the recorder and usually listing the plant species on which each bee is foraging. This has become a standard and repeatable approach that is non-destructive and widely recognised in the fields of entomology and agro-ecology. The transect method (also referred to as line-transect or belt method) was originally proposed by Banaszak (1980) and Teräs (1983) who recognised the need for a standardised method for achieving quantitative estimates of bee density in different habitats. It has since been used in major large-scale studies such as the Farm Scale Evaluations of genetically modified herbicide-tolerant crops (Roy et al., 2003) and in evaluations of the benefits of agri-environment schemes for bees across England (Pywell et al., 2006) and other European countries (Kleijn et al., 2006). The transect method is also used across a variety of habitat types in the national Butterfly Monitoring Scheme in Britain (Pollard and Yates, 1993) and elsewhere in Europe (van Swaay, 1990).

Essential criteria include that transect recorders are experienced in field identification, that walking speed and transect width remain constant and that transects are conducted under weather conditions suitable for bee activity. Maintaining a fixed transect area throughout the season also allows estimates of forage availability to be made as this is undoubtedly a major driver of bumblebee density and abundance on a given transect. It is important to recognise, however, that as bumblebees are central place foragers with colony size varying between species, the abundance of foragers on a transect does not necessarily relate to the number of colonies in that area or to their reproductive success in terms of queens and males produced (as would determine the effective population size). Instead, the transect estimates illustrate how attractive an area is in terms of floral resources for bees nesting in the vicinity. This emphasises the importance of only recording foraging bees and not bees in flight which may simply be travelling to utilise a habitat patch beyond the transect.

Alternative low-cost methods that are commonly used to sample flower-visiting insects include sweep-netting and fixed 'quadrat' observations. Sweep-netting can allow for accurate identification in the lab, but additional benefits are limited. This method was used to sample bumblebees in evaluations of the Arable Stewardship Scheme in England (Allen et al., 2001) but apart from yielding little data, was found to be destructive to both bees and flowers and potentially also dangerous to surveyors when large catches were involved. In addition, as originally pointed out by Banaszak (1980), sweeping may not capture all bee species (including *Bombus* spp.) as they tend to forage on flowers at different heights within a sward. I have also used fixed 'quadrat' observations to investigate the habitat use of bumblebees over large areas of grassland under different management regimes (Carvell, 2002). This approach requires considerable replication to counter the heterogeneity of forage patches within an area and is perhaps less suited than transects to the assessment of linear habitat features in agricultural landscapes. It should, however, not be ruled out in focused studies of bee behaviour or plant-pollinator interactions such as those constructing visitation webs (e.g. Gibson et al., 2006).

1.5.2 Pollen load analysis

The foraging behaviour of bumblebees has been extensively studied, in relation to the energetics of flight (Heinrich, 1979), their choice of flower species (e.g. Heinrich, 1976; Ranta and Lundberg, 1980; Fussell and Corbet, 1992) and exploitation of patchy resources in the landscape (Osborne and Williams, 2001; Goulson, 2003). Foraging studies looking at flower choice and dietary preference for different plant species have, especially in recent years, tended to focus on the flower visits of individuals observed on transect walks (as above) or timed observations at forage patches. These are likely to reflect the often wide range of plant species visited for nectar, but may not identify those species which are particularly important as pollen sources (Ranta and Lundberg, 1981; Goulson and Darvill, 2004).

The pollen loads collected by bees are good indicators of flower constancy, the tendency to restrict their visits to flowers of a single species (Waser, 1986). They also provide a useful means of comparing the foraging specializations of different bee species, which are apparent at most foraging sites due to factors such as differences in tongue length and flower handling ability (Ranta and Lundberg, 1980). This thesis explores the use of pollen load analysis to supplement measures of bumblebee visitation from transect walks (Chapters 4 and 5), particularly in the context of the value of restored habitats as sources of nectar and pollen in the farmed landscape.

References

Alford, D.V., 1975. Bumblebees. Davis-Poynter, London.

Alford, D.V., Ed., 1980. Atlas of the Bumblebees of the British Isles. Institute of Terrestrial Ecology, Cambridge, UK.

Anonymous, 1995. Biodiversity - The UK Steering Group Report. Volume 2 Action Plans. HMSO, London.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P., Walker, S., 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conservation Biology 12, 8-17.

Allen, D.S., Gundrey, A.L., Gardner, S.M., 2001. Bumblebees. Technical annex to Ecological Evaluation of the Arable Stewardship Pilot Scheme 1998-2000. ADAS, Wolverhampton, UK.

Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology & Evolution 14, 63-68.

Banaszak, J., 1980. Studies on methods of censusing the numbers of bees (Hymenoptera: Apoidea). Polish Ecological Studies 6, 355-366.

Benton, T., 2006. Bumblebees. Collins, London.

Buchmann, S.E., Nabhan, G.P., 1996. The Forgotten Pollinators. Island Press, Washington DC, USA.

Carvell, C., 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. Biological Conservation 103:33-49.

Corbet, S.A., 2000. Conserving compartments in pollination webs. Conservation Biology 14, 1229-1231.

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

Defra, 2001. The Countryside Stewardship Scheme: New Arable Options for 2002. Department for Environment, Food and Rural Affairs, London.

Defra, 2005a. Environmental Stewardship: Entry Level Stewardship Handbook. Department for Environment, Food and Rural Affairs, London.

Defra, 2005b. Environmental Stewardship: Higher Level Stewardship Handbook. Department for Environment, Food and Rural Affairs, London.

Dicks, L.V., 2002. The structure and functioning of flower-visiting insect communities on hay meadows. PhD thesis. University of Cambridge, Cambridge, UK.

Dramstad, W.E., 1996. Do bumblebees (Hymenoptera: Apidae) really forage close to their nests? Journal of Insect Behavior 9, 163-182.

Edwards, M., 1998. UK BAP Bumblebee Working Group Report, 1998. Unpublished report for the UK BAP Bumblebee Working Group, Midhurst, UK.

Falk, S., 1991. A review of the scarce and threatened bees, wasps and ants of Great Britain. Nature Conservancy Council, Peterborough, UK.

Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2006. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. Plos Biology 4, 129-135.

Free, J.B., 1993. Insect Pollination of Crops, 2nd edition. Academic Press, London.

Free, J. B. and Butler, C. G., 1959. Bumblebees. Collins, London.

Fuller, R.M., 1987. The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930-84. Biological Conservation 40, 281-300.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R., Carter, N., 1995. Population declines and range contractions among lowland farmland birds in Britain. Conservation Biology 9, 1425-1441.

Fussell, M., Corbet, S.A., 1992. Flower usage by bumblebees: a basis for forage plant management. Journal of Applied Ecology 29, 451-465.

Gibson, R.H., Nelson, I.L., Hopkins, G.W., Hamlett, B.J., Memmott, J., 2006. Pollinator webs, plant communities and the conservation of rare plants: arable weeds as a case study. Journal of Applied Ecology 43, 246-257.

Goulson, D., 2003. Bumblebees: their behaviour and ecology. Oxford University Press.

Goulson, D., Darvill, B., 2004. Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? Apidologie 35, 55-63.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. Biological Conservation 122, 1-8.

Haines-Young, R. (editor) 2000. Accounting for nature: assessing habitats in the UK countryside. DETR: London.

Hawkins, R.P., 1961. Observations on the pollination of red clover by bees. Annals of Applied Biology 49, 55 - 65.

Heinrich, B., 1976. The foraging specializations of individual bumblebees. Ecological Monographs 46, 105-128.

Heinrich, B., 1979. Bumblebee Economics. Harvard University Press, Cambridge, MA.

Jordan, W. R., Gilpin, M. E., Aber, J. D., 1987. Restoration ecology: a synthetic approach to ecological research. Cambridge University Press, Cambridge, UK.

Kells, A.R., Goulson, D., 2003. Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. Biological Conservation 109, 165-174.

Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? Journal of Applied Ecology 40, 947-969.

Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., De Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Johl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecology Letters 9, 243-254.

Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, A., Goulson, D., 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. Molecular Ecology 14, 1811-1820.

Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences of the United States of America 99, 16812-16816.

Kwak, M., van den Brand, C., Kremer, P., Boerrigter, E., 1991. Visitation, flight distances and seed set in the rare species *Phyteuma nigrum* (Campanulaceae). Acta Hort. 288, 303-307.

Muller, C.B., Schmid-Hempel, P., 1992. Correlates of reproductive success among field colonies of *Bombus lucorum* - the importance of growth and parasites. Ecological Entomology 17, 343-353.

Neal, P.R., 1998. Pollinator restoration. Trends in Ecology & Evolution 13, 132-133.

Osborne, J. L., Corbet, S.A., 1994. Managing habitats for pollinators in farmland. Aspects of Applied Biology 40; Arable farming under CAP reform, 207-215.

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

Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. Journal of Applied Ecology 36, 519-533.

Pollard, E., Yates, T.J., 1993. Monitoring Butterflies for Ecology and Conservation. Chapman and Hall, London.

Pollard, E., Moss, D. & Yates, T.J., 1995. Population trends of common British butterflies at monitored sites. Journal of Applied Ecology 32: 9-16.

Preston, C. D., Pearman, D. A., Dines, T.D. (2002). New Atlas of the British and Irish Flora. Oxford University Press, Oxford, UK.

Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W., Peel, S., 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. Journal of Applied Ecology 39, 294-309.

Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., Critchley, C.N.R., Sherwood, A., 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 129, 192-206.

Ranta, E., Lundberg, H., 1980. Resource partitioning in bumblebees: the significance of differences in proboscis length. OIKOS 35, 298-302.

Ranta, E., Lundberg, H., 1981. Food niche analyses of bumblebees: a comparison of three data collecting methods. OIKOS 36, 12-16.

Rasmont, P., 1988. Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera. Apidae, Bombinae). PhD Thesis. Faculté des Science Agronomique de l'Etat, Gembloux, Belgium.

Roy, D.B., Bohan, D.A., Haughton, A.J., Hill, M.O., Osborne, J.L., Clark, S.J., Perry, J.N., Rothery, P., Scott, R.J., Brooks, D.R., Champion, G.T., Hawes, C., Heard, M.S., Firbank, L.G.,

2003. Invertebrates and vegetation of field margins adjacent to crops subject to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 358, 1879 - 1898.

Saville, N.M., Dramstad, W.E., Fry, G.L.A., Corbet, S.A., 1997. Bumblebee movement in a fragmented agricultural landscape. Agriculture, Ecosystems and Environment 61, 145-154.

Sladen, F. W. L., 1912. The Humble-bee, its life history and how to domesticate it. Macmillan & Co. Ltd., London.

Smart, S.M., Firbank, L.G., Bunce, R.G.H., Watkins, J.W., 2000. Quantifying changes in abundance of food plants for butterfly larvae and farmland birds. Journal of Applied Ecology 37, 398 – 414.

Stace, C., 1997. New Flora of the British Isles. Cambridge University Press, Cambridge, UK.

Steffan-Dewenter, I., Tscharntke, T., 1999. Effects of habitat isolation on pollinator communities and seed set. Oecologia 121, 432 – 440.

Steffan-Dewenter, I., Potts, S.G., Packer, L., 2005. Pollinator diversity and crop pollination services are at risk. Trends in Ecology & Evolution 20, 651-652.

Svensson, B., Lagerlöf, J., Svensson, Bo. G., 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agriculture, Ecosystems and Environment 77, 247-255.

Teräs, I., 1983. Estimation of bumblebee densities (*Bombus*: Hymenoptera, Apidae). Acta Entomologica Fennica 42, 103-113.

UK Biodiversity Group, 1998. UK Biodiversity Group Tranche 2 Action Plans: Invertebrates, vol. IV. English Nature, Peterborough, UK.

van Swaay, C.A.M., 1990. An assessment of the changes in butterfly abundance in The Netherlands during the 20th Century. Biological Conservation 52, 287-302.

Vickery, J., Carter, N., Fuller, R.J., 2002. The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. Agriculture Ecosystems & Environment 89, 41-52.

Walther-Hellwig, K., Frankl, R., 2000. Foraging distances of *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae). Journal of Insect Behavior 13, 239-246.

Waser, N. M., 1986. Flower constancy: definition, cause and measurement. American Naturalist 127, 593-603.

Westrich, P., 1996. The problems of partial habitats. In The Conservation of Bees. eds A. Matheson, S.L. Buchmann, C. O'Toole, W. P., I.H. Williams. Academic Press, London, UK.

Williams, P.H., 1982. The distribution and decline of British bumblebees (*Bombus* Latr.) Journal of Apicultural Research 21 (4), 236-245.

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

Willmer, P.G. et al, 1994. The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. Ecological Entomology 19, 271 – 284.

Table 1.1 Summary of the current known distribution and conservation status of British *Bombus* species (excluding subgenus *Psithyrus*).

***Bombus* species**	**Distribution in Britain ***	**Conservation status/ comment**	**Ecology summary †**
Bombus lucorum (Linnaeus)	Universal		Short-tongued, nests underground, urban/woodland edge
Bombus terrestris (Linnaeus)	Universal	More frequent in south	Short-tongued., nests underground, urban/woodland edge
Bombus pratorum (Linnaeus)	Universal	Very common in gardens	Short-tongued, nests variable, urban/woodland edge
Bombus lapidarius (Linnaeus)	Universal	Scarce in N Scotland	Medium-tongued, nests variable-underground, urban/woodland edge
Bombus pascuorum (Scopoli)	Universal		Long-tongued, carder bee nests on surface, urban/woodland edge
Bombus hortorum (Linnaeus)	Universal		Long-tongued, nests variable, urban/woodland edge
Bombus jonellus (Kirby)	Universal, local		Short-tongued, nests variable, urban/woodland edge and moorland
Bombus soroeensis (Fabricius)	Universal, local		Medium-tongued, nests underground, open grassland
Bombus muscorum (Linnaeus)	Universal, local to Northern	EN Species Recovery, proposed BAP	Long-tongued, carder bee nests on surface, open grassland
Bombus monticola (Fabricius)	Northern, high ground in south	EN Species Recovery, proposed BAP	Medium-tongued, nests variable, open grassland and moorland
Bombus distinguendus (Morawitz)	Northern, local	UK BAP species	Long-tongued, nests underground, open grassland
Bombus magnus (Kruger)	Northern		Short-tongued, often grouped with *B. lucorum*
Bombus ruderarius (Muller)	Southern	EN Species Recovery, proposed BAP	Long-tongued, nests on surface, open grassland
Bombus humilis (Illiger)	Southern, local	UK BAP species	Long-tongued, carder bee nests on surface, open grassland
Bombus sylvarum (Linnaeus)	Southern, local	UK BAP species	Long-tongued, carder bee nests on surface, open grassland
Bombus ruderatus (Fabricius)	Southern, local	UK BAP species	Long-tongued, nests underground, open grassland
Bombus subterraneus (Linnaeus)	Southern, local/ Extinct	UK BAP species, prob. extinct	Long-tongued, nests underground, open grassland

***Bombus* species cont.**	**Distribution in Britain** *	**Conservation status/ comment**	**Ecology summary** †
Bombus cullumanus (Kirby)	Extinct since 1950's	Extinct	Medium-tongued, open grassland
Bombus pomorum (Panzer)	Extinct since 1864	Extinct	Long-tongued, open (damp) grassland
Bombus hypnorum (Linnaeus)	Introduced	First recorded 2001	Short-tongued, urban/woodland edge on continent

* Range descriptions are based on updates of the Bumblebee Distribution Maps Scheme (Alford,1980) and patterns identified by Williams (1982). Some have been compiled by the Bees, Wasps and Ants Recording Society and published in recent Newsletters, and others are based on current knowledge of the International Bee Research Association, Mike Edwards and Murdo Macdonald (personal communication). Most represent the known post-1970 to present distribution of each bumblebee (*Bombus*) species.

Universal = occurs throughout the British Isles; Universal, local = occurs throughout the British Isles but is restricted in abundance, even within main area of distribution; Northern = restricted to, or with strong bias to the north of the Humber-Mersey line; Northern, local = restricted to the extreme north of Scotland; Southern = restricted to, or with strong bias to the south of the Humber-Mersey line; Southern, local = restricted to the southern coastal band running south from Norfolk in the east an up to the Isle of Anglesey in the west, having seriously declined since the 1970's.

† Based on descriptions from Edwards and Williams (2004) and Benton (2006).

2. Declines in forage availability for bumblebees at a national scale

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Appendix 2B is included in the thesis to demonstrate additional analyses that were carried out on changes in grass species associated with bumblebee nesting habitats.

Abstract

We assessed national scale changes in the forage plants of bumblebees in Britain, as a means of providing quantitative evidence for the likely principal cause of declines in bumblebee species. We quantified the relative value of native and long-established plant species as forage (nectar and pollen) resources for bumblebees by collating visitation data from 14 field sites across Britain. Twentieth Century changes in range and frequency of these forage plants were assessed using data from the *New Atlas of the British and Irish Flora* (1930-69 to 1987-99) and the Countryside Surveys of Britain (1978 to 1998). Forage plants declined in both large-scale range and local-scale frequency between the two survey periods. These changes were of greater magnitude than changes in other native plant species, reflecting serious reductions in quality of foraging habitats for bees as well as a general decline in insect-pollinated plants. Seventy-six percent of forage plants declined in frequency within 1-km squares, including those (e.g. *Trifolium pratense*) of particular value for threatened bumblebee species. We consider how our findings relate to other recorded changes in the British flora, how they may help to explain declines in bumblebees and how they could contribute to a conservation strategy.

Keywords

Bombus, forage plants, habitat quality, pollinators, conservation

2.1 Introduction

Resource availability is often a critical factor in determining the distribution and abundance of species, and it is recognised that reductions in habitat quality as well as quantity are likely to cause population declines (Schultz and Dlugosch, 1999). Many social bumblebee (*Bombus* Latr.) species have undergone serious declines in recent decades across Europe and North America (Williams, 1982; Rasmont, 1988; Buchmann and Nabhan, 1996). Several factors have been suggested as possible contributors to these declines, including competition from the honeybee (*Apis mellifera*), changes in climate and the effects of predators and parasites (Williams, 1986). However, the principal factor is likely to have been the loss and degradation of habitats and critical food resources due to changes in land-use and agricultural practices (Goulson et al., 2005; Williams, 2005).

In Britain, as in other parts of Europe, the intensification of agricultural practices since the 1940s has resulted in the fragmentation, degradation and loss of semi-natural habitats (Robinson and Sutherland, 2002). For example, the area of unimproved lowland grassland in Britain is reported to have declined by over 90% between 1932 and 1984 (Fuller, 1987). Bumblebees forage for the colony as well as themselves, but only store several days' worth of reserves, so therefore require an almost continuous supply of food resources (nectar and pollen) within foraging distance from the nest throughout the period of colony activity (Prŷs-Jones and Corbet, 1991). Flower-rich, extensively managed vegetation is therefore considered an essential component of the agricultural landscape for bumblebees, providing foraging resources as well as nesting, mating and hibernation sites (Banaszak, 1992; Williams, 1986).

Analyses of change in the distributional ranges of British bumblebees have highlighted the likely extent of declines during the 20th Century. By the 1980s, only six of Britain's 19 *Bombus* species remained throughout their pre-1960 range (Williams, 1982). Three species are now considered to have become extinct, four (*Bombus distinguendus*, *B. humilis*, *B. ruderatus* and *B. sylvarum*) are currently on the UK Biodiversity Action Plan as priorities for conservation and others remain under threat (UK Biodiversity Group, 1998). This situation may threaten the pollination of many wild flowers and entomophilous crops (such as field bean, clover and various fruits) for which bumblebees are especially important (Corbet et al., 1991). They are therefore a key component of agricultural and semi-natural ecosystems that require urgent conservation.

The causes of rarity and decline among British bumblebees have recently been discussed by Goulson et al. (2005) and Williams (2005). They concluded that a combination of factors including a species' proximity to the edge of its European range and degree of food-plant or habitat specialization are likely to determine its sensitivity to environmental change, but noted that further studies on the rarer bumblebee species are still required. While these ecological factors continue to be debated, evidence of specific changes in abundance of essential habitat components, namely forage plants which provide nectar and pollen resources, has been largely anecdotal or derived at local scales. At the scale of individual sites, there is a link between the abundance and diversity of bumblebees and that of their preferred forage plant species (Bäckman and Tiainen, 2002; Carvell, 2002). More specifically, the abundance of the most rewarding forage plants at a site seems to be more important for many bee species than overall flowering plant diversity (Williams, 1989). Rasmont (1988) suggested that the loss of Fabaceae, historically sown as fodder crops, from grassland systems in France and Belgium was the major driver of declines in the longer-tongued bumblebees. However, quantitative evidence for declines or increases in forage plant abundance at national scales and over relevant time periods is so far lacking. It is important to understand the extent and direction of these changes in order to design appropriate measures to conserve bumblebee populations.

Attempts to quantify large-scale changes in biodiversity are often hindered by the quality and availability of data on species distributions (Thomas et al., 2004). However, repeated and systematic surveys in Britain over the past 30 to 50 years have generated two datasets which allow national changes in range and abundance of vascular plant species to be assessed. The *New Atlas of the British and Irish Flora* can be used to study change in number of occupied 10-km squares between 1930-69 and 1987-99 (Preston et al., 2002). This spans the likely period of most serious decline in bumblebee species (Williams, 1982). At a more detailed scale, the Countryside Surveys of Britain recorded the changing presence of all vascular plant species in fixed plots within 259 1-km squares between 1978 and 1998 (Haines-Young et al., 2000). These changes in species frequency have been used to infer changes in plant abundance between the two survey periods (Smart et al., 2005). The Countryside Surveys are likely to have covered the later phase of the period of bumblebee declines, but offer the most useful measure of national scale change in habitat quality.

In this paper we collate a number of datasets documenting bumblebee visitation to specified plant species in Britain, to produce a list of important nectar and pollen sources. We analyse changes in range and frequency of these forage plant species to quantify changes in resource availability for bumblebees at a national scale. We also consider whether the magnitude of such changes may help to explain 20th Century declines in British bumblebees. The forage species list is not exhaustive, and does not include entomophilous crops or garden flowers, but represents the collective findings of available surveys which meet particular criteria. Furthermore, the analysis is restricted to native species and long-established aliens (archaeophytes) (Preston et al., 2004), both because the value of recently introduced plant species (neophytes) as forage plants is less well known, and because numerical estimates of the spread of invasive plant species are influenced to a greater degree than natives by changes in recording practice.

2.2 Methods

2.2.1 Collation of bumblebee forage plant data

A number of datasets containing information on bumblebee forage plant visitation across Britain were collated. Data from both published and unpublished studies were used but, in order to ensure consistency, the following criteria were applied.

1. All studies presented data as the number of bumblebee visits to a specified list of flowering plant species from one site (where more than one site was sampled during a study, datasets were considered separately). Studies conducted in gardens alone were excluded, as were those concentrating on crop species. Data was also restricted to flowering plant species classified as natives, probable natives or archaeophytes in Britain.
2. Bumblebee visits were given to species level, but not necessarily separated by caste (we assume therefore that plants visited by queens, workers and males were represented in the collated data, even if not in all studies).
3. Bumblebees were recorded using a standardised bee walk transect (Banaszak, 1980) or similar method.
4. All studies were conducted within Britain, and over at least a two week time period up to and including the year 2000.

Datasets from a total of 14 study sites were found to match these criteria (Table 2.1), and were used to derive a list of visits by individual bumblebee species to specific forage plants. The studies encompassed a wide range of semi-natural habitats (including a limited number within intensively farmed landscapes) and geographical locations across Britain.

To measure the relative value of each plant species as a forage resource, a 'forage index' was calculated. A simple average across sites of number of bee visits to each plant species was not an appropriate measure of relative importance, as the forage plant species by sites table was unbalanced (i.e. many plant species were present at just a few sites and a more limited number present at most sites). Also, due to differences in habitat type and quality between study sites, overall visitation rates were higher in some datasets than others. To compensate for these effects, a general linear model (Ryan et al., 2000) of the form,

$$\log(y_{ij} + 1) = \mu + \alpha_i + \beta_j + \varepsilon_{ij}$$

was applied to the data, where y_{ij} is the number of visits to plant species *i* at a site *j*. μ is a constant and the coefficients α_i and β_j are effects for species and sites respectively. The forage index was calculated as a least-squares mean for each plant species; in effect this provides a geometric mean number of visits to each plant species, allowing for missing values.

Because of difficulties in comparing visitation data from different study sites (Williams, 2005), forage indices were not calculated for individual *Bombus* species. Forage indices were calculated for all social *Bombus* species grouped, and also for two summary classes of longer- and shorter-tongued species. Long-tongued species included *B. hortorum, B. pascuorum, B. humilis, B. ruderarius, B. sylvarum, B. muscorum* and *B. distinguendus* and short to medium-tongued species included *B. terrestris, B. pratorum, B. lapidarius, B. lucorum* and *B. jonellus*, based on Williams (1989) and Prŷs-Jones and Corbet (1991). These are not absolute classifications of tongue length as this can vary between species and among castes of the same species.

2.2.2 Quantifying range changes (1930-69 to 1987-99)

Changes in the distributional range of bumblebee forage plants were quantified at the 10-km square scale using records collated for the periods 1930-69 and 1987-99 (Preston et al., 2002). In order to compensate for variations in recording intensity and geographical coverage, changes in range size were assessed using a 'change index' (Telfer et al., 2002). The full details of this change index are already described, but the method is briefly outlined here. The 2788 10-km grid squares which were surveyed in both recording periods were defined (excluding Ireland), and the proportion of these squares in which each species was recorded was calculated for each period and then logit-transformed. A weighted linear regression model was fitted to the relationship between these counts, and the standardised residual for each species taken to represent an index of its change in range size relative to the trend across all species (Telfer et al., 2002). Thus, while the change index does not represent species range increases or decreases in absolute terms, it allows an assessment of the performance of each species between the two periods in relation to the 'average' species. Plant nomenclature follows Stace (1997).

2.2.3 Quantifying frequency changes (1978 to 1998)

Changes in forage plant species frequency were based on data recorded at the 1-km square scale in 1978 and 1998 as part of the Countryside Survey (CS) (Haines-Young et al., 2000). A total of 259 1 x 1 km sample squares were selected at random from 32 land classes representing physiographically similar sampling domains across Britain. Within each square, a number of fixed plots were established. These plots covered both linear features, including hedgerows, stream sides and road verges (all $10m^2$) as well as fields and unenclosed land (all 200 m^2). Within each plot (n=1572), the presence (frequency) of all vascular plant species was recorded once in 1978 and again in 1990 and 1998. Further information on the CS approach and recording methodology can be obtained from Haines-Young et al. (2000) and Smart et al. (2005).

Changes in plot frequency of individual plant species between 1978 and 1998 for which CS data were available were assessed by calculating the percentage change in number of occupied plots between the two survey periods (referred to as relative % change). All CS plots that contained a recorded presence for a species in 1978 and 1998 were used, with the minimum sample size for analysis set at six occurrences in either year.

2.2.4 Analysis

For the CS data on species plot frequency, recorder intensity and geographical coverage were the same for each survey, therefore magnitude of change could be assessed. For each species, the change in number of occupied plots between 1978 and 1998 as a proportion of the total number of plots sampled (1572) was analysed using the *Z*-test for two proportions.

Differences between the mean range and frequency change in bumblebee forage plants and the mean change in range and frequency of all other non-forage plant species were analysed using two-sample T-tests. Analyses were repeated using randomisation tests that do not make assumptions about the distribution of the data (Manly, 1997), but these are not presented here as they did not change the results. Only species treated as natives, probable natives or archaeophytes (plants believed to have become established before 1500) by Preston et al. (2002, 2004) were included in the analyses. Species which had a British range size of less than 500 10-km squares (Preston et al., 2002), were removed from the list of non-forage plants to be comparable with the selected bee forage species that all occurred in more than 500 10-km squares. The grasses (Poaceae) were also excluded from the list of non-forage plants for this comparison. Relationships between the forage indices for all *Bombus* species, the long- or short-tongued species groups and forage plant species change were also assessed, using regression analyses, in order to determine whether the magnitude of recorded change was greater for more important forage plants.

2.3 Results

2.3.1 Bumblebee forage plants and the 'forage index'

A total of 145 plant species were identified as forage resources for bumblebees at the 14 study sites from which datasets were collated (Table 2.1). Of these species, 43% represented the Fabaceae (15%), Asteraceae (15%) and Lamiaceae (13%) and the majority were perennial or biennial. Plants with the highest overall forage index included *Ballota nigra*, *Centaurea nigra*, *Teucrium scorodonia* and *Lamium album*, though the latter two species were only visited by bees at one site. The long-tongued *Bombus* species group had high forage index values for *Ballota nigra*, *Trifolium pratense* and other Fabaceae whereas the shorter-tongued species showed a tendency to visit *Centaurea nigra*, *Rubus fruticosus* and other Asteraceae, with lower forage indices for the Fabaceae (Table 2.2). Data on changes in range and abundance of native and long-established forage plant species from the *New Atlas* and Countryside Survey were available for 97 and 68 respectively (see Appendix 2A; key species in Table 2.2). These lists included most species visited by bees at two or more sites and representatives from the majority of plant families in the full list.

2.3.2 Range changes in forage plants (1930-69 to 1987-99)

Of the 97 bumblebee forage plant species, 71% had a negative change index. Forage plants had significantly lower change indices than other, non-forage plant species ($n = 671$) ($t = -2.22$, df = 155, $P<0.05$; Figure 2.1a). Bumblebee forage plants have thus declined in range size between 1930-69 and 1987-99 relative to other native or long-established species. Forage species with the largest negative change index included *Leucanthemum vulgare* (-1.14) and *Lamium purpureum* (-1.09), and the largest positive change index was for *Leontodon autumnalis* (+1.32). There was no significant relationship between the forage index of plants for all *Bombus* species grouped and their change index values (Table 2.2). The same was true when this analysis was repeated using the forage indices of long- and short- tongued species.

2.3.3 Frequency changes in forage plants (1978 to 1998)

Within Countryside Survey plots, 76% of bumblebee forage plant species declined and 24% increased in frequency between 1978 and 1998. Forage plants showed a significantly greater decline in CS plot frequency than other, non-forage plant species ($n = 257$) ($t = -3.07$, df = 211, $P<0.01$; Figure 2.1b). Summing the total extent of decline in terms of number of plots from which a forage species was 'lost' (1012), this far exceeded the number of plots in which a species was 'gained' (105). In terms of magnitude of change for individual species, 26 of the 68 species tested showed significant changes in plot frequency ($P<0.05$), but 24 of these were declines (Appendix 2A). Notable declines were recorded for *Centaurea nigra*, *Lathyrus pratensis*, *Leucanthemum vulgare*, *Lotus corniculatus, Rhinanthus minor* and *Trifolium pratense*. Forage species showing the greatest relative increase in plot frequency included *Ballota nigra* and *Odontites vernus*, though 1978 frequency was very low for these two species (Table 2.2). There was no significant relationship between the forage index of plants for all *Bombus* species grouped and their relative percentage change in plot frequency (Table 2.2). Analysing these data according to bee tongue-length, a positive relationship was found between the forage indices for long-tongued species and percentage change in plot frequency ($r^2 = 9.8$, $P<0.01$), although this trend was influenced by high forage indices for the two plant species (*Ballota nigra* and *Odontites vernus*) which more than doubled in plot occupancy between the two surveys.

2.4 Discussion

This study was designed to broadly quantify 20th Century changes in availability of forage resources for bumblebees at a national scale using the best available data. Overall, a large proportion of forage plants declined in both large-scale range and local-scale frequency between the two survey periods of the *New Atlas* and Countryside Survey (CS). These changes were of greater magnitude than changes in other native and long-established plant species, reflecting serious reductions in the quality of foraging habitats for bees as well as a general decline in insect-pollinated plants.

The negative impacts of agricultural intensification on particular groups of animals and plants in Britain have been well recognised (Rich and Woodruff, 1996; Chamberlain et al., 2000; Robinson and Sutherland, 2002) and our results are consistent with these studies. The general trend for plants has been an increase in species characteristic of fertile habitats and decrease in species (often specialists) characteristic of less fertile, semi-natural habitats such as calcareous grassland (Preston et al., 2002). The former include some species which provide forage for bumblebees (e.g. *Cirsium arvense*), as well as the larval food plants (e.g. *Urtica dioica*) of certain butterfly species which have also increased since the 1970's (Smart et al., 2000). However, the majority of bumblebee forage plants are nectariferous perennials or biennials, often typical of established semi-natural vegetation receiving infrequent disturbance. It is therefore perhaps not surprising that as a group, they have declined relative to the 'average' native or archaeophyte species. These declines in range and abundance reflect the degradation of quality of foraging habitats for bumblebees in British landscapes which apparently persisted into the latter part of the 20th Century. Such changes can also be explained by recorded trends in specific management practices across England and Wales. Between 1962 and 1995 for example, large increases in silage production and autumn-sown cereals were accompanied by decreases in hay production, temporary clover leys and undersowing of legumes (Chamberlain et al., 2000).

A decline in forage resources is likely to impact upon bumblebees by affecting both the fitness of individual colonies within each season and persistence of populations between years, depending on the scale at which it is considered. At the local scale, a reduction in nectar and pollen availability within the foraging range of the nest limits colony growth and, ultimately, the reproduction of sexuals (Goulson et al., 2002; Pelletier and McNeil, 2003). Our results from the CS dataset suggest that native forage species important during all stages of colony activity declined between 1978 and 1998. Significant decreases in plot frequency were found for spring forage plants such as *Ajuga reptans*, *Lamium purpureum* and *Salix cinerea* and mid- to late-season forage plants such as *Centaurea nigra*, *Lathyrus pratensis*, *Lotus corniculatus*, *Rhinanthus minor* and *Trifolium pratense*. The total extent of these declines in terms of the likely loss of forage was not compensated for by the increases shown by some species, although we discuss some of the caveats associated with these data below.

Given their relatively large foraging ranges (Darvill et al., 2004), bumblebees might be expected to be capable of adapting to these local-scale reductions in forage, if sufficient resources persisted elsewhere within their population range. However, our results at the larger scale, represented by change in number of occupied 10-km squares from the *New Atlas*, suggest that on the whole this may not have been possible. Since the 1940s, despite being geographically widespread species, bumblebee forage plants have been lost from a significant number of 10-km squares within their range (assuming, as seems likely, that the relative change in forage plants represents an absolute decline). As well as contributing to reduced colony densities at the local to regional scale, this may have restricted the dispersal distances of new queens from their natal colonies, either before or after hibernation, and thereby affected their capacity for population expansion. A much greater understanding of the dispersal abilities of bumblebees (Mikkola, 1978) is required to fully assess the potential of populations to track the changing distribution of forage resources at different spatial scales.

The general response to reduced forage resources suggested above is likely to vary considerably between species, as evidenced by the different patterns of response to 20th Century environmental change shown by bumblebee species in Britain and elsewhere (Goulson et al., 2005; Williams, 2005). This may be due to a combination of ecological, behavioural and morphological factors. For example, the effect of local decreases in forage abundance may be stronger for those species with shorter foraging ranges or more specific dietary preferences. Although we did not distinguish between pollen and nectar provision, the Fabaceae are thought to be especially important pollen sources for the longer-tongued species (Goulson et al., 2005), as reflected here by higher forage indices. The loss of Fabaceae within semi-natural vegetation may have particularly affected this group of bumblebees, some of which have been suggested to have relatively short foraging ranges (Knight et al., 2005). These inter-species differences, combined with the difficulties in measuring preference for particular forage plants (e.g. Williams, 2005), may explain why our forage index did not relate to the recorded changes in plant species. The studies from which visitation data were collated to produce the forage index represented a variety of semi-natural habitats at sites with and without the rarer *Bombus* species, with only heathlands (and to an extent farmland) being underrepresented. But we could not allow for the super-abundance of particular forage plants at certain sites, or for patterns of flower visitation which might have been revealed by studies conducted in the early 20th Century, prior to bumblebee declines. The forage index provides a useful measure of the relative value of plant species to long- vs short-tongued species, and of certain groups of plants to all species, but it should not be interpreted as a definitive measure of floral preference by all bumblebees.

By focusing on native and long-established plant species associated with semi-natural habitats, our analysis did not consider the potentially positive effect that introduced plant species, including garden exotics and entomophilous crops, could have on bumblebee populations. For example, the increase in area of oil-seed rape in England and Wales since the 1970s (Chamberlain et al., 2000) has probably benefited shorter-tongued species such as *Bombus terrestris* (Westphal et al., 2003). Exotic species within gardens, such as *Pulmonaria officinalis* and *Nepeta x faassenii*, may also be important in some situations where native sources of forage are scarce or temporally unavailable (Macdonald, 1998). There is also evidence that urban areas support higher concentrations of nests of the short-tongued *B. terrestris* than arable or mixed farmland (Chapman et al., 2003; Knight et al., 2005) and that nests of this species grow more quickly in gardens than in mixed farmland (Goulson et al., 2002).

In drawing conclusions, we note the caveats associated with comparing the results of two large surveys conducted across different spatial and temporal scales (Preston et al., 2002; Wilson et al., 2004). The direction of change detected by each survey was not the same for every plant species, although the general pattern of forage declines was consistent. Declines in local or regional plant abundance could go undetected at the 10-km scale. Likewise the CS plot data may underestimate the degree of habitat degradation, as plant frequency has some shortcomings as a functional measure of the quality of floral resources available to bumblebees. For example, changes in the cutting management of permanent grassland might reduce the number of flowers and alter sward structure but would not necessarily be detected as changes in plant abundance or plot frequency. We have not considered changes in availability of bumblebee nesting sites here, as it is difficult to quantify the variety of characteristics associated with nest site preferences of the different species (but see Appendix 2B for supplementary analyses of change in grass species associated with bumblebee nesting habitats). However, many species rely on undisturbed grassy vegetation with a tussocky structure, often using the abandoned nests of small mammals (Kells and Goulson, 2003). The response of vole numbers to intensification and the loss of suitable grasslands (Gorman and Reynolds, 1993) is an indication that nesting sites for bumblebees may have declined alongside forage plants, and should be considered in the design of conservation measures.

2.4.1 Conclusions: towards effective conservation and further research

This study has produced the first quantitative evidence for 20th Century declines in resource availability for bumblebees at a national scale in Britain, yet there is scope for much further work of this nature, such as that applied to British butterflies (Wilson et al., 2004). Analyses of changes in plant species range at a regional level suggest that certain forage species declined more seriously in East Anglia (representing much of Williams' (1982) 'central impoverished region' of England) than in other UK regions (Preston et al., 2003). Yet populations of some rare *Bombus* species still persist in central and eastern England, albeit at apparently low densities (Carvell et al., 2006). The question of whether declines in bumblebee populations have depressed crop productivity or the reproductive potential of wild plants in Europe is still under debate (Ghazoul, 2005). However, bee diversity and proximity to natural habitats have been shown to enhance both crop productivity (Kremen et al., 2002) and seed set of isolated plants (Steffan-Dewenter and Tscharntke, 1999), strengthening the conservation argument. Declines in a large number of insect-pollinated native plant species in Britain, as evidenced here, combined with declines in bumblebee species are undoubtedly a cause for concern. More detailed studies of recorded changes in bumblebee distribution and plant abundance and the functional links between plants and pollinators are required to address these questions.

An opportunity now exists to use knowledge from this and other studies to inform targeted habitat restoration, to reintroduce important forage plants to the farmed landscape through agri-environment schemes (Carvell et al., 2004; Pywell et al., 2005). A delay in this reintroduction of resources could further threaten populations of the rarer bumblebees which are mainly restricted to designated sites (Carvell, 2002). We recommend species such as *Trifolium pratense, Lotus corniculatus* and *Centaurea nigra* as components of wildlife seed mixtures. As well as the evidence that these are important forage plants to a range of *Bombus* species which have declined in the countryside, they have also been shown to perform well during restoration experiments (Pywell et al., 2003). Sympathetic management of vegetation along hedgerows and woodland edges should also encourage plants such as *Ajuga reptans* and *Lamium album* to provide spring forage. These recommendations are summarised in Table 2.3. Furthermore, it will be important to implement these practical measures which increase resources for bumblebees at scales and in regions which will influence national trends. This highlights the need for experimental and monitoring approaches focused up to the landscape scale, and on the population responses of rare as well as common *Bombus* species.

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Appendix 2A. Supplementary data

A supplementary appendix with forage index and change data for the full list of forage plant species considered in the analyses.

Appendix 2B. Analyses of change in bumblebee nesting habitats.

Notes and data on analyses of change in grass species associated with nesting habitats for bumblebees are presented here but were not included in the published version of this chapter.

References

Alford, D.V., 1975. Bumblebees. Davis-Poynter, London.

Bäckman, J.P.C., Tiainen, J., 2002. Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera : *Bombus* and *Psithyrus*). Agriculture Ecosystems & Environment 89, 53-68.

Banaszak, J., 1980. Studies on methods of censusing the numbers of bees (Hymenoptera: Apoidea). Polish Ecological Studies 6, 355-366.

Banaszak, J., 1992. Strategy for Conservation of Wild Bees in an Agricultural Landscape. Agriculture Ecosystems & Environment 40, 179-192.

Buchmann, S.E., Nabhan, G.P., 1996. The Forgotten Pollinators. Island Press, Washington DC.

Carvell, C., 2000. Studies of the distribution and habitat requirements of *Bombus sylvarum* (the Shrill Carder Bee) and other bumblebees at Castlemartin Range, Pembrokeshire and Kenfig National Nature Reserve, Glamorgan and surrounding areas. Report for Countryside Council for Wales, Bangor, UK.

Carvell, C., 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. Biological Conservation 103, 33-49.

Carvell, C., Meek, W.R., Pywell, R.F., Nowakowski, M., 2004. The response of foraging bumblebees to successional change in newly created arable field margins. Biological Conservation 118, 327-339.

Carvell, C., Pywell, R.F., Heard, M.S., Meek, B., 2006. The potential value of Environmental Stewardship Schemes for the BAP bumblebee, *Bombus ruderatus* (Fabricius) (Hymenoptera: Apidae). Entomologist's Gazette 57, 91-97.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubb, M., 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. Journal of Applied Ecology 37, 771-788.

Chapman, R.E., Wang, J., Bourke, A.F.G., 2003. Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. Molecular Ecology 12, 2801-2808.

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

Darvill, B., Knight, M.E., Goulson, D., 2004. Use of genetic markers to quantify bumblebee foraging range and nest density. Oikos 107, 471-478.

Dicks, L.V., Corbet, S.A., Pywell, R.F., 2002. Compartmentalization in plant-insect flower visitor webs. Journal of Animal Ecology 71, 32-43.

Fuller, R.M., 1987. The changing extent and conservation interest of lowland grasslands in England and Wales - a review of grassland surveys 1930-84. Biological Conservation 40, 281-300.

Ghazoul, J., 2005. Buzziness as usual? Questioning the global pollination crisis. Trends in Ecology & Evolution 20, 367-373.

Gorman, M.L., Reynolds, P., 1993. The impact of land-use change in voles and raptors. Mammal Review 23, 121-126.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. Biological Conservation 122, 1-8.

Goulson, D., Hughes, W.O.H., Derwent, L.C., Stout, J.C., 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. Oecologia 130, 267-273.

Haines-Young, R.H., Barr, C.J., Black, H.I.J., Briggs, D.J., Bunce, R.G.H., Clarke, R.T., Cooper, A., Dawson, F.H., Firbank, L.G., Fuller, R.M., Furse, M., Gillespie, M.K., Hill, R., Hornung, M., Howard, D.C., McCann, T., Morecroft, M.D., Petit, S., Sier, A.R.J., Smart, S.M., Smith, G.M., Stott, A.P., Stuart, R.C., Watkins, J.W., 2000. Accounting for nature: assessing habitats in the UK countryside. Report for Department of the Environment, Transport and the Regions, London.

Hughes, L., 1998. The Great Yellow Bumblebee, *Bombus distinguendus*; aspects of habitat use, phenology and conservation on the Machair of the Outer Hebrides, UK. MSc thesis. University College London, UK.

Kells, A.R., Goulson, D., 2003. Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. Biological Conservation 109, 165-174.

Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, A., Goulson, D., 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. Molecular Ecology 14, 1811-1820.

Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences of the United States of America 99, 16812-16816.

Macdonald, M.A., 1998. Feeding ecology of some *Bombus* and *Psithyrus* bumblebees (Hym., Apidae) in northern Scotland. The Scottish Naturalist 110, 51-104.

Manly, B.F.J., 1997. Randomization, bootstrap and Monte Carlo methods in biology, 2nd edn. Chapman & Hall, London, UK.

Mikkola, K., 1978. Spring migrations of wasps and bumblebees on the southern coast of Finland (Hymenoptera: Vespidae and Apidae). Annales Entomol. Fennici 44, 10-26.

Pelletier, L., McNeil, J.N., 2003. The effect of food supplementation on reproductive success in bumblebee field colonies. Oikos 103, 688-694.

Pickett, H., 2000. Bumblebee (*Bombus*) abundance, diversity and activity in relation to field margin habitat type. MSc thesis. University of Liverpool, UK.

Preston, C.D., Pearman, D.A., Dines, T.D., 2002. New Atlas of the British and Irish Flora. Oxford University Press, Oxford, UK.

Preston, C.D., Telfer, M.G., Roy, D.B., Carey, P.D., Hill, M.O., Meek, W.R., Rothery, P., Smart, S., Smith, G.M., Walker, K.J. & Pearman, D.A., 2003. The Changing Distribution of the Flora of the United Kingdom: Technical Report C01093. NERC Centre for Ecology and Hydrology, Huntingdon, UK.

Preston, C.D., Pearman, D.A., Hall, A.R., 2004. Archaeophytes in Britain. Botanical Journal of the Linnean Society 145, 257-294.

Prŷs-Jones, O.E., 1982. Ecological studies of foraging and life history in bumblebees. PhD thesis. University of Cambridge, UK.

Prŷs-Jones, O.E., Corbet, S.A., 1991. Bumblebees, 2nd edn. Richmond Publishing Company, Slough, UK.

Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L.I.Z., Walker, K.J., Rothery, P., 2003. Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40, 65-77.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R., Sherwood, A., 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 121, 479-494.

Rasmont, P., 1988. Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera. Apidae, Bombinae). PhD thesis. Faculté des Science Agronomique de l'Etat, Gembloux, Belgium.

Rich, T.C.G., Woodruff, E.R., 1996. Changes in the vascular plant floras of England and Scotland between 1930-1960 and 1987-1988: the BSBI monitoring scheme. Biological Conservation 75, 217-229.

Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology 39, 157-176.

Ryan, B.F., Joiner, B.L., Ryan, T., 2000. MINITAB Handbook, Fourth Edition. Brooks Cole, Florence KY.

Saville, N.M., 1993. Bumblebee ecology in woodlands and arable farmland. PhD thesis. University of Cambridge, UK.

Schultz, C.B., Dlugosch, K.M., 1999. Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. Oecologia 119, 231-238.

Smart, S.M., Bunce, R.G.H., Marrs, R., LeDuc, M., Firbank, L.G., Maskell, L.C., Scott, W.A., Thompson, K., Walker, K.J., 2005. Large-scale changes in the abundance of common higher plant species across Britain between 1978, 1990 and 1998 as a consequence of human activity: Tests of hypothesised changes in trait representation. Biological Conservation 124, 355-371.

Smart, S.M., Firbank, L.G., Bunce, R.G.H., Watkins, J.W., 2000. Quantifying changes in abundance of food plants for butterfly larvae and farmland birds. Journal of Applied Ecology 37, 398-414.

Stace, C., 1997. New Flora of the British Isles. Cambridge University Press, Cambridge, UK.

Steffan-Dewenter, I., Tscharntke, T., 1999. Effects of habitat isolation on pollinator communities and seed set. Oecologia 121, 432-440.

Telfer, M.G., Preston, C.D., Rothery, P., 2002. A general method for measuring relative change in range size from biological atlas data. Biological Conservation 107, 99-109.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T., Lawton, J.H., 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303, 1879-1881.

UK Biodiversity Group, 1998. UK Biodiversity Group Tranche 2 Action Plans: Invertebrates, vol. IV. English Nature, Peterborough, UK.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. Ecology Letters 6, 961-965.

Williams, P., 2005. Does specialization explain rarity and decline British bumblebees? - A response to Goulson et al. Biological Conservation 122, 33-43.

Williams, P.H., 1982. The distribution and decline of British bumblebees (*Bombus* Latr.). Journal of Apicultural Research 21, 236-245.

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

Williams, P.H., 1989. Why are there so many species of bumble bees at Dungeness? Botanical Journal of the Linnean Society 101, 31-44.

Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B., Kunin, W.E., 2004. Spatial patterns in species distributions reveal biodiversity change. Nature 432, 393-396.

Table 2.1 Sources of data on bumblebee forage plant visitation.

Year of study	UK Site Location	Habitat types surveyed	No. of forage plants visited *	No. of social *Bombus* species	Reference
1999	Salisbury Plain Training Area, Wiltshire	Unimproved calcareous grassland	20	8	Carvell (2002)
2000	Castlemartin Range, Pembrokeshire, SW Wales	Unimproved mesotrophic grassland	9	10	Carvell (2000)
2000	Kenfig NNR, Glamorgan, S Wales	Mesotrophic and dune grassland	22	10	Carvell (2000)
1999	Shelfanger, Norfolk	Ancient hay meadow	13	6	Dicks et al. (2002)
1999	Hickling Broad NNR, Norfolk	Restored hay meadow	12	6	Dicks et al. (2002)
1998	South Uist, Western Isles, Scotland	Machair dune grasslands	11	5	Hughes (1998)
1998	Western Isles, Scotland	Machair dune grasslands	9	5	Macdonald, unpublished
1997	Strathpeffer, Highland Region, Scotland	Village edge and farmland	63	4	Macdonald (1998)
2000	Malton, North Yorkshire	Arable farmland, field margins	7	6	Pickett (2000)
1978	Wicken Fen, Cambridgeshire	Fen meadow	34	7	Prŷs-Jones (1982)
1990	Madingley Wood, Cambridgeshire	Woodland	24	6	Saville (1993)
1990	Croxton, West Cambridgeshire	Woodland and arable farmland	21	6	Saville (1993)
1982	Dungeness, Kent	Dune ridge grasslands	13	12	Williams (1989)
1983	Shoreham, Kent	Arable farmland and woodland edge	17	7	Williams (1989)

* a few species were excluded from the analysis if there was insufficient data from both plant surveys, or if they were considered recently established alien species (neophytes).

Table 2.2 Forage index and change data for bumblebee forage plant species for which both *New Atlas* and Countryside Survey (CS) data were available, and which were visited by bumblebees at two or more study sites.

Plant species	Forage index all *Bombus*	Forage index long-tongued	Forage index short-tongued	Number of study sites with bee visits	New Atlas Change index (1930-69 to 1987-99)	CS plot frequency 1978	CS plot frequency 1998	CS Relative % change 78-98	Z-test † significance
Ajuga reptans	2.17	2.08	0.89	2	-0.56	32	18	-43.75	*
Arctium agg.	1.48	1.35	0.14	2	0.05	16	15	-6.25	ns
Ballota nigra	3.85	3.56	0.89	2	-0.37	5	14	180.00	*
Bryonia dioica	1.03	0.74	0.40	3	-0.50	11	5	-54.55	ns
Centaurea nigra	3.82	2.66	3.32	7	-0.25	135	73	-45.93	***
Chamerion angustifolium	2.50	1.45	2.27	7	-0.01	65	46	-29.23	ns
Cirsium arvense	2.85	1.69	2.47	8	0.47	319	311	-2.51	ns
Cirsium palustre	3.36	2.79	2.19	3	0.15	131	117	-10.69	ns
Cirsium vulgare	2.82	2.24	1.90	8	0.80	228	163	-28.51	***
Convolvulus arvensis	2.65	0.85	2.76	3	-0.70	78	87	11.54	ns
Epilobium hirsutum	3.75	3.14	2.65	4	0.12	41	32	-21.95	ns
Filipendula ulmaria	1.55	-0.05	1.74	3	-0.10	110	84	-23.64	*
Glechoma hederacea	1.70	1.33	0.74	2	-0.56	65	57	-12.31	ns
Iris pseudacorus	1.36	1.05	0.40	2	0.16	12	13	8.33	ns
Lamiastrum galeobdolon	1.25	-0.20	1.53	2	1.07	6	5	-16.67	ns
Lathyrus pratensis	2.38	2.21	0.75	5	-0.17	101	56	-44.55	***
Leucanthemum vulgare	2.79	0.97	2.28	3	-1.14	20	7	-65.00	**
Lotus corniculatus	2.89	2.23	1.86	9	1.09	134	98	-26.87	**
Lychnis flos-cuculi	1.62	1.64	0.19	2	-0.79	13	11	-15.38	ns
Mentha aquatica	2.80	2.26	1.09	2	-0.11	38	23	-39.47	*
Odontites vernus	2.92	2.43	1.70	5	-0.46	6	16	166.67	*
Prunella vulgaris	2.00	1.80	0.57	7	0.60	178	145	-18.54	*
Ranunculus acris	0.78	0.76	0.01	2	0.30	205	191	-6.83	ns
Rhinanthus minor	2.85	2.39	1.67	7	-0.49	29	6	-79.31	***
Rubus fruticosus agg.	3.47	2.45	3.29	6	-0.29	279	275	-1.43	ns
Senecio jacobaea	2.29	0.70	2.34	5	0.11	109	115	5.50	ns
Stachys sylvatica	1.89	1.81	0.19	3	-0.49	50	51	2.00	ns
Trifolium dubium	1.19	0.76	0.50	2	-0.11	43	35	-18.60	ns
Trifolium pratense	3.31	3.26	0.91	8	-0.18	153	93	-39.22	***
Trifolium repens	2.36	1.64	1.79	10	1.31	576	507	-11.98	**
Vicia cracca	2.65	2.44	0.53	6	-0.37	30	35	16.67	ns

† the Z-test assessed change in the number of occupied CS plots between 1978 and 1998 as a proportion of the total number of plots sampled: ns = not significant; * $P<0.05$; ** $P<0.01$; *** $P<0.001$. Species in bold type showed a significant decline in CS plot frequency.

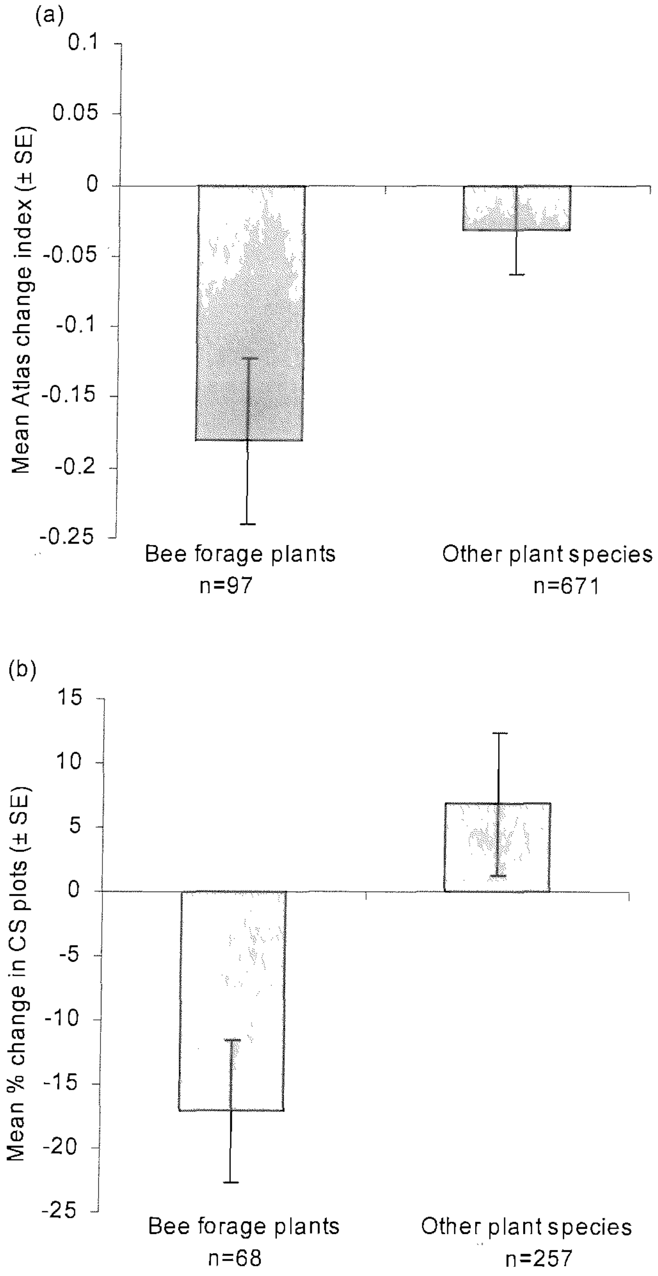
Table 2.3 Recommended forage plant species for wildlife seed mixtures and other restoration schemes in agricultural landscapes.

Plant species	Rank performance *
Ajuga reptans	
Anthyllis vulneraria	11
Ballota nigra	
Centaurea nigra	5
Centaurea scabiosa	15
Cirsium vulgare	
Dipsacus fullonum	
Echium vulgare	
Glechoma hederacea	
Hypochaeris radicata	6
Knautia arvensis	14
Lamium album	
Lamium purpureum	
Lathyrus pratensis	8
Leucanthemum vulgare	1
Lotus corniculatus	3
Odontites vernus	
Prunella vulgaris	4
Rhinanthus minor	7
Rubus fruticosus agg.	
Salix cinerea	
Stachys officinalis	12
Stachys sylvatica	
Succisa pratensis	13
Symphytum officinale	
Thymus polytrichus	10
Trifolium pratense	2
Vicia cracca	9

* Species ranked in order of decreasing performance based on measures of relative success in establishment and persistence in grassland restoration experiments from Pywell et al. (2003), updated to include more recent studies (unpublished). Species with no ranking can be encouraged along hedgerows and woodland edges, particularly to provide spring forage. Note that other plant species not listed here may be equally valuable to bumblebees in certain regions.

Figure 2.1 Changes in range size (a) and frequency (b) of bumblebee forage plants vs all other native and long-established plant species in Britain.

Range changes from 1930-69 to 1987-99 were measured by the Atlas change index for 10-km squares. Frequency changes from 1978 to 1998 were measured as relative % change in frequency of occupied Countryside Survey plots within 1-km squares.



Appendix 2A. Forage index and change data for the full list of native and long-established bumblebee forage plant species considered in the analyses. *New Atlas* data were available for 97 species and Countryside Survey (CS) data for 68 species. † the *Z*-test assessed change in the number of occupied CS plots between 1978 and 1998 as a proportion of the total number of plots sampled: ns = not significant; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Plant Species	Forage index all *Bombus*	Forage index long-tongued	Forage index short-tongued	No. study sites with bee visits	*New Atlas* Change Index	CS plots 1978	CS plots 1998	CS relative % change 78-98	Z-test † significance
Ajuga reptans	2.17	2.08	0.89	2	-0.56	32	18	-43.75	*
Anthyllis vulneraria	2.73	2.48	1.39	3	0.45				
Arctium minus	1.49	1.35	0.14	2	-0.41	16	15	-6.25	ns
Ballota nigra	3.85	3.56	0.89	2	-0.37	5	14	180.00	*
Bryonia dioica	1.03	0.74	0.40	3	-0.50	11	5	-54.55	ns
Calluna vulgaris	1.60	0.67	1.81	1	-0.64	332	297	-10.54	ns
Caltha palustris	0.90	0.33	0.64	1	-0.26	17	11	-35.29	ns
Campanula latifolia	1.31	0.95	1.11	1	-0.23				
Cardamine pratensis	0.78	0.72	0.15	1	0.42	93	92	-1.08	ns
Carduus crispus	3.02	2.51	1.93	3	-0.18				
Centaurea cyanus	7.06	3.06	6.90	1	-0.39				
Centaurea nigra	3.82	2.66	3.32	7	-0.25	135	73	-45.93	***
Centaurea scabiosa	2.65	1.55	1.90	1	-0.49				
Chaerophyllum temulum	1.39	0.77	1.10	1	-0.64				
Chamerion angustifolium	2.50	1.45	2.27	7	-0.01	65	46	-29.23	ns
Cirsium arvense	2.85	1.69	2.47	8	0.47	319	311	-2.51	ns
Cirsium dissectum	3.04	2.47	0.64	1	-0.14				
Cirsium palustre	3.36	2.79	2.19	3	0.15	131	117	-10.69	ns
Cirsium vulgare	2.82	2.24	1.90	8	0.80	228	163	-28.51	***
Clematis vitalba	2.98	1.00	3.36	1	0.00	11	7	-36.36	ns
Clinopodium vulgare	1.27	1.30	0.00	2	-0.67				
Convolvulus arvensis	2.65	0.85	2.76	3	-0.70	78	87	11.54	ns
Crataegus monogyna	0.78	0.72	0.15	1	-0.76	201	206	2.49	ns
Cytisus scoparius	2.57	-0.43	3.06	1	0.00	13	5	-61.54	*
Digitalis purpurea	3.39	3.44	0.01	1	0.72	70	86	22.86	ns
Dipsacus fullonum sens.lat.	2.00	1.71	0.95	3	0.82				
Echium vulgare	4.07	3.47	3.02	3	-0.24				
Epilobium hirsutum	3.75	3.14	2.65	4	0.12	41	32	-21.95	ns
Erica tetralix	2.61	1.65	2.72	1	-0.91	199	162	-18.59	*

Plant Species	**Forage index all *Bombus***	**Forage index long-tongued**	**Forage index short-tongued**	**No. study sites with bee visits**	***New Atlas* Change Index**	**CS plots 1978**	**CS plots 1998**	**CS relative % change 78-98**	**Z-test † significance**
Eupatorium cannabinum	3.47	1.58	3.64	1	-0.15	3	6	100.00	ns
Filipendula ulmaria	1.55	-0.05	1.74	3	-0.10	110	84	-23.64	*
Frangula alnus	4.04	3.19	3.13	1	-0.16				
Geum urbanum	0.78	0.72	0.15	1	-0.53	41	42	2.44	ns
Glechoma hederacea	1.70	1.33	0.74	2	-0.56	65	57	-12.31	ns
Helianthemum nummularium	2.01	1.51	1.81	1	-0.70				
Heracleum sphondylium	1.48	0.72	1.25	1	0.08	269	191	-29.00	***
Hyacinthoides non-scripta	1.19	0.72	0.85	1	-0.41	44	31	-29.55	ns
Hypericum hirsutum	0.98	0.77	0.41	1	-0.18				
Hypochaeris radicata	1.99	0.97	1.30	2	0.61				
Iris pseudacorus	1.36	1.05	0.40	2	0.16	12	13	8.33	ns
Knautia arvensis	1.81	0.47	1.25	2	-0.88				
Lamiastrum galeobdolon	1.25	-0.20	1.53	2	1.07	6	5	-16.67	ns
Lamium album	4.40	3.81	1.34	1	-0.65	48	51	6.25	ns
Lamium purpureum	0.91	0.95	0.01	1	-1.09	46	23	-50.00	**
Lapsana communis	0.98	0.07	1.10	1	-0.47	47	45	-4.26	ns
Lathyrus pratensis	2.38	2.21	0.75	5	-0.17	101	56	-44.55	***
Leontodon autumnalis	0.96	0.29	1.06	1	1.33				
Leucanthemum vulgare	2.79	0.97	2.28	3	-1.14	20	7	-65.00	**
Linaria vulgaris	2.91	2.84	0.23	1	-0.80				
Lonicera periclymenum	2.41	2.46	0.01	1	-0.11	33	27	-18.18	ns
Lotus corniculatus	2.89	2.23	1.86	9	1.09	134	98	-26.87	**
Lotus pedunculatus	3.26	2.87	1.94	1	-0.06	30	29	-3.33	ns
Lychnis flos-cuculi	1.62	1.64	0.19	2	-0.79	13	11	-15.38	ns
Lythrum salicaria	4.43	3.86	0.64	1	-0.08				
Melilotus altissimus	3.31	2.57	2.31	2	0.73				
Mentha aquatica	2.80	2.26	1.09	2	-0.11	38	23	-39.47	*
Odontites vernus	2.92	2.43	1.70	5	-0.46	6	16	166.67	*
Ononis repens	2.87	1.87	1.87	2	-0.45				
Ononis spinosa	0.85	1.15	-0.40	1	-0.82				
Orchis morio	0.94	1.34	-0.13	1	-0.98				
Origanum vulgare	3.41	2.03	3.56	1	-0.10				

Plant Species	Forage index all *Bombus*	Forage index long-tongued	Forage index short-tongued	No. study sites with bee visits	*New Atlas* Change Index	CS plots 1978	CS plots 1998	CS relative % change 78-98	Z-test † significance
Papaver rhoeas	1.32	0.29	1.19	1	-0.41	19	9	-52.63	*
Pilosella officinarum	2.24	1.15	1.54	1	-0.59	46	13	-71.74	***
Potentilla palustris	1.51	0.34	1.30	1	-0.21	6	1	-83.33	*
Potentilla reptans	0.78	0.72	0.15	1	-0.62	87	69	-20.69	ns
Primula veris	1.34	0.65	0.97	1	-0.32	9	4	-55.56	ns
Prunella vulgaris	2.00	1.80	0.57	7	0.60	178	145	-18.54	*
Prunus avium	2.23	-0.43	2.72	1	1.29				
Ranunculus acris	0.78	0.76	0.01	2	0.30	205	191	-6.83	ns
Ranunculus repens	4.18	2.43	4.07	1	0.55	561	501	-10.70	*
Rhinanthus minor	2.85	2.39	1.65	7	-0.49	29	6	-79.31	***
Rubus caesius	2.68	2.08	2.00	4	-0.34				
Rubus fruticosus agg.	3.47	2.45	3.29	6	-0.29	279	275	-1.43	ns
Rubus idaeus	3.73	2.86	3.73	1	-0.09	19	8	-57.89	*
Salix cinerea	4.08	1.25	4.43	1	0.84	22	7	-68.18	**
Scrophularia nodosa	0.98	0.77	0.41	1	-0.37	9	3	-66.67	ns
Senecio jacobaea	2.29	0.70	2.34	5	0.11	109	115	5.50	ns
Sinapis arvensis	2.51	0.38	2.23	1	-1.76	16	10	-37.50	ns
Solanum dulcamara	1.09	0.95	0.28	2	-0.11				
Sonchus arvensis	1.60	1.02	0.64	1	-0.12	22	13	-40.91	ns
Stachys officinalis	2.56	2.40	1.21	1	-0.62	6	7	16.67	ns
Stachys palustris	4.02	3.42	1.34	1	0.01	7	8	14.29	ns
Stachys sylvatica	1.89	1.81	0.19	3	-0.49	50	51	2.00	ns
Succisa pratensis	5.60	5.01	2.03	1	-0.57	109	133	22.02	ns
Symphytum officinale	6.05	5.37	4.23	1	0.34				
Taraxacum agg.	1.60	1.02	0.64	1	0.43	431	441	2.32	ns
Teucrium scorodonia	6.67	4.33	6.77	1	-0.69	34	26	-23.53	ns
Thalictrum flavum	1.60	0.33	1.74	1	-0.53				
Thymus polytrichus	3.26	0.38	2.98	1	-0.64	42	35	-16.67	ns
Trifolium dubium	1.19	0.76	0.50	2	-0.11	43	35	-18.60	ns
Trifolium pratense	3.31	3.26	0.91	8	-0.18	153	93	-39.22	***
Trifolium repens	2.36	1.64	1.79	10	1.31	576	507	-11.98	**
Ulex europaeus	0.91	-0.43	1.40	1	-0.34				
Vicia cracca	2.65	2.44	0.53	6	-0.37	30	35	16.67	ns
Vicia sativa	1.18	1.57	-0.27	1	0.19	31	18	-41.94	ns
Vicia sepium	3.66	3.71	0.01	1	-0.43	67	39	-41.79	**
Viola tricolor	0.77	0.51	-0.04	1	-1.52	10	1	-90.00	**

Appendix 2B. Analyses of change in bumblebee nesting habitats.

It is important when assessing patterns of habitat loss for any species to consider their full range of habitat requirements, and for bumblebees this includes nesting, mating and hibernation sites as well as the forage resources (arguably the most limiting habitat component) considered in this chapter. Mating and male patrolling sites are typically linear features with established vegetation and open flowers so the results already presented suggest that these are likely to have declined along with nectar and pollen sources. Nest site characteristics are highly variable, both between and within species (e.g. Kells and Goulson, 2003), and the same is probably true for hibernation sites although less is known about these (Alford, 1975). Hence it is difficult to quantify these habitat components to the same degree as foraging habitats. Nevertheless, the two national datasets on plant species change allowed us to consider a subset of grass species as indicators of potential increases or decreases in availability of nest sites, particularly for the carder bees such as *Bombus pascuorum*. These bee species tend to nest above ground within established vegetation using dried grasses and moss to construct the nest and regulate brood temperature, as opposed to other species such as *B. lapidarius* which nest below ground in a variety of sheltered situations. Change was assessed, using the same approach as in the main paper, for 11 species of fine-leaved and tussock-forming grasses associated with established vegetation such as might be found along banks, hedgerows and verges and used either directly by queen bumblebees founding nests in the spring or by small mammals whose holes or nests are subsequently used by bumblebees (Alford, 1975).

Results and discussion

Of the 11 grass species, 45% had negative and 55% had positive change index values (see table). Their mean change index (+0.51 ±0.29) did not differ significantly from that of all other native grass species (+0.34 ±0.10, $n = 56$) ($t = 0.55$, df = 12, $P>0.05$), suggesting that grasses associated with nesting habitat have not declined in 10-km range size between the two periods 1930-69 and 1987-99 relative to other grass species of comparable native status and range. Two of the 11 grass species showed significant declines in CS plot frequency, and the remaining nine species increased between 1978 and 1998, though this increase was only significant for *Festuca rubra* (Table 3). There was no significant difference between mean % change in occupied plots for the 11 nesting grasses (12.74 ±8.6) and all other native grass species (11.6 ±15.0, $n = 39$) ($t = 0.07$, df = 47, $P>0.05$).

Changes in range and CS plot frequency for grass species associated with bumblebee nesting habitats. † the Z-test assessed change in the number of occupied CS plots between 1978 and 1998 as a proportion of the total number of plots sampled: ns = not significant; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Grass species	New Atlas Change index (1930-69 to 1987-99)	CS plot frequency 1978	CS plot frequency 1998	CS Relative % change 78-98	Z-test † significance
Anthoxanthum odoratum	0.90	362	366	1.10	ns
Arrhenatherum elatius	0.37	307	319	3.91	ns
Bromopsis erecta	-0.01	4	5	25.00	ns
Cynosurus cristatus	0.02	202	203	0.50	ns
Dactylis glomerata	-0.06	583	503	-13.72	**
Elytrigia repens	-0.01	239	271	13.39	ns
Festuca pratensis	-0.16	8	15	87.50	ns
Festuca rubra agg.	2.96	317	409	29.02	***
Holcus lanatus	1.34	664	675	1.66	ns
Phleum pratense sens.lat.	-0.33	213	174	-18.31	*
Poa pratensis sens.lat.	0.60	256	282	10.16	ns

Based on these results it appears that, in contrast to forage plants, grasses associated with bumblebee nesting habitats did not in general experience significant declines during the 20th Century. However, the decline shown for the tussock-forming species *Dactylis glomerata* in both surveys is an indication that vegetation structure and availability of sites for surface-nesting species have been reduced, as seems likely given changes in agricultural practice. Again, it is important to note that plant frequency and occupancy of 10-km squares may not be an effective functional measure of sward structure or habitat quality for nesting. Four of the five predominantly surface-nesting bumblebee species which are probably more susceptible to the effects of mechanical disturbance in grasslands are rare and declining (e.g. *Bombus sylvarum*), so the potential influence of nest site limitation should not be dismissed in the design of restoration schemes.

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

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Abstract

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

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

3.1 Introduction

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

In recent years there have been attempts to restore and maintain habitats which enhance biodiversity in the agricultural landscape (Bignal, 1998). Policy developments within the UK agri-environment schemes (e.g. the Countryside Stewardship Scheme (DEFRA, 2003)) offer increased opportunities to achieve this restoration, particularly on arable field margins which are a key feature of British farmland (Marshall, 1998; Marshall and Moonen, 2002). Bumblebees are known to benefit from the presence of flowering perennial herb species, ideally in unfragmented species-rich grasslands (Carvell, 2002). However, they can also utilize forage resources in patches of established semi-natural vegetation such as field margins, green lanes (Croxton et al., 2002) and other habitat islands, due to their ability to fly considerable distances from the nest (Fussell and Corbet, 1991; Saville et al., 1997; Osborne et al., 1999; Bäckman and Tiainen, 2002). In addition to a season-long supply of suitable forage resources, bumblebees also require nesting sites, mating and hibernation areas, although there is little information describing the latter two requirements (Alford, 1969; 1975). Forage and nesting sites are currently more accessible targets for habitat restoration, and although in this paper we focus on foraging bumblebees, it is likely that, once established, suitable foraging habitats in non-cropped areas also have the potential to support nest sites (Svensson et al., 2000).

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

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

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

3.2 Methods

3.2.1 Site description and margin treatments

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

1. Natural regeneration, unsown, 6m wide;
2. Sown 'tussocky' grass mixture, 6m wide;

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

Details of the sown mixtures are given in Table 3.3. Plant species nomenclature follows Stace (1997). In April 2000, a selective graminicide was applied at 6.25 g ai/ha (= 0.5 l/ha Fusilade-5) to the 'wildflower' treatments and the wildflower half of the 'split' margin treatments to control blackgrass, *Alopecurus myosuroides* and sterile brome, *Anisantha sterilis*. Following establishment, all plots (except those cropped to the edge) were cut and the herbage removed using a forage harvester in May 2000. In late August 2000 the two treatments containing wildflowers were cut to around 10cm, with the cuttings removed. In late August 2001, the natural regeneration plots were cut as a means of controlling a developing thistle problem (see discussion), with the cuttings left. Subsequent management was focused on the 'wildflower' treatments, and wildflower half of the 'split' plots, which received an annual cut during late August 2001 and 2002, with cuttings removed.

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

3.2.2 Bumblebee monitoring

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

3.2.3 Flower abundance scores

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

1. 1-25 flowers
2. 26-200 flowers
3. 201-1000 flowers
4. 1001 - 5000 flowers
5. Superabundant - more than 5000 flowers.

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

3.2.4 Data Analysis

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

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

3.3 Results

3.3.1 Differences in bumblebee abundance between field margin treatments

Over the duration of this study, a total of 2,241 foraging bumblebees were recorded, with the average number of individuals per plot on each sampling date remaining fairly consistent across the years (4.6 in 2000; 5.1 in 2001 and 4.0 in 2002). There were significant differences between field margin treatments in terms of mean total bumblebee numbers in each year, and across all years combined (Figure 3.1: ANOVA, $F_{4,8} = 25.67$, $p<0.001$ in 2000; $F_{4,8} = 10.07$, $p<0.01$ in 2001; $F_{4,8} = 5.15$, $p<0.05$ in 2002 and $F_{4,8} = 18.92$, $p<0.001$ for all years). However, the preferred treatments were not the same each year, as confirmed by Tukey's pairwise comparisons. In 2000, significantly more bumblebees were recorded in the wildflower and 'split' tussocky grass & wildflower treatments than in all others ($p<0.01$), but in 2001, the natural regeneration treatment was preferred, attracting significantly more bumblebees than the tussocky grass and cropped treatments ($p<0.01$). The pattern in 2002 was similar to that of 2000, with highest numbers in the two treatments sown with the 'wildflower' mixture, although there were no significant pairwise comparisons ($p>0.05$). When the mean number of bumblebees per plot was calculated across all years, abundance was highest in the wildflower and 'split' plots, and significantly different in these compared to only the tussocky grass and cropped plots ($p<0.01$).

Differences between years were tested for each margin treatment in turn. Significance was only detected for the natural regeneration treatment ($F_{2,4} = 20.06$, $p<0.01$), where many more bees were recorded during 2001 (Figure 3.1) in response to the increased thistle population (see section 3.3.3). In all other treatments bumblebee numbers were relatively consistent over the three years. In general, no significant differences between the three replicates were apparent, although the high numbers in the natural regeneration treatment in 2001 were mainly biased towards two replicates.

3.3.2 Bumblebee species

Six social bumblebee species were recorded, all known to be fairly widespread across the UK (Williams, 1982). Table 3.1 shows differences in abundance of each species between the margin treatments in 2001 and 2002. *Bombus lapidarius* accounted for around 50% of observations in each year, followed by *B. pascuorum*. *B. terrestris/lucorum* and *B. hortorum* were observed less frequently, and *B. pratorum* was scarce, accounting for less than 1% of observations. Patterns of abundance across treatments were generally consistent between species, with the natural regeneration treatment being preferred in 2001 (though never significantly different to those sown with the 'wildflower' mixture $p<0.05$), and the wildflower, followed by 'split', treatment preferred in 2002. Statistical significance between treatments was not always achieved for species recorded in lower numbers (Table 3.1).

3.3.3 Differences in flower abundance between field margin treatments

Both the mean flower abundance score for all species grouped and the species richness of plants in flower over the sampling period differed significantly between field margin treatments (Table 3.2). As expected, abundance and species richness were higher in plots featuring the sown 'wildflower' mixture than in all other treatments (Tukey's pairwise comparisons; $p<0.01$). This response was consistent in 2001 and 2002.

Lists of sown and unsown flowering plant species recorded on the field margins in 2001 and 2002 are given in Table 3.4, with mean abundance scores shown to indicate relative flowering in each year. Species were grouped according to various characteristics (ie. their life history, whether sown in the mixtures or visited by foraging bumblebees) in order to examine patterns of occurrence across the margin treatments (Table 3.2). As expected, sown species were significantly more abundant in the 'wildflower' and 'split' plots than in all others, and achieved notably higher mean abundance scores in 2002, the third year after establishment. This group consisted mostly of perennials, except *Rhinanthus minor* which accounts for the flowering annuals occurring in the sown treatments. In contrast, flowers of unsown species were significantly more abundant in the natural regeneration treatment than in all others except the crop in 2001. This was due to patches of *Cirsium vulgare* (a biennial), flowering during 2001, but mainly absent during 2002 (Table 3.4) when there was no significant difference in unsown species between the treatments.

3.3.4 Forage plant preferences

The flowering plant species receiving the most foraging visits differed in each year of this study (Figure 3.2), reflecting the relative abundance of those species flowering on the field margin treatments. In 2000, more than 90% of visits were to the annual species *Centaurea cyanus* (during the restricted July sampling period), whereas in 2001 and 2002 visits were more evenly spread across several species, with concentration on *C. vulgare* and *Lotus corniculatus* respectively. It is interesting to note that some species scoring highly in terms of flower abundance (e.g. *Leucanthemum vulgare*) received a low proportion of bumblebee visits. Figure 3.3 shows the flower visits of three *Bombus* species in 2001 and 2002. Despite the dominance of *C. vulgare* in 2001 and *L. corniculatus* in 2002, some differences in other utilized forage species are apparent. For example, *B. lapidarius* (the shorter-tongued species here) visited *Senecio jacobaea* and *L. vulgare*, whereas the longer-tongued *B. pascuorum* and *B. hortorum* visited *R. minor* and *Prunella vulgaris* and in 2002, *Lathyrus pratensis.*

3.3.5 Temporal changes in bumblebee and flower abundance

Patterns of bumblebee activity throughout each season clearly reflected temporal changes in flower abundance on each margin treatment (Figure 3.4a – d). During 2001, the increase in bumblebees on the natural regeneration treatment towards the end of the season reflected the increase in flowering (mainly of *Cirsium vulgare*) in that treatment, although the wildflower and split treatments provided a more continuous supply of forage plants (Figure 3.4a and b). For 2002, the data demonstrate a continuous supply of flowers in the wildflower and split treatments, with little influence from the natural regeneration plots (Figure 3.4c and d).

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

3.4 Discussion

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

The two margin treatments containing the sown 'grass and wildflower' mixture were of value to bumblebees in all three years after establishment. Most of the seed mixture components flowered between May and late August, with a few exceptions (e.g. *Geranium pratense* and *Malva moschata*) which failed to establish well at this site. Despite the absence of flower abundance scores from 2000, the data on foraging preferences and from additional vegetation surveys (Meek et al., 2002), combined with these results from 2001 and 2002 show a clear pattern of succession on the sown treatments. The annual Cornflower (*C. cyanus*), thought to be an important pollen source (Engels et al., 1994), was the dominant forage species in year one, with the perennial sward developing and flowers such as *Centaurea nigra, L. corniculatus* and *L. pratensis* increasing in abundance over the second and third years. In addition to providing attractive forage species for bumblebees, it is likely that the sown wildflower treatments significantly reduced the cover of pernicious annual weeds as observed elsewhere (Marshall and Nowakowski, 1995; Meek et al., 2002).

The natural regeneration treatment, although less costly than the sown mixture option, was inconsistent both between years and across replicates in terms of flowering plant and bumblebee abundance. Patches of flowering thistles, *Cirsium vulgare* and to a lesser extent *C. arvense*, were prominent in 2001 on two replicates and attracted foraging bumblebees of several species. Male bumblebees emerging towards the end of the season are particularly attracted to their flowers which appear at this time (e.g. Barrow, 1983). Whilst being attractive nectar sources (see also Feber et al., 1996), these thistles are pernicious weeds and are not considered agriculturally acceptable, requiring control under the UK Injurious Weeds Act of 1959 (www.defra.gov.uk/environ/weedsact/default.htm). In our experiment, cutting at the end of August prevented *C. vulgare* from re-occurring the following year, as would be expected from this monocarpic biennial. Subsequently however, few other species in the developing perennial sward of the regeneration treatment produced flowers that were attractive to foraging bees. There is therefore no guarantee that field margins left to natural regeneration will provide a sustained supply of suitable forage for bumblebees, unless detailed knowledge of the seed or bud bank is available. Furthermore, natural regeneration may take at least five years to produce the equivalent diversity and density of perennial forage plants to sown swards, as suggested by Corbet (1995) when considering Schmidt's analysis of a 10-year succession (Schmidt, 1976, as listed in Ellenberg, 1988).

The six *Bombus* species recorded during this study all belonged to the 'mainland ubiquitous group' (Williams, 1982), which is the usual assemblage found on arable farmland in the UK (Fussell and Corbet, 1991; Kells et al., 2001). *B. pratorum* accounted for a low proportion of records in both 2001 and 2002, but this is perhaps not surprising as the species tends to be observed more frequently in gardens (Prŷs-Jones and Corbet, 1991), possibly due to its agility in foraging at a range of flower depths and angles such as might be found in horticultural situations. *B. pratorum* is also known to establish its colonies early so worker numbers peak in advance of the other species. This highlights the importance of the sampling period which, in this study, could have been brought forward to early May to assess whether the margin treatments provided resources for queens and early workers during colony initiation. The results suggest that this could be the case for the treatments containing sown wildflowers, but not for the natural regeneration, tussocky grass or cropped treatments.

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

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

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

Conclusions

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

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References

Alford, D.V., 1969. The study of the hibernation of bumblebees. Journal of Animal Ecology 38, 149-170.

Alford, D.V., 1975. Bumblebees. Davis-Poynter, London.

Alford, D.V., Ed., 1980. Atlas of the Bumblebees of the British Isles. Institute of Terrestrial Ecology, Cambridge, UK.

Bäckman, J-P. C., Tiainen, J., 2002. Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). Agriculture, Ecosystems and Environment 89, 53-68.

Banaszak, J., 1980. Studies on methods of censusing the numbers of bees (Hymenoptera: Apoidea). Polish Ecological Studies 6, 355-366.

Banaszak, J., 1996. Ecological bases of conservation of wild bees. In Matheson, A., Buchmann, S.L., O'Toole, C., Westrich P., Williams, I.H. (Eds.), The Conservation of Bees. Linnean Society Symposium Series 18. Academic Press, London.

Barrow, D.A., 1983. Ecological studies on bumblebees in South Wales with special reference to resource partitioning and bee size variation. PhD thesis, University of Wales, Cardiff.

Bignal, E.M., 1998. Using an ecological understanding of farmland to reconcile nature conservation requirements, EU agriculture policy and world trade agreements. Journal of Applied Ecology 35, 949-954.

Carreck, N.L., Williams, I.H., Oakley, J.N., 1999. Enhancing farmland for insect pollinators using flower mixtures. In Field Margins and buffer zones: ecology, management and policy. Aspects of Applied Biology 54, 101-108.

Carreck, N.L. & Williams, I.H., 2002. Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. Journal of Insect Conservation 6: 13-23.

Carvell, C., 2002. Habitat use and conservation of bumblebees (*Bombus* spp) under different grassland management regimes. Biological Conservation 103, 33-49.

Carvell, C., Pywell, R.F., Smart, S.M., Roy, D., 2001. Restoration and management of bumblebee habitat on arable farmland: literature review. DEFRA Contract report BD1617. Centre for Ecology and Hydrology, Monks Wood, Cambridgeshire, UK.

Corbet, S.A., Williams, I.H., 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., 1995. Insects, plants and succession: advantages of long-term set-aside. Agriculture, Ecosystems and Environment 53, 201 – 217.

Corbet, S.A., 2000. Conserving compartments in pollination webs. Conservation Biology 14 (5), 1229 – 1231.

Cowgill , S.E, Wratten, S.D., Sotherton, N.W., 1993. The selective use of floral resources by the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) on farmland. Annals of Applied Biology 122: 223-231.

Croxton, P.J., Carvell, C., Mountford, J.O., Sparks, T.H., 2002. A comparison of green lanes and field margins as bumblebee habitat in an arable landscape. Biological Conservation 107, 365-374.

Defra, 2003. The Countryside Stewardship Scheme: Information and how to apply. Department for Environment, Food and Rural Affairs, London, UK.

Dramstad, W., Fry, G., 1995. Foraging activity of bumblebees in relation to flower resources on arable land. Agriculture, Ecosystems and Environment 53, 123-135.

Edwards, M., 2001. UK BAP Bumblebee Working Group Report, 2001. Unpublished report for the UK BAP Bumblebee Working Group, Midhurst, UK.

Ellenberg, H., 1988. Vegetation Ecology of Central Europe. Cambridge University Press, Cambridge.

Engels, W., Schulz, U. & Radle, M.,1994. Use of the Tübingen mix for bee pasture in Germany. In Forage for bees in an agricultural landscape, ed A. Matheson, pp. 57-65. International Bee Research Association, Cardiff.

Feber, R.E., Smith, H., Macdonald, D.W., 1996. The effects on butterfly abundance of the management of uncropped edges of arable fields. Journal of Applied Ecology 33, 1191 – 1205.

Firbank, L.F., Asteraki, E., Chamberlain, D.E., Gough, S., Haysom, K. Petit, S.E., Pywell, R.F., Warman, E.A. and Vickery, J.A., 2001. Development and validation of a methodology for the condition assessment of extensively managed arable habitats (OC9801). Final report to Department of Environment, Food and Rural Affairs. Centre for Ecology and Hydrology, Merlewood, UK.

Free, J.B., 1993. Insect Pollination of Crops. 2nd Edition. Academic Press, London.

Fussell, M., Corbet, S.A., 1991. Forage for bumblebees and honey bees in farmland: a case study. Journal of Apicultural Research 30, 87-97.

Fussell, M., Corbet, S.A., 1992a. Flower usage by bumblebees: a basis for forage plant management. Journal of Applied Ecology 29, 451-465.

Fussell, M., Corbet, S.A., 1992b. The nesting places of some British bumble bees. Journal of Apicultural Research 31, 32-41.

Goulson, D., Hughes, W.O.H., Derwent, L.C., Stout, J.C., 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. Oecologia 130, 267-273.

Haines-Young, R. (editor), 2000. Accounting for nature: assessing habitats in the UK countryside. Department of the Environment, Transport and the Regions, London.

Holm, S.N., 1966. The utilization and management of bumble bees for red clover and alfalfa seed production. Annual Review of Entomology 11, 155-182.

Kells, A.R., Holland, J.M., Goulson, D., 2001. The value of uncropped field margins for foraging bumblebees. Journal of Insect Conservation 6, 13-23.

Kwak, M., van den Brand, C., Kremer, P., Boerrigter, E., 1991. Visitation, flight distances and seed set in the rare species *Phyteuma nigrum* (Campanulaceae). Acta Hort. 288, 303-307.

Lagerlöf, J., Stark, J., Svensson, B., 1992. Margins of agricultural fields as habitats for pollinating insects. Agriculture, Ecosystems and Environment 40, 117-124.

MAFF, 1999. The Countryside Stewardship Scheme: Arable Stewardship, Information and how to apply. Ministry of Agriculture, Fisheries and Food Publications, London.

Marshall, E.J.P., 1998. Guidelines for the siting, establishment and management of arable field margins, beetle banks, cereal conservation headlands and wildlife seed mixtures. MAFF Project report BD0412. IACR Long Ashton, Bristol, UK.

Marshall, E.J.P., Moonen, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agriculture, Ecosystems and Environment, 89, 5-21.

Marshall, E.J.P., Nowakowski, M., 1995. Successional changes in the flora of a sown field margin strip managed by cutting and herbicide application. Brighton Crop Protection Conference – Weeds. pp. 973-978. British Crop Protection Council, Surrey, UK.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. & Nowakowski, M., 2002. The effect of arable field margin composition on invertebrate biodiversity. Biological Conservation 106, 259-271.

Miller, P.C.H., Lane, A.G., 1999. Relationship between spray characteristics and drift risk into field boundaries of different structure. In Field Margins and buffer zones: ecology, management and policy. Aspects of Applied Biology 54, 45-51.

Murdoch, W.W., 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. Ecological Monographs 39, 335-354.

Osborne, J.L., Corbet, S.A., 1994. Managing habitats for pollinators in farmland. In Arable farming under CAP reform. Aspects of Applied Biology 40, 207-215.

Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. Journal of Applied Ecology 36, 519-533.

Prŷs-Jones, O.E., Corbet, S.A., 1991. Bumblebees. 2nd edn. Naturalists' Handbooks 6. The Richmond Publishing Co. Ltd., Slough, UK.

Ranta, E., Lundberg, H., 1980. Resource partitioning in bumblebees: the significance of differences in proboscis length. OIKOS 35, 298-302.

Rasmont, P., 1988. Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera. Apidae, Bombinae). PhD Thesis. Faculté des Science Agronomique de l'Etat, Gembloux, Belgium.

Saville, N.M., Dramstad, W.E., Fry, G.L.A., Corbet, S.A., 1997. Bumblebee movement in a fragmented agricultural landscape. Agriculture, Ecosystems and Environment 61, 145-154.

Schmidt, W., 1976. (cited in Ellenberg, 1988). Ungestorte und gelenkte Sukzession auf Brachackern. Habil. Schr. Gottingen.

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

Stace, C., 1997. New Flora of the British Isles. Cambridge University Press, Cambridge, UK.

Steffan-Dewenter, I., Tscharntke, T., 1999. Effects of habitat isolation on pollinator communities and seed set. Oecologia 121, 432 – 440.

Stoate, C., Boatman, N.D., Borralho, R.J., Rio Carvalho, C., de Snoo, G.R., Eden, P., 2001. Ecological impacts of arable intensification in Europe. Journal of Environmental Management. 63: 337-365.

Svensson, B., Lagerlöf, J., Svensson, Bo. G., 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agriculture, Ecosystems and Environment 77, 247-255.

Swash, G., Belding, R., 1999. Arable reversion in Environmentally Sensitive Area and Countryside Stewardship Schemes: Guidelines for project officers. Farming and Rural Conservation Agency, UK.

Thomas, C.F.G., Marshall, E.J.P., 1999. Arthropod abundance and diversity in differently vegetated margins of arable fields. Agriculture Ecosystems and Environment 72: 131-144.

Williams, P.H., 1982. The distribution and decline of British bumblebees (*Bombus* Latr.) Journal of Apicultural Research 21 (4), 236-245.

Willmer, P.G., Bataw, A.A.M., Hughes, J.P., 1994. The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. Ecological Entomology 19, 271 – 284.

Table 3.1 Bumblebee abundance by species on the different margin types.

		Field margin type					**ANOVA 2001**	
a) ***Bombus*** **species 2001**	% of all records	Natural regeneration	Tussocky grass	Wildflower	Tussocky & wildflower	Cropped	F 4,8	Sig. level
B. terrestris/lucorum	15.1	1.83 ±0.62 b	0.10 ±0.06 a	0.93 ±0.41 ab	0.97 ±0.35 ab	0 a	5.52	*
B. lapidarius	49.8	6.53 ±3.51 c	0.27 ±0.27ab	4.20 ±1.97 bc	1.50 ±0.51 ac	0.17 ±0.12 a	7.45	**
B. pratorum	0.5	0.07 ±0.07	0.00	0.07 ±0.03	0.00	0.00	1.02	ns
B. pascuorum	22.7	3.23 ±1.99 b	0.30 ±0.25 a	1.27 ±0.47 ab	0.97 ±0.30 ab	0.00 a	5.91	**
B. hortorum	11.9	1.37 ±0.72	0.23 ±0.19	0.87 ±0.38	0.53 ±0.26	0.03 ±0.03	3.60	ns

		Field margin type					**ANOVA 2002**	
b) ***Bombus*** **species 2002**	% of all records	Natural regeneration	Tussocky grass	Wildflower	Tussocky & wildflower	Cropped	F 4,8	Sig. level
B. terrestris/lucorum	7.5	0.00	0.03 ±0.03	0.79 ±0.42	0.67 ±0.34	0.00	3.66	ns
B. lapidarius	54.2	0.00	0.03 ±0.03	6.88 ±3.44	3.76 ±1.84	0.03 ±0.03	4.65	*
B. pratorum	0.8	0.00	0.00	0.09 ±0.05	0.06 ±0.03	0.00	3.16	ns
B. pascuorum	29.2	0.09 ±0.00	0.12 ±0.12	3.45 ±1.73	2.09 ±0.77	0.00	4.87	*
B. hortorum	8.3	0.00	0.00	0.94 ±0.69	0.67 ±0.42	0.03 ±0.03	2.47	ns

Numbers represent mean number of bumblebees per plot, per sampling date, with ± standard errors. Means within a row followed by different letters (a, b, c) are significantly different ($p<0.05$) following Tukey's Honest Significant Difference tests. * $p<0.05$; ** $p<0.01$; *** $p<0.001$; ns, not significant.

Table 3.2 Abundance of flowers, grouped by various ecological characteristics, on the different margin treatments.

	Field margin type					**ANOVA**	**2001**
a) Flower 'group' 2001	Natural regeneration	Tussocky grass	Wildflower	Tussocky & wildflower	Cropped	F 4,8	Sig. level
Annuals	0.47 ±0.33 ab	0.07 ±0.03 a	2.93 ±0.35 c	2.57 ±0.18 bc	1.97 ±0.78 ac	8.63	**
Perennials & Biennials	5.77 ±1.18 b	2.03 ±0.95 ab	11.10 ±1.23 c	10.07 ±1.30 c	1.37 ±0.72 a	26.59	***
Sown species	0.57 ±0.26 a	0.83 ±0.39 a	12.57 ±1.14 b	10.97 ±0.94 b	0.10 ±0.10 a	105.05	***
Unsown species	5.67 ±1.42 b	1.27 ±0.58 a	1.47 ±0.34 a	1.67 ±0.47 a	3.23 ±1.16 ab	5.19	*
Bee forage species [f]	4.73 ±0.94 a	1.60 ±0.78 a	11.73 ±1.58 b	10.40 ±1.27 b	1.40 ±0.68 a	32.25	***
Non-bee forage species	1.50 ±0.61 ab	0.50 ±0.29 a	2.30 ±0.15 b	2.23 ±0.09 b	1.93 ±0.59 ab	4.81	*
Abundance score all flowers	6.23 ±1.31 a	2.10 ±0.97 a	14.03 ±1.47 b	12.63 ±1.24 b	3.33 ±1.24 a	24.87	***
Species richness of plants in flower	3.80 ±0.76 ab	1.83 ±0.94 a	6.30 ±0.35 b	5.90 ±0.68 b	1.93 ±0.47 a	10.99	**

	Field margin type					**ANOVA**	**2002**
b) Flower 'group' 2002	Natural regeneration	Tussocky grass	Wildflower	Tussocky & wildflower	Cropped	F 4,8	Sig. level
Annuals	0.09 ±0.05	0.03 ±0.03	2.33 ±0.90	2.52 ±1.06	2.36 ±1.45	2.88	ns
Perennials & Biennials	3.27 ±0.52 a	1.97 ±0.84 a	15.03 ±2.52 b	13.00 ±2.41 b	1.73 ±0.93 a	19.60	***
Sown species	0.79 ±0.36 a	1.18 ±0.66 a	16.00 ±3.14 b	14.00 ±3.10 b	0.06 ±0.06 a	25.73	***
Unsown species	2.58 ±0.41	0.82 ±0.19	1.36 ±0.28	1.52 ±0.31	4.03 ±1.85	2.42	ns
Bee forage species	1.76 ±0.53 a	1.39 ±0.74 a	11.88 ±3.68 b	10.97 ±3.09 b	1.03 ±0.37 a	10.49	**
Non-bee forage species	1.61 ±0.08 ac	0.60 ±0.12 a	5.48 ±0.43 b	4.55 ±0.33 bc	3.06 ±1.43 ab	7.87	**
Abundance score all flowers	3.36 ±0.55 a	2.00 ±0.84 a	17.36 ±3.41 b	15.55 ±3.40 b	4.09 ±1.79 a	14.34	***
Species richness of plants in flower	2.52 ±0.44 a	1.61 ±0.63 a	7.18 ±0.82 b	6.61 ±0.99 b	2.94 ±1.16 a	13.32	***

Numbers represent the mean flower abundance score per plot, per sampling date, ± standard errors. Letters and significance levels as in Table 3.1.

Table 3.3 Details of sown mixtures established on the replicated field margin experiment in 1999.

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

Table 3.4 List of flowering plant species recorded on the field margins in 2001 and 2002. Mean flower abundance scores across all treatments are shown.

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

Figure 3.1 Change in total bumblebee abundance on the different margin treatments over three years.

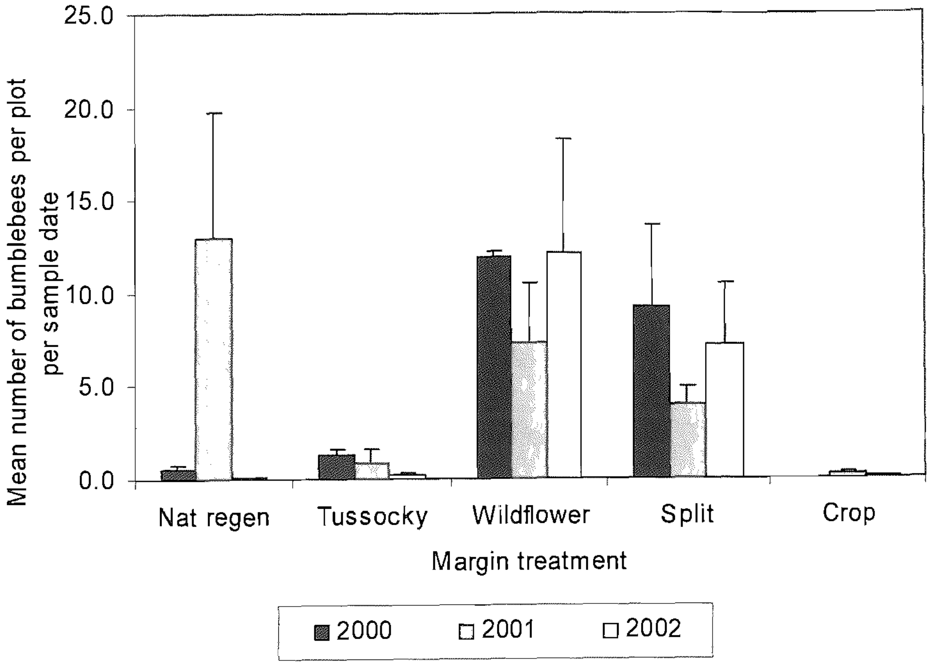


Figure 3.2 Flower preferences of foraging bumblebees (all species) across all margin treatments in each year, for species receiving 30 or more visits in total.

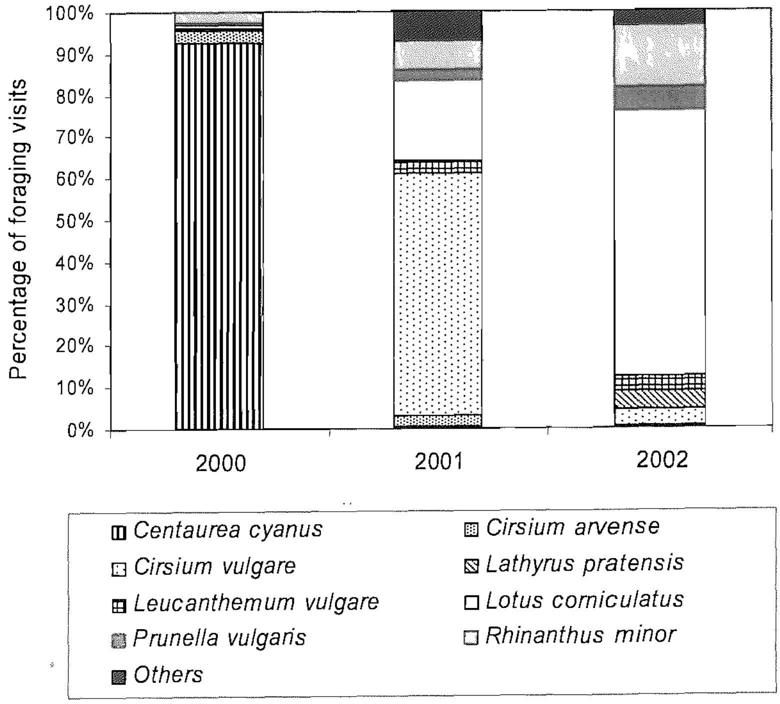
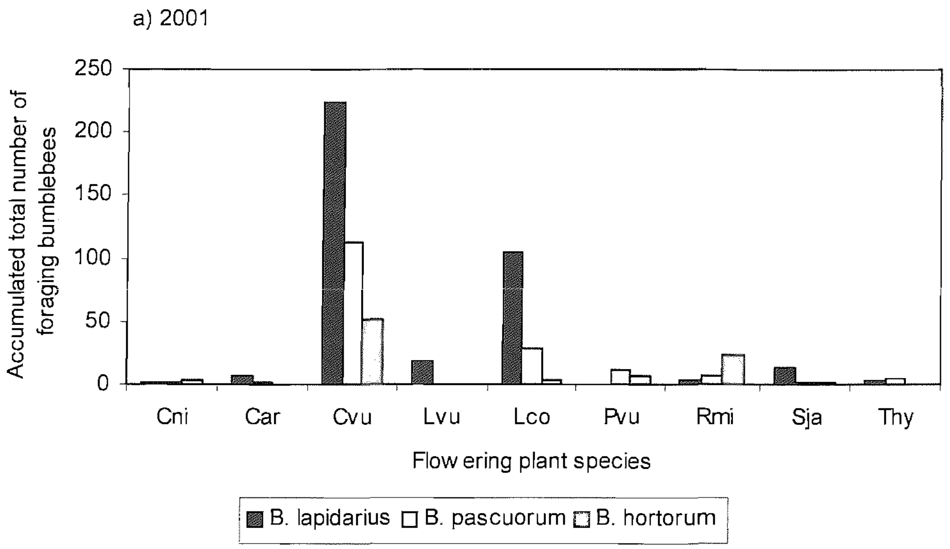


Figure 3.3 Flower visits of three bumblebee species during a) 2001 and b) 2002. Key to plant species as follows: Cni, *Centaurea nigra*; Car, *Cirsium arvense*; Cvu, *Cirsium vulgare*; Lpr, *Lathyrus pratensis*; Lvu, *Leucanthemum vulgare*; Lco, *Lotus corniculatus*; Pvu, *Prunella vulgaris*; Rmi, *Rhinanthus minor*; Rra, *Raphanus raphanistrum*; Sja, *Senecio jacobaea*; Thy, *Trifolium hybridum*.


a) 2001

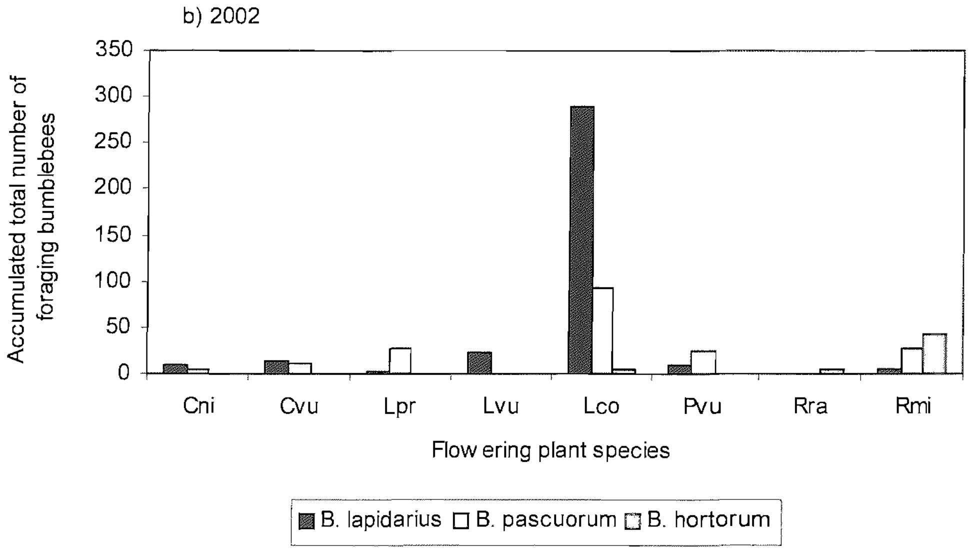
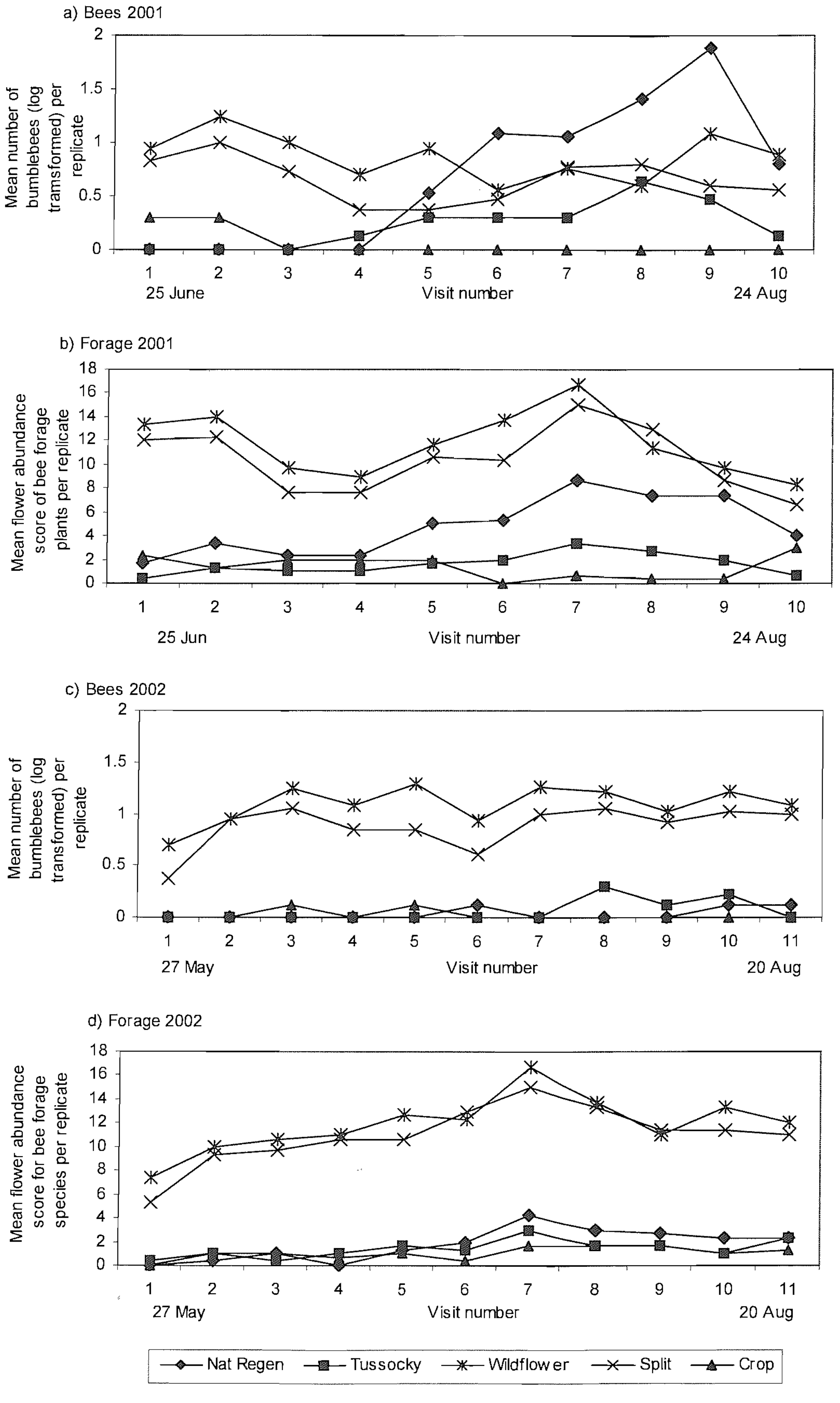

b) 2002

Figure 3.4 Temporal changes in abundance of a) bumblebees in 2001, b) flowers of bumblebee forage species in 2001, c) bumblebees in 2002 and d) flowers of forage species in 2002, across the different field margin treatments.



4. Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis

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Abstract

The value of introduced seed mixtures in providing forage for bumblebees on farmland was assessed by direct observation of individuals and analysis of pollen loads. Two mixtures of perennial grasses and wildflowers were compared with an annual mix of mostly seed-bearing crops over three years. Foraging bees showed contrasting patterns of visitation depending on species. Longer-tongued *Bombus* species preferred the perennial mixtures in which *Trifolium pratense* was dominant, whilst shorter-tongued *Bombus* and honeybees, *Apis mellifera*, visited mainly *Borago officinalis* in the annual mix. These patterns were supported by analysis of pollen loads from *B. pascuorum* and *B. terrestris*, both species showing a high degree of flower constancy to sown species. The relative specialisation of different bee species towards certain plant families, and the flowering phenology of seed mix components, must be considered in the design of agri-environment measures to conserve these and other pollinators.

Keywords: bumblebees/ foraging/ pollen/ seed mixture/ restoration

4.1 Introduction

Bumblebees (*Bombus* spp.) provide an essential pollination service for many entomophilous crops and wild flowers, and are therefore an integral component of agricultural and semi-natural ecosystems (Kevan, 1991; Free, 1993). However, evidence suggests that bumblebees have declined dramatically across Europe and North America in recent decades (Rasmont and Mersch, 1988; Kosior, 1995; Buchmann and Nabhan, 1996). Of the assemblage of 25 Bombus species in the UK, three species have become extinct and several more have shown marked contractions in range, four of which are on the UK Biodiversity Action Plan as priorities for conservation (Williams, 1982; Anon., 1995). These declines are thought to be largely due to the intensification of agriculture, which has also affected many other wild pollinators (Kevan, 1991). Changes in land use and agricultural practices have resulted in the loss of both nesting and foraging habitats, in particular the abundance of key forage plant species associated with semi-natural habitats (Fuller, 1987; Corbet et al., 1991; Haines-Young, 2000). Thus, there is an urgent need to restore and maintain habitats of value for bumblebees and other pollinating insects in intensively managed agricultural landscapes. This has been recognised at a global level by the launch of the International Pollinator Initiative (Dias et al., 1999).

Although they can be seen on a number of different flowers, many bumblebee species preferentially visit perennials from the Fabaceae, Lamiaceae and Asteraceae such as *Trifolium pratense*, *Lamium album* and *Centaurea nigra* (eg. Fussell and Corbet, 1992; Goulson and Darvill, 2004). The flowers of certain annuals such as *Borago officinalis* (borage), *Centaurea cyanus* (cornflower), and *Raphanus sativus* (fodder radish) can also be attractive to some species (Carreck et al., 1999). Recent developments in European agri-environmental policy have encouraged the introduction of such species to uncropped areas on farmland (Marshall and Moonen, 2002). For example, in England, legumes (Fabaceae) have been recommended as components of a new option for arable land under the Environmental Stewardship Scheme, referred to as the 'pollen and nectar flower mixture'. Annual species, such as R. sativus, are often included in mixtures of seed-bearing crops under the 'wild bird seed mixture' option to provide winter food and cover for farmland birds (http://www.defra.gov.uk/erdp/schemes/es/default.htm).

Uncropped field margins sown with perennial wildflower mixtures have been shown to significantly enhance the abundance and diversity of nectar- and pollen-feeding insects compared with margins sown with tussocky grass mixtures, conventional crops, treated as conservation headlands or ploughed and left to regenerate naturally (Meek et al., 2002; Carvell et al., 2004; Pywell et al., 2005). However, the flowering component of these mixtures has not been specifically designed to provide the range and succession of forage plants required by bumblebees (Bombus spp.). Nectar and pollen are required throughout the colony's active period from late April to September, and any gap in flowering due to management actions or flowering phenology in components of the sown mixture could be detrimental to colony development. In addition, bumblebees have varying tongue lengths depending on species which, amongst other factors, determine their preferences for certain forage plants (Pyke, 1982; Prŷs-Jones and Corbet, 1991). Within species the different sexes may also visit different flowers. Therefore conservation of the full bumblebee assemblage (in terms of foraging resources) requires a range of flowers from which nectar and pollen are accessible (Ranta and Lundberg, 1980; Harder, 1985).

The aim of this study was to assess the relative value of three contrasting seed mixtures (all available as options under the Environmental Stewardship Scheme) in providing resources for foraging bumblebees on an arable farm. Most studies of foraging bees tend to focus on the flower visits of individuals observed on localised transect walks, and sometimes note whether nectar, pollen, or both are being collected (e.g. Fussell and Corbet, 1992; Goulson and Darvill, 2004). No studies to date have examined the value of restored habitats by analysing the composition of pollen loads collected by foraging workers, although these can give us useful information about the flowers from which they are obtaining pollen, and about their relative importance based on the proportion of species in each sample (e.g. Brian, 1951; Westrich and Schmidt, 1986). Bumblebees require pollen for their reproduction as it is the sole protein source for developing larvae, and recent evidence suggests that adult workers have an ongoing need for pollen throughout their lives (Smeets and Duchateau, 2003). It is therefore important to assess whether newly restored habitats on farmland are providing this resource, if they are to promote conservation of the bumblebee fauna. In this study, we supplemented direct observations of foraging individuals on the three sown mixtures with the collection and analysis of pollen loads from two *Bombus* species, *B. pascuorum* and *B. terrestris/lucorum*, to represent both the long- and short-tongued species guilds respectively.

4.2 Methods

4.2.1 Study site and experimental design

Research was conducted on an intensively managed arable farm of 164 ha, in North Yorkshire, UK (Lat. 54°05'N, Long. 0°49'W; 40m above mean sea level). This is a demonstration farm which aims to show that practical wildlife conservation and profitable farming can be effectively integrated (http://www.f-e-c.co.uk). Three seed mixtures were sown along the margin of a large arable field on 17th April 2001. Plots were 30 m long x 6 m wide, each replicated five times following a randomised block design. The treatments comprised two mixtures of native perennial grasses and wildflowers (one 'basic' with three herbaceous species and one 'diverse' with 18 herbs) and one of predominantly seed-bearing cover crops sown annually (Table 4.1). In terms of seedbed preparation, plots containing the two perennial mixtures were ring rolled (levelled), and those with the annual mixture were ring rolled and harrowed prior to sowing. Subsequent management involved an application of slug pellets and insecticide (to control weevils on the *Trifolium pratense*) during the second month of establishment. The perennial plots were cut three times during 2001, with the cuttings removed, to ensure successful establishment, and again in early April and late August 2002. The annual treatments were ploughed and re-sown with the same mixture in March 2002 and again in March 2003.

4.2.2 Bumblebee activity

During 2001, bumblebee activity was recorded on 24th and 25th July, to obtain preliminary data on the use of the different mixtures in the establishment year. In 2002, records were made on 12 sampling dates between 28th May and 20th August. In 2003, records were made on 7 dates between 14th May and 11th August. All sampling was conducted between 0930 and 1700h, and during dry weather when the ambient temperature was above 15°C. On each sampling date, transects were walked along the centre of all plots, recording foraging bumblebees and honeybees, and the flower species on which each bee was first seen, within 2 m to each side of the observer. *Bombus terrestris* (L.) and *B. lucorum* (L.) workers cannot always be reliably distinguished in the field (Prŷs-Jones and Corbet, 1991), if considered as two species, so were collectively recorded as *B. terrestris/lucorum*. We refer to this species pair as *B. terrestris* from here. Males were recorded separately from females for *Bombus lapidarius* only, as sex separation of other species in the field can be unreliable. The cuckoo bumblebees (subgenus *Psithyrus* spp. auct.) were recorded together as a group for analysis.

4.2.3 Flower abundance

In order to gain a measure of forage availability and the success in establishment and flowering of sown species, the number of flowers/inflorescences of each plant species present within each plot was estimated using a 5-point scale: 1= 1-25 flowers; 2= 26-200 flowers; 3= 201-1000 flowers; 4= 1001-5000 flowers; 5= > 5000 flowers (as in Carvell et al., 2004). One flower 'unit' was counted as an umbel (e.g. *Daucus carota*), head (e.g. *T. pratense*), spike (e.g. *Ononis spinosa*) or capitulum (e.g. *Centaurea nigra*). Plant species nomenclature follows Stace (1997). Flower abundance scores were recorded on every sampling date, immediately following bumblebee transects.

4.2.4 Collection and analysis of pollen loads

Pollen loads were collected from two species commonly occurring at the study site; *B. pascuorum* (Scopoli) and *B. terrestris*, on three dates: 10th, 11th and 12th July 2002, approaching the peak of colony activity in these species (Prŷs-Jones and Corbet, 1991). Within each plot, the first ten workers of either *B. terrestris* or *B. pascuorum* that were observed to be carrying pollen loads were caught. A single complete pollen load was removed from each bee using a fresh cocktail stick, whilst the bee was restrained using a marking cage with soft plunger. The *Bombus* species, flower species on which it was foraging, plot number and treatment were recorded on a label which was placed with the pollen load in a sample tube, and this was cooled at 5 °C for preservation prior to analysis. Weather conditions were noted, but remained fine throughout the three sampling days.

All pollen samples were processed by mixing and embedding as a thin layer in glycerine jelly and mounting on a microslide (Westrich and Schmidt, 1986). Samples were analysed using a light microscope to identify a) the pollen genera and where possible the most likely plant species from which they were collected according to the exine morphology and grain size, and b) an estimate of the percentage species composition of each pollen load based on a count of 200 grains per sample. Species present in trace amounts comprising less than 1% of a load were regarded as possible contamination and were excluded from the analysis. Pollen identifications were made with the aid of reference collections and a full list of plant species in flower at the study site during the period of pollen collection. Where the determination of pollen types to species level was not possible, they were identified to species 'group' or plant family level (e.g. *Trifolium repens/ hybridum*).

4.2.5 Data analysis

Bumblebee and honeybee counts were summed for each year to calculate seasonal averages (ie. the mean number observed by direct observation per sample date on each plot). These bumblebee means were log-transformed to stabilise the variance prior to analysis. Flower scores of individual plant species were also summarised as seasonal averages, giving a mean score per plot. To compare the total estimated flower abundance of all species in flower between treatments, species abundance scores were expressed as the median value for each range as follows: Score 1 = 13 flowers; 2 = 113 flowers; 3 = 600.5 flowers; 4 = 3000.5 flowers; 5 = 15000 flowers. These data were combined into two variables according to whether species had been sown or unsown in the seed mixtures. Differences in bumblebee abundance, flower abundance and species richness (number of species in flower) between the three treatments in each year were tested by two-way ANOVA, including replicates and treatments as factors. Tukey's Honest Significant Difference test was performed on all analyses to assess pairwise differences between the treatments. To examine the possible effects of flower density on differences in bumblebee abundance between treatments, ANCOVAs were performed with 'total number of flowers per plot' (sown and unsown) as the covariate. Changes in flower abundance of key forage species over each sampling season were also examined. Standard deviations on the mean flower scores for each date were calculated as a measure of continuity in forage supply.

The data on pollen load composition were assessed in terms of the total number of species represented within each load (species richness) and the relative proportions of each plant species present. Differences in species richness and percentage of each pollen species per load as sampled from the three treatments were tested by two-way ANOVA, again with Tukey's test for pairwise differences between treatments.

4.3 Results

4.3.1 Flower abundance

Many species sown in the mixtures established well during their first year (2001; Table 4.2). By 2002, all three herb species in plots sown with the basic perennial mix had established, and 12 of the 18 herbs sown in the diverse perennial mix were recorded (though not always in flower). The two perennial treatments contained a significantly higher number of unsown flowers (annuals such as *Capsella bursa-pastoris*, *Matricaria* spp. and *Myosotis arvensis*) than the annual treatment during 2001. This proportion of unsown species decreased in 2002, and flower abundance of sown species increased, with no significant difference between treatments indicating similar flower abundance within each plot (Table 4.2). A similar pattern was shown during 2003, although statistical significance was achieved with a higher number of sown flowers in the diverse perennial than basic and annual treatments, as expected from the composition of the seed mixtures.

Flower scores for individual species differed significantly between treatments according to the mixtures in which they were sown (Table 4.3). The occurrence of a few flowers in plots where a species was not sown is likely to be due to occasional spread of material, including flower heads, by machinery during cutting at the end of the season. Of the dominant flowering components, red clover, *Trifolium pratense* had similarly high mean abundance scores in both perennial mixtures, whereas borage, *Borago officinalis* had mean scores of 2.5 and 1.9 in 2002 and 2003 respectively in the annual mixture. These means (calculated as seasonal averages) are lower than expected given the high density of *B. officinalis* flowers observed, but are explained by changes in flower abundance over each sampling season (Figure 4.2). *T. pratense* flowers were relatively abundant on all sampling visits from late May to August, with a relatively low standard deviation on the mean scores per plot for each year indicating a continuous forage supply (2002 = 0.7, 2003 = 1.4). *B. officinalis* only began flowering around late June, and the results suggest a decrease in flowering towards the end of August, with higher standard deviations than *T. pratense* (2002 = 2.1, 2003 = 2.0).

Climatic conditions within the region of the study site (Northeast England) were relatively stable during the study, with average yearly temperatures of 8.9°C , 9.5°C and 9.6°C and a total rainfall of 786 mm, 905 mm and 616 mm in 2001, 2002 and 2003 respectively (http://www.metoffice.com/climate/uk/). These patterns were similar to the UK average, perhaps with the exception of a lower rainfall during the winter of 2001-2002. This had no apparent detrimental effect on establishment of the seed mixtures.

4.3.2 Bumblebee abundance

Six social *Bombus* species were recorded, representing the assemblage most commonly found in the UK. There were significant differences in the total number of bumblebees (altogether 4,925 individuals) visiting the three mixtures in all sampling years (see Table 4.2). Abundance was highest on the annually sown mixtures in each year, with numbers in the perennial treatments increasing as the mixtures established. Honeybees were restricted almost entirely to the annual mixture, although numbers fell in 2002 and 2003 (hive density in the surrounding landscape was not recorded). Abundance of each *Bombus* species differed significantly between treatments (Figure 4.1). While *B. terrestris/lucorum*, and *B. pratorum* (shorter-tongued species) and honeybees visited the annual mixture almost exclusively, *B. lapidarius* (also a relatively short-tongued species) visited all mixtures and was the most commonly recorded species. *B. pascuorum* and *B. hortorum* (longer-tongued species) preferred the two perennial treatments, but there were no significant differences between the number of visits to the basic and diverse mixtures. Few cuckoo bumblebees visited the margins, but those that were recorded *(Bombus (P.) vestalis* and *Bombus (P.) barbutellus*) showed a significant preference for the annual mixture in 2002 only. When the 'total number of flowers per plot' was added as a covariate to the analysis of differences in bumblebee abundance between treatments, there was no significant effect of this covariate, and the treatment differences described above were unaffected. Thus bumblebee abundance was apparently more strongly related to seed mixture composition than total flower abundance.

4.3.3 Bee activity

Patterns of forage plant visitation as recorded by direct observation suggest a preference for *Borago officinalis* flowers by the shorter-tongued bumblebees (*B. terrestris* and *B. pratorum*) and honeybees, though these visits were restricted mainly to July and August (Table 4.4). The longer-tongued species (*B. pascuorum* and *B. hortorum*) showed a preference for *Trifolium pratense*, with visits recorded on all sampling dates from May to August. As suggested by the abundance data, *B. lapidarius* was intermediate in its flower preferences, visiting a range of species but particularly *Centaurea nigra* in 2003. More than 50% of these visits to *C. nigra* were by males. Of the additional species sown in the diverse perennial mixture that were not included in the basic mix, only *Ononis spinosa* was visited more than five times by foraging bumblebees.

4.3.4 Pollen load analysis

A total of 149 pollen load samples were analysed; 44 from *B. terrestris* and 105 from *B. pascuorum*, this difference being due to the tendency for *B. terrestris* to forage from the annual mixture and *B. pascuorum* from both perennial mixtures. Overall, a high proportion of the pollen collected was from plant species sown in the experimental mixtures (88% of all loads in *B. pascuorum* and 73% in *B. terrestris*) rather than from other farm habitats. *Borago officinalis* and *Trifolium pratense* were the only two plant species for which the mean percentage per load of pollen differed significantly between the three mixtures. They tended to dominate loads sampled from the mixtures in which they were sown (Table 4.5).

The typical composition of pollen loads collected by each bee species revealed contrasting preferences for certain plant species (Tables 4.5 and 4.6). *B. terrestris* loads contained pollen from nine species, but only 32% of loads were of mixed species. *Borago officinalis* pollen dominated 70% of samples, often being the sole pollen type present. Pollens from the unsown species *Papaver rhoeas* and *Rubus fruticosus* were also present in some samples, and, where they occurred, constituted up to 90% or 100% of the load. In contrast, *B. pascuorum* loads represented 13 plant species, but contained mainly *T. pratense* pollen, which occupied a significantly higher percentage per load sampled from the perennial than the annual mixtures (Table 4.5). Many of these loads were of mixed species (53%), containing additional pollen from *Lathyrus pratensis* and the unsown *Trifolium repens/ hybridum* and *Stachys sylvatica.*

The composition of a bumblebees' pollen load did not always relate to the forage plant species on which it had been caught. Of the seven loads from *B. pascuorum* workers sampled on *B. officinalis* in the annual mixture, only three were dominated by *B. officinalis* pollen, with others comprising mainly *Trifolium* species (Table 4.5) and one with 90% *Linaria vulgaris* pollen. The information on forage plant preferences that was gained from pollen load analysis is compared with that from direct observations during July 2002 in Table 4.6.

4.4 Discussion

4.4.1 Annual and perennial mixtures

This study confirms that British bumblebee species show marked differences in their choice of forage plants and highlights some important factors to be considered in the future management of habitats for bumblebees in agricultural areas. When annual and perennial flower mixtures composed of different species were offered together at the same site patterns of visitation, especially for pollen collection, contrasted between bee species. The mixture comprising annual seed-bearing crops attracted all six *Bombus* species, but particularly the short-tongued *Bombus terrestris/lucorum*, and it was virtually the only treatment in which honeybees were recorded. This reflected the abundance of *Borago officinalis* (borage), which has been shown both to dominate within annual mixtures and attract short-tongued bumblebees and honeybees in other studies, along with the non-native species *Phacelia tanacetifolia* (phacelia) (Williams and Christian, 1991; Carreck et al., 1999; Walther-Hellwig and Frankl, 2000). Additional species sown in the annual mixture (eg. *Linum usitatissimum* and *Melilotus officinalis*) contributed little to flower abundance or bumblebee diversity, so could be excluded from the mix in future or replaced with other nectar rich annuals such as *Centaurea cyanus* or *Vicia sativa* which may improve its value for longer-tongued bumblebees. However, the primary function of these annual mixtures as an agri-environmental measure is to provide winter food and cover for seed-eating farmland birds (Stoate et al., 2003). The design of such mixtures could be improved to benefit both groups, by providing winter seed for birds and summer pollen and nectar sources for bumblebees and other pollinators.

Previous observations of foraging bees on *Borago officinalis* have indicated that it may be visited mainly for nectar and not for pollen (Engels et al., 1994; Carreck and Williams, 1997), hence although agronomically viable in the UK, it may be a less valuable forage species than certain perennials. From our results, this was not the case for the short-tongued *B. terrestris*, as *Borago officinalis* pollen constituted a large part of its pollen diet. However, pollen sampling was only carried out during a limited period in July, and our counts of flower abundance showed that during both years, *B. officinalis* flowers were unavailable during May and June, thus restricting bee visitation at these times. This suggests that annual mixtures should either be sown sequentially (Carreck and Williams, 2002) or include a wider range of forage species to benefit bees and other pollinators throughout their individual and colony lifespans. Furthermore, due to its annual nature, this option does not allow the establishment of vegetation suitable as nesting habitat for bumblebees (Svensson et al., 2000).

Treatments containing the perennial mixtures were visited mainly by the two longer-tongued bumblebee species, *Bombus pascuorum* and *Bombus hortorum*. This reflected the large number of *Trifolium pratense* flowers, particularly in 2002 when the proportion of unsown species in the sward had decreased. The lower number of these bumblebees recorded on average in 2003 may have been due to the reduction in availability of *T. pratense* flowers from July onwards (Figure 4.2) or an increase in forage supply elsewhere within their foraging range, although we cannot account for the latter. *Bombus lapidarius* also visited the perennial treatments to forage mainly on *Centaurea nigra*, *T. pratense* and *Lotus corniculatus*. These patterns generally follow the well documented tendency for bumblebees to utilize flowers with corolla lengths which correspond to their tongue length (e.g. Ranta and Lundberg, 1980; Fussell and Corbet, 1992), with *B. lapidarius* showing a tendency to be intermediate in its forage preferences between the longer- and shorter-tongued groups (as in Goulson et al., 2005). Furthermore, that *B. lapidarius* males visited *C. nigra* almost exclusively suggests that purely legume-based forage patches may not cater for the requirements of both bumblebee sexes.

The importance of *T. pratense* as a pollen source for *B. pascuorum* was evident in our study, as shown by Brian (1951) in the UK, and Anasiewicz and Warakomska (1977) in Poland. Analyses of pollen loads and the pollen collecting behaviour of the rare long-tongued bumblebee species *B. sylvarum* and *B. humilis* in the UK also revealed a strong preference for pollens from the Fabaceae, particularly *Trifolium* spp. (Edwards, pers. comm.; Goulson and Darvill, 2004). This may reflect the nutritional quality of Fabaceae pollen for bumblebees, which is yet to be determined. As the need to re-introduce *T. pratense* to farmland areas and enhance bumblebee populations increases, native seed sources are becoming costly and difficult to obtain. Mixtures with agricultural varieties of this and other legume species are currently being tested by the authors alongside other agri-environmental measures within a multi-site experiment, and show potential to benefit the longer-tongued bumblebee assemblage in particular.

In terms of the relative value of the 'basic' and 'diverse' perennial mixtures tested in this study, both the direct foraging observations and pollen data suggest that the additional species in the 'diverse' mixture contributed little to bumblebee activity, at least during the first three years of development. *Lathyrus pratensis* may be an important component of sown perennial mixtures as it is likely to develop and prolong the value of this restored habitat for bumblebees (e.g. Carvell et al., 2004). Considering the costs of native wildflower seed, some other species could be excluded from the mix, but a proportion of open-flowered composites (Asteraceae, eg. *Leontodon hispidus*) or umbellifers (Apiaceae, eg. *Daucus carota*) should remain to provide resources for other social or solitary bees, butterflies and hoverflies (eg. Feber et al., 1996; Westrich, 1996). In addition, the potential for perennial mixtures or other measures to provide early season forage plants for bumblebee queens has yet to be realised and requires further investigation.

4.4.2 Pollen analysis vs direct observation methods

Differences between the preferred forage plants of *B. terrestris* and *B. pascuorum* as identified by direct observation were further emphasized by differences in the pollen loads they collected. It is not surprising that most of the pollen types identified were from flower species in the sown mixtures (eg. *B. officinalis* and *T. pratense*), as these were the species which bumblebees were visiting when caught (as in Yalden, 1982). Still, this highlights the functional importance of the introduced mixtures in providing forage resources relative to the existing farmed landscape. A high degree of flower constancy during each foraging trip was evident from the many single-species samples, as well as fidelity to the experimental treatments, suggesting that many bumblebees were foraging exclusively on the sown mixtures, at least during the peak of colony activity.

Several plant species from beyond the experimental area were present in the pollen loads, including *Papaver rhoeas*, *Stachys sylvatica* and *Rubus fruticosus*. That these species had been visited was not apparent by direct observation alone. Mapping the locations and flowering times of these species relative to the experimental margin would in future allow us to examine farm-scale movements of bumblebees, based on the pollen types collected by each individual in a foraging trip. Our data also suggest that, in suitable habitats, *B. pascuorum* may be able to exploit a similarly wide range of plant species for pollen as *B. terrestris*. Although *B. terrestris* is considered the most polylectic of bumblebee species, this may be primarily an artefact of its high relative abundance throughout much of Europe (Goulson, 2003). That *B. pascuorum* has the potential to obtain pollen from a wide range of species (although it prefers to specialise on the Fabaceae) may explain why it is one of only two longer-tongued *Bombus* species remaining common in the UK (Williams, 1982; Goulson, 2003).

4.4.3 Conclusions and implications for bumblebee conservation

The effects of habitat change in many European agricultural landscapes have resulted in bumblebee communities dominated by relatively short-tongued species such as *B. terrestris* and *B. lapidarius* (Walther-Hellwig and Frankl, 2000; Pywell et al., 2005). These species may well benefit from temporary forage resources such as mass flowering crops, as suggested by Westphal et al., (2003), or annually sown mixtures including *Borago officinalis*, as in this study. However, we argue that these foraging resources alone are not sufficient to conserve the full bumblebee assemblage in agricultural ecosystems. Perennial forage plants such as *Trifolium pratense* are highly valuable, particularly as pollen sources, for the long-tongued species. These bumblebees are required to perform a pollination service that cannot be replaced by short-tongued species or honeybees (Corbet, 2000). Our study provides useful evidence of foraging by long- and short-tongued bumblebee species in habitats created from carefully selected perennial and annual seed mixtures. Further research at a larger scale is now required to fully assess the impacts of introduced foraging habitats on bumblebee populations, rather than simply on the abundance or activity of individuals. In conclusion, we recommend two key factors which should be considered in the design of agri-environmental schemes aiming to conserve bumblebees and other pollinators in agricultural ecosystems: i) the relative specialisation of different bumblebee species towards certain plant families for nectar and pollen collection, in particular the association of long-tongued species with the Fabaceae, and ii) the flowering phenology of species chosen as seed mixture components for habitat restoration.

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References

Anasiewicz, A., Warakomska, Z. (1977) Pollen food of the Bumble-bees (*Bombus Latr. Hymenoptera*) and their association with the plant species in the Lubin region. Ekologia Polska 25, 309-322.

Anon. (1995) Biodiversity – The UK Steering Group Report. Volume 2 Action Plans. HMSO London.

Brian, A.D. (1951) The pollen collected by bumble-bees. J. Anim. Ecol. 20, 191 – 194.

Buchmann, S.E., Nabhan, G.P. (1996) The Forgotten Pollinators. Island Press, Washington DC, USA, 292 pp.

Carreck, N.L., Williams, I.H. (1997) Observations on two commercial flower mixtures as food sources for beneficial insects in the UK. J. Agricultural Science, Cambridge 128, 397-405.

Carreck, N.L., Williams, I.H., Oakley, J.N. (1999) Enhancing farmland for insect pollinators using flower mixtures. In Field margins and buffer zones: ecology, management and policy. Asp. Appl. Biol. 54, 101-108.

Carreck, N.L., Williams, I.H. (2002) Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. J. Insect Conserv. 6, 13-23.

Carvell, C., Meek., W.R., Pywell., R.F., Nowakowski, M. (2004) The response of foraging bumblebees to successional change in newly created arable field margins. Biol. Conserv. 118, 327-339.

Corbet, S.A., Williams, I.H., 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. (2000) Conserving compartments in pollination webs. Conserv. Biol. 14 (5), 1229 – 1231.

Dias, B.S.F., Raw, A., Imperatri –Fonseca, V.L. (1999) International Pollinators Initiative: The São Paulo Declaration on Pollinators. Report on the Recommendations of the Workshop on the Conservation and Sustainable Use of Pollinators in Agriculture with Emphasis on Bees. Brasília: Brazilian Ministry of the Environment (MMA)1999. 66 pp.

Engels, W., Schulz, U., Radle, M. (1994) Use of the Tübingen mix for bee pasture in Germany. In *Forage for bees in an agricultural landscape*. pp. 57-65. Matheson, A. (Ed) International Bee Research Association, Cardiff.

Feber, R.E., Smith, H., Macdonald, D.W. (1996) The effects on butterfly abundance of the management of uncropped edges of arable fields. J. Appl. Ecol. 33, 1191 – 1205.

Free, J.B. (1993) Insect Pollination of Crops, 2nd edition. Academic Press, London, UK.

Fuller, R. M. (1987) The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930-84. Biological Conservation 40, 281-300.

Fussell, M., Corbet, S.A. (1992) Flower usage by bumblebees: a basis for forage plant management. J. Appl. Ecol. 29, 451-465.

Goulson, D. (2003) Bumblebees: their behaviour and ecology. Oxford University Press, Oxford.

Goulson, D., Darvill, B. (2004) Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? Apidologie 35, 55-64.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. & Knight, M.E. (2005) Causes of rarity in bumblebees. Biological Conservation 122, 1-8.

Haines-Young, R. (editor) (2000) Accounting for nature: assessing habitats in the UK countryside. Department of the Environment, Transport and the Regions, London.

Harder, L.D. (1985) Morphology as a predictor of flower choice by bumblebees. Ecology 66, 198-210.

Kevan, P.G. (1991) Pollination: keystone process in sustainable global productivity. Acta Hort. 288, 103-110.

Kosior, A. (1995) Changes in the fauna of bumble-bees (*Bombus* Latr.) and cuckoo-bees (*Psithyrus* Lep.) of selected regions in southern Poland. pp. 103-111 in: Banaszak, J. (Ed.) Changes in Fauna of Wild Bees in Europe. Pedagogical Univ., Bydgoszcz, Poland.

Marshall, E.J.P., Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. Agric. Ecosyst. Environ. 89, 5-21

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H., Nowakowski, M. (2002) The effect of arable field margin composition on invertebrate biodiversity. Biol. Conserv. 106, 259-271.

Prŷs-Jones, O.E., Corbet, S.A. (1991) *Bumblebees. Naturalists' Handbooks 6.* The Richmond Publishing Co. Ltd., Slough.

Pyke, G.H. (1982) Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. Ecology 63, 555-573.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R. & Sherwood, A. (2005) Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation* 121: 479-494.

Ranta, E., Lundberg, H. (1980) Resource partitioning in bumblebees: the significance of differences in proboscis length. Oikos 35, 298-302.

Rasmont, P., Mersch, P. (1988) Première estimation de la dérive faunique chez les bourdons de la Belgique (Hymenoptera: Apidae). Ann. Soc. Roy. Zool. Belgique 118, 141-147.

Smeets, P., Duchateau, M.J. (2003) Longevity of *Bombus terrestris* workers (Hymenoptera: Apidae) in relation to pollen availability, in the absence of foraging. Apidologie 34, 333-337.

Stace, C. (1997) *New Flora of the British Isles.* Cambridge University Press, Cambridge, UK.

Stoate, C., Szczur, J., Aebischer, N.J. (2003). Winter use of wild bird cover crops by passerines on farmland in northeast England. Bird Study 50, 15-21.

Svensson, B., Lagerlöf, J., Svensson, Bo. G. (2000) Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agric. Ecosyst. Environ. 77, 247-255.

Walther-Hellwig, K., Frankl, R. (2000) Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae) in an agricultural landscape. J. Appl. Entomol. 24, 299-306.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T. (2003) Mass flowering crops enhance pollinator densities at a landscape scale. Ecology Letters 6, 961-965.

Westrich, P. (1996) The problems of partial habitats. In Matheson, A., Buchmann, S.L., O'Toole, C., Westrich P., Williams, I.H. (Eds.), The Conservation of Bees. Linnean Society Symposium Series 18. Academic Press, London.

Westrich, P., Schmidt, K. (1986) Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hynemoptera, Apoidea). Linzer Biol. Beitr. 18, 341-360.

Williams, P.H. (1982) The distribution and decline of British bumblebees (*Bombus* Latr.) J. Apic. Res. 21 (4), 236-245.

Williams, I.H., Christian, D.G. (1991) Observations on *Phacelia tanacetifolia* Bentham (Hydrophyllaceae) as a food plant for honey bees and bumble bees. J. Apic. Res. 30 (1), 3 – 12.

Yalden, P.E. (1982) Pollen collected by the bumblebee *Bombus monticola* Smith in the Peak District, England. J. Natural History 16, 823 – 832.

Table 4.1 Seed mixture details (* Wildflower seed was of native lowland UK provenance, purchased from a commercial seed house)

Mixture type	**Basic perennial Grass & wildflower***	**Diverse perennial Grass & wildflower***	**Annual cover crop**
Recommended seeding rate	37 kg/ha	37 kg/ha	5.5 kg/ha

Scientific name	**Common name (UK)**	**% composition**	**% composition**	**Scientific name**	**Common name (UK)**	**% composition**
Centaurea cyanus	Cornflower		0.2	*Borago officinalis*	Borage	34
Centaurea nigra	Black Knapweed	2	1.5	*Raphanus sativus*	Fodder Radish	22
Daucus carota	Wild Carrot		1	*Linum usitatissimum*	Linseed	11
Knautia arvensis	Field Scabious		1.5	*Sinapis alba*	Mustard	11
Lathyrus pratensis	Meadow Vetchling		0.5	*Melilotus officinalis*	Yellow-blossom Clover	22
Leontodon hispidus	Rough Hawkbit		1			
Leucanthemum vulgare	Oxeye Daisy		2			
Linaria vulgaris	Common Toadflax		3			
Lotus corniculatus	Bird's-foot Trefoil	3	1.5			
Odontites verna	Red Bartsia		0.2			
Ononis spinosa	Spiny Restharrow		0.5			
Primula veris	Cowslip		0.5			
Prunella vulgaris	Selfheal		0.3			
Silene latifolia	White Campion		1			
Stachys officinalis	Betony		1			
Ranunculus acris	Meadow Buttercup		2.5			
Taraxacum officinalis	Dandelion		0.5			
Trifolium pratense	Red Clover	15	2			
Agrostis capillaris	Common Bent	5	5			
Cynosurus cristatus	Crested Dogstail	30	30			
Festuca rubra ssp commuata	Chewing's Fescue	10	10			
Festuca rubra ssp juncea	Slender Red Fescue	20	20			
Poa pratensis	Smooth Meadow Gras	15	15			
Number of herb species		3	18			5
Number of grass species		5	5			
Total no. of species		**8**	**23**			**5**

Table 4.2 Differences in number of bumblebees, honeybees, mean total number of flowers and richness of species in flower per sampling date on the three seed mixtures in each year (ns, not significant; * $P<0.05$; ** $P<0.01$; *** $P<0.001$; Means within a row followed by different letters are significantly different at $P<0.05$)

Year		**Basic Perennial**	**Diverse Perennial**	**Annual**	**$F_{2,8}$**	**ANOVA Sig.**
2001	All bumblebees	5.1 ab	3.8 a	12.5 b	5.5	*
(July only)	Honeybees	0.0 a	0.0 a	17.1 b	58.7	***
	Total number sown flowers	2093.5 a	1578.7 a	15000.0 b	362.1	***
	Sown species richness	2.0 b	2.4 b	1.0 a	26.0	***
	Total number unsown flowers	26697.0 b	19430.2 b	143.0 a	17.4	***
	Unsown species richness	5.6 b	6.4 b	3.0 a	33.9	***
2002	All bumblebees	12.6 a	10.8 a	24.9 b	58.5	***
(whole season)	Honeybees	0.0 a	0.0 a	7.0 b	322.9	***
	Total number sown flowers	7540.5	6063.5	6245.9	4.1	ns
	Sown species richness	3.1 b	5.2 c	1.5 a	499.1	***
	Total number unsown flowers	313.3 ab	156.2 a	670.3 b	4.7	*
	Unsown species richness	2.0	1.9	2.2	2.0	ns
2003	All bumblebees	16.4 a	13.3 a	20.6 b	15.6	**
(whole season)	Honeybees	0.2 a	0.2 a	4.5 b	71.5	***
	Total number sown flowers	5133.2 a	11030.1 b	5274.3 a	33.9	***
	Sown species richness	3.0 b	5.7 c	0.7 a	554.2	***
	Total number unsown flowers	122.1	79.6	215.8	0.8	ns
	Unsown species richness	1.4	1.3	1.6	0.4	ns

Table 4.3 Differences in mean flower abundance scores of sown species per sampling date for the three sown mixtures (treatments) in 2002 and 2003. (Figures are in bold where a species was sown; ns, not significant; * P<0.05; ** P<0.01; *** P<0.001; Means within a row followed by different letters are significantly different at P<0.05)

	2002					2003				
Sown species	**Basic Perennial**	**Diverse Perennial**	**Annual**	$F_{2,8}$	ANOVA Sig. 2002	**Basic Perennial**	**Diverse Perennial**	**Annual**	$F_{2,8}$	ANOVA Sig. 2003
Borago officinalis	0.00 a	0.00 a	**2.50 b**	1800.0	***	0.00 a	0.00 a	**1.91 b**	1122.3	***
Centaurea nigra	**0.65 b**	**0.58 b**	0.00 a	230.2	***	**1.03 b**	**1.09 b**	0.00 a	686.0	***
Daucus carota	0.02 a	**0.88 b**	0.00 a	93.5	***	0.03 a	**0.83 b**	0.00 a	69.2	***
Knautia arvensis	0.00 a	**0.12 b**	0.00 a	5.4	*	0.00 a	**0.26 b**	0.00 a	13.5	**
Lathyrus pratensis	0.00 a	**0.10 b**	0.00 a	6.0	*	0.00 a	**0.80 b**	0.00 a	120.6	***
Leucanthemum vulgare	0.15 a	**2.15 b**	0.00 a	312.8	***	0.00 a	**2.66 b**	0.00 a	455.2	***
Lotus corniculatus	**1.87 b**	**1.90 b**	0.02 a	131.0	***	**2.46 b**	**2.54 b**	0.00 a	1393.3	***
Melilotus officinalis	0.00 a	0.00 a	**0.65 b**	9.9	**	0.00	0.00	**0.11**	4.6	*
Ononis spinosa	0.00 a	**0.60 b**	0.00 a	152.5	***	0.00 a	**0.83 b**	0.00 a	841.0	***
Plantago lanceolata	0.67 b	1.13 c	0.05 a	59.1	***	0.89 b	1.29 c	0.00 a	99.4	***
Prunella vulgaris	0.03 a	**0.38 b**	0.00 a	51.3	***	0.00 a	**0.26 b**	0.00 a	23.1	***
Raphanus sativus	0.03 a	0.00 a	**1.00 b**	71.1	***	0.00 a	0.00 a	**1.57 b**	93.1	***
Silene latifolia	0.28 b	**0.20 ab**	0.05 a	6.1	*	0.29 b	**0.09 ab**	0.00 a	6.2	*
Sinapis alba	0.02 a	0.00 a	**1.42 b**	80.7	***	0.00 a	0.00 a	**1.14 b**	213.3	***
Trifolium pratense	**4.15 b**	**3.97 b**	0.08 a	1156.8	***	**3.09 b**	**3.09 b**	0.00 a	1138.0	***

Table 4.4 Foraging visits of bumblebees and honeybees recorded by direct observation. (Plant species receiving fewer than 5 visits in both years were excluded; (s) = species sown in the experimental mixtures; Flowering periods refer to presence of flowers across all mixtures for both years in half-months as follows: 5.0 = 1-15 May; 5.5 = 16-31 May; 6.0 = 1-15 June; 6.5 = 16-30 June etc.)

		Bee species (% of total visits to each plant species across all mixtures and all dates within each year)											
	Flowering	*B. terrestris/ luc*		*B. lapidarius*		*B. pratorum*		*B. pascuorum*		*B. hortorum*		*Honeybees*	
Forage plant species	**period**	2002	2003	2002	2003	2002	2003	2002	2003	2002	2003	2002	2003
Borago officinalis (s)	6.5-8.5	97.6	87.4	61.4	28.2	99.3	93.2	1.0	5.7	0.6		98.4	57.7
Centaurea nigra (s)	7.0-8.5	0.2	8.0	17.4	59.1			2.4	9.0		1.4		6.0
Cirsium vulgare	7.0-8.5	0.3	0.8	2.4	0.7			0.4	0.8				
Lotus corniculatus (s)	5.5-8.5	0.2		4.3	2.4			0.9	27.1			0.2	
Ononis spinosa (s)	7.5-8.5		1.5		0.3			1.0	7.4				0.6
Raphanus sativus (s)	6.0-8.5	0.3	1.1	4.0	6.9		6.2	0.8	0.8	0.3		1.2	35.7
Sinapis alba (s)	6.0-8.5			0.6									
Trifolium pratense (s)	5.0-8.5	0.9	0.4	6.6	1.4	0.9		92.0	45.2	99.2	98.6	0.2	
Trifolium repens	5.0-8.5	0.6	0.8	3.3	0.9			1.4	4.1				

Table 4.5 Differences in mean species richness of pollen loads and mean % of *B. officinalis* and *T. pratense* pollen per load sampled from the three mixtures in 2002. (ns, not significant; * $P<0.05$; ** $P<0.01$; *** $P<0.001$; Means within a row followed by different letters are significantly different at $P<0.05$)

		Basic Perennial	**Diverse Perennial**	**Annual**	**$F_{2,8}$**	**ANOVA Sig.**
B. terrestris	Pollen load species richness	0.00	0.60	1.35	3.6	ns
	% *Borago officinalis* pollen	0.00 a	0.00 a	70.76 b	283.6	***
	% *Trifolium pratense* pollen	0.00	0.00	2.22	1	ns
B. pascuorum	Pollen load species richness	1.59	1.59	2.14	0.1	ns
	% *Borago officinalis* pollen	1.02 a	0.00 a	42.86 b	9.9	**
	% *Trifolium pratense* pollen	75.53 b	85.41 b	18.57 a	22.3	***

Table 4.6 Comparison of forage plant preferences as derived from pollen analysis and direct observation methods. Data represent mean % per pollen load from July 2002 pollen analysis ± SE, and % of visits from direct observations during July 2002 only ((s) = species sown in the experimental mixtures).

	B. terrestris		***B. pascuorum***	
Pollen / Forage plant species	Pollen analysis n= 44 loads	Direct observation n= 595 visits	Pollen analysis n= 105 loads	Direct observation n= 562 visits
Borago officinalis (s)	69.55 ± 6.26	99.32	3.30 ± 1.58	1.07
Centaurea nigra (s)				0.18
Chamaenerion angustifolium			0.19 ± 0.19	
Cirsium vulgare	0.02 ± 0.02		0.57 ± 0.35	
Hypericum spp.			0.38 ± 0.38	
Impatiens glandulifera			0.38 ± 0.38	
Lathyrus pratensis/ Vicia cracca (s)			5.26 ± 1.64	
Linaria vulgaris (s)	0.45 ± 0.45		1.54 ± 0.94	
Lotus corniculatus (s)		0.16	1.68 ± 0.90	0.89
Papaver rhoeas	10.91 ± 4.20			
Rubus fruticosus	11.36 ± 4.28		1.84 ± 1.02	
Sinapis/ Raphanus (s)	2.02 ± 1.82			
Stachys sylvatica	1.36 ± 1.01		1.37 ± 0.57	
Trifolium pratense (s)	2.27 ± 2.27		75.62 ± 3.17	96.98
Trifolium repens/ hybridum	0.45 ± 0.45	0.50	6.73 ± 1.77	0.89
Viola arvensis			0.05 ± 0.05	

Figure 4.1 Abundance of different bumblebee species and honeybees on each forage mixture in 2002 and 2003. Treatment differences are shown above each species as follows (ANOVA, df = 2,8): ns, not significant; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

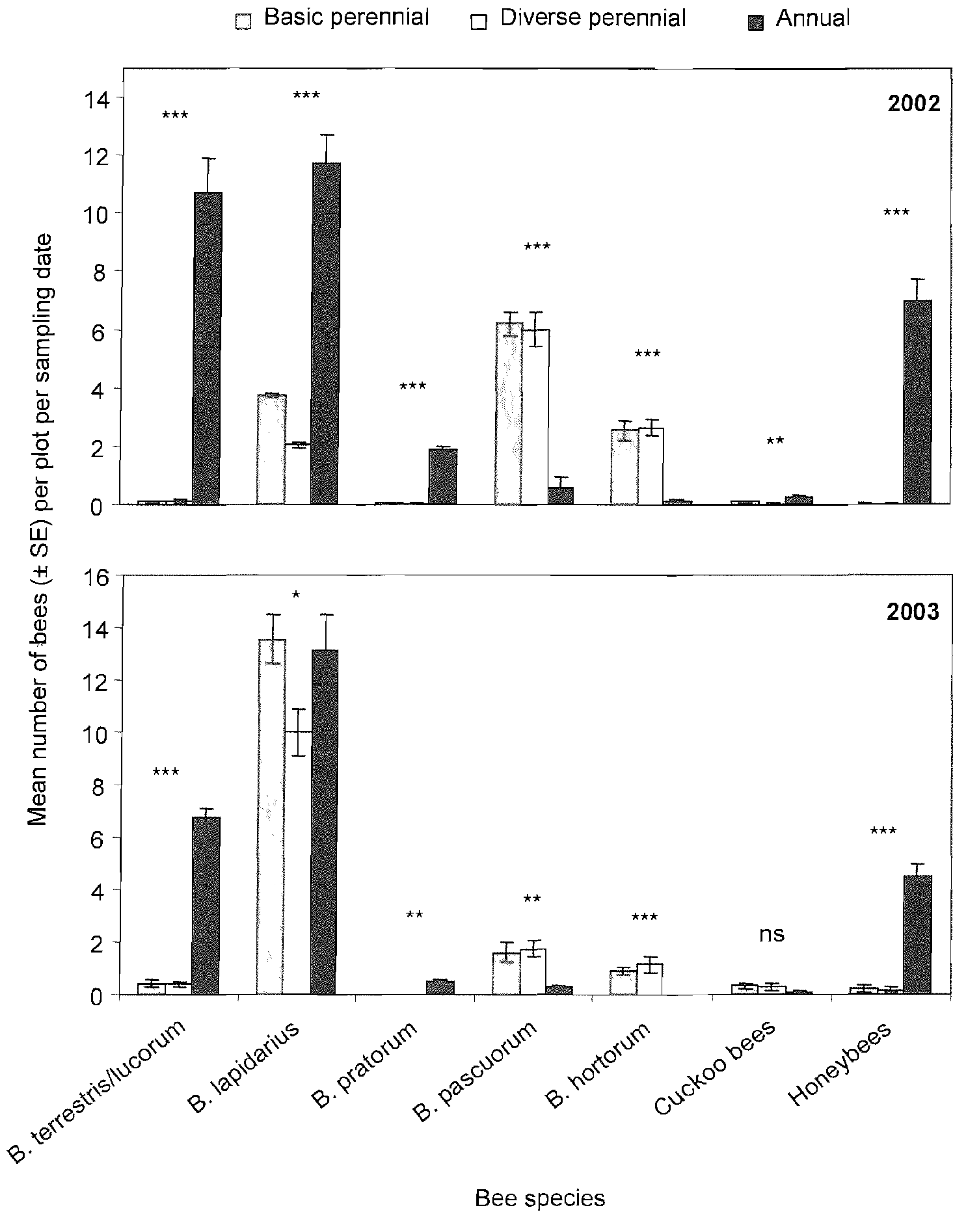
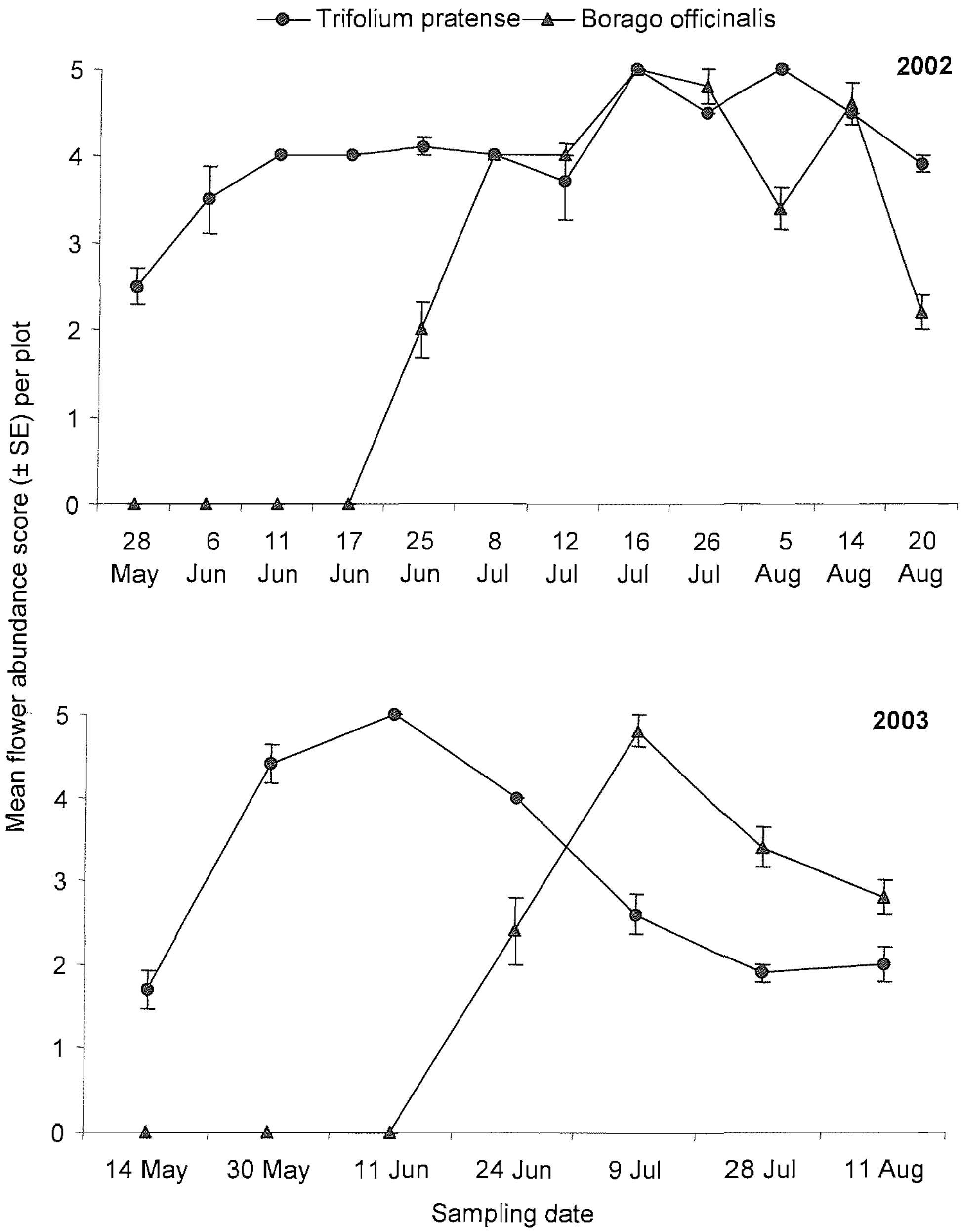


Figure 4.2 Flowering phenology of red clover, *Trifolium pratense* (mean of scores from basic and diverse perennial mixtures) and borage, *Borago officinalis* (scores from annual mixture) in 2002 and 2003.



5. Utilisation of pollen resources by bumblebees in an enhanced arable landscape

Abstract

Pollen is an essential resource for bumblebees, yet this is often overlooked in studies of their foraging requirements. The decline of bumblebees across the UK and rest of Europe has prompted conservation measures to consider the provision of pollen as well as nectar resources, particularly in intensive agricultural landscapes. This study was carried out to investigate the utilisation of pollen from different forage plants by two bumblebee species with contrasting ecologies (*Bombus pascuorum* and *Bombus terrestris/lucorum*) across an enhanced arable landscape. An area of 1.96 km^2, centred on an arable farm in northeast England, was divided into grid squares of 100m x 100m. Pollen loads were sampled from foraging workers in eight random squares within the centre of this grid, and every square was surveyed in detail to map the distribution and abundance of all plants in flower.

The two bumblebee species showed specialization towards pollen from contrasting species. *B. pascuorum* visited flowers of 23 different species to collect pollen, but many loads were dominated by species from the Fabaceae, especially *Trifolium pratense*. *B. terrestris/lucorum* loads contained pollen from 17 species, with fewer mixed loads, and *Borago officinalis* was the dominant pollen type. The majority of pollen loads of both bee species were dominated by species which had been sown in mixtures under the Countryside Stewardship Scheme. Although several unsown species were visited for pollen, they were only present in a few loads and at low proportions, thus pollen load diversity was not related to flowering plant diversity within squares. Calculation of a pollination probability index (PPI) showed that bumblebees tended to collect largest amounts of conspecific pollen from their preferred pollen forage plants (ie. *Trifolium pratense, Borago officinalis*). Maps of flower abundance and distribution showed that the study landscape contained many diverse patches of flowering plants, particularly of the Fabaceae. Knowledge of the locations of these relative to the pollen-sampled squares and composition of pollen loads provided evidence of spatial foraging patterns which could not have been gained by field observation alone.

5.1 Introduction

Bumblebees depend heavily on nectar and pollen resources from flowers in order to develop and maintain their colonies. Nectar provides a source of carbohydrates for energy, and pollen is the colony's only source of protein and is essential for the development of larvae. The foraging behaviour of bumblebees has been extensively studied, in relation to the energetics of flight (Heinrich, 1979), their choice of flower species (Free, 1970; Heinrich, 1976; Ranta and Lundberg, 1980; Fussell and Corbet, 1992a) and exploitation of patchy resources in the landscape (Osborne and Williams, 2001; Goulson, 2003). The majority of foraging studies on flower choice have, particularly in recent years, tended to focus on the flower visits of individuals observed on localised transect walks. These are likely to reflect the often wide range of plant species visited for nectar, but may not identify those species which are particularly important as pollen sources (Ranta and Lundberg, 1981; Carvell et al., 2006; Goulson and Darvill, 2003).

Analysis of the pollen loads carried by foraging bees can give us useful information about the flowers from which they are obtaining pollen, and about their relative importance based on the proportion of species in each sample (Brian, 1951; Westrich and Schmidt, 1986). The pollen loads collected by bees are good indicators of flower constancy, the tendency to restrict their visits to flowers of a single species (Waser, 1986; Ne'eman et al., 1999). They also provide a useful means of comparing the foraging specializations of different bee species, which are apparent at most foraging sites due to factors such as differences in tongue length and flower handling ability (Ranta and Lundberg, 1980).

The loss of nectar and pollen sources from the countryside is likely to have been a major factor causing the declines suffered by many bumblebee species in the UK (Williams, 1982; Corbet et al., 1991). A recent analysis of change in abundance of selected bumblebee forage plant species during the 20th Century found that more than 70% declined in both 10-km range and frequency of occupied 1-km sample squares (Carvell et al., 2001). Declining species included *Trifolium pratense* which is often cited as a major pollen source for the rarer bumblebees (Edwards, 2001). As bumblebees are key pollinators of many entomophilous crops and native plant species, their decline has serious implications for the yields and conservation of these (Corbet et al., 1991; Free, 1993). It is therefore critical that habitat restoration measures such as those now available in Europe within the agri-environment schemes (Defra, 2002) offer options to restore both nectar and pollen resources in order to maintain and enhance bumblebee populations in the agricultural landscape.

Arable field margins sown with wildflower seed mixtures have been shown to significantly enhance the local abundance and diversity of nectar and pollen-feeding insects, especially bumblebees (eg. Meek et al., 2002; Carvell et al., 2004). A preliminary analysis of pollen loads from bees foraging at such margins suggested that each *Bombus* species may have strong preferences for certain flower species in terms of the pollen types it collects (Carvell et al., 2006). Plant species in sown mixtures also constituted a high proportion of most pollen loads, suggesting that newly created habitats can have an important functional role in providing pollen as well as nectar for bumblebees on farmland. However, the relative value of these, compared to other newly created or existing semi-natural habitats on the farm, in terms of providing pollen resources, has not been tested. Furthermore, bumblebees are known to forage over wide areas which are likely to extend beyond field and even farm boundaries (Osborne et al., 1999; Goulson and Stout, 2001). With this in mind, foraging studies still rarely seek to map the abundance of every species in flower within the foraging range of the bumblebees under study. Sampling pollen loads from bumblebees foraging at known locations, together with knowledge of pollen availability in the local landscape, allows us to assess spatial foraging patterns in such a way that cannot be achieved by field observations alone.

The aims of this study are as follows:

1. To investigate the utilisation of pollen from different forage plant species by two bumblebee species with contrasting ecologies (*Bombus pascuorum* and *Bombus terrestris/lucorum*) across an enhanced arable landscape;
2. To record the distribution and abundance of flowering plants in the landscape as a means of mapping availability of pollen resources, and
3. To use pollen load analysis to assess spatial foraging patterns of *B. pascuorum* and *B. terrestris/lucorum* across the farmed landscape.

5.2 Methods

5.2.1 Study area

This study was conducted on Manor Farm and surrounding farmland, Eddlethorpe, near Malton in North Yorkshire (Lat. 54°05'N, Long. 0°49'W), over a total area of 1.96km2 (196ha). Manor Farm is a modern, intensively managed arable enterprise of 164ha where the 'Manor Farm Project' was established in 1998 to demonstrate that practical wildlife conservation and profitable farming can be effectively integrated. Many areas of the farm have been enhanced with newly planted field margins, blocks or corners either as part of the Countryside Stewardship Scheme or ongoing experiments. These provide a variety of flower-rich foraging habitats for bumblebees, together with existing semi-natural habitats at field and woodland edges, and a species rich meadow to the west of the farm.

5.2.2 Experimental design and sampling

The study area of 1.96km^2 was divided into 196 grid squares, each 100m x 100m (Figure 5.1). The sampling of bumblebee pollen loads and mapping of pollen availability were carried out during the week of 14th – 18th July 2003.

Mapping pollen availability

In order to create a detailed map of pollen availability within the study area, each grid square was surveyed to identify and score all plant species in flower. Flowers were scored according to their coverage of the entire square (the 'widespread' score) and then according to their local abundance in patches where they occurred in that square (the 'local' score, based on the DAFOR system) as follows:

Widespread flower scores		**Local flower scores**	
1	1-6 % coverage	1	Rare
2	7-12% coverage	2	Occasional
3	13-25% coverage	3	Frequent
4	26-50% coverage	4	Abundant
5	51-100% coverage	5	Dominant

Of the 196 grid squares, 154 contained plant species in flower at the time of the survey. These data on flower abundance within each square were spatially referenced onto the OS map and sampled grid using ArcView GIS 3.2 software, to give a distribution and abundance map for each species in flower within the study area.

Sampling pollen loads

Pollen loads were sampled from bumblebees within a central area of the larger grid, measuring 0.36 km^2. A systematic random sample of eight grid squares which contained adequate forage resources to attract pollen-collecting bumblebees (either *Bombus pascuorum* (Scopoli) or *B. terrestris/lucorum* (L.)) was selected (Figure 5.1). This left a minimum distance of 400m (or 300m in one case) from any 'pollen-sampled' square to the limit of the pollen availability map. *B. terrestris* and *B. lucorum* workers cannot be reliably distinguished in the field, so are treated as a species pair which is referred to as *B. terrestris* from here. Within each of the eight squares, the first 15 workers of either species encountered with full pollen baskets were caught. A single complete pollen load was removed from each bee using a clean cocktail stick, whilst the bee was restrained using a marking cage with soft plunger. The species of bee, plant species on which the bee was foraging when caught and grid square location were recorded on a label which was placed with the pollen load in a small sample tube, and this was cooled for preservation prior to analysis. For squares in which a full sample of 15 workers could not be seen, the observer continued searching for up to 60 minutes until no further pollen-collecting bumblebees were encountered, and then moved on to the next square. Pollen sampling was undertaken between 10.00hrs and 18.00hrs during dry, sunny weather (weather conditions were noted during sampling).

5.2.3 Analysis and interpretation of pollen samples

Each pollen sample was processed by embedding as a thin layer in glycerine jelly and mounting on a microslide (Westrich and Schmidt, 1986). Samples were analysed using a light microscope to identify a) the pollen genera and where possible the most likely plant species from which they were collected according to exine morphology and grain size, and b) an estimate of the percentage species composition of each pollen load based on a count of 200 grains per sample. Species present in trace amounts comprising less than 1% of a load were regarded as contamination and were excluded from the subsequent data. For each load, any pollen species occupying a proportion greater than 50% was defined as dominant. Pollen identifications were made with the aid of reference collections and a full list of plant species in flower at the study site during the period of pollen collection. Where the determination of pollen types to species level was not possible, they were identified to plant family level.

5.2.4 Data Analysis

The data were analysed in four stages; firstly, we examined the distribution and abundance of different flowering plant species across the study landscape. Secondly, the pollen load characteristics of *B. pascuorum* and *B. terrestris* were compared by looking at both the number of loads in which different plant species were present, and the mean proportion of each pollen species per load across all loads. Thirdly, differences between the sample squares in terms of the diversity of pollen loads collected by bumblebees, and the relationship between flowering plant diversity and pollen load diversity per square were examined. Finally spatial relationships between flowering plants and the pollen loads collected by bumblebees were examined. To assign a single flower abundance score for further analysis, the relationship between the mean 'local' and 'widespread' flower scores per square for each species was examined. Simple linear regression showed these two variables to be highly correlated ($F_{1,163}$= 1953.52, $P<0.001$, $r^2 = 0.92$), with perhaps a tendency for local scores to be higher where species had been sown in field margins or corners. The local scores were applied for subsequent analysis as we considered these to be a more biologically relevant unit of forage availability to a bumblebee. Several of the analyses involved assessments of species diversity which were represented by calculating Simpson's diversity index, taking into account both the number and relative proportion of every plant species in a sample, as explained below.

Simpson's diversity index

The species diversity of each pollen load was represented by calculating Simpson's diversity index (Begon et al., 1990):

$$\text{Simpson's index} = \frac{1}{\sum_{i=1}^{S} Pi^2}$$

where S is the total number of species in the pollen load, and P*i* is the proportion of the load occupied by the *i*th species. Larger values indicate higher diversity.

For each of the *Bombus* species studied, the mean proportion of each pollen type per load across all loads was calculated. In order to compare the breadth of the pollen diets of *B. pascuorum* and *B. terrestris*, Simpson's index was calculated from these means to represent the diversity of pollen types collected overall.

Simpson's index was also calculated for the diversity of plant species in flower in each sample square, with S equal to the total number of flowering species in the square, and P*i* as the proportion of the summed 'local' abundance scores occupied by the *i*th species.

The diversity (Simpson's index) of pollen loads collected by bumblebees from each forage plant species on which those bees were caught was also calculated. These values were compared using a one-way ANOVA. Tukey's honest significant difference test was also performed to assess differences between species.

Differences between sampled squares

Differences in the mean diversity of pollen loads of each *Bombus* species sampled from each of the eight grid squares were tested using a one-way ANOVA, with Tukey's honest significant difference test. The effect of flowering plant diversity on pollen load diversity was examined by simple linear regressions, with both diversity of all plant species per square and diversity of bumblebee pollen forage species per square as explanatory variables.

Differences between forage plant species

To examine the relationship between the forage plant species on which a bumblebee was caught and the composition of its pollen load, we calculated the Pollination Probability Index (PPI) as proposed by Ne'eman et al. (1999). This index for pollen load analysis aims to reflect flower constancy at the pollinator population level, and may also serve as an estimation for pollination probability. For each forage plant species on which bumblebees were caught during sampling, the mean proportion of conspecific pollen per load was calculated (PCP). The proportion of bees (out of the total number observed) carrying conspecific pollen was also calculated for each forage plant species (PBP). The pollination probability index was then calculated as follows: PPI = PCP x PBP. The PPI varies from 0 in cases where bees did not collect any conspecific pollen, to 1 in cases where all bees collected only conspecific pollen from that particular forage species.

Spatial relationships between bumblebee pollen loads and plant species in flower

The test whether the proportion of a pollen species collected was related to flower abundance of that plant species across the whole study area (1.96 km^2) simple linear regression was used. For further analyses, we attempted to relate the proportion of each pollen type in the 'average' bees' load with flower abundance within a radius of 0m (ie. the sample square), 100m, 200m, and so on, from where that load was sampled, using regressions. However, problems were encountered in the interpretation of these data due to the heterogeneity of the local landscape in terms of flowering plant distribution, and small sample sizes for several pollen types. Furthermore, the majority of pollen loads contained species flowering in the sample square, so the regression models were most significant at a radius of zero metres.

Further analyses therefore focused on the two preferred major pollen sources for *B. pascuorum* and *B. terrestris* in our study area: *Trifolium pratense* and *Borago officinalis* respectively. A Chi-squared test was used to test for significant differences between the proportion of bumblebees carrying each pollen species at different distances from the nearest known flowering patch of that plant species. Distances between sampled squares were calculated as centre-to-centre distance to the nearest 100m, using Pythagoras calculations for diagonals.

All statistical analyses were performed using Minitab 13 statistical software (Ryan et al., 2000).

5.3 Results

In total, 107 pollen samples were analysed, with a few missing data points due to a lack of pollen-collecting bumblebees at certain forage patches. Workers of *Bombus pascuorum* were more numerous than *Bombus terrestris* at the study site, probably as a result of the plant species composition of the relevant forage patches being more preferable to the former species. Hence, 79 pollen samples were collected from *B. pascuorum* and 28 from *B. terrestris.*

5.3.1 The 'pollen landscape' of Manor Farm

The distribution and relative abundance of key bumblebee forage plant species in flower within the study area during sampling are shown in Figure 5.2. Many species occur along boundary features of the landscape such as field margins, particularly where they have been sown on the farm (eg. *Borago officinalis* and *Lotus corniculatus*). Where they appear to flower in the centre of fields, species have often been sown either as part of a wild bird mix (eg. *Dipsacus fullonum*), a wildflower 'island' disconnected from the margin (eg. *Lathyrus. pratensis*) or as part of an organic grass ley (eg. *T. pratense* to the north-west of the sample grid). In total, 165 plant species were recorded in flower across the study area during the sampling week. A full species list of these, along with their mean flower abundance scores per square, is given in Appendix 5A.

5.3.2 Pollen load characteristics of B. pascuorum and B. terrestris

Pollen load analysis showed that *B. pascuorum* had visited flowers of at least 23 different species, assuming that pollen grains only classified to genus level or of 'unknown' identity were from single species (Table 5.1a). Seventy-six per cent of *B. pascuorum* pollen loads were mixed, but many of these mixed loads were dominated by one species. Species from the Fabaceae were present in 95% of all loads, notably *Trifolium pratense*, *Lotus corniculatus*, *Lathyrus pratensis* and *Trifolium repens/hybridum*, and where present, these occupied on average between 46% and 70% of the load. *T. pratense* was present in 14 loads at over 90%, and is referred to from here as the preferred pollen species for *B. pascuorum*. Other pollen sources were members of the Scrophulariaceae, Lamiaceae and Asteraceae, each present in 17% of loads (Table 5.1a), but only on average at between 5% and 30%. Overall, the Simpson's diversity index for the pollen diet of *B. pascuorum* in this study was 6.1.

Pollen loads from *B. terrestris* were from 17 species overall, with a Simpson's index of 4.5 indicating a narrower diet breadth than for *B. pascuorum*. Thirty-two per cent of the 28 loads were of mixed species. *Borago officinalis* was the dominant pollen source (Table 5.1b), present in 46% of loads occupying an average of 87% per load (referred to as the preferred pollen species of *B. terrestris*). Other notable pollen sources were from the Fabaceae (mainly *T. repens/hybridum*), Asteraceae and Dipsacaceae (*Dipsacus fullonum*) present in 36%, 18% and 11% of all loads respectively. Of the pollen species only present in single loads, *Ononis spinosa*, *Filipendula ulmaria* and *Rubus fruticosus* constituted over 50%, and *Mentha* spp. was the only pollen type in one particularly large load. Others, such as *T. pratense*, *Chamerion angustifolium* and *Arctium minus* were present at less than 20% of the load.

In terms of whether pollen sources had been sown on or around the farm in mixtures as part of the Countryside Stewardship Scheme or other habitat enhancement, the data show that both bumblebee species visited a similar number of unsown and sown species to collect pollen (Tables 5.1a and b). However, the unsown species tended to be present in only a few loads and at low proportions.

5.3.3 Differences between forage plant species

The forage plant species on which a bumblebee was caught during sampling did not necessarily relate to the composition of the pollen load carried by that bee (Figure 5.3). There were significant differences between the number of *B. pascuorum* workers caught on a plant species and the number of pollen loads in which that plant species was dominant at over 50% (Chi-squared value = 35.68, df = 6, $P<0.001$; excluding species with counts less than 5). This difference was not significant for *B. terrestris* (Chi-squared value = 2.53, df = 2, ns).

Pollen loads sampled from bees foraging at their preferred pollen species tended to contain a lower diversity of pollen types than less preferred species, such as *B. pascuorum* on *Trifolium pratense* and *B. terrestris* on *Borago officinalis* (Table 5.2). This tendency was just not significant for *B. pascuorum* (ANOVA on mean Simpson's index per load sampled from each forage plant species $F_{10,68} = 1.91$, $P = 0.059$) but was significant for *B. terrestris* ($F_{6,21} = 17.36$, $P<0.001$). Furthermore, the PCP, PBP and PPI values presented in Table 5.2 were generally highest for the preferred pollen species of each *Bombus* species.

5.3.4 Differences between sampled squares

There were no significant differences in the diversity of *B. pascuorum* pollen loads collected from the eight sample squares (ANOVA on Simpson's index; $F_{7,71} = 1.37$, ns). *B. terrestris* pollen loads were of significantly different diversity between the sampled squares (ANOVA $F_{5,22} = 5.34$, $P<0.01$), but this appeared to relate more to the presence of *Borago officinalis* from which single species loads were collected rather than to the overall diversity of forage plants per square. Linear regressions showed that there was no significant effect of flowering plant diversity per square, either of all plant species or only bumblebee pollen forage species, on the diversity of pollen loads of either bee species.

5.3.5 Spatial relationships between bumblebee pollen loads and plant species in flower

Overall, there was a significant positive relationship between the mean proportion of pollen species in *B. pascuorum* loads and their flower abundance across the study area ($F_{1,17} = 1953.52$, $P<0.01$, $r^2 = 0.30$). This relationship was not significant for *B. terrestris* pollen loads, suggesting that preferred pollen sources of these species were not generally abundant across the landscape.

For each plant species from which bees collected pollen, counts were made of the number of conspecific loads which had been sampled from bees foraging in squares where its flowers were absent (Table 5.1a and b). All squares within which *B. pascuorum* loads were sampled were within 200m of the nearest flowering *T. pratense* patch. However, our data show that of the 27 loads containing *T. pratense* pollen, six were sampled from bees at least 100m from the nearest patch and nine were sampled from bees at least 200m from the nearest patch of flowers (Figure 5.4). There were significant differences between the proportion of *B. pascuorum* carrying *T. pratense* pollen at 0m, 100m and 200m from the nearest known patch of flowers (Chi-squared value = 30.07, df = 2, $P<0.001$).

All squares in which pollen-collecting *B. terrestris* were sampled were within 200m of the nearest flowering *Borago officinalis* patch. The majority of loads sampled were from bees within the same square as a patch of *B. officinalis* flowers (ie. at 0m), and two loads were from bees in squares at

100m from the nearest patch. These differences were significant (Chi-squared value = 15.45, df = 2, P<0.001).

Further interesting patterns of forage utilisation are revealed by examining the distribution of flower species only present in a small number of pollen loads. For example, of the four loads of *B. pascuorum* containing *Lamium purpureum*, two were sampled at 400m from the nearest patch of flowers, and two at 500m from the nearest patch. This is the furthest pollen-foraging distance for which we have evidence for *B. pascuorum* from this study, although of course we cannot be certain that the *L. purpureum* pollen was collected from the flower patches mapped within the study area. For *B. terrestris*, a single load sampled from a worker foraging at *Dipsacus follonum* contained 100% pollen from *Mentha* spp., the nearest flowering patch of which was 600m away.

5.4 Discussion

The bumblebees in our study area appear to collect the majority of their pollen from a few plant species ('majors') and much smaller amounts from many others ('minors', as referred to by Heinrich, 1976). This tendency is well recognised in the literature, as is the tendency for the major pollen species to differ between bumblebee species (eg. Brian, 1951; Free, 1970; Heinrich, 1976). *Bombus pascuorum* pollen loads contained an overwhelming amount of pollen from the Fabaceae, particularly *Trifolium pratense*. Brian (1951) found that pollen from *T. pratense* was the major constituent of larval cells in *B. pascuorum* nests in Scotland, and other studies have revealed similar preferences for this and other Fabaceae by the longer-tongued *Bombus* species (Anasiewicz and Warakomska, 1977; Edwards, 2001; Carvell et al., 2006). *Bombus terrestris* (and *B. lucorum*), both short-tongued species, tended to collect pollen from *Borago officinalis*, and *Trifolium repens/hybridum* could also be considered a major pollen source as it constituted a high proportion of loads where present. Species from the Asteraceae, Dipsacaceae, Rosaceae and an unidentified pollen type were present as minors. These preferences to plant family are similar to those suggested in other studies, although the species may differ according to local abundance (Brian, 1951; Carvell et al., 2006).

Simpson's index for the diversity of pollen types collected was higher for *B. pascuorum* (6.1) than for *B. terrestris/lucorum* (4.5), suggesting that at this site *B. pascuorum* has a broader pollen diet. That the index has low sensitivity to sample size (Magurran, 1988) is important here as the greater abundance of *B. pascuorum* led to a larger sample of pollen loads for this species. However, it is interesting that these findings compare with those of Goulson and Darvill (2003) who examined the flower visits of several bumblebee species across a large area of diverse unimproved grassland and found a positive relationship between worker abundance and diet breadth. Even though our results come from a relatively small sample of loads from *B. terrestris*, these are likely to represent the behaviour of most individuals. According to Free (1970), bumblebees tend to exhibit day-to-day constancy as well as constancy during a foraging trip. Free (1970) also found that although pollen collecting behaviour of *B. lucorum* workers was fairly similar within one colony, workers of another colony made different use of the surrounding flora, suggesting that the colony may influence an individual's choice of forage. This should be noted when interpreting analysis of pollen loads from bees in the field, rather than from the nest.

The forage plant species on which a bumblebee was caught did not always relate to the composition of the pollen load carried by that bee, highlighting the value of the pollen analysis method in studying bumblebee forage preferences. For example, *B. pascuorum* was often seen foraging at *Dipsacus follonum* and *Prunella vulgaris*, yet these species barely featured in the pollen loads, so may be visited primarily for nectar. Considering this, it is not surprising that pollen loads sampled from the major pollen plants of both *Bombus* species tended to contain a lower diversity of species than those from their minors. Furthermore, the diversity of pollen loads sampled from any one square was not related to flowering plant diversity within that square, indicating that pollen collection at the local scale does not follow the general tendency for diversity of visited plants to be correlated with plant species richness, at least where preferred forage plants are present (eg. Carvell, 2002).

The pollination probability index (PPI) (Ne'eman et al., 1999) allowed us to examine these patterns more closely. The PPI was higher for bumblebees caught foraging at their preferred pollen forage plants, suggesting that in the landscape around Manor Farm they may be more efficient as pollinators of these plant species than other less favoured pollen source species. Care should be taken with the use and interpretation of this index, as bumblebees may not serve as legitimate pollinators of all plant species visited for pollen (Westrich, pers. comm.). However, this result could have implications for plant conservation. If preferred pollen source species such as *T. pratense* are sown as part of a mixture of either native wildflower species (as in the current UK Countryside Stewardship Arable option R3 with GX supplement) or agricultural legumes (as in Arable option WM2, the pollen and nectar mix; Defra, 2002) they may themselves have a high probability of pollination, but may in turn reduce the chances of other species in the mixture or in adjacent habitats being pollinated by bumblebees. Further research is required in this area. We would expect the average UK farm to support an assemblage of five or six *Bombus* species with a range of flower preferences, along with other insect pollinators, so if chosen carefully then most species in a sown mixture could have equal pollination probability.

The quality of our study landscape for foraging bumblebees, at least during the July sampling period, was evident from the mapped abundance and distribution of preferred forage plant species. The presence of a species-rich meadow and organic farm to the north-west, combined with the network of sown flower-rich habitats on Manor Farm itself make it atypical of the arable landscape of the UK (Meek et al., 2003). This landscape clearly favours *B. pascuorum* to a greater extent than *B. terrestris* in terms of available pollen sources (especially during mid to late summer), as all four Fabaceae species were sown in several mixtures. It is therefore no surprise that the proportion of pollen species in *B. pascuorum* loads was related to their flower abundance both across the study area, and also, for the majority of loads, in the square from which they were sampled. Most squares in which *T. pratense* flowers were absent contained one of the other favoured Fabaceae species, although several *B. pascuorum* pollen loads (15) in these squares contained *T. pratense* pollen, possibly collected from up to 200m away. Further evidence of non-local foraging activity in *B. pascuorum* came from the presence of *Lamium purpureum* pollen in loads sampled up to 500m from the nearest known patch of its flowers. Taken together, these results suggest that many *B. pascuorum* workers may have been undertaking short foraging flights with guaranteed rewards, thus increasing colony efficiency and fecundity. Some individuals, however, may have been travelling larger distances over several fields in order to profit from forage plants in the sown mixtures. Our 500m distance concurs with the minimum estimate of maximum foraging distance of 449m for *B. pascuorum* recently found using microsatellite markers by Knight et al. (2005).

For *B. terrestris*, the greater proportion of unsown species collected in pollen loads and lack of pollen-foraging workers in several sample squares, suggest that apart from *Borago officinalis* sown into a seed-bearing mixture for wild birds, enhancement on this particular farm was less favourable. *B. terrestris* and other short-tongued bumblebee species have been less affected than longer-tongued species by the loss of semi-natural habitats in agricultural landscapes (Williams, 1982; Edwards, 2001). This may be partly due to their wide foraging ranges, as evidenced here (up to 600m) and in other studies to be potentially greater than for *B. pascuorum* (Walther-Hellwig and Frankl, 2000; Knight et al., 2005). *B. terrestris* also emerge from hibernation early in spring, when mass-flowering crops such as oilseed rape can provide valuable forage resources (Westphal et al., 2003) which may boost colony development. However, suitable pollen resources must be made available to these species throughout their seasonal development, particularly in areas with few mass-flowering crops or existing semi-natural habitats.

In summary, this study has confirmed that bumblebees have clear preferences for certain pollen types which vary between species. The distribution and abundance of preferred pollen types across a landscape are likely to affect the observed pattern of flower visitation to these and other forage plant species. Our approach could be greatly enhanced with knowledge of the nest locations of the sampled bees, although these are difficult to find (Fussell and Corbet, 1992b). From the limited evidence available, bumblebee colonies do appear to attain larger size and forage closer to the nest in areas with a greater density and diversity of suitable flowers (Brian, 1954; Goulson et al., 2002). Thus in an arable landscape with spatially and temporally patchy resources, workers may regularly forage at plants separated by hundreds of meters in a single foraging trip, in order to fill their pollen baskets.

Further research is required to ascertain how pollen species differ in their quality or nutritional value for bees, which may be related to protein content (Cook et al., 2003). Utilisation and availability of pollen sources early in the season should also be considered, although at present no other study has mapped the local landscape in terms of its pollen resources to this level of detail. We stress the importance of considering the pollen requirements of different bumblebee species in the design of restoration measures to conserve populations and retain their important pollination service across agricultural landscapes.

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References

Anasiewicz, A., Warakomska, Z., 1977. Pollen food of the Bumble-bees (*Bombus Latr. Hymenoptera*) and their association with the plant species in the Lubin region. Ekologia Polska 25, 309-322.
Begon, M., Harper, J.L., and Townsend, C.R., 1990. Ecology; individuals, populations and communities. Second Edition. Blackwell Scientific Publications, UK.
Brian, A.D., 1951. The pollen collected by bumble-bees. Journal of Animal Ecology 20, 191 – 194.
Brian, A.D., 1954. The foraging of bumblebees. Bee World 35: 61-67, 81-91.
Carvell, C., 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. Biological Conservation 103, 33-49.
Carvell, C., Pywell, R.F., Smart, S. & Roy, D., 2001. Restoration and management of bumblebee habitat on arable farmland: literature review. DEFRA Contract report BD1617. Centre for Ecology and Hydrology, Monks Wood, Cambridgeshire, UK.
Carvell, C., Meek., W.R., Pywell., R.F., Nowakowski, M., 2004. The response of foraging bumblebees to successional change in newly created arable field margins. Biological Conservation 118, 327-339.
Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F., Nowakowski, M., 2006. Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. Apidologie 37, 326-340.

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

Defra, 2002. The Countryside Stewardship Scheme: New Arable Options for 2002. Department for Environment, Food and Rural Affairs, London.

Edwards, M., 2001. UK BAP Bumblebee Working Group Report, 2001. Unpublished report for the UK BAP Bumblebee Working Group, Midhurst, UK.

Free, J.B., 1970. The flower constancy of bumblebees. Journal of Animal Ecology 39, 395-402.

Free, J.B., 1993. Insect Pollination of Crops, 2nd edition. Academic Press, London, UK.

Fussell, M., Corbet, S.A., 1992a. Flower usage by bumblebees: a basis for forage plant management. Journal of Applied Ecology 29, 451-465.

Fussell, M., Corbet, S.A., 1992b. The nesting places of some British bumble bees. Journal of Apicultural Research. 31, 32-41.

Goulson, D., 2003. Bumblebees: their behaviour and ecology. Oxford University Press.

Goulson, D., Stout, J.C., 2001. Homing ability of the bumblebee *Bombus terrestris*. Apidologie 32, 105-112.

Goulson, D., Hughes, W.O.H., Derwent, L.C., Stout, J.C., 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. Oecologia 130: 267-273.

Goulson, D., Darvill, B., 2003. Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? Apidologie 34, 1-9.

Heinrich, B., 1976. The foraging specializations of individual bumblebees. Ecological Monographs 46, 105-128.

Heinrich, B., 1979. *Bumblebee Economics*. Harvard University Press, Cambridge, MA.

Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, A., Goulson, D., 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology*, **14**, 1811-1820.

Magurran, A.E., 1988. Ecological diversity and its management. Princeton University Press, Princeton.

Meek, W.R., Carvell, C., Pywell, R.F., Nowakowski, M., Sparks, T.H., Loxton, R.G., Skidmore, P., Bell, D., Croxton, P.J., Warman, E.A., Löbel, S., & Walker, K.J., 2002. The Buzz Project: technical report 2002. Report to the Farmed Environment Company Ltd. (www.f-e-c.co.uk). CEH, Monks Wood, UK.

Meek, B., Pywell, R., Sparks, T., Nowakowski, M., Loxton, D., Carvell, C., Hammond, M., Croxton, P., Skidmore, P., Shore, R., Turner, D., Bell, D., Singer, E., Gowing, R., Farrant, C., Iliffe, L., Pickett, H., Shadrack, A., Warman, E., Löbel, S., Walker, K., Westrich, P., 2003. Ecological assessments and monitoring of Manor Farm, N Yorks: Final Technical report 1999 – 2002. Unpublished report to the Farmed Environment Company. CEH Monks Wood, UK.

Ne'eman, G., Dafni, A., Potts, S.G., 1999. A new pollination probability index (PPI) for pollen load analysis as a measure for pollination effectiveness of bees. Journal of Apicultural Research 38, 19-23.

Osborne, J.L., Williams, I.H., 2001. Site constancy of bumble bees in an experimentally patchy habitat. Agriculture, Ecosystems and Environment 83, 129 – 141.

Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. Journal of Applied Ecology 36, 519-533.

Ranta, E., Lundberg, H., 1980. Resource partitioning in bumblebees: the significance of differences in proboscis length. OIKOS 35, 298-302.

Ranta, E., Lundberg, H., 1981. Food niche analyses of bumblebees: a comparison of three data collecting methods. OIKOS 36, 12-16.

Ryan, B.F., Joiner, B.L., Ryan, T., 2000. MINITAB Handbook, Fourth Edition, Brooks Cole, Florence KY.

Walther-Hellwig, K., Frankl, R., 2000. Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae) in an agricultural landscape. Journal of Applied Entomology 124, 299-306.

Waser, N. M., 1986. Flower constancy: definition, cause and measurement. American Naturalist 127, 593-603.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. Ecology Letters 6, 961-965.

Westrich, P., Schmidt, K., 1986. Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hynemoptera, Apoidea). Linzer Biol. Beitr. 18, 341-360.

Williams, P.H., 1982. The distribution and decline of British bumblebees (*Bombus* Latr.) J. Apic. Res. 21 (4), 236-245.

Table 5.1a Composition of pollen loads collected by *Bombus pascuorum* (n=79), ranked in descending order by the mean percentage of each pollen type per load.

(s = species sown on the farm; u = species not sown and naturally occurring; b = both sown and naturally occurring; note that *Trifolium repens* and *T. hybridum* pollen types could not be distinguised during analysis)

Pollen species or type	**Family**	**Sown on Manor Farm?**	**Mean % pollen per load**	**±SE mean**	**Number of loads containing pollen species**	**Number of loads from squares where pollen absent**
Trifolium pratense	Fabaceae	s	22.18	4.28	27	15
Lotus corniculatus	Fabaceae	b	21.58	4.23	27	0
Lathyrus pratensis	Fabaceae	b	18.78	3.48	32	2
Trifolium repens/ hybridum	Fabaceae	b	16.65	3.58	25	4
Rhinanthus minor	Scrophulariaceae	s	4.44	1.59	13	0
Unknown	Unknown	u	2.97	1.71	3	-
Vicia cracca	Fabaceae	b	2.59	1.78	3	0
Ononis spinosa	Fabaceae	s	1.77	1.30	2	1
Stachys officinalis	Lamiaceae	u	1.65	1.28	9	1
Centaurea nigra	Asteraceae	s	1.50	0.71	10	0
Lamium purpureum	Lamiaceae	u	1.46	1.15	4	4
Dipsacus follonum	Dipsacaceae	s	0.70	0.52	3	1
Chamaenerion angustifolium	Onagraceae	u	0.63	0.63	1	0
Rubus fruticosus	Rosaceae	u	0.63	0.45	2	2
Rosaceae type	Rosaceae	u	0.51	0.51	1	-
Fabaceae type	Fabaceae	s	0.51	0.51	1	-
Centaurea cyanus	Asteraceae	s	0.25	0.25	1	1
Geranium spp.	Geraniaceae	u	0.25	0.25	1	1
Hypericum spp.	Hypericaceae	u	0.25	0.25	1	1
Lathyrus pratensis/ Vicia cracca	Fabaceae	b	0.25	0.25	1	1
Prunella vulgaris	Lamiaceae	s	0.25	0.25	1	0
Cirsium vulgare	Asteraceae	u	0.17	0.13	3	1
Impatiens glandulifera	Balsaminaceae	u	0.01	0.01	1	1

Table 5.1b Composition of pollen loads collected by *Bombus terrestris* (n=28), ranked in descending order by the mean percentage of each pollen type per load.

(s = species sown on the farm; u = species not sown and naturally occurring; b = both sown and naturally occurring)

Pollen species or type	**Family**	**Sown on Manor Farm?**	**Mean % pollen per load**	**±SE mean**	**Number of loads containing pollen species**	**Number of loads from squares where pollen absent**
Borago officinalis	Boraginaceae	s	40.57	9.28	13	2
Trifolium repens/ hybridum	Fabaceae	b	17.50	7.23	5	1
Unknown	Unknown	u	9.32	4.98	5	-
Dipsacus follonum	Dipsacaceae	s	8.93	5.18	3	0
Centaurea cyanus	Asteraceae	s	6.43	4.49	2	2
Mentha spp.	Lamiaceae	u	3.57	3.57	1	1
Lotus corniculatus	Fabaceae	b	3.32	2.41	2	0
Ononis spinosa	Fabaceae	s	2.86	2.86	1	0
Cirsium vulgare	Asteraceae	u	1.96	1.79	2	0
Filipendula ulmaria	Rosaceae	u	1.79	1.79	1	0
Rubus fruticosus	Rosaceae	u	1.61	1.61	1	0
Melilotus altissima	Fabaceae	u	0.71	0.71	1	1
Trifolium pratense	Fabaceae	s	0.64	0.64	1	0
Impatiens glandulifera	Balsaminaceae	u	0.36	0.36	1	1
Chamaenerion angustifolium	Onagraceae	u	0.18	0.18	1	0
Ericaceae type	Ericaceae	u	0.18	0.18	1	1
Arctium minus	Asteraceae	u	0.07	0.07	1	0

Table 5.2 Simpson's diversity index and calculation of the Pollination Probability Index for each forage plant species on which bumblebees were caught.

PCP = the mean proportion of conspecific pollen in each pollen load

PBP = the proportion of bumblebees (out of N caught) carrying conspecific pollen

PPI = the calculated pollination probability index (see section 2.4.2)

B. pascuorum

Forage plant species	**N caught**	**Simpsons mean**	**± SE**	**PCP**	**PBP**	**PPI**
Centaurea nigra	2	2.11	0.89	0.17	0.50	0.083
Chamaenerion angustifolium	1	2.00	*	0.50	1.00	0.500
Dipsacus fullonum	12	1.32	0.11	0.04	0.17	0.006
Lathyrus pratensis	17	1.81	0.27	0.41	0.82	0.335
Lotus corniculatus	14	1.25	0.09	0.62	0.64	0.396
Prunella vulgaris	9	2.33	0.38	0.02	0.11	0.002
Rhinanthus minor	2	1.94	0.84	0.23	1.00	0.225
Stachys officinalis	7	1.38	0.27	0.17	0.86	0.146
Trifolium pratense	9	1.19	0.11	0.76	0.89	0.680
Trifolium repens	3	1.53	0.43	0.80	1.00	0.800
Vicia cracca	3	1.03	0.03	0.68	1.00	0.683

B. terrestris

Forage plant species	**N caught**	**Simpsons mean**	**± SE**	**PCP**	**PBP**	**PPI**
Arctium minus	1	1.04 a	*	0.02	1.00	0.020
Borago officinalis	12	1.01 a	0.01	0.92	0.92	0.840
Chamaenerion angustifolium	1	2.20 b	*	0.05	1.00	0.050
Dipsacus fullonum	7	1.16 a	0.14	0.36	0.43	0.153
Lotus corniculatus	2	2.69 b	0.31	0.47	1.00	0.465
Ononis spinosa	1	1.49 a	*	0.80	1.00	0.800
Trifolium repens	4	1.12 a	0.12	0.75	0.75	0.563

ANOVA on mean Simpsons index per load from each forage plant species; $F_{10,68} = 1.91$, $P = 0.059$ for *B. pascuorum* and $F_{6,21} = 17.36$, $P<0.001$ for *B. terrestris*. Means with different letters are significantly different (Tukey's test $P<0.05$).

Figure 5.1 Map of Manor Farm and the surrounding landscape showing the study area within sampled grid squares (n=196) and squares selected for pollen load sampling (n=8).
OS Grid Reference for the south-western corner of the study area is SE763649.

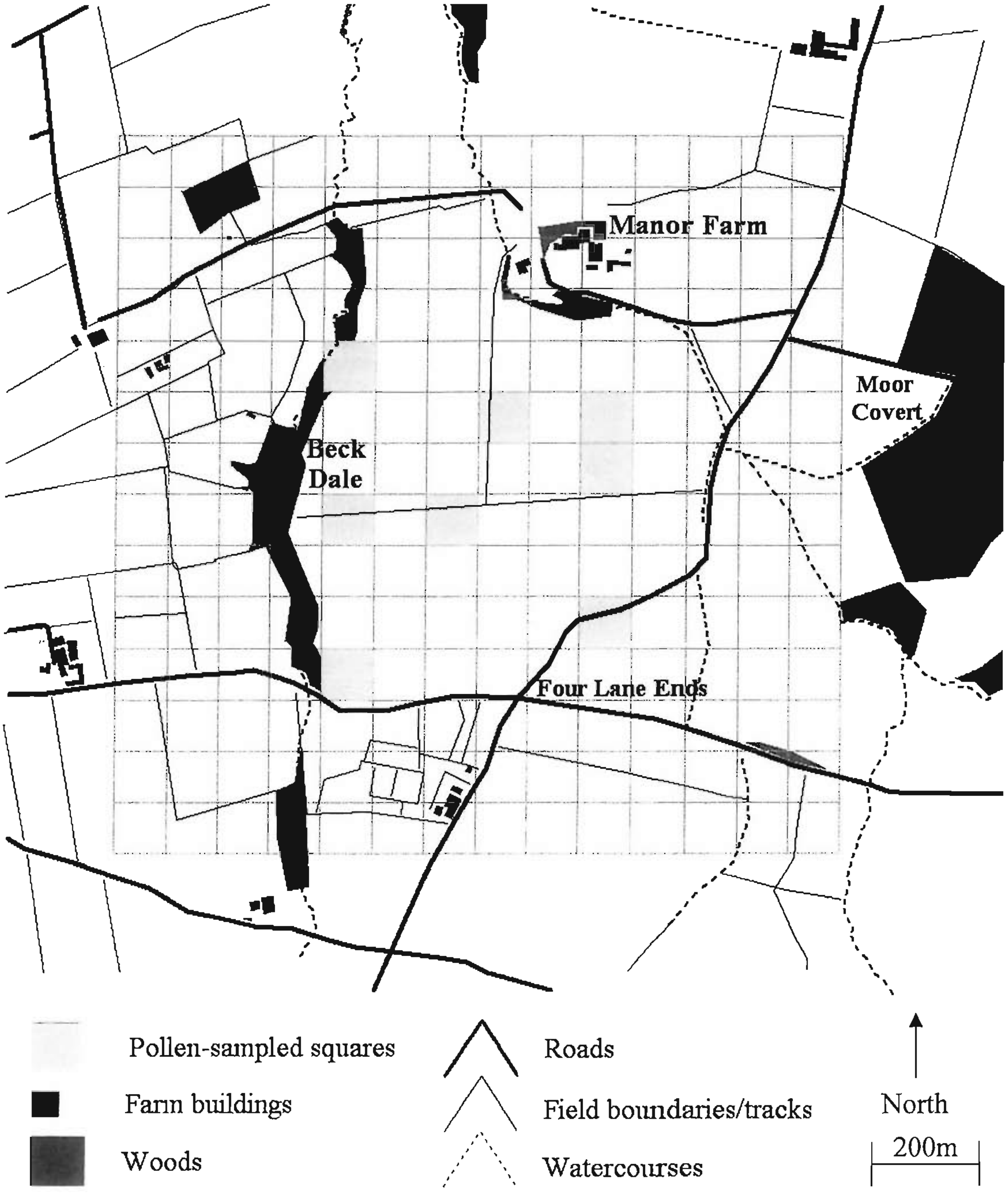
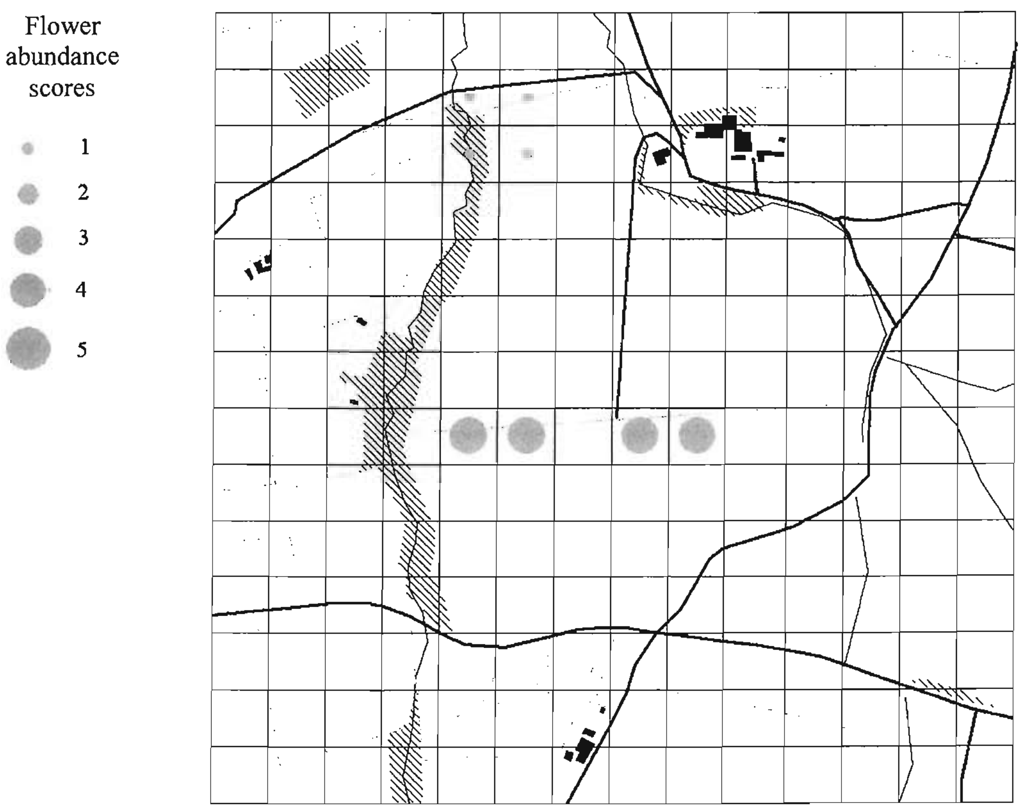
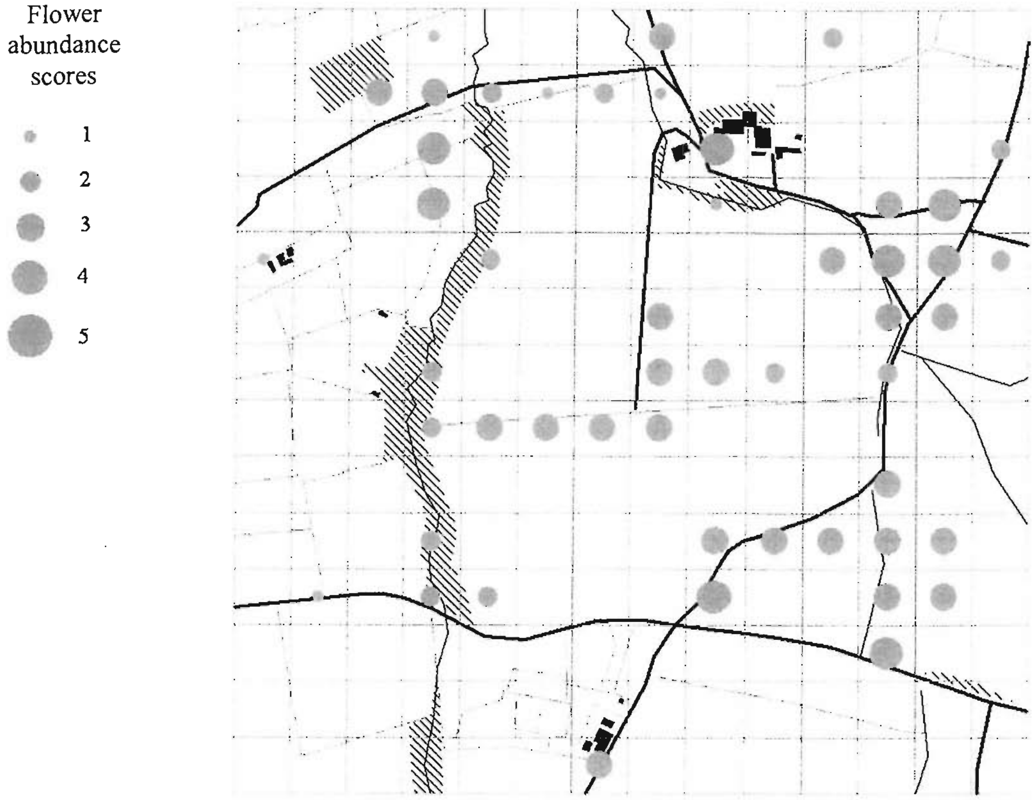


Figure 5.2 Maps showing the distribution and relative abundance of plant species in flower within the study area between 14th – 18th July 2003. Scores relating to the 'local' abundance of flowers in patches where they occurred are shown for key bumblebee pollen sources; a) *Borago officinalis*, b) *Centaurea nigra*, c) *Dipsacus follonum*, d) *Lathyrus pratensis*, e) *Lotus corniculatus*, f) *Rubus fruticosus*, g) *Trifolium repens/hybridum*, h) *Trifolium pratense*. (s = species sown on the farm; u = species not sown and naturally occurring; b = both sown and naturally occurring; see methods section 2.2.1 for explanation of flower scores; key to map symbols and scale as in Figure 1)

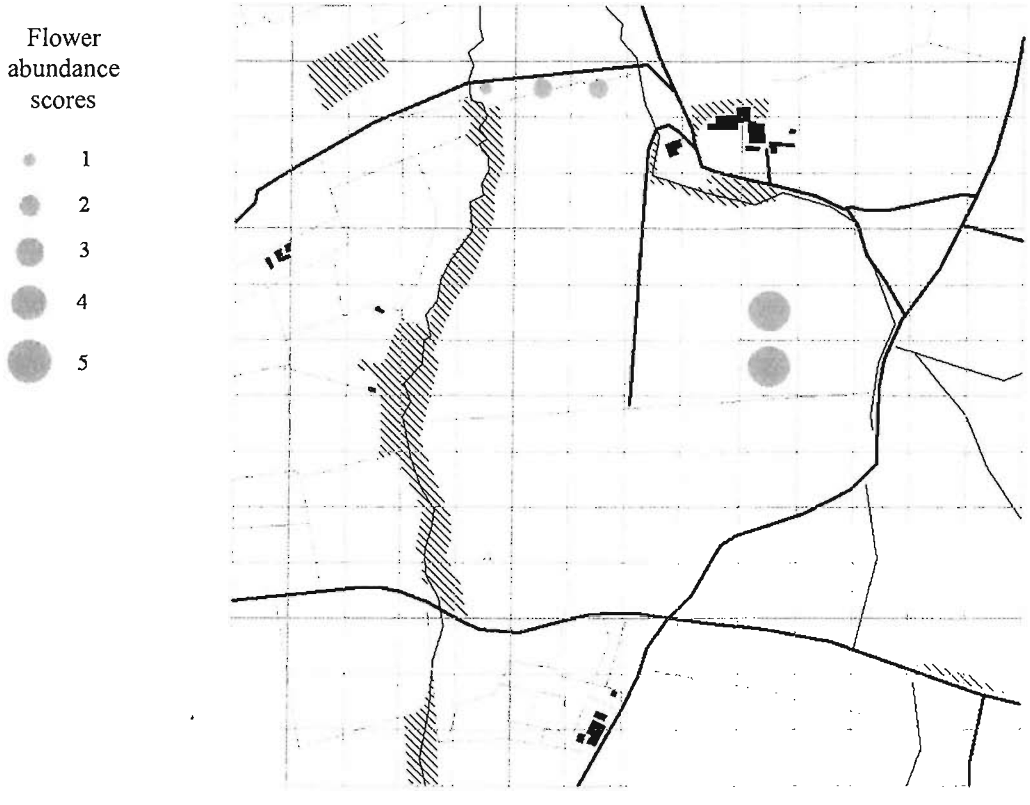
a) *Borago officinalis* (s)



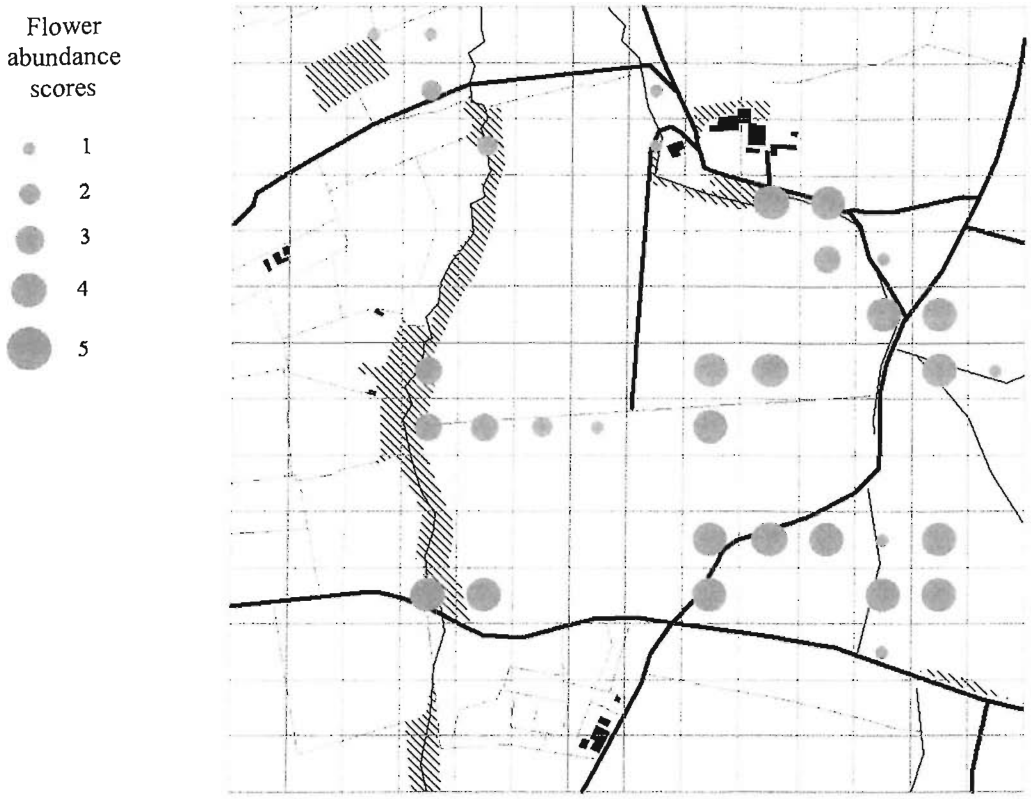
b) ***Centaurea nigra*** **(s)**



c) ***Dipsacus follonum*** **(s)**



d) *Lathyrus pratensis* (b)



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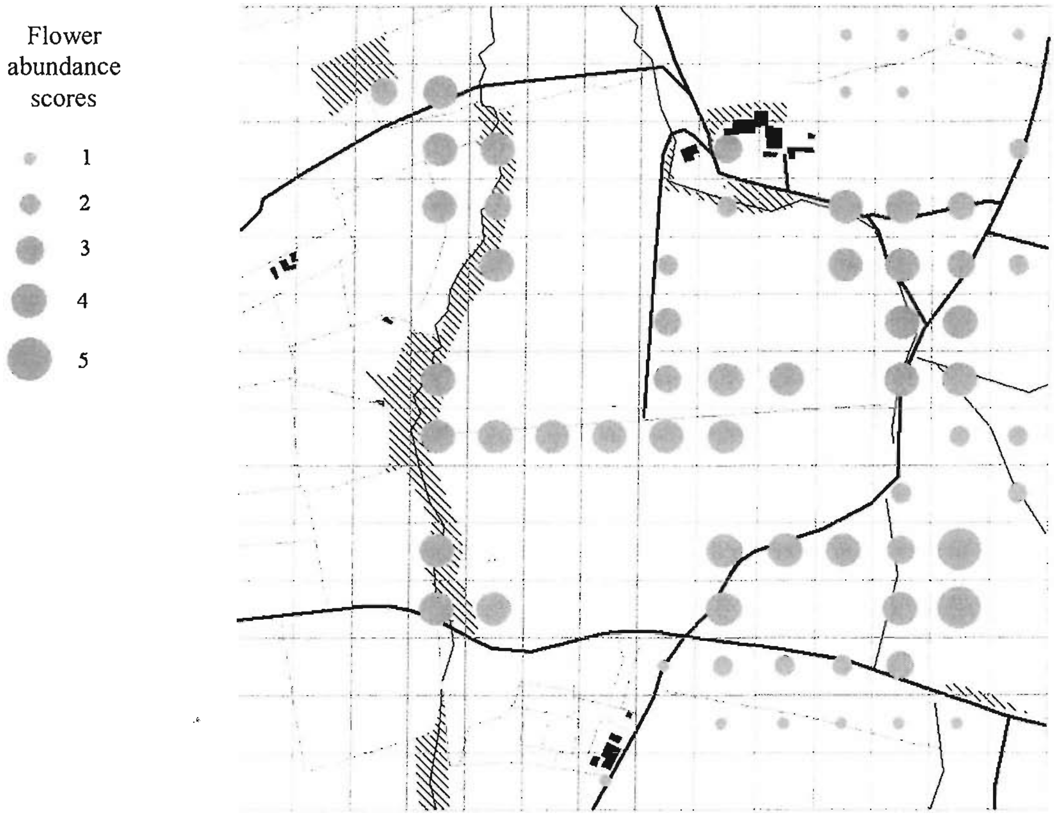
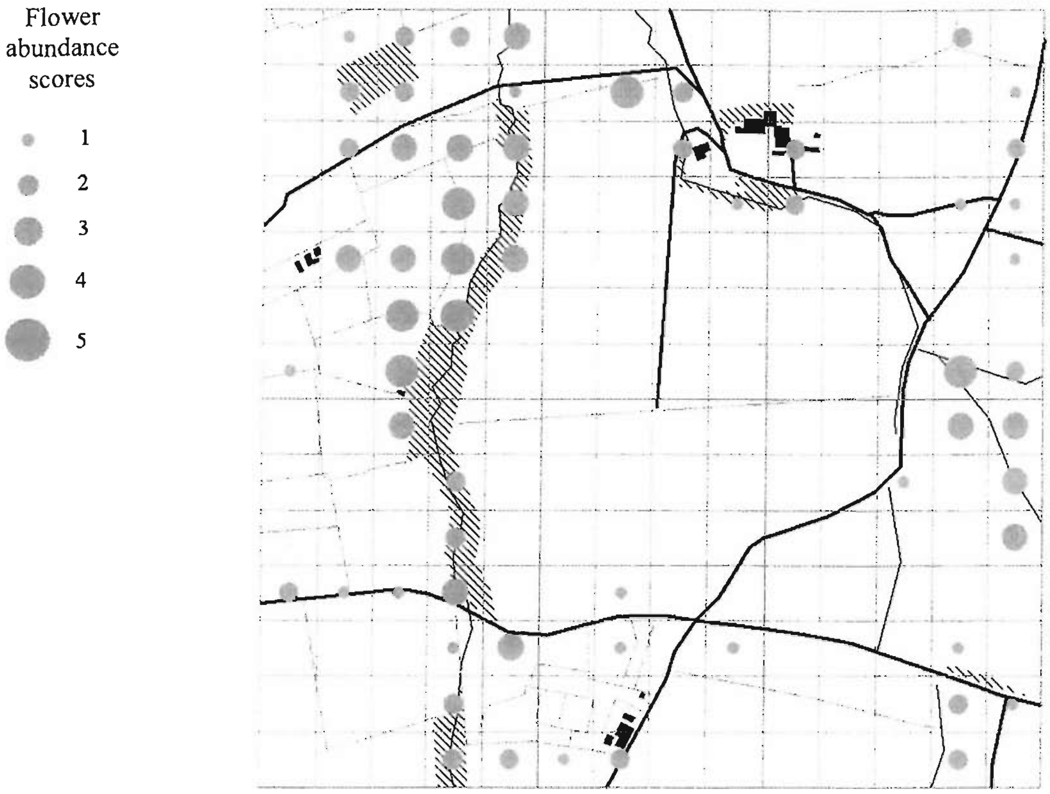
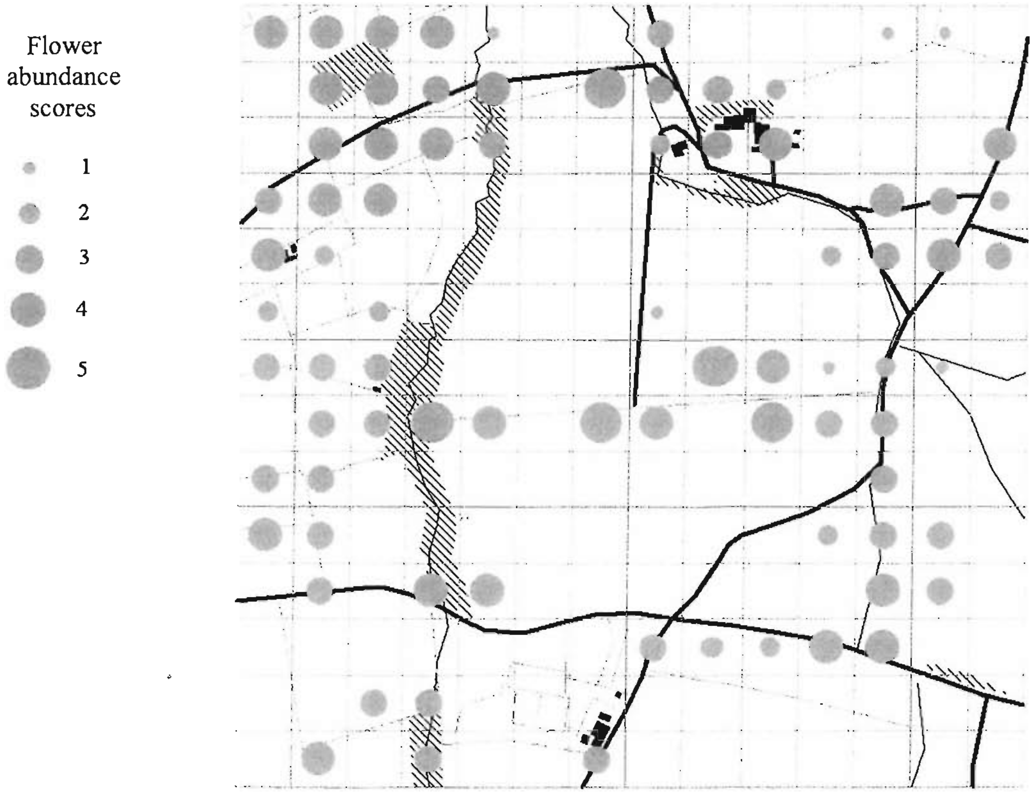
e) *Lotus corniculatus* (b)



f) *Rubus fruticosus* (u)



g) *Trifolium repens/hybridum* (b : species not distinguished in pollen analysis so combined here)



h) ***Trifolium pratense*** **(s)**

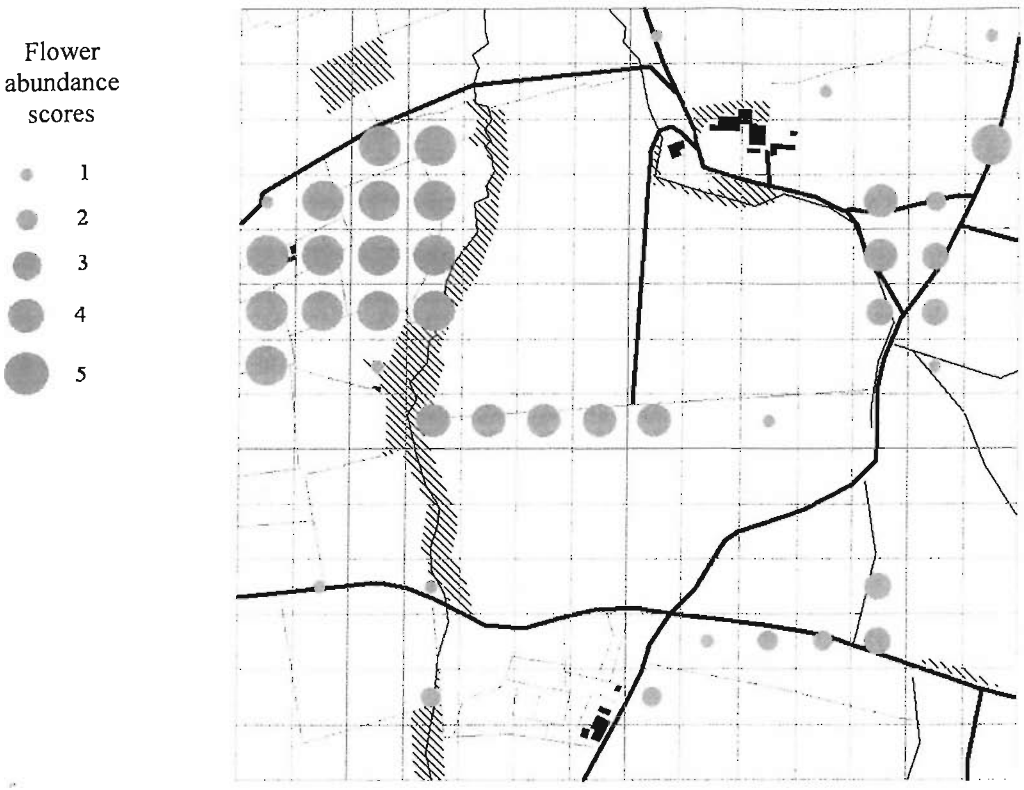
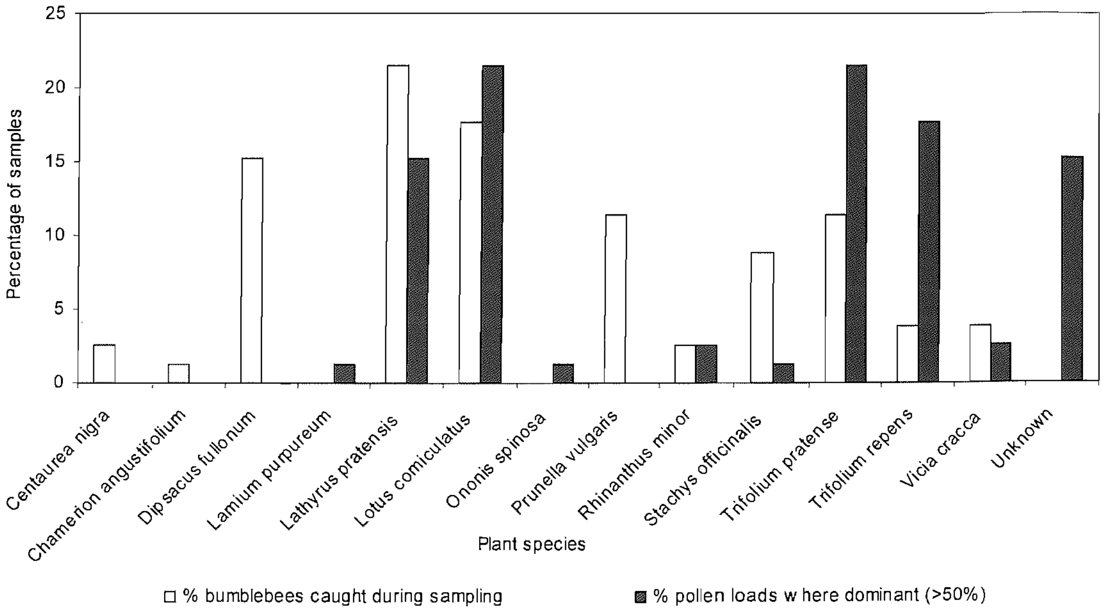


Figure 5.3 Comparison of forage plant species as observed during sampling with those dominating pollen loads for a) *B. pascuorum* and b) *B. terrestris/lucorum*.
(the unknown category refers to pollen loads which contained no dominant species (>50%) or in one case which was dominated by an unknown pollen species)

a) B. pascuorum



b) B. terrestris/lucorum

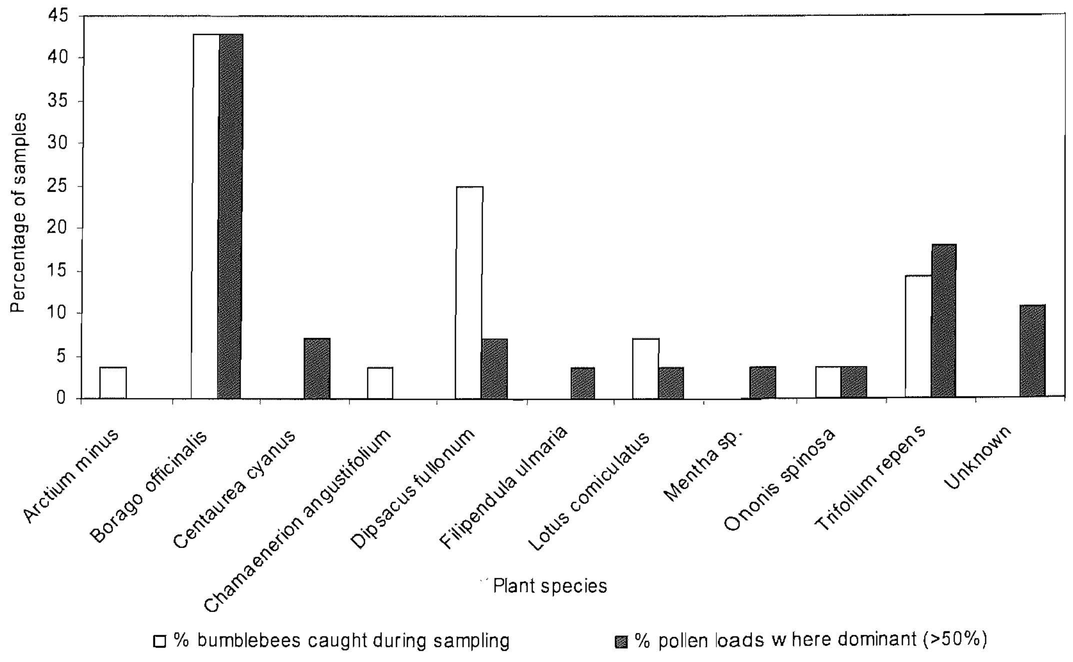
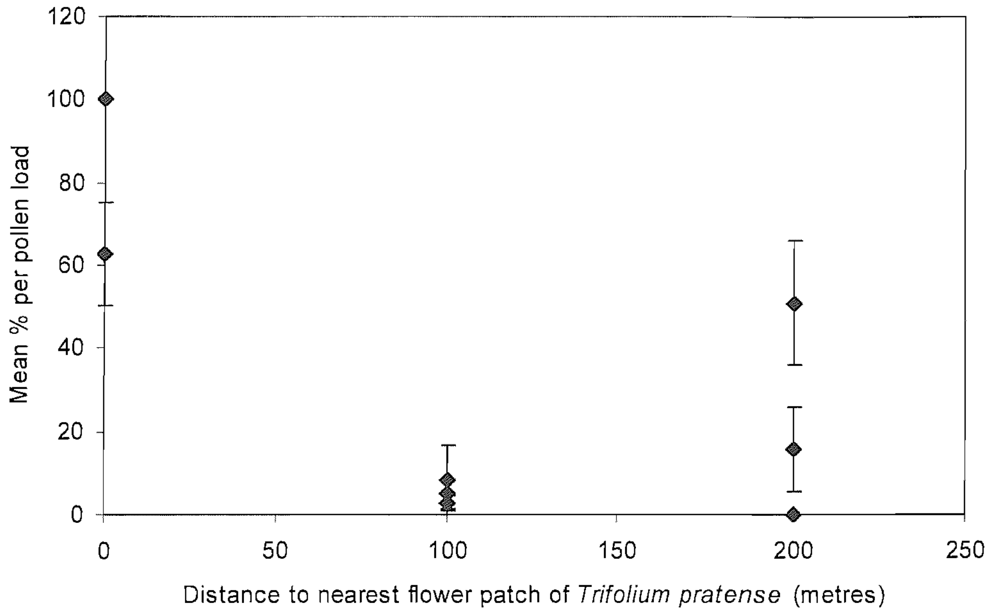


Figure 5.4 Relationship between the percentage of *Trifolium pratense* pollen in pollen loads of *Bombus pascuorum* and distance to the nearest patch of flowering *T. pratense* (each point represents the mean % per pollen load sampled from one grid square, ± stand errors).



Appendix 5A. Species list of plant species in flower within the study area, 14th – 18th July 2003. Values represent mean 'local' and 'widespread' scores per square, with standard deviations to indicate variability across the site; garden varieties and crops are shown with common names.

	Local Score		**Widespread Score**	
Flowering plant species	Mean	St Dev	Mean	St Dev
Achillea millefolium	0.58	1.12	0.34	0.78
Aegopodium podagraria	0.01	0.14	0.01	0.07
Aethusa cynapium	0.01	0.10	0.01	0.10
Agrostemma githago	0.01	0.14	0.01	0.07
Alchemilla mollis	0.01	0.07	0.01	0.07
Alliaria petiolata	0.01	0.07	0.01	0.07
Anagallis arvensis	0.02	0.21	0.01	0.07
Anchusa arvensis	0.03	0.21	0.04	0.33
Anthriscus sylvestris	0.01	0.07	0.01	0.07
Arctium minus	0.13	0.51	0.08	0.27
Ballota nigra	0.01	0.07	0.01	0.07
Barbarea intermedia	0.01	0.14	0.01	0.07
Barbarea vulgaris	0.01	0.07	0.01	0.07
Bellis perennis	0.02	0.23	0.02	0.16
Borago officinalis	0.13	0.73	0.05	0.22
Brassica napus	0.03	0.17	0.04	0.26
Buddleija davidi	0.01	0.07	0.01	0.07
Calystegia sepium	0.02	0.12	0.02	0.12
Calystegia silvatica	0.19	0.73	0.07	0.25
Campanula rotundifolia	0.04	0.28	0.06	0.46
Capsella bursa-pastoris	0.33	1.02	0.17	0.61
Carduus nutans	0.04	0.36	0.03	0.30
Centaurea cyanus	0.27	0.96	0.13	0.50
Centaurea nigra	0.68	1.25	0.45	1.01
Chaerophyllum temulentum	0.01	0.14	0.01	0.07
Chamerion angustifolium	0.79	1.48	0.41	0.89
Chenopodium album	0.10	0.48	0.04	0.20
Chrysanthemum segetum	0.02	0.16	0.01	0.10
Circaea lutetiana	0.08	0.47	0.07	0.38
Cirsium arvense	1.43	1.63	0.81	1.17
Cirsium palustre	0.17	0.67	0.14	0.55
Cirsium vulgare	0.84	1.27	0.72	1.25
Conium maculatum	0.04	0.28	0.03	0.19
Convolvulus arvensis	0.01	0.14	0.01	0.07
Conyza canadensis	0.04	0.30	0.05	0.34
Crepis capillaris	0.17	0.65	0.15	0.61
Dactylorhiza fuchsii	0.06	0.32	0.10	0.56
Daucus carota	0.34	1.02	0.21	0.75
Dipsacus fullonum	0.08	0.54	0.04	0.28
Echinops sphaerocephalus	0.01	0.07	0.01	0.07
Echium plantagineum	0.01	0.07	0.01	0.07

Cont.	**Local Score**		**Widespread Score**	
Flowering plant species	Mean	St Dev	Mean	St Dev
Epilobium ciliatum	0.42	1.11	0.45	1.26
Epilobium hirsutum	0.52	1.13	0.28	0.64
Epilobium obscurum	0.15	0.59	0.16	0.62
Epilobium palustre	0.01	0.14	0.01	0.07
Epilobium parviflorum	0.18	0.54	0.39	1.20
Epilobium tetragonum	0.01	0.07	0.01	0.07
Erodium cicutarium	0.01	0.07	0.02	0.21
Eupatorium cannabinum	0.01	0.14	0.01	0.07
Euphorbia exigua	0.01	0.07	0.01	0.07
Fallopia convolvulus	0.06	0.39	0.03	0.22
Filipendula ulmaria	0.44	1.17	0.23	0.73
Fumaria officinalis	0.02	0.21	0.01	0.07
Galeopsis bifida	0.02	0.14	0.05	0.37
Galeopsis tetrahit	0.06	0.35	0.03	0.17
Galium aparine	0.20	0.78	0.08	0.34
Galium uliginosum	0.03	0.24	0.06	0.46
Galium verum	0.24	0.83	0.15	0.58
Geranium dissectum	0.04	0.28	0.02	0.14
Geranium molle	0.01	0.14	0.01	0.14
Geranium pratense	0.02	0.12	0.02	0.12
Geranium pusillum	0.03	0.30	0.03	0.30
Geranium pyrenaicum	0.02	0.16	0.01	0.10
Geranium robertianum	0.11	0.50	0.09	0.40
Geranium sp.	0.22	0.71	0.17	0.57
Geum urbanum	0.03	0.16	0.03	0.16
Heracleum sphondylium	0.17	0.53	0.17	0.61
Hieracium sp.	0.01	0.07	0.01	0.07
Hypericum pulchrum	0.02	0.20	0.03	0.32
Hypericum tetrapterum	0.02	0.12	0.02	0.12
Hypericum sp.	0.04	0.23	0.05	0.34
Hypochaeris radicata	0.09	0.42	0.16	0.75
Impatiens glandulifera	0.03	0.26	0.01	0.10
Knautia arvensis	0.06	0.23	0.07	0.36
Lamium album	0.04	0.21	0.03	0.17
Lamium hybridum	0.01	0.14	0.02	0.21
Lamium purpureum	0.05	0.26	0.05	0.23
Lapsana communis	0.15	0.52	0.09	0.28
Lathyrus pratensis	0.48	1.20	0.27	0.75
Leontodon hispidus	0.02	0.12	0.03	0.30
Leucanthemum vulgare	0.55	1.09	0.39	0.95
Ligustrum ovalifolium	0.02	0.29	0.01	0.07
Lonicera periclymenum	0.07	0.35	0.04	0.20
Lotus corniculatus	0.98	1.57	0.55	1.04
Lotus uliginosus	0.25	0.92	0.15	0.65

Cont.	**Local Score**		**Widespread Score**	
Flowering plant species	Mean	St Dev	Mean	St Dev
Lychnis flos-cuculi	0.01	0.07	0.01	0.07
Lysimachia punctata	0.01	0.10	0.01	0.10
Malva moschata	0.10	0.36	0.17	0.69
Malva sylvestris	0.01	0.14	0.01	0.07
Malva sp. Garden	0.01	0.07	0.01	0.07
Matricaria discoidea	0.58	1.27	0.28	0.69
Matricaria recutita	0.82	1.43	0.36	0.67
Medicago lupulina	0.02	0.21	0.01	0.07
Mentha arvensis	0.02	0.17	0.02	0.12
Mentha aquatica	0.01	0.07	0.02	0.21
Mentha sp.	0.03	0.19	0.03	0.25
Myosotis arvensis	0.72	1.32	0.40	0.84
Odontites verna	0.01	0.07	0.01	0.07
Onobrychis viciifolia	0.02	0.12	0.02	0.12
Ononis spinosa	0.02	0.12	0.02	0.12
Papaver argemone	0.01	0.07	0.01	0.07
Papaver rhoeas	0.63	1.05	0.45	0.82
Persicaria lapathifolia	0.13	0.54	0.08	0.34
Persicaria maculosa	0.54	1.17	0.32	0.76
Pilosella officinalis	0.01	0.07	0.01	0.07
Plantago lanceolata	0.25	0.72	0.24	0.81
Polygonum aviculare	0.44	1.14	0.22	0.67
Potentilla erecta	0.13	0.70	0.11	0.59
Potentilla fruticosa	0.01	0.07	0.01	0.07
Potentilla reptans	0.04	0.26	0.03	0.16
Prunella vulgaris	0.57	1.23	0.32	0.77
Pulicaria dysenterica	0.02	0.23	0.01	0.10
Ranunculus acris	0.22	0.62	0.25	0.87
Ranunculus flammula	0.01	0.07	0.01	0.07
Ranunculus repens	0.57	1.09	0.47	1.05
Raphanus raphanistrum	0.11	0.47	0.07	0.31
Rhinanthus minor	0.37	1.02	0.28	0.91
Rorippa nasturtium-aquaticum	0.03	0.29	0.01	0.10
*Rosa sp. (*Garden)	0.01	0.07	0.01	0.07
Rubus fruticosus	0.68	1.15	0.42	0.75
Rumex obtusifolius	0.02	0.23	0.01	0.10
Sambucus nigra	0.06	0.24	0.06	0.24
Sanguisorba officinalis	0.01	0.07	0.02	0.21
Scrophularia auriculata	0.16	0.61	0.10	0.39
Senecio jacobaea	0.48	0.89	0.53	1.19
Senecio sylvaticus	0.04	0.30	0.04	0.33
Senecio vulgaris	0.54	1.27	0.47	1.26

Cont.	**Local Score**		**Widespread Score**	
Flowering plant species	Mean	St Dev	Mean	St Dev
Silene alba	0.01	0.07	0.01	0.07
Silene latifolia	0.06	0.24	0.06	0.24
Silene dioica	0.24	0.66	0.21	0.62
Silene noctiflora	0.02	0.21	0.01	0.07
Sinapis arvensis	0.01	0.07	0.01	0.07
Sisymbrium officinalis	0.05	0.27	0.03	0.17
Solanum dulcamara	0.01	0.07	0.01	0.07
Sonchus arvensis	0.19	0.62	0.16	0.54
Sonchus asper	0.19	0.59	0.14	0.49
Stachys officinalis	0.14	0.70	0.11	0.59
Stachys sylvatica	0.35	0.83	0.24	0.64
Stellaria graminea	0.22	0.87	0.14	0.66
Stellaria media	0.10	0.56	0.04	0.22
Symphytum x uplandicum	0.01	0.07	0.01	0.07
Taraxacum officinale agg.	0.08	0.30	0.10	0.51
Torilis japonica	0.07	0.37	0.05	0.21
Tragopogon pratensis	0.01	0.10	0.01	0.10
Trifolium campestre	0.06	0.34	0.06	0.39
Trifolium dubium	0.40	1.07	0.22	0.66
Trifolium hybridum	0.16	0.57	0.12	0.48
Trifolium pratense	0.70	1.54	0.48	1.18
Trifolium repens	1.32	1.65	0.81	1.29
Trifolium rep/hyb	1.48	1.90	0.93	1.48
Tripleurosp inodorum	0.24	0.75	0.13	0.38
Verbascum thapsus	0.01	0.07	0.01	0.07
Veronica persica	0.13	0.59	0.06	0.24
Vicia cracca	0.58	1.25	0.35	0.89
Vicia sativa	0.02	0.16	0.01	0.10
Vicia sepium	0.01	0.07	0.01	0.07
Vicia tetrasperma	0.14	0.65	0.09	0.49
Viola arvensis	0.34	0.90	0.19	0.57
Viola tricolor	0.01	0.07	0.01	0.07
CANTERBURY BELLS Campanula	0.01	0.07	0.01	0.07
LINSEED	0.03	0.25	0.02	0.14
MUSTARD	0.01	0.07	0.01	0.07
FODDER RADISH	0.03	0.21	0.02	0.12
POTATO	0.01	0.10	0.01	0.10
TREE MALLOW	0.01	0.07	0.01	0.07

6. Comparing the efficacy of agri-environment schemes to enhance bumblebee abundance and diversity on arable field margins

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Summary

1. Declines in abundance and diversity of bumblebees (*Bombus* spp.) in Europe have been linked to agricultural intensification and the resulting loss of suitable foraging and nesting habitats. Environmental Stewardship (ES) is a new scheme in England offering the opportunity to restore habitats of value for these important pollinators to agricultural land. Scientific evaluation of options prescribed within the scheme is essential to ensure that their objectives are met and that the benefits can be realised by the full bumblebee species assemblage. We compared the efficacy of different ES options for field margins and arable land to enhance the abundance and diversity of flowering resources and foraging bumblebees. Our study was conducted over three years using a multi-site experiment.

2. Overall, uncropped margins sown with mixtures containing nectar and pollen-producing plants were more effective in providing bumblebee forage than margins sown with a grass mix, allowed to regenerate naturally or managed as cropped conservation headlands.

3. A mixture of agricultural legumes established quickly and attracted on average the highest total abundance and diversity of bumblebees, including the rare, long-tongued species *Bombus ruderatus* and *B. muscorum*. However, marked differences were observed between species and sexes in their responses to margin management over time.

4. A diverse mixture of native wildflowers, including *Trifolium pratense* and *Centaurea nigra*, attracted more of the shorter-tongued *Bombus* species and provided greater continuity of forage resources, especially early in the season. Allowing *Cirsium* spp. to flower on such margins also increased their attractiveness to male bumblebees.

5. *Synthesis and applications.* Our results suggest that the legume-based 'pollen and nectar flower mix', as prescribed under Entry Level Stewardship, can quickly provide a highly attractive forage resource for bumblebees, but that issues of seasonal flowering phenology and longevity of the mixture need to be addressed. Establishment of 'floristically enhanced margins' under Higher Level Stewardship will be important to provide diverse perennial communities of forage plants and support a greater range of *Bombus* species and other pollinators. The population-level responses of bumblebees to introduced seed mixtures and other agri-environment options require further study in order to maximise the benefits of such schemes in intensively farmed landscapes.

Key-words: agri-environment, *Bombus*, bumblebees, arable farmland, forage plants

6.1 Introduction

The intensification of agriculture in Western Europe over recent decades has led to declines in the populations of many wild plant and animal species formerly characteristic of farmland (Robinson & Sutherland 2002). In order to reverse these declines, the Common Agricultural Policy has adopted provisions for EU member states to operate agri-environment schemes (EEC regulation 2078/92). These cover a range of objectives which differ depending on country or region, but all include measures whereby farmers are paid to manage their land for the benefit of particular habitats and species (Ovenden, Swash & Smallshire 1998). In England, a new agri-environment scheme has recently been adopted which takes forward the two largest existing schemes, Environmentally Sensitive Areas (ESAs) and the Countryside Stewardship Scheme (CSS) (Defra 2005a, 2005b). Environmental Stewardship (ES) represents a commitment of increased funds towards environmental protection, with greater rewards for farmers participating at higher levels. It is therefore essential that management options within the scheme are subject to scientific evaluation such that they are successful in attracting the desired species onto farmland (Kleijn & Sutherland 2003; Knop *et al.* 2006). In this study we assessed the effects of ES options for arable land on an important group of pollinating insects, bumblebees, and their forage plants over three years using a multi-site experiment.

Bumblebees (*Bombus* spp.) are considered important as pollinators due to their roles in enhancing the yields of entomophilous crops (Corbet, Williams & Osborne 1991; Free 1993), particularly fruit crops (Willmer, Bataw & Hughes 1994) and in maintaining populations of native plant species which have been fragmented within the agricultural landscape (Steffan-Dewenter & Tscharntke 1999). However, many bumblebee species have shown declines in abundance and contractions in range across Europe and North America since the mid-twentieth century (Williams 1982; Rasmont 1988; Buchmann & Nabhan 1996). In the UK, three species have been declared extinct and up to half the remaining 22 species are under threat (Edwards & Jenner 2005).

Their requirements for a season-long supply of pollen and nectar sources and undisturbed nesting, mating and hibernation sites make bumblebees susceptible to the effects of intensive farming. Changes in management practice, such as the conversion of species-rich hay meadows for silage production and the degradation of perennial vegetation in field margins and hedgerows, are likely to have had detrimental effects on all *Bombus* species (Osborne & Corbet 1994). Some species, including *Bombus sylvarum* and *Bombus ruderatus*, are thought to have been particularly affected by the loss of unimproved grassland in the UK (Fuller 1987), and are listed on the Biodiversity Action Plan (Anonymous 1999). Suitable management of semi-natural areas where their populations persist is a conservation priority (Carvell 2002), but the potential to provide resources for these rarer species on farmland requires further investigation. While the more common species may benefit from mass flowering crops such as oilseed rape (*Brassica napus* ssp. *oleifera*)

(Westphal, Steffan-Dewenter & Tscharntke 2003), these temporary forage resources alone are unlikely to be sufficient to sustain their colonies throughout the season, or to support the full species assemblage in agricultural landscapes. Agri-environment schemes therefore offer an important opportunity to restore habitats of value to bumblebees in intensively farmed areas.

One objective of the UK agri-environment schemes is to enhance the abundance and diversity of flowering plant species within arable systems through changes in management within or at the margins of fields. Field margins are a key feature of agricultural landscapes and there are well documented agronomic and ecological reasons why they have become the focus of management options within the schemes (Marshall & Moonen 2002; Defra 2005a, 2005b). Margins act as buffers to protect hedgerows against pesticide and fertilizer drift, prevent the spread of pernicious weeds into crops, and provide important refuge habitats for wildlife (Marshall & Moonen 2002; Meek *et al.* 2002; Critchley *et al.* 2004). Initial assessments of these management options suggested that the potential benefits for bumblebees were mixed (Kells, Holland & Goulson 2001; Kleijn *et al.* 2001; Goulson *et al.* 2002), despite positive effects being recognised for other taxa. Conservation headlands, where pesticide and herbicide applications at the crop edge are reduced, are more likely to encourage annual plants than perennials and biennials which are the preferred forage species for most bumblebees (Fussell & Corbet 1992; Dramstad & Fry 1995; Critchley *et al.* 2004). Uncropped margins left to regenerate naturally may provide suitable forage species on some sites but can encourage pernicious weeds such as *Cirsium* spp. and take several years to develop suitable mid-successional communities (Corbet 1995; Carvell *et al.* 2004).

Sowing a mixture of annual or perennial grassland species on arable field margins has been shown to overcome some of the above restrictions and significantly enhance the abundance and diversity of bumblebees and their forage plants (Carreck & Williams 2002; Meek *et al.* 2002; Carvell *et al.* 2004; Pywell *et al.* 2005). However, these studies have either been conducted at a single location or during a single year, where factors such as soil geology, the local *Bombus* species assemblage, climatic conditions and timing in relation to the establishment of field margin habitats may influence the outcome. Furthermore, many agri-environment scheme assessments have been compromised by a lack of standardised management practices or seed mixtures across study sites, caused by variation in farmer expertise and understanding of the desired plant communities (Kleijn *et al.* 2001). Options for field margins and arable land within the new Environmental Stewardship scheme in England are accompanied by clear management guidelines involving standard agricultural techniques (Defra 2005a, 2005b). They may require greater intervention in the early stages to achieve successful establishment (Marshall & Nowakowski 1995), but the outcome is likely to better resemble the intended vegetation community and habitat quality for target species, and thus achieve the objectives of the scheme. To our knowledge, there have so far been no comprehensive assessments of the effects of these new ES options with standardised management prescriptions on any taxon.

We present results from a multi-site experiment conducted over three years, in which we tested the following hypotheses:

H1: Field margin management according to different ES options has significant effects on the abundance and diversity of flowering resources and foraging bumblebees;

H2: The effects of margin management on bumblebees and their forage resources change over time, between years;

H3: The effects of seed mixture composition on flowering resources and foraging bumblebees change during the season.

The results are discussed in terms of the efficacy of different ES options in attracting foraging bumblebees, and the potential role of agri-environment schemes in enhancing and sustaining bumblebee populations on arable farmland.

6.2 Methods

6.2.1 Study sites and experimental treatments

The experiment was conducted at six sites across central and eastern England (Figure 6.1). All sites were predominantly arable farms with soil types ranging from clay in the east to sandy or variable loams in central and northern locations. At each of the six sites, experimental plots were established in September 2001 along two cereal field margins (replicates) within the same field, in all cases but one on opposite sides, with an east and west aspect. Plots were contiguous, measuring 50-m long and 6-m wide. On each replicate margin, plots were managed according to one of six treatments detailed in Table 6.1, five of which represented current and forthcoming agri-environment options and one which represented conventional crop management as a control. Treatments were randomly assigned to plots at each site, with the exception of the crop and conservation headland which were assigned at random to either end of each replicate to enable annual farming operations. Details of the seed mixtures used in the three sown treatments are given in Appendix 6A.

6.2.2 Flowering resources

To gain a measure of forage availability and assess seasonal change in flowering resources within treatments, an estimate of the number of flowering units present within each plot was made. This was done following each bumblebee transect (see below), from May to late August in the years 2002, 2003 and 2004. All flowering dicotyledon species were identified in the field (following Stace 1997), and the following scores used to describe their abundance:

1. 1 - 25 flowers
2. 26 - 200 flowers
3. 201 - 1000 flowers
4. 1001 - 5000 flowers

5. more than 5000 flowers (super-abundant)

One flower 'unit' was counted as a single flower or in the case of multi-flowered stems as an umbel (e.g. *Daucus carota*), head (e.g. *Trifolium pratense*), spike (e.g. *Rhinanthus minor*) or capitulum (e.g. *Centaurea nigra*).

6.2.3 Bumblebee monitoring

Bumblebee activity was recorded from May to late August, with between six and eleven sampling visits to each site in 2002, and nine visits to each site in 2003 and 2004. Bumblebee nests are difficult to reliably locate by any standardised sampling method, and techniques to estimate the effects of field-scale management on populations were not developed at the start of the study (Knight *et al.* 2005). We therefore used standardised counts of foraging bumblebees visiting flowers within the field margin plots to measure the relative attractiveness of treatments and potential for forage provision. On each visit, foraging bumblebees were counted along 6-m wide transects, with the recorder walking down the centre line of each field margin plot (as in Banaszak 1980; Carvell *et al.* 2004). The direction in which margins were walked was varied between visits. The plant species on which each bumblebee was first seen foraging was noted. All *Bombus* species were recorded, but *Bombus terrestris* and *Bombus lucorum* were collectively recorded, as workers of these species cannot be reliably distinguished in the field. Any other individuals that could not be readily identified whilst foraging, such as *Bombus muscorum*, were captured and examined with a hand lens. The different castes (queen, worker, male) were recorded separately for *Bombus lapidarius* only, as sex separation of other species in the field can be unreliable. The cuckoo bumblebees (now subgenus *Psithyrus*, brood parasites of the social *Bombus* species) were counted together as a group for analysis. Bumblebee nomenclature follows Prŷs-Jones & Corbet (1991).

Transects were carried out between 10.00 and 17.00 when weather conformed to criteria for the UK Butterfly Monitoring Scheme (temperature above 13°C with at least 60% clear sky, or 17°C in any sky conditions, with no count at all if raining) (Pollard & Yates 1993). The ambient temperature, percentage sunshine and wind speed were recorded at the end of each transect walk.

6.2.4 Data analysis

Flowering plant abundance scores were expressed as the interval median value for each range, to give an estimate of the number of flowering units on each sampling visit, as follows: Score 1 = 13 flowers; 2 = 113 flowers; 3 = 600.5 flowers; 4 = 3000.5 flowers; 5 = 15000 flowers. These data were summed into three variables according to a) whether a plant had been sown as part of the experiment, b) unsown and c) whether visited by foraging bumblebees.

The mean number of flowers, bumblebees and species richness of plants in flower or bumblebees recorded per plot, per sampling visit was calculated. This summarised data across the season in each year and between replicates at each site. The bee count data were log-transformed prior to analysis to normalise residual variation. Within-year differences between margin treatments in summary flower variables, in abundance of the eight most visited forage plants and in abundance of each bumblebee species, total bees and species richness were tested by Analysis of Variance (ANOVA), including site and treatment as factors (H1). Multiple pairwise comparisons were carried out on the means using Tukey's Honest Significant Difference tests. Repeated measures ANOVA was performed to test for average treatment effects across all years, and to assess whether these changed over time between years (H2).

Patterns of forage plant visitation by the different *Bombus* species were examined using Principal Components Analysis (PCA) on the proportion of visits by each bee species to each plant species averaged over the three years, using Canoco software, version 4.5 (ter Braak & Šmilauer 1998). A separate PCA was carried out to examine the foraging visits of the different castes of *Bombus lapidarius*.

To test whether the effects of treatment changed during the season (H3) bumblebee and flower means were further summarised according to the early season (May/June) versus mid-late season (July/August) sampling visits in each year. A preliminary nested ANOVA was performed on the log-transformed bumblebee means to examine the effects of site, treatment, year and season, and to test all the two-factor and three-factor interactions containing these terms. As bumblebees were most strongly influenced by margins sown with the wildflower or pollen and nectar seed mixtures, further analysis on seasonal effects examined just these two treatments. Repeated measures ANOVA was used to assess whether the observed treatment effects of seed mixture composition on flowering resources and bumblebee abundance differed between the early and mid-late season time periods (H3).

All ANOVA and repeated measures ANOVA analyses were undertaken using SAS 9.1 statistical software (SAS Institute Inc. 2004).

6.3 Results

6.3.1 Effects of Environmental Stewardship options on flower abundance and species richness

The field margin treatments established with relative consistency across all six sites, with the majority of sown species flowering on at least one sampling visit by the second, if not the first year. Dicot flower abundance and the number of species in flower (richness) varied between treatments and years as the vegetation communities developed over time (Table 6.2). All summary variables and key bee forage plants showed significant treatment by year interactions, with the exception of *Cirsium vulgare* and *Onobrychis viciifolia*. The pollen and nectar mixture produced the highest total flower abundance in the first year, nearly double that of the wildflower mixture, mainly due to the rapid establishment of *Trifolium hybridum*. This was replaced by *Trifolium pratense* in 2003 and an increasing number of *Lotus corniculatus* flowers in 2004, with the overall abundance of bee forage flowers remaining most constant between years in this treatment. The wildflower mixture produced few flowers, particularly of bee forage plants, in its first year, but numbers increased in 2003 and 2004 as the proportion of unsown species declined and the mixture established its perennial nature. Of the sown native species, *Leucanthemum vulgare* and *Achillea millefolium* achieved the highest mean flower scores at most sites, but only received 0.1% of foraging visits.

Flower abundance of unsown species was highest in the annually cultivated natural regeneration treatment, though only significantly so in 2002. The most prominent nectar source species in this treatment was *C. vulgare*. The presence of arable weed species was generally suppressed in the sown, compared to unsown or cropped treatments. Flower abundance and richness in the conservation headland treatment were never significantly higher than in the crop or tussocky grass treatment (Table 6.2), highlighting the lack and inconsistency of pollen and nectar sources provided by this field margin option.

6.3.2 Effects of Environmental Stewardship options on bumblebee abundance and species richness

During the three years of the experiment and across all six study sites, a total of 12,462 bumblebees representing nine social bumblebee species and at least three cuckoo bee species (subgenus *Psithyrus*) was recorded. These included three species considered rare and declining in the UK, *Bombus muscorum* (at the site in Essex), *Bombus ruderatus* (in Cambridgeshire and Bedfordshire) and *Bombus ruderarius* (at all sites except in N. Yorkshire and Bedfordshire), as well as the six ubiquitous species most commonly observed on farmland; *Bombus terrestris* and *Bombus lucorum* (recorded together), *Bombus pratorum*, *Bombus lapidarius*, *Bombus pascuorum* and *Bombus hortorum*, which were recorded at all sites.

Field margins sown with the legume-based pollen and nectar mixture attracted the highest total number and species richness of foraging bees in all years, with on average up to 269 times more bees recorded in this treatment than in the crop and conservation headlands (Table 6.3). Bumblebee abundance was also significantly higher on the pollen and nectar treatment than the natural regeneration and tussocky grass treatments in all years. The effects of site were not significant, but the overall treatment effects showed significant changes over time. In the natural regeneration treatment, total bumblebee abundance and richness decreased in the second and third years (2003 and 2004). In contrast, abundance and richness increased in the wildflower margins over time, showing no significant difference between this and the pollen and nectar treatment during the third year (Table 6.3). Overall, there was a positive correlation between the mean estimated number of flowers of bee forage plant species and mean total number of bumblebees per plot (Pearson's correlation coefficient 0.81, $P<0.001$; Figure 6.2).

At the species level, there were significant differences between margin treatments in abundance of the more common *Bombus* species, although these were not always consistent between species and years (Table 6.3). *B. lapidarius* and *B. pascuorum*, the most commonly recorded species, were significantly more abundant in the pollen and nectar treatment than in all others. In the third year *B. lapidarius* was also recorded in higher numbers in the wildflower margins than in other treatments. *B. hortorum* preferred the pollen and nectar mixture, but in 2003 and 2004 differences between this and the wildflower treatment were not significant. *B. terrestris*, *B. lucorum* (recorded together) and *B. pratorum* were recorded in lower numbers, and their visits were more evenly distributed between the natural regeneration, tussocky grass, wildflower and pollen and nectar treatments. The cuckoo bumblebees showed mixed preferences in each year, but with a tendency to be more abundant where the flowering seed mixtures were sown.

The three declining UK *Bombus* species were generally recorded in low numbers (Table 6.3), and significant differences in abundance between treatments were not detected. At sites where they occurred, the majority of individuals were recorded in the pollen and nectar, followed by wildflower treatment. For example, 98% of all records of *B. ruderatus* were from the pollen and nectar mixture.

6.3.3 Bumblebee forage plant visitation

Overall, 40 plant species were visited for pollen and/or nectar, including sown and unsown species. For all *Bombus* species and all years combined, 92% of visits were to just six species: *T. pratense* (agricultural and native varieties), *T. hybridum*, *L. corniculatus* (agricultural and native varieties) and *C. vulgare*. Patterns of forage plant visitation contrasted between species, as summarised by Principal Components Analysis. The first and second components accounted for 86% and 10% of variation respectively (Figure 6.3). The first axis separated the group of longer-tongued *Bombus*, including the rarer species, on the basis of their visits to *T. pratense*. The second axis separated the remaining four social *Bombus* species which are shorter-tongued and visited mainly *T. hybridum*, *L. corniculatus* and *C. vulgare*. The cuckoo bumblebees were placed centrally between these groups. A Chi-square test, based on a contingency table with total visits to the top ten forage species by the more commonly recorded bee species, confirmed these differences in flower choice between bee species ($P<0.001$).

PCA on the foraging visits of *B. lapidarius* revealed further contrasts between the different castes of this species (Figure 6. 4). The first component accounted for 63% of variation, separating queens on the basis of their visits to *T. pratense*. Of these, visits by early queens in May tended to be to the native variety in the wildflower mixture and those by the later, newly emerged queens to the agricultural variety in the pollen and nectar mixture. The second axis accounted for a further 21% of variation and separated workers on association with *L. corniculatus*, *Centaurea nigra* and

T. hybridum and males on the basis of their visits to *C. vulgare*. A Chi-square test, based on a contingency table with total visits to the top ten forage species by each caste, confirmed these differences in flower choice between queens, workers and males of *B. lapidarius* (P<0.001).

6.3.4 Seasonal differences

Seasonal differences were detected in the effects of seed mixture composition (of the wildflower and pollen and nectar mixtures) on flower and bumblebee abundance. When the effects of season were added as an interaction term to the nested ANOVA on total bumblebee abundance, the three-factor interaction was not significant ($F_{2,10}$ = 1.88; P = 0.20), suggesting that the strong treatment by season interaction ($F_{1,5}$ = 27.45; P<0.01) did not vary between years. Data were therefore averaged across the three years for the repeated measures ANOVA on seasonal effects.

Flower abundance of all forage plants grouped showed a significant treatment by season interaction ($F_{1,5}$ = 23.1; P<0.01), with on average more flowers in the wildflower than pollen and nectar mixture during May/June, but the pollen and nectar mixture providing more forage during July/August (Figure 6.5a). This was reflected in the bumblebee response. Bee abundance was significantly greater in the wildflower than pollen and nectar mixture during May/June for *B. hortorum* ($F_{1,5}$ = 51.6; P<0.01) and *B. terrestris* ($F_{1,5}$ = 24.9; P<0.01), and all the common *Bombus* species were more abundant in the pollen and nectar than wildflower treatment during July/August ($F_{1,5}$ = 101.8; P<0.001 for total bees, with a significant treatment by season interaction $F_{1,5}$ = 27.3; P<0.01) (Figure 6.5b). The plant species most influencing these trends were *T. pratense* and *L. corniculatus*, both showing significant effects of season on differences between treatments ($F_{1,5}$ = 18.5; P<0.01 and $F_{1,5}$ = 26.6; P<0.01 respectively). The native varieties sown in the wildflower mixture began flowering in early May, producing more flowers than the agricultural varieties in the pollen and nectar mixture early in the season. This pattern was reversed during July/August when the agricultural varieties reached peak flowering (Figure 6.6).

6.4 Discussion

The management of arable field margins according to different options under Environmental Stewardship (ES) had significant effects on bumblebees and their forage plants, confirming our first hypothesis. These effects were consistent across the six farms on which the experiment was conducted. Uncropped margins sown with a mixture containing four agricultural legume species attracted on average the highest abundance and diversity of bumblebees, including rare species. However, marked differences were observed between bumblebee species and amongst the sexes within species in their responses to margin management, which can be explained in part by differences in their foraging preferences. Our assessment of changes in flower abundance also revealed seasonal differences in forage provision, and significant changes in the composition of flowering plant species over three years depending on management option and seed mixture composition, confirming our second and third hypotheses. These results are discussed in terms of the potential role of different ES options in enhancing and sustaining bumblebee populations on arable farmland, both at the Entry Level (ELS) (Defra 2005a) which is open to all farmers and the Higher Level (HLS) (Defra 2005b) which offers greater rewards to land managers for the delivery of a wider range of biodiversity benefits on targeted sites such as those with existing high priority environmental features.

Removing arable field margins from the cropping system can potentially provide increased forage resources for bumblebees, as well as a greater diversity of habitats for other invertebrates (Feber, Smith & Macdonald 1996; Meek *et al.* 2002; Asteraki *et al.* 2004). Whilst conservation headlands may encourage more annual plants than a conventionally managed crop (Critchley *et al.* 2004), our results showed that this did not translate to an overall increase in either flower abundance and richness of species in flower or the number and species of bumblebees recorded. Allowing natural regeneration on uncropped cultivated margins is a relatively simple management option which could achieve widespread uptake within the ELS and HLS schemes, creating opportunities for rare arable plants (Bill Meek, unpublished data). However, bumblebee and forage plant abundance were only significantly higher on this option than on cropped margins during the first year after establishment, despite the occurrence of *Cirsium vulgare* which was attractive to the shorter-tongued species, and particularly male *Bombus lapidarius*. It is possible that bees were less likely to visit this treatment when greater floral rewards were present in adjacent field margin plots. When tested in isolation, naturally regenerated margins can provide enhanced foraging habitat when compared to conservation headlands (Kells *et al.* 2001). In general though, this management option is unlikely to provide a sufficient density or diversity of bumblebee forage resources unless injurious weeds such as *Cirsium* spp. are allowed to persist, which carries agronomic problems, or vegetation is left uncultivated and a perennial sward established over time (Carvell *et al.* 2004).

Sowing a mixture of perennial grass and wildflower or legume species has clear advantages in terms of further enhancing the quality of arable field margins for bumblebees. The positive response of different species to increased densities of their preferred forage plants has been well documented, both in semi-natural and agricultural landscapes (e.g. Dramstad & Fry 1995; Bäckman & Tiainen 2002; Carvell 2002). Our study suggests that it is the composition and seasonal flowering patterns of seed mixtures which are the most important factors influencing the abundance and diversity of bumblebees attracted to ES options for sown margins.

The 'pollen and nectar flower mixture', containing at least three legume species (at 20% of the mix) and non-aggressive grasses (at 80%), can be sown on arable field margins or set-aside land under both ELS and HLS schemes (Defra 2005a). This option may be of high conservation value for some of Britain's rarer bumblebees as the legume component attracted three species not commonly recorded on farmland; the Biodiversity Action Plan (BAP) species *Bombus ruderatus*, confirming preliminary observations by Pywell *et al.* (2005), and two species proposed for inclusion in the UK BAP, *B. muscorum* and *B. ruderarius* (Stuart Roberts, pers. comm.). However, this seed mixture had several shortcomings as a means of providing sustained forage throughout the season. The low abundance of flowers during May and June implied that it would not fully cater for bumblebee colonies in the early stages of their development. The use of alternative varieties of *Trifolium* spp., or changes in the cutting management of such margins could be investigated in order to extend their flowering time. Also, despite establishing quickly and flowering well in the first two years, the results suggested a reduction in flower abundance of the two *Trifolium* species in the pollen and nectar mixture along with a decrease in bee density in the third year. Re-sowing may therefore be necessary as the grass component of the mixture becomes dominant. Furthermore, the legume species tested in our study did not appear wholly suitable as forage plants for the shorter-tongued species (e.g. *B. terrestris* or *B. pratorum*) or more specifically for males (e.g. *B. lapidarius*). An additional ELS option, the 'wild bird seed mixture' (EF2) offers the opportunity to sow appropriate forage plants, such as *Borago officinalis*, for these species, and could complement the pollen and nectar mixture if established on other parts of the farm (Defra 2005a; Carvell *et al.* 2006).

Sowing a more diverse mixture of native wildflowers (at 20% of the mix) and non-aggressive grasses (at 80%) on arable margins or set-aside land is an option available under the HLS scheme (Defra, 2005b). Our results suggest that despite, on average, a lower density of bees and forage flowers, this option has the potential to cater across the whole season for a wider range of species than the pollen and nectar mixture as currently prescribed. This observation is supported by a study of bumblebees on field margins in Finland, where although bee density was strongly related to margin width and flowering of the most visited forage species, *Trifolium medium*, species diversity did not follow this pattern and was only enhanced with the presence of plant species such as *Knautia arvensis* and *Galeopsis speciosa* (Backman & Tiainen 2002). As well as *Trifolium pratense* and *Lotus corniculatus*, the mixture we tested contained species from the Asteraceae such as *Centaurea nigra*, which were attractive to both sexes of the shorter-tongued *Bombus* species. These additional plant species are likely to enhance the value of field margins for other pollinators such as solitary bees and butterflies (Feber, Smith & Macdonald 1996; Westrich 1996). Agronomically, the wildflower mixture did not fully establish until its second year, but the resulting perennial vegetation is likely to persist over a five to ten-year timescale (Pywell *et al.* 2002). The native legume varieties sown here flowered significantly earlier than their agricultural equivalents, attracting the longest-tongued species, *Bombus hortorum*, as well as queens of *B. lapidarius*, for which other resources on farmland are often scarce in the early summer. By sowing both varieties in the same mixture, season-long forage could be provided. However, the implications for competition between species and conservation of genetic diversity within species require further consideration if native and agricultural cultivars are to be sown together (Walker *et al.* 2004).

The tendency for bumblebees to show species-specific preferences for certain flowers or plant families, as demonstrated in this study, has been well recognised (Heinrich, 1976). Although we did not differentiate between pollen and nectar collection, evidence from other studies suggests that it may be the high value of legume (Fabaceae) pollen to the longer-tongued species, especially those founding colonies relatively late in the season, which accounts for their large number of visits to *T. pratense* and other Fabaceae (Brian 1951; Goulson & Darvill 2004; Carvell *et al.* 2006). This apparent specialisation on plant species which have declined in the countryside, combined with proximity to their European range edges, may be the principal cause of rarity and decline in British bumblebees (Goulson *et al.* 2005; Williams 2005). Thus by restoring legume-rich habitats in arable areas the assumption is that rare species can benefit within their range, as evidenced here. However, Williams (2005) highlights some of the problems associated with comparing forage plant preferences, as they depend on the abundance of each bee species and availability of each forage plant at particular study sites. The consistent management of treatments across our six sites ensured that flower abundances of forage species were similar, although the *Bombus* species assemblages differed depending on region. In this case the Principal Components Analysis, which accounted for a high percentage of variation in visitation patterns, described the contrasts in forage use between bumblebee species and explained the observed differences in their abundance between ES options.

Having gained evidence of the field-scale effects of different margin management options on bumblebees and their forage plants, the question remains as to how these effects might translate to the landscape-scale. Habitat heterogeneity has been reduced by intensification in agricultural landscapes at a range of spatial scales, with consequences for many taxa (Benton, Vickery & Wilson 2003; Tscharntke *et al.* 2005). Agri-environment schemes do not currently promote habitat heterogeneity as a stated aim. However, the potentially widespread establishment of options such as the pollen and nectar mixture under Entry Level Stewardship, interspersed with fewer but high quality diverse wildflower mixtures under Higher Level Stewardship, is likely to significantly enhance the heterogeneity and quality of the English lowland landscape for bumblebees. The relatively large foraging ranges of many species may enable them to exploit these new habitats, at least at the farm-scale (Osborne *et al.* 1999; Steffan-Dewenter *et al.* 2002; Knight *et al.* 2005), although the dispersal abilities of bumblebees are still poorly understood. Furthermore, we did not assess the use of different ES options as nesting sites due to the difficulty of locating nests of all species, and the limited total area under study. The tussocky grass mixture tested here is likely to provide suitable nesting habitat if left undisturbed (Kells & Goulson 2003), but interactions between the nesting and foraging components of introduced habitats require further investigation. It is also important that more direct measurements of colony density (Chapman, Wang & Bourke

2003; Knight *et al.* 2005) are employed to assess whether the abundance and species richness benefits shown in this study translate to increased population density and persistence of bumblebee species in enhanced agricultural landscapes.

Conclusions

This study provides the first comprehensive assessment of the effects of different management options for arable land as prescribed under the new Environmental Stewardship scheme on a high profile group of insects. As predicted, uncropped margins sown with mixtures containing nectar and pollen-producing plants were more effective in providing bumblebee forage than margins sown with a grass mix, allowed to regenerate naturally or managed as conservation headlands. Our results suggest that uptake of selected options within Entry Level Stewardship in England could have a positive impact on bumblebees, including species of conservation concern. As with all such agri-environment initiatives, factors such as temporal variation in resource provision within the period of insect activity, and longer-term value as newly established vegetation communities change over time must be considered in the design of management guidelines. Additional options within Higher Level Stewardship are likely to be important in meeting these needs. Environmental Stewardship therefore provides a mechanism for enhancing the currently impoverished *Bombus* assemblages of intensively managed landscapes, and potentially facilitating the pollination of certain crops and wildflowers, though these associations have yet to be tested directly (Ghazoul 2005). The population-level responses of bumblebees to introduced seed mixtures and other agri-environment options still require better understanding in order to maximise the benefits of such schemes in intensively farmed landscapes.

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References

Anonymous (1999) UK Biodiversity Group Tranche 2 Action Plans. Volume IV - invertebrates. English Nature, Peterborough, UK.

Asteraki, E.J., Hart, B.J., Ings, T.C. & Manley, W.J. (2004) Factors influencing the plant and invertebrate diversity of arable field margins. *Agriculture Ecosystems and Environment*, **102**, 219-231.

Backman, J.P.C. & Tiainen, J. (2002) Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera : *Bombus* and *Psithyrus*). *Agriculture Ecosystems and Environment*, **89**, 53-68.

Banaszak, J. (1980) Studies on methods of censusing the numbers of bees (Hymenoptera: Apoidea). *Polish Ecological Studies*, **6**, 355-366.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, **18**, 182-188.

Brian, A.D. (1951) The pollen collected by bumble-bees. *Journal of Animal Ecology*, **20**, 191-194.

Buchmann, S.E. & Nabhan, G.P. (1996) *The Forgotten Pollinators*. Island Press, Washington DC, USA.

Carreck, N.L. & Williams, I.H. (2002) Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *Journal of Insect Conservation*, **6**, 13-23.

Carvell, C. (2002) Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation*, **103**, 33-49.

Carvell, C., Meek, W.R., Pywell, R.F. & Nowakowski, M. (2004) The response of foraging bumblebees to successional change in newly created arable field margins. *Biological Conservation*, **118**, 327-339.

Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F. & Nowakowski, M. (2006) Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. *Apidologie,* **37**, 326-340.

Chapman, R.E., Wang, J. & Bourke, A.F.G. (2003) Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. *Molecular Ecology*, **12**, 2801-2808.

Corbet, S.A. (1995) Insects, Plants and Succession - Advantages of long-term set-aside. *Agriculture Ecosystems and Environment*, **53**, 201-217.

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

Critchley, C.N.R., Allen, D.S., Fowbert, J.A., Mole, A.C. & Gundrey, A.L. (2004) Habitat establishment on arable land: assessment of an agri- environment scheme in England, UK. *Biological Conservation*, **119**, 429-442.

Defra. (2005a) Environmental Stewardship: Entry Level Stewardship Handbook. Department for Environment, Food and Rural Affairs, London.

Defra. (2005b) Environmental Stewardship: Higher Level Stewardship Handbook. Department for Environment, Food and Rural Affairs, London.

Dramstad, W. & Fry, G. (1995) Foraging activity of bumblebees (Bombus) in relation to flower resources on arable land. *Agriculture Ecosystems and Environment*, **53**, 123-135.

Edwards, M. & Jenner, M. (2005) *Field guide to the bumblebees of Great Britain and Ireland.* Ocelli, UK.

Feber, R.E., Smith, H. & Macdonald, D.W. (1996) The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology*, **33**, 1191-1205.

Free, J.B. (1993) *Insect Pollination of Crops*, 2nd edition. Academic Press, London.

Fuller, R.M. (1987) The changing extent and conservation interest of lowland grasslands in England and Wales - a review of grassland surveys 1930-84. *Biological Conservation*, **40**, 281-300.

Fussell, M. & Corbet, S.A. (1992) Flower usage by bumble-bees: a basis for forage plant management. *Journal of Applied Ecology*, **29**, 451-465.

Ghazoul, J. (2005) Buzziness as usual? Questioning the global pollination crisis. *Trends in Ecology and Evolution*, **20**, 367-373.

Goulson, D. & Darvill, B. (2004) Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? *Apidologie*, **35**, 55-63.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. & Knight, M.E. (2005) Causes of rarity in bumblebees. *Biological Conservation*, **122**, 1-8.

Goulson, D., Hughes, W.O.H., Derwent, L.C. & Stout, J.C. (2002) Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia*, **130**, 267-273.

Heinrich, B. (1976) The foraging specializations of individual bumblebees. *Ecological Monographs*, **46**, 105-128.

Kells, A.R. & Goulson, D. (2003) Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological Conservation*, **109**, 165-174.

Kells, A.R., Holland, J.M. & Goulson, D. (2001) The value of uncropped field margins for foraging bumblebees. *Journal of Insect Conservation*, **5**, 283-291.

Kleijn, D., Berendse, F., Smit, R. & Gilissen, N. (2001) Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature*, **413**, 723-725.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947-969.

Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, A. & Goulson, D. (2005) An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology*, **14**, 1811-1820.

Knop, E., Kleijn, D., Herzog, F. & Bernhard, S. (2006) Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology*, **43**, 120-127.

Marshall, E.J.P. & Nowakowski, M. (1995) Successional changes in the flora of a sown field margin strip managed by cutting and herbicide application. In *Brighton Crop Protection Conference - Weeds*, pp. 973-978. British Crop Protection Council, Surrey, UK.

Marshall, E.J.R. & Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture Ecosystems and Environment*, **89**, 5-21.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. & Nowakowski, M. (2002) The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, **106**, 259-271.

Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R. & Edwards, A.S. (1999) A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology*, **36**, 519-533.

Osborne, J.L. & Corbet, S.A. (1994) Managing habitats for pollinators in farmland. *Aspects of Applied Biology*, **40**, 207-215.

Ovenden, G.N., Swash, A.R.H. & Smallshire, D. (1998) Agri-environment schemes and their contribution to the conservation of biodiversity in England. *Journal of Applied Ecology*, **35**, 955-960.

Pollard, E. & Yates, T.J. (1993) *Monitoring Butterflies for Ecology and Conservation.* Chapman and Hall, London.

Prŷs-Jones, O.E. & Corbet, S.A. (1991) *Bumblebees*, 2nd edition. Richmond Publishing Company, Slough, UK.

Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W. & Peel, S. (2002) Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology*, **39**, 294-309.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R. & Sherwood, A. (2005) Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation*, **121**, 479-494.

Rasmont, P. (1988) Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera: Apidae, Bombinae). PhD, Faculté des Science Agronomique de l'Etat, Gembloux, Belgium.

Robinson, R.A. & Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, **39**, 157-176.

SAS Institute Inc. (2004) SAS® 9.1.2 Qualification Tools User's Guide. Cary, NC.

Stace, C. (1997) *New Flora of the British Isles.* Cambridge University Press, Cambridge, UK.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. & Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, **83**, 1421-1432.

Steffan-Dewenter, I. & Tscharntke, T. (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia*, **121**, 432-440.

ter Braak, C.J.F. & Šmilauer, P. (1998) CANOCO reference manual and user's guide to CANOCO for Windows: Software for canonical community ordination (version 4). Microcomputer Power, Ithaca, NY.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, **8**, 857-874.

Walker, K.J., Hodder, K., Bullock, J. & Pywell, R.F. (2004). A review of the potential effects of seed sowing for habitat re-creation on the conservation of infraspecific biodiversity. Defra report BD1447. NERC Centre for Ecology and Hydrology, UK.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, **6**, 961-965.

Westrich, P. (1996). The problems of partial habitats. In *The Conservation of Bees.* (eds A. Matheson, S.L. Buchmann, C. O'Toole, W. P. & I.H. Williams). Academic Press, London.

Williams, P. (2005) Does specialization explain rarity and decline British bumblebees? - A response to Goulson *et al. Biological Conservation*, **122**, 33-43.

Williams, P.H. (1982) The distribution and decline of British bumble bees (*Bombus* Latr). *Journal of Apicultural Research*, **21**, 236-245.

Willmer, P.G., Bataw, A.A.M. & Hughes, J.P. (1994) The superiority of bumblebee to honeybees as pollinators - insect visits to raspberry flowers. *Ecological Entomology*, **19**, 271-284.

Table 6.1 Arable field margin treatments and management details with corresponding agri-environment scheme options.

* under the prescriptions, selected herbicide application is permitted only to control pernicious weeds or invasive alien species (Defra, 2005a, 2005b).

				Agri-Environment Scheme Options		
Experimental treatment	**Abbreviation**	**Description**	**Management**	2002 Countryside Stewardship Scheme	2004/5 Entry Level Stewardship (ELS)	2005 Higher Level Stewardship (HLS)
Crop	Crop	Conventional arable crop management (the control)	Managed as rest of the field in cereal crop rotation	N/A	N/A	N/A
Conservation Headland	Cons head	Arable crop managed to encourage broad-leaved annuals on 6 m margin	Sown with cereal crop as rest of field; herbicide and insecticide application restricted *	CH1	EF9	N/A
Natural Regeneration	Nat regen	Uncropped 6 m margin cultivated to encourage rare annual plants	Cut early September every year; cuttings left; lightly cultivated in late September every year; no herbicide, pesticide or fertiliser *	R3 with natural regeneration	EF11	HF20
Tussocky grass mixture	Grass	6 m margin sown with 5 tussock forming grass species at 20 kg ha^{-1}	Sown in September 2001; cut in May and September 2002; uncut thereafter; no herbicide, pesticide or fertiliser *	R3 with sown grass mixture	EE3	N/A
Wildflower mixture	Wildflower	6 m margin sown with 21 native wildflower species and 4 fine grass species at 37 kg ha^{-1}	Sown in September 2001; cut in May and early September 2002 then only in September 2003/4; cuttings removed; no herbicide, pesticide or fertiliser *	R3 with GX supplement	EE3	HE10
Pollen and nectar mixture	Pollen & nectar	6 m margin sown with 4 agricultural legume species and 4 fine grass species at 20 kg ha^{-1}	Sown in September 2001; cut in May and early September 2002 then only in September 2003/4; cuttings removed; no herbicide, pesticide or fertiliser *	WM2	EF4	HE10

Table 6.2 Means and test statistics (ANOVA) for treatment differences in flower abundance and richness.

Values represent the mean estimated number of flowers or plant species in flower (richness) per plot (50 x 6-m), per sampling visit, averaged across the six sites. Individual species are those which received the highest percentage of foraging visits, presented in decreasing order from the left (AG = agricultural legume, NAT = native variety). Calculation of 'Total bee forage species' included all 40 plant species visited.

ns = not significant; **P*<0.05; ***P*<0.01; ****P*<0.001.

	Field margin treatment	*Trifolium pratense* AG	*Trifolium hybridum*	*Lotus corniculatus* AG	*Cirsium vulgare*	*Trifolium pratense* NAT	*Lotus corniculatus* NAT	*Centaurea nigra*	*Onobrychis viciifolia*	Total bee forage species	Sown species	Unsown species
2002	Crop	0.0 b	0.0 b	0.0 b	0.2	0.0 b	0.0 b	0.0 b	0.0 b	7.7 b	0.3 c	28.9 b
	Cons head	0.0 b	0.0 b	0.0 b	0.0	0.0 b	0.0 b	0.0 b	0.0 b	210.5 b	0.0 c	370.3 b
	Nat regen	0.2 b	0.2 b	0.3 b	39.6	0.2 b	0.7 b	0.0 b	0.0 b	919.6 b	13.9 c	3435.3 a
	Grass	0.4 b	2.5 b	0.5 b	10.0	0.3 b	0.7 b	0.0 b	0.0 b	342.1 b	10.6 c	1167.7 b
	Wildflower	0.0 b	8.8 b	0.0 b	4.8	281.0 a	140.6 a	8.3 a	1.2 b	750.8 b	2995.2 b	1108.7 b
	Pollen & nectar	917.8 a	4143.5 a	1327.2 a	3.0	0.0 b	0.0 b	0.0 b	16.6 a	6528.4 a	6407.3 a	810.3 b
2002 ANOVA	F $_{5,25}$	93.64	29.06	8.03	2.15	9.58	19.87	4.88	4.37	33.76	31.45	8.50
	Significance	***	***	***	ns	***	***	**	**	***	***	***
2003	Crop	0.0 b	0.0 b	0.2 b	0.5	0.0 b	0.0 b	0.4 b	0.0 b	328.6 b	3.2 b	757.5 ab
	Cons head	0.1 b	0.0 b	0.0 b	0.1	0.0 b	0.0 b	0.0 b	0.0 b	333.5 b	1.3 b	1291.8 al
	Nat regen	0.5 b	1.8 b	0.1 b	28.0	0.1 b	0.2 b	0.2 b	0.0 b	220.6 b	45.7 b	1951.2 a
	Grass	2.7 b	7.3 b	5.8 b	30.2	0.5 b	0.5 b	0.5 b	0.4 b	171.9 b	61.6 b	201.7 b
	Wildflower	0.1 b	42.3 b	1.0 b	47.2	2519.1 a	1527.9 a	46.1 a	2.4 b	4321.6 a	9901.8 a	99.8 b
	Pollen & nectar	4091.8 a	1274.9 a	866.7 a	53.6	0.0 b	0.0 b	0.4 b	71.4 a	6375.0 a	6321.6 a	144.4 b
2003 ANOVA	F $_{5,25}$	12.53	7.49	7.52	1.12	10.69	6.13	8.49	2.98	15.17	17.77	4.63
	Significance	***	***	***	ns	***	***	***	*	***	***	**
2004	Crop	0.0 b	0.2 b	0.1 b	0.5 b	0.0 b	0.0 b	0.0 b	0.0 b	577.9 b	2.7 b	1191.6
	Cons head	0.1 b	2.5 b	0.2 b	0.0 b	0.0 b	0.1 b	0.0 b	0.0 b	542.5 b	4.3 b	1281.4
	Nat regen	1.9 b	3.2 b	0.4 b	30.9 a	0.2 b	0.0 b	0.5 b	0.0 b	523.8 b	22.4 b	1098.6
	Grass	1.4 b	23.2 b	4.3 b	8.7 ab	0.7 b	7.8 b	1.3 b	0.0 b	153.7 b	112.2 b	136.7
	Wildflower	0.0 b	267.2 ab	0.0 b	10.4 ab	562.9 a	2954.4 a	75.0 a	4.2 b	4241.9 a	7446.3 a	90.6
	Pollen & nectar	2183.4 a	1182.9 a	2214.9 a	11.6 ab	5.6 b	1.1 b	0.1 b	30.7 a	5708.4 a	5666.5 a	130.7
2004 ANOVA	F $_{5,25}$	6.06	3.55	11.65	2.66	11.98	13.23	33.04	5.17	14.68	31.71	2.38
	Significance	***	**	***	*	***	***	***	**	***	***	ns
Repeated measures ANOVA F $_{10,50}$	Treatment	18.87 ***	20.54 ***	15.91 ***	1.94 ^{ns}	12.52 ***	10.67 ***	24.40 ***	3.82 *	33.51 ***	43.11 ***	8.82 ***
	Year	4.20 *	10.46 ***	2.82 ^{ns}	3.17 ^{ns}	9.06 **	10.65 **	11.69 ***	2.32 ^{ns}	1.88 ^{ns}	4.57 *	3.04 ^{ns}
	Year x Treatment	4.19 ***	12.06 ***	2.82 **	1.02 ^{ns}	9.08 ***	10.58 ***	10.91 ***	2.24 ^{ns}	3.09 **	4.78 ***	3.45 **

Table 6.3 Means, sample sizes and test statistics (ANOVA) for treatment differences in bumblebee abundance and richness. Values represent the mean number of bees per plot (50 x 6-m), per sampling visit, averaged across the six sites. Results for all species are presented for consistency, but where fewer than 10 individuals of a species were recorded in any year ANOVA was not performed. Rare species are shown in bold. ns = not significant; **P*<0.05; ***P*<0.01; ****P*<0.001.

	Field margin treatment	*B. terrestris/ lucorum*	*B. lapidarius*	*B. pratorum*	*B. pascuorum*	*B. hortorum*	***B. ruderarius***	***B. muscorum***	***B. ruderatus***	Cuckoo bees	Total bees
2002	Sample size	233	1637	4	1120	110	6	15	9	41	3175
	Crop	0.00 c	0.01 c	0.00	0.00 c	0.00 b	0.00	0.00	0.00	0.00 b	0.01 c
	Cons head	0.02 c	0.04 c	0.00	0.00 c	0.00 b	0.00	0.00	0.00	0.00 b	0.06 c
	Nat regen	1.16 bc	2.16 b	0.04	0.22 c	0.00 b	0.00	0.00	0.00	0.02 ab	3.59 b
	Grass	0.27 bc	0.55 bc	0.01	0.06 c	0.00 b	0.00	0.00	0.00	0.01 ab	0.91 bc
	Wildflower	0.05 c	0.73 bc	0.00	1.64 b	0.32 b	0.00	0.00	0.00	0.01 b	2.75 b
	Pollen & nectar	1.09 ab	14.57 a	0.00	10.28 a	0.92 a	0.07	0.16	0.11	0.40 a	27.59 a
2002 ANOVA	$F_{5,25}$	4.67	25.70	1.62	120.05	11.48	1.00	1.00	1.00	3.20	32.21
	Significance	**	***	-	***	***	-	ns	-	*	***
2003	Sample size	110	2237	1	2573	724	8	19	65	119	5856
	Crop	0.04	0.03 d	0.00	0.01 c	0.00 b	0.00	0.00	0.00	0.00	0.07 d
	Cons head	0.03	0.04 d	0.00	0.01 c	0.00 b	0.00	0.00	0.00	0.01	0.08 d
	Nat regen	0.17	1.16 cd	0.00	0.25 c	0.00 b	0.00	0.00	0.00	0.16	1.73 cd
	Grass	0.19	1.26 c	0.00	0.35 c	0.06 b	0.00	0.00	0.00	0.28	2.13 c
	Wildflower	0.27	4.67 b	0.01	2.91 b	1.76 a	0.02	0.06	0.00	0.16	9.83 b
	Pollen & nectar	0.33	13.56 a	0.00	20.30 a	4.89 a	0.06	0.12	0.60	0.50	40.36 a
2003 ANOVA	$F_{5,25}$	2.89	51.73	1.00	27.58	17.35	0.85	1.00	1.00	2.17	55.82
	Significance	*	***	-	***	***	-	ns	ns	ns	***
2004	Sample size	144	1403	10	1494	197	1	4	27	151	3431
	Crop	0.14	0.31 b	0.00 b	0.04 c	0.04 b	0.00	0.00	0.00	0.04 c	0.56 b
	Cons head	0.12	0.47 b	0.00 b	0.03 e	0.02 b	0.00	0.00	0.00	0.16 bc	0.80 b
	Nat regen	0.33	0.79 b	0.01 b	0.13 c	0.00 b	0.00	0.00	0.00	0.08 c	1.34 b
	Grass	0.17	0.42 b	0.00 b	0.15 c	0.10 b	0.00	0.01	0.01	0.11 bc	0.96 b
	Wildflower	0.34	3.99 a	0.07 a	1.95 b	0.56 ab	0.00	0.00	0.01	0.63 ab	7.56 a
	Pollen & nectar	0.23	7.01 a	0.01 b	11.54 a	1.10 a	0.01	0.03	0.23	0.38 bc	20.54 a
2004 ANOVA	$F_{5,25}$	0.64	19.63	4.23	19.32	4.43	1.00	1.00	1.16	3.59	24.10
	Significance	ns	***	**	***	**	-	-	ns	*	***
Repeated measures	Treatment	3.85 *	42.11 ***	-	43.29 ***	16.35 ***	-	1.00 ns	1.05 ns	4.16 **	49.82 ***
ANOVA $F_{10,50}$	Year	2.54 ^{ns}	4.75 *	-	4.47 *	15.97 ***	-	1.06 ns	0.95 ns	4.66 *	5.77 **
	Year x Treatment	2.96 ***	7.35 ***	-	1.28 ^{ns}	6.81 ***	-	1.00 ns	0.97 ns	1.91 ^{ns}	4.93 ***

Figure 6.1 Map of England and Wales showing locations of the six sites where the field margin experiment was conducted.

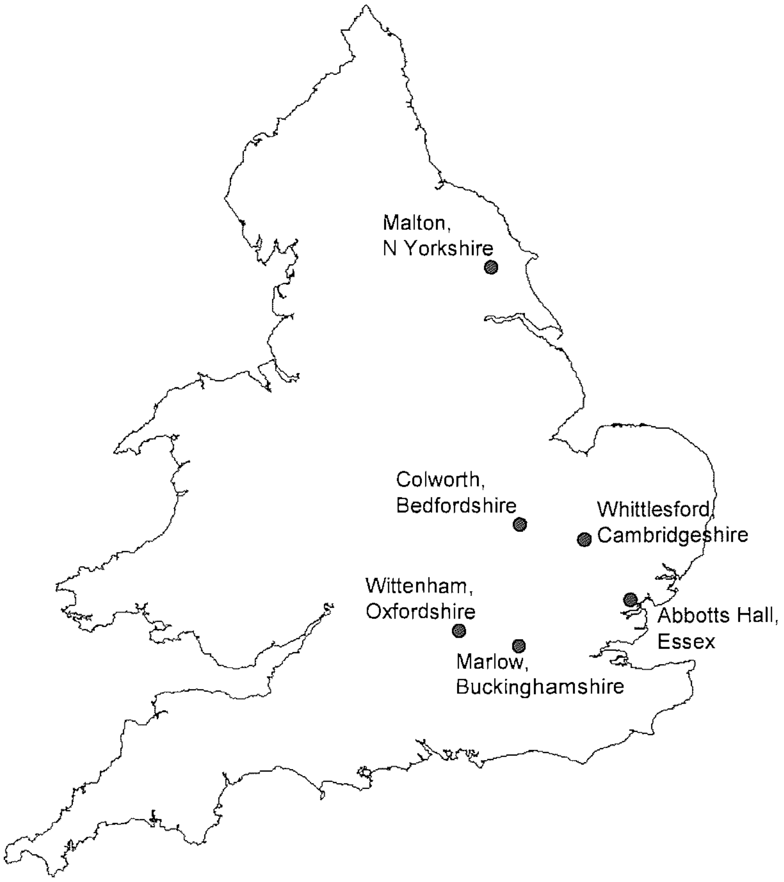


Figure 6.2 The relationship between flower abundance of bee forage species and total bumblebee abundance on different ES field margin options. Values represent the log transformed mean number of bees per plot at each site, averaged over three years.

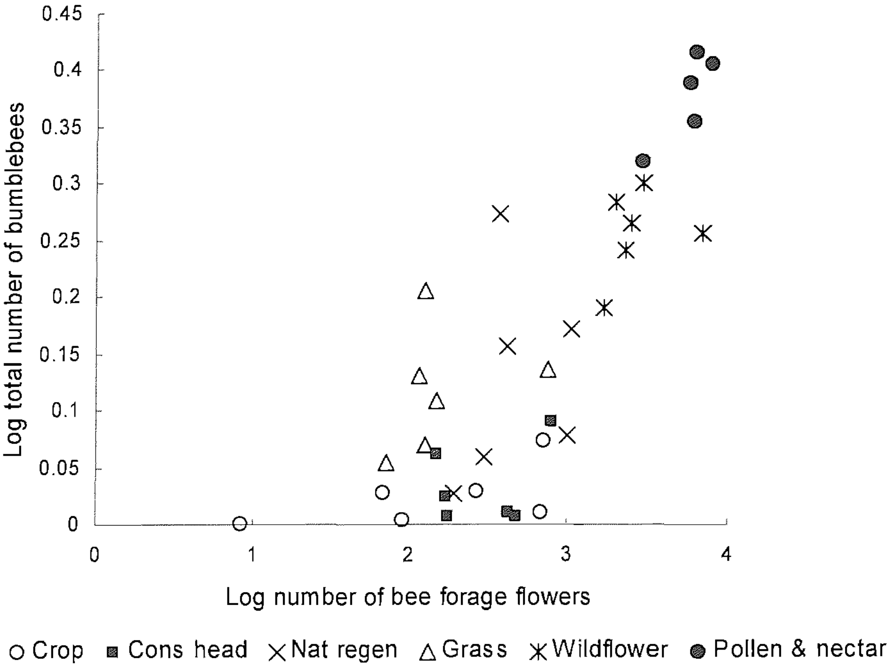


Figure 6.3 Principal Components Analysis biplot based on the proportion of visits to different plant species by foraging bumblebees of each species. Abbreviations of bumblebee species names: prato = *B. pratorum*; terluc = *B. terrestris/lucorum*; lapid = *B. lapidarius*; musco = *B. muscorum*; pascu = *B. pascuorum*; horto = *B. hortorum*; rudri = *B. ruderarius*; rudtu = *B. ruderatus*; cucko = cuckoo bumblebees. Abbreviations of plant species (in italics): Cir vulg = *Cirsium vulgare*; Lot corn = *Lotus corniculatus*; Tri hybr = *Trifolium hybridum*; Tri prat = *Trifolium pratense*; others = e.g. *Centaurea nigra*, *Rhinanthus minor*, *Papaver rhoeas*, *Brassica napus*, *Dipsacus fullonum*. Visits to native and agricultural varieties of *T. pratense* and *L. corniculatus* were combined for this analysis.

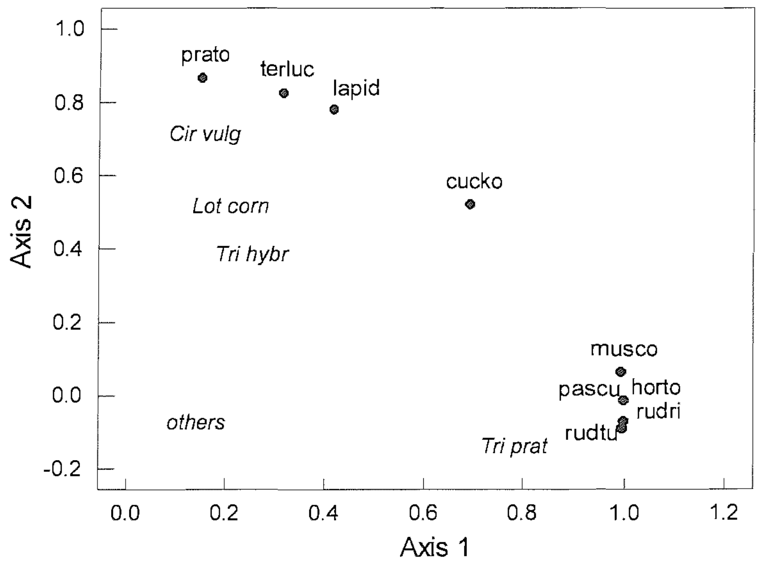


Figure 6.4 Principal Components Analysis biplot based on the proportion of visits to different plant species by different castes of *Bombus lapidarius*. Abbreviations of plant species as in Fig. 2, also: Cen nigr = *Centaurea nigra*; Dip full = *Dipsacus fullonum*. Visits to native and agricultural varieties of *T. pratense* and *L. corniculatus* were combined.

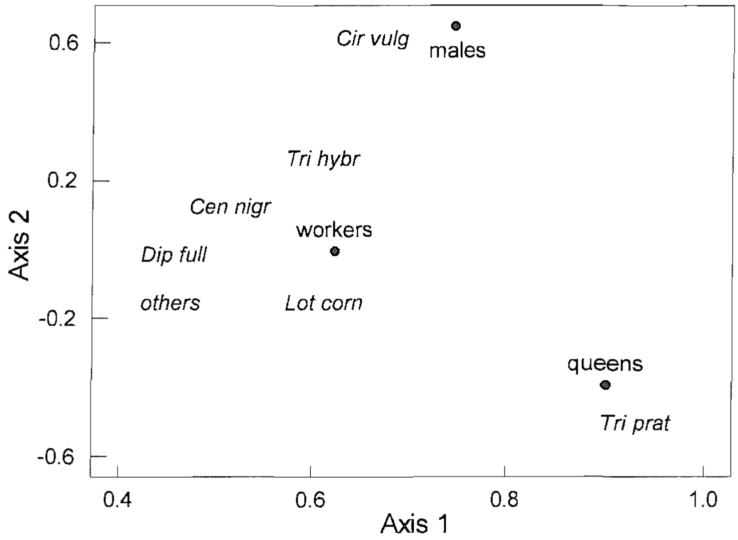


Figure 6.5 Seasonal effects of seed mixture composition on abundance of a) all flowers of bumblebee forage plants and b) all bumblebee species. White bars = early (May/June) transects; grey bars = late season (July/August) transects.

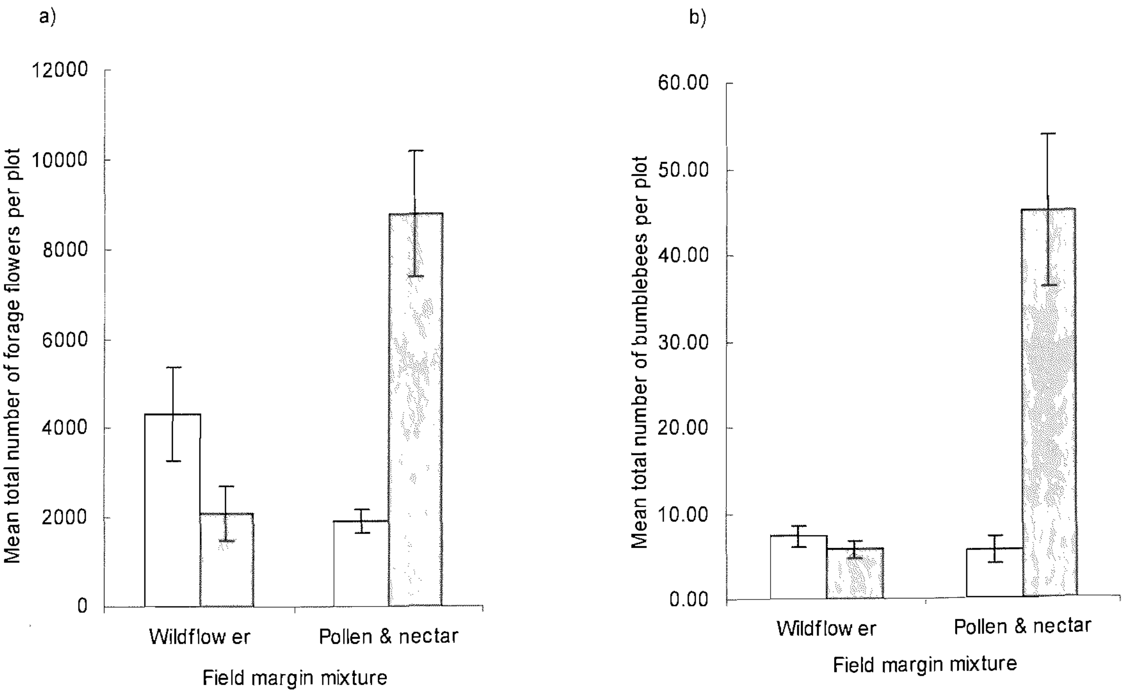
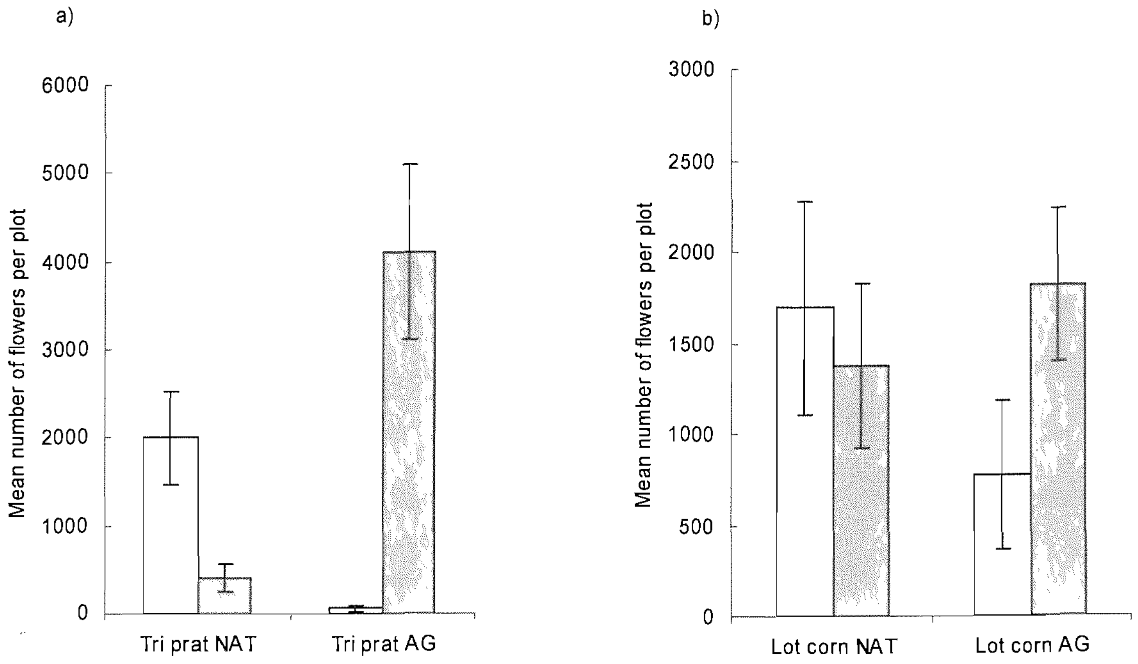


Figure 6.6 Seasonal differences in flower abundance of native vs agricultural varieties of a) *Trifolium pratense* and b) *Lotus corniculatus* in wildflower (NAT) and pollen and nectar (AG) mixtures. White bars = early (May/June) transects; grey bars = late season (July/August) transects.



Appendix 6A Seed mixture details for the three sown arable field margin treatments.

Wildflower (37 kg ha^{-1})	% of mixture
Grasses (80%)	
Cynosurus cristatus	24
Festuca rubra ssp commutata	28
Festuca rubra ssp juncea	16
Poa pratensis	12
Flowers (20%)	
Achillea millefolium	0.5
Centaurea nigra	1
Centaurea scabiosa	0.5
Daucus carota	1
Knautia arvensis	1.5
Leucanthemum vulgare	1.5
Leontodon hispidus	0.5
Lotus corniculatus	0.5
Lychnis flos-cuculi	0.5
Galium verum	1
Malva moschata	1
Plantago lanceolata	1
Plantago media	1
Primula veris	1
Prunella vulgaris	0.5
Ranunculus acris	2
Rhinanthus minor	1
Rumex acetosa	0.5
Sanguisorba minor	2
Silene dioica	1.5
Trifolium pratense	0.5

Tussocky grass (20 kg ha^{-1})	% of mixture
Cynosurus cristatus	20
Dactylis glomerata	10
Festuca pratensis	30
Festuca rubra ssp commutata	30
Poa pratensis	10

Pollen and nectar (20 kg ha-1)	% of mixture
Grasses (80%)	
Cynosurus cristatus	24
Festuca rubra ssp commutata	28
Festuca rubra ssp juncea	16
Poa pratensis	12
Legumes (20%)	
Trifolium pratense	6
Trifolium hybridum	3
Lotus corniculatus	5
Onobrychis viciifolia	6

7. Synthesis and final discussion

7.1 Synthesis of research

The research presented in this thesis has made a substantial contribution to our knowledge of some of the likely causes of bumblebee declines in Britain, and of the responses of different bumblebee species to various methods of habitat restoration. By quantifying the declines in range and frequency of forage plants which occurred during the 20th Century, I have provided new evidence of the loss of key nectar and pollen resources in the wider countryside. The severity and consistency of these declines across plant species are of concern not only from the perspective of food availability for bumblebees and other nectar and pollen-feeding insects, but also from the perspective of the native flora. A large number of previously widespread perennials and biennials (and arguably many other insect-pollinated plants not examined here) have become less common than before the onset of agricultural intensification. Balanced against this, the increase in growing of mass-flowering crops such as oilseed rape (*Brassica napus*) and more recently borage (*Borago officinalis*) and linseed (*Linum usitatissimum*), combined with the continued popularity of gardening in the UK, may enhance populations of some bumblebee species. However these changes are unlikely to cater for the full species assemblage of bumblebees or to compensate for the loss of seasonal continuity in forage provision typically achieved by natural and semi-natural plant communities. The findings in Chapter 2 therefore strengthen the argument for restoring bumblebee forage (and nesting) resources on farmland via the agri-environment schemes (AES), and recommend a list of plant species that can be included in seed mixtures. I will return to the subject of pollination and the implications of habitat restoration for native plant populations and crop yields later in this discussion.

The field margin experiment set up on Manor Farm in North Yorkshire and described in Chapter 3 provided an opportunity to study the response of foraging bumblebees to a series of management options for habitat restoration at a single site over three years. These management options represented prescriptions available under the UK Countryside Stewardship Scheme which, although not originally targeted at pollinating insects, had the potential to provide nectar and pollen sources and this required testing. The results were predictable in that where flower abundance of suitable forage plants (either introduced in seed mixtures or naturally established) was highest, bumblebee densities were also highest. Importantly though, the study demonstrated the need to consider successional changes in field margin vegetation both within and between years as a measure of success in establishment and persistence of the desired plant community. It also provided the first scientific evaluation of the benefits for bees of sown versus unsown management options for arable land within the Countryside Stewardship Scheme (CSS).

Findings from the first field margin study helped to inform the design of an experiment to investigate the value of three targeted bumblebee seed mixtures for potential inclusion in future CSS options. It had become clear that the Fabaceae (legumes) were an important forage resource for several species (Edwards, 2002; Goulson and Darvill, 2004), so *Trifolium pratense* was added as a key component of both 'diverse' and 'basic' perennial seed mixtures (having been absent from the first experiment) to be compared with an annual mixture containing *Borago officinalis* and other seed-bearing crops. The experiment further demonstrated the successional nature of flowering in different components of the seed mixtures and the influence this change in forage availability can have on forager densities. It also showed that when presented with a choice the shorter-tongued bumblebee species, as well as honeybees *Apis mellifera*, preferentially foraged at open-flowered annuals such as *B. officinalis*, whereas the longer-tongued species preferred perennials such as *T. pratense* as expected. Mixtures sown under the CSS would therefore need to contain this variety of plant species in order to benefit the full assemblage of social bee species. During the study, two prescriptions were introduced as New Arable Options in the CSS which closely mirrored the annual and basic perennial mixtures sown here. These were referred to as a wild bird seed mix (option WM1) and pollen and nectar mixture (option WM2) (Defra, 2001).

The novelty of this experiment (Chapter 4) was in the analysis of pollen loads, supplementing transect-based observations of foragers, as a means of better assessing the functional value of introduced forage mixtures for *Bombus pascuorum* and *B. terrestris*. High proportions of the loads carried by both species whilst visiting the experimental mixtures comprised pollen from sown plant species (*T. pratense* and *B. officinalis*). This suggests that many foragers may have been travelling directly from their nests to collect pollen and nectar from the sown mixtures without visiting additional patches of forage in between. This in turn suggests that the mixtures were providing a significant proportion of the pollen resource for developing larvae in nests local to the experimental margin and thereby enhancing colony fitness (Sutcliffe and Plowright, 1990). Several workers visiting the margin were also carrying pollen from plant species flowering elsewhere on the farm such as *Papaver rhoeas* and *Stachys sylvatica*, indicating that the sown mixtures were not consistently diverting all foragers away from existing native plant populations.

Chapter 5 describes a study which was designed to expand on the pollen analysis work from bees visiting a single field margin (as in Chapter 4). This involved constructing a map of pollen availability across the entire farm and relating it to the composition of pollen loads sampled from foraging workers in known grid squares. Despite fairly small sample sizes, the results confirmed the preferences for contrasting pollen types shown by *B. pascuorum* and *B. terrestris*. They highlighted the degree of flower constancy in terms of pollen collection which can occur, regardless of flowering plant diversity in a given forage patch. The study also provided some evidence of the spatial nature of foraging patterns which could be further investigated using this approach. The composition of several sampled pollen loads suggested that in a landscape with spatially and temporally patchy resources, 'constancy' is not an exclusive foraging strategy, and that workers may regularly forage at plants separated by hundreds of meters in a single foraging trip.

Finally, the results of a comparative study of different options for arable field margin management within the AES are presented (Chapter 6). This study allowed the generality of the response of foraging bumblebees shown at Manor Farm (Chapter 3) to be tested across six farms in central and eastern England, bringing the opportunity to observe rare as well as common *Bombus* species. While in general the response was consistent across all farms, marked differences in forage provision and bumblebee species composition were shown both within seasons and between years, depending on management option and seed mixture composition. Taken together with the other studies these findings suggest that given appropriate management, and for most arable situations, introduced seed mixtures, newly created habitats can attract large numbers of bumblebees, including rare species, and supply a significant proportion of their foraging resources which would otherwise be absent from the arable landscape.

7.2 Critique of methods used

While significant progress has been made in achieving the aims of the thesis, there are a few caveats connected to the methods I have used. These are worthy of discussion here as they are relevant to the interpretation of the data but have only been briefly highlighted in the submitted papers.

7.2.1 Transects

The transect method was used to estimate abundance of foraging bumblebees on the various experimental field margins and hence compare the attractiveness of different management options in terms of providing floral resources for bees nesting in the vicinity. This has allowed management recommendations to be made, but what do the results tell us about repeatability of the findings or the status of the bumblebee populations under study? A quantitative comparison of the mean total bumblebee density per square metre estimated using transects in this thesis versus equivalent estimates from other studies in agricultural landscapes is shown in Table 7.1. Where different habitat types were assessed, transect data for that providing the highest density of forage plants was selected. An encouraging result is the relative similarity in densities recorded on the Manor Farm experiment in Chapter 4 with those on the pollen and nectar mixture in the six site experiment in Chapter 6 (ranging from 0.08 – 0.1 per m^2). These also concur with densities recorded by Pywell et al. (2005b; 2006) on field margins in England sown with flower-rich mixtures under AES, and with densities on field margins in Sweden sown with a clover-based mixture (Lagerlof et al., 1992). Similarities with the other studies are less clear, and these data serve to highlight the main caveats associated with the interpretation of data from transects conducted at different sites and in differently structured landscapes.

Firstly, bumblebee density in a given habitat patch cannot be considered in isolation from the surrounding matrix of available habitats. An increasing number of studies have attempted to relate both species richness and density of flower-visiting bumblebees to landscape variables such as the proportion of arable land or grassland (Steffan-Dewenter and Tscharntke, 1999; Bäckman and Tiainen, 2002; Mand et al., 2002; Steffan-Dewenter et al., 2002; Hirsch et al., 2003; Westphal et al., 2003; Pywell et al., 2006). Several have identified positive correlations between species richness and the availability of semi-natural habitats, consistent with the effects of agricultural intensification on habitat quality for declining *Bombus* species (e.g. Pywell et al., 2006). However, the relationship with bumblebee density is less conclusive and may depend to a large extent on the species under study and the scale at which analyses are conducted (Steffan-Dewenter et al., 2002).

For example, Westphal et al. (2003) found that availability of semi-natural habitats at scales up to 3 km did not affect the density of *B. terrestris* agg., *B. lapidarius* and *B. pascuorum* foragers on plots of *Phacelia tanacetifolia* in agricultural areas of Germany. Density was, however, related to the availability of mass flowering crops (mainly oilseed rape). In contrast, across the different regions of England, Pywell et al. (2006) found that density of long-tongued bumblebees (e.g. *B. pascuorum* and *B. hortorum*) on flower-rich field margins was highest in regions with mixed farming (hence more semi-natural habitat). This density parameter was also positively related to the number of ES margins sown with the 'pollen and nectar' mixture within the 10-km square. Are more bumblebees attracted to a flower-rich strip between arable fields because other resources within foraging range are scarce, or because that landscape supports more successful colonies? Conversely, in a more heterogeneous landscape, should we expect to record fewer foragers per unit area, because they are dispersed across a greater number of available forage patches? The potential for transect-based observations to fully answer these questions may be limited. However, novel techniques using molecular microsatellite markers have recently been developed which allow the number of colonies represented by workers sharing a forage patch to be estimated, by identifying related sisters among a sample (Chapman et al., 2003; Darvill et al., 2004; Knight et al., 2005). Using this approach across a variety of sites could offer a powerful means of comparing nest densities and foraging ranges in differently structured landscapes.

Secondly, at a more local scale, the density of foragers on a transect is likely to relate to its area (assuming even forage plant distribution) and to the size of the patch in which it is located. The design of our field margin experiments allowed patch size to remain constant (within studies), and transects covered the entire area of each treatment patch. Studies have shown, however, that more foragers are attracted to larger patches, that they generally spend more time in larger patches and visit more flowers while resident in them (Goulson, 2003; Cresswell and Osborne, 2004). Sowig

(1989) also found that patch size of forage plants affected the species composition of visiting bumblebees, with short-tongued species dominating in larger patches. This suggests that caution should be taken when comparing, for example, the very high bumblebee density per m^2 estimated by Walther-Hellwig and Frankl (2000) in *T. pratense* fields with that from transects along linear features (Table 7.1).

Thirdly, within a forage patch, many factors influence whether a bee will choose to visit one forage species or plant over another. These include flower morphology, flower age, scent, colour, availability of nectar and pollen and prior visitation by nest mates, conspecifics or other insect species (e.g. Heinrich, 1976; Goulson et al., 1998; Goulson, 2003). Foragers may, for example, abandon specialisation in favour of generalisation when their preferred flowers are scarce (Kunin and Iwasa, 1996; Chittka et al., 1997). In two of my experiments (Chapters 4 and 6), bees were presented with a choice of a clover-dominated mixture or a more diverse wildflower mixture containing clover flowers dispersed among other rewarding species. Might foragers have switched to these other species and disproportionately avoided clovers in the more diverse mixture? Evidence from the *B. pascuorum* pollen loads suggested that this did not occur to a significant degree, although of course we cannot be sure how long workers had been resident in each plot when pollen sampling occurred. Whatever the factors influencing flower choice, it is assumed here that differential visitation rates of individuals or species are an indicator of those resources (or management options) that are most or least likely to enhance colony success and thereby benefit the local population.

7.2.2 Pollen load analysis

The merits of analysing pollen loads collected by workers in contrasting forage patches have been outlined above (Section 7.1 and in the relevant chapters). Based on the high degree of flower constancy and high pollination probability index (PPI) shown for preferred forage plants, it was concluded that these plant species (e.g. *T. pratense*) may have a higher probability of pollination by bumblebees than other less favoured pollen source species on the farm (Chapter 5). However, pollen was sampled only from the corbiculae or pollen baskets where it may be less readily available for pollination than when scattered on the hairs of a bees' thorax (Ne'eman et al., 1999). I am aware of no studies that have compared the composition of pollen types actively combed into the corbiculae and intended for transport to the nest with those found elsewhere on the bee. It would be interesting to know if these were closely correlated as if not, the contents of a pollen load alone may be a poor indicator of pollination probability.

Finally, answering further questions about the farm-scale movements of bumblebees between nests and forage patches may not be possible without knowledge of their nest locations which are extremely hard to find. Recently, colonies imported from commercial breeders (Goulson et al., 2002; Ings et al., 2006) or reared in captivity from native queens (Muller and Schmid-Hempel

1992; Pelletier and McNeil, 2003; Osborne, pers. comm.) have been used as surrogates for naturally founded nests to study aspects of their survival and pollen foraging. Further studies of this nature are urgently required on a range of bumblebee species in order to better understand the effects of different landscape attributes on colony success and the influence of agri-environment schemes on these interactions.

Table 7.1 Bumblebee density estimates from different studies using transects conducted in agricultural landscapes. (* this may represent an over-estimate as the data were scaled up by the authors from counts in 2 x 2m quadrats within *T. pratense* fields)

Author	Location	Habitat	Approx. flower density	Social *Bombus* Castes (P = *Psithyrus*)	Mean number bumblebees per transect over season	Unit area of transect, m^2	Mean Bumblebee density per m^2
Carvell et al. (Ch 3)	Manor Farm, Yorkshire	Wildflower mix	moderate - high	W + Q + M	12.2	432	0.03
Carvell et al. (Ch 4)	Manor Farm, Yorkshire	Basic perennial clover mix	high	W + Q + M	14.5	180	0.08
Carvell et al. (Ch 4)	Manor Farm, Yorkshire	Annual borage mix	high	W + Q + M	22.8	180	0.13
Carvell et al. (Ch 6)	6 sites C & E England	Pollen & nectar legume mix	high	W + Q + M	29.5	300	0.10
Pywell et al., 2005b	E Anglia & W Midlands	Wildlife seed mix	moderate - high	W + Q + M (+ P)	37.5	600	0.06
Pywell et al., 2006	England regions	Pollen & nectar legume mix	high	W + Q + M	42.8	600	0.07
Kells et al., 2001	W Midlands	Uncropped margins	moderate	W + Q + M (+ P)	22.1	25	0.88
Edwards, 2005	4 sites C England	Pollen & nectar legume mix	high	W + Q + M	172.9	200	0.86
Walther-Hellwig & Frankl, 2000	W Germany	*Trifolium pratense* field	high	W + Q + M (+ P)	447 *	400	1.12
Walther-Hellwig & Frankl, 2000	W Germany	Roadside verge	low - moderate	W + Q + M (+ P)	8	400	0.02
Bäckman & Tiainen, 2002	S Finland, Porkkala	Field margins	high	W + Q + M (+ P)	2338	10000	0.23
Lagerlof et al., 1992	Uppsala, Sweden	*Trifolium pratense* margin mix	high	W + Q + M	1.3	20	0.07

7.3 The potential role of habitat restoration and enhancement for the conservation of bumblebee species in Britain

In considering whether the restoration and enhancement of habitats for bumblebees in agricultural landscapes can play a significant role in their conservation, a number of questions need to be addressed. These fall into four general areas, some of which have been considered directly in this thesis and others which I will discuss in the context of requirements for further research:

1. the quality of the existing landscape for bumblebees: should restoration be targeted to particular landscape types?
2. the relative suitability of restoration measures for different bumblebee species: can similar measures cater for all species and how much habitat is required?
3. the implications for other taxa (particularly other pollinating insects and insect-pollinated plants): do field margin mixtures facilitate pollination of nearby crops and native plants? and
4. the ability of the current policy framework to deliver what is required to conserve sustainable bumblebee populations in the wider countryside.

7.3.1 Landscape quality and targeting

What defines the quality of the existing agricultural landscape for bumblebees and should habitat restoration be targeted for maximum effect? This is likely to depend on a combination of farming type and management intensity (Tscharntke et al., 2005). The arable flora has become progressively impoverished for bumblebees as a result of the increased use of fertilisers and efficiency of modern herbicides and pesticides, combined with the actual loss of uncropped habitats (e.g. Smart et al. 2005). Although the land area under cereal cropping in the UK has marginally reduced over the last decade, approximately 4.4 million hectares are under arable farming, representing 26% of the total area of agricultural land (Defra, 2006). As already discussed, the recent suggestion that oilseed rape enhances colony fitness such that it could make a significant contribution to bumblebee conservation (Westphal et al., 2003) is only likely to hold true if mass flowering crops with alternative flowering periods such as borage, lupins and sunflowers are also grown. A switch to spring sowing of entomophilous crops, as encouraged under the new AES, may also extend their flowering periods and hence increase the availability of large areas of forage. However these may still pose a risk if pesticide applications are involved (Thompson, 2001). Ultimately, the enhancement of bumblebee habitats in predominantly arable landscapes such as in Central and Eastern England will be best achieved via an increase in area of uncropped land. Options for arable land under ES, as shown here (Chapter 6), have much potential to provide both short- and longer-term foraging habitats on this uncropped land. These habitats can attract bumblebees within a year of establishment, even in landscapes which are characterised by high proportions of arable land.

Forage may be the most limiting factor for bumblebee populations but it is not the only habitat component requiring conservation. Undisturbed nesting and hibernation sites are also essential and are likely to be particularly scarce in intensive arable areas Fussell and Corbet, 1992). Goulson (2003) points out that as early as the 1940s, Skovgaard argued for the protection of uncultivated refuges on agricultural land to provide bumblebee nest sites. Although nest site provision has not been quantified here (due to practical constraints on locating successfully established nests) two other studies have assessed nest site preferences in agricultural areas by observing queens performing nest-searching behaviour. Svensson et al. (2000) found that over a total transect distance of approximately 96 km through intensive and wooded farmland in Sweden, 147 nest-searching queens were encountered. Interestingly, when Kells and Goulson (2003) surveyed 86 km of extensively (and organically) farmed land in Hampshire, UK, using an apparently similar approach, they encountered 1287 nest-searching queens of similar species composition. If this difference reflects queen and potential nest density in the two landscapes, it confirms that greater proportions of semi-natural habitat in boundaries and open grassland are preferable. The planting and conservation of hedgerows (Croxton et al. 2004) and establishment of undisturbed tussocky grass margins or 'beetlebanks' via ES, in addition to forage mixtures, can increase nesting opportunities for both underground and surface-nesting bumblebees on farmland.

This thesis has not specifically investigated the effects of habitat management for bumblebees in areas of grassland and livestock farming. I have previously shown that extensive cattle grazing is the most effective management regime across large areas of unimproved grassland to create flower-rich swards which support a diverse bumblebee community (Carvell, 2002). This situation is not, however, typical of most of the UK. Permanent agricultural grassland (over 5 years) and grassland under 5 years old covers respectively 5.7 and 1.2 million hectares in the UK, representing approximately 40% of agricultural land (Defra, 2006). Intensive reseeding and application of inorganic fertilisers in place of traditional hay production and clover leys (Chamberlain et al., 2000) have left most of these lowland grasslands structurally uniform and species poor. Even the 30% of land covered by rough grazing is subject to high stocking densities, with restricted floral resources for bees.

There has been considerable research effort into the restoration and re-creation of species-rich grasslands via, for example, long-term reversion of arable land (Pywell et al., 2002; Walker et al., 2004). Options for this re-creation are available under HLS (Defra, 2005b), but may only be feasible in a few situations close to existing species-rich grassland due to the limiting processes involved. Opportunities for more widespread enhancement of buffer strips and field corners on intensive grassland are available under ELS (including by sowing pollen and nectar mixtures, option EG3; Defra, 2005a). Few studies have quantified the benefits of these options for pollinators, although initial results from the PEBIL project in SW England suggest that margins of grass fields sown or undersown with a legume-based mixture can attract large numbers of bumblebees (www.rdg.ac.uk/caer/project_pebil). Priority should now be given to research into agronomic aspects of these management options on both arable land and grassland. Given successful establishment, how long can they be expected to provide sustained forage resources (Chapter 6)? Should the fine grass component be replaced with *Lolium perenne* on intensive grassland or removed altogether?

Ultimately, the restoration or re-creation of bumblebee habitats may prove most effective in areas of mixed farming where existing populations are available to colonise them (Pywell et al., 2006; Figure 7.1). In addition, organic farming offers great potential because of the tendency for smaller field sizes and use of rotations involving legumes such as *T. pratense*. A recent study found up to thirteen times more foraging bumblebees on 'small' organic farms than on large conventional farms in Sweden (Belfrage et al., 2005). However, the question remains as to how we can best measure or quantify 'effective' restoration. This could be defined as having been achieved when an area has reached its potential to support stable or increasing bumblebee populations over time. The transect-based data presented here did not give a clear indication of this pattern, although bumblebee density per square metre at Manor Farm was nearly three times higher in plots from the second study (Chapter 4) compared to the first (Chapter 3) following increased habitat creation across the whole farm (Table 7.1). The genetic techniques outlined above probably offer the most powerful tool for assessing the effectiveness of AES in enhancing populations in different regions and landscape types, at least for the common *Bombus* species for which adequate sample sizes can be obtained (Knight et al., 2005; also see www.ceh.ac.uk/sections/epms/bumblebee). The implications for rare and declining species are considered in the following section.

7.3.2 Consequences for different bumblebee species

Throughout this thesis, emphasis has been given to the forage plant preferences of the different species and how these affect their responses to different field margin management regimes. In particular, the importance of long corolla flowers for the longer-tongued bumblebees, as evidenced by high proportions of nectar and pollen-foraging visits to *T. pratense*, *T. hybridum*, *Lotus corniculatus*, *Lathyrus pratensis* and *Rhinanthus minor*, highlights the value of these species when sown in mixtures. The data have also confirmed the attractiveness of particular species to males (e.g. *Centaurea nigra* to *B. lapidarius*) and queens at the beginning and end of the season. It seems we now have sufficient information from which to create the 'best' mixture, whether it be a legume-based 'pollen and nectar mix' (ideally with the addition of *C. nigra* or *Centaurea cyanus*), an annual 'cover crop' which could contain both long and short corolla forage plants or a more diverse and longer-lived wildflower mix. It is likely that a combination of these mixtures sown along different field margins on a farm may be the best means of providing forage for the full bumblebee species assemblage over the season. Many seed merchants have responded to the increased demand for such mixtures and now advertise a range of 'bee-friendly' products (e.g. www.cotswoldseeds.com/ environmental; www.wildseed.co.uk; Richard Brown pers. comm.).

However, as discussed in Chapter 2, there are many other differences in ecological and behavioural traits between *Bombus* species, besides flower preferences, that are likely to have determined their responses to agricultural change and will naturally determine their responses to agri-environment schemes. These include the timing of queen emergence, preferred nesting habitat, colony size, nest density, foraging range, dispersal ability and range size (see Edwards and Williams (2004), Williams (2005) and Benton (2006) for full accounts). While the six common or 'universal' species appear able to locate and utilise newly created forage patches on arable farmland (with the possible exception of *B. pratorum* which may generally be more common in gardens), can the same be said of the rarer species? Evidence accumulated over the past few years suggests that it can, given sufficient proximity to existing populations, as outlined in the following examples. This is important if AES and other conservation efforts are to succeed in increasing species richness of bumblebee communities as well as the density of individual species.

In this study, *Bombus ruderatus* (a BAP species) was recorded on farms in Cambridgeshire and Bedfordshire and, together with other field margin studies, these observations have significantly extended the known coverage of occupied 10-km squares for the species (Carvell et al., 2006). The three rare carder bumblebees, *B. muscorum* (proposed BAP species), *B. humilis* (BAP species) and *B. sylvarum* (BAP species) have a strong association with unimproved grasslands, but each was recorded on arable field margins sown with the 'pollen and nectar mix' surveyed by Pywell et al. (2006) in at least one of the regions containing known populations. *B. muscorum* and *B. humilis*, which have predominantly coastal distributions, have also shown signs of persistence at suitably managed foraging habitats in excess of 10 km from their known strongholds such as Romney Marsh in Kent (Edwards, pers. comm.), the Essex coast (*B. muscorum*; Benton, 2006; this study) and urban nature reserves or ex-industrial sites along the Thames estuary (*B. humilis*; Chapman, 2004). *B. sylvarum* has probably suffered the most serious decline of the three species, yet in South Wales, foraging workers have been recorded on organic farms up to 4 km from the core population at Castlemartin Ranges and at a restored mining site 8 km from the core at Kenfig National Nature Reserve (Carvell, 2000). Both sites supported very high densities of preferred forage plants through to early autumn (e.g. *Trifolium pratense* and *Odontites vernus*), a condition that is perhaps more important for *B. sylvarum* than for the other two species (Benton, 2006).

While a full discussion of the implications of habitat restoration for every British bumblebee species is not feasible here, three further species warrant a brief note. *B. distinguendus*, like the four mentioned above, is a long-tongued species which appears to be declining rapidly. However, it may never have been abundant in England and Wales, and now survives only in northern Scotland, where it is the focus of much autecological and conservation-based research (Edwards, 2001; Charman pers. comm.). For *B. distinguendus*, habitat restoration is likely to apply mainly in the form of grazing management and preservation of the species-rich machair grasslands in these areas, rather than targeted sowing of field margins under AES in lowland landscapes. The same may be true for *B. monticola* (proposed BAP species) and partly also for *B. jonellus*. Both species are short to medium-tongued and have a strong association with heathland and moorland habitats in western and northern upland areas. Studies have confirmed the importance of bilberry (*Vaccinium myrtillus*) and heathers (*Erica cinerea, E. tetralix*) as pollen and nectar sources from these core habitats. However, for *B. monticola* in particular, these species alone do not provide sufficient continuity of forage so the presence of adjacent grassland habitats containing *Lotus corniculatus* and *Trifolium repens* is essential for colony survival (Hewson, 2000; Edwards, 2002). Both Entry and Higher Level Stewardship options for the uplands (Defra, 2005c) aimed at reducing grazing intensity in such grasslands and maintaining early-successional flowering on moorland habitats (e.g. former 'Environmentally Sensitive Areas') are likely to contribute to the conservation of *B. monticola* and *B. jonellus*, which may never be a common feature of lowland agricultural landscapes.

Providing suitable foraging habitats within range of existing populations can therefore attract many of the rarer bumblebee species to agricultural areas, but how much of this suitable habitat is required to sustain populations? The relationship between local habitat quality and quantity at the larger scale is complex, and it is still not clear to what extent an area of good quality habitat (e.g. a field margin with high density of forage plants) is equivalent to a greater area of lower quality habitat (Thomas et al., 2001). Most insects in fragmented agricultural landscapes are thought to exist as metapopulations, with colonisation between sub-populations depending on their size, degree of habitat connectivity and dispersal ability of the species (Hanski and Gilpin, 1991). Bumblebees have a low effective population size, being social insects for which the reproductive population is a function of the number of successful nests rather than the number of individuals. They may therefore be particularly susceptible to inbreeding and other effects suffered by isolated sub-populations (Chapman and Bourke, 2001), and as a consequence, require large areas of habitat to maintain genetic viability and optimal nest density.

The available evidence (though anecdotal) suggests that for species with specialised requirements such as *B. sylvarum* and *B. humilis*, at least 10 km^2 of suitable habitat may be needed, as no surviving populations in Britain are known from areas smaller than this (Edwards, 2001). I have estimated the *B. sylvarum* metapopulation at Castlemartin in South Wales to exist over at least 30 km^2, with 'satellite' colonies surviving on habitat patches isolated by at least 4 km from the core population. Together with *B. muscorum*, these species appear to have more restricted foraging ranges (perhaps in the order of 300 – 1000 metres) (Walther-Hellwig and Frankl, 2000) and smaller colony sizes than the more common and widespread species such as *B. terrestris* and *B. lapidarius* which often forage at more than 1 km and sometimes up to 5 km from the nest, thus may be better able to exploit newly created habitats in the agricultural matrix (Osborne et al., 1999; Knight et al., 2005).

Direct measures of queen dispersal ability are still lacking, but a recent study by Darvill et al. (2006) provides alarming evidence that isolated sub-populations of *B. muscorum* exhibit reduced genetic diversity compared to common species such as *B. pascuorum*, and may suffer from inbreeding. Genetic differentiation was evident between all populations separated by 10 km or more, suggesting that dispersal rarely occurs over a greater distance than this. The two populations sampled in south east England and separated by 49 km were, however, more heterozygous with higher allelic richness than those on the Hebridean islands (Darvill et al., 2006). Until recently, these populations were probably part of a larger *B. muscorum* metapopulation extending across southern England. If this situation is representative of other rare *Bombus* species, it underlines the urgency for habitat creation in order to prevent genetic bottlenecks and reduced effective population sizes. Furthermore, if the effects of climate warming intensify, habitat 'corridors' may be required to facilitate the ability of species to track the distribution of suitable climates (Warren et al., 2001).

In conclusion, based on the available evidence, the provision of two to three flower-rich field margins covering in total around one hectare within each square kilometre of agricultural land, linking larger areas of extensively managed semi-natural grassland, may be sufficient to sustain bumblebee metapopulations. The time needed to establish gene flow across newly created habitats may be longer for some of the rarer species, and this should be monitored using appropriate techniques, but colonisation and exchange is likely to occur if the right habitats are sustained. Whether considering currently rare or widespread and common species, efforts should undoubtedly be focused not on individual farms or sites, but at landscape and regional scales.

7.3.3 Implications for other taxa

The restoration of suitable habitats for bumblebees is likely to benefit a large number of other taxa in agroecosystems. Many of these taxa have also been the targets of AES or Biodiversity Action Plans, and can be considered beneficial species in terms of providing ecosystem services such as biological control and pollination (Marshall and Moonen, 2002). Other pollinating insects, especially solitary bees, honeybees, butterflies and hoverflies (Syrphidae), share nectar and pollen source species with bumblebees and have been shown to benefit from flower mixtures sown in a variety of agricultural situations (Lagerlof et al., 1992; Feber et al., 1996; Meek et al., 2002; Carreck and Williams, 2002; Pywell et al., 2004; Pontin et al., 2006). Some (e.g. solitary bees and hoverflies) may prefer to visit open-flowered species such as the Asteraceae, rather than the long-corolla species preferred by long-tongued bumblebees (Cowgill et al., 1993; Westrich, 1996), so seed mixture composition can be adjusted to attract a greater diversity of pollinators. In the field margin experiment described in Chapter 6, suction sampling and sweep-netting revealed that the diverse wildflower mixture was attractive to the widest range of invertebrates when compared to the other treatments (Meek et al., 2004). The 'pollen and nectar mixture' did, however, attract large numbers of butterflies and other flower visiting insects, and provided vegetation structure suitable for canopy-dwelling spiders and bugs. It is important to acknowledge the possibility that introduced flower mixtures may lead to unwanted non-target effects, such as an increase in pest populations (Baggen et al., 1999). The dynamics of multiple species responses to introduced habitats require further investigation, but research to date suggests that the benefits as discussed here are likely to far outweigh any costs.

The provision of suitable bumblebee nesting habitats along hedgerows and field margins is also likely to benefit animals which require a dense, sheltered vegetation structure. These include overwintering beetles and spiders (Pywell et al., 2005a), small mammals (Gorman and Reynolds, 1993) and some foraging and breeding birds (Marshall and Moonen, 2002; Vickery et al., 2004). Furthermore, bumblebee foragers and nests are predated to varying degrees by insectivorous birds, badgers, shrews and mice (Alford, 1975; Goulson, 2003) so an increase in bumblebee populations could provide a direct food source for these animals. Bumblebees also support a diverse array of parasites, commensals and parasitoids that feed on the adults, larvae or nest material.

These associations, combined with their importance as pollinators of several crops and many native plant species (as outlined in Chapter 1), make bumblebees 'keystone' species whose removal from agricultural landscapes could have serious consequences for the rest of the ecosystem (Kevan, 1991). They can also be considered 'umbrella' species, requiring a range of habitats at large spatial scales which support many other taxa (Simberloff, 1998), and 'indicators' of functioning and productive ecosystems because of their sensitivity to environmental change (Kevan, 1999). However, there is much potential for further research on the interactions between bumblebees, the plants they pollinate and the ecosystems supporting both bees and plants. How might the restoration and creation of flower-rich habitats, and the spatial distribution of these, influence plant-pollinator interactions in agricultural systems? Are they more likely to facilitate pollination of crops and native plants, or compete with these for pollinators?

The growing recent interest in describing plant-pollinator interactions takes us some way to answering these questions, although whether plant reproduction (seed set) is limited by pollination in many species is still subject to debate (Burd, 1994; Dicks, 2002; Ashman et al., 2004). There is evidence that seed-set in small, isolated plant populations is enhanced by bee visitation, that isolation from patches of semi-natural habitat results in decreased abundance and species richness of flower-visiting bees, and that this in turn results in reduced seed set (Steffan-Dewenter and Tscharntke, 1999; Hirsch et al., 2003). This suggests that by linking isolated habitat patches in the landscape and increasing local bee abundance, introduced flower mixtures along arable field margins are likely to facilitate interactions between bees and existing rare arable plants (see also Gibson et al., 2006). In this thesis, the analysis of pollen loads from both *B. pascuorum* and *B.*

terrestris foraging respectively at clover- and borage-dominated mixtures revealed visitation to less common species in the local landscape up to 600 metres away.

Crop pollination by native bees (of watermelon, *Citrullus lanatus*, in California) is enhanced on farms adjacent to or supporting a high proportion of semi-natural habitat (Kremen et al., 2004), although further evidence of this interaction for entomophilous crops in European landscapes is required. Whether field margin mixtures enhance pollination in adjacent crops at the local level probably depends on the flowering phenology and relative attractiveness of plants in the margin versus the crop (Pontin et al., 2006). Perhaps ensuring minimal overlap in flowering times between field margin and crop would reduce the risk of a negative competitive response occurring for pollinators. However, if margins sown with suitable forage plants can enhance bumblebee densities at the colony and population level, then this may translate to a facilitatory effect on crop pollination at least in the medium to long term.

7.3.4 The policy framework

Finally, what are the likely costs of these restoration measures to the farming industry, and is the current policy framework sufficient to deliver what is required? Agri-environment schemes (AES) are the most important policy instruments to protect biodiversity in agricultural landscapes, and all EU member-countries are obliged to develop and implement them. AES cover around 25% of all farmland in the 15 older EU countries (EU, 2005), costing up to 3.7 billion Euros a year (EEA 2002). Biodiversity conservation is, however, only one of several scheme objectives, many of which are broad and lack specific targets, making cost-benefit analyses difficult. Recent evaluation studies have questioned the effectiveness of European AES in conserving biodiversity, especially of rare species, thus creating concern amongst practitioners and scientists (Kleijn and Sutherland, 2003; Kleijn et al., 2006; Potts et al., 2006; Whitfield, 2006). Kleijn et al. (2006) tested an arguably limited number of management options and their small sample sizes may have precluded the detection of rare invertebrates. In many cases, positive effects of AES might only be apparent in the long term, so agreements would need to last for longer than the current 5 or 10 years. However, this thesis, along with studies on other taxa (e.g. Vickery et al., 2004; Walker et al., 2006), demonstrates that targeted, evidence-based habitat creation under Environmental Stewardship can provide almost immediate benefits to both widespread and rare bumblebee species. Whether these translate to reversed declines and population growth will require further monitoring.

AES payments in England have formed an increasing proportion of CAP subsidies since the decoupling of farm income from production in 2005 (Defra, 2006). While earlier schemes (not open to all farmers) perhaps failed to achieve widespread coverage of many options, around 13,000 land managers have taken up ELS agreements since August 2005 (www.defra.gov.uk/erdp/schemes/es/default). Uptake of the 'pollen and nectar mixture' option extends to around 700 agreements covering up to 700 hectares (Rural Development Service, pers. comm.). This suggests that there is potential for more widespread sowing of flower mixtures within existing agreements, but that better communication of management prescriptions and training of farmers is required. The seed mixture trialled in Chapter 6 is cost-effective at around £90 per hectare (€134), and offers a high proportion of the farmer's 'points target' (450 points per ha) for acceptance into the ELS scheme. This means of providing high quality foraging habitats for bumblebees is also fairly reliable, with agricultural legumes in the mixture establishing readily on fertile soils. The more diverse grass and wildflower mixture may prove more costly at between £300 and £850 per hectare (€446 - €1,263), but payments under HLS are designed to cover these costs. The availability of advisory networks and technology transfer groups such as the Farmed Environment Company (www.farmedenvironment.co.uk) will be important to ensure effective targeting and management of all scheme prescriptions.

To enable the conservation of British bumblebees and other taxa associated with agricultural landscapes, AES should be viewed as complementary to other policy instruments such as national BAPs. These exist for habitats and species both within and outside farmed areas (Figure 7.1). The UK BAP requires, for example, that the biodiversity of some 15,000 ha of cereal field margins is 'improved and restored' by 2010 (www.ukbap.org.uk/habitats). This target may soon be updated to specify flower-rich field margins providing pollen and nectar sources (Rural Development Service, pers. comm.). There are also targets aiming to restore up to 2000 ha of lowland calcareous grassland and lowland meadows of wildlife value at carefully targeted sites by 2010. For the five BAP *Bombus* species, current targets are perhaps less specific, but the need to combine habitat management on SSSIs with that under AES is clearly stated. This will in future require more effective targeting in areas surrounding known populations, as at present, information on the distributions of rare bumblebees available to RDS project officers within Defra may be out of date (Smallshire, pers. comm.). The restructuring of government agencies to form *Natural England* should ensure better integration of actions carried out under the BAP and AES. Greater consideration should also be given to the wider conservation benefits that AES may bring to non-farmed habitats, such as SSSIs, by restoring or 'softening' the agricultural matrix that separates them (Donald and Evans, 2006).

7.3.5 Conclusion and recommendations

In conclusion, I refer to an illustration that summarises the potential effectiveness of AES for conserving bumblebees in relation to landscape type and farming intensity (Figure 7.1). If 'effectiveness' is measured as the enhancement of bumblebee abundance and diversity, the shape of the curve is due to the availability of regional species pools for colonisation of restored habitats (start and end points may vary in different countries). As suggested by Tscharntke et al. (2005), and evidenced here, suitably managed AES options in 'simple' or typical agricultural landscapes can be highly effective. In 'cleared' landscapes with almost no semi-natural habitat, species pools may be inadequate to produce a measurable response to habitat management. Although such landscapes may be absent from Britain, the potential for AES to operate in intensive arable regions of eastern England and boost bumblebee numbers for additional benefits such as crop pollination should not be overlooked. In diverse landscapes supporting larger amounts of existing semi-natural habitat (e.g. within SSSIs), carefully targeted AES (see table) can also provide valuable habitats that are exploited by bumblebees, including rare species. However, in these areas schemes should be accompanied by habitat preservation and restoration to enhance floral diversity and nesting sites via other policy instruments, such as the Biodiversity Action Plan.

The recommendations of the thesis can be summarised as follows:

- Arable field margins are best enhanced for bumblebees by introducing seed mixtures of suitable nectar and pollen-producing plants (see Ch 1, Table 1.3; Ch 6, Appendix 6A);
- The management of forage mixtures in both arable and grassland situations requires further research to ensure a seasonal succession of flowering and better longevity. Interactions between forage mixtures and within-field flowering crops also require further study;
- The response of bumblebee populations to agri-environment schemes may be more effectively measured by techniques focusing on colony dynamics and nest density than by transect-based estimates of forager density on localised habitat patches. Knowledge of potential correlations between genetic estimates of nest density and transect counts could better inform future monitoring approaches;
- Better understanding of the metapopulation structure and dispersal ability of bumblebees is required in order to predict their response to management changes at the landscape scale, and determine interactions between agricultural land and protected semi-natural areas;
- Future success will require close links between policy makers, land managers and ecologists. It will also require a commitment to monitoring on the scale of a national scheme that enables the effects of habitat restoration on rare and common bumblebees to be studied, as well as interactions with other components of agricultural ecosystems.

Landscape type	Cleared	Simple	Complex/ Diverse
Farming type	Arable or grassland 'prarie'; absent from Britain?	Arable, grassland or mixed; much of Britain	Mixed organic or very low input; including or surrounding nature reserves, SSSIs etc.
Habitat management	Habitat creation?	Habitat creation and restoration via agri-environment schemes (AES)	Habitat preservation and restoration
Policy instrument		Environmental Stewardship (mainly Entry Level) with Single Farm Payment; Cereal field margin BAP	Environmental Stewardship (mainly Higher Level) with Single Farm Payment; Habitat and species BAPs; SSSIs
Best AES options for bumblebees		Pollen and nectar flower mix EF4/EG3 Wild bird seed mix (+ nectar/pollen-rich plants) EF2/EG2 Field corner management (+ grass and flower mix if seed bank poor) EF1/EK1 Uncropped, cultivated margins (depending on site conditions) EF11	Floristically enhanced grass margin HE10 Enhanced wild bird seed mix HF12 Maintenance, restoration and creation of species-rich, semi-natural grassland HK6 – HK8 Hay-making supplement HK18 Restoration of moorland and upland heathland HL10/HL11

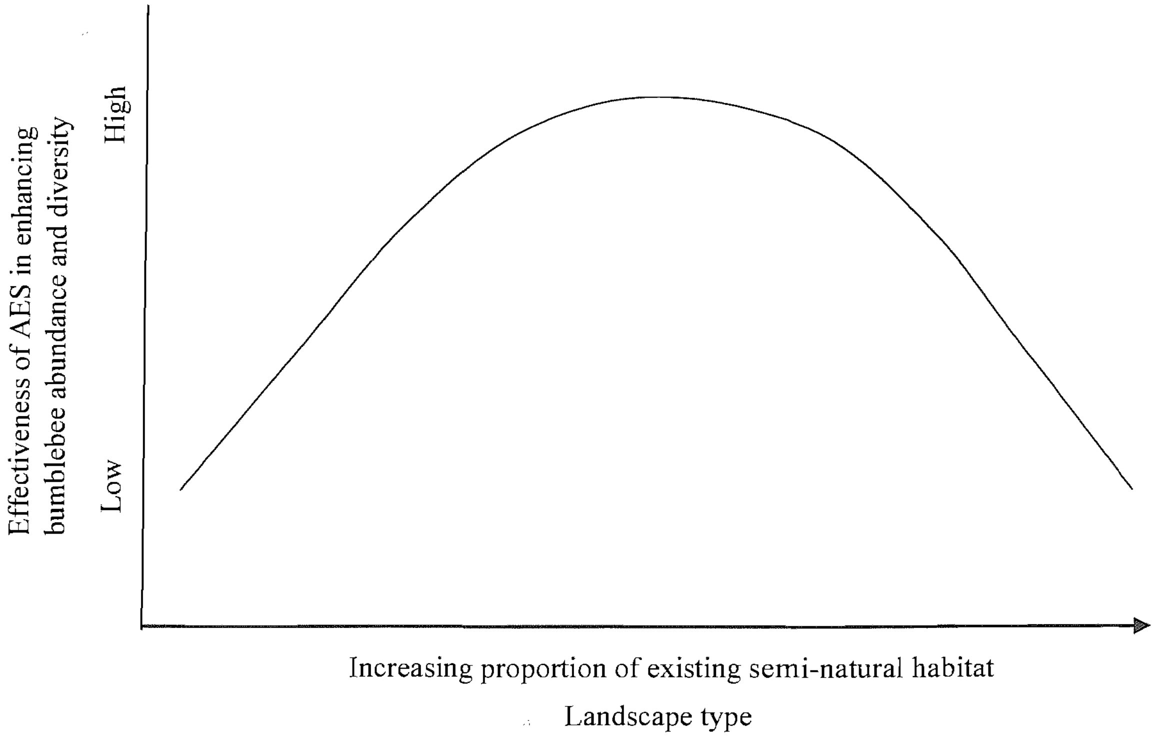


Figure 7.1 Illustration of the potential effectiveness of agri-environment schemes (AES) for conserving bumblebees in relation to landscape type and farming intensity (redrawn from Tscharntke et al., 2005). The table aligns with the graph, AES options referring to those available in England. See text for further explanation, section 7.3.5.

Full Bibliography

Alford, D.V., 1969. The study of the hibernation of bumblebees. Journal of Animal Ecology 38, 149-170.

Alford, D.V., 1975. Bumblebees. Davis-Poynter, London.

Alford, D.V., Ed., 1980. Atlas of the Bumblebees of the British Isles. Institute of Terrestrial Ecology, Cambridge, UK.

Anasiewicz, A., Warakomska, Z., 1977. Pollen food of the Bumble-bees (*Bombus Latr. Hymenoptera*) and their association with the plant species in the Lubin region. Ekologia Polska 25, 309-322.

Anonymous, 1995. Biodiversity - The UK Steering Group Report. Volume 2 Action Plans. HMSO, London.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P., Walker, S., 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conservation Biology 12, 8-17.

Allen, D.S., Gundrey, A.L., Gardner, S.M., 2001. Bumblebees. Technical annex to Ecological Evaluation of the Arable Stewardship Pilot Scheme 1998-2000. ADAS, Wolverhampton, UK.

Ashman, T.L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mazer, S.J., Mitchell, R.J., Morgan, M.T., Wilson, W.G., 2004. Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. Ecology 85, 2408-2421.

Asteraki, E.J., Hart, B.J., Ings, T.C., Manley, W.J., 2004. Factors influencing the plant and invertebrate diversity of arable field margins. Agriculture Ecosystems & Environment 102, 219-231.

Bäckman, J.P.C., Tiainen, J., 2002. Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera : *Bombus* and *Psithyrus*). Agriculture Ecosystems & Environment 89, 53-68.

Baggen, L.R., Gurr, G.M., Meats, A., 1999. Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. Entomologia Experimentalis et Applicata 91, 155-161.

Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology & Evolution 14, 63-68.

Banaszak, J., 1980. Studies on methods of censusing the numbers of bees (Hymenoptera: Apoidea). Polish Ecological Studies 6, 355-366.

Banaszak, J., 1992. Strategy for Conservation of Wild Bees in an Agricultural Landscape. Agriculture Ecosystems & Environment 40, 179-192.

Banaszak, J., 1996. Ecological bases of conservation of wild bees. In Matheson, A., Buchmann, S.L., O'Toole, C., Westrich P., Williams, I.H. (Eds.), The Conservation of Bees. Linnean Society Symposium Series 18. Academic Press, London.

Barrow, D.A., 1983. Ecological studies on bumblebees in South Wales with special reference to resource partitioning and bee size variation. PhD thesis, University of Wales, Cardiff.

Begon, M., Harper, J.L., and Townsend, C.R., 1990. Ecology; individuals, populations and communities. Second Edition. Blackwell Scientific Publications, UK.

Belfrage, K., Bjorklund, J., Salomonsson, L., 2005. The effects of farm size and organic farming on diversity of birds, pollinators, and plants in a Swedish landscape. Ambio 34, 582-588.

Benton, T., 2006. Bumblebees. Collins, London.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution 18, 182-188.

Bignal, E.M., 1998. Using an ecological understanding of farmland to reconcile nature conservation requirements, EU agriculture policy and world trade agreements. Journal of Applied Ecology 35, 949-954.

Brian, A.D., 1951. The pollen collected by bumble-bees. Journal of Animal Ecology 20, 191 – 194.

Brian, A.D., 1954. The foraging of bumblebees. Bee World 35, 61-67; 81-91.

Buchmann, S.E., Nabhan, G.P., 1996. The Forgotten Pollinators. Island Press, Washington DC, USA.

Burd, M., 1994. Bateman Principle and Plant Reproduction - the role of pollen limitation in fruit and seed set. Botanical Review 60, 83-139.

Carreck, N.L., Williams, I.H., 1997. Observations on two commercial flower mixtures as food sources for beneficial insects in the UK. Journal of Agricultural Science, Cambridge 128, 397-405.

Carreck, N.L., Williams, I.H., Oakley, J.N., 1999. Enhancing farmland for insect pollinators using flower mixtures. In Field Margins and buffer zones: ecology, management and policy. Aspects of Applied Biology 54, 101-108.

Carreck, N.L., Williams, I.H., 2002. Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. Journal of Insect Conservation 6, 13-23.

Carvell, C., 2000. Studies of the distribution and habitat requirements of *Bombus sylvarum* (the Shrill Carder Bee) and other bumblebees at Castlemartin Range, Pembrokeshire and Kenfig National Nature Reserve, Glamorgan and surrounding areas. Countryside Council for Wales, Bangor, UK.

Carvell, C., 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. Biological Conservation 103, 33-49.

Carvell, C., Meek, W.R., Pywell, R.F., Nowakowski, M., 2004. The response of foraging bumblebees to successional change in newly created arable field margins. Biological Conservation 118, 327-339.

Carvell, C., Pywell, R.F., Heard, M.S., Meek, B., 2006. The potential value of Environmental Stewardship Schemes for the BAP bumblebee, *Bombus ruderatus* (Fabricius) (Hymenoptera: Apidae). Entomologist's Gazette 57, 91 - 97.

Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F., Nowakowski, M., 2006. Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. Apidologie 37, 326-340.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubb, M., 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. Journal of Applied Ecology 37, 771-788.

Chapman, R.E., 2004. The Foraging Ecology and Conservation of Bumblebees in Urban Areas. PhD thesis. University College London.

Chapman, R.E., Bourke, A.F.G., 2001. The influence of sociality on the conservation biology of social insects. Ecology Letters 4, 650-662.

Chapman, R.E., Wang, J., Bourke, A.F.G., 2003. Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. Molecular Ecology 12, 2801-2808.

Chittka, L., Gumbert, A., Kunze, J., 1997. Foraging dynamics of bumble bees: Correlates of movements within and between plant species. Behavioral Ecology 8, 239-249.

Corbet, S.A., 1995. Insects, plants and succession: advantages of long-term set-aside. Agriculture, Ecosystems & Environment 53, 201 – 217.

Corbet, S.A., 2000. Conserving compartments in pollination webs. Conservation Biology 14, 1229-1231.

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

Cowgill, S.E., Wratten, S.D., Sotherton, N.W., 1993. The selective use of floral resources by the hoverfly *Episyrphus-balteatus* (Diptera, Syrphidae) on farmland. Annals of Applied Biology 122, 223-231.

Cresswell, J.E., Osborne, J.L., 2004. The effect of patch size and separation on bumblebee foraging in oilseed rape: implications for gene flow. Journal of Applied Ecology 41, 539-546.

Critchley, C.N.R., Allen, D.S., Fowbert, J.A., Mole, A.C., Gundrey, A.L., 2004. Habitat establishment on arable land: assessment of an agri- environment scheme in England, UK. Biological Conservation 119, 429-442.

Croxton, P.J., Carvell, C., Mountford, J.O., Sparks, T.H., 2002. A comparison of green lanes and field margins as bumblebee habitat in an arable landscape. Biological Conservation 107, 365-374.

Croxton, P.J., Franssen, W., Myhill, D.G., Sparks, T.H., 2004. The restoration of neglected hedges: a comparison of management treatments. Biological Conservation 117, 19-23.

Darvill, B., Ellis, J.S., Lye, G.C., Goulson, D., 2006. Population structure and inbreeding in a rare and declining bumblebee, *Bombus muscorum* (Hymenoptera : Apidae). Molecular Ecology 15, 601-611.

Darvill, B., Knight, M.E., Goulson, D., 2004. Use of genetic markers to quantify bumblebee foraging range and nest density. Oikos 107, 471-478.

Defra, 2001. The Countryside Stewardship Scheme: New Arable Options for 2002. Department for Environment, Food and Rural Affairs, London.

Defra, 2003. The Countryside Stewardship Scheme: Information and how to apply. Department for Environment, Food and Rural Affairs, London, UK.

Defra, 2005a. Environmental Stewardship: Entry Level Stewardship Handbook. Department for Environment, Food and Rural Affairs, London.

Defra, 2005b. Environmental Stewardship: Higher Level Stewardship Handbook. Department for Environment, Food and Rural Affairs, London.

Defra, 2005c. Environmental Stewardship; look after your land and be rewarded. Department for Environment, Food and Rural Affairs, London.

Defra, 2006. Agricultural quick statistics. http://statistics.defra.gov.uk/esg/quick/agri.asp

Dias, B.S.F., Raw, A., Imperatri –Fonseca, V.L., 1999. International Pollinators Initiative: The São Paulo Declaration on Pollinators. Report on the Recommendations of the Workshop on the Conservation and Sustainable Use of Pollinators in Agriculture with Emphasis on Bees. Brasília: Brazilian Ministry of the Environment (MMA) 1999. 66 pp.

Dicks, L.V., 2002. The structure and functioning of flower-visiting insect communities on hay meadows. PhD thesis. University of Cambridge, Cambridge, UK.

Dicks, L.V., Corbet, S.A., Pywell, R.F., 2002. Compartmentalization in plant-insect flower visitor webs. Journal of Animal Ecology 71, 32-43.

Donald, P.F., Evans, A.D., 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. Journal of Applied Ecology 43, 209-218.

Dramstad, W.E., 1996. Do bumblebees (Hymenoptera: Apidae) really forage close to their nests? Journal of Insect Behavior 9, 163-182.

Dramstad, W., Fry, G., 1995. Foraging activity of bumblebees in relation to flower resources on arable land. Agriculture, Ecosystems and Environment 53, 123-135.

Edwards, M., 1998. UK BAP Bumblebee Working Group Report, 1998. Unpublished report for the UK BAP Bumblebee Working Group, Midhurst, UK.

Edwards, M., 2001. UK BAP Bumblebee Working Group Report, 2001. Unpublished report for the UK BAP Bumblebee Working Group, Midhurst, UK.

Edwards, M., 2002. UK BAP Bumblebee Working Group Report, 2002. Unpublished report for the UK BAP Bumblebee Working Group, Midhurst, UK.

Edwards, M., 2005. Syngenta 'Operation Bumblebee' Monitoring Report, 2005. Unpublished report for Syngenta Crop Protection UK Ltd., Midhurst, UK.

Edwards, M., Williams, P.H., 2004. Where have all the bumblebees gone, and could they ever return? British Wildlife June 2004, 305-312.

Edwards, M., Jenner, M., 2005. Field guide to the bumblebees of Great Britain and Ireland. Ocelli, UK.

EEA, 2002. Environmental signals 2002 - Benchmarking the Millennium. European Environment Agency, Copenhagen.

Ellenberg, H., 1988. Vegetation Ecology of Central Europe. Cambridge University Press, Cambridge.

Engels, W., Schulz, U. & Radle, M., 1994. Use of the Tübingen mix for bee pasture in Germany. In: Forage for bees in an agricultural landscape, ed A. Matheson, pp. 57-65. International Bee Research Association, Cardiff.

EU, 2005. Agri-environment Measures - Overview on general principles, types of measures and application. European Commission - Directorate General for Agriculture and Rural Development.

Falk, S., 1991. A review of the scarce and threatened bees, wasps and ants of Great Britain. Nature Conservancy Council, Peterborough, UK.

Feber, R.E., Smith, H., Macdonald, D.W., 1996. The effects on butterfly abundance of the management of uncropped edges of arable fields. Journal of Applied Ecology 33, 1191-1205.

Firbank, L.F., Asteraki, E., Chamberlain, D.E., Gough, S., Haysom, K. Petit, S.E., Pywell, R.F., Warman, E.A. and Vickery, J.A., 2001. Development and validation of a methodology for the condition assessment of extensively managed arable habitats (OC9801). Final report to Department of Environment, Food and Rural Affairs. Centre for Ecology and Hydrology, Merlewood, UK.

Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2006. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. Plos Biology 4, 129-135.

Free, J.B., 1970. The flower constancy of bumblebees. Journal of Animal Ecology 39, 395-402.

Free, J.B., 1993. Insect Pollination of Crops, 2nd edition. Academic Press, London.

Free, J. B. and Butler, C. G., 1959. Bumblebees. Collins, London.

Fuller, R.M., 1987. The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930-84. Biological Conservation 40, 281-300.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R., Carter, N., 1995. Population declines and range contractions among lowland farmland birds in Britain. Conservation Biology 9, 1425-1441.

Fussell, M., Corbet, S.A., 1991. Forage for bumblebees and honey bees in farmland: a case study. Journal of Apicultural Research 30, 87-97.

Fussell, M., Corbet, S.A., 1992. Flower usage by bumblebees: a basis for forage plant management. Journal of Applied Ecology 29, 451-465.

Fussell, M., Corbet, S.A., 1992. The nesting places of some British bumble bees. Journal of Apicultural Research 31, 32-41.

Ghazoul, J., 2005. Buzziness as usual? Questioning the global pollination crisis. Trends in Ecology & Evolution 20, 367-373.

Gibson, R.H., Nelson, I.L., Hopkins, G.W., Hamlett, B.J., Memmott, J., 2006. Pollinator webs, plant communities and the conservation of rare plants: arable weeds as a case study. Journal of Applied Ecology 43, 246-257.

Gorman, M.L., Reynolds, P., 1993. The impact of land-use change in voles and raptors. Mammal Review 23, 121-126.

Goulson, D., 2003. Bumblebees: their behaviour and ecology. Oxford University Press, Oxford.

Goulson, D., Hawson, S.A., Stout, J.C., 1998. Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species. Animal Behaviour 55, 199-206.

Goulson, D., Stout, J.C., 2001. Homing ability of the bumblebee *Bombus terrestris*. Apidologie 32, 105-112.

Goulson, D., Hughes, W.O.H., Derwent, L.C., Stout, J.C., 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. Oecologia 130, 267-273.

Goulson, D., Darvill, B., 2004. Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? Apidologie 35, 55-63.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. Biological Conservation 122, 1-8.

Haines-Young, R. (editor) 2000. Accounting for nature: assessing habitats in the UK countryside. DETR: London.

Hanski, I., Gilpin, M., 1991. Metapopulation Dynamics - Brief-History and Conceptual Domain. Biological Journal of the Linnean Society 42, 3-16.

Harder, L.D., 1985. Morphology as a predictor of flower choice by bumblebees. Ecology 66, 198-210.

Hawkins, R.P., 1961. Observations on the pollination of red clover by bees. Annals of Applied Biology 49, 55 - 65.

Heinrich, B., 1976. The foraging specializations of individual bumblebees. Ecological Monographs 46, 105-128.

Heinrich, B., 1979. Bumblebee Economics. Harvard University Press, Cambridge, MA.

Hewson, R., 2000. Food availability and foraging by moorland bumblebees *Bombus* spp. Naturalist 125, 61-68.

Hirsch, M., Pfaff, S., Wolters, V., 2003. The influence of matrix type on flower visitors of *Centaurea jacea* L. Agriculture, Ecosystems & Environment 98, 331-337.

Holm, S.N., 1966. The utilization and management of bumble bees for red clover and alfalfa seed production. Annual Review of Entomology 11, 155-182.

Hughes, L., 1998. The Great Yellow Bumblebee, *Bombus distinguendus*; aspects of habitat use, phenology and conservation on the Machair of the Outer Hebrides, UK. MSc thesis. University College London, UK.

Ings, T. C., Ward, N. L., Chittka, L., 2006. Can commercially imported bumble bees out-compete their native conspecifics? Journal of Applied Ecology (online doi: 10.1111/j.1365-2664.2006.01199.x)

Jordan, W. R., Gilpin, M. E., Aber, J. D., 1987. Restoration ecology: a synthetic approach to ecological research. Cambridge University Press, Cambridge, UK.

Kells, A.R., Holland, J.M., Goulson, D., 2001. The value of uncropped field margins for foraging bumblebees. Journal of Insect Conservation 6, 13-23.

Kells, A.R., Goulson, D., 2003. Preferred nesting sites of bumblebee queens (Hymenoptera : Apidae) in agroecosystems in the UK. Biological Conservation 109, 165-174.

Kevan, P.G., 1991. Pollination: keystone process in sustainable global productivity. Acta Horticulturae 288, 103-110.

Kevan, P.G., 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. Agriculture Ecosystems & Environment 74, 373-393.

Kleijn, D., Berendse, F., Smit, R., Gilissen, N., 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413, 723-725.

Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., De Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Johl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecology Letters 9, 243-254.

Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? Journal of Applied Ecology 40, 947-969.

Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, A., Goulson, D., 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. Molecular Ecology 14, 1811-1820.

Knop, E., Kleijn, D., Herzog, F., Bernhard, S., 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. Journal of Applied Ecology 43, 120-127.

Kosior, A., 1995. Changes in the fauna of bumble-bees (*Bombus* Latr.) and cuckoo-bees (*Psithyrus* Lep.) of selected regions in southern Poland. pp. 103-111 In: Banaszak, J. (Ed.) Changes in Fauna of Wild Bees in Europe. Pedagogical Univ., Bydgoszcz, Poland.

Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences of the United States of America 99, 16812-16816.

Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P., Thorp, R.W., 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecology Letters 7, 1109-1119.

Kunin, W., Iwasa, Y., 1996. Pollinator foraging strategies in mixed floral arrays: Density effects and floral constancy. Theoretical Population Biology 49, 232-263.

Kwak, M., van den Brand, C., Kremer, P., Boerrigter, E., 1991. Visitation, flight distances and seed set in the rare species *Phyteuma nigrum* (Campanulaceae). Acta Hort. 288, 303-307.

Lagerlof, J., Stark, J., Svensson, B., 1992. Margins of agricultural fields as habitats for pollinating insects. Agriculture Ecosystems & Environment 40, 117-124.

Macdonald, M.A., 1998. Feeding ecology of some *Bombus* and *Psithyrus* bumblebees (Hym., Apidae) in northern Scotland. The Scottish Naturalist 110, 51-104.

MAFF, 1999. The Countryside Stewardship Scheme: Arable Stewardship, Information and how to apply. Ministry of Agriculture, Fisheries and Food Publications, London.

Magurran, A.E., 1988. Ecological diversity and its management. Princeton University Press, Princeton.

Mand, M., Mand, R., Williams, I.H., 2002. Bumblebees in the agricultural landscape of Estonia. Agriculture, Ecosystems and Environment 89, 69-76.

Manly, B.F.J., 1997. Randomization, bootstrap and Monte Carlo methods in biology, 2nd edn. Chapman & Hall, London, UK.

Marshall, E.J.P., 1998. Guidelines for the siting, establishment and management of arable field margins, beetle banks, cereal conservation headlands and wildlife seed mixtures. MAFF Project report BD0412. IACR Long Ashton, Bristol, UK.

Marshall, E.J.P., Moonen, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agriculture Ecosystems & Environment 89, 5-21.

Marshall, E.J.P., Nowakowski, M., 1995. Successional changes in the flora of a sown field margin strip managed by cutting and herbicide application. Brighton Crop Protection Conference – Weeds. pp. 973-978. British Crop Protection Council, Surrey, UK.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H., Nowakowski, M., 2002. The effect of arable field margin composition on invertebrate biodiversity. Biological Conservation 106, 259-271.

Meek, B., Pywell, R., Sparks, T., Nowakowski, M., Loxton, D., Carvell, C., Hammond, M., Croxton, P., Skidmore, P., Shore, R., Turner, D., Bell, D., Singer, E., Gowing, R., Farrant, C., Iliffe, L., Pickett, H., Shadrack, A., Warman, E., Löbel, S., Walker, K., Westrich, P., 2003. Ecological assessments and monitoring of Manor Farm, N Yorks: Final Technical report 1999 – 2002. Unpublished report to the Farmed Environment Company. NERC Centre for Ecology and Hydrology, Monks Wood, Cambridgeshire, UK.

Meek, B., Carvell, C., Pywell, R.F., Nowakowski, M., Sparks, T., Loxton, D., Skidmore, P., Bell, D., Croxton, P., Warman, E.A., Lobel, S., Walker, K.J., 2004. The BUZZ project: Year 3 Technical report. NERC Centre for Ecology and Hydrology, Monks Wood, Cambridgeshire, UK.

Mikkola, K., 1978. Spring migrations of wasps and bumblebees on the southern coast of Finland (Hymenoptera: Vespidae and Apidae). Annales Entomol. Fennici 44, 10-26.

Miller, P.C.H., Lane, A.G., 1999. Relationship between spray characteristics and drift risk into field boundaries of different structure. In Field Margins and buffer zones: ecology, management and policy. Aspects of Applied Biology 54, 45-51.

Muller, C.B., Schmid-Hempel, P., 1992. Correlates of reproductive success among field colonies of *Bombus lucorum* - the importance of growth and parasites. Ecological Entomology 17, 343-353.

Murdoch, W.W., 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. Ecological Monographs 39, 335-354.

Neal, P.R., 1998. Pollinator restoration. Trends in Ecology & Evolution 13, 132-133.

Ne'eman, G., Dafni, A., Potts, S.G., 1999. A new pollination probability index (PPI) for pollen load analysis as a measure for pollination effectiveness of bees. Journal of Apicultural Research 38, 19-23.

Osborne, J. L., Corbet, S.A., 1994. Managing habitats for pollinators in farmland. Aspects of Applied Biology 40; Arable farming under CAP reform, 207-215.

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

Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. Journal of Applied Ecology 36, 519-533.

Osborne, J.L., Williams, I.H., 2001. Site constancy of bumble bees in an experimentally patchy habitat. Agriculture, Ecosystems and Environment 83, 129 – 141.

Ovenden, G.N., Swash, A.R.H., Smallshire, D., 1998. Agri-environment schemes and their contribution to the conservation of biodiversity in England. Journal of Applied Ecology 35, 955-960.

Pelletier, L., McNeil, J.N., 2003. The effect of food supplementation on reproductive success in bumblebee field colonies. Oikos 103, 688-694.

Pickett, H., 2000. Bumblebee (*Bombus*) abundance, diversity and activity in relation to field margin habitat type. MSc thesis. University of Liverpool, UK.

Pollard, E., Yates, T.J., 1993. Monitoring Butterflies for Ecology and Conservation. Chapman and Hall, London.

Pollard, E., Moss, D. & Yates, T.J., 1995. Population trends of common British butterflies at monitored sites. Journal of Applied Ecology 32: 9-16.

Pontin, D.R., Wade, M.R., Kehrli, P., Wratten, S.D., 2006. Attractiveness of single and multiple species flower patches to beneficial insects in agroecosystems. Annals of Applied Biology 148, 39-47.

Potts, S.G., Bradbury, R.B., Mortimer, S.R., Woodcock, B.A., 2006. Commentary on Kleijn et al. 2006. Ecology Letters 9, 254 - 256.

Preston, C. D., Pearman, D. A., Dines, T.D., 2002. New Atlas of the British and Irish Flora. Oxford University Press, Oxford, UK.

Preston, C.D., Telfer, M.G., Roy, D.B., Carey, P.D., Hill, M.O., Meek, W.R., Rothery, P., Smart, S., Smith, G.M., Walker, K.J. & Pearman, D.A., 2003. The Changing Distribution of the Flora of the United Kingdom: Technical Report C01093. NERC Centre for Ecology and Hydrology, Huntingdon, UK.

Preston, C.D., Pearman, D.A., Hall, A.R., 2004. Archaeophytes in Britain. Botanical Journal of the Linnean Society 145, 257-294.

Prŷs-Jones, O.E., 1982. Ecological studies of foraging and life history in bumblebees. PhD thesis. University of Cambridge, UK.

Prŷs-Jones, O.E., Corbet, S.A., 1991. Bumblebees, 2nd edn. Richmond Publishing Company, Slough, UK.

Pyke, G.H., 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. Ecology 63, 555-573.

Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W., Peel, S., 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. Journal of Applied Ecology 39, 294-309.

Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L.I.Z., Walker, K.J., Rothery, P., 2003. Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40, 65-77.

Pywell, R.F., Warman, E.A., Sparks, T.H., Greatorex-Davies, J.N., Walker, K.J., Meek, W.R., Carvell, C., Petit, S., Firbank, L.G., 2004. Assessing habitat quality for butterflies on intensively managed arable farmland. Biological Conservation 118, 313-325.

Pywell, R.F., James, K.L., Herbert, I., Meek, W.R., Carvell, C., Bell, D., Sparks, T.H., 2005a. Determinants of overwintering habitat quality for beetles and spiders on arable farmland. Biological Conservation 123, 79-90.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R., Sherwood, A., 2005b. Providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 121, 479-494.

Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., Critchley, C.N.R., Sherwood, A., 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 129, 192-206.

Ranta, E., Lundberg, H., 1980. Resource partitioning in bumblebees: the significance of differences in proboscis length. OIKOS 35, 298-302.

Ranta, E., Lundberg, H., 1981. Food niche analyses of bumblebees: a comparison of three data collecting methods. OIKOS 36, 12-16.

Rasmont, P., Mersch, P., 1988. Première estimation de la dérive faunique chez les bourdons de la Belgique (Hymenoptera: Apidae). Annales de la Societe Royale Zoologique de Belgique 118, 141-147.

Rasmont, P., 1988. Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera. Apidae, Bombinae). PhD Thesis. Faculté des Science Agronomique de l'Etat, Gembloux, Belgium.

Rich, T.C.G., Woodruff, E.R., 1996. Changes in the vascular plant floras of England and Scotland between 1930-1960 and 1987-1988: the BSBI monitoring scheme. Biological Conservation 75, 217-229.

Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology 39, 157-176.

Roy, D.B., Bohan, D.A., Haughton, A.J., Hill, M.O., Osborne, J.L., Clark, S.J., Perry, J.N., Rothery, P., Scott, R.J., Brooks, D.R., Champion, G.T., Hawes, C., Heard, M.S., Firbank, L.G., 2003. Invertebrates and vegetation of field margins adjacent to crops subject to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 358, 1879 - 1898.

Ryan, B.F., Joiner, B.L., Ryan, T., 2000. MINITAB Handbook, Fourth Edition. Brooks Cole, Florence KY.

SAS Institute Inc., 2004. SAS® 9.1.2 Qualification Tools User's Guide. Cary, NC.

Saville, N.M., 1993. Bumblebee ecology in woodlands and arable farmland. PhD thesis. University of Cambridge, UK.

Saville, N.M., Dramstad, W.E., Fry, G.L.A., Corbet, S.A., 1997. Bumblebee movement in a fragmented agricultural landscape. Agriculture, Ecosystems and Environment 61, 145-154.

Schmidt, W., 1976. (cited in Ellenberg, 1988). Ungestorte und gelenkte Sukzession auf Brachackern. Habil. Schr. Gottingen.

Schultz, C.B., Dlugosch, K.M., 1999. Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. Oecologia 119, 231-238.

Simberloff, D., 1998. Flagships, umbrellas, and keystones: Is single-species management passe in the landscape era? Biological Conservation 83, 247-257.

Sladen, F. W. L., 1912. The Humble-bee, its life history and how to domesticate it. Macmillan & Co. Ltd., London.

Smart, S.M., Firbank, L.G., Bunce, R.G.H., Watkins, J.W., 2000. Quantifying changes in abundance of food plants for butterfly larvae and farmland birds. Journal of Applied Ecology 37, 398 – 414.

Smart, S.M., Bunce, R.G.H., Marrs, R., LeDuc, M., Firbank, L.G., Maskell, L.C., Scott, W.A., Thompson, K., Walker, K.J., 2005. Large-scale changes in the abundance of common higher plant species across Britain between 1978, 1990 and 1998 as a consequence of human activity: Tests of hypothesised changes in trait representation. Biological Conservation 124, 355-371.

Smeets, P., Duchateau, M.J., 2003. Longevity of *Bombus terrestris* workers (Hymenoptera: Apidae) in relation to pollen availability, in the absence of foraging. Apidologie 34, 333-337.

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

Sowig, P., 1989. Effects of flowering plants patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera, Apidae). Oecologia 78, 550-558.

Stace, C., 1997. New Flora of the British Isles. Cambridge University Press, Cambridge, UK.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421-1432.

Steffan-Dewenter, I., Tscharntke, T., 1999. Effects of habitat isolation on pollinator communities and seed set. Oecologia 121, 432-440.

Steffan-Dewenter, I., Potts, S.G., Packer, L., 2005. Pollinator diversity and crop pollination services are at risk. Trends in Ecology & Evolution 20, 651-652.

Stoate, C., Boatman, N.D., Borralho, R.J., Rio Carvalho, C., de Snoo, G.R., Eden, P., 2001. Ecological impacts of arable intensification in Europe. Journal of Environmental Management. 63: 337-365.

Stoate, C., Szczur, J., Aebischer, N.J., 2003. Winter use of wild bird cover crops by passerines on farmland in northeast England. Bird Study 50, 15-21.

Sutcliffe, G.H., Plowright, R.C., 1990. The effects of pollen availability on the development time in the bumble bee *Bombus terricola* K. (Hymenoptera: Apidae). Canadian Journal of Zoology 68, 1120-1123.

Svensson, B., Lagerlof, J., Svensson, B.G., 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agriculture Ecosystems & Environment 77, 247-255.

Swash, G., Belding, R., 1999. Arable reversion in Environmentally Sensitive Area and Countryside Stewardship Schemes: Guidelines for project officers. Farming and Rural Conservation Agency, UK.

Telfer, M.G., Preston, C.D., Rothery, P., 2002. A general method for measuring relative change in range size from biological atlas data. Biological Conservation 107, 99-109.

Teräs, I., 1983. Estimation of bumblebee densities (*Bombus*: Hymenoptera, Apidae). Acta Entomologica Fennica 42, 103-113.

ter Braak, C.J.F., Šmilauer, P., 1998. CANOCO reference manual and user's guide to CANOCO for Windows: Software for canonical community ordination (version 4). Microcomputer Power, Ithaca, NY.

Thomas, C.F.G., Marshall, E.J.P., 1999. Arthropod abundance and diversity in differently vegetated margins of arable fields. Agriculture Ecosystems and Environment 72: 131-144.

Thomas, J.A., Bourne N. A. D., Clarke, R. T., Stewart, K. E., Simcox, D. J., Pearman, G S, Curtis R., Goodger B., 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings of the Royal Society B 268, 1791-1796.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T., Lawton, J.H., 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303, 1879-1881.

Thompson, H.M., 2001. Assessing the exposure and toxicity of pesticides to bumblebees (*Bombus* sp.). Apidologie 32, 305-321.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecology Letters 8, 857-874.

UK Biodiversity Group, 1998. UK Biodiversity Group Tranche 2 Action Plans: Invertebrates, vol. IV. English Nature, Peterborough, UK.

van Swaay, C.A.M., 1990. An assessment of the changes in butterfly abundance in The Netherlands during the 20th Century. Biological Conservation 52, 287-302.

Vickery, J., Carter, N., Fuller, R.J., 2002. The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. Agriculture Ecosystems & Environment 89, 41-52.

Vickery, J.A., Bradbury, R.B., Henderson, I.G., Eaton, M.A., Grice, P.V., 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. Biological Conservation 119, 19-39.

Walker, K.J., Stevens, P.A., Stevens, D.P., Mountford, J.O., Manchester, S.J., Pywell, R.F., 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biological Conservation 119, 1-18.

Walker, K.J., Hodder, K., Bullock, J., Pywell, R.F., 2004. A review of the potential effects of seed sowing for habitat re-creation on the conservation of infraspecific biodiversity. Defra report BD1447. NERC Centre for Ecology and Hydrology, UK.

Walker, K.J., Critchley, C.N.R., Sherwood, A., Large, R., Nuttall, P., Hulmes, S., Rose, R., Moy, I., Towers, J., Hadden, R., Larbalestier, J., Smith, A.D., Mountford, J.O., Fowbert, J.A., 2006. Effectiveness of new agri-environment schemes in conserving arable plants in intensively farmed landscapes. NERC Centre for Ecology and Hydrology, Monks Wood, UK.

Walther-Hellwig, K., Frankl, R., 2000. Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., apidae), in an agricultural landscape. Journal of Applied Entomology 124, 299-306.

Walther-Hellwig, K., Frankl, R., 2000. Foraging distances of *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae). Journal of Insect Behavior 13, 239-246.

Waser, N. M., 1986. Flower constancy: definition, cause and measurement. American Naturalist 127, 593-603.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D., Thomas, C.D., 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414, 65-69.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. Ecology Letters 6, 961-965.

Westrich, P., 1996. The problems of partial habitats. In The Conservation of Bees. eds A. Matheson, S.L. Buchmann, C. O'Toole, W. P., I.H. Williams. Academic Press, London.

Westrich, P., Schmidt, K., 1986. Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hynemoptera, Apoidea). Linzer Biol. Beitr. 18, 341-360.

Whitfield, J., 2006. How green was my subsidy? Nature 439, 908 - 909.

Williams, P.H., 1982. The distribution and decline of British bumblebees (*Bombus* Latr.) Journal of Apicultural Research 21 (4), 236-245.

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

Williams, P.H., 1989. Why are there so many species of bumble bees at Dungeness? Botanical Journal of the Linnean Society 101, 31-44.

Williams, P., 2005. Does specialization explain rarity and decline British bumblebees? - A response to Goulson et al. Biological Conservation 122, 33-43.

Williams, I.H., Christian, D.G., 1991. Observations on *Phacelia tanacetifolia* Bentham (Hydrophyllaceae) as a food plant for honey bees and bumble bees. Journal of Apicultural Research 30, 3 – 12.

Willmer, P.G., Bataw, A.A.M., Hughes, J.P., 1994. The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. Ecological Entomology 19, 271 – 284.

Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B., Kunin, W.E., 2004. Spatial patterns in species distributions reveal biodiversity change. Nature 432, 393-396.

Yalden, P.E., 1982. Pollen collected by the bumblebee *Bombus monticola* Smith in the Peak District, England. Journal of Natural History 16, 823 – 832.

Arable field margin sown with a mixture of agricultural legumes
(*Trifolium pratense*, *Trifolium hybridum* and *Lotus corniculatus*)