



Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae)

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ABSTRACT

Bumblebees (*Bombus* spp.) play a key role within agricultural systems as pollinators of crops and wild flowers. However, this taxon has suffered severe declines as a result of agricultural intensification. Conservation efforts largely focus on providing forage resources for bumblebees through the summer, but providing suitable habitat during the period of nest foundation in early spring could be a more effective method of boosting local bumblebee populations. This study assesses the attractiveness of three different farmland habitat types (hedgerow, field margin and grassland), and the relative merits of respective land management prescriptions under the Scottish Rural Stewardship scheme to nest site searching and foraging bumblebee queens during the period of queen emergence and colony foundation. Hedgerows were the least attractive habitat type to spring queens. Rural Stewardship species-rich grassland comprised a complex vegetation structure attracting nest site searching queens, whilst grassland that had been abandoned allowing natural regeneration contained more flowers, attracting foraging queens. Field margin habitats were the most attractive habitat type, and Rural Stewardship field margins attracted both nest site searching and foraging queens at relatively high densities. This management option consisted of a sown grass mix, giving rise to the complex vegetation structure preferred by nest site searching queens, but regular disturbance allowed invasion by early flowering bumblebee forage plants. These findings suggest that it should be possible to develop simple combined management strategies to provide both suitable nesting sites and spring forage resources on farmland, promoting bumblebee colony foundation and therefore abundance in the agricultural environment.

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1. Introduction

Agricultural intensification has caused the decline of many native plant and animal species in the UK and western Europe (Donald et al., 2001; Wilson et al., 1999). The drive towards self-sufficiency that followed the World Wars led to the destruction of vast areas of natural and semi-natural habitat to be replaced by large-scale and more intensively managed farmland. Such changes in countryside management have led to the loss of farmland biodiversity havens such as hedgerows and hay meadows, giving rise instead to a uniform rural landscape of large monocultures divided by simpler field boundary features (Stoate et al., 2001). In the UK, bumblebees (*Bombus* spp.) have suffered severe declines as a result of this agricultural intensification and it is widely accepted that these are directly related to declines in the wild flowers upon which they rely. It has been shown that many

of the forage plants that bumblebees prefer have declined disproportionately (Carvell et al., 2006a), and that those species of bumblebee that have suffered the most severe declines tend to be those that display least plasticity in forage plant preferences (Goulson and Darvill, 2004; Goulson et al., 2005).

Bumblebees play a key role within agricultural systems, providing a pollination service that can increase yields of many flowering crops (Corbet et al., 1991). Many of the wildflower species associated with the rural environment also rely on bumblebee populations for survival (reviewed in Osborne and Williams, 1996). The provision of sufficient resources to support large, diverse bumblebee populations is therefore likely to provide both economic advantages and broader conservation benefits.

In recent years, an increasing awareness of the negative effects of intensive farming on native biodiversity has led to the implementation of a number of government-funded agri-environment schemes across Europe (Kleijn and Sutherland, 2003). One principle aim of these schemes is to restore and create areas of semi-natural habitat on farmland and thereby increase landscape heterogeneity. The management options presented in these

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schemes are often designed with target species in mind, and these commonly include game animals, beneficial invertebrates and rare arable plants. However, it is assumed that the improvement of farmland for these species will also provide benefits for a wider range of non-target flora and fauna. The value of these schemes across different taxa is widely debated, but many studies do indicate that certain schemes are of conservation value. For example, benefits of agri-environment prescriptions have been shown for many insects, birds, small mammals and wildflowers (e.g. Marshall et al., 2006; MacDonald et al., 2007). One of the most popular forms of conservation management has been arable field margin management, and suitably managed field margins are recognized as havens for biodiversity (Marshall and Moonen, 2002).

The effects of field margin management options on bumblebee communities have been the focus of many studies in recent years, particularly in England, and it has been found that those options involving the sowing of annual or perennial wildflowers or agricultural cultivars of legume species can have positive effects on the abundance and diversity of foraging bumblebees (Carreck and Williams, 2002; Meek et al., 2002; Carvell et al., 2004, 2006b, 2007; Pywell et al., 2005, 2006). It has also been suggested that it may be possible to develop a management strategy that will combine high quality forage with nest site provision for bumblebees (Carvell et al., 2004). However, the suitability of these schemes for providing nesting habitat has not been evaluated, and almost all studies of agri-environment schemes and bumblebees to date have focussed on populations of worker bees in the summer. Paradoxically, it is arguable that habitat quality in early spring may be the most important factor determining bumblebee abundance, for at this time of year queens first emerge after diapause and must find a suitable nest site and single-handedly rear the first cohort of workers (Goulson, 2003).

The availability of sufficient nest sites is vital, yet this requirement is often overlooked. Little is known about bumblebee nest site preferences as nests are inconspicuous although broad species-specific differences are understood. For example in the UK, species such as *Bombus terrestris* and *Bombus lucorum* tend to nest under the ground whilst species such as *Bombus pascuorum* prefer to nest on the ground surface. In both cases there appears to be a strong tendency towards the use of abandoned nests of other small animal species such as small mammals or birds (Rasmont et al., 2008). Nest-searching bumblebees have been found to be associated with linear features such as hedgerows and woodland edges, and also with tall, tussocky grassland (Fussell and Corbet, 1992; Kells and Goulson, 2003). However, these habitat types have declined as a result of agricultural intensification and it is possible that this has resulted in increased competition for nesting sites. It is notable that the bumblebee species that have shown the greatest declines in the UK tend to be those that emerge from hibernation later in the year and their declines may be at least partially accounted for by an increase in competition for nesting sites, with surface nesters such as *Bombus muscorum* competing with the earlier emerging *B. pascuorum* and subterranean nesters such as the late emerging *Bombus soroensis* competing with earlier emerging *B. terrestris* and *B. lucorum*. Indeed, a recent study in the USA has shown that bumblebee abundance in urban parks is limited by nest site availability (McFrederick and LeBuhn, 2006).

The availability of forage in close proximity to the nest must also be crucial in spring. The bumblebee queen must incubate the brood clump, so it seems unlikely that queens are able to embark on lengthy foraging trips (Cresswell et al., 2000). A recent study in the UK has shown that bumblebee nests appear to be more common in gardens than they are in the countryside (Osborne et al., 2008) and this may reflect a paucity of suitable nesting habitat and/or a shortage of early forage to support nests in the rural environment. Encouraging bumblebees to nest on farmland by offering suitable nesting

habitat in combination with plentiful spring forage may help to ensure efficient pollination of crops as well as many wildflowers associated with the farmland environment.

Although most studies of agri-environment scheme suitability for bumblebees have focussed on field margin management, other management options are also likely to influence bumblebee populations. For example, the sowing of tussocky grass strips adjacent to, or bisecting crop fields, restoration or creation of hedgerows and wooded areas and restoration or creation of species-rich grasslands are all likely to promote the sorts of vegetation structure generally associated with nesting bumblebees. However, to date there have been few attempts to quantify the value of these schemes for bumblebees.

We use a paired-farm comparison to quantify the relative value of three management options offered as part of the Scottish Rural Stewardship scheme 2004 for nest site searching and foraging spring bumblebee queens (similar or identical schemes are available in England and Wales). The aim of the study is to assess the potential of these schemes to promote nest foundation and thereby enhance bumblebee abundance in the agricultural environment.

2. Methods

2.1. Study sites

Ten predominantly arable low lying (0–200 m altitude) farms in East and Central Scotland were chosen for inclusion in this study. Five of these were participants of the Scottish Rural Stewardship scheme (referred to hereafter as RSS) and as such, had signed up to a management plan beginning in 2004. The management plan for each farm consisted of at least one each of the following management prescriptions (adapted from Anon 2006).

2.1.1. Management of grass margin or beetle bank in arable fields

This prescription involves sowing or maintaining a crop-adjacent strip of land between 1.5 and 6 m wide with a suitable mix of grass species, and is specifically targeted at fields containing an arable crop. The application of fertilisers is forbidden and grazing is not allowed until the crop has been harvested.

The aim of this prescription is to provide a refuge for beneficial insects as well as cover for birds. However, the prescription results in the establishment of large areas of tussocky, undisturbed grassland which may also be of benefit to nesting bumblebees.

2.1.2. Management or creation and management of species-rich grassland

The former stipulates restrictions on the mowing or grazing of existing areas of unimproved grassland between the months of March and August. The latter involves the removal of existing vegetation cover of an area followed by priming of the land (e.g. by reducing soil fertility and/or removing weed species) and the establishment of a new sward using a low productivity grass and herb mix.

The aim of these prescriptions is to promote the growth and spread of flowering plants and other grassland species. One of the goals was that these should be of conservation value to pollinator species including butterflies and bumblebees, providing a source of wildflowers on which they can feed. The tussocky structure of this grassland may also provide nesting sites for surface-nesting bumblebees as well as attracting small mammals which in turn may provide nest sites for subterranean-nesting species.

2.1.3. Management of hedgerows

This prescription involves managing hedgerows by filling in gaps and limiting cutting to once every 3 years at most and only

in the winter. The hedge-bottom vegetation must not be mown and pesticides must not be applied.

The aim of this prescription is to promote the growth of a diverse hedge-bottom flora as well as to provide shelter for birds, small mammals and invertebrates. Additionally, this scheme may provide a source of bumblebee forage as well as attracting small mammals and birds that will provide nesting sites for bumblebees.

The remaining five farms used in this study were chosen as counterparts for each RSS farm. This was based on three criteria:

1. The paired farm must not be involved in ANY agri-environment scheme.
2. The paired farm must be within 5 km of the corresponding RSS farm.
3. The proportion of the farm dedicated to different land use types must be broadly similar to that of its counterpart.

This design aimed to control variation in bumblebee abundance based on locality and land use.

2.2. Sampling methods

On each farm six 100 m transects were chosen. On RSS farms, these represented:

FM1. An arable field margin managed according to the grass margin/beetlebank prescription.

FM2. A conventionally managed arable field margin.

G1. An area of grassland managed according to the species-rich grassland prescription.

G2. An area of unfarmed grassland not under any management prescription, referred to from hereon as non-prescription grassland.

H1. A hedgerow managed according to RSS guidelines.

H2. A conventionally managed hedgerow.

On non-stewardship farms, two each of transects G2, FM2 and H2 were chosen to represent the three habitat types (uncultivated grassland, arable field margin and hedgerow). Transects were chosen at random from a farm map prior to visiting the sites themselves. Transects on each pair of farms were matched for aspect and land usage in the adjacent field(s). Grassland transects were set up through the area of grassland rather than at the boundary and when surveying hedgerow transects, bees were only recorded when nest site searching or foraging at the base of the hedge. The edge of the recording area for hedgerow transects was defined by the centre of the hedge, allowing accurate observations of abundances of nest site searching queens.

Non-prescription grassland sites (G2) were areas of land that were largely free from management practices, therefore representing a naturally regenerated grassland habitat. Disturbance to these areas was minimal although vegetation was generally cut back once or twice a year. RSS species-rich grassland (G1) sites used in this study were sown with a wild flower and grass seed mix in 2004, thus allowing 3 years for the sown mix to become established. Each year, the sites were not mown or grazed from the middle of March to the middle of August to allow season-long flowering, but all were topped at the end of this period to encourage floral diversity. (Under the RSS management prescription, grazing is suggested as an alternative to topping but this method was not used at any of the study sites.)

The hedgerows surveyed in this study (H1 and H2) were hawthorn (*Crataegus monogyna*) or blackthorn (*Prunus spinosa*) dominated and these did not come into flower until the very end of the recording period. *Ulex europaeus*, other *Prunus* spp. and *Cytisus*

scoparius were also occasional components of the hedgerows themselves. In both RSS and conventionally-managed hedgerows, the hedge-bottom flora was dominated by grass species. *Taraxacum officinale*, *Lamium album* and *Lamium purpureum* were minor components of hedge-bottom flora in both types of hedgerow.

Each pair of farms was visited once a week over a 5 week period between 14th April and 16th May 2008. Paired farms were surveyed on the same day so that data collected for each partner on each visit were directly comparable, controlling for differences in weather and date. The order in which the farms were visited and the transects walked was randomised to control for any effect of time of day. Data were collected in dry conditions and temperatures ranged from 5 °C at the beginning of the recording period to 25 °C later in the season. During each transect walk, the number of bumblebee queens seen within 3 m either side of the transect was recorded. In cases where habitat strips were less than 6 m wide, this involved counting any bees observed in the adjacent crop. No fields included in the study contained spring flowering crops. Bees observed were categorised into nest site searching queens (those demonstrating the characteristic slow zigzag flight associated with nest site searching behaviour in bumblebees) and foraging queens and were identified to species level. Each individual was recorded once according to the first behaviour observed. Individuals crawling in vegetation were observed to see whether nest site searching behaviour would commence and if not, the individual was not recorded. The flower on which each foraging queen was found was also recorded.

Abundance of nest site searching queens was used as a measure of the suitability of habitat for nesting bumblebees. It could be argued that numbers of nest site searching queens may not be a good indicator of habitat suitability, as an abundance of nest site searching queens could simply indicate that nest sites are scarce and that the time taken for any individual bumblebee queen to find a suitable nest site is therefore longer. However, this seems unlikely as bumblebee queens should have become adapted to search in those habitat types most likely to yield high quality nest sites (and see Section 4).

In addition to the bumblebee counts, the number of individual inflorescences open for each flowering plant species seen in each sampling area was estimated every time a transect was walked. All flowers observed along any given transect walk were recorded, but only those on which bumblebees had been observed to forage were included in data analysis.

On each farm, an additional 30 min search was made per time-point in which additional areas of suitable habitat were searched and foraging bumblebee queens and flower abundance were recorded as above. These data were used to get a more robust picture of the usage of floral resources by bumblebee queens (for example by revealing whether bees were using flowering trees not present in transects).

A basic vegetation survey was also carried out for each transect in week 2 of the recording period. Margin width and vegetation height were measured and the proportion of land covered by grasses, broad-leaved species, vegetation litter, exposed earth and moss was estimated.

2.3. Analysis

All analyses were carried out using SPSS 16.0.

2.4. Timing of queen activity

A repeated measures analysis of variance was used to investigate species-specific differences in changes in bumblebee abundance over time. Data were combined from transects to give

total observations for each species and time point at each farm and were then square root transformed to normalise the data.

2.5. Queen forage plant usage

A chi-square test of independence was used to examine differences in forage use between species based on all the data collected, both on transect walks and during the additional 30 min recording period. Only the three most commonly observed bumblebee species (*B. terrestris*, *B. pascuorum* and *Bombus hortorum*) and the four most popular forage plants (*Prunus* spp., *L. album*, *L. purpureum* and *Symphytum officinale*) were included in this analysis as inclusion of other species would have resulted in expected frequencies of below five rendering the data unsuitable for chi-square analysis.

2.6. Effects of habitat type and management practice

Two levels of analysis were conducted on bumblebee and flower abundance: the first only included RSS farms and assessed the effects of habitat type (e.g. field margin) and whether the habitat was prescription or non-prescription (“land management type”). The second assessed the effects of habitat type and whether the farm was in a RSS scheme (“farm type”) across both RSS and conventional farms. Details of these analyses are outlined below.

All of the following analyses were calculated using bee or flower abundance per transect summed over all time points.

There were insufficient observations to analyse bee species separately but an examination of the data revealed no evidence for species-specific differences in relation to the explanatory variables examined.

2.6.1. Effects of habitat type and management practice on bumblebee and flower abundance within Rural Stewardship participant farms

In order to assess the effect of RSS scheme prescriptions on bumblebee queen abundance, a Poisson loglinear analysis was carried out with farm, habitat type (hedge, field margin or grassland) and land management practice (RSS or conventional) as potential explanatory factors. Flower abundance, including only those species on which bumblebee queens had been observed to forage, was included as a covariate. This analysis only included data collected on RSS participant farms in order to exclude any effects of overall farm management. Separate analyses were carried out on nest site searching and foraging bumblebee queens. A two-way interaction effect between habitat type and land management practice was also tested for in the analysis relating to nest site searching bumblebee queens. Low numbers of foraging bumblebees were observed so an interaction effect could not be included in the analysis for foraging bumblebees. The final explanatory model was created by step-wise removal of non-significant factors.

A general linear model with normal errors was also carried out to assess the effect of RSS scheme prescriptions on flower abundance (log transformed), with farm, habitat type (hedge, field margin or grassland) and land management practice (RSS or conventional) as explanatory variables. A two-way interaction effect between habitat type and land management practice was also included.

2.6.2. Comparison of conventionally managed land on Rural Stewardship participant vs. conventionally-managed farms

In order to identify effects of RSS participation on bumblebee abundance (nest sites searching and foraging), a Poisson loglinear analysis was carried out with locality (each farm pair being classed as one locality), habitat type and farm type as explanatory variables and flower abundance as a covariate. These analyses excluded data collected on RSS managed habitat types (so that equivalent habitats were being compared on each farm type).

Again, a two-way interaction effect between habitat type and farm type was included for the nest site searching analysis, but not for foraging bumblebees as numbers observed were low. The final explanatory models were created by step-wise removal of non-significant factors.

The effect of farm type on flower abundance was investigated using an additional generalized linear model with site, habitat type and farm type as explanatory variables. A two-way interaction effect between habitat type and farm management practice was also tested for. Flower abundance data were log transformed prior to analysis in order to normalise the data.

Subgenus *Psithyrus* species (kleptoparasitic bumblebees) were not included in any data analysis as they display different life history strategies to those of social *Bombus* species, and only small numbers were observed. It is likely that management benefiting social bumblebees will also profit these species as their numbers are likely to be directly influenced by the abundance of their host species.

3. Results

3.1. Bee species

During the course of the study, six species of true bumblebee were recorded, but the majority of observations (over 90%) belonged to just four. These were *B. terrestris* (29.4%), *B. pascuorum* (24.2%), *B. lucorum* (22.3%), and *B. hortorum* (16.7%). *Bombus pratorum* and *Bombus lapidarius* were also observed in small numbers (5.0% and 2.3% of observations, respectively). Fewer than 0.5% of observations were of cuckoo bumblebees (those belonging to the subgenus *Psithyrus*).

3.2. Timing of queen activity

Abundance of bumblebee queens changed over the course of the study, with low numbers observed in mid April increasing towards the end of April, then declining ($F_{(1, 54)} = 20.02$, $p < 0.001$). Species-specific differences were also found, with numbers of *B. terrestris* and *B. lucorum* peaking approximately a week earlier than *B. hortorum* and *B. pascuorum*, which reached their maximum in early May ($F_{(5, 54)} = 5.15$, $p = 0.001$, Fig. 1). The abundance of

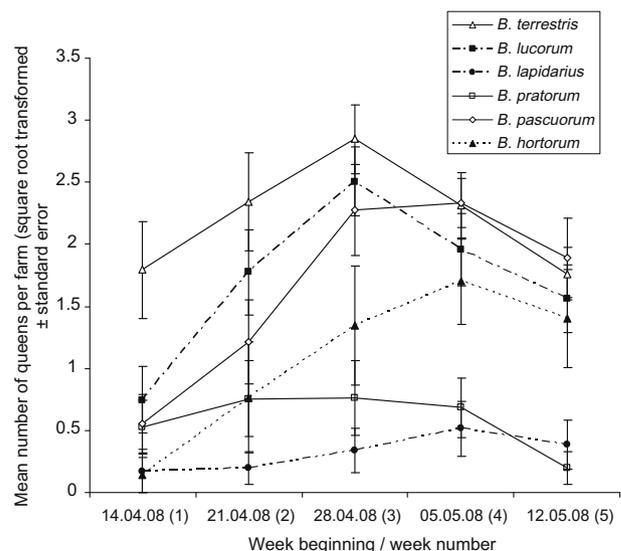


Fig. 1. Number of queens of each species observed averaged across all farms at each time point.

queens of *B. pratorum* observed shows no clear peak, but decline towards the end of the recording period in mid May. Sightings of *B. lapidarius* were rare and no clear pattern is evident in the timings of observations of this species.

Small numbers of workers of each species except for *B. lapidarius* were also observed during the final 3 weeks of observations.

3.3. Queen forage plant usage

Bumblebee queens were seen foraging on 24 different plant species spanning 13 different families. However, most of these plant species individually accounted for a very small percentage of observations. Over 60% of bumblebee flower visits were to white dead nettle (*L. album*), red dead nettle (*L. purpureum*), cherry (*Prunus* spp.) and comfrey (*S. officinale*) (Table 2). Combined, these plant species made up only 21% of inflorescences of bumblebee forage plants observed.

Clear species-specific differences were observed in queen forage use between these four plant species ($\chi^2_6 = 167.33$, $p < 0.001$, Fig. 2). *B. lucorum* and *B. terrestris* were most commonly observed foraging on *Prunus* blossoms, whilst the longer tongued *B. hortorum* and *B. pascuorum* were observed most commonly on long-corolla flowers such as *S. officinale*, *L. purpureum* and *L. album*. *B. hortorum* was observed particularly often on *L. album*. *B. lapidarius*, *B. pratorum* and *B. lucorum* were excluded from statistical analysis as the number of observations for these species was low.

3.4. Effects of habitat type and management practice on bumblebee and flower abundance within Rural Stewardship participant farms

Summary data on the vegetation characteristics of the different habitat types are presented in Table 1.

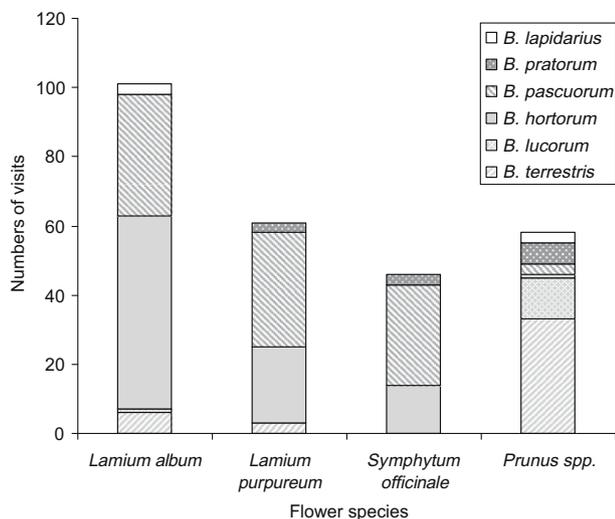


Fig. 2. Numbers of visits by bumblebee queens of each species to the four main forage plants.

Table 1

Average width and vegetation characteristics of transect types. Standard errors are in brackets.

	Width of margin (m)	Height of vegetation (m)	Grass spp. (% cover)	Vegetation litter (% cover)	Exposed earth (% cover)	Broad-leaved spp. (% cover)	Moss (% cover)
RSS species-rich grassland	N/A	1.30 (0.21)	46.4 (17.33)	13.8 (12.35)	27.2 (9.43)	8.6 (2.80)	4.0 (2.53)
Conventional grassland	N/A	1.00 (0.14)	47.4 (5.92)	2.0 (1.36)	8.9 (3.62)	40.9 (5.57)	0.73 (0.67)
RSS hedgerows	2.40 (0.92)	0.96 (0.15)	48.6 (13.88)	8.6 (4.95)	38.4 (16.02)	4.2 (1.83)	0.2 (0.20)
Conventional hedgerow	1.78 (0.59)	0.53 (0.15)	56.5 (8.91)	5.0 (1.72)	19.7 (5.95)	15.1 (4.39)	3.6 (3.45)
RSS field margin	6.20 (1.06)	1.39 (0.07)	71.8 (8.32)	0.6 (0.40)	25.8 (7.10)	1.6 (1.60)	0.2 (0.20)
Conventional field margin	1.81 (0.54)	0.64 (0.10)	64.1 (5.30)	1.9 (1.35)	17.2 (4.31)	16.8 (4.35)	0.07 (0.67)

Nest site searching bumblebee queens were observed more frequently in field margin habitats (FM1 and FM2) than in grassland habitats (G1 and G2), and more frequently in grassland habitats than in hedgerow habitats (H1 and H2) ($\chi^2_2 = 21.17$, $p < 0.001$, Fig. 3). Land managed according to RSS prescriptions (FM1, G1 and H1) also attracted greater numbers of nest site searching queens than conventionally managed land (FM2, G2 and H2) on the same farm ($\chi^2_1 = 8.93$, $p = 0.003$). The effect of land management (RSS versus conventional) on nest site searching bumblebee abundance was the same across all habitat types (interaction effect, $\chi^2_1 = 0.27$, $p = 0.607$).

Habitat type did not explain the variation in the abundance of foraging bumblebee queens observed between transects ($\chi^2_2 = 2.33$, $p = 0.313$), but the effect of land management practice was significant ($\chi^2_1 = 4.25$, $p = 0.039$) with foraging bumblebees observed more frequently on RSS habitat than on conventional habitat. Interaction effects could not be examined as observations of foraging bumblebee queens were few, but these data suggest that greater abundances of foraging bumblebee queens were attracted to RSS field margins (FM1) than conventionally managed field margins (FM2), whilst conversely, non-prescription grassland (G2) appeared to be more attractive to foraging bumblebees than RSS species-rich grassland (G1) (Fig. 3). No difference was evident between RSS and conventionally-managed hedgerows (H1 and H2) (Fig. 3).

Habitat type was a strong predictor of the abundance of bumblebee forage flowers within RSS participant farms ($\chi^2_2 = 9.91$, $p = 0.007$). Flower abundance was greatest in the field margin habitat type (FM1 and FM2) and lowest in the hedgerow habitat type

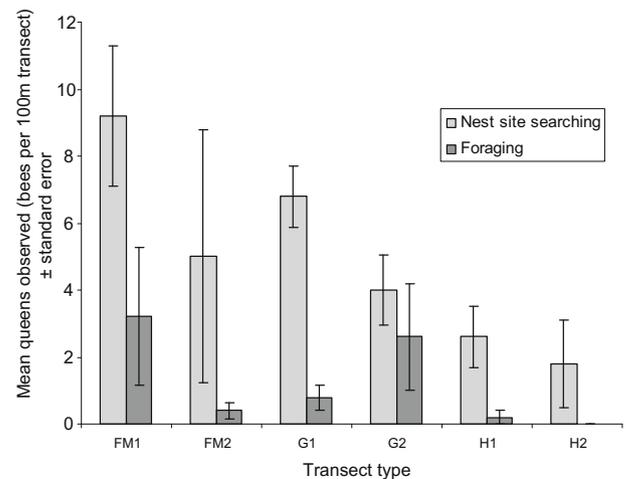


Fig. 3. Mean number of bumblebee queens observed per transect for each transect type on Rural Stewardship participant farms. (Data summed over all time-points, and pooled for bee species.) FM1 = Rural Stewardship arable field margin, FM2 = conventionally-managed field margin, G1 = Rural Stewardship species-rich grassland, G2 = non-prescription grassland, H1 = Rural Stewardship hedgerow, H2 = conventionally-managed hedgerow.

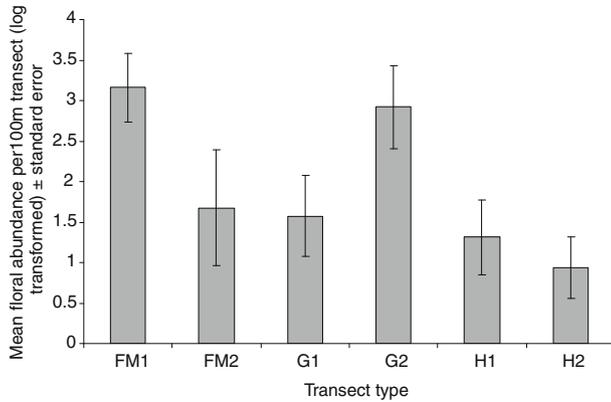


Fig. 4. Mean number of inflorescences per transect (log transformed) for each transect type on Rural Stewardship participant farms. (Data summed over all time points.) Key to transect types as in Fig. 3.

(H1 and H2) (Fig. 4). There was a significant interaction between habitat type and land management practice ($\chi^2 = 10.20$, $p = 0.006$), resulting from the low abundance of flowers observed in RSS species-rich grassland (G1) compared to non-prescription grassland (G2). Flower abundance did not differ between sites ($\chi^2_4 = 6.41$, $p = 0.171$).

Transect types containing more flowers attracted significantly more foraging bumblebee queens ($\chi^2_1 = 17.8$, $p < 0.001$), but flower abundance had no effect on the abundance of nest site searching queens ($\chi^2_1 = 0.45$, $p = 0.503$, Figs. 3 and 5).

3.5. Comparison of conventionally managed land on Rural Stewardship participant vs. conventionally-managed farms

Results for the effects of habitat type and land management practice on bumblebee abundance within RSS participant farms are presented in Table 3. A significant interaction effect was found between farm type and habitat type, with nest site searching bumblebee queens being observed more frequently in field margins (FM2) on RSS participant farms than on conventional farms, but as frequently on non-prescription grassland (G2) and along hedgerows (H2) on both RSS participant farms and conventionally-managed farms (Fig. 5a). Again, abundance of bumblebee forage plant inflorescences had no effect on numbers of nest site searching bumblebee queens observed ($\chi^2_1 < 0.001$, $p = 0.994$).

Habitat type was the best predictor of foraging bumblebee abundance Table 3. Foraging queens were observed most frequently in non-prescription grassland (G2) habitat type and were much less abundant in the field margin and hedgerow habitat types (FM2 and H2) (Fig. 5b). When considering only conventionally-managed habitats, RSS participant farms attracted fewer foraging bumblebee queens than conventionally-managed farms. Again, number of bumblebee forage plant inflorescences was a significant predictor of abundance of foraging bumblebee queens. However, the data were insufficient to provide a reliable assessment of any interaction effects between habitat type and farm type.

The locality of each farm pair was a significant predictor of the abundance of both nest site searching and foraging bumblebee queens (Table 3).

Flower abundance differed between habitat types, again being highest in the grassland habitat type (G2) and lowest in the hedgerow habitat type (H2) ($\chi^2_2 = 13.81$, $p = 0.001$, Fig. 5c). No overall effect of farm type was observed nor was there an interaction between farm type and habitat ($\chi^2_1 = 0.42$, $p = 0.518$, $\chi^2_2 = 2.80$,

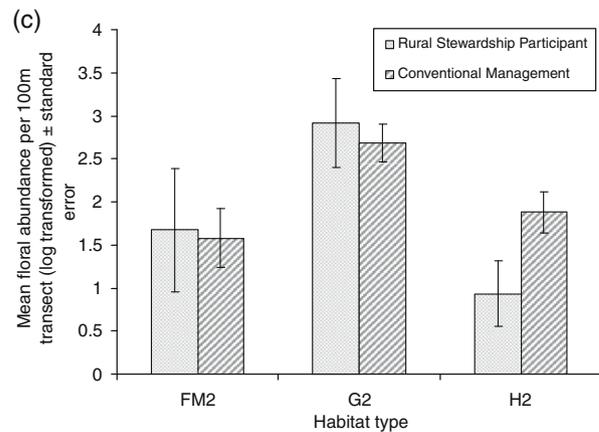
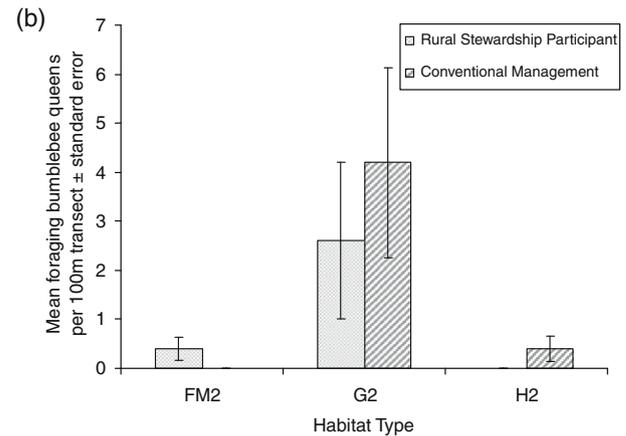
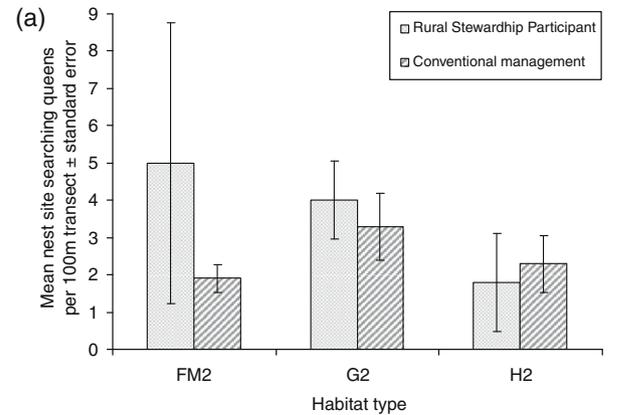


Fig. 5. (a) Mean number of nest site searching queens per transect on conventionally-managed habitat types on Rural Stewardship participant vs. conventionally-managed farms. (b) Mean number of foraging queens per transect on conventionally-managed habitat types on Rural Stewardship participant vs. conventionally-managed farms. (c) Mean number of inflorescences per transect on conventionally-managed habitat types on Rural Stewardship participant vs. conventionally-managed farms. (Data summed over all time points, only conventionally-managed habitat included.) Key to transect types as in Fig. 3.

$p = 0.247$, respectively). There was also no effect of locality on flower abundance ($\chi^2_4 = 5.17$, $p = 0.271$).

4. Discussion

4.1. Bee species

All social bumblebees observed belonged to the 'big six' British bumblebee species, so-called because they are common and wide-

Table 2
Numbers of foraging visits made by queens of the six species observed to different flower species from both 100 m transect walks and additional 30 min farm searches.

Bumblebee species	Asteraceae		Boraginaceae			Brassicaceae		Caryophyllaceae		Fabaceae			Grossulariaceae	
	<i>Taraxacum officinale</i>		<i>Pentaglottis viridis</i>	<i>Pulmonaria officinalis</i>	<i>Symphytum officinale</i>	<i>Aubrieta</i> spp.	<i>Raphanus raphanistrum</i>	<i>Silene dioica</i>		<i>Cytisus scoparius</i>	<i>Viccia cracca</i>	<i>Ulex europaeus</i>	<i>Ribes sanguineum</i>	<i>Ribes uva-crispa</i>
<i>Flower species</i>														
<i>B. terrestris</i>	10	0	2	0	0	0	0	0	3	0	4	10	0	
<i>B. lucorum</i>	0	0	1	0	1	0	0	3	0	12	6	1		
<i>B. pascuorum</i>	11	1	8	29	1	0	0	4	2	1	1	0		
<i>B. pratorum</i>	7	0	4	3	0	1	0	0	0	0	2	1		
<i>B. lapidarius</i>	0	0	0	0	1	0	0	0	0	2	0	0		
<i>B. hortorum</i>	1	0	9	14	0	0	1	1	0	7	0	0		
Total	29	1	24	46	3	1	1	11	2	26	19	2		
	Lamiaceae				Ranunculaceae	Rosaceae			Salicaceae	Sapindaceae	Scrophulariaceae	Violaceae	Totals	
	<i>Glechoma hederacea</i>	<i>Lamiasstrum galeobdolon</i>	<i>Lamium album</i>	<i>Lamium purpureum</i>	<i>Ranunculus ficaria</i>	<i>Crataegus monogyna</i>	<i>Malus</i> spp.	<i>Prunus</i> spp.	<i>Salix</i> spp.	<i>Aesculus hippocastanum</i>	<i>Cymbalaria muralis</i>	<i>Viola odorata</i>		
<i>B. terrestris</i>	0	0	6	3	0	0	5	33	8	1	0	0	85	
<i>B. lucorum</i>	0	0	1	0	0	0	2	12	7	0	0	0	46	
<i>B. pascuorum</i>	0	0	2	35	33	1	0	0	3	0	1	1	1	
135														
<i>B. pratorum</i>	1	0	0	0	3	1	1	0	6	2	0	0	0	
32														
<i>B. lapidarius</i>	0	0	3	0	0	0	0	0	3	1	0	0	0	
10														
<i>B. hortorum</i>	0	0	56	22	0	0	0	0	1	0	0	0	0	
112														
Total	1	2	101	61	2	1	7	58	18	2	1	1	420	

Table 3
Table of results for the effects of habitat type and farm management practice on bumblebee abundance on Rural Stewardship vs. Conventionally managed farms using Poisson loglinear analyses with nest site searching and foraging bumblebees as response variables.

	Nest site searching bees			Foraging bees		
	Wald chi-square	Degrees of freedom	P value	Wald chi-square	Degrees of freedom	P value
(Intercept)	75.76	1	<0.001	15.51	1	<0.001
Habitat type	5.76	2	0.056	35.46	2	<0.001
Farm management type	2.56	1	0.110	5.51	1	0.019
Locality	36.28	4	<0.001	17.83	4	0.001
Flower abundance	–	–	–	4.69	1	0.030
Habitat type * Land management type	6.69	2	0.035	–	–	–

spread throughout most of the British Isles. The relative abundances of each species recorded in this study are largely consistent with those reported in previous studies on farmland in England. However, there was a notable scarcity of *B. lapidarius*, a species that usually accounts for a high proportion of bumblebee observations in this type of study (Kells et al., 2001; Carvell et al., 2004, 2006b; Pywell et al., 2005). This may be due in part to the fact that *B. lapidarius* is at the northern edge of its range in Scotland (Goulson et al., 2005) and is therefore likely to be less common here than in England where previous work has been carried out. However, in addition to this, *B. lapidarius* was found to be unusually rare in the north of the UK in 2008 (Bumblebee Conservation Trust “Bee-watch” Survey, unpublished data), possibly as a result of poor weather in the period of 2007–2008 which may have differentially affected this species at the edges of its range.

4.2. Timing of queen activity and species-specific patterns

It is well documented that bumblebee species differ in their choice of forage plant (Alford, 1975), and these differences were apparent in this study. As was expected, short-tongued species such as *B. terrestris* and *B. lucorum* were more frequently observed foraging on flowers with short corolla lengths, in this case largely *Prunus* spp. (excluding *P. spinosa*), whilst *B. hortorum* and *B. pascuorum* (the two longer tongued species represented in this study) were more frequently observed feeding on flowers with long corolla lengths, particularly *L. album*, *L. purpureum* and *S. officinale*.

Bumblebee activity varied between species with peak activity levels being reached first by *B. pratorum* between the 21st and 28th April, then by *B. terrestris* and *B. lucorum* and finally by *B. hortorum* and *B. pascuorum* in the week of the 5th May. Similar abundances of each species of bumblebee were observed displaying foraging behaviour over the course of the study, but nest site searching behaviour was more commonly displayed by *B. terrestris* and *B. lucorum* than by other species (notably *B. hortorum* and *B. pascuorum*). These patterns reflect known phenological differences between these different species (Goulson et al., 2005). As the study was carried out early in the year, it would be expected that the lag time between queen emergence and commencement of nest site searching behaviour would result in earlier emerging species such as *B. terrestris* and *B. lucorum* being represented in higher abundances in the subset of queens searching for nest sites.

4.3. Effects of habitat type and management practice on bumblebee and flower abundance

A comparison of habitat types managed either conventionally or according to RSS prescriptions within the same farms allowed the local effects of each management prescription to be assessed excluding any influence of whole farm management, whilst comparing the same conventionally-managed habitat types on RSS participant farms and conventionally-managed farms allowed examination of effects of RSS participation at the farm scale.

Non-prescription grasslands (G2) tended to be relatively rich in broad-leaved plants including several spring-flowering forage plants such as *L. album* and *L. purpureum*, and as a result, this habitat type attracted the greatest abundance of foraging bumblebee queens. RSS species-rich grassland sites (G1) contained fewer spring forage flowers and this translated into a lower abundance of foraging bumblebee queens. This is in marked contrast to previous studies carried out in England, which have shown that arable field margins sown with a grass and wildflower mix (similar to that used in the RSS species-rich grassland prescription) were of greater value for providing bumblebee forage than those allowed to undergo naturally regeneration (Carvell et al., 2004; Pywell et al., 2005). However, these studies focussed on foraging workers in summer, thus not addressing provision of spring forage to support queens early in the year. Unimproved grassland prescriptions usually aim to promote legumes such as *Trifolium pratense* and *Lotus corniculatus*, which flower in late spring and summer. These prescriptions provide little during the early stages of colony foundation and development.

Despite the low availability of spring forage, nest site searching bumblebee queens were observed more frequently on RSS species-rich grassland (G1) than on non-prescription grassland (G2). This is not unexpected as at this time of year, these areas appeared to be dominated by grasses, giving rise to a tall, dense and tussocky vegetation structure with few spring-flowering plants. Such habitat is probably ideal for providing suitable nest sites for bumblebees as it creates the sheltered sites at the base of grass plants favoured by surface-nesters and also attracts small mammals that will give rise to nest sites suited to colonisation by subterranean nesters.

Conventionally managed field margins (FM2) appeared to be of little benefit to foraging bumblebee queens, containing few spring flowering bumblebee forage plants and attracting low numbers of foraging bumblebees. However, management according to the RSS arable field margin prescription (FM1) resulted in a marked increase in the abundance of early forage flowers for bumblebees (notably *L. purpureum*, *S. officinale*, *Silene dioica* and *U. europaeus*) and an associated increase in abundance of foraging bumblebee queens observed, despite the lack of forbs included in the seed mix sown under this management prescription. Similarly, conventionally managed field margins (FM2) attracted fewer nest site searching bumblebee queens than RSS margins (FM1), which attracted the greatest number of nest site searching bumblebee queens of all habitat types studied. The grass mix sown on RSS managed field margins had become established over the 3 years since the scheme was implemented and the vegetation structure of these margins were similar to that of the RSS species-rich grassland. However, they appeared to receive more disturbance (e.g. as a result of the movement of farm machinery) than did the species-rich grassland, facilitating invasion by other plant species including those favoured by foraging bumblebee queens, notably *L. purpureum*, which is indicated as an important source of spring forage in this study. These findings suggest that RSS field margins are able both to provide suitable nesting habitat and to enhance spring for-

age availability for bumblebees which should promote colony foundation and early growth in these areas as a result.

Of the three broad habitat types examined, hedgerows appeared to be of least benefit to spring bumblebee queens. Although one of the aims of the RSS prescription for hedgerow management was to promote the development of a diverse hedge-bottom flora, abundance of spring bumblebee forage was found to be low in both conventionally managed and RSS hedgerows (H2 and H1, respectively) and this translated into low numbers of foraging queens in both management types. Despite the suggestion from previous studies that hedgerows are preferred nesting habitat for at least some of the bumblebees commonly recorded in this study (Kells and Goulson, 2003), nest site searching queens were found to be scarce in this habitat type.

Despite clear differences between the vegetation associated with RSS hedgerows and conventionally-managed hedgerows, there was no evidence for a difference in attractiveness to nest site searching queens between the two hedgerow types. Although the vegetation associated with RSS hedgerows looked superficially like that of the RSS field margins and the species-rich grassland, RSS hedgerows seemed to be much less attractive to nest site searching queens. A possible explanation for this is that both the species-rich grassland and the field margin management prescriptions involve the sowing of a seed mix whilst the vegetation associated with RSS managed hedge bottoms is a result of natural regeneration. More detailed analysis of the vegetation associated with these scheme types may help to explain the differences observed here.

When considering only habitats managed conventionally (i.e. FM2, G2, H2) there were some interesting interacting effects of habitat type and farm management on the abundance of nest site searching queens. It is sometimes argued that farmers choosing to adopt agri-environment schemes are likely to be more environmentally aware and may therefore manage their land differently to those farmers that choose not to take part in such schemes (even when managing features that are not specifically included in their agri-environment scheme agreement). The data presented here suggest that such differences probably do exist, for example nest site searching queens were more abundant in field margins on farms with RSS agreements than on equivalent margins on conventional farms, even when these were not part of management agreements. However, this could also be due to an effect of the management agreements on bumblebee abundance at the farm scale such that bumblebee numbers were generally higher on RSS managed farms than on conventionally-managed farms.

It could be argued that numbers of nest site searching queens may not be a good indicator of subsequent nest density or even of habitat suitability (see Section 2). However, the data presented in this study correspond well with what would be expected given the body of evidence for bumblebee nest site choice already present in the literature (Sladen, 1912; Alford, 1975; Svensson et al., 2000; Kells and Goulson, 2003). This suggests that abundance of nest site searching bumblebees is a reasonable measure for assessing the relative quality of habitat for nesting bumblebees, although we accept that evidence for this would require both the density of nest-searching queens and then the density of subsequent nests.

5. Conclusions

The maintenance of a healthy and diverse assemblage of wild bees in the rural environment can ensure maximum yields from flowering crops with little or no input from expensive commercially reared or domesticated pollinators (Kremen et al., 2004; Mohr and Kevan, 1987). It is also of value for conservation, promoting the survival of wildflower species associated with rural environments (Osborne and Williams, 1996). Of all the wild bees native to the UK, bumblebees are almost certainly the most impor-

tant wild pollinator taxa (Goulson, 2003), but the maintenance of robust bumblebee populations requires the provision of suitable resources. Perhaps the most critical period for the establishment of strong bumblebee populations is spring, when a queen must locate a suitable nesting site and single-handedly feed and incubate her first brood of workers.

We found that Rural Stewardship species-rich grassland and field margin prescriptions provide benefits for spring bumblebee queens, and that the field margin prescription creates habitat that is both attractive to nest site searching bumblebee queens and provides spring foraging resources, presumably promoting colony foundation and early growth in these areas. Notably, species-rich grassland prescriptions were favoured by nest-searching bumblebees and are likely to provide plentiful forage in summer, but they provided little early spring forage. In contrast, unsown grasslands created by natural regeneration were rich in spring flowers such as *Lamium* spp. and appeared to provide a valuable forage resource at this time. Our findings demonstrate that it is possible to provide both spring forage and sites attractive to nest-searching bees by the implementation of a small number of simple management prescriptions, and that this may be an effective method of promoting bumblebee population density in agricultural environments.

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References

- Alford, D.V., 1975. Bumblebees. Davis Poynter Ltd., London.
- Anon., 2006. The Rural Stewardship Scheme. Scottish Executive, p. 114.
- 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., Meek, W.R., Pywell, R.F., Nowakowski, M., 2004. The response of bumblebees to successional change in newly created arable field margins. *Biological Conservation* 118, 327–339.
- Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D., Goulson, D., 2006a. Declines in forage availability for bumblebees at a national scale. *Biological Conservation* 132, 481–489.
- Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F., Nowakowski, M., 2006b. Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. *Apidologie* 37, 326–340.
- Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D., Nowakowski, M., 2007. Comparing the efficiency of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology* 44, 29–40.
- Corbet, S., 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.
- Cresswell, J.E., Osborne, J.L., Goulson, D., 2000. An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Economic Entomology* 25, 249–255.
- Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird population. *Proceedings of the Royal Society of London Series B* 268, 25–29.
- Fussell, M., Corbet, S.A., 1992. The nesting places of some British bumble bees. *Journal of Apicultural Research* 31, 32–41.
- Goulson, D., 2003. Bumblebees: 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, 55–63.
- Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. *Biological Conservation* 122, 1–8.
- 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., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology* 40, 947–969.
- 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.
- MacDonald, D.W., Tattershall, F.H., Service, K.M., Firbank, L.G., Feber, R.E., 2007. Mammals, agri-environment schemes and set-aside—what are the putative benefits? *Mammal Review* 37, 259–277.
- 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., West, T.M., Kleijn, D., 2006. Impacts of an agri-environment field margin prescription on the flora and fauna of arable farmland in different landscapes. *Agriculture, Ecosystems and Environment* 113, 36–44.
- McFrederick, Q.S., Lebuhn, G., 2006. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? *Biological Conservation* 129, 372–382.
- Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H., Nowakowski, M., 2002. The effect of arable field margin composition on invertebrate diversity. *Biological Conservation* 106, 259–271.
- Mohr, N.A., Kevan, P.G., 1987. Pollinators and pollination requirements of lowbush blueberry (*Vaccinium angustifolium* Ait. and *V. myrtilloides* Michx.) and cranberry (*V. macrocarpon* Ait.) in Ontario with notes on highbush blueberry (*V. corymbosum* L.) and lingonberry (*V. vitis-idaea* L.). *Proceedings of the Entomological society of Ontario* 118, 149–154.
- Osborne, J.L., Williams, I.H., 1996. Bumblebees as pollinators of crops and wild flowers. In: Matheson, A. (Ed.), *Bumblebees for Pleasure and Profit*. IBRA, Cardiff, pp. 24–32.
- Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J., Sanderson, R.A., 2008. Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology* 45, 784–792.
- 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 forage 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.
- Rasmont, P., Murat Aytekin, A., Suleyman Kacar, M., 2008. Ousting of the Common Redstart (*Aves: Turdidae: Phoenicurus phoenicurus*) from its nest by the bumblebee *Bombus niveatus vorticatus* (Hymenoptera: Apidae). *Annales de la Société Entomologique de France* 44, 251–255.
- Sladen, F.W.L., 1912. *The Humble-Bee, its Life History and How to Domesticate it*. Macmillan and Co. Ltd.
- 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 Ecological Management* 63, 337–365.
- Svensson, B., Lagerlof, J., Svensson, B.G., 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems and Environment* 77, 247–255.
- Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., Bradbury, R.B., 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems and Environment* 75, 13–30.