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Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK

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Abstract

Bumblebees (*Bombus* spp.) have undergone a documented Europe-wide decline in recent years, mostly attributable to destruction of forage and nest sites caused by agricultural intensification. This study was set up to quantify species-specific nest-site preferences of observed UK species for various types of field and forest boundary habitat. In total, 1287 observations were made of seven common bumblebee species; nest-searching behaviour was taken as being indicative of nest site preference. There was interspecific variation in preferred habitat, with some species found to be much more specific in their choice of nest site than others. A strong association was found between those species that are known to prefer subterraneous nesting and those habitats that contained banks (*Bombus terrestris*, *B. lapidarius* and *B. lucorum*); other species were strongly associated with tussock-type vegetation (*B. pascuorum*, *B. hortorum* and *B. ruderarius*). In order to safeguard the continued existence of bumblebee species it is clear that a variety of field and forest boundary types need to be conserved; this has positive implications for the conservation of other species of flora and fauna associated with agroecosystems. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: *Bombus* spp.; Nest-searching; Field boundary; Forest boundary; Tussock; Bank

1. Introduction

That nest-choice preference is species specific amongst bumblebees has been demonstrated in previous studies (see e.g. Sladen, 1912; Skovgaard, 1936; Free and Butler, 1959; Svensson and Lundberg, 1977; Richards, 1978; Harder, 1986; Fussell and Corbet, 1992a; Svensson et al., 2000). Some species are known to prefer to nest subterraneously, (e.g. *Bombus terrestris, B. lucorum, B. lapidarius, B. ruderatus*), whilst others prefer to nest on or just below the soil surface (e.g. *B. hortorum, B. pascuorum, B. sylvarum, B. humilis, B. muscorum, B. ruderarius*). Species such as *B. lapidarius* and *B. pratorum* can be very opportunistic in their nest choice, and utilise things such as birds' nests and anthropogenic artefacts (Fussell and Corbet, 1992a; Svensson et al., 2000). Bowers (1985) has suggested that queen nest site selection is governed by different evolutionary forces to those that influence the success of the resultant colony. Intrinsic factors determining acceptability as a nest site include degree of shelter, soil drainage, heat absorption, and those factors that are species specific. There may be a trade-off between shelter and degree of warmth from direct sunlight (i.e. more exposed sites), and Skovgaard (1945) has suggested that south-facing banks may be least popular.

In recent years there has been a documented decline in bumblebee species numbers and species diversity across Europe (Rasmont et al., 1992) [France], (Kwak and Tieleman, 1994) [The Netherlands], (Berezin et al., 1995) [Russia], (Kosior, 1995) [southern Poland]). Within the UK, local species diversity and density have become altered; a huge central area of the country now contains only six resident species (out of a total of 19; Williams, 1982, 1989). Agricultural intensification is known to be responsible for a decline in forage resources; a drive to increase field sizes has also decreased the area available for nest sites. (e.g. Pollard et al., 1974; Williams, 1986; Ricketts et al., 2001). The abandoned burrows of small mammals and tussocky areas where the different bumblebee species commonly build their nests are

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generally found along field boundaries; this is where queens are often found in nest-searching flight (Svensson et al., 2000), but these habitat types are amongst the first to be lost in any intensification of the farming system.

Finding existing nests in the field is difficult, and only a small proportion of nests are ever located (Svensson and Lundberg, 1977; Donovan and Wier, 1978; Fussell and Corbet, 1992a). Previous studies of bumblebee nesting behaviour have placed artificial nest boxes in the field, but the uptake rates of these are generally very poor (Norgaard Holm, 1966; Richards, 1973, 1978; MacFarlane et al., 1983; Fussell and Corbet, 1992a). Alternatively, observed nest-searching behaviour of bumblebee queens has been used as an indicator of preferred nest site, as a larger amount of data can be generated in this way. This method of extrapolating nest-site preference from search data has previously been used in similar studies in other countries (see Svensson et al., 2000). Nest-searching queens display a typical behaviour pattern very different from that of foraging individuals. This comprises a characteristic zigzag flight trajectory, low over the ground, with stops to investigate potential nest sites. This study was set up to compile detailed information on the relative nest-site preferences of those British bumblebee species recorded across different habitats. It is hoped that results will give a basis for field boundary management, which could be used in conjunction with studies of foraging preferences, to enable farmers to manage habitats to encourage bumblebees.

2. Methods

2.1. Study site

This study was carried out on the Cholderton Estate, near Andover, on the Wiltshire/Hampshire border, UK. The estate is managed in a way that is beneficial to wildlife. Most of the study area is chalk downland, and a mixed farming system is in place. The estate also contains stands of mixed deciduous woodland, and many fields are bounded by this on at least one side.

2.2. Study design

Two different habitat types were studied—

Habitat 1: field–field edges. Borders running between two large agricultural fields
Habitat 2: field–forest edges. Borders running between a large agricultural field and mixed woodland

Within each of the habitat types, three different boundary types were characterised—

1. Fence. Fields or field and forest separated by a fence with no associated hedge-type vegetation.
2. Hedgerow. A continuous boundary of dense, shrubby, vegetation separating fields, or field and forest, and containing typical hedgerow flora.
3. Gapped-out hedgerow. Older hedge banks where the flora has become impoverished through lack of management. These generally consisted of a row of mature trees typical of hedgerow species, such as hawthorn (*Crataegus monogyna*), with gaps in between.

These three boundary types could be sub-divided into four distinct edge types—

1. Nothing. No associated vegetation in the case of fences, or no vegetation except that which constitutes the hedgerow in the other two boundary types.
2. Bank. Edges where the boundary was located on top of a bank at least 15 cm high (maximum bank height was 30 cm).
3. Tussock. An edge containing a densely vegetated, grass-dominated strip.
4. Bank and tussock. Edges containing a combination of types 2 and 3 above.

The occurrence of nest-searching queens was quantified along 100 m transects laid out along field edges. Pollard's transect method for butterfly recording was used (Pollard et al., 1975; Pollard, 1977), with all queens searching 0.5 m either side of the transect recorded. Queens exhibiting both typical nest-searching flight low over the ground, and those observed crawling on the ground (Lundberg and Svensson, 1975), were included in the analysis. Every effort was made to avoid pseudo-replication.

Observations were carried out during a 6-week period from 25 April until 1 June 2001, with 3 days of observations being made each week. There was no replication of transects walked within the weeks, but there was replication between the weeks. Equal numbers of edge types were studied within each boundary type, and equal numbers of boundary types within each habitat. In total 432 transects were walked along each habitat type, 24 per day of observations.

Bumblebee nomenclature follows Prys-Jones and Corbet (1991). Female bumblebees that are capable of egg laying, but which have not founded a nest are properly known as gynes (Michener, 1974). However, this is interchangeable with 'queen' in the literature, and so queen will be the term used here.

2.3. Analysis

Univariate ANOVA using GLM (SPSS, 1998) was used to analyse the data from this study, with each edge type entered as fixed factors. Observations within and between weeks were summed for the purpose of this analysis (Table 1).

3. Results

3.1. Total numbers of bumblebee species observed

A total of 1287 observations of nest-searching queens were made during this study (Table 1). The most commonly recorded species were *B. terrestris* and *B. pascuorum*, accounting for 577 observations (44.83%), whereas there were only 85 observations of *B. ruderarius* (6.60% of the total; Table 1).

3.2. Timing of emergence

Emergence of *B. terrestris*, *B. lapidarius*, *B. lucorum* and *B. pascuorum* queens had commenced prior to the initiation of this study. *B. terrestris* numbers peaked in week 4 (16–18 May), and then underwent a sharp decline; *B. pascuorum* exhibited a similar pattern, though the decline was not as steep, and numbers were still relatively high at the end of the study. *B. lapidarius* and *B. lucorum* numbers remained relatively constant for the first 4 weeks of observations, but declined towards zero over the next 2 weeks. Emergence of *B. hortorum*, *B. ruderarius* and *B. pratorum* queens was evident by week 2 (2–4 May); *B. ruderarius* and *B. pratorum* numbers peaked at week 4, and had declined to low levels by week 6 (30 May–1 June), whilst *B. hortorum* numbers were still increasing at this point (week 6; see Fig. 1).

3.3. Habitat preferences

Different *Bombus* species had specific preferences in terms of investigation of potential nest sites. The seven species that were observed are considered in turn.

Table 1
Total number of observations of nest-searching queens of each species for the duration of this experiment, expressed as a percentage of the total number of observations of all species

Species	Number of observations	Percentage of observations
B. terrestris	329	25.56
B. lapidarius	167	12.98
B. lucorum	152	11.81
B. pascuorum	248	19.27
B. hortorum	174	13.52
B. ruderarius	85	6.60
B. pratorum	132	10.26
Total	1287	100

3.3.1. B. terrestris

B. terrestris queens showed no preference for nest searching in either field–field or field–forest habitats, or according to boundary type (Table 2; Fig. 2). However, edge type was found to be significant, with queens preferring to nest search in edge types 2 and 4 (Table 2; Fig. 3). Both these edge types contained banks, with type 4 also containing a tussocky grass strip. This pattern is apparent across both habitat and boundary types. There was no significant two-way interaction between any of the factors for this species (Table 2).

3.3.2. B. lapidarius

The majority of *B. lapidarius* queens were observed along field–field boundaries (Fig. 2). They also exhibited a significant preference according to boundary type, with most queens nest, searching along fences (boundary 1; Fig. 3). Like *B. terrestris*, queens of this species also preferred searching along those edge types that contained banks, specifically those in field–field boundaries (Table 2; Fig. 3). There was a significant two–way interaction between habitat and boundary; those boundaries with gapped out hedges had many queens searching along them in field–field habitats, but very few in field–forest habitats. There was also a two-way interaction between boundary and edge type, with those edge types containing banks and tussocks disproportionately preferred when occurring along fences.

3.3.3. B. lucorum

B. lucorum displayed a significant preference for nest searching along those boundaries that contained hedges, either gapped-out, or managed. There was also a preference for those edge types that contained banks (Table 2): this pattern is evident across both habitats (Fig. 3). The only significant two-way interaction for this species was between boundary type and edge type (Table 2); the preference of nest-searching queens for banks along those boundaries with hedges was not displayed along fenced boundaries.

3.3.4. B. pascuorum

B. pascuorum queens were observed significantly more often along field–forest habitats (Fig. 2). Those boundaries with hedges were preferred over boundaries with fences (Table 2). In both habitats and across all boundary types, many more individuals were observed along those edge types that contained tussocks (types 3 and 4; Fig. 3). With the exception of fenced boundaries along forest edges, more *B. pascuorum* queens were recorded from those tussocky habitats not containing banks, than from those that did. There is a significant two-way interaction between habitat and edge type for this species (Table 2); along field–forest habitats there were more observations of *B. pascuorum* queens along those edges with bank and tussock, than along these same

Table 2
Results of Univariate ANOVA (SPSS, 1998) one-way and two-way analyses of the data[a]

	Habitat	Boundary	Edge	Habitat×Boundary	Habitat×Edge	Boundary×Edge
B. terrestris	0.034n.s.	0.973n.s.	20.225***	(0.196n.s.)	(1.967n.s.)	(0.642n.s.)
B. lapidarius	73.870***	23.205***	31.676***	5.977*	11.274***	3.329*
B. lucorum	0.032n.s.	33.588***	33.923***	(2.012n.s.)	(0.446n.s.)	10.335*
B. pascuorum	7.191**	22.569***	93.970***	(0.393n.s.)	2.904*	7.562*
B. hortorum	0.201n.s.	1.293n.s.	20.639***	(0.486n.s.)	(0.161n.s.)	(1.895n.s.)
B. ruderarius	0.092n.s.	1.753n.s.	14.597***	(0.487n.s.)	7.049*	(0.487n.s.)
B. pratorum	4.006*	2.047n.s.	2.527n.s.	(1.048n.s.)	(0.913n.s.)	(0.779n.s.)

[a] There were no significant interactions for three-way ANOVA. Those numbers in brackets represent non-significant two-way interactions, which were then removed from the analysis, and the data re-analysed. $n. = 432$ for habitat, $n = 288$ for boundary, $n = 216$ for edge.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

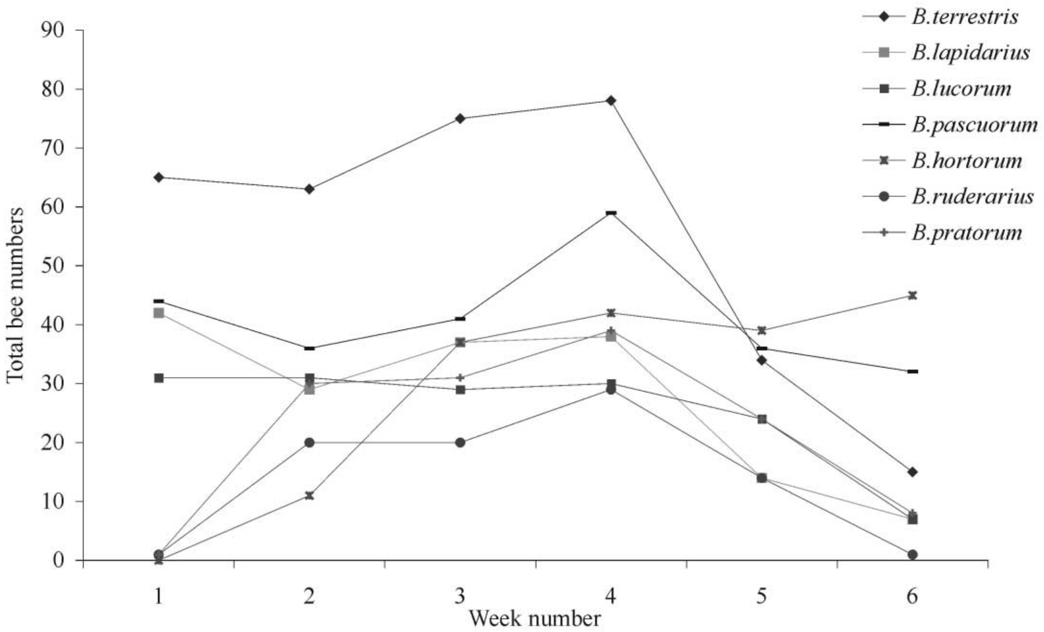

Fig. 1. Patterns of abundance of nest-searching queens of the different species through time.

edge types in field–field habitats. There is also a significant two-way interaction between boundary type and edge type; more queens were observed along tussocky edges (types 3 and 4) next to hedges (boundary types 2 and 3) than next to fences (type 1) in both habitats (Fig. 3).

3.3.5. B. hortorum

B. hortorum queens were not found to exhibit a preference for nest sites based on habitat type or on boundary type as quantified in this study (Table 1; Fig. 2). However, these queens were found to nest, search significantly more often along those edge types that contained tussocks (types 3 and 4); this behaviour was evident across all boundary and habitat types (Fig. 3). There were no significant two-way interactions between any of the factors for this species (Table 2).

3.3.6. B. ruderarius

No significant difference was found between habitats and between boundary types for nest searching *B. ruderarius* queens (Fig. 2). However, edge type was found to have a significant effect on numbers of queens observed (Table 1). Most queens of this species were recorded along tussocky edges (types 3 and 4; Fig. 3). There was also a significant interaction between habitat and edge type (Table 2), with more *B. ruderarius* queens observed nest searching along tussocky edges with banks in field–forest habitats, and more observed nest searching along tussocky edges without banks in field-

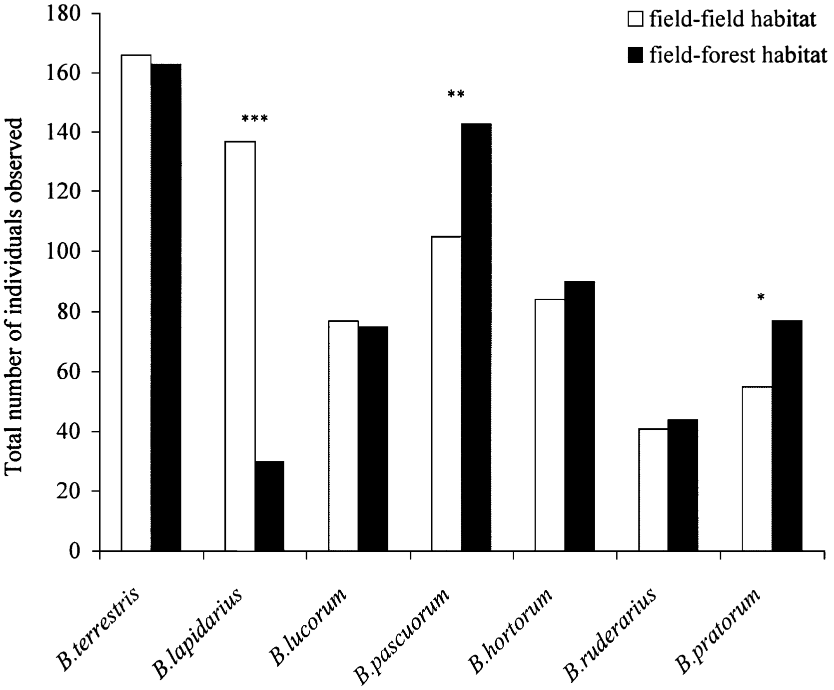

Fig. 2. Total numbers of each *Bombus* species queen observed in the two habitats across the duration of this study. $^{*}P<0.05$, $^{**}P<0.005$, $^{***}P<0.001$.

field habitats (Fig. 3). There were also more queens recorded along type 1 edges (no banks or tussocks) in field–forest than field–field habitats, although numbers were much lower than those observed along edge types with tussocks (Fig. 3).

3.3.7. B. pratorum

Significantly more *B. pratorum* queens were recorded from field–forest habitats than field–field habitats (Table 2; Fig. 2). Boundary type and edge type were not found to have a significant effect on occurrence of nest-searching queens (Table 2), and there were no two-way interactions between any of the factors. Fig. 3 illustrates that nest-searching queens of this species were observed across all boundary and edge types in approximately equal numbers.

4. Discussion

4.1. Individual species preferences

B. terrestris is known from previous studies to nest subterraneously. Here we took a preference for searching along banks (especially type 2 edges, which contained no tussocks), to indicate a tendency towards subterraneous nesting. The work of Svensson et al. (2000) recorded the majority of observations of nest-searching queens of this species in areas of open ground, although here there seemed to be no preference between open ground and forest boundaries. Although significantly more queens were observed nest searching in those edge types that contained banks, there were *B. terrestris* queens recorded in edges that did not. This species is known to be adaptable in choice of nest site, and can utilise anthropogenic artefacts (Fussell and Corbet, 1992a).

B. lapidarius displayed a strong preference for nest searching along the more open habitats in this study, especially along banks. There have been similar findings for this species from other studies (Skovgaard, 1936; Svensson et al., 2000). On the field–field boundaries, *B. lapidarius* was found most often along fences, which afford the least shelter of all boundary types, but there is a trade-off here with degree of warmth from the sun (Svensson et al., 2000). *B. lapidarius* workers begin foraging later in the day than those of other species, and finish earlier (Hasselrot, 1960); they have a higher temperature threshold (Prys-Jones and Corbet, 1991), and nest location in open areas may be taking maximum advantage of the heat reservoir effect of the soil (Fussell and Corbet, 1992a). Nests of this species are more often found in locations with all-day exposure to direct sunlight, than those of any other species (Fussell and Corbet, 1992a). Svensson et al. (2000) found that *B. lapidarius* queens did not nest search along habitats containing tussocks; results here were similar, indicating that this species rarely founds nests in above ground vegetation. There may be an avoidance of nesting in heavily vegetated areas, as nests here are likely to be shaded. Alford (1975), von Hagen (1986), and Westrich (1989) all mention that *B. lapidarius* may nest above ground; this species is known to take advantage of

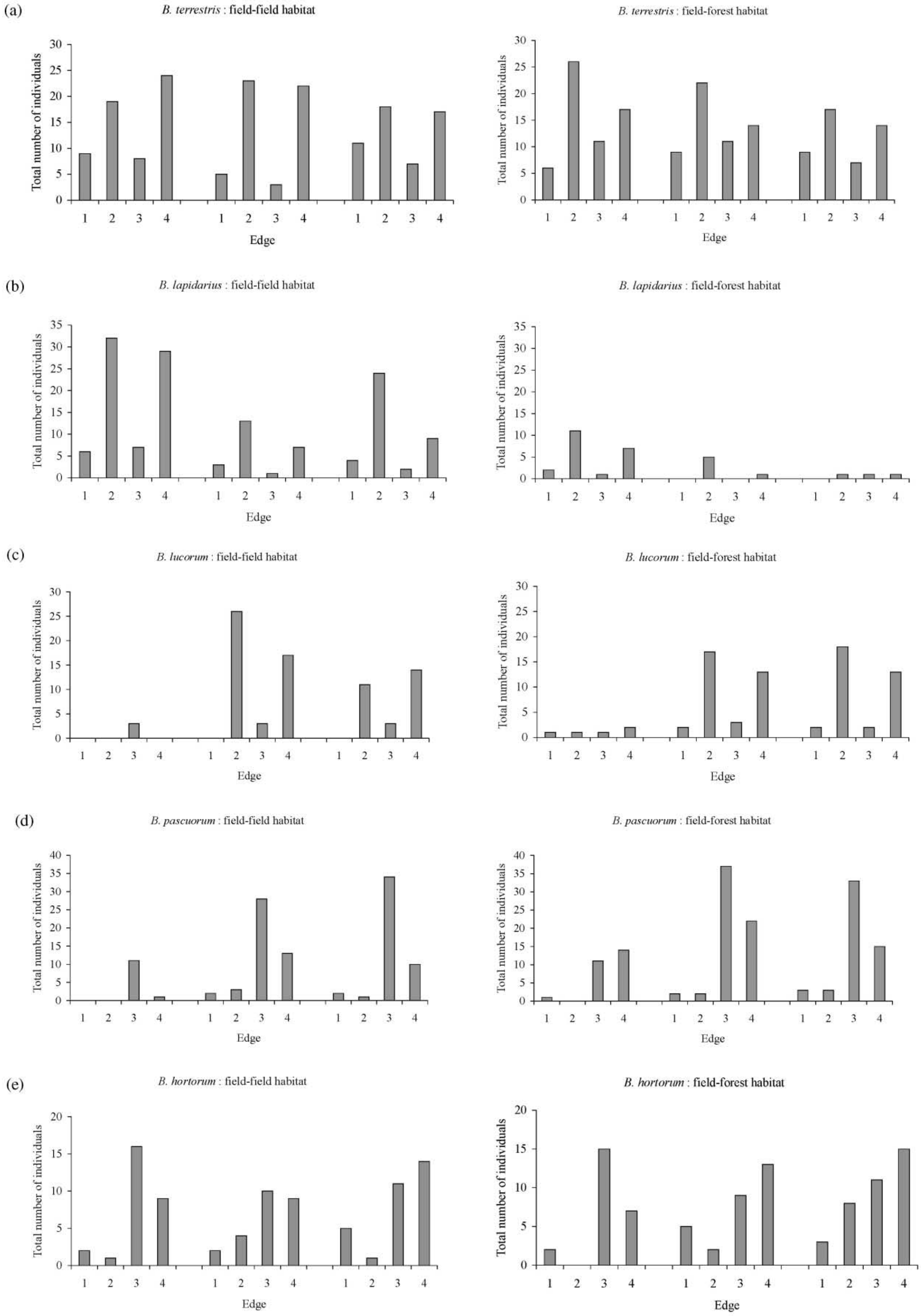

Fig. 3. Boundary and edge type preferences for nest-searching bumblebee queens in two different habitats. Boundary types were as follows: (1) fenced; (2) managed hedge; (3) gapped-out hedge. Edge types were (1) no bank or vegetation; (2) bank only; (3) tussock only; (4) bank and tussock.

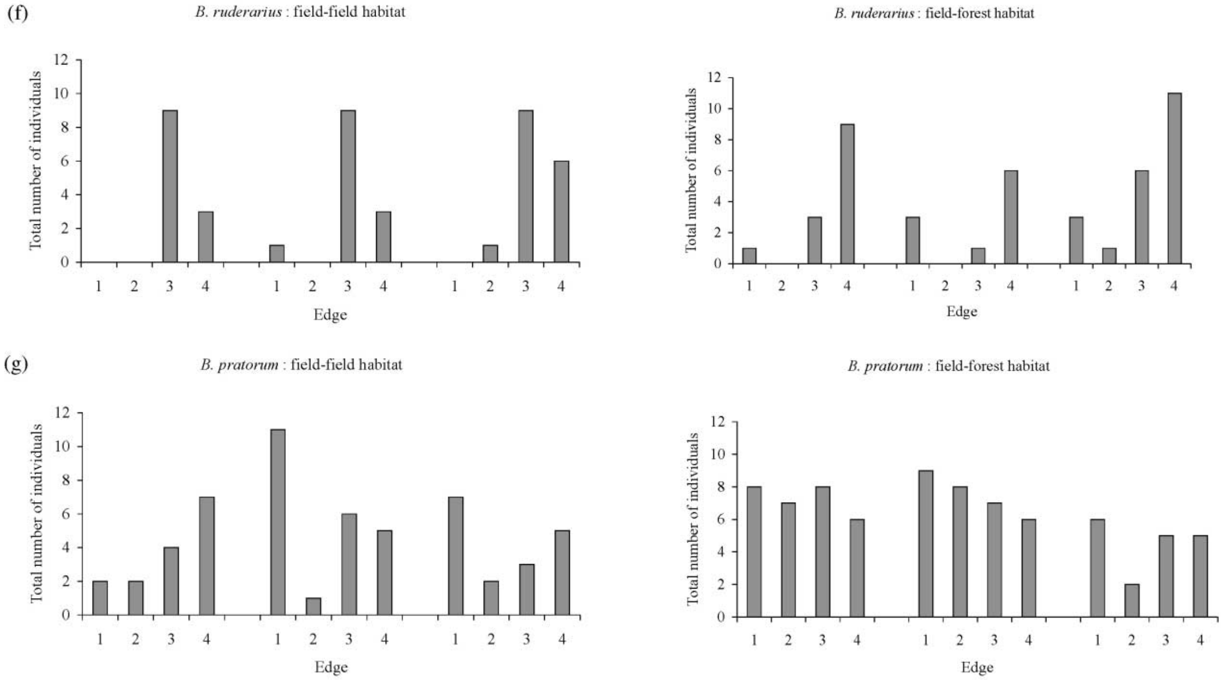

Fig. 3. (*continued*).

anthropogenic artefacts (Prys-Jones and Corbet, 1991), and sites such as wall cavities may offer ideal unshaded nest sites.

No difference was found between occurrence of nest searching on open ground and on forest boundaries for *B. lucorum*, although there was a preference towards banks along boundaries with a hedge structure; these may be more sheltered than boundaries that only have fences along their length. Svensson et al. (2000) also found that although this species displayed variety in terms of where individuals searched, overall there was a preference for sheltered boundaries. Those *B. lucorum* queens recorded in southern Sweden (Svensson et al., 2000) were also associated with the presence of tussocks, but here the presence of banks seemed to play an important part in nest-site choice.

The majority of *B. pascuorum* queens were observed along boundaries that afforded some degree of shelter, a pattern that was apparent in both habitats. There was a strong preference towards those edges that contained tussocky vegetation within these boundary types. Svensson et al. (2000) found that *B. pascuorum* queens were most prevalent along forest boundaries in southern Sweden, however Svensson and Lundberg (1977), working in northern Sweden, found a preference for open areas with tussocks. This may depend on the degree of shelter and the amount of direct sunlight afforded by the location (Svensson et al., 2000).

B. hortorum queens were observed searching for nests in either habitat in approximately equal numbers. This species also did not seem to exhibit a preference for boundary type. However, significantly more observations were made along those edges that contained tussocks. The literature suggests that *B. hortorum* nests are found in a diversity of sites, with some studies reporting an association between these and the presence of hedges and banks (Skovgaard, 1936; Fussell and Corbet, 1992a); this was not the case here.

B. ruderarius belongs to the mainland ubiquitous species group of Williams (1982, 1986). It is less common than the other members of this species group, although it may be locally abundant. This species is known to nest on the soil surface of the ground; here it was seen to search along field and forest edges that had tussocks.

B. pratorum is known to be one of the most opportunistic bumblebee species in terms of where it builds its nests. There is some evidence in this study of a slight preference towards forest boundaries, but queens were observed nest searching along the whole range of boundary and edge types.

4.2. Parasitism

It is important to remember that the findings of this study can only give an indication of individual species nest-site preference, and are not necessarily indicative of the abundance of successful nests. Spring queen numbers may bear very little relationship to the number of viable nests founded. The nematode *Sphaerularia bombi*, which acts to arrest ovary development (Pouvreau, 1962; McCorquodale et al., 1998), may disrupt the mechanism of female orientation and affect nest-seeking behaviour (Lundberg and Svensson, 1975). Parasitised queens remain on the wing for much longer than conspecific healthy queens, and are found on typical hibernation sites (north-facing banks) appearing to try to dig into the soil, or to force themselves under vegetation (Alford, 1975); parasitised queens do not found nests. Queens in this study exhibited characteristic nest-searching behaviour, and not that of parasitised individuals. Large numbers of nests founded by queens free from *S. bombi* fail before workers and/or reproductives are produced. This can be due to factors such as predation, disturbance from both human and environmental stochastic events, and usurpations, from both conspecifics and *Psithyrus* spp. Hobbs et al. (1962), and Richards (1978) found that approximately 15% of nests of one species within their study area in western Canada experienced usurpation attempts. As the season progresses, local extinctions and the successful production of reproductives are highly correlated with local floral diversity and density (Pyke, 1979, 1980; Bowers, 1985).

4.3. Timing of emergence

The earlier a species emerges from hibernation, the more choice one would imagine it has in terms of possible nest sites. However, later emergence has advantages in that new nest sites may become available as the season progresses, and weather and resources may be more favourable to colony founding. There may also be lower pressure from parasitism by *Psithyrus* spp. There is probably a degree of trade-off between early and late establishment (Richards, 1978). Here, the three that preferentially searched along banks (*B. terrestris, B. lapidarius, B. lucorum*) were already abundant by the start of the study, whilst of the three species that preferred tussocks (*B. pascuorum, B. hortorum, B. ruderarius*), *B. hortorum* and *B. ruderarius* were only beginning to emerge (Fig. 1). Potential nest sites along banks are likely to be more visible earlier in the season, before becoming covered with vegetation, whilst tussocks are likely to offer better cover later in the season. Emergence patterns of queens of all species were slightly later in this study than may be expected in southern England; the study site was on elevated chalk downland and relatively exposed, and ambient temperatures would have been lower than those on surrounding land with a greater degree of shelter.

4.4. Spatial patterns of nest founding

There is considerable spatial variation in the patterns of *Bombus* nest founding. Harder (1986) found a random pattern of dispersal of 35 bumblebee nests of five different species within one field in Ontario, Canada. Nest-site abundances, both relative and absolute, vary from year to year (Bohart and Knowlton, 1952; Teräs, 1976; Thomson, 1978). The pattern of establishment of subterranean nests is likely to be a reflection of the nesting habits of the local small mammal population. The density of small mammals is independent of the density of nest-seeking queens (Harder, 1986). Svensson and Lundberg (1977) working on bumblebee nests in northern Sweden found that all excavated subterraneous nests were located in what were previously rodent nests. They suggested that with peaks in rodent population dynamics, many ‘extra’ nests are created; these are then left empty when numbers fall below peak levels, and *Bombus* species can colonise these without competition or parasitism from rodents (Svensson and Lundberg, 1977). Individual *Bombus* species success is highly variable between years, and some years are more favourable overall for *Bombus* spp. than others. All this influences the numbers of queens produced at the end of the colony life cycle, and the numbers emerging from hibernation in the spring. Some authors believe that there may be competition for nest sites (Ranta, 1982), but this has been refuted by others (Pyke, 1982). If competition does occur, it probably differs between habitats, and between years.

Although recent work has indicated that bumblebees forage further from their nests than previously thought (Riley et al., 1996; Osborne et al., 1999; Walther-Hellwig and Frankl, 2000), the maximal observed home range is no more than 1750 m (Walther-Hellwig and Frankl, 2000), and on average may be much less than this (Kevan and Baker, 1983; Bowers, 1985; Rotenberry, 1990). Successful nests will require a continuum of forage resources from crops or other food sources within the home range (Dukas and Edelstein-Keshet, 1998; Cresswell et al., 2000).

4.5. Conservation of suitable nest sites

The availability of nest sites is obviously important to the survival of *Bombus* spp. (Tscharntke et al., 1998). Many potential nest sites have been destroyed by landscape modification (Rasmont et al., 1992), as most bumblebee nest sites are found along uncultivated field boundaries (Banaszak, 1983; von Hagen, 1994). Those habitats that have been much disturbed and cultivated are of least value to bumblebee queens as potential nest sites (Fussell and Corbet, 1992a). Remaining potential nest sites exist mainly on scattered remnants of semi-natural habitat (Saville et al., 1997), and it is important that these are conserved, along with habitats such as field and forest boundaries that contain banks and tussock-type vegetation. As an initial step, priority may be given to habitat conservation depending on the crops grown in the surrounding landscape. Those *Bombus* species with the longest tongues (*B. hortorum, B. pascuorum*) are necessary for the pollination of crops such as beans and red clover, and tend to prefer nest sites containing tussocks, whilst those short-tongued species (*B. terrestris, B. lapidarius*) that preferentially nest along banks are successful pollinators of crops with smaller, more open flowers, such as rape and apples (Ranta and Lundberg, 1980; Fussell and Corbet, 1991, 1992b).

Field boundaries have become a major refuge for many arthropod species once common on farmland (Lagerlof and Wallin, 1993). Many widely distributed bird species utilise hedgerows, and areas that are otherwise inhospitable to woodland species may contain hedgerows that are used as winter habitats or dispersal routes (Fuller et al., 2001). Conservation of such areas should aid not only bumblebees, but many other species of fauna as well (Kells et al., 2001).

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References

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

Banaszak, J., 1983. Ecology of bees (*Apoidea*) of agricultural landscape. Polish Ecological Studies 9, 421–505.

Berezin, M.V., Beiko, V.B., Berezina, N.V., 1995. Bumblebees of the Moscow region. Entomologist's Monthly Magazine 131, 259–268.

Bohart, G.E., Knowlton, G.F., 1952. Yearly population fluctuation of *Bombus morrisoni* at Freedonia, Arizona. Journal of Economic Entomology 45, 890–891.

Bowers, M.A., 1985. Bumblebee colonisation, extinction and reproduction in subalpine meadows in north-eastern Utah. Ecology 66, 914–927.

Cresswell, J.E., Osborne, J., Goulson, D.G., 2000. An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. Ecological Entomology 25, 249–255.

Donovan, B.J., Wier, S.S., 1978. Development of hives for field population increase, and studies on the life-cycles of the four species of introduced bumblebees in New Zealand. New Zealand Journal of Agricultural Research 21, 733–756.

Dukas, R., Edelstein-Keshet, L., 1998. The spatial distribution of colonial food provisioners. Journal of Theoretical Biology 190, 121–134.

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

Fuller, R.J., Chamberlain, D.E., Burton, N.H.K., Gough, S.J., 2001. Distributions of birds in lowland agricultural landscapes of England and Wales: how distinctive are bird communities of hedgerows and woodland? Agriculture Ecosystems and Environment 84, 79–92.

Fussell, M., Corbet, S.A., 1991. Forage for bumble bees and honeybees 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 bumblebees. Journal of Apicultural Research 31, 32–41.

Harder, L.D., 1986. Influences on the density and dispersion of bumble bee nests (Hymenoptera, Apidae). Holarctic Ecology 9, 99–103.

Hasselrot, T.B., 1960. Studies on Swedish bumblebees (genus *Bombus* Latr.): their domestication and biology. Opuscula Entomologica Supplementum 17, 1–192.

Hobbs, G.A., Nummi, W.O., Virostek, J.F., 1962. Managing colonies of bumble bees (Hymenoptera: Apidae) for pollination purposes. Canadian Entomologist 94, 1121–1132.

Kells, A.R., Holland, J.M., Goulson, D., 2001. The value of uncropped field margins for foraging bumblebees (*Bombus* spp.). Journal of Insect Conservation 1–9.

Kevan, P.G., Baker, H.G., 1983. Insects as flower visitors and pollinators. Annual Review of Entomology 28, 407–453.

Kosior, A., 1995. Changes in the fauna of bumblebees (*Bombus* Latr.) and cuckoobees (*Psithyrus* Lep.) of selected regions in southern Poland. In: Banaszak, J. (Ed.), Changes in Fauna of Wild Bees in Europe. Pedagogical University, Bydgoszcz, pp. 103–111.

Kwak, M.M., Tieleman, I., 1994. Het Hommelleven. Jeugdbondsuitgeverij en strichting Uitgeverij KNNV. Utrecht, Netherlands.

Lagerlof, J., Wallin, H., 1993. The abundance of arthropods along two field margins with different types of vegetation composition: an experimental study. Agriculture, Ecosystems and Environment 43, 141–154.

Lundberg, H., Svensson, B.G., 1975. Studies on the behaviour of *Bombus* Latr. species (Hym., Apidae) parasitized by *Sphaerularia bombi* Dufour (Nematoda) in an alpine area. Norwegian Journal of Entomology 22, 129–134.

MacFarlane, R.P., Griffen, R.P., Read, P.E.C., 1983. Bumblebee management options to improve "Grasslands Pawera" red clover seed yields. Proceedings of the New Zealand Grassland Association 44, 47–53.

McCorquodale, D.B., Beresford, R.G., Francis, J.M., Thomson, C.E., Bartlett, C.M., 1998. Prevalence of Sphaerularia bombi (Nematoda: Tylenchida: Sphaerulariidae) in bumble bee queens (Hymenoptera: Apidae) on Cape Breton Island, Nova Scotia, Canada. Canadian Entomologist 130, 877–882.

Michener, C.D., 1974. Social Behaviour of the Bees. Harvard University Press, Cambridge, MA.

Norgaard Holm, S., 1966. The utilisation and management of bumble bees for red clover and alfalfa seed production. Annual Review of Entomology 11, 155–182.

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 bumblebee foraging range and constancy, using harmonic radar. Journal of Applied Ecology 38, 519–533.

Pollard, E., 1977. A method for assessing chages in the abundance of butterflies. Biological Conservation 12, 115–134.

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

Pollard, E., Hooper, M.D., Moore, N.W., 1974. Hedges. Collins, London.

Pouvreau, A., 1962. Contribution a l'etude de *Sphaerularia bombi* parasite des reines de bourdons. Annals Abeille 5, 181–199.

Prys-Jones, O.E., Corbet, S.A., 1991. Bumblebees. Richmond Publishing Company, Slough.

Pyke, G.H., 1979. Optimal foraging in bumblebees: rule of movement between flowers within inflorescences. Animal Behaviour 27, 1167–1181.

Pyke, G.H., 1980. Optimal foraging in bumblebees: calculation of net rate of energy intake and optimal patch choice. Theoretical Population Biology 17, 232–246.

Pyke, G.H., 1982. Local geographic distribution of bumblebees near Crested Butte, Colorado: competition and community structure. Ecology 63, 555–573.

Ranta, E., 1982. Species structure of north European bumblebee communities. Oikos 38, 202–209.

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

Rasmont, P., Gaspar, C., LeClerq, J., Jacob-Remacle, A., Pauly, A., 1992. The faunistic drift of Apoidea in Belgium. In: Bruneau, E. (Ed.), Bees for Pollination. Proceedings of an EC Workshop. Brussels. 2–3 March 1992. Commission of the European Communities, Brussels, pp. 65–86.

Richards, K.W., 1973. Biology of *Bombus polaris* Curtis and *B. hyperboreus* Schonherr at Lake Hazen, Northwest Territories (hymenoptera: Bombini). Quaestiones entomologicae 9, 115–157.

Richards, K.W., 1978. Nest-site selection by bumblebees (Hymenoptera: Apidae) in southern Alberta. Canadian Entomologist 110, 301–318.

Ricketts, T.H., Daily, G.C., Erhlich, P.R., Fay, P.R., 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. Conservation Biology 15, 378–388.

Riley, J.A., Smith, A.D., Reynolds, D.R., Edwards, A.S., Osborne, J.L., WIlliams, I.H., Carreck, N.L., Poppy, G.M., 1996. Tracing bees with harmonic radar. Letters to Nature 379, 29–30.

Rotenberry, J.T., 1990. Variable flower phenology: Temporal resource heterogeneity and its implications for flower visitors. Holoarctic Ecology 13, 1–10.

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.

Skovgaard, O.S., 1936. Rodkloverens bestovning, humlebier og humleboer. Raekke, Denmark.

Skovgaard, O.S., 1945. Rodkloverns Bestoving, Humlebier og Humbleboer. Kl danske vidensk Selsk Nat og mth Ser. 6, 1–140.

Sladen, F.W.L., 1912. The Bumble-bee: its Life History and How to Domesticate it. MacMillan, London, UK.

SPSS, 1988. SPSS for Windows: Advanced Statistics. Release 9.0. SPSS, Chicago.

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.

Svensson, B.G., Lundberg, H., 1977. Distribution of bumble bee nests in a subalpine/alpine area in relation to altitude and habitat (Hymenoptera, Apidae). Zoon 5, 63–72.

Teräs, I., 1976. Bumblebees, *Bombus* Latr. (Hymenoptera, Apidae), on red clover in South Savo, Finland. Annals Agricultures Fennoscandia 15, 116–127.

Thomson, J.D., 1978. A local replacement of *Bombus ternarius* by *Bombus terricola* in northern Wisconsin (Hymenoptera: Apidae). Great Lakes Entomology 11, 101–103.

Tscharntke, T., Gathmann, A., Steffan-Dewenter, I., 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. Journal of Applied Ecology 35, 708–719.

von Hagen, E., 1986. Hummeln. Neumann-Neudamn, Melsungen, Germany.

von Hagen, E., 1994. Hummeln bestimmen. Ansiedeln, Vermehren, Schutzen. Naturbuch-Verlag, Augsburg.

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

Westrich, P., 1989. Die Bienen Baden-Wurttembergs, vol. 1. Ulmer Verlag, Stuttgart.

Williams, P.H., 1982. The distribution and decline of British bumble bees (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.