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Causes of rarity in bumblebees

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Abstract

Many bumblebee (*Bombus*) species are thought to have declined in abundance in the last 50 years, while a small number of species remain abundant. Here we examine which factors render some British bumblebee species more susceptible to environmental change than others. We present forage data on workers of 15 bumblebee species gathered from 172 one hour searches conducted at sites in southern UK, the Hebrides (western Scotland) and in New Zealand (to which UK bumblebees were introduced). We also review data on distribution, phenology and tongue length of these species. Overall, Fabaceae appear to be the major pollen source for most bumblebee species. In particular, long-tongued, late emerging species such as *Bombus ruderatus*, *Bombus humilis* and *Bombus subterraneus* specialize heavily in gathering pollen from Fabaceae, and this group of bumblebee species have all declined. Some of them are also at the edge of their geographic range in the UK, which may have rendered them more sensitive to environmental change. The decline of many bumblebee species is probably attributable largely to the loss of unimproved flower-rich grasslands, a habitat rich in Fabaceae. The bumblebee species that remain abundant are mostly short-tongued species that emerge early in the season and have less specialized diets; these species are very common in suburban gardens where they are able to exploit the broad range of floral resources. A third group of bumblebees are strongly associated with Ericaceae in moorland and heathland habitats, and have probably always had restricted distributions. A small number of species are not so easily categorised. *Bombus soroeensis* and *B. ruderarius* are not dietary specialists, nor are they close to the limit of their geographic range, but nevertheless they have declined. Much of the ecology of rare bumblebee species remains poorly understood and in need of further study.

Keywords: Hymenoptera; *Bombus*; Abundance; Tongue length; Pollen; Competition

1. Introduction

Many bumblebee species have suffered declines in recent decades, both in Europe and in North America (Peters, 1972; Williams, 1982, 1986; Rasmont, 1995; Kosior, 1995; Buchmann and Nabhan, 1996; Westrich, 1996; Westrich et al., 1998). Of the 25 species known from the UK, three species are extinct and several more are now confined to a handful of sites and have uncertain futures. The consensus is that declines in numbers of bumblebees are linked to the intensification of farming practices (Williams, 1986; Osborne and Corbet, 1994; Goulson, 2003).

The plight of our bumblebee fauna deserves particular attention because loss of bee species will almost certainly have repercussions for other wildlife. A large number of wild plants are pollinated predominantly or exclusively by bumblebees, sometimes by particular species of bumblebee (Corbet et al., 1991; Osborne et al., 1991). Thus it seems probable that reductions in the abundance and species richness of bumblebees may lead to widespread changes in plant communities (Corbet et al., 1991). These changes will have further knock-on effects for associated herbivores and other animals dependent on plant resources.

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Although many bumblebee species have become more scarce, a small subset of species (six in the UK) remain abundant and ubiquitous. At present we have little indication as to why bumblebee species differ so widely in their abundance and susceptibility to environmental change. Morphologically, all species are remarkably similar, the only obvious differences being variation in size and tongue length. They have broadly similar annual life cycles (although a few species are partially bivoltine), and all depend exclusively on nectar and pollen for food. Most species do not have precise habitat requirements, so far as is known (Williams, 1986).

For practical reasons, most studies of bumblebee ecology and behaviour focus on the common species, notably *Bombus terrestris*, *Bombus lucorum*, *Bombus lapidarius*, *Bombus pratorum*, *Bombus pascuorum* and *Bombus hortorum* in much of Europe. For most of the approximately 40 remaining European bumblebee species, we have very little information on forage use, or indeed on any other aspects of their ecology. A recent study in southern UK suggested that rare bumblebees may have more specialized diets, while those species that remain abundant are generalists (Goulson and Darvill, 2004). Thus studies of the forage used by common species may be of little help in developing appropriate conservation strategies for the rare ones. Ecological studies of rare and declining species are urgently needed if appropriate conservation measures are to be deployed. In particular, we need to improve our understanding of the causes of rarity in bumblebees.

Here we quantify and compare forage use by a broad range of UK bumblebee species to test whether rarity is correlated with dietary specialization. We quantify the tongue length of these species, since tongue length is likely to constrain foraging behaviour. We also review data on latitudinal range, phenology, and UK distribution, in an attempt to understand what factors determine bumblebee abundance and susceptibility to environmental change.

2. Methods

Bumblebee forage use was quantified using the same methodology at 172 sites in three geographic regions: southern UK (Salisbury Plain, S. Wales, S. Essex, N. Kent, Dungeness, Somerset levels) (68 sites); the Hebrides, western Scotland (34 sites), central South Island, New Zealand (70 sites). Regions were selected on the basis of supporting a broad range of bumblebee species, and individual study sites within regions were chosen to provide abundant bumblebee forage and often because previous records suggested that rare bumblebee species were present. The New Zealand bumblebee fauna was deliberately introduced at the end of the 19th century from the UK (Hopkins, 1914), and includes two species which are now exceedingly rare or extinct in the UK.

Studies were carried out between June and August 2002 (southern UK), January 2003 (New Zealand), and June–August 2003 (southern UK and Inner Hebrides). Each site consisted of a circle of approximately 100 m radius, and was searched for one man hour. All searches were conducted between 0800 and 1700 h, and during warm dry weather favourable to bee activity. All *Bombus* species were recorded. In areas where both were present (southern UK), no attempt was made to distinguish workers of *B. terrestris* and *B. lucorum* (to do so would have been very time-consuming and unreliable in the field). However, the small numbers of male *lucorum* recorded at the southern UK study sites (male *terrestris* and *lucorum* are readily distinguished) suggest that the majority of workers were *B. terrestris*. Other species that are difficult to distinguish on the wing, such as *B. humilis* and *Bombus muscorum*, were captured and examined with a hand lens. The area was searched systematically, to avoid recording the same bees more than once, but this probably occasionally occurred. The flower species that the bee visited was recorded, and the bee was briefly observed to determine whether it was collecting pollen or nectar. Bees were classified as nectar collectors (those not collecting pollen) or pollen collectors (those observed actively grooming pollen into their corbiculae), but it must be noted that most pollen collectors were also collecting nectar. The total number of inflorescences within the search area (the circle of 100 m radius) was estimated for each forage species present.

The proportion of visits by workers of each bee species to each plant family was examined using principal components analysis in SPSS 11.0, with separate analyses for pollen-collecting and nectar-collecting visits.

Tongue lengths were measured for dry museum specimens of workers of each species (length of the glossa plus prementum, following Prys-Jones and Corbet (1991)), since tongue length is known to influence floral preferences. Sample size was ten for all species except *Bombus distinguendus* (4) and *Bombus monticola* (6).

3. Results and discussion

3.1. Forage use

Our analyses rely on surveys conducted at a large number of sites differing greatly in habitat type and floral availability. The forage used by each bee species is clearly constrained by availability, so that for example bees on Salisbury Plain cannot visit *Erica* spp. because none are available. This does not mean that they would not visit them given the opportunity. Thus our forage data should not be interpreted as a measure of floral preference, but rather as a measure of forage use in the sites where rare bees persist. Our study sites include almost all of the sites in England and New Zealand known to support a rich assemblage of bumblebee species, and also representative sites from the Hebrides. For some species, such as *Bombus sylvarum*, we visited all known UK populations, so our measure of forage use should be accurate.

A striking feature of the data is the large number of visits by workers of almost all bee species to Fabaceae, notably *Trifolium pratense*, particularly when collecting pollen (Table 1). This species alone accounted for 28.8% of all pollen-collecting visits, while Fabaceae as a whole received 61.1% of all pollen-collecting visits (Table 2). The only other substantial source of pollen was Ericaceae (*Calluna* and *Erica* spp.), but it must be noted that these visits were largely confined to three bumblebee species, *Bombus magnus*, *Bombus jonellus* and *Bombus muscorum smithianus*, which appear to be heath/moorland specialists to varying degrees. Less important sources of pollen included Scrophulariaceae (largely *Odontites verna*), Boraginaceae, Lamiaceae and Rosaceae.

When collecting nectar, forage use by workers was markedly different. Although Fabaceae were still the most visited plant family, both Asteraceae and Boraginaceae were also visited at high frequency (Table 2). The single most popular species for nectar collection was *Echium vulgare*, which alone comprised 21.4% of all bee visits. Among the Asteraceae, the main nectar sources were *Centaurea* and *Cirsium* spp. (Table 3). The contrast between bumblebee forage use when collecting pollen versus nectar is most marked in the Asteraceae, which are frequently visited for nectar but very rarely for pollen, despite often having conspicuous and abundant pollen. This is particularly noticeable in *Cirsium* spp.; when bees gather nectar from *Cirsium* flowers they often become liberally coated in pollen but rarely groom this pollen into their corbiculae (D.G. pers. obs.). It seems that Asteraceae pollen has properties that render it less attractive to bumblebees than alternatives such as Fabaceae, but what these might be remains unknown. One possibility that has not been investigated is that nitrogen-fixing Fabaceae may provide pollen that is richer in protein (Goulson and Darvill, 2004). Variation in pollen quality, and its significance to foraging bees, has received very little attention.

Principal components analysis summarised that 71.1% and 15.7% of variation in visitation patterns to different plant families when collecting pollen could be explained by the first and second principal components, respectively (Fig. 1(a)). Principal component one sepa-

Table 2
Forage use by bumblebees when collecting pollen and nectar, expressed as a percentage of all visits recorded

Species	Pollen	Nectar
Asteraceae	2.2	21.9
Boraginaceae	4.1	21.4
Ericaceae	13.5	3.1
Fabaceae	61.1	36.8
Lamiaceae	2.5	3.5
Rosaceae	4.1	1.5
Scrophulariaceae	5.8	3.2

Data are combined for all bee species, castes and sites.

Table 1
Forage use by bumblebees collecting pollen

Species	% of visits	Cumulative %	Family
Trifolium pratense	28.8	28.8	Fabaceae
Trifolium repens	10.1	38.9	Fabaceae
Calluna vulgaris	9.0	46.7	Ericaceae
Lotus corniculatus	8.5	56.4	Fabaceae
Erica cinerea	4.4	60.8	Ericaceae
Onobrychis viciifolia	4.2	65.0	Fabaceae
Melilotus altissima	4.1	69.1	Fabaceae
Echium vulgare	3.6	73.5	Boraginaceae
Odontites verna	3.0	75.7	Scrophulariaceae
Rubus fruticosus	2.8	78.4	Rosaceae
Hypericum perforatum	1.9	80.4	Guttiferae
Potentilla erecta	1.5	81.8	Rosaceae
Erica tetralix	1.4	83.3	Ericaceae
Papaver rhoeas	1.2	84.5	Papaveraceae
Rhinanthus minor	1.1	85.6	Scrophulariaceae
Taraxacum officinale	1.1	86.7	Lamiaceae
Prunella vulgaris	0.9	26.8	Lamiaceae
Vicia sepium	0.9	27.7	Fabaceae
Vicia cracca	0.7	89.2	Fabaceae
Lupinus arboreus	0.7	89.8	Fabaceae

Only the 20 most visited plants are included, ranked according to the number of visits (for all bee species, castes and sites combined). $N = 3029$.

Table 3
Forage use by bumblebees collecting only nectar

Species	% of visits	Cumulative %	Family
Echium vulgare	21.4	21.4	Boraginaceae
Trifolium pratense	18.5	39.8	Fabaceae
Trifolium repens	9.3	40.0	Fabaceae
Centaurea debeauxii	7.7	56.9	Asteraceae
Centaurea scabiosa	4.4	61.2	Asteraceae
Cirsium vulgare	3.4	64.7	Asteraceae
Erica cinerea	2.9	67.6	Ericaceae
Lotus corniculatus	2.1	69.7	Fabaceae
Cirsium arvense	2.0	71.7	Asteraceae
Odontites verna	1.9	24.4	Scrophulariaceae
Taraxacum officinale	1.8	75.3	Lamiaceae
Melilotus altissima	1.7	77.0	Fabaceae
Vicia cracca	1.3	78.3	Fabaceae
Calluna vulgaris	1.3	79.6	Ericaceae
Knautia arvensis	1.2	80.8	Dipsacaceae
Thymus pulegioides	1.1	20.7	Lamiaceae
Rubus fruticosus	1.1	26.2	Rosaceae
Calystegia silvatica	1.1	27.3	Convolvulaceae
Fuschia sp.	1.1	85.2	Onagraceae
Escallonia sp.	0.9	86.1	Other

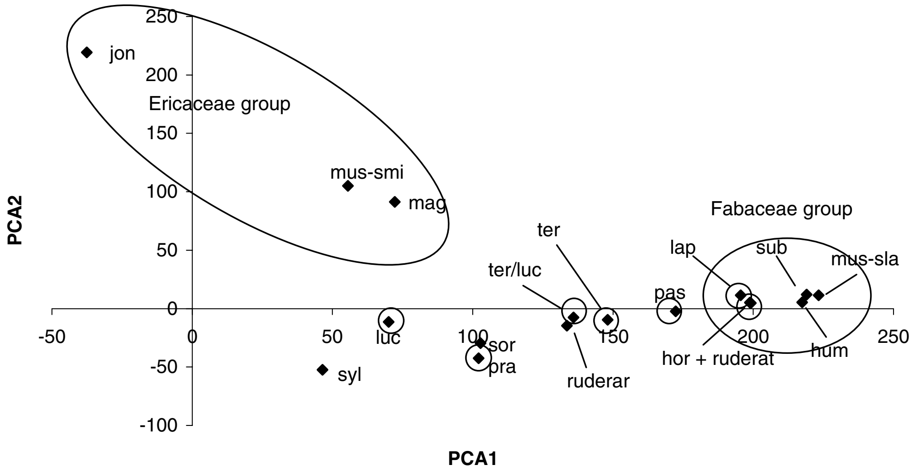
The 20 most visited plants are included, ranked according to the number of visits (for all bee species, castes and sites combined). $N = 3370$.

rated species largely on the basis of their usage of Fabaceae, with a cluster of mainly longer tongued bee species specializing in collecting Fabaceae pollen (ranked in declining order; *B. muscorum sladeni*, *Bombus subterraneus*, *B. humilis*, *B. ruderatus*, *B. hortorum*, *B. lapidarius* and *B. pascuorum*). It is interesting to note that the first four species are rare and declining, while those with a less pronounced association with Fabaceae remain relatively abundant. There was a significant positive correlation between principal component one and tongue length (Pearson's correlation coefficient 0.495, $p = 0.043$).

The second axis reflected visitation to Ericaceae, and so separates moorland species from the remainder. It highlights the extreme specialization of *B. jonellus* in this respect, while *B. magnus* and *B. muscorum smithianus* are also largely found on or near moorland, but these two species do collect pollen from plant families other than Ericaceae, notably from Fabaceae. The remaining species are not heavily dependent on either Fabaceae or Ericaceae for pollen, and would appear to be more generalized. This group includes the highly polylectic species *B. terrestris*, *B. lucorum* and *B. pratorum*, but also three rare and declining species, *B. ruderarius*, *B. sylvarum* and *B. soroeensis*.

PCA on nectar-collecting visits was less revealing. The first and second principal components accounted for 47.7% and 16.1% of variation, respectively (Fig. 1b). The first component is once again closely correlated with use of Fabaceae, while the second is positively correlated

(a) Pollen



(b) Nectar

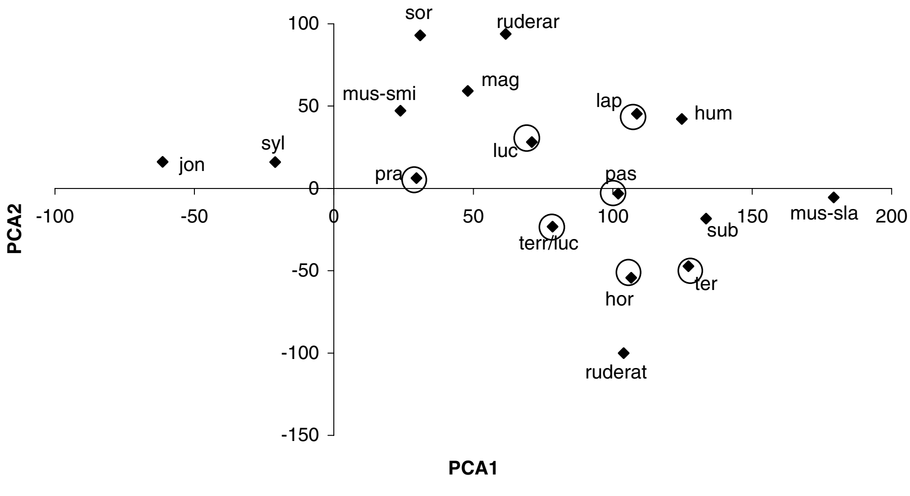


Fig. 1. The proportion of visits to different plant families by workers of each bumblebee species was subjected to principal components analysis, and the first two components are plotted here. Combined data for *B. terrestris*/*lucorum* from southern UK is plotted separately to *B. terrestris* alone (New Zealand data) and *B. lucorum* alone (Hebridean data). The 'big six' bumblebee species are circled. (a) Pollen-collecting visits; the first and second component account for 71.1% and 15.7% of variation in forage use, respectively. Component 1 is strongly correlated with visits to Fabaceae, while component two is correlated with visits to Ericaceae. (b) Nectaring visits; the first and second components account for 47.7% and 16.1% of variation, respectively. The first component is correlated with use of Fabaceae, while the second is primarily correlated with use of Asteraceae.

with use of Asteraceae and negatively correlated with visits to Boraginaceae. However, no clear groups are evident. It has previously been found that bumblebees are more polylectic when gathering nectar than when gathering pollen (Goulson and Darvill, 2004; Goulson and Hanley, in press), which may explain the absence of clear patterns. For both pollen and nectar collection, the 'big six' common bumblebee species tend to fall centrally within the scatter of bee species, suggesting a lower degree of dietary specialization (Fig. 1). This concurs with previous studies which have found that abundant bumblebee species tend to have broader diets (Rasmont, 1988; Goulson and Darvill, 2004; Goulson and Hanley, in press).

Our studies were conducted at the time of peak worker activity for most species, and so few data were obtained on queen foraging which tends to occurs earlier in the season. Adequate forage availability for queens is vital for nest foundation, and so further studies of queen forage use would be valuable.

3.2. Causes of rarity in bumblebees

The only previous detailed attempt to explain patterns of abundance of UK bumblebees was made by Williams (1988). He sensibly argued that rare species tended to be those near the edge of their latitudinal range. Such species are presumably poorly adapted to local conditions and thus can only survive in high quality habitats; when these become degraded, they are the first species to disappear. Several species that have declined are indeed at the northern edge of their range in the UK: *B. sylvarum*, *B. humilis*, *B. ruderarius*, *B. ruderatus*, and *B. subterraneus* (Table 4). However, this theory alone is not adequate to explain patterns in bumblebee declines. Both *B. lapidarius* and *B. terrestris*, the two most common UK bumblebees, are also close to the northern limit of their range. The strongest population of *B. ruderarius* found in our study was the furthest north, in the Hebrides. And *B. soroeensis*, which would appear to be near the centre of its range in the UK, is rare and seemingly in decline. An alternative but mutually compatible explanation as to why species at the northern edge of their range have declined is that these species are confined to the south in the UK, and this region has experienced greater agricultural intensification than any other. To distinguish these hypotheses it is worth considering whether species near the centre of their geographic range have declined more in the south than in the north (which we would predict if declines were driven by agricultural intensification). It seems that *B. muscorum sladeni* (the southern race) has probably declined more than *B. muscorum smithianus* (the Hebridean race). Recent searches by the authors for *B. soroeensis* in southern localities known to have formerly supported this species have found only one southern population (Salisbury Plain), and almost all recent

Table 4
Attributes of bumblebee ecology, gleaned from personal observation and from Sladen (1912), Løken (1973), Alford (1975), Prys-Jones and Corbet (1991), Goodwin (1995) and Edwards (1998, 1999, 2000, 2001)

Species	Study regions	Sample size	Subgenus	Tongue length	Emergence time	UK status	UK position relative to European distribution
terrestris/lucorum	SUK	703	Bombus	–	–	–	–
terrestris	NZ	882	Bombus	7.6 ± 0.5	Early	Widespread, common	Northern edge
lucorum	Heb	218	Bombus	7.5 ± 0.5	Early	Widespread, common	Central
magnus	Heb	149	Bombus	8.0 ± 0.6	Mid	Local	Central
lapidarius	SUK + Heb	1010	Melanobombus	7.7 ± 0.4	Mid	Widespread, common	Northern edge
pascuorum	SUK + Heb	457	Thoracobombus	8.5 ± 0.6	Mid	Widespread, common	Central
humilis	SUK	197	Thoracobombus	8.1 ± 0.5	Late	Rare, declining	Northern edge
ruderarius	Heb	181	Thoracobombus	8.5 ± 0.6	Mid	Rare, declining	Northern edge
sylvarum	SUK	80	Thoracobombus	8.8 ± 0.7	Late	Rare, declining	Northern edge
muscorum sladeni	SUK	91	Thoracobombus	8.7 ± 0.6	Late	Rare, probably declining	Central
muscorum smithianus	Heb	455	Thoracobombus	8.9 ± 0.6	Late	Local	Central
hortorum	SUK + NZ + Heb	1008	Megabombus	12.5 ± 0.8	Mid	Widespread, common	Central
ruderatus	NZ	292	Megabombus	11.6 ± 0.7	Mid	Rare, declining	Northern edge
subterraneus	NZ	38	Subterraneo-bombus	9.3 ± 0.6	Late	Extinct	Northern edge
distinguendus	–	–	Subterraneo-bombus	9.7 ± 0.6	Late	Rare, declining	Central
soroeensis	SUK	60	Kallobombus	6.5 ± 0.4	Late	Rare, declining	Central
pratorum	SUK	120	Pyrobombus	7.3 ± 0.4	Early	Widespread, common	Central
monticola	–	–	Pyrobombus	7.5 ± 0.5	Mid	Rare, declining	
jonellus	Heb	265	Pyrobombus	6.4 ± 0.3	Variable	Local	Central

Sample size refers to the number of foraging records obtained for each species. Note that tongue lengths differ slightly from those in Goulson and Darvill (2004), reflecting differences in the individual bees that were measured. Those for *B. monticola* and *B. distinguendus* are based on old UK museum specimens. Emergence times are not precise, and depend greatly on latitude. For southern UK they are crudely classified as: Early = March–April, mid = April to mid May, late = May onwards. In the Hebrides, emergence is approximately 2 months later.

records are from the north (M. Edwards, pers. comm.). *B. distinguendus* is now extinct throughout England but survives in the far north of Scotland and the Hebrides. It seems likely that declines of rare bumblebees have been greatest in the south (particularly the Midlands, East Anglia and the south east), but accurate distribution and abundance data is not available to answer this question convincingly.

It has often been suggested that long-tongued bumblebees have declined most (Rasmont, 1988; Prys-Jones and Corbet, 1991). Examination of the UK species suggests that this is broadly true, although there are notable exceptions. If we crudely classify the UK non-*Psithyrus* bumblebees into short (⩽8 mm), medium (8–9 mm) and long (>9 mm) tongued species, then four of the 'big six' bumblebees are short tongued. This category also includes three heathland specialists (*B. magnus*, *B. jonellus* and *B. monticola*) and the rare and declining *B. soroeensis*. The medium-tongued bees comprise only the subgenus *Thoracobombus*, of which four are rare and declining while *B. pascuorum* remains common. The long-tongued bees includes three very rare and declining species, *B. ruderatus*, *B. distinguendus* and *B. subterraneus*, and the ubiquitous *B. hortorum*.

Our data suggest that long-tongued species tend to be those that specialize in collecting pollen from Fabaceae, a plant family that includes many species with deep corollae. Those bee species with the most pronounced specialization in this respect are all rare, and it seems likely that their dietary specialization is in part the cause of their rarity. Previous studies have shown the importance of Fabaceae, and in particular of *T. pratense*, as forage species for bumblebees in both the UK and northern Europe (Skovgaard, 1936; Teräs, 1985; Jennersten et al., 1988; Carvell, 2002; Goulson and Darvill, 2004). Rasmont (1988) argued that the decline of long-tongued bumblebees in France and Belgium is largely attributable to a decline in leguminous fodder crops once grown to feed horses. Similarly, the long-tongued *B. ruderatus* and *B. subterraneus* appear to be in decline in New Zealand as a result of reduced sowing of *T. pratense* for fodder (Goulson and Hanley, in press). In Europe, the switch from Fabaceae-rich hay meadows to silage for providing winter fodder for cattle has probably had a large impact on the availability of floral resources for bumblebees (Goulson, 2003). Indeed, surveys have shown that both *T. pratense* and *L. corniculatus* have declined in the UK (Grime et al., 1988; Rich and Woodruff, 1996), and these two species together comprised 37.3% of all pollen-collecting visits by bumblebees. The decline of these and other legume species is likely to have had severe repercussions for UK *Bombus* species that specialize in collecting forage from Fabaceae.

Conversely, four of the six bumblebee species that remain common and widespread in the UK have broad diets when collecting both nectar and pollen. It is presumably their dietary flexibility that has enabled these species to flourish in urban areas where there are many cultivated flowers from diverse taxa, but rather few of their natural forage resources (Goulson et al., 2002). It has previously been argued that the apparent specialisation of rare bumblebee species and generalisation of common ones is an artefact of sample size; common bees are recorded often and therefore are recorded visiting more plant species (Williams, 1989). They are also likely to occupy a broader range of habitats, and hence encounter more plant species. However, our approach of examining the proportion of visits to different plant families is not greatly affected by sample size, and in our data set specialisation is not related to numbers of records obtained when collecting either nectar or pollen (sample sizes are given in Table 4). For example, *B. lapidarius* and *B. hortorum* both belong to the group of Fabaceae specialists, but were the two most frequently recorded species, while *B. pratorum* and *B. soroeensis* were recorded comparatively rarely but nonetheless appear to be generalists.

The abundance of *B. hortorum* is a conundrum. It has one of the longest tongues of any European species. It is less specialized in its diet than some long and medium-tongued species (Fig. 1), but nonetheless shows a strong association with Fabaceae. So why has it fared so well? Interspecific competition is thought to be important in bumblebee communities (Inouye, 1978; Pyke, 1982). It may be that the dwindling numbers of deep flowers are sufficient to support one long-tongued species but no more. *B. hortorum* is near the centre of its range in the UK, while the only other species with a very long tongue, *B. ruderatus*, is near the edge of its range, which may make it more susceptible to habitat loss or competition.

Our data strongly suggest that long-tongued Fabaceae specialists are not the only bumblebees to have suffered declines. *B. soroeensis*, *B. ruderarius* and *B. sylvarum* are all now exceedingly rare throughout most of the UK, and have undoubtedly declined, but all three are moderately polylectic in both pollen and nectar collection, and *B. soroeensis* is short-tongued. As we have seen, *B sylvarum* is at the edge of its range, with a distribution concentrated in southern England where agricultural changes have been great, and this may explain its decline. But *B. soroeensis* is in the centre of its range, and *B. ruderarius* has strong populations in Scotland.

A final correlate of rarity appears to be emergence time (Table 4). Bumblebee species differ greatly in the time of year at which queens emerge from hibernation; the earliest species emerge in February, while other species do not appear until late May. All five of the early and early/mid emerging species are in the 'big six'. All of the late emerging species have declined (with the possible exception of the moorland bee *B. muscorum smithianus*). Most late emerging species are medium or long tongued. It has been suggested that early emerging species are associated with woodland or woodland edges, where many plants flower in early spring before the canopy closes, while late emerging species are associated with unimproved grassland (M. Edwards, pers. comm.), although this hypothesis remains to be adequately tested. Late emergence for grassland species is necessary because few grassland plants flower before May in the UK, and most of the deep-flowered Fabaceae visited by long-tongued species do not flower until June. The greatest change to agriculture in western Europe in the last 50 years has been the loss of unimproved grasslands (hay meadows, calcareous grassland, etc.), and this may explain why late-emerging long-tongued bumblebees have been most severely affected.

4. Conclusions

Declines in abundance and range of bumblebee species can largely be explained by a combination of factors. Longer-tongued, late-emerging species associated with meadow flora such as Fabaceae are at high risk because a high proportion of unimproved grassland has been lost (Howard et al., 2003). Species at the northern edge of their range may be threatened because they are poorly adapted to the UK climate and/or because their southerly distribution has exposed them to the most intensive agricultural changes. Declines in some species, such as *B. soroeensis* and *B. ruderarius*, cannot be adequately explained by these factors, and may relate to other aspects of their ecology such as nesting requirements, about which we know very little. At present our knowledge of the changing distributions and habitat requirements of most of the rarer bumblebee species is scant, and further studies are urgently needed. In the meantime, restoration of Fabaceae-rich grasslands (particularly containing *T. pratense*) would seem to be the most sensible strategy for the conservation of many of the more threatened bumblebee species.

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