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Does specialization explain rarity and decline among British bumblebees? A response to Goulson et al.

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Abstract

Recent studies of British bumblebees have proposed a seemingly simple explanation for the decline in some species: that greater dietary specialization among the rarer species has put them at greater risk. However, comparisons of dietary specialization require: (1) that bees have access to the same dietary options among which to make their choices; (2) that the differing relative breadths of dietary choices made are not obscured by the differing sample sizes among bee species. Using one of the few suitable data sets, I find no evidence for a relationship between, on the one hand, rarity or declines in British bumblebees and, on the other, their dietary breadths, the strengths of their dietary preferences, or their proboscis lengths (which influence dietary choices). In contrast, there is support for a relationship between rarity or declines within Britain and the sizes of species' European ranges, particularly when these measures are adjusted to represent their ranges near sea level. Adjusted range sizes may reflect overall niche breadth and perhaps climatic and habitat specialization. This is not to say that climate change is the driving factor for declines or that changing food-plant availability is unimportant, but that climatic and habitat specialization may be a better indicator of risk of decline, which deserves further study.

Keywords: Biodiversity loss; Species richness; Species assemblages; Community structure; Faunal change

1. Introduction

There is substantial agreement that some of the rarer social bumblebee species (genus *Bombus*, excluding the subgenus *Psithyrus*) have declined and, in some cases at least, are still declining in the extents of their distribution ranges throughout Britain (e.g. Free and Butler, 1959; Alford, 1975; Williams, 1982; Prys-Jones and Corbet, 1987; Benton, 2000; Carvell, 2002; Edwards, 2003; Goulson, 2003; Macdonald, 2003; Edwards and Williams, 2004). The question of what causes bumblebee rarity and declines is important because the social species are popular and valuable pollinators (Osborne and Williams, 1996), so there is strong interest in their conservation.

Recently, Goulson and Darvill (2004) and Goulson et al. (2004) have concluded that declines are explained by a food-plant specialization hypothesis. This proposes that: (1) the rarer bumblebees, in terms of their distribution throughout Britain, have; (2) narrower dietary breadth for both nectar and pollen; (3) that this is the result of greater specialization in their foraging behaviour, which; (4) because of changes in plant communities, has caused a decline (reduction) in the extent of their distribution ranges within Britain. Narrower food-plant specialization is also suggested to be associated among bumblebee species with longer proboscides (see also Prys-Jones and Corbet, 1987; Rasmont, 1988). Proboscis length has been shown previously to have a major influence on flower choice (Brian, 1957).

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Most studies exclude the social parasites (subgenus *Psithyrus*) because their distributions are governed by different processes, particularly regarding the added importance of the densities of colonies of the host species.

Most people studying the problem of bumblebee declines agree broadly that changes in land use, acting through changes in the availability of forage plants, is at least one important factor in causing the declines of some bumblebee species in Britain (op. cit.). The debate concentrates on the ecological mechanism by which this has its effect, and in particular, on the meaning of the word 'specialization' in this context. Based on dictionary definitions (e.g. Onions, 1973), *preference* might be used where a bumblebee species will like or choose one or more food-plant species over others, but will still use some of the less preferred species at a lower rate, or when the more preferred species are rare or absent. Unfortunately, *specialization* might then be used to describe both (1) a greater degree of narrowness in this preference; and (2) the more extreme situation where a bumblebee species is exclusively limited by choice to a particular food-plant species, or to a well-defined group of food-plant species. All of these cases involve the distinguishing characteristic of active choice by a forager of the flowers of one plant species and rejection of those of another. Consequently, both 'specialization' and 'preference' would be inappropriate terms for situations where bees visit a plant frequently simply because either the bee species or the plant species is abundant. In this case they would be expected to encounter one another frequently by chance alone. This distinction is important because of the potential ecological implications of discovering specialist dependencies by bumblebee species on particular food-plant species.

The food-plant specialization hypothesis can be seen as a particular case of familiar ideas of species occupying more or less specialized niches (Hutchinson, 1957). Taking a macroecological perspective (Brown, 1995; Gaston and Blackburn, 2000), I have described a simple visualization (a 'marginal mosaic' model: Williams, 1985, 1988, 1989b) for how bumblebee species near the edges of their geographic ranges, or with particularly narrow ranges (i.e. those populations near their niche limits), might have marginal growth rates, be present at lower local densities, and be most patchy in their local distributions. With reductions in foraging profits and consequent further reductions in density, these species would be most likely to be extirpated locally and so show range declines. Consequently, it is not necessarily specialization in particular food-plants that is limiting, but possibly specialization in other aspects of the niche. This idea could encompass several possible mechanisms. As a first step, the relationships between species' declines within Britain and their European range sizes (as a measure of their relative niche breadths), or proximity to their range edges (as a measure of proximity to their niche envelopes), needs to be assessed.

The food-plant specialization hypothesis was rejected by Williams (1985, 1989b). However, there are challenges in how to measure all of the factors involved. Here, I apply improved methods in an effort to avoid some of the pitfalls in assessing the relationships.

2. Methods

2.1. Measuring rarity and decline in British distribution ranges

Williams (1982) provided the first quantitative description of declines in the extent of the distributional ranges of bumblebees in Britain. That study used data from a national grid of 10 × 10 km cells in the Bumblebee Distribution Maps Scheme (BDMS) atlas (Anonymous, 1980; Fig. 1). However, because the aim was to describe regional patterns, the data were combined to a coarser spatial scale, that of Watsonian vice-counties.

Studying regional patterns by using data compiled at a coarser scale has three advantages. First, at the 10 km scale, many cells have not been sampled for bumblebees (Anonymous, 1980). While variation in sampling effort necessarily remains at the coarser scale, at least most area units have received some sampling effort. Second, at the 10 km scale, distributions may be genuinely more patchy, not only because species depend on habitats that are patchy at this scale, but also because of potential metapopulation effects whereby some suitable patches may be unoccupied for part of the time. Particularly for species near the edges of their ranges, metapopulation processes might cause distributions at fine scales to change frequently even if they were at equilibrium (Doherty Jr. et al., 2003), adding to the complexity of the analysis. Third, species at low density may be on the verge of detectability at many sites (Williams, 2000; Doherty Jr. et al., 2003), so there may be more sampling error for presence data at the 10 km scale than for pooled data at coarser scales.

Analysing data compiled on a regular rectangular grid has advantages over using irregular polygons of different sizes, such as vice-counties. For this study, the most important advantage is that the inland cells have equal areas, which helps to reduce biases for any comparisons of species richness among areas that might be expected to arise from species-area effects (e.g. Connor and McCoy, 1979; coastal cells are not excluded from this analysis because of the importance of coastal distributions). Consequently, the analysis is moved to a coarser (regional) scale by using a rectangular grid of 50 × 50 km cells (Fig. 1).

For lack of more precise information, measuring range declines from the BDMS data has to depend on

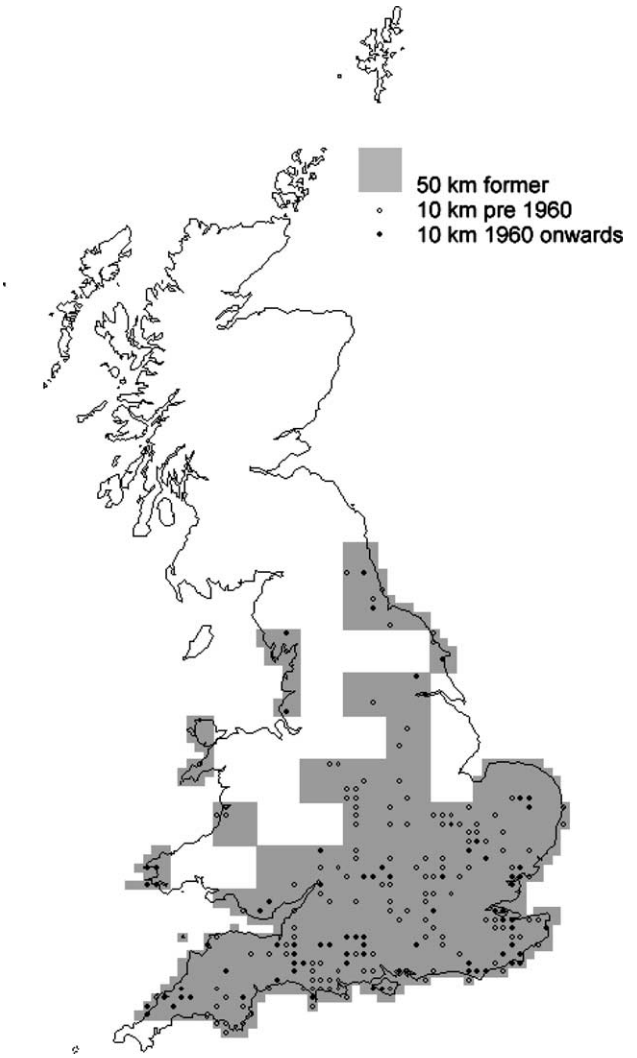


Fig. 1. Map of the distribution of *B. sylvarum* (a rare declining species) from the BDMS data plotted as: black spots, at the scale of 10 × 10 km grid cells for 1960 onwards records; open circles, at the scale of 10 × 10 km grid cells for pre 1960 records; grey squares, at the scale of 50 × 50 km grid cells for former regional range (pre 1960 and 1960 onwards records combined).

the crude assumptions that a '1960 onwards' record on the published map implies its pre 1960 presence (precluded from appearing on the map, Fig. 1), and so shows a continuing presence of the species. In contrast, a 'pre 1960' record on the map implies its post 1960 absence (from no 1960 onwards record shown on the map, Fig. 1) and a local extirpation of the species. Some of the problems with these data and with their interpretation have been discussed previously (e.g. Williams, 1982, 2000).

Former British range sizes of species are measured using BDMS data from counts of numbers of cells on a 50 km grid for the combined pre 1960 and 1960 onwards records. *Declines* in British range are measured using BDMS data from the proportional change in the numbers of cells on a 50 km grid: (pre 1960 records)/(pre 1960 + 1960 onwards records). *Present* British range sizes are measured using BDMS data from counts of numbers of cells on a 50 km grid for the 1960 onwards records (Table 1).

2.2. Measuring relative dietary breadth

Quantitative comparisons of food-plant choices by foraging bumblebees are fraught with difficulties. There is plenty of evidence that these bees seek to optimise their choices in a variety of ways (e.g. Heinrich, 1979), so it is important that data be collected under comparable conditions.

The greatest problem in studying the choices that foraging bees make is that all of the bees in the study should be exposed to the same array of options. Consequently, data cannot be pooled from many separate surveys (or from different parts of the season), each with its different set of bumblebee species and its own restricted array of food-plant options. Thus, if *Bombus monticola* and bilberry were surveyed only in Scotland, and *Bombus subterraneus* were surveyed only in areas without bilberry in Kent, then there would be no way to compare preferences by *B. monticola* and *B. subterraneus* for bilberry (or, strictly speaking, even for plant families, if there were a possibility of choice constraints at the level of plant species).

Because there are few sites where most of the bumblebee species occur together, where they might choose among the same plants, so there are correspondingly few data sets that permit genuine quantitative comparisons of forager choices. One of these is from Dungeness in Kent. A plot of 72 ha was sampled intensively between 26th July and 8th August 1982. This area is sufficiently small that all parts are potentially within the foraging range of a single worker (e.g. Cresswell et al., 2000; Walther-Hellwig and Frankl, 2000; Kreyer et al., 2004). About 1115 visits by workers for nectar or for nectar and pollen (only a very few visits exclusively for pollen were excluded and no nectar robbing was seen) by 13 species of social bumblebees to 13 species of plants were logged (non-destructively) from a single traverse using a modified belt-transect method (Williams, 1989a; Table 4). Proboscis-length measurements for workers of the 13 bumblebee species are taken from Williams (1989a) (Table 1).

A second major problem for measuring dietary breadth is a statistical artefact that can arise as an effect of the differing sample sizes among bumblebee species (Williams, 1989b). The rarer bumblebee species will be recorded as making fewer visits to flowers, and as a direct consequence of this rarity alone, it is likely that they will be recorded as visiting fewer plant species. This is not the same as foragers of a rarer bumblebee species choosing to visit a narrower range of plant species.

Table 1
Values for measurements compiled for the correlation analysis

Species	BDMS former range (no. 50 km cells)	BDMS range decline (proportion 50 km cells)	Rarefied dietary breadth (no. plant species in 20 visits)	Maximum dietary preference (obs−exp)/exp	Adjusted total European range (no. EA cells)	Northern European range (no. EA cells)	Adjusted southern European range (no. EA cells)	European range-edge proximity (see text)
soroeensis	88	0.454	–	–	[12]	4	[0]	0.00
muscorum	127	0.165	–	10.99	16	4	4	0.53
humilis	71	0.352	7.19	4.27	15	3	4	0.57
ruderarius	89	0.191	–	29.97	15	3	4	0.57
sylvarum	57	0.350	8.37	4.93	14	2	4	0.43
pascuorum	134	0.000	6.73	3.68	17	3	6	0.53
hortorum	142	0.007	4.73	6.14	17	4	5	0.62
ruderatus	52	0.423	3.94	16.00	13	0	5	0.00
subterraneus	45	0.733	–	27.77	15	3	4	0.57
distinguendus	75	0.666	–	–	12	4	0	0.00
jonellus	116	0.146	4.72	7.68	[12]	4	[0]	0.00
pratorum	127	0.000	3.63	3.54	15	3	4	0.57
monticola	70	0.157	–	–	[9]	3	[0]	0.00
lucorum	148	0.000	3.99	35.20	16	4	4	0.53
terrestris	111	0.018	2.43	0.31	17	1	8	0.18
lapidarius	110	0.127	4.05	3.08	16	3	5	0.56
cullumanus	8	1.000	–	–	9	0	2	0.00

EA stands for equal-area grid cells over Europe. Brackets show which European range sizes have been adjusted to sea level (see text). Pocket makers include *muscorum* to *distinguendus* ; pollen storers include *jonellus* to *cullumanus*; *soroeensis* belongs to neither group.

While it is important to have adequate samples for each bumblebee species, the problem for this comparison is that the samples should be of similar sizes among the species.

The most direct and easily interpreted way of overcoming the sample-size effect in measuring dietary breadth is to compare how many plant species the different bee species would be expected to visit for a standardised number of visits by each bee species. This can be achieved by using a rarefaction procedure (Hurlbert, 1971; Heck et al., 1975; Gotelli and Colwell, 2001). Here, a sub-sample of 20 visits is made from the observed frequency distribution of visits by each bee species, but chosen at random without replacement 1000 times. This provides an estimate of the mean number of plant species from a particular plant assemblage that each bumblebee species would be expected to visit within 20 flower visits. For the Dungeness data, there are insufficient records of *Bombus ruderarius*, *Bombus muscorum*, and *B. subterraneus* to permit this technique to be applied to these species, but it still allows comparison among the remaining 10 species. These include the rarer and declining species *Bombus sylvarum*, *Bombus humilis*, *Bombus jonellus*, and *Bombus ruderatus* (Table 1). The precision of the estimate for each bumblebee species will still depend on the number of visits per bee species.

2.3. Measuring relative dietary preference

Here, specialization is taken to be the result of an active preference for one plant species over others. Just as when comparing dietary breadth, if the choices that the bees make are to be studied, then all of the bees in the study must be exposed to the same array of options. Data cannot be pooled from multiple surveys, each with its different set of bumblebee species and its own restricted array of food-plant options. Again, the Dungeness data provide one of the few data sets with many of the rarer bumblebee species to fulfil these requirements.

Assessing which flowers are suitable and available to bumblebee foragers, both in terms of which plant species and in terms of which flowers on a plant, is highly problematic (reviewed by e.g. Williams, 1985). Consequently, it is considered impossible to assess preferences in an absolute sense (in relation to what is available), but only preferences of one bumblebee species in relation to those of other bumblebee species, by looking at their relative patterns of food-plant visitation.

Relative preferences of bumblebee species can be studied by comparing the deviations of their observed frequencies of flower visits from those expected using a contingency table (Williams, 1989a). The frequencies of visits that would be expected if foragers were unselective and encountered the same flowers, but in proportion to the total numbers of recorded visits, can be calculated from the product of the marginal totals of recorded visits (total numbers of visits by one bee species × total number of visits to one plant species) divided by the total of all visits to all flowers (1115 for the Dungeness data). An index of preference of a bee for a plant is provided by the deviation of observed from expected frequencies of visits, divided by the expected frequency (these values may be positive or negative). The strongest preference is the largest positive index value (Table 1).

2.4. Measuring European range sizes and proximity to range edges

Measuring range sizes and proximity to range edges in Europe is not straightforward because many species that occur near sea level in the north of the continent are restricted to high altitudes in the south. For comparability with species' declines in Britain, records should only be admitted for comparison if they are from the same range of altitudes as are represented extensively within Britain (taken to be 0–750 m). In the absence of this information, only a preliminary crude assessment can be made. This uses records mapped on a grid of equal-area cells (Fig. 4, for details of data and grid see Williams (1998)), although the cells are very large (611,000 km^2). The European grid then consists of 20 cells in a box extending from 31°13′N, 10°0′W to 71°43′N, 30°0′E (no records of these species are known from further north; one cell with records for *Bombus lapidarius* from southern Morocco is excluded). I adjust the European range measure to exclude from these data records for southern Europe (the Alps, Pyrenees, etc.) for those species that rarely occur there at low altitudes. Using altitudinal range data for Languedoc–Roussillon from Rasmont (1988), the records excluded from the southern data are for species with less than 10% of records from below 825 m in this part of southern Europe: *B. jonellus*, *B. monticola*, and *Bombus soroeensis* (Table 1). Unfortunately, altitudinal range data from Languedoc–Roussillon cannot be used in a simple way to represent altitudinal ranges at the more northerly latitude of Britain, because altitudinal ranges (not just mean altitudes) are expected to vary within species with latitude (Gorodkov, 1986a,b).

Formulating a representative measure of range-edge proximity is even more problematic with the coarse-scale global grid data. The problem can be simplified by concentrating on latitudinal ranges. There is then one row of occupied cells north of Britain (the northern band), two rows spanning Britain, and two rows south of Britain (the southern band). The number of cells occupied by each species within the northern and southern bands is counted separately and divided by the species' adjusted European range size to give the proportion of the European range that falls within each band. The scores are standardised against the maximum observed scores within the northern and southern bands respectively, to give the proximity scores the same range of possible values in the northern and southern bands. Then for each species in turn, the minimum of the two northern and southern edge-proximity scores is taken as the measure of its proximity (distance) to its nearest range edge (Table 1).

Data compilation, mapping, rarefaction, and contingency tables were made with programs written for this paper in C. Spearman rank correlations were tested using STATISTICA 6.

3. Results

3.1. Rarity and decline in British regional ranges

Former distribution ranges from the BDMS data at the scale of 10 and 50 km grids are inevitably positively correlated ($r_s = 0.91$). Fig. 2 shows that species with intermediate regional range sizes within Britain are disproportionately rarer within regions.

Changing scale from 10 to 50 km grid cells with the BDMS data shows a similar pattern of changes in the distribution of species richness to the pattern reported previously from classifications of vice-counties (Williams, 1982). Using 50 km grid cells, the former distribution of social bumblebees (Fig. 3(a)) shows hotspots of richness in central and southern Britain. The declines in social bumblebees (Fig. 3(b)) are concentrated in central England. The resulting 'present' distribution of social bumblebees (Fig. 3(c)) shows hotspots of remaining richness in regions nearer the coasts of England and Wales, but with a new coldspot of reduced species richness in central England.

Worker proboscis length for the 13 species at Dungeness is uncorrelated with British former regional range size among species ($r_s = -0.31$, $p > 0.05$) and is uncorrelated with regional decline among species ($r_s = 0.40$, $p > 0.05$) in the BDMS data. Therefore there is no evidence for a relationship between rarity or declines in British bumblebees and their proboscis lengths in these data.

3.2. Correlating rarity and decline with dietary breadth

The raw data for numbers of food-plant species visited are positively correlated with the number of forager visits recorded among species in the Dungeness data ($r_s = 0.78$, $p < 0.05$). However, after rarefaction, relative dietary breadth is uncorrelated with the number of forager visits recorded among species in the Dungeness data ($r_s = -0.01$, $p > 0.05$). Therefore the rarefaction procedure has reduced the effect of differing sample sizes among bumblebee species. In contrast, the Simpson index, used to measure dietary breadth by Goulson and Darvill (2004), was confirmed as remaining positively correlated with the number of forager visits recorded among species in the Dungeness data ($r_s = 0.75$, $p < 0.05$).

Relative dietary breadth in the Dungeness data is uncorrelated with British former regional range size among species ($r_s = -0.12$, $p > 0.05$) and is uncorrelated

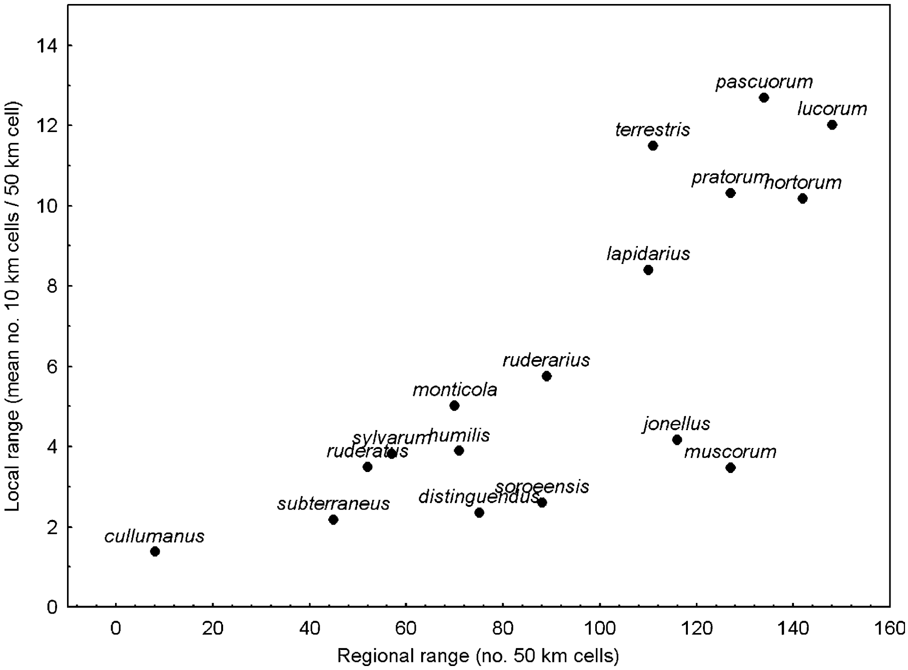


Fig. 2. Scatterplot showing the relationship between the former ranges of British bumblebee species (pre 1960 and 1960 onwards in the BDMS data) measured (x-axis) as numbers of 50 × 50 km grid cells and (y-axis) as mean numbers of 10 × 10 km grid cells per occupied 50 × 50 km grid cell.

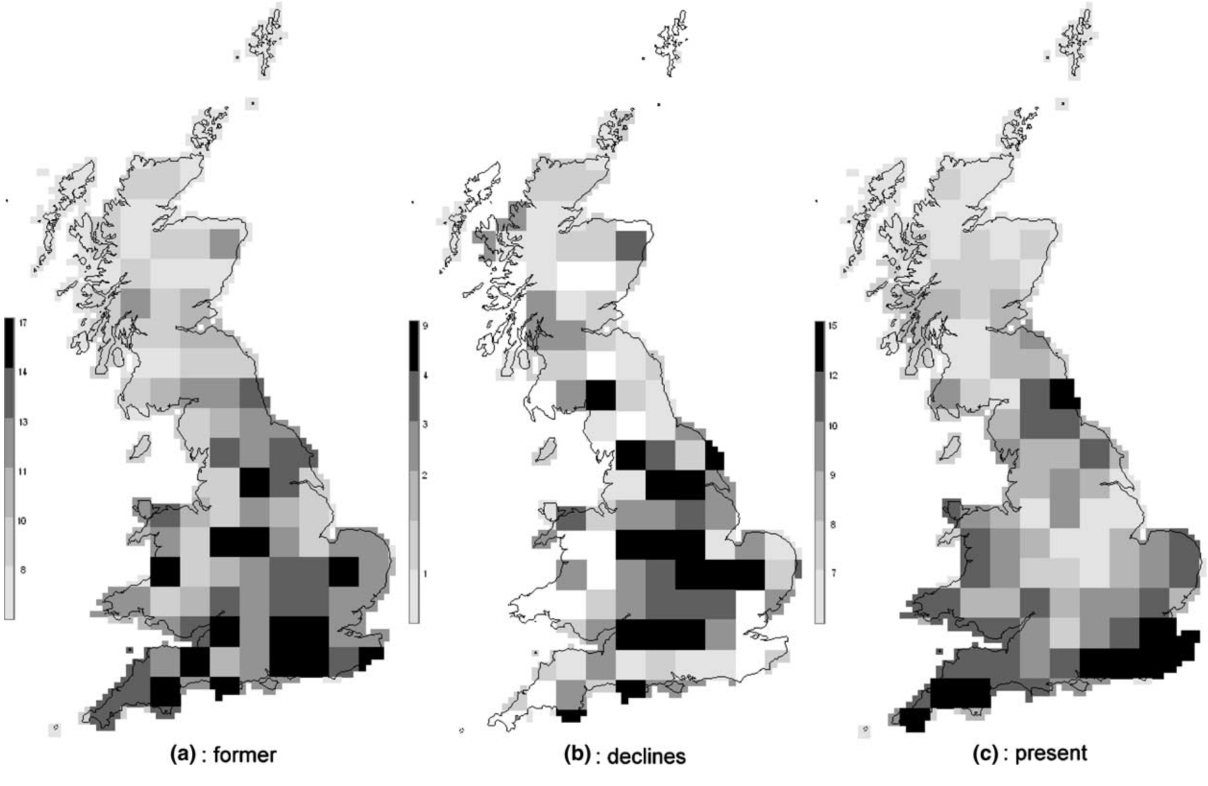


Fig. 3. Maps of species richness for British bumblebees from the BDMS data measured at the scale of 50 × 50 km grid cells for: (a) former richness (pre 1960 and 1960 onwards records); (b) declines in richness (pre 1960 records); (c) present richness (1960 onwards records). Equal-frequency grey-scale classes are used to maximise differentiation among regions.

with regional decline among species ($r_s = 0.26$, $p > 0.05$) in the BDMS data. Relative dietary breadth is also uncorrelated with worker proboscis length among species ($r_s = 0.28$, $p > 0.05$). Therefore there is no evidence for a relationship between rarity or declines in British bumblebees and their dietary breadths in these data.

3.3. Correlating rarity and decline with dietary preference

Relative maximum dietary preference is negatively correlated with the number of forager visits recorded among species in the Dungeness data ($r_s = -0.85$, $p < 0.05$). One possible interpretation is that this may show a saturation of the limited numbers of at least some of the available food-plant species by the most abundant bee species, forcing these bees to visit more plant species than expected by chance.

Relative maximum dietary preference in the Dungeness data is uncorrelated with British former regional range size among species ($r_s = -0.07$, $p > 0.05$) and is uncorrelated with regional decline among species ($r_s = 0.34$, $p > 0.05$) in the BDMS data. Relative maximum dietary preference is also uncorrelated with worker proboscis length among species ($r_s = 0.15$, $p > 0.05$). Therefore there is no evidence for a relationship between rarity or declines in British bumblebees and the strengths of their dietary preferences in these data.

3.4. Correlating rarity and decline with European range sizes and edges

Adjusted European range size is positively correlated with British former regional range size among species ($r_s = 0.68$, $p < 0.05$) and is negatively correlated with regional decline among species ($r_s = -0.65$, $p < 0.05$) in the BDMS data. However, European range-edge proximity is uncorrelated with British former regional range size among species ($r_s = 0.37$, $p > 0.05$) and is uncorrelated with regional decline among species ($r_s = -0.35$, $p > 0.05$) in the BDMS data. Therefore, there is no support for a relationship between latitudinal range-edge proximity and rarity or decline among species in these data, but there is support for a relationship with adjusted European range size. Without the adjustment, the relationships of rarity and decline with European range size are weaker (former regional range size: $r_s = -0.65$, $p < 0.05$; regional decline: $r_s = -0.55$, $p < 0.05$). Adjusted European range size is also uncorrelated with worker proboscis length among species ($r_s = 0.11$, $p > 0.05$).

4. Discussion

4.1. Caveats

None of the factors measured here (Table 1) could properly be considered to have caused range declines, because none of them represents any form of state *change*. Nonetheless, they may still be helpful in identifying the species that are most at risk of decline.

Some species have continued to decline since the BDMS survey. *B. sylvarum*, *B. ruderatus*, and *B. subterraneus* have all disappeared from Dungeness (which was the last known outpost of *B. subterraneus* in Britain) in the last 15 years (pers. obs.). On the other hand, some species now have broader recorded ranges. *Bombus terrestris* and *B. lapidarius* have been expanding in Scotland (Macdonald, 2001). *B. soroeensis* has been fluctuating in density in Scotland (Macdonald, 2000) and has recently been recorded from many more localities in southern England (Else, 2000). *B. soroeensis* is easily overlooked and some of its habitats have been previously inaccessible military ranges, so it may have been under recorded, rather than showing an expanding range. However, recent records include the first record in 1998 of *B. soroeensis* from Dungeness (collected from the RSPB reserve by B. Pinchen), where I had not seen it previously, despite regular searches between 1974 and 1997. Furthermore, *Bombus hypnorum* has been recorded as new to the British fauna (Goulson and Williams, 2001). It may require many years of time-series data before all of these population fluctuations or changes can be understood. Nonetheless, it is widely assumed that, rather than all of the declines considered here being merely stochastic changes across some European populations (and the same species at least are declining in some other parts of Europe: e.g. Rasmont, 1988), the declines are responses to environmental driving factors. Correlation analyses such as this will need to be followed up with more detailed studies of proposed mechanisms.

4.2. Interpretation for specialization

Narrow food-plant specialization has been described for a few bumblebee species in Europe, such as *Bombus consobrinus* (Løken, 1961, 1973). However, even in this case, a narrow food-plant preference could be a dynamic, optimising response to limited food choices, rather than an innate recognition of a particular food-plant taxon (Williams, 1989a). Extreme food-plant specialization such as this might be expected only in unusual circumstances, because it could impose a serious disadvantage for social organisms that need to maintain colonies with high energy demands beyond the flowering period of any one plant species.

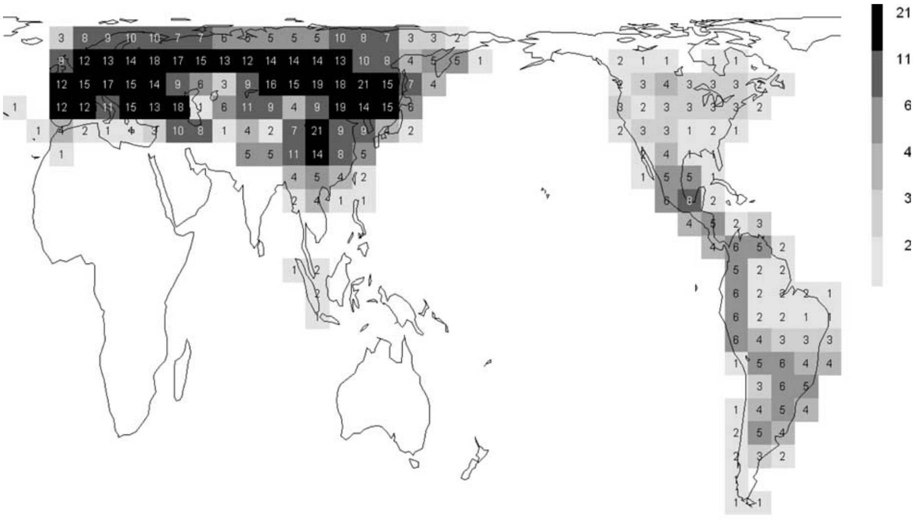
The results of the analysis in this paper show that neither relative dietary breadth nor preference among bumblebee species at Dungeness, when adjusted appropriately for varying sample sizes among bumblebee species, explains the relative rarity or decline of bumblebee species in Britain. Some of the issues affecting the degree to which the BDMS data can be considered representative of distributions are discussed by Williams (1982, 2000). The more recent, specimen-referenced Bees Wasps and Ants Recording Scheme (BWARS) data were unavailable for this analysis. It may also be that the Dungeness data are unrepresentative of dietary breadth and specialization patterns among British bumblebees in general. Unfortunately, as yet I know of no other foraging data that can provide the same comparability among as many species and thereby permit an independent assessment. These data were collected to represent nectar foraging and it is easily conceivable that pollen specialization would have more explanatory power. We urgently need further studies of pollen foraging by bumblebees, and particularly studies from more sites where many of the rare and declining species persist. Studies of the effects of food-plant availability at the critical early stages of colony development might also yield greater insights.

The marginal mosaic model (Williams, 1985) could explain how a general reduction in bumblebee food resources (e.g. reduced flower density) could affect the rarer species the most. The regionally rarer species tend to be found at lower local abundances where they are present (Williams, 1988), so if abundances were decreased further across all species of bumble bees, it is likely to be the least abundant species that would be extirpated first. Thus it might be an interaction between an as yet unidentified aspect of niche specialization affecting regional range sizes, on the one hand, and any land-use changes reducing food-plant availability, on the other, that explains the observed selective pattern of greater range reduction in the rarer species.

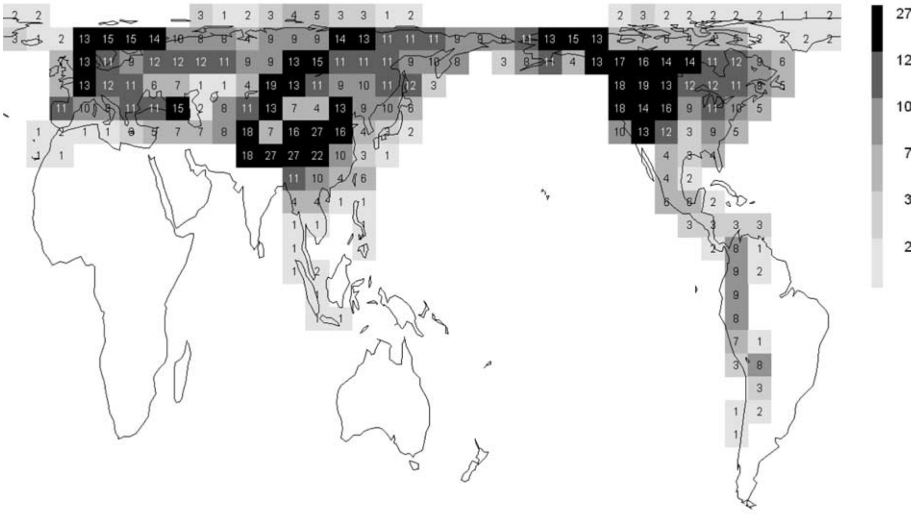
While declines in food-plant density may lead to local losses of some of the rarer bumblebees, increases in food plants may be insufficient to ensure recovery. For example, a wildflower nursery was established in 1987 extending over more than 16 ha near Nottingham in the central impoverished region of Britain (the central coldspot in Fig. 3(c)). The nursery has a much higher density of bumblebees than the surrounding countryside (visited in July 1997), which may reflect a genuine increase in local bumblebee populations. Nonetheless, these bumblebees are all of the common species. The rare and declining species are apparently not quick to colonise areas of newly increased resources such as this. In contrast, in Uppland (Sweden) at the far northern edges of their ranges, the rare and declining species *B. subterraneus* and *B. sylvarum* are persisting at Linnaeus's Hammarby house (visited in June 1998). This stands in one of many small islets of low intensity land use and of high food-plant density (80 ha), while the surrounding land has been subject to intensification of arable agriculture and pesticide use with declines in food plants (B. Cederberg, in litt.). Conservation of this monument may have contributed indirectly to their persistence by providing a continuity of rich food-plant resources over the last two centuries. Continuity in high food-plant availability is likely to be especially important if rare bumblebees are not good colonisers of isolated patches of favourable habitat. The effect of landscape-scale patterns will be need to be examined (e.g. Kreyer et al., 2004; Westphal et al., 2004). Detailed studies of bumblebee faunas in relation to the history of land use, to the sizes of patches of suitable habitat, and to inter-patch distances, may be possible in a few areas. These might permit an assessment of the importance of patch size and pattern, and of bumblebee dispersal.

In contrast to dietary specialization, the present results show that relative rarity and decline among British bumblebees are related to their European range sizes. Range sizes have been interpreted as an expression of the relative breadths of the ecological niches among species (see Gaston and Blackburn, 2000), at least when they are not severely constrained by barriers of drastically different and unsuitable habitat and when ranges across entire continents are included. Here, the European range has been adjusted to give a better representation of species' latitudinal ranges near sea level. Particularly because this adjustment improves the correlations, one possibility is that it is the relative degree of specialization in species' climatic or habitat tolerances that is important (Williams, 1988), rather than the overall extent of its geographical area of occurrence (such as a 'mass effect' of total population size, see Gaston and Blackburn, 2000). Viewed from this perspective, a species' former coarse-scale regional distribution (50 km grey squares in Fig. 1) may be constrained more by its climatic tolerances, whereas the species' fine-scale local distribution (10 km black spots in Fig. 1) within this region may be limited more by whether its food and habitat requirements are met at particular sites. However, coarse-scale declines in bumblebees do not appear to be associated with climate change. The rarer northern and southern species have both declined in range, but in opposite directions. This is inconsistent with either simple climate warming or cooling. In contrast, coarse-scale changes in habitat and food availability from changes in national agricultural policy have been proposed as explanations of coarse-scale declines in bumblebee ranges (e.g. Williams, 1989b). If these climate, habitat, and food factors are all important, then the extent to which they might compensate for one another would be interesting to assess. The failure to find effects of range-edge proximity on extirpation patterns cf. Doherty Jr. et al. (2003) may be real, but confirmation from better data on European ranges is needed.

What might the principal habitat factors be? At an even larger scale, all of the species showing more than a 25% range decline in Table 1 (except *Bombus cullumanus*) are 'pocket makers,' rather than 'pollen storers,' in the sense of Sladen (1912). Although not well supported by morphological characters (Williams, 1995), there has recently been support for two broadly corresponding monophyletic groups from molecular data (Kawakita et al., 2003; S. Cameron and H. Hines, in litt.; *B. soroeensis* falls outside either group, Table 1). Species of both groups are commonly found in forested regions, although fine-scale studies from Europe, Asia, and North America all show that bumblebees are more abundant in clearings and along forest edges than under closed canopy woodland (Bowers, 1985; Williams, 1988, 1991; Kreyer et al., 2004). Looking at the differences between the biomes where the two groups are particularly rich in species (Fig. 4), there are more pocket makers in temperate grassland and steppe biomes (richest in the steppes of Inner Mongolia), whereas there are more pollen storers in montane and arctic biomes (richest in the mountains of the Himalaya). This distinction is not exclusive and exceptions are known in both groups (e.g. *B. cullumanus* is a chalk-grassland pollen storer, see Yarrow (1954)). Nevertheless, in Britain the declining pocket-making species are also associated with open grassy habitats with a lack of recent or drastic human disturbance (Williams, 1988; Carvell, 2002; Edwards, 2003). Some of these grassland habitats have high, relatively uniform densities of food plants, which may simply be very favourable for all bumblebees. But in addition, British pocket makers tend to be later nesting (Williams, 1989a; Edwards and Williams, 2004) and it appears that at least some of the grassland habitats with the declining pocket makers have few or none of the early food plants required by the early nesting pollen storers (Edwards, 2003; Edwards and Williams, 2004). If this reduces the density of pollen storers, then it might reduce the competition experienced by the rare pocket makers nesting later in the season (Edwards, 2003; Edwards and Williams, 2004). Thus conversion of these grassland habitats, even by management as apparently benign as augmenting the early season forage plants, could present a particular threat to the rare and declining bumblebee species.



(a): pocket makers



(b): pollen storers

Fig. 4. Maps of species richness of bumblebees among equal-area (611,000 km^2) grid cells (for details of the grid and data, see Williams, 1998) for: (a) pocket makers; (b) pollen storers. Equal-frequency grey-scale classes are used to maximise differentiation among regions.

In summary, bumblebee declines may not be explained by narrow food-plant specialization in these data, but may yet be explained in part by specialization in other aspects of their niches, including preferred climate and habitats. This is not to say that bumblebees do not show food-plant preferences, merely that the strengths of these preferences are unrelated to relative declines among species. Furthermore, while particular food-plant taxa may not be recognised instinctively, food plants with certain characteristics, irrespective of taxon, are known to be preferred (Brian, 1957). Short-term food-plant preferences, as a dynamic response to changing relative profitability among food plants, are well documented for bumblebees (e.g. Heinrich, 1979).

4.3. Implications for conservation

The debate concerning bumblebee specialization may be of little consequence for conservation at many of the sites studied in southern England. It could be argued that all that conservationists in these areas need to know is which plants are visited frequently, not why, because it may be sufficient as a 'rule of thumb' to ensure that these plants (such as Fabaceae and especially red clover) are available in large numbers (Edwards, 2003; Edwards and Williams, 2004). However, the question of why is still of concern to theoretical ecology, and ultimately will be of concern to conservationists when faced with similar problems, but in the context of different food-plant floras. For example, at Dungeness, the highest frequencies of visits (pollen and nectar visits not discriminated) were to plants of the families Lamiaceae, Boraginaceae, and Rosaceae, while in some alpine situations (Kashmir, Sichuan), more visits (particularly for pollen) may go to Ranunculaceae and Scrophulariaceae (Williams, 1991; unpublished data).

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References

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

Anonymous., 1980. Atlas of the bumblebees of the British Isles. Institute of Terrestrial Ecology, Cambridge.

Benton, T., 2000. The Bumblebees of Essex. Lopinga Books, Wimbish.

Bowers, M.A., 1985. Bumble bee colonization, extinction, and reproduction in subalpine meadows in northeastern Utah. Ecology 66, 914–927.

Brian, A.D., 1957. Differences in the flowers visited by four species of bumble-bees and their causes. Journal of Animal Ecology 26, 71–98.

Brown, J.H., 1995. Macroecology. University of Chicago Press, Chicago.

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

Connor, E.F., McCoy, E.D., 1979. The statistics and biology of the species-area relationship. American Naturalist 113, 791–833.

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. Ecological Entomology 25, 249–255.

Doherty Jr., P.F., Boulinier, T., Nichols, J.D., 2003. Local extinction and turnover rates at the edge and interior of species' ranges. Annales Zoologici Fennici 40, 145–153.

Edwards, M., 2003. UK BAP Bumblebee Working Group Report, Midhurst, 2002, pp. 1–45.

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

Else, G.R., 2000. Observations on *Bombus soroeensis* (F.) *B. humilis* Illiger and *B. muscorum* (L.) on Salisbury Plain, Wiltshire, in 1998–2000. BWARS Newsletter Autumn 2000, 5–6.

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

Gaston, K.J., Blackburn, T., 2000. Pattern and process in macroecology. Blackwell Science, Oxford.

Gorodkov, K.B., 1986a. Three-dimensional climatic model of potential range and some of its characteristics II. Entomological Review 65, 1–18.

Gorodkov, K.B., 1986b. Three-dimensional climatic model of potential range and some of its characteristics I. Entomological Review 65, 19–35.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4, 379–391.

Goulson, D., Williams, P., 2001. *Bombus hypnorum* (Hymenoptera: Apidae), a new British bumblebee. British Journal of Entomology and Natural History 14, 129–131.

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

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

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2004. Causes of rarity in bumblebees. Biological Conservation, in press, doi:10.1016/j.biocon.2004.06.017.

Heck, K.L., Belle, G.v., Simberloff, D., 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology 56, 1459–1461.

Heinrich, B., 1979. Bumblebee economics. Cambridge, Massachusetts.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52, 577–586.

Hutchinson, G.R.E., 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22, 415–427.

Kawakita, A., Sota, T., Ascher, J., Ito, M., Tanaka, H., Kato, M., 2003. Evolution and phylogenetic utility of alignment gaps within intron sequences of three nuclear genes in bumble bees (*Bombus*). Molecular Biology and Evolution 20, 87–92.

Kreyer, D., Oed, A., Walther-Hellwig, K., Frankl, R., 2004. Are forests potential landscape barriers for foraging bumblebees. Landscape scale experiments with *Bombus terrestris* agg. and

Bombus pascuorum (Hymenoptera, Apidae). Biological Conservation 116, 111–118.

Løken, A., 1961. *Bombus consobrinus* Dahlb., an oligolectic bumble bee (Hymenoptera, Apidae). Transactions of the XI International Congress of Entomology, Vienna 1, 598–603.

Løken, A., 1973. Studies on Scandinavian bumble bees (Hymenoptera, Apidae). Norsk Entomologisk Tidsskrift 20, 1–218.

Macdonald, M., 2000. Observations on *Bombus soroeensis* (Fabr.) (Hym., Apidae) in northern Scotland. The Scottish Naturalist 112, 45–53.

Macdonald, M., 2001. The colonisation of northern Scotland by *Bombus terrestris* (L.) and *B. lapidarius* (L.) (Hym., Apidae), with comments on the possible role of climate change. Entomologist's Monthly Magazine 137, 1–13.

Macdonald, M., 2003. Bumblebees. Scottish Natural Heritage, Battleby.

Onions, C.T., 1973. The shorter Oxford English dictionary on historical principles. Clarendon Press, Oxford.

Osborne, J.L., Williams, I.H., 1996. Bumble bees as pollinators of crops and wild flowers. In: Matheson, A. (Ed.), Bumble Bees for Pleasure and Profit. IBRA, Cardiff, pp. 24–32.

Prys-Jones, O.E., Corbet, S.A., 1987. Bumblebees. Cambridge University Press, Cambridge.

Rasmont, P., 1988. Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae). Pages 309 + lxi. Faculté des Sciences agronomiques de l'Etat, Gembloux.

Sladen, F.W.L., 1912. The Bumble-bee, its Life History and How to Domesticate it, with Descriptions of all the British Species of *Bombus* and *Psithyrus*. MacMillan, London.

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

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2004. The relative importance of local habitat quality and regional landscape characteristics on the densities of bumble bees. Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie 14, 493–496.

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

Williams, P.H., 1985. On the distribution of bumble bees (Hymenoptera, Apidae) with particular regard to patterns within the British Isles. Pages 180. Department of Applied Biology. University of Cambridge, Cambridge.

Williams, P.H., 1988. Habitat use by bumble bees (*Bombus* spp.). Ecological Entomology 13, 223–237.

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

Williams, P.H., 1989b. Bumble bees – and their decline in Britain. Central Association of Bee-Keepers, Ilford Available from: www.nhm.ac.uk/entomology/bombus/decline.html.

Williams, P.H., 1991. The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini). Bulletin of the British Museum (Natural History) (Entomology) 60, 1–204.

Williams, P.H., 1995. Phylogenetic relationships among bumble bees (*Bombus* Latr.): A reappraisal of morphological evidence. Systematic Entomology 19, 327–344.

Williams, P.H., 1998. An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). Bulletin of The Natural History Museum (Entomology) 67, 79–152 (updated at www.nhm.ac.uk/entomology/bombus).

Williams, P.H., 2000. Some properties of rarity scores used in site quality assessment. British Journal of Entomology and Natural History 13, 73–86.

Yarrow, I.H.H., 1954. Some observations on the genus *Bombus*, with special reference to *Bombus cullumanus* (Kirby) (Hym. Apidae). Journal of the Society for British Entomology 5, 34–39.