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Bombus

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B. subterraneus at Dungeness in 1982
(unrecorded in Britain since 1988)

Distribution and decline of British bumblebees

This page is based on a Central Association of Bee-Keepers pamphlet (Williams, 1989*b*)

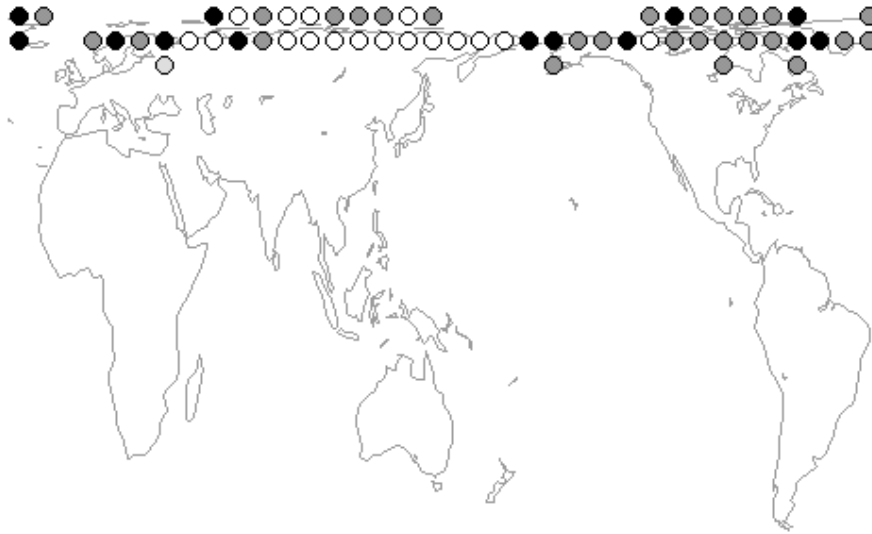
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During the 1970s, considerable effort went into mapping the distributions of [British bumblebees](#). The Bumblebee Distribution Maps Scheme (abbreviated below to BDMS) produced an atlas of these insects for Britain and Ireland (Alford, 1980). This drew particular attention to the apparent changes in populations of these important pollinators (Alford, 1973). It has also provided useful material for advancing an understanding of the factors that may have brought about these changes.

My interest in this field developed through attempts to describe general patterns in bumblebee distributions. These patterns can be found at many different scales, ranging from those among continents to those within fields (Williams, 1985*a*).

Patterns worldwide

Bumblebees include about [249 species](#) worldwide. They rank among the most abundant flower visitors in alpine, cool temperate, and even arctic environments of the northern continents (see the map below). In the tropics and the southern continents, they are native only in Southeast Asia and South America, where their centres of diversity are in the high mountains (Williams, 1985*b* [[map](#)]). This pattern of worldwide distribution has undoubtedly been limited in part by poor opportunities for them to reach areas that are now known to be favourable to them, such as New Zealand [[introduced species](#)][see also [biogeographic regions](#)]. In contrast, the other social long-tongued bees, such as honey bees and stingless bees, have their centres of diversity further south in the tropical lowlands (e.g. Ruttner, 1987) [[maps of honey bees and stingless bees](#)].

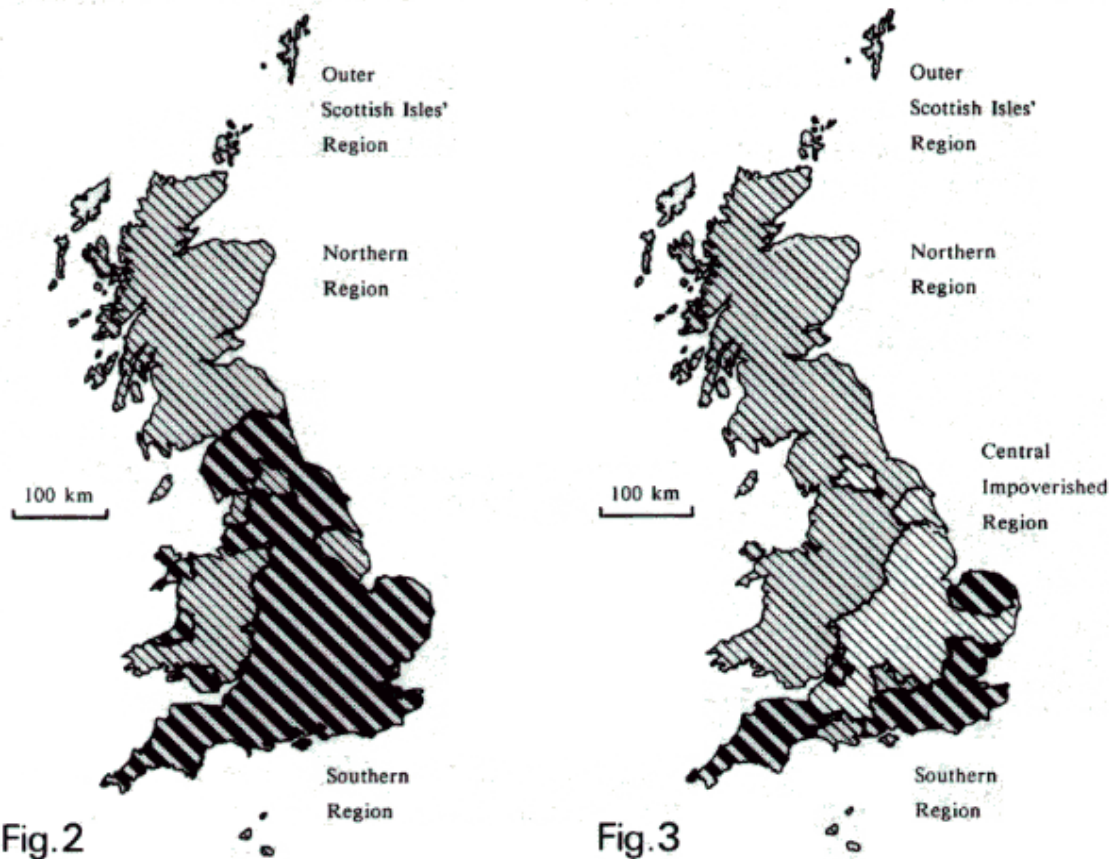


Above: map showing the recorded distribution of *B. (Alpinobombus) hyperboreus*, one of the most northerly distributed of all bumblebees, among equal-area (611,000 km²) grid cells, with black spots for specimens identified by PHW, grey spots for literature records, and white spots for expected distribution.

The worldwide distribution of bumblebees in regions with cool and strongly seasonal climates may be related to two factors. First, the combination of annual colony development with solitary hibernation by queens provides an energy-inexpensive way of passing predictable, long periods of unfavourable conditions. In comparison, it is likely to be relatively energy-expensive to keep a colony of honey bees sufficiently warm through long cold winters. Second, bumblebees have been shown to be able to choose to regulate their body temperatures particularly effectively when necessary, so that they can forage profitably at lower temperatures than honey bees (Heinrich, 1979). Bumblebees are therefore relatively cold-adapted insects, and in Britain the group is not close to the extremes of its latitudinal range. [Many British species have very broad distributions in the Palearctic Region and were consequently among the first species to be described.]

Patterns within Britain

Within Britain, regional differences in the bumblebee fauna can be summarised from the BDMS atlas maps to show the major shared patterns. This is done by classifying together regions with similar species, and then classifying together species with similar regional distributions (Williams, 1982). The large Watsonian vice-counties were used as area units, rather than BDMS atlas 10 x 10 km grid cells, because at this stage it is the broad regional patterns that are of interest. When all BDMS data are included in the analysis as an estimate of distributions before 1960 (assuming that '1960 onwards' records imply the presence of a species before 1960, although range expansions cannot be detected in these data), three main groups of species are distinguished because of their differing distributions among three regions (maps below).



Above left: map showing pre-1960 distribution of *Bombus* species (excluding *Psithyrus*) in England, Wales and Scotland, from a classification of all BDMS vice-county records. Above right: map showing post-1960 distribution, from a classification of '1960 onwards' BDMS vice-county records (Williams, 1982).

- **Mainland Ubiquitous Species** (diagonal lines - all regions except the Outer Scottish Isles' Region): *B. hortorum*, *B. pascuorum*, *B. pratorum*, *B. lucorum* (and *magnus*), *B. terrestris*, *B. lapidarius* and *B. ruderarius*.
- **'Widespread' Local Species**, after 1960 more northern and western (dots - all regions except the Central Impoverished Region): *B. monticola*, *B. jonellus*, *B. soroeensis* and *B. muscorum*.
- **Southern Local Species** (broad stripes - just the Southern Region): *B. subterraneus*, *B. ruderatus*, *B. sylvarum* and *B. humilis*.

[[click here for colour maps of species richness for the three species groups among 10 x 10 km grid cells from BDMS 1960-onwards data](#)]

As early as 1959, Free & Butler wrote that '*It is commonly supposed that the bumblebee population has declined in recent years.*' Evidence for this can now be seen in the BDMS atlas, which distinguishes pre-1960 and 1960 onwards records. Another summary (British map in figure 3 above), this time for the 1960 onwards records alone, shows that two of the three groups of species have retreated within Britain, so that only the Mainland Ubiquitous Species remain strongly represented in the Central Impoverished Region. This analysis shows that it is the loss of just certain species from central England that is most dramatic. Changes in distribution such as this provide opportunities to exclude some factors and so narrow the range of those that are likely to have a strong influence on species' distributions.

To help characterise the three groups of species with different regional patterns of distribution within Britain, it is useful to compare their distributions elsewhere in Europe, such as Scandinavia (Løken, 1973) and in the Alps (Pittioni, 1937). Many of the species overlap broadly in distribution across Europe, but differences in the regional and altitudinal limits of the groups of species can be found. The first group, the **MAINLAND UBIQUITOUS SPECIES**, remains strongly represented throughout mainland Britain, both

before and after 1960. These species generally do not reach distributional limits within the lowlands of Britain and most are found broadly across Scandinavia and the Alps. After 1960, the second group, the '*WIDESPREAD LOCAL SPECIES*', have become more restricted, with most recent records coming from the north and west of Britain, although some of the species also occur in the south, particularly near the coasts. This group of species is strongly represented in the arctic region of northern Scandinavia. They do occur further south in Europe, but mostly at higher altitudes, and especially in the Alps. *B. muscorum* is unusual because it occurs mainly near coasts, both in northern and southern parts of western Europe. The third group, the '*SOUTHERN LOCAL SPECIES*', has also become more restricted in Britain after 1960, but has retreated largely in the opposite direction, to the far south. These species reach their northern limits within Britain and southern Scandinavia and occur only at lower altitudes in the Alps. At least in Europe, their pre-1960 northern limits follow just to the south of the July mean 15° C isotherm (Williams, 1986). Their northern limits may be even closer to the northern European 250 mm contour of water deficit (the difference between average annual precipitation and evapo-transpiration, mapped by Polunin & Walters, 1985). Thus in Britain, the regionally restricted species seem to be near their range limits as governed by climate, and it is these species that have been in apparent decline.

More recently it has been possible to describe the climatic niches of a few species more precisely, based on their distributions in western Europe (Williams et al., 2007 [pdf]). This appears to support the idea that (1) the declining species are those with narrower climatic specialization; and (2) that it is areas closest to the edges of their climatic niches where they are likely to be most vulnerable.

Patterns within Kent

To find out more about the differences between the species of the three groups, their distribution was studied in Kent, within the Southern Region of Britain, where all three groups can still be found together. The bumblebee records collected by Gerald Dicker and Eric Philp (unpublished) using a 2 x 2 km grid were used, because these are closer to the size of the foraging areas used by individual bumblebee colonies.

The bumblebees that appear to be nearer the edges of their ranges in Britain are also found at only a very few localities within this range in Kent, where they all tend to occur together (see the map below). These have been called the 'local' species (Southern Local Species, Widespread Local Species), as opposed to the 'ubiquitous' species (Mainland Ubiquitous Species), which occur almost everywhere both in Kent and elsewhere in the lowlands of mainland Britain. In Kent, the distinction between these two groups is very marked (Williams, 1988).

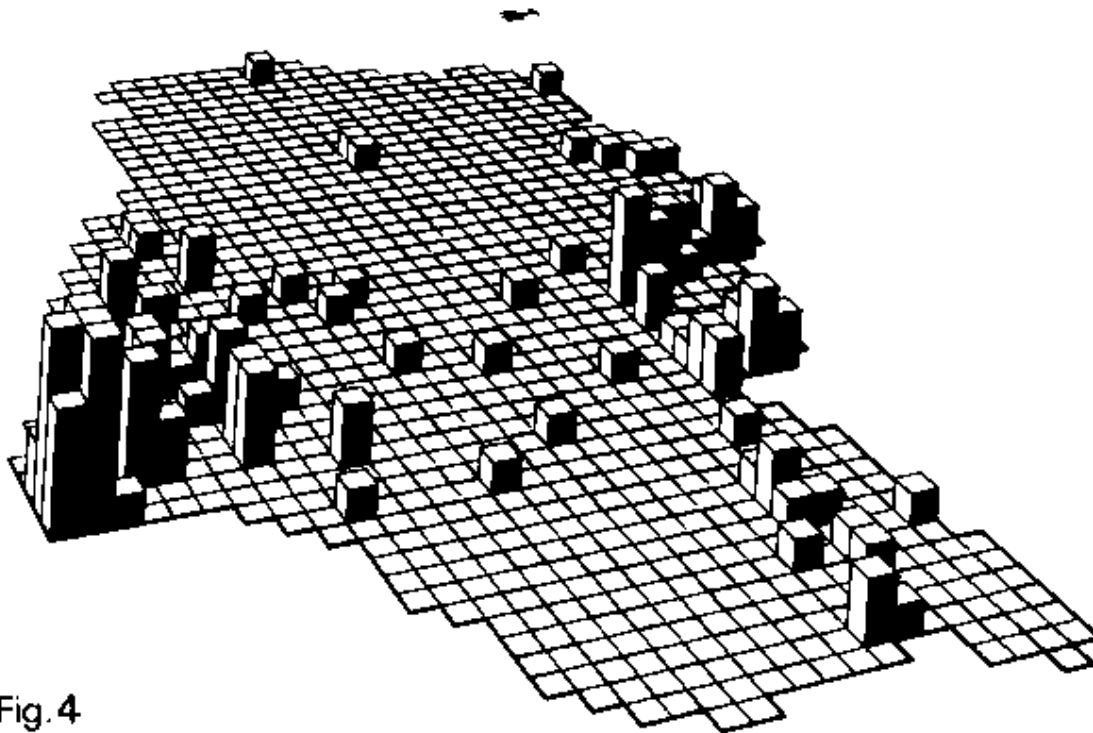


Fig. 4

Above: map showing numbers of local bumblebee species (0-6 species) recorded on a 2 x 2 km grid in Kent by G. Dicker and E. Philp (unpublished) 1972-1978 (Williams, 1988). The grid is viewed from across Folkestone towards London, which lies beneath the north pointer. Dungeness, on the southern coast, is on the far left. The Swale marshes, on the mid-northern coast, to the right. Shoreham is near the top of the grid.

[\[click here for a colour map of species richness for the local species among 2 x 2 km grid cells from 1972-onwards data\]](#)

In 1983 I set out to try to characterise those localities that support the local species (as well as the ubiquitous species) in Kent. Only 20 sites could be surveyed, because the different species are active at slightly different times of the year (e.g. Prys-Jones & Corbet, 1987; Williams, 1989a), so in order to obtain comparable local counts of bumblebees, these counts could be made during only a short period of the summer. The results showed that although the local species had previously been recorded from all of these 20 sites, the local species could still be found at just 10 of them.

I used Tansley's (1939) lists of plants associated with each of 16 major kinds of vegetation to describe the habitat at each site. First, I looked for the greatest variation in vegetation composition among the sites (the principal components analysis in Williams, 1988). Coincidentally, this sorted the sites into two groups: one group with the local bumblebee species; and one group without them. It showed that the sites with the local bumblebees also had many of the plants of saltmarsh, shingle, sand dune, and to a much lesser extent, of old meadow (see figure 5 below: x axis).

Second, another approach is to search for the 'discriminant function' that best separates the two groups of sites. This simply attempts to find which among all of the kinds of vegetation scored are the best indicators for the presence of the local bumblebees (see figure 5 below: y axis). The results are very similar, which is shown in the comparison in figure 5 by the clusters of points on the graph in the lower left and upper right quadrants. But this analysis shows that, in addition, hedgerow and heath are also particularly good indicators. The difference is caused by the greater sensitivity of the second method to kinds of vegetation that are only weakly variable, but which vary more closely in step with the presence of the local bumblebees.

Comparison of two analyses of vegetation as habitats for the local bumble bees
(for both analyses, positive values are associated with presence of the local bees).

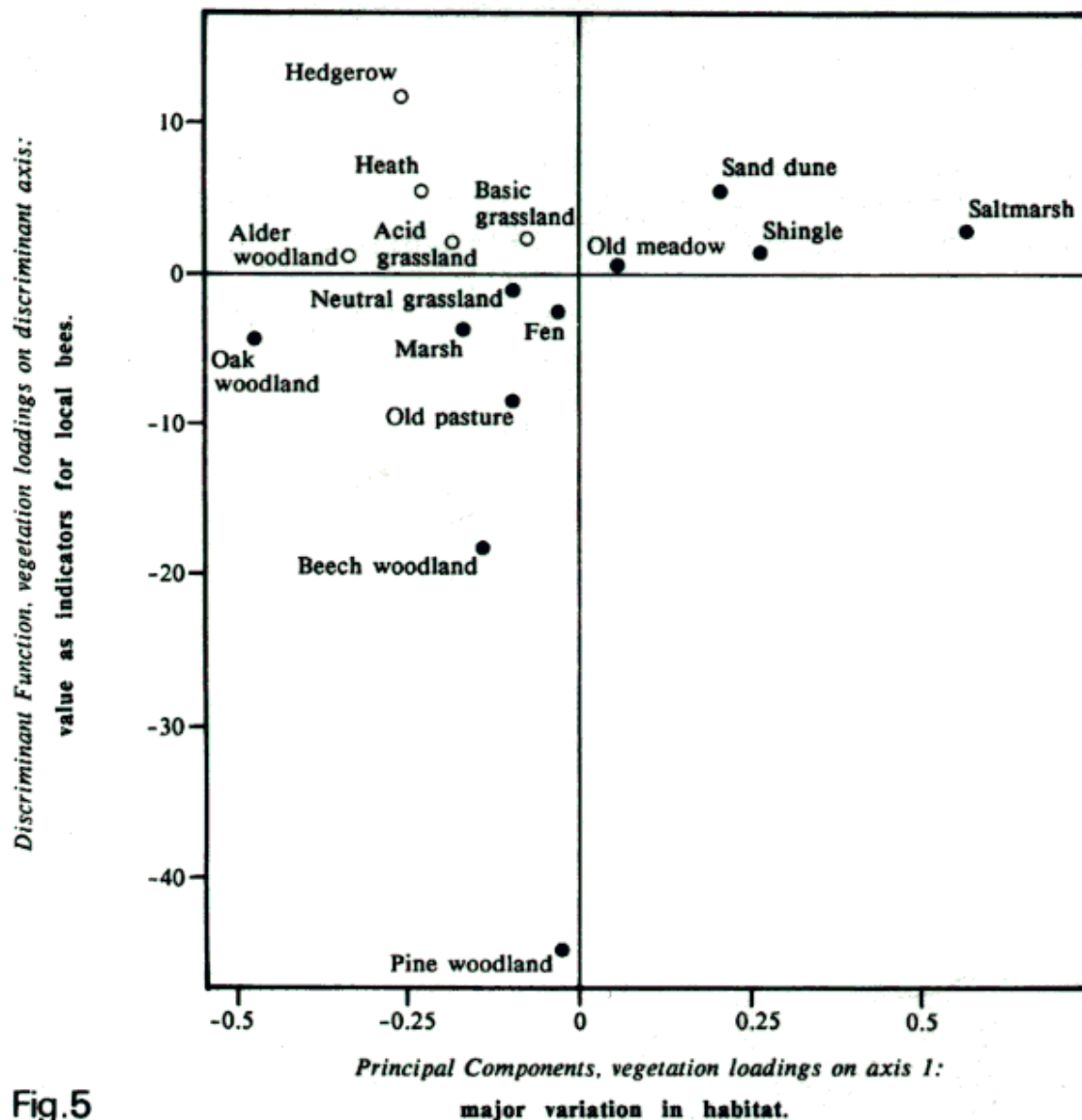


Fig.5

Above: graphical comparison of two analyses (x axis: PCA and y axis: discriminant function) of variation in vegetation at 20 sites in Kent that were surveyed in 1983. Both analyses distinguish completely between the 10 sites with the local species and the 10 sites without them. Similar results between the two analyses are shown by the dark circles in the lower left quadrant (vegetation associated with species-poor sites) and upper right quadrants (vegetation associated with species-rich sites). Divergent results between the two analyses are shown by open circles, which are concentrated in the upper left quadrant.

Hedgerow, as used here, also includes woodland edge and scrub vegetation. It includes the longest list of plants from Tansley (1939) among all of the kinds of vegetation in this analysis. Consequently, it may be a better indicator of the general degree of loss of plant diversity than assessments of the other kinds of vegetation. The link between higher floral diversity and lack of drastic disturbance over a long period has been especially well documented for hedgerows (Pollard, Hooper & Moore, 1974).

Heath is particularly interesting in the context of habitats for local bumblebees, because heathland is also important to many of the solitary wasps and some of the solitary bees that are locally restricted in southern Britain (George Else, pers. comm.). The richest single site for local bumblebees in Kent, Dungeness, has a particularly large number of Tansley's shingle plants. But much of Dungeness has also

been classified in the past as heath in its broadest sense (Hubbard, 1970). This is not the same as heath in the strict sense, because even the Common heather or Ling, *Calluna vulgaris* (L.) Hull, is absent from most of Dungeness.

All of these kinds of vegetation characterising the sites where the local bumblebee species persist share a common feature, in that they all present open (often grassy) habitats with a lack of recent or drastic disturbance. Crucially, these sites also support a greater abundance of the ubiquitous species than the other sites, so they appear to be more favourable to all bumblebees, irrespective of whether they belong to the regionally and locally restricted species or not (Williams, 1988).

Comparison of local foraging patterns

In order to find out what is special about the species-rich localities for bumblebees in Kent, I have been visiting Dungeness since 1974. By the 1980s, this area may have more species of bumblebees than anywhere else in Britain. In the summer of 1982, July and August were spent recording flower visits by bumblebees over a survey area of 72 ha. The analysis of foraging patterns concentrates on records collected during two weeks at the peak of foraging activity, when competition is expected to be most intense. This is the period when young queens and males are being reared. The results are compared with the pattern of flower visits seen during the same period of 1983 at Shoreham. This is a more typical, species-poor locality, also in Kent. The comparison allows a test of three ideas about what governs the number of bumblebee species at a locality (Williams, 1989a).

(1) The **specialist hypothesis** is that the presence of a particular species of bee (and therefore the number of species of bees) might depend on the presence of a particular food-plant species, if the bees were extreme specialists. Løken (1961, 1973) has found that the Scandinavian bumblebee *B. consobrinus* Dahlbom showed a strong preference for visiting flowers of Northern wolfsbane, *Aconitum septentrionale* Koelle. In Scandinavia, the distribution of the bee is restricted to the area within the distribution of the plant, although the bee is believed to occur with other species of *Aconitum* in areas eastwards to the Pacific coast. In Kent, the preferred food plants of the local bumblebee species can be identified at Dungeness as those which were visited more often than expected by chance alone. But contrary to what is expected from the specialist hypothesis, these bees were not associated with these plants where they occurred throughout Kent.

For an update on the discussion of the role of food-plant specialization and bumblebee declines, see Goulson *et al.* (2005) and Williams (2005 [PDF]).

(2) The **diversity hypothesis** is that the presence of a species of bee might depend on the presence of food plants of kinds not used by other bees, so that the species of bee is not excluded by competition. For example, Inouye (1977) applied this competition-based idea to bumblebees. He expected that there would be a higher diversity of bumblebees where there is a higher diversity of food plants, provided that there is a broad range of flower depths available. In Kent, at Dungeness where the diversity of bumblebees is highest in terms of numbers of bumblebee species, the diversity of food plants used is actually lower than at the species-poor site at Shoreham. This result, contrary to the diversity hypothesis, is obtained irrespective of whether food-plant diversity is measured (a) as the number of species of food-plants used; (b) as the range of flower depths used; or (c) as how evenly the bees shared their visits among the food plants (a more even sharing of visits would represent a pattern of more diverse flower use).

(3) The **abundance hypothesis** is that the presence of a species of bee might be governed by the balance between local energy resources, in the form of food, and local energy 'costs', which are likely to be influenced by local climate. This is described by a simple macroecological model of distribution, which has been elaborated to account for the patterns described here (see the diagram below). It is based on the idea that the individuals of a species share a similar physiology that works better in a region with a near-optimum climate for that species (e.g. Andrewartha & Birch, 1954; Hengeveld & Haeck, 1981). Where the individuals find themselves a long way from this optimum, food availability may not always be sufficient to cover local 'costs', so that the species will not persist at every locality. Consequently, this model could account for the more patchy distributions of species nearer to the edges of their distributions. In Kent for instance, the bumblebee species nearer their distribution limits are also more patchy. Furthermore, a concentric pattern can be seen even within the British range of some species that are 'sub-central' here in their global distributions, such as *B. lapidarius* and *B. ruderarius* (see Alford, 1980 [maps]). These species are nearly ubiquitous in south-eastern England, but are much more local in

northern England, and reach their northern limits in Scotland. Yet the distribution patterns of some species are very patchy even in the central regions of their distributions. This can also be accounted for by the model, either if some widespread patches of habitat were to provide very little food, or if the species' range of tolerances on either side of the optimum were very narrow. The latter may be the case for some of the Southern Local Species in particular. Thus the model implies that locally abundant food could sometimes compensate for locally suboptimal climate for some species (Williams, 1985a, 1988, Williams et al., 2007 [pdf]).

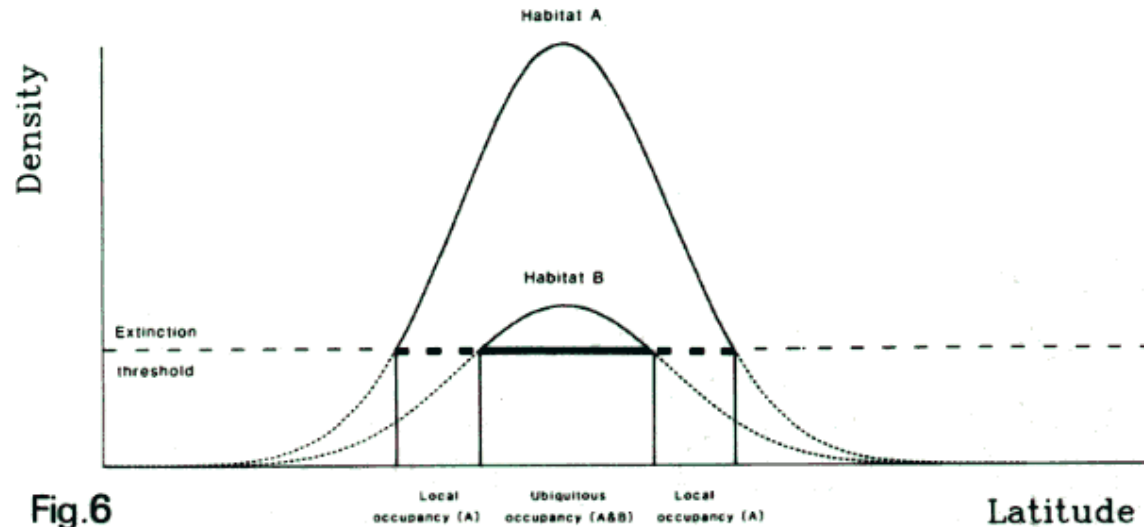


Fig.6 Above: diagram of a 'marginal mosaic' model describing regional patterns of favourability of habitats for a single species. In this simplified illustration, the environment is assumed to consist of a mosaic of just two kinds of habitats, with higher (habitat A) and lower (habitat B) food availability. The local abundance of the species within each kind of habitat depends on the local foraging profitability, which in turn depends on local climate and hence (ignoring the effect of altitude) on latitude. This results in the two density curves showing higher values centred on the climatic optimum for the species. If there is a lower limit to the density of the species without it going locally extinct (shown by the horizontal dotted line), then the species could have different latitudinal limits in the different kinds of habitat. Consequently, in regions nearer the edges of its distribution range, a species may be more locally restricted to just those habitats with most food (Williams, 1985a, 1988, Williams et al., 2007 [pdf]).

Food resources are very difficult to measure directly over a whole site. There are severe difficulties in accounting for variations in reward among flowers, both within and between flower patches, and how these vary with time of day, with weather, and with visits by bumblebees and other insects.

Another approach has been to examine the foraging patterns of the bumblebees themselves and to interpret these in the context of optimal foraging theory (see Cheverton, Kacelnik & Krebs, 1985, and references therein). This is possible because bumblebees appear to show highly optimised foraging behaviour. For example, bumblebee foragers learn to visit flowers with a depth similar to their individual tongue lengths (e.g. Brian, 1957; Heinrich, 1979; Morse, 1982; Plowright & Laverty, 1984). One explanation is that this results from a trade-off between the sugar reward, which is greater in deeper flowers (Prys-Jones, 1982), and costs in the form of the time taken to collect the reward, which increases dramatically when the flower is deeper than the bee's tongue length (Harder, 1983). Any departure from this pattern of flower choice is likely to reduce the profitability of foraging below the maximum that could be achieved.

As expected, the relationship between tongue length and flower choice was found at both Dungeness and Shoreham. Intriguingly, the tongue lengths among the fewer bumblebee species foraging at Shoreham were similar to those at Dungeness (which has the same species as the whole of Kent), so there is no evidence that only species with shorter or longer tongues survive at the more species-poor locality, Shoreham (see histograms below). Neither were the bees at Shoreham more evenly different from one another in tongue length, which might have been expected if there were competitive 'thinning' of species

(Williams, 1988).

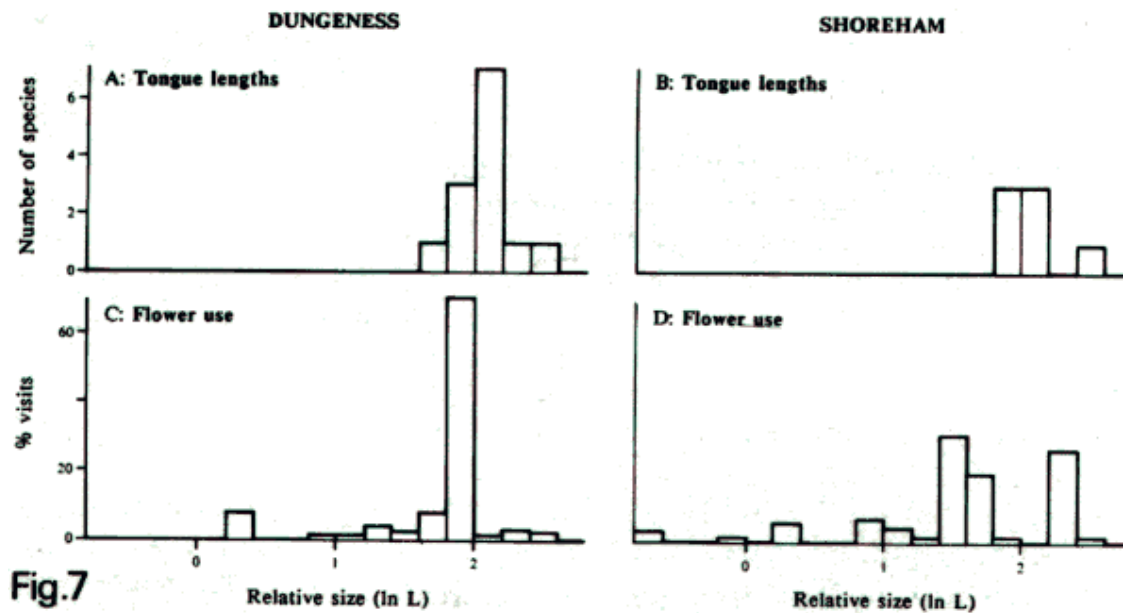


Fig.7 Above: histograms showing numbers of species of bumblebees with different tongue lengths at Shoreham and Dungeness in Kent, together with the overall frequency of visits to flowers of different depths at the two sites, both by relative size (natural logarithm of length in mm) (Williams, 1989a). All records are for workers during two weeks at the peak of foraging activity, when very few queens or males and no 'robbing' of flowers were seen. (A) bumblebee tongue lengths at Dungeness; (B) the same at Shoreham; (C) flower use at Dungeness as a percentage of visits by bumblebees to different flower depth classes; (D) the same at Shoreham.

However, although at Dungeness the bumblebees visited flowers closely similar in depth to their own tongue lengths (histograms A,C above), at Shoreham many of the bees visited flowers that were significantly shallower than the lengths of their tongues (histograms B, D above). This appears to be because there are not enough of the deeper, more rewarding flowers for bumblebees at Shoreham. Thus the crucial characteristic of the favourable habitats at the sites where the local bumblebee species persist may be that there are just more (a higher density) of the most profitable food-plants at these sites (Williams, 1985a, 1989a). The generality of this pattern throughout Kent has still to be tested.

The changing environment and declines in British bumblebees

So why have we lost so many of the bumblebee species from central England? Elsewhere I have reviewed some of the many possible factors, including competition from the honey bee, the effects of predation and parasites, and the effects of insecticides and herbicides (Williams, 1986; see also Alford, 1973). None of these agents is known either to select against the local species alone, or to have changed particularly in central England. This is not to deny them a role in the decline of bumblebees (especially for pesticides), it is merely that they are unlikely to be the principal factors. However, two other factors, climate and vegetation, have been suggested here as having particularly strong influences on bumblebee distributions.

Climatologists had claimed that the climate in Britain had warmed between 1850 and 1930, but had then showed a trend towards cooling in the period covering the second date class of records (1960-1976) in the BDMS atlas. bumblebee distribution limits seem to show some relationship to differences in summer climate with latitude and altitude. Therefore, cooling might account for the southward retreat of the Southern Local Species. However, cooling cannot easily account for the northerly retreat of the Widespread Local Species, unless a particularly strong increase in climatic variance is to blame (Williams et al., 2007 [pdf]). Records of these species are generally more frequent in the north and at

slightly higher altitudes in central Europe, so they might have been expected to be favoured by a slight cooling of the climate in Britain. Thus climate is unlikely to be the sole or major factor.

Vegetation can be profoundly affected by land use and one of the largest proportional changes in Britain this century has been through rapid urbanisation. All bumblebees, and especially the local species, have been shown to be favoured by certain kinds of vegetation. The ubiquitous species of bumblebees may remain abundant, or may even increase in abundance, in mature gardens in towns, though it is possible that shortages of food immediately after land clearance for building could eliminate the local species, which are not known to survive well in these areas. Nevertheless, urbanisation is not likely to have affected the broader regional distribution of bumblebees, because few of the vice-counties (the units used in the regional classification) even approach complete urban development.

More than 80% of the total land area of Britain is used for agriculture and since the Second World War, government policy and resulting economic pressure has driven a pronounced intensification of agriculture with an acceleration of mechanisation. There is still a preponderance of arable farming (especially wheat) in eastern England and a preponderance of livestock in the wetter west and north. But inevitably under this economic pressure, much land that was previously considered to be of borderline profitability (especially wet grassland), and frequently allowed to remain relatively undisturbed, has been reclaimed for cultivation, particularly in the central lowlands. Field under-drainage, which has been most extensive in the central and eastern counties, has usually been the prelude to the conversion of pastures back to arable use and to the first-time cultivation of pasture land, including alluvial meadows and marsh. The Midlands have been most affected by increases in the arable area and, although the eastern counties have remained largely arable in their farming, field sizes have been increased to facilitate mechanisation, especially by the removal of hedges. All of these changes are likely to have reduced the amount of particularly favourable habitat that has a greater abundance of the better food plants for bumblebees (Williams, 1985a, 1986).

The importance of changes in agricultural land use for the decline of British bumblebees is supported by anecdotal evidence from a few, well documented localities such as Wicken Fen in central England. It also appears to be continuing in the southern region at localities such as the Rother Levels in Kent (Williams, 1986). [Since 1989, the species *B. subterraneus*, *B. ruderatus* and *B. sylvarum* may also have disappeared from Dungeness, although *B. soroeensis* has been recorded there for the first time.]

Bumblebee declines elsewhere in Europe

In the former East Germany, a similar decline in most of the same species has been reported by Peters (1972). He believed that this was caused by a trend towards uniformity in agricultural landscapes and by the use of pesticides.

In Belgium and northern France, a decline in many of the same bumblebees has been described by Rasmont (1988). He also concluded that this has been caused primarily by degradation of open habitats with a consequent loss of food plants. He placed particular emphasis on plants of the families Leguminosae and Compositae for the local and declining species of bumblebees.

Rasmont (1988) found that in a survey of the Languedoc-Rousillon region of southern France, the more locally restricted bumblebees visited a narrower range of food plants. He concluded that the between how many food plants a bumblebee species uses and how widespread it is explains why some species are more widespread than others. However, this relationship is expected as an effect of sample size alone. This explanation was rejected because he found no correlation between the average local abundance of a bee species and the total number of food plants recorded for it from Languedoc-Rousillon. However, the pattern might be obscured because so many different climatic regions and habitats were included: the Languedoc-Rousillon survey area includes a broad altitudinal and climatic range, which is equivalent to several regions of the kind defined for Britain. For instance, some of the French bumblebees are restricted to the subalpine zone, so even if they were locally abundant and using many food-plant species, their total number of food plants for Languedoc-Rousillon could still amount to fewer than for the more widespread species, simply because they are rarer when considered among all samples.

The pattern whereby the local bumblebees use a narrower range of food plants than the ubiquitous bumblebees was not found at Dungeness (Median test for a difference between the numbers of food-plant species used by ubiquitous and local species of bumblebees at Dungeness, Fisher exact $p = 0.38$), where two of the local species actually visited more species of food plants than any of the ubiquitous

species. But when the comparison was extended to all 20 of the sites surveyed in Kent, where the local species tend to be much less abundant, then a correlation was found between the average local number of bees per species and the average local number of food-plant species for that bee species (Kendall correlation, $\tau = 0.94$, $p < 0.001$). Thus smaller sample sizes for the rarer local species alone, rather than narrower food-plant specialisation, may be sufficient to explain why the locally restricted bumblebees may appear to use fewer food-plant species.

Food-plant specialization was also proposed as an explanation for bumblebee declines in Britain by Goulson *et al.* (2005), but the apparent relationship disappeared when allowance was made for factors such as sample size (Williams, 2005 [PDF]).

A correlation between bumblebee range sizes and numbers of food plants used would not be expected to result from innate specialisation by the local bees to particular plant species. Previous studies have shown that bumblebees usually learn to visit the most rewarding flowers that happen to be common in their local foraging areas (e.g. Heinrich, 1979). Furthermore, the test of the specialist hypothesis at Dungeness showed that the local bees are not distributed together with the same preferred food plants throughout Kent.

Conclusion

This brief summary of bumblebee distributions and their decline in Britain shows that undoubtedly many factors in the changing environment *could* have contributed to the impoverishment of the bumblebee fauna in some areas. A general problem in the interpretation of distribution patterns is that these factors may be closely correlated with one another, so that their effects would be much more difficult to disentangle were it not for the changes in bumblebee distributions in the last few decades.

If it were necessary to identify the single most important factor to have affected the decline of British bumblebees then this study helps by showing that it is the loss of open habitats rich in certain kinds of food plants that is the most likely candidate. More precisely, it may not be necessarily a reduction in the number of species of flowering plants at a locality that is important, but rather a decrease in the abundance of the most rewarding food plants. Since most worker bumblebees in Kent have tongue lengths in the range 5-13 mm, and more especially in the range 7-9 mm (figure 7A), then flowers with similar depths are likely to be most valuable (Williams, 1985a, 1989a).

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