Where have all the bumblebees gone, and could they ever return?

Mike Edwards and Paul Williams

If you were asked to name ten insects to be found in the British countryside it is likely that 'bumblebees' would be high on your list. The deep, loud buzz of a nest-searching queen is a sign of spring, whilst the busy flight of a foraging worker is frequently used as a metaphor for summer in literature. Folk-histories record country children searching out bumblebee nests in order to steal the thimble-sized pot of honey, whilst manual workers cutting hay cursed the scythe-stroke which disturbed the nest. Entomologists up to the Second World War hardly bothered to record the presence of bumblebee species in their accounts, comments such as '*Bombus sylvarum* everywhere as usual' (Hallett, 1928) and the presence of a few specimens of many of the British species in provincial museum collections testifying to their ubiquity. The usefulness of bumblebees in pollinating the then agriculturally vital clover crops was well known at the turn of the 20th century, with species being introduced into New Zealand in order to establish the clover-based pastures which supported the development of the New Zealand milk, lamb and wool industries.

The overall pattern of bumblebee life history has been well known for a hundred years and was well documented by F.W. Sladen (1912). However, there is still a lack of detailed autecological knowledge for individual species. Later accounts draw heavily on Sladen's observations. It is probable that this reflects the decline in some bumblebee populations during the second half of the 20^{th} century as much as any lack of detailed research. For instance, Free and Butler (1968) writing in the late 1960s, clearly had personal experience of most of the British species, whilst Alford (1975), writing less than a decade later, was unable to give first-hand experience for many of these.

Bumblebees and BAPs

The results of a bumblebee mapping scheme that collected data up to 1976 were published during 1980 (IBRA, 1980). These maps appeared to confirm that many species were not as widely distributed as was once thought. At this time, research was going on in a group centred around Dr Sarah Corbet at Cambridge. Oliver Prys-Jones was studying flower preferences of the common species (see Prys-Jones & Corbet, 1987) and one of us (PW) was looking into how this might affect changing patterns in distribution, particularly for the rarer species (see www.nhm.ac.uk/entomology/bombus/declines.htm). During the mid 1990s, when the Biodiversity Action Plan was being formulated, these observations, together with the experience of other entomologists, resulted in five species being put forward for more detailed study under the BAP process. These were *B. distinguendus, B. humilis, B. ruderatus, B. subterraneus* and *B. sylvarum*.

Of the five BAP bumblebees, *B. sylvarum* was chosen for the first list of 100 BAP Priority Species for initial study. The reasons for so doing were several. It is a species that was known to be formerly widespread in southern and midland England and southern Wales; the IBRA Atlas appeared to show a decline by the beginning of 1970s; it was rarely encountered by entomologists during the 1980s; and it is a distinctive bee, so that historic records are unlikely to include many misidentifications.

The results of an initial survey of post-1970 locations for this species in England during the summer of 1997, funded by English Nature and WWF (UK), were dramatic. After six man-weeks of searching, only two workers were found, one in north Kent and one on Salisbury Plain Training Area! At the same time, rather better hopes were raised by a survey for *B. distinguendus* in the Outer Hebrides, funded by Scottish Natural Heritage, where a good population was found still to be present and distributed across at least three of the larger islands.

It was suspected from this survey, as from previous analysis (Williams, 1988), that the habitat needs of the BAP bumblebees were broadly similar. At the end of 1997, it was decided to investigate the BAP bumblebees as a group rather than species by species. Accordingly, the Bumblebee Working Group was set up by the three Country Government Conservation Agencies (Countryside Council for Wales, English Nature and Scottish Natural Heritage), RSPB and WWF (UK). These bodies and the BWG became the lead partners for these species under the BAP process. The five species initially chosen represented almost one-third of the eighteen British species of social bumblebees recognised in the 1980 Atlas (there are a further six socially parasitic species). Confirming earlier analysis (Williams, 1982), it soon became clear that the status of a further five species (*B. jonellus, B, monticola, B. muscorum, B. ruderarius* and *B. soroeensis*) also gave reason for concern.

In the event, this concern has been shown to be fully justified for at least three of the additional species: *B. monticola, B. muscorum* and *B. ruderarius.* Research into these species has subsequently been supported by English Nature's Species Recovery Programme. The status of *B. soroeensis* remains unclear, largely because of the difficulty of reliable field identification, but it is likely to be declining; only that of *B. jonellus* appears to be of more limited concern within Britain as a whole.

For some time, populations of many species of bumblebee have been known to be declining on the mainland of Europe. Much evidence is anecdotal, although a review of the status of European bumblebee species is shortly to be published by Prof. P. Rasmont of the Université de Mons-Hainaut in Belgium. On a more restricted level, the status of bees in Baden-Württemburg (south-western Germany) has been well documented over the past twenty years (Westrich, 1989, and pers. comm). Here severe declines are shown for the same species (as well as some non-British species) as are a cause for concern in Britain.

Foraging for pollen

Much modern research into bumblebees has concentrated on the economics of foraging, using the common species. This has concentrated on the profitability of nectar collection, in the belief that this is the limiting factor. There has been relatively little research into the kinds of pollen which are being gathered (with the notable exception of investigations into *B. monticola* in the Peak District (Yalden, 1982). Many members of the BWG had previously been more involved with solitary bees than the social bumblebees. Among solitary bees, many species have very strong preferences in the pollen which they collect. It was, perhaps, inevitable that we should look at this previously neglected area of bumblebee foraging.

Our initial field studies led us to believe that, although true oligolecty (specialisation on pollen from one plant species or family) would be an unlikely strategy for long-season bumblebee species (as expected in theory: Williams, 1989), many species were quite fussy about which pollens they collected. Pollen provides the major building material for growing larvae, so studying the collection of pollen could help our understanding of bumblebee ecology. This idea was further supported when we discovered that when commercially-reared bumblebee colonies (usually *B. terrestris*) start to fail, the first remedy is to change the source of the pollen which they are being fed.

Hints that pollen collection can be an important consideration for bumblebees and that bumblebee pollen foraging preferences can lead to flower specialisation are provided by studies of the structural specialisation of the flowers of two species of Lousewort *Pedicularis* sp. reported in *The Pollination of Flowers* (Proctor & Yeo, 1973). One of the two Louseworts provides no nectar at all, but both are visited regularly for pollen by bumblebees. The anthers are held in a curved 'tube' and the pollen is released through interaction with specific sections of the body of the visiting bumblebee. One Lousewort (with nectar) flowers in early spring and is visited by queen bumblebees; the anther tube in this species is curved to fit between the head and thorax of the large queens and the pollen is rubbed off between the two body parts. The second species (with no nectar) flowers later; the tube in this case is curved to fit between the thorax and abdomen of the smaller workers. These release pollen by vibrating their thoracic muscles which, in turn, shakes the anthers violently so that a cloud of pollen envelops the bee and is then combed off into the pollen baskets on the legs. Similar situations occur in the Himalaya of Kashmir (Williams, P.H., 1991).

Our initial studies of *B. distinguendus* on the Outer Hebrides during early August 1997 linked this species with areas of machair habitat with two factors in common: plentiful Red Clover *Trifolium pratense* and flowering Black Knapweed *Centaurea nigra*. These two plants were regular components of areas of machair that are grazed by cattle during the winter only; but are missing, or very suppressed, where there is fenced sheep-grazing, or a very high density of rabbits. We collected a number of samples of pollen from workers. Subsequent analysis showed that Red Clover and, to a lesser extent, Black Knapweed, were indeed strongly represented.

Clearly, as the bumblebee colony had been present earlier in the year before the Red Clover was flowering, this is not the whole story. Indeed, we were not sure whether the link with Knapweed signified merely that this plant grows in areas with suitable nest sites. It may be that Knapweed is simply a convenient place to sit (many of the bees were males). Studies carried out during the next two years in machair habitats identified Bird's-foot Trefoil *Lotus corniculatus* as an important early pollen source and Marsh Woundwort *Stachys palustris* as an additional later-season source. But the strong link, in the Western Isles, with the overall machair habitat was confirmed.

Confirmation of these plants as pollen sources was obtained by collecting pollen loads from foraging bumblebees (*B. distinguendus* and other species) and analysing them. Whilst not exhaustive, the list of pollen sources for bumblebees highlights the overall importance of three plant families: Fabaceae, Lamiaceae and Scrophulariaceae. The results also hint strongly that individual bumblebee species exhibit differences between a) preferred plant species and b) their tendency to collect loads from single plant species or mixed plant species loads. Claire Carvell, working on a three-year Centre for Hydrology and Ecology/Farmed Environment Company study funded by English Nature, recently obtained further evidence of choices among plants being made by different bumblebee species (Carvell et al., 2003). Given the choice of adjacent plots which contained either (predominately) flowering Borage *Borago officinalis* or (predominately) flowering Red Clover the species visiting the flowers fell into two groups. *B. terrestris, B. lucorum, B. pratorum* and Honeybees *Apis mellifera* mainly visited the Borage, and *B. hortorum* and *B. pascuorum* mainly visited the Clover. Whilst *B. lapidarius* showed a preference for visiting Borage, it also made 40% of visits to other species growing in the plots. Analysis of pollen loads for two of the species confirmed this dichotomy, with *B. terrestris* having pollen mostly from the Borage and *B. pascuorum* having pollen mostly from the Clover. This pattern was repeated in further investigations of pollen specialisation in 2003. These results underline the dangers inherent in treating all bumblebees as a uniform group as far as foraging is concerned.

This must lead on to asking what is special about the preferred pollens. Preliminary work by Dave Goulson (pers. comm.) at Southampton University has shown a significant difference between the protein content of pollen from different plant families. Pollen from Fabaceae has in the order of twice the protein content of pollen from Asteraceae or Apiaceae, although there are individual differences between species. Much more research needs to be done here.

Foraging distance and area

Studies on individual solitary bee species have suggested that they are able to forage efficiently over considerable distances. These may be up to 5 km in one case in Southern Germany, where Paul Westrich has studied colonies of the mining bee *Andrena agilissima* (pers. comm.). One of us (ME) knows of nesting aggregations of *Andrena florea* that are more than 1 km from the nearest pollen foraging source, flowers of White Bryony *Bryonia dioica*. Nevertheless, there has been a strong argument from energetics that such distances represent unusual situations and that most bees will visit resources near to the nest, rather than far away. Recently, Juliet Osborne, using radar-tracking studies at Rothamsted, has shown that most foraging bumblebee workers were leaving the nest and travelling considerable distances, certainly in excess of four hundred metres (the point at which radar contact was lost, not the foraging location!), before commencing to forage. In doing so, they were ignoring resources nearer to the nest (Osborne et al., 1999). This accords with our observations that marked individuals are rarely found close to the nest.

Nests of different bumblebee species probably forage over differently-sized areas; the same may well be true regarding nest density; small colony species such as *B. humilis* having more densely spaced nests than species with large colonies, such as *B. terrestris.* We have tried to establish measures of the density of bumblebee nests, but this has proved very difficult. We can say that no population of the BAP species has been found to occupy a landscape area (population range) which is less than 10 km^2, and the occupied area is usually much greater (some populations of *B. humilis* occupy the smallest known population ranges). Most bumblebee nests fail to produce new sexuals, succumbing to predators and parasites before new queens are produced. This means that the true mean density of bumblebees (as successful reproductive individuals) is quite low, probably for some species in the order of 1-2 nests per km^2. This also agrees with the observed need for large population ranges. Within these population ranges there may well be sites which have a higher density of successful nests, but nowhere do these appear to be sustained without a much larger area of lower-density occupation.

Possible reasons for declines

The question of whether there are any similarities between the strongly-declining species and those which are still relatively frequent has been examined. One favoured hypothesis has been that it is the long-tongued species that are declining. These species are often associated with more complex flowers. However, two species, *B. hortorum* and *B. pascuorum,* are longer-tongued and still widespread, whilst two short-tongued species, *B.*

monticola and *B. soroeensis,* are much more restricted and currently declining.

One of us has described (Williams, 1988, 1989) how the species that are closer to the cores of their global ranges within Britain are the more widespread and abundant species, whereas the species that are in the margins of their global ranges here are more patchy, tend to be less abundant, and are more likely to have declined. This may be most obvious for species pairs such as *B. distinguendus* (now restricted to N. Scotland) and *B. subterraneus* (formerly southern, but now extinct in Britain). Compared to globally widespread species like *B. lucorum*, *B. hortorum*, and *B. pascuorum*, these more narrowly-distributed species may be less efficient in making more bees in some habitat types. With narrower ranges, these species appear to have correspondingly narrower climatic tolerances for activity, and seem to need correspondingly higher densities of the most suitable flowers for the economics of their populations to allow them to stay in business. Recent analysis of published bumblebee and plant distribution data also refutes the over-riding influence of tongue length of individual bumblebee species as a cause of the decline and suggests a stronger association with the decline in some plant communities - S. Gray & A.F. G. Bourke, unpublished. The same species are becoming rarer throughout their whole European range and some of our largest remaining populations of scarcer species are on extensive, flower-rich grasslands, such as the Castlemartin Ranges in West Wales. Indeed, one species, *B. ruderatus*, has its main relict populations in a few flower-rich sites near the centre of that part of Britain that had been judged to be the most impoverished for bumblebees.

During our studies it has become clearer that the timing of queen emergence and the presence of a plentiful supply of suitable forage flowers at this time is likely to be an important factor in deciding which species are able to occupy an area permanently. Clearly there exists for all species the need for provision of suitable forage throughout the life of the colony and dramatic interruptions of forage supply are lethal for any bumblebee colony.

Looking at bumblebee species according to the timing of queen emergence and the timing of first flower flushes leads to two main habitat/bumblebee groupings:

(1) Woodland edges (and gardens) favour species that have early-emerging queens. These queens are able to forage at the early flowers which typically grow in such sheltered situations (March-May, depending on latitude).

(2) Extensive areas of open grasslands (wet or dry) flower much later (May to July, according to latitude). These favour species which have later-emerging queens (May to July, according to latitude).

Queens are more likely to found their nests where there are plentiful resources. An early-emerging queen is very unlikely to stay long on the open grassland of Salisbury Plain, or on the Somerset Levels in March! By the time the open-ground areas come into flower, it is too late for early-emerging species, which must already have established their nests where the early flower flushes allowed. However, the later queens are then ideally placed to found nests in the more empty, later-flowering areas. These distinctions are not hard and fast, as woodland-edge species may often be found with open-ground species, because there is nothing to stop a bumblebee flying over large areas of open ground to forage at suitable resources. Conversely, the practice of establishing clover-rich (late-flowering) meadows as part of agricultural systems may allow the open-ground species to establish nests within an essentially woodland-edge situation.

B. jonellus seems to belong to both groups, according to latitude and/or altitude. It is rare, however, for other open-ground species to be found in garden and woodland habitats. This may be, in part, a reflection of the relative scarcity of the open-ground species. Some long-tongued species occur in the garden and woodland-edge group and some short-tongued species occur in the open-ground group. The full relationship between species is undoubtedly complex and perhaps no single answer can account for all the differences that have been noted so far.

The British species are grouped by the proposed habitat association below, together with an assessment of their current status and conservation priority. Note that a third group is formed by the socially parasitic species.

One of the main aims of the Biodiversity Action Plans for these bumblebees is to reverse the current declines; is this likely to be possible? Early results from increasing the availability of legume flowers, notably Red Clover, have been very encouraging. During the first three years of a trial of arable farm margins sown with agricultural legume mixes on Romney Marsh there was a three-hundred-fold increase in the total number of bumblebees recorded on fixed-time transect walks. Unfortunately, these trials did not include control transects of fields without sown legume margins, so it is possible that the observed changes might be attributable to a more widespread change in overall bumblebee populations. However, once these margins lost their high density of flowering legumes (in year four) the numbers of bumblebees fell dramatically.

Also in the Romney Marsh area, at RSPB Dungeness Reserve, changes were made to grazing regimes which allowed native legumes to flower where before there was little flower present. Again, numbers of bumblebees of all species, but most notably of *B. humilis* and *B. muscorum,* have increased in the suitably managed areas during the five year period of the study. In this project counts have been repeated at other locations on Dungeness and the observed increase is more clearly attributable to the presence of the additional flower resources. The first two years' results from more extensive and well-controlled experimentation under the Farmed Environment Company/Centre for Ecology and Hydrology Buzz Project also show a strong link between high bumblebee abundance and the provision of additional suitable forage areas, especially legumes, in the farmed environment.

We are firmly of the opinion that the current limiting factor for all species is the lack of suitable forage resources. Providing these at a suitable density and ensuring that forage continuity is maintained are cornerstones of this part of the plan. We consider this to be completely achievable, given sufficient political will and good farming advice. Agri-environment agencies have accepted the need for the inclusion of bumblebee habitat within schemes and a Scheme Option (WM2) provides a cheap mix of agricultural legumes which can be sown to provide suitable mid- to late-summer forage. This is a good, fire-fighting start and may be all that is appropriate, or achievable, in some farming situations. However, we still need to learn more about creating better-quality and more permanent habitat to provide suitable foraging, nesting and hibernating resources. We also need to know much more about the landscape scales that are appropriate for effective restoration programmes. Cooperative research projects involving BWG, Government Agricultural Agencies and Research Foundations, The Natural History Museum, RSPB, The Farmed Environment Company and a number of University Departments are all working at improving our ability to halt the decline in habitat quality. The real challenge will be to provide habitat restoration procedures that provide resources to a much broader range of organisms than just bumblebees, whilst not making unrealistic demands on agriculture, which is, after all, what feeds us humans.

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Table 1 The British species are grouped below by the proposed habitat association, together with an assessment of their current status and conservation priority.

Group 1 Garden/woodland-edge species, widespread, often frequent in gardens.

B. hortorum	long-tongued, underground or surface nesting.
B. hypnorum	short-tongued, underground, surface or above-ground nesting (new to Britain).
B. lapidarius	mid-tongued, underground nesting.
B. lucorum	short-tongued, underground nesting.
B. pascuorum	long-tongued, surface nesting.
B. pratorum	short-tongued, underground nesting, surface or above-ground nesting.
B. terrestris	short-tongued, underground nesting.

Intermediate

B. jonellus	short-tongued, underground, surface or above-ground nesting. It is regularly double-brooded in the south, with early-emerging queens. It is also typical of open heathland and moorland habitats, where queens are late-emerging. In the north the queens are late-emergers only. Here it is one of the commonest bumblebees of open moorland.

Group 2 Open-ground species associated with flower-rich grasslands, rarely found in gardens, unless adjacent to other suitable habitat. All are declining, some more than others. One is recently extinct in Britain. Similar declines throughout Europe. Declines are most marked in the areas of most intensive agriculture (excluding heavily wooded areas, which are unsuitable anyway).

B. distinguendus	long-tongued, underground nesting, now NW Scotland only (Biodiversity Action Plan priority species = BAP).
B. humilis	long-tongued, surface nesting, now S England and Wales only, largely coastal. (BAP).
B. monticola	short-tongued, underground or surface nesting, upland species associated with tall moorland vegetation, especially bilberry areas, but also uses legume pollen. (Species Recovery Programme = SRP. Will be put forward for inclusion in BAP at next review.)
B. muscorum	long-tongued, surface nesting, largely northern and coastal. (SRP)
B. ruderarius	long-tongued, surface nesting, largely southern. (SRP)
B. ruderatus	long-tongued, underground nesting, southern. (BAP)
B. soroeensis	mid-tongued, underground nesting. Biology unclear, but associated with extensive flowery grasslands and moorland throughout Britain. (SRP)
B. sylvarum	long-tongued, underground or surface nesting, southern. On verge of extinction in Britain. (BAP)
B. subterraneus	long-tongued, underground nesting, southern. Extinct in Britain in the past 15 years.

Group 3 social parasites (Cuckoos). All are associated with at least one widespread species, although most will attack some of the scarce species when possible. Formerly considered to be a separate genus, *Psithyrus*. All widespread, although populations do have regional differences and numbers fluctuate year by year and over longer time-scales. There is no data on relationship with the density of host populations.
B. barbutellus, B. bohemicus, B. campestris, B. rupestris, B. sylvestris, B. vestalis

Open grasslands, such as on Salisbury Plain, provide very poor floral resources early in the season (top), **but by mid June** (below) **they have a super-abundance of flowers**. Mike Edwards.

Arable margins at Old Romney sown with agricultural legumes, providing excellent foraging resources for bumblebees. Mike Edwards.

Less continuous grazing of grasslands at Dungeness RSPB Reserve transformed grasslands with few flowering plants to areas with a plentiful supply of flowering legumes and other plants. Mike Edwards.