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

Queen *Bombus sylvarum* on clover. This bumblebee is a BAP Priority Species. Peter Harvey

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

***Bombus pascuorum* is one of the bumblebees that can often be seen feeding in gardens.** David Element

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, despite all this, there is still a lack of detailed aut-ecological knowledge for individual species. Later accounts draw heavily on Sladen's observations. It is probable that this reliance reflects the decline in some bumblebee populations during the second half of the 20th century as much as it does any lack of detailed research. For instance, Free & Butler (1959), writing in the late 1950s, clearly had personal experience of most of the British species, whilst Alford (1975), writing less than a 20 years 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 so widely distributed as was once thought. At this time, research was being carried out by 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 (BAP) 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 *Bombus distinguendus*, *B. humilis*, *B. ruderatus*, *B. subterraneus* and *B. sylvarum*.

Of the five BAP bumblebees, *Bombus sylvarum* was included in 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 the 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, carried out during the summer of 1997 and 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 *Bombus 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 (BWG) was set up by the three Country 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 18 British species of social bumblebee recognised in the 1980 IBRA Atlas (there are a further six socially parasitic species, the 'cuckoo bumblebees'). Confirming earlier analysis (Williams 1982), it soon became clear that the status of a further five species (*Bombus 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

***Bombus hortorum* is a relatively common long-tongued bumblebee.** Mike Edwards

***Bombus humilis* is a scarce bumblebee mostly found in southern coastal regions.** Peter Harvey

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 Université de Mons-Hainaut, in Belgium. On a more restricted level, the status of bees in Baden-Württemberg (south-western Germany) has been well documented over the past 20 years (Westrich 1989 and pers. comm.). Here, severe declines have been shown for the same species as those which are causing concern in Britain (as well as for some non-British species).

Foraging for pollen

Much modern research into bumblebees has concentrated on the economics of foraging, using the common species. This has focused 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 *Bombus monticola* in the Peak District: Yalden 1982). Many members of the BWG had previously been more involved with solitary bees than with the social bumblebees. Among solitary bees, many species have very strong preferences in the pollen which they collect. It was therefore, 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, and studying the collection of pollen could therefore help our understanding of bumblebee ecology. This idea was further supported when we discovered that, when commercially reared bumblebee colonies (usually *Bombus terrestris*) start to fail, the first remedy is to change the source of the pollen with 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 North American lousewort *Pedicularis* reported by Proctor *et al.* (1996). 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, and these release

The machair on South Uist has a plentiful supply of flowering plants, making it an ideal foraging habitat for species such as *Bombus distinguendus*. Robin Bush/Nature Photographers

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 1991).

Our initial studies of *Bombus 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 Common Knapweed *Centaurea nigra*. These two plants were regular components of areas of machair that are grazed by cattle during the winter only; but they are missing, or very suppressed, where there is fenced sheep-grazing, or a very high density of Rabbits *Oryctolagus cuniculus*. We collected a number of samples of pollen from workers. Subsequent analysis showed that Red Clover and, to a lesser extent, Common 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. We were not sure whether the link with Common Knapweed signified merely that this plant grows in areas with suitable nest sites. It may be that the 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 Common 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.

These plants were identified as pollen sources by collecting pollen loads from foraging bumblebees (*Bombus distinguendus* and other species) and then analysing them. Whilst not exhaustive, the list of pollen sources for bumblebees highlighted the overall importance of three plant families: Fabaceae (legumes), Lamiaceae (deadnettles and allies) and Scrophulariaceae (figworts and allies). 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 (predominantly) flowering Borage *Borago officinalis* or (predominantly) flowering Red Clover, the species visiting the flowers fell into two groups: *B. terrestris, B. lucorum, B. pratorum* and Honeybees *Apis mellifera* mainly visited Borage; *B. hortorum* and *B. pascuorum* mainly visited Red Clover. Whilst *B. lapidarius* showed a preference for 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 Borage and *B. pascuorum* having pollen mostly from Red 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, so 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

Bumblebee covered in pollen.
N A Callow/Nature Photographers

has shown a significant difference in 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 (composites) or Apiaceae (umbellifers), 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 5km in one case in southern Germany, where Paul Westrich (pers. comm.) has studied colonies of the mining bee *Andrena agilissima*. One of us (ME) knows of nesting aggregations of *Andrena florea* that are more than 1km 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 worker bumblebees were leaving the nest and travelling considerable distances, certainly in excess of 400m (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, and the same may well be true regarding nest density. Small-colony species, such as *Bombus humilis*, have more densely spaced nests than do 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 10km^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 a new sexual generation, 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 one or two 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, *Bombus 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 more widespread and abundant, whereas those that are at the margins of their global ranges 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 *Bombus distinguendus* (now restricted to north Scotland) and *B. subterraneus* (formerly southern, but now extinct in Britain). Compared with globally widespread species, such as *B. lucorum*, *B. hortorum* and *B. pascuorum*, these more narrowly distributed species may be less efficient in producing new generations in some habitat types. With narrower ranges, the species appear to have correspondingly narrower climatic tolerances for activity, and seem to need correspondingly higher densities of the most suitable

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, nesting underground or at surface
B. hypnorum	short-tongued, nesting underground, at surface or above ground (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, nesting underground, at surface or above ground
B. terrestris	short-tongued, underground-nesting

Intermediate

B. jonellus	short-tongued, nesting underground, at surface or above ground. 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. In Britain, 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 in any case unsuitable).

B. distinguendus	long-tongued, underground-nesting, now north-west Scotland only (BAP priority species)
B. humilis	long-tongued, surface-nesting, now southern England and Wales only, largely coastal (BAP priority species)
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 priority species)
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 priority species)
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 are no data on relationship with the density of host populations.

B. barbutellus, B. bohemicus, B. campestris, B. rupestris, B. sylvestris, B. vestalis

flowers for their populations to survive. Recent analysis of published bumblebee and plant distribution data also refutes the overriding influence of tongue length of individual bumblebee species as a cause of declines and suggests a stronger association with the declines in some plant communities (S Gray & A F G Bourke unpub.). 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 are likely to be important factors 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.

Examination of bumblebee species according to the timing of queen emergence and the timing of first flower flushes leads to two main habitat/bumblebee groupings (see Table 1).

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 grassland (wet or dry) which flower much later (May to July, according to latitude), favour species which have later-emerging queens.

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 less occupied, 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.

Bombus 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.

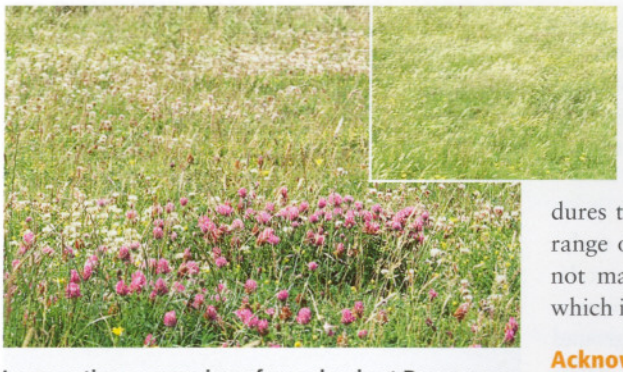
One of the main aims of the Biodiversity Action Plans for these bumblebees is to reverse the current declines in their populations. Early results related to increasing the availability of flowering legumes, notably Red Clover, have been very encouraging. During the first three years of a trial in which arable farm margins were sown with agricultural legume mixes on Romney Marsh, Kent, there was a 300-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

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

changes may be attributable to a more widespread change in overall bumblebee populations in the area. 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 the RSPB Dungeness Reserve, changes were made to grazing regimes which allowed native legumes to flower where few flowers were present before. Again, numbers of bumblebees of all species, but most notably of *Bombus humilis* and *B. muscorum*, increased in the suitably managed areas during the five-year period of the study. In this project,

Arable field 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 (top) **to areas with a plentiful supply of flowering legumes and other plants** (above).
Mike Edwards

counts have been repeated at other locations on Dungeness and the observed increase is more clearly attributable to the presence of the additional flowering. 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 a continuity of suitable forage flowers 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. Co-operative 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 implement habitat restoration procedures that provide resources for 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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