

# Bumblebee vulnerability and conservation world-wide\*

Paul H. WILLIAMS<sup>1</sup>, Juliet L. OSBORNE<sup>2</sup>

<sup>1</sup> Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

<sup>2</sup> Department of Plant and Invertebrate Ecology, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK

Received 6 October 2008 – Revised 13 January 2009 – Accepted 15 January 2009

**Abstract** – We review evidence from around the world for bumblebee declines and review management to mitigate threats. We find that there is evidence that some bumblebee species are declining in Europe, North America, and Asia. People believe that land-use changes may be having a negative effect through reductions in food plants in many parts of the world, but that other factors such as pathogens may be having a stronger effect for a few species in some regions (especially for *Bombus* s. str. in North America). Evidence so far is that greater susceptibility to land-use change is associated world-wide with small climatic ranges, range edges, and late-starting colony-development cycles. More evidence is needed on the roles of pollen specialization, nest sites, hibernation sites, and pesticides. It is still too early to assess the success of schemes aimed at improving forage in agricultural and conservation areas. However, schemes aimed at raising public awareness have been very successful. Until proven safe, we recommend that live bumblebees should not be moved across continents or oceans for commercial pollination.

**bumblebee / *Bombus* / threat / vulnerability / decline / conservation**

## 1. INTRODUCTION

Conservation means different things to different people, because it depends ultimately on people's personal values. The largest quantified value of bumblebees comes from their pollination services to agriculture, which are worth billions of dollars annually (e.g. Dias et al., 1999; Goulson, 2003; Winter et al., 2006). Bumblebees are also immensely popular with great cultural value in north temperate regions (e.g. Milne, 1926). However, both of these values could arguably be satisfied largely by the very few commercially reared species, so conservation policies based on these values alone could in principle permit most bumblebee species to go extinct. In contrast, the value of bumblebee pollination services to natural ecosystems, as well as their biodiversity val-

ues, require the persistence of many or all of the 250 or so bumblebee species world-wide.

People are also likely to see different goals for conservation in different contexts. For example, we might see as high priorities the species most at risk of global extinction (e.g. IUCN, 2001), such as *Bombus franklini* (Frisson) (Thorp, 2005). Alternatively, we might be more concerned about the loss of species from a particular country like Britain (e.g. Anonymous, 1994), even though the latter species might remain widespread elsewhere in the world (e.g. *B. subterraneus* (Linnaeus), which has many recent records from Sweden to Iran and Mongolia). Although these priorities could conflict, both are valid in their respective contexts.

There have been many reviews of bumblebee declines and the need for their conservation (e.g. Williams P.H., 1986; Rasmont and Mersch, 1988; Benton, 2000; Kearns and Thomson, 2001; Goulson, 2003; Edwards and Williams P.H., 2004; Benton, 2006; Goulson

Corresponding author: P.H. Williams,

[paw@nhm.ac.uk](mailto:paw@nhm.ac.uk)

\* Manuscript editor: Tomas Murray

et al., 2008). This review differs by considering evidence *world-wide* for extinction and decline and discusses the factors that threaten the persistence of bumblebee species and the factors that influence which species are most susceptible. We note which species world-wide have become most threatened and which areas of the world support the largest numbers of threatened species (we do not consider the parasitic species of the subgenus *Psithyrus*, because information is too sparse). We then discuss conservation-management strategies and finish with suggestions for future work.

## 2. EVIDENCE FOR DECLINES

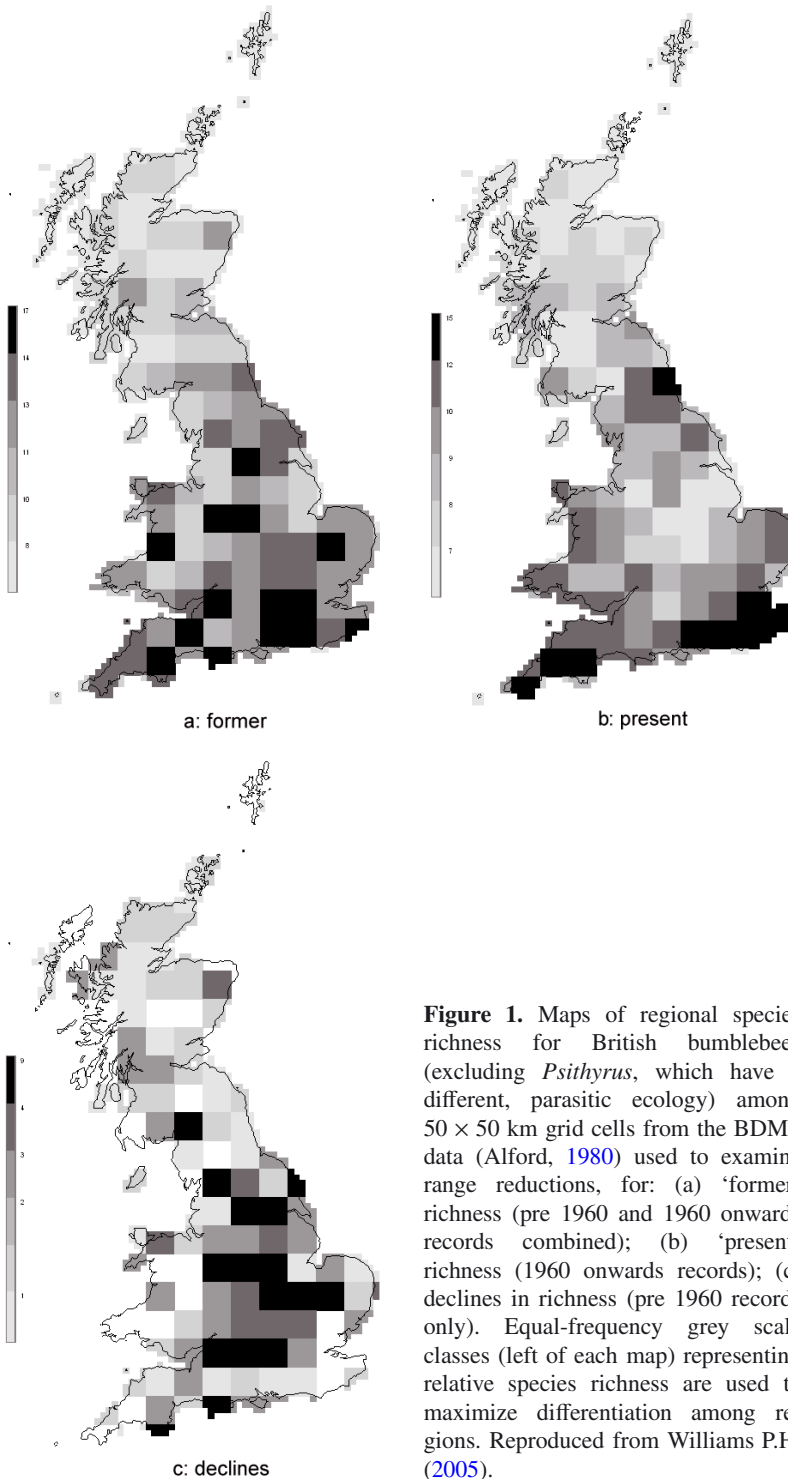
Most concern about bumblebee conservation has come from widespread perceptions that many bumblebee species have declined in local abundance and in their range extent (i.e. through local extirpations), without going globally extinct. The dates and rates of these changes are often very uncertain, because baseline data for comparisons are rarely available. Data collected 50–100 years ago using standardised and repeatable sampling methods for measuring abundance are almost completely lacking, but fortunately there are data on range extent that can provide information.

The earliest worries about changes in the status of bumblebee species were expressed in Britain by Free and Butler (1959), who wrote that “*It is commonly supposed that the bumblebee population has declined in recent years*”. Some species had been completely lost from Britain. For *B. pomorum* (Panzer), there had only ever been a few records from the south-east coast of Britain before the last record in 1864, so that it may never have been a long-term part of the fauna (Alford, 1975). For *B. cullumanus* (Kirby), females were always rare and especially difficult to identify, making it unlikely to be recorded, although the more easily recognized males were recorded regularly from the southern chalk grasslands until ‘c. 1941’ (Williams P.H., 1982). Now it appears that *B. subterraneus* may have joined this list of losses (Edwards and Williams P.H., 2004). Although once described as common

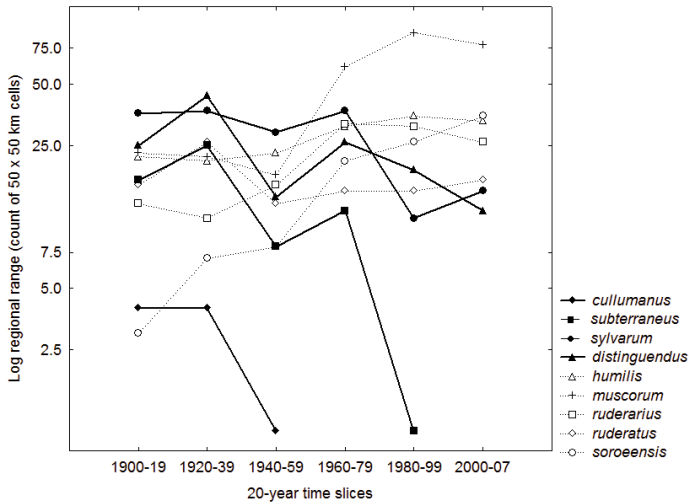
and even locally abundant (Sladen, 1912), it subsequently became less common (Yarrow in Free and Butler, 1959) or scarce (Alford, 1975), but was then seen regularly in only low numbers at Dungeness on the south-east coast (Williams P.H., 1989b), until the last individual was found in a pitfall trap in 1988. Since then, repeated visits have found no more individuals.

Among all British species, strong regional range reductions seemed to be apparent in the maps for the 1960 onwards data collected by the Bumblebee Distribution Maps Scheme (BDMS: Alford, 1980). This pattern becomes less sensitive to heterogeneity in local sampling effort (Williams P.H., 2000) when the data are plotted as maps of regional range using large area units (Williams P.H., 1982, 2005). For example, Figure 1 compares the declines in regional species richness (although it cannot show any effects of range expansions), showing the strongest declines in central England. Of the 16 currently persisting non-parasitic bumblebee species in Britain (excluding *B. magnus* Vogt and *B. cryptarum* (Fabricius), which cannot yet be recognised reliably in both sexes and castes without recourse to molecular methods, Murray et al., 2008), more than half have been suggested to be rare and in decline (Williams P.H., 1986; Goulson, 2003; Edwards and Williams P.H., 2004; Goulson et al., 2005; Benton, 2006). These authors agree on declines for *B. distinguendus* Morawitz, *B. humilis* Illiger, *B. muscorum* (Linnaeus), *B. ruderatus* (Fabricius), *B. subterraneus*, and *B. sylvarum* (Linnaeus). Other species that have been suggested to be rare or declining are *B. jonellus* (Kirby), *B. monticola* Smith, *B. ruderarius* (Müller), and *B. soroeensis* (Fabricius). Although there is evidence that these latter species remain widespread in at least some regions (Williams P.H., 1985; Else, 2000), they will still need to be monitored.

The time course for the declines of some British species can be better resolved from the specimen data compiled by the Bees Wasps and Ants Recording Society (BWARS), because their regional ranges can be plotted for successive 20-year time periods (Fig. 2). Although the sampling effort is not uniform, this



**Figure 1.** Maps of regional species richness for British bumblebees (excluding *Psithyrus*, which have a different, parasitic ecology) among  $50 \times 50$  km grid cells from the BDMS data (Alford, 1980) used to examine range reductions, for: (a) 'former' richness (pre 1960 and 1960 onwards records combined); (b) 'present' richness (1960 onwards records); (c) declines in richness (pre 1960 records only). Equal-frequency grey scale classes (left of each map) representing relative species richness are used to maximize differentiation among regions. Reproduced from Williams P.H. (2005).



**Figure 2.** Trends in regional range size within Britain by 20-year time slices for the more regionally-restricted (Fig. 1) bumblebee species as counts of occupied  $50 \times 50$  km grid cells from the BWARS data (2008).

is less of a problem when measuring regional ranges (Williams P.H., 2005). For *B. humilis*, *B. muscorum*, *B. ruderarius*, *B. ruderatus* and *B. soroensis*, there is little evidence of decline in range extent. Their broad trend towards apparent gradual increase is likely to be due more to increasing numbers of recorders and increasing recorder mobility with cars, rather than to increasing bumblebee range sizes. Similarly, the apparent dip during the 1940–59 period for all plotted species is likely to be due to the second world war and the weakened economy in its immediate aftermath temporarily constraining recording effort. However, in contrast to these background patterns, Figure 2 does appear to show gradual declining trends in regional range over the entire period of a century, not only for the now extirpated *B. subterraneus* and *B. cullumanus*, but also for *B. sylvarum* and *B. distinguendus*. If the 1940–1959 war years are excluded, these declines are most pronounced between the 1960–79 and the 1980–99 time periods. The apparent slight increase in regional range for *B. sylvarum* between the 20 years up to 1999 and the following eight years is also likely to be due to increasing sampling effort, thanks to BWARS and the Bumblebee Work-

ing Group. Similar declines over a period of several decades in some bumblebee species have also been reported more broadly in Europe (e.g. Rasmont and Mersch, 1988; Berezin et al., 1996; Rasmont et al., 2005; Fitzpatrick et al., 2007; Kosior et al., 2007). However, *B. subterraneus*, *B. cullumanus*, *B. sylvarum* and *B. distinguendus* all remain common in some areas either further south in Europe (*B. sylvarum*) or further east beyond Europe.

In North America, the situation appears to be more complicated. Some non-parasitic species may be showing similar gradual declines over decades to those described for some species in Europe (e.g. *B. fervidus* (Fabricius), *B. pensylvanicus* (DeGeer), and *B. vagans* Smith in Ontario: Colla and Packer, 2008; also *B. borealis* Kirby, *B. ternarius* Say, *B. fraternus* (Smith), *B. pensylvanicus* and *B. vagans* in Illinois: Gixti et al., 2009; and *B. fervidus californicus* Smith and *B. pensylvanicus sonorus* Say in California: R. Thorp, in litt.). In contrast, other species of the subgenus *Bombus* (*B. terricola* Kirby [including the western colour forms, *B. terricola occidentalis* Greene], and more especially *B. franklini* (Frison) and *B. affinis* Cresson) have shown a precipitous collapse in numbers of

records in a short period between 1995–2000 across all or much of their ranges (e.g. Thorp, 2005; Thorp and Shepherd, 2005; Colla and Packer, 2008). For example, *B. terricola* and *B. affinis* were two of the commonest bumblebees seen in southern Ontario by one of us in 1983 (PW, unpubl. data.), but only two individuals of *B. terricola* and no *B. affinis* were seen during broad sampling in eastern North America (including Ontario) in every year from 2002–2008 (although other occasional records exist for this period, see below). *B. terricola* is now being reported from more areas again in 2007–2008 (S. Cameron; S. Colla, unpubl. data).

In Asia, declines in some Chinese bumblebee species are beginning to be suspected (Yang, 1999; Xie et al., 2008). For the exceptionally rich fauna of Sichuan, the high and middle elevation mountain faunas (2000–4500 m) appear to remain relatively intact, whereas the low elevation fauna of the Sichuan Basin (500–1999 m) has many old records but few records from the last ten years (Williams P.H. et al., 2009b). In Japan, rapid declines are as in North America particularly affecting the species of the subgenus *Bombus* (Matsumura et al., 2004; Inoue et al., 2008).

### 3. THREATENING FACTORS

What is *driving* bumblebee declines around the world? Conservation efforts are only likely to be successful if the causes of the declines are correctly diagnosed so that appropriate mitigation can be applied. Any amount of forage resource provision is unlikely to solve the problem if populations are being limited by disease, or if ranges are contracting because of climate change. Of course, the factors that threaten a species or population may be multiple, correlated, interacting, and may differ among areas making the precise contributions of particular causes difficult to establish.

Climate change is currently a popular explanation for changes in distribution ranges, especially with a general warming of the climate in western Europe (e.g. Thomas et al., 2006). This could be affecting bumblebees directly, or indirectly via their food plants, or

even via their nest sites (e.g. via small mammals or flooding). Recent range expansions of *B. terrestris* (Linnaeus) and *B. lapidarius* (Linnaeus) in Scotland may be related to climatic warming (Macdonald, 2001). However, climatic warming has been rejected as a general explanation for declines in British bumblebees (Williams P.H., 1986, 1989a), because while some species have retreated northwards (e.g. *B. distinguendus*), others have simultaneously retreated southwards (e.g. *B. sylvarum*). Therefore a simple unidirectional change in Britain's climate could not explain these opposing geographical range shifts. Nonetheless, it remains possible that an increase in the climatic variance could have affected adversely both the warm- and cool-adapted bumblebee species simultaneously, by alternately imposing increasingly extreme cool and extreme warm climates (Williams P.H. et al., 2007). More detailed studies are needed, and future impacts of expected climatic change should be anticipated.

Changing agricultural policy and practices have often been identified as driving the land-use changes that are likely to have contributed substantially to many bumblebee declines, especially in Europe (e.g. Williams P.H., 1986; Rasmont and Mersch, 1988; Goulson, 2003; Edwards and Williams P.H., 2004; Benton, 2006; Goulson et al., 2008), but also in North America (Stephen, 1955; Colla and Packer, 2008; Grixti et al., 2009), and in China (Yang, 1999; Xie et al., 2008). Most bumblebee species in Britain have broadly similar habitat requirements, with a general preference for flower-rich open grassland or heath (Williams P.H., 1988; Carvell, 2002; Goulson et al., 2006). The situation in North America (Bowers, 1985; Hines and Hendrix, 2005; Hatfield and LeBuhn, 2007; PW, pers. obs.) and Asia (Williams P.H., 1991; Williams P.H. et al., 2009b) appears to be broadly similar, but at higher elevations at lower latitudes. Nonetheless, quantitative local surveys in southern Britain found that bumblebee density and species richness are both generally lower in the more intensively farmed areas than in some open semi-natural areas (Williams P.H., 1988). There is no doubt that in Europe and North America agricultural

landscapes have changed substantially in the last 50 years. Among the now widespread and intensified agricultural practices in Europe that have been suggested to harm bumblebees are: (1) increased field sizes to facilitate mechanized cultivation, with the removal of hedgerows and orchards, and drainage or reclamation of marginal grasslands and wetlands, especially in central and eastern Britain (Williams P.H., 1986; Fig. 1); (2) drainage and 'improvement' of grasslands with fertilizers for increased livestock densities, especially in northern and western Britain (Williams P.H., 1986; Goulson et al., 2005; wetter mountain meadows are known to support more bumblebee species in North America: Bowers, 1985; Hatfield and LeBuhn, 2007); (3) the shift from clover leys and hay to silage production for fodder (Rasmont, 1988; Carvell et al., 2006a); (4) loss of rotations of legume crops by replacement with continuous cereals with chemical fertilizers (Edwards, 1999; Kleijn and Raemakers, 2008); (5) application of pesticides (Williams P.H., 1986; Williams I.H. and Carreck, 1994; Kevan et al., 1997) and (6) more frequent or intensive cutting or grazing of grassland (Carvell, 2002; Hatfield and LeBuhn, 2007; Xie et al., 2008).

Bumblebee-forage plants generally now have reduced ranges and frequency in Britain (Carvell et al., 2006a; Kleijn and Raemakers, 2008). Detailed studies of foraging patterns have pointed to the importance of declining bumblebees of large areas of high densities of a set of particularly favourable food-plants (Williams P.H., 1986; 1989b), which are often (but not always) species of legumes (Rasmont and Mersch, 1988; Goulson et al., 2005; Rasmont et al., 2005), and especially (in agricultural landscapes) red clover (Rasmont and Mersch, 1988; Carvell, 2002; Edwards and Williams P.H., 2004; Goulson and Darvill, 2004; Rasmont et al., 2005; Kleijn and Raemakers, 2008). Not only is a plant's corolla depth and nectar reward likely to be important in relation to declines (Williams P.H., 1989b), but so too is the protein content (quality) of the plant's pollen (Génissel et al., 2002; Goulson and Darvill, 2004; Kleijn and Raemakers, 2008).

Intensification of agriculture in Europe has resulted in a coarser-grained landscape, with less complexity of habitat per unit area (Westphal et al., 2006; Osborne et al., 2008b) and with loss of habitats containing many evenly distributed food plants (Williams P.H., 1986). Often food plants have in effect become highly concentrated in large blocks of mass-flowering crops which are likely to concentrate bumblebee foraging effort in space and time (Westphal et al., 2003), as just a short part of colony development. If these crops cover a substantial proportion of the landscape, then they may affect overall abundance and colony growth (Westphal et al., 2006). Bumblebees are very flexible in their utilisation of floral resources and are probably buffered against some level of fragmentation and patchiness by their ability to forage at long range from the colony (Osborne et al., 2008b; Goulson and Osborne, in press), by their communication (Dornhaus and Chittka, 2001), and by their accurate memory of the location of forage sites (Osborne et al., 1999; Osborne and Williams I.H., 2001). Low food-plant diversity per se is not always associated with low bumblebee diversity (Williams P.H., 1989a, b).

It is less easy to find evidence of whether changing land-use is affecting bumblebee populations via nesting or hibernation opportunities. The availability of suitable nest sites and the distribution of bumblebee colonies is far less easy to assess than forage availability and worker activity, so there are correspondingly fewer data (Skovgaard, 1936; Richards, 1978; Harder, 1986; Fussell and Corbet, 1992; Osborne et al., 2008a). Intensive management of crops and grassland (ploughing and cutting) has led to bumblebee nests being concentrated in the less disturbed edge features around fields, such as hedgerows, fence-lines and unmanaged strips of vegetation (Fussell and Corbet, 1992; Svensson et al., 2000; Kells and Goulson, 2003; Osborne et al., 2008a). Keeping grass cut short severely affects the survival of surface nests (Fussell and Corbet, 1992). That bumblebees can be flexible about nesting sites may be evidenced by Dungeness, which in the period 1970–1990 probably had the largest bumblebee fauna in Britain, despite being almost covered with

a coarse shingle substrate that restricts nest-site choices by bumblebees. Very little is known about differences among species in hibernation-site requirements or whether this implies constraints on any species.

Introduction of exotic bumblebees (*B. terrestris*) has been shown to be correlated with declines of native bumblebees (*B. hypocrita* Pérez) since 1995 in Japan (Matsumura et al., 2004; Inoue et al., 2008). In one study no evidence of competition was found (Nagamitsu et al., 2006), but elsewhere it was claimed that *B. terrestris* is out-competing *B. hypocrita* for suitable underground nest sites (Inoue et al., 2008). However, it is also possible that *B. terrestris* is seeking usurpation of established colonies of *B. hypocrita*, so that it is actually the small colonies with workers, brood, and food stores that are the subject of competition, rather than the nest sites (Alford, 1975). Introduction of exotic species is potentially a serious problem. Other species may also compete with bumblebees (Stout and Morales, 2009).

The need for a complete set of 'partial habitats' for different activities, including feeding, nesting, hibernation, and mating, has been emphasized by some people (Westrich, 1989; Benton, 2006). Although different bumblebee species often use very particular parts of habitats for mate-searching (Svensson, 1979), when these habitats are unavailable, species with even very unusual mate-searching behaviours can show remarkable plasticity (Williams P.H., 1991), so that lack of particular 'mating habitats' is unlikely to be a threat to populations.

Although there are many predators of bumblebees (Alford, 1975; Goulson, 2003; Benton, 2006), there is little evidence for substantial increases in their numbers or in increasing selective effects that might have driven declines in particular bumblebee species. Mortality from impact with the growing number of cars might act like predation, but this has been discounted (Rasmont and Mersch, 1988). There is some evidence that among road kills of bumblebees, the declining species can actually be disproportionately under-represented relative to the common species, possibly because they are often 'door-step' foragers and do not cross roads

away from their preferred habitats (Williams P.H., 1985). The effects of collecting by entomologists have also been discounted (Rasmont and Mersch, 1988).

In contrast, there is evidence of pathogen spillover to wild bumblebees around commercial glasshouses where bumblebees are imported for crop pollination (Colla et al., 2006; Otterstatter and Thomson, 2008). It has been suggested that introductions between 1992–1994 (to the field as well as to glasshouses) of bumblebees that were reared in Europe may have been a key driver for the sharp declines since 1995 in a small group of closely related North American bumblebee species (Thorp, 2003; Thorp and Shepherd, 2005; Winter et al., 2006; Colla and Packer, 2008), although so far this is unproven. With regard to the future health of bumblebee populations, we may also need to consider new pests and diseases. Small hive beetle (*Aethina tumida* Murray) and deformed wing virus currently threaten honeybee populations and both have been shown to survive on bumblebees (Spiewok and Neumann, 2006; Genersch et al., 2006). Commercial movement of bumblebees with pathogens potentially poses a severe threat.

Pesticides could affect bumblebee populations either directly, as insecticides that kill bumblebees (Williams P.H., 1986; Thompson, 2001), or indirectly, as herbicides that kill their food plants (Williams P.H., 1986; Williams I.H. and Carreck, 1994). The importance of these chemicals as drivers of species declines remains unclear (Colla and Packer, 2008) because as yet it is difficult to separate the impact of pesticides on bee populations from the effects of other environmental factors in the landscape. It is possible that impacts have been worse in North America than Europe.

For insecticides, there are a few documented local cases of acute poisoning leading to changes in local abundance of bumblebees (e.g. Kevan and Plowright, 1989; Kevan et al., 1997). It is likely that incidents of honeybee poisoning from insecticides will also have affected wild bees (studies suggest pesticide toxicity is similar for bumblebees and honeybees: Thompson and Hunt, 1999; Thompson, 2001). Confirmed incidents of honeybee poisoning have decreased dramatically in the UK

and Germany since the 1990s (Barnett et al., 2007; Brasse, 2003), although in 2008 there was a severe incident where at least 12 000 honeybee colonies were killed by Clothianidin (active ingredient of PonchoPro®), due to mistakes made in the dressing and sowing of maize seed (Rosenkrantz and Wallner, 2008; see also De La Rúa et al., 2009). This is likely to have had a catastrophic effect on wild bees in the area, although they were not monitored. Rasmont et al. (2005) suggest that such acute poisoning is likely to be limited to local events, and rigorous regulatory processes ensure that modern insecticides, if used according to the guidelines, should present little risk to honeybees (Lewis et al., 2007). However, very little is known about the importance of chronic and sub-lethal effects in the field (Thompson, 2001; Thompson and Maus, 2007). Thomson and Hunt (1999) highlight the need to consider bumblebees in pesticide risk assessments more thoroughly, because they forage earlier in the morning and foraging queens are especially vulnerable when crops are sprayed in the spring.

The use of herbicides to kill flowering plants in intensively managed grassland and crops may be an important driver of bumblebee declines on a global scale (Williams P.H., 1986; Rasmont and Mersch, 1988; Kearns and Thomson, 2001; Rasmont et al., 2005; Colla and Packer, 2008). In managed grassland, there is no doubt that floral diversity and abundance are reduced by the use of herbicides (and also by frequent mowing or grazing, fertilizer input, and the sowing of competitive grass species). In arable fields, effective control of broad-leaved weeds with herbicide reduces the densities of foraging bees (Haughton et al., 2003; Hawes et al., 2003).

Urbanisation is likely to have had mixed and complex effects on bumblebee populations (Williams P.H., 1986, Goulson et al., 2002; Chapman et al., 2003; Osborne et al., 2008a). Increased areas of land are covered in concrete, tarmac, or buildings, at the expense of semi-natural vegetation (Gaston et al., 2005). However, many countries have a complex of suburban gardens, parks, and roadside verges, and these contain an enhanced variety of plant species, which produce nectar and pollen

throughout the year, together with a variety of nesting sites (McFrederick and LeBuhn, 2006). In suburban gardens, foragers are often abundant (Williams P.H., 1986, 1989a; Tommasi et al., 2004) and the density of bumblebee nests is higher than in any equivalent area of arable countryside (Osborne et al., 2008a) and colonies can grow faster and larger (Goulson et al., 2002). Even in the centres of cities as large as London (UK) and New York, several species are present. In Europe, *B. hypnorum* (Linnaeus), is a species that is actually positively associated with human habitation (Løken, 1973).

Recently it has become possible to study genetic variation within populations of the different bumblebee species in relation to their abundances and declines (Darvill et al., 2006; Ellis et al., 2006; Goulson et al., 2008). Whether population-genetic effects are an initial driver of bumblebee declines, perhaps compounding the effects of e.g. reduced resources or pathogens, or whether they are merely a consequence of populations becoming small or fragmented for other reasons, is not yet clear (Zayed, 2009). Discerning cause from effect by looking for population genetic changes over the last 50 years is the subject of current research in North America. Studies of the current and historical genetic structure of populations using microsatellites are underway (S. Cameron, in litt.).

In summary, it is likely that to some extent the most important threats to bumblebees differ among different regions of the world. It is also likely that the action of these threats could be asynchronous among regions. For example, the changes in agricultural land use that are already familiar in western Europe may only just be beginning to have a strong effect in the recent EU Accession Countries of eastern Europe (Goulson, 2007).

#### 4. CHARACTERISTICS OF THE MOST SUSCEPTIBLE SPECIES

Different degrees of decline among bumblebee species might imply that some species are more susceptible than others to threatening factors. Many authors have suggested species characteristics that they believe are associated



with greater susceptibility to decline and extinction.

The most susceptible species are likely to be those with the lowest maximum intrinsic rates of increase throughout their geographical ranges, because they will be less able to recover quickly from any reductions in population size. These species might be expected to be those that produce fewer young queens and males per colony, which in turn might be the species with the smallest maximum colony sizes. Reliable comparative data on any of these aspects are difficult to obtain, in part because colony sizes are often very variable within species (Plowright, 1977). Large random samples would be needed, but colonies are often difficult to find, especially when small (Free and Butler, 1959; Osborne et al., 2008a). However, the relationship is not straightforward, because in Britain *B. pascuorum* (Scopoli) shows little susceptibility to decline (see above) but tends to have small colonies (Cumber, 1949). Ultimately we need to know what affects rates of increase.

Variations in bumblebee susceptibility to threat factors such as pesticides have yet to be studied (Thompson, 2001). For threats from pathogens and parasites, there are data for differences among bumblebee species in the parasite load (number of parasite species per average individual of a host species, Durrer and Schmid-Hempel, 1995). Parasite load increases with the range size, abundance, and colony size, but not with body size of the host bumblebee species, so that rare bumblebee species harbour lower loads than common species. However, variations in susceptibility to parasites and pathogens among bumblebee species remain largely unknown, although the microsporidian *Nosema bombi* Fantham and Porter is less infectious but causes higher mortality when spread from *B. terrestris* to *B. lapidarius* and *B. hypnorum* (Schmid-Hempel and Loosli, 1998).

Declines of bumblebees driven by reductions in density of the most suitable food plants have attracted the most research attention, and there have been many suggestions as to what confers greater susceptibility on some bumblebee species than on others. These factors include: (1) intensified compe-

tion with other bumblebee species (Inouye, 1977; Simberloff and Boecklen, 1981; Ranta, 1982; Williams P.H., 1985, 1988); (2) narrower climatic range (Williams P.H., 1985, 1988, 2005; Fitzpatrick et al., 2007; Williams P.H. et al., 2007); (3) closer proximity to climatic range edge (Williams P.H., 1985, 1988, 2005; Fitzpatrick et al., 2007; Williams P.H. et al., 2007); (4) narrower food-plant specialization, either at the level of plant families or plant species (Williams P.H., 1985, 1989b, 2005; Rasmont, 1988; Rasmont and Mersch, 1988; Goulson and Darvill, 2004; Fitzpatrick et al., 2007; Kleijn and Raemakers, 2008); (5) greater tongue length (Goulson et al., 2005, 2006, 2008; Rasmont et al., 2005; Williams P.H., 2005); and (6) a later start to annual activity (Edwards, 2003; Edwards and Williams P.H., 2004; Fitzpatrick et al., 2007).

To assess which characteristics are most generally and strongly shared by the bumblebee species showing the strongest declines from food-plant reductions world-wide, a recent study correlated measurements of declines with measurements of the species' characteristics (above) within each of the almost completely independent bumblebee faunas of three continents – from Europe (Britain: Dungeness), North America (Canada: Guelph), and Asia (China: Hongyuan) (Williams P.H. et al., 2009a). In Britain, unfortunately only Dungeness has a large data set from one homogeneous site in which many species were co-occurring. Also included in the tests were McKinney's (1997) susceptibility factors for vertebrates of large body size and small geographic range size. A meta-analysis showed that decline was significantly positively correlated as a common effect among faunas only with species that have: (1) narrower, more specialized, climatic ranges; (2) closer proximity (for a particular study site) to the species' climatic range edges relative to its climatic range centre; and (3) a later start to the species' annual activity. Long tongues and food-plant specialization were not associated with declines across the three continents in these data. It was suggested that species starting later in the year might be at a particular disadvantage when they have long colony cycles if there were then losses of food plants in late summer.

Removing the two species of the subgenus *Bombus* from the Canadian analysis further strengthened the correlations, which would be expected if these particular species are declining not because of food-plant losses but because of pathogens (see above).

In addition to these factors, recent results show that specialization for pollen sources alone is greater among declining bumblebee species than the others, at least in western Europe (Kleijn and Raemakers, 2008). This specialization applies at the level of plant genera or species, but not at the level of plant families. Earlier studies of food-plant specialization had either included nectar or had not investigated pollen loads directly (above). Most had confounded greater specialization with smaller samples for the rarer bumblebee species (Williams P.H., 2005). Truly narrow food-plant specialization by bumblebees (e.g. Løken, 1961) might be expected only in regions with very short summers and an abundant food-plant species, because otherwise the nutritional demands of long-lived colonies would require multiple food-plant species flowering in succession through the season (Williams P.H., 1989b). Pollen from some plant species may be nutritionally more valuable than others for all bumblebee species (Génissel et al., 2002; Hanley et al., 2008), but for whatever reason, the declining bumblebee species may be especially susceptible to decreases in these food plants (Kleijn and Raemakers, 2008). As with the three factors identified in the meta-analysis across the three continents, differing susceptibilities among bumblebee species to pollen quality may be related to their efficiencies in gathering resources and turning them into sufficient new bees for population persistence as constrained by climate (Williams P.H. et al., 2007). Viewed within this framework, a possibility that remains unexplored is that the declining species might be more susceptible to reductions in their specialist pollen species especially nearer to the edges of their climatic ranges.

To turn the results of the meta-analysis around, the least vulnerable (and potentially the most invasive) bumblebee species are likely to be among the more climatically

widespread of the relatively early emerging species. In mid-temperate regions, these species belong to the subgenera *Bombus* and *Pyrobombus*. These are also the subgenera to which all of the commercially reared species belong (Winter et al., 2006), increasing the risk of escape (e.g. Colla et al., 2006) and the introduction of both invasive bumblebee species and of their pathogens.

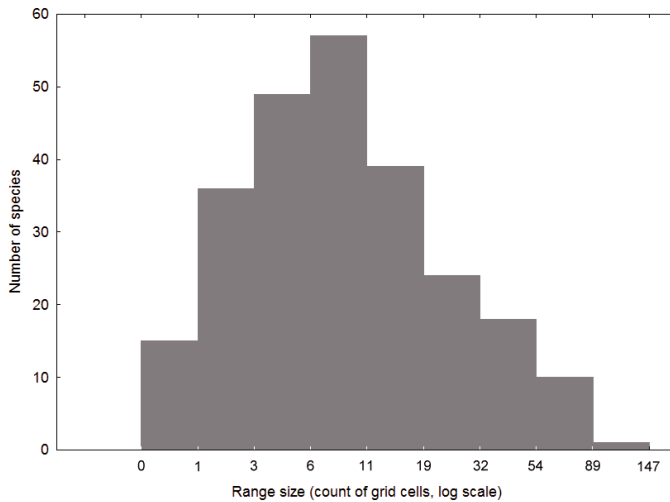
## 5. SPECIES MOST VULNERABLE WORLD-WIDE

Vulnerability is a product of both the intensity of threatening factors (Sect. 3) and the particular species' susceptibility (Sect. 4) to those factors. There have been assessments of the conservation status of bumblebees, but only for some species in Europe and North America (e.g. Sárospataki et al., 2005; Thorp and Shepherd, 2005; Fitzpatrick et al., 2006; Kosior et al., 2007; Grixti et al., 2009). Here we draw attention to some of the species world-wide that might be at greatest risk of global extinction and therefore of most interest for the global Red-Listing process, by considering the likely application of IUCN (2001, 2008) criteria for all of the world's bumblebee species across their entire ranges (Tab. 1). This version compiled from existing data sources cannot be definitive. Inevitably it will need to be substantially revised with quantitative contributions from a broad panel of regional specialists when these become available (Rodrigues et al., 2006). However, an early start to this process is encouraged (IUCN, 2001).

It could be argued that almost all bumblebee species are DATA DEFICIENT, or that most have been NOT EVALUATED thoroughly (in the sense of IUCN, 2001, 2008). However, at the very least, global distribution maps for all species (Williams P.H., 1998) make some preliminary comparisons possible. These maps have been compiled on a coarse-scale equal-area grid, so counts of the numbers of occupied cells (Fig. 3) provide comparable estimates of the global ranges among species. The relatively low number of bumblebee species with a recorded range size of just one cell

**Table I.** Preliminary assessment of the conservation status (IUCN, 2001, 2008) of bumblebee species across their entire ranges in relation to complete extinction (so species that are threatened in some European countries but which have unthreatened Asian populations may be considered of least concern). Many provisional judgments (marked \*) are based on the frequency with which recent specimens have been seen in collections around the world. All species not listed here are considered to be of LEAST CONCERN.

Category	<i>Bombus</i> species	Criterion	Source	Location
EXTINCT	<i>rubriventris</i>	unrecorded since Lepeletier, 1835 (date of specimen unknown)	Williams, 1998	Brazil or Caribbean
	<i>melanopoda</i>	unrecorded since Cockerell, 1910 (date of specimen 1878–1883)	Williams, 1998	S Sumatra
CRITICALLY ENDANGERED	<i>franklini</i>	A2: > 80% population reduction since 1995 (inferred), causes may not be reversible and may not yet have ceased, based on few records of individuals in the last 4 years	IUCN, 2008; Thorp, 2005; Thorp & Shepherd, 2005	S Oregon + N California
	<i>affinis</i>	A2: > 80% population reduction since 1995 (inferred), causes may not be reversible and may not yet have ceased, based on very few records of individuals in the last 4 years	Thorp & Shepherd, 2005; Colla & Packer, 2008	E North America
ENDANGERED	<i>terricola</i> (including the western colour form <i>occidentalis</i> )	A2: > 50% population reduction since 1995 (inferred), causes may not be reversible and may not yet have ceased, based on very few records of individuals in the last 4 years, at least in the south-eastern and south-western quarters of its range	Thorp & Shepherd, 2005; Colla & Packer, 2008	North America
VULNERABLE	<i>confusus</i> , <i>cullumanus</i> , <i>fragrans</i>	A2: substantial decline in area of occurrence and numbers of records in > 50% of the range since 1950	*	Europe
NEAR THREATENED	<i>genalis</i> , <i>irisanensis</i>	A2: no records known since 1983	*	Asia
	<i>gerstaeckeri</i> , <i>inexpectatus</i> , <i>mucidus</i> , <i>pomorum</i> , <i>sulfureus</i> , <i>velox</i>	small area of occurrence (most 1-2 grid cells), few sites since 1980, habitat at least potentially under human threat	*	Europe
	<i>haueri</i> , <i>macgregori</i> , <i>trinominatus</i>	small area of occurrence (most 1-2 grid cells), few records since 1980, habitat at least potentially under human threat	*	Central America
	<i>abnormis</i> , <i>angustus</i> , <i>braccatus</i> , <i>makarjini</i> , <i>mirus</i> , <i>monozonus</i> , <i>simillimus</i>	small area of occurrence (most 1-2 grid cells), few records since 1980, habitat at least likely to be under human threat	*	Asia (incl. China)
	<i>atripes</i> , <i>sporadicus</i>	formerly widespread, no records seen since 1995, habitat at least likely to be under human threat	*	China
LEAST CONCERN	<i>mlokosiewitzii</i> , <i>perezi</i>	small area of occurrence (1-2 grid cells), some records since 1980 or else habitat inaccessible, and habitat not known to be under immediate human threat	*	Europe
	<i>avinoviellus</i> , <i>beaticola</i> , <i>fedschenkoi</i> , <i>formosellus</i> , <i>himalayanus</i> , <i>kotzschii</i> , <i>luteipes</i> , <i>parthenius</i> , <i>pressus</i> , <i>obtusus</i> , <i>oceanicus</i> , <i>richardsiellus</i> , <i>semenovianus</i> , <i>sonani</i> , <i>superbus</i> , <i>tanguticus</i>	small area of occurrence (1-2 grid cells), some records since 1980 or else habitat inaccessible, and habitat not known to be under immediate human threat	*	Asia



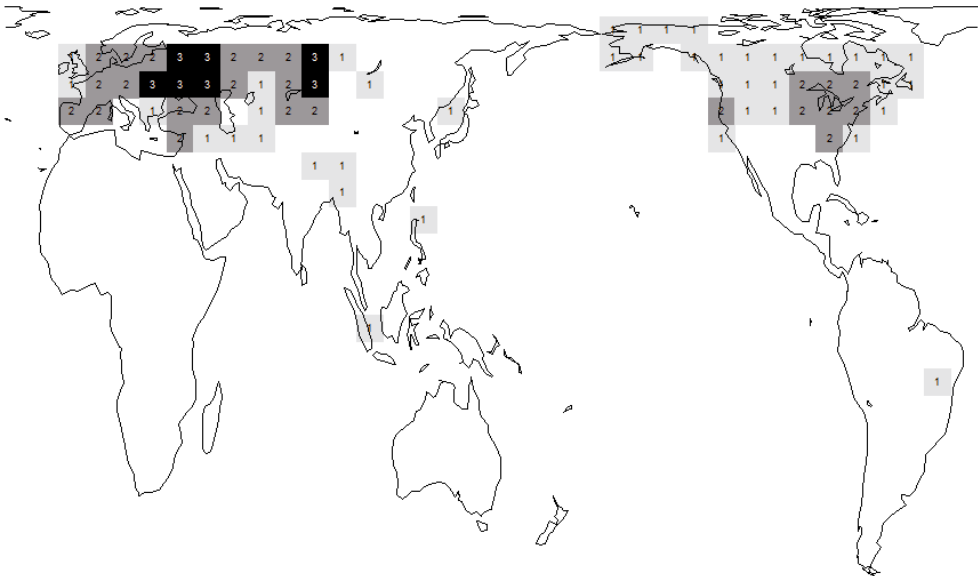
**Figure 3.** Histogram of the frequency of range sizes among bumblebee species worldwide ( $x$  axis log transformed). Range sizes are measured as counts of the numbers of occupied equal-area grid cells (area of each c. 611000 km<sup>2</sup>, see Fig. 4), updated from Williams P.H. (1998).

(Fig. 3) shows that the chosen grid is not too coarse for this purpose. Provisionally we consider the remaining species listed by Williams P.H. (1998) but not included in Table I to be of LEAST CONCERN, but this will need to be revisited when more data are available.

Global extinctions can be difficult to prove, so unsurprisingly there are few known cases for bumblebees. World-wide, *B. rubriventris* Lepeletier shows the strongest evidence for global extinction (Williams P.H., 1998). This distinctive looking species is known from a single specimen, collected from an uncertain locality in the Americas, at an unknown date prior to its description in 1835. Another species known from a single specimen is *B. melanopoda* Cockerell. This was collected in Sumatra, probably between 1872–1883 (Williams P.H., 1998). However, this specimen is entirely black, like most Sumatran bumblebees, making it very difficult to be sure that this species has not been overlooked subsequently. There is always a problem of ensuring that survey effort has been sufficient to detect the presence of a species when it is present at only very low density. This is also problematic for better known species, such as the recent suggestion that the always narrowly distributed *B. franklini* from

the border area between Oregon and California (Thorp et al., 1983) may have gone extinct (Buchmann et al., 2008), even though it was last sighted as recently as 2006 (R. Thorp, in litt.). This species has recently been listed as CRITICALLY ENDANGERED by IUCN (2008). *B. affinis* has also shown a sudden and dramatic decline throughout its range, although occasional individuals have continued to be seen up to 2008 (J. Ascher; S. Cameron; S. Colla, in litt.).

World-wide, the geographical pattern of species of conservation concern (Fig. 4) shows that hotspots of threatened species are concentrated in the north temperate zone. In contrast, the rich bumblebee faunas of the tropical mountains of southern Asia and South America appear as relatively cold spots. What the hotspots in the Old World appear to show is the threat to faunas of the northern grassland steppes, which have already been largely converted for agriculture. In Europe, several species that formerly had broad ranges (*B. confusus*, Schenck, *B. cullumanus*, *B. fragrans* (Pallas)) have become very rare (Berezin et al., 1996; Rasmont et al., 2005; Kosior et al., 2007). To the east in southern Siberia, *B. fragrans* has also become very rare and *B. confusus* has become rare, although



**Figure 4.** Map of the world (excluding Antarctica) plotting counts of the numbers of species from the categories EXTINCT, CRITICALLY ENDANGERED, ENDANGERED, and VULNERABLE from Table I on an equal-area grid (area of each c. 611 000 km<sup>2</sup>). Grid cells are scored as occupied by a species for its total known and expected historical native distribution, not for its current distribution. Cells are defined by intervals of 10 ° longitude and by varying intervals of latitude (bumblebee data updated from Williams P.H., 1998). Cylindrical equal-area projection.

*B. cullumanus* (as the yellow-banded colour form, *B. cullumanus serrisquama* Morawitz) remains common in some localities (A. Byvaltsev, in litt.). Further east in Asia, many species have very restricted mountain distributions, but there is no evidence as yet of strong declines and most have been found when appropriate habitats have been searched (e.g. Williams P.H., 1991; Williams P.H. et al., 2009b). Exceptions appear to be *B. genalis* Friese (eastern Himalaya), and *B. irisanensis* Cockerell (Philippines), for which we can find no post-1983 records. In North China, *B. sporadicus* Nylander (subgenus *Bombus*, a close relative of the most strongly declining North American species) is well represented in collections from before 1991, but has not been re-recorded in the many more recent samples. In North America, we see in Figure 4 the ranges of the species of the subgenus *Bombus*, which may be threatened by pathogens (see above). In Central America, several species (*B. haueri* Handlirsch, *B. macgregori* Labougle and Ayala, *B. trinominatus* Dalla Torre) have very re-

stricted mountain distributions, or their habitats are under threat (R. Ayala, in litt.). In South America, most species are more broadly distributed (even in the Andes) and appear still to be present (if not abundant) when appropriate areas are searched (e.g. despite few recent published records for *B. brevivillus* Franklin from Brazil, the species does not appear to be threatened, G. Melo, in litt.). Some species of the subgenus *Cullumanobombus* in the broad sense remain poorly known both taxonomically and in terms of their conservation status. Many other species world-wide may be NEAR THREATENED (Tab. I). However, the present information on population sizes and threats is generally very imprecise and urgently needs to be improved.

## 6. MITIGATION MANAGEMENT

To date, most practical initiatives to slow or reverse the declines in bumblebees, and to raise public awareness, are concentrated in

western European countries, and most of the published examples are from Britain (Corbet et al., 1994; Carvell, 2002; Carvell et al., 2004, 2007). Substantial information on the ecology and local distribution of uncommon species has been collected in Britain (see above) via BWARS and the Bumblebee Working Group to inform the UK government's Biodiversity Action Plan (e.g. Edwards, 2003), which aims to prioritise threatened species and develop management plans to ensure their survival. However, often the initiatives aimed at increasing bumblebee populations are targeted at species that are not considered rare or endangered. Mitigation strategies have attempted to increase nesting site availability, forage availability, or both, by sensitive habitat management. Some of these strategies have been trialed first to examine effects on populations (Kleijn and Sutherland, 2003; Carvell et al., 2004, 2007), but others have been recommended on the assumption that improving habitat quality and quantity will result in increased populations of bumblebees (Matheson, 1994).

Trials using a variety of nest boxes to increase nesting opportunities in Canada and in Britain have had mixed success (Fye and Medler, 1954; Richards, 1978; Edwards, 2003). Low occupancy rates (although see Richards, 1978) could have resulted because the design of the boxes was not attractive to queens, or because nest sites are not limiting the populations in these particular areas. Trials to test whether increasing forage availability enhances bee populations are difficult. The simplest response variable is the number of bees visiting flowers in the area, or the density of foragers, but this may not reflect the actual nesting density or reproductive success (the most important factor with respect to population size) because of flexible foraging ranges and differences in the numbers of workers per colony. If foraging resources in an area are meagre, then bees are likely fly further to reach flowers and forager density may appear high locally due to a concentration effect. Therefore while this may give good information on whether the forage is useful to the bees, only experiments measuring colony growth and reproductive success over time can

answer whether a particular management strategy is successful, and ecologists are still in the early stages of achieving this (Goulson et al., 2002; Carvell et al., 2008).

Many countries (particularly within the EU and more recently in North America) have land management and stewardship schemes, aimed at improving farmed landscapes for sustainable production, biodiversity and ecosystem service provision (Vaughan et al., 2004; Rural Development Service, 2005; Berenbaum et al., 2007). These schemes provide incentives for farmers and land managers to encourage wildlife on their land by taking up different management options, such as planting new hedgerows, leaving field edges uncultivated, allowing regeneration of wild flowers in margins, or planting wild flower mixtures to encourage flower-visiting insects (Pywell et al., 2006; Carvell et al., 2007). These broad schemes are not specific to the declining species of bumblebees, but some of them are targeted to particular groups of bees. For example, in Britain, the 'nectar and pollen' mixture of wild plants that is recommended for sowing in field margins is targeted to provide flowers with long corollae, aimed at attracting and supporting bumblebee species with long tongues (Carvell, 2006b; Carvell et al., 2007). Flower mixtures certainly attract large numbers of foraging bumblebees (Carvell et al., 2004, 2007; Marshall et al., 2006; Pywell et al., 2006), but the degree to which these schemes actually increase bumblebee populations on a landscape scale in the long term remains to be seen (Williams, 2005; Carvell et al., 2007; Heard et al., 2007). The recent trend towards organic farming may also have had some effect on bumblebee populations (Rundlof et al., 2008).

Land managers of conservation areas and reserves are also starting to take advice on how best to maintain and increase bumblebee populations, particularly where they have populations of species considered to be in decline. In Britain there are active habitat management plans to increase areas of flower-rich grassland at sites where there are populations of bumblebee species that are targets of the Government's Biodiversity Action Plans (e.g. on Salisbury Plain, owned by the Ministry

of Defence; and on the Scottish Isles and at Dungeness, reserves owned by the Royal Society for the Protection of Birds).

Over the last fifteen years there has been a substantial increase in the number of organizations raising public awareness of the 'plight' of bumblebees. Examples are known from the Netherlands (Kwak, 1996), the USA (Arkansas Natural Heritage Commission; Xerces Society), and Britain (Fussell and Corbet, 1992; Osborne et al., 2008a). There are currently at least seven voluntary bumblebee surveys being co-ordinated in Britain. These surveys raise the profile of declining bumblebees and serve as a route to disseminate information to members of the public and to policy makers on how to encourage bumblebee nesting and flower visiting in gardens and in public areas. In 2006, the BumbleBee Conservation Trust (BBCT) in Britain was formed to educate and inform the public, and to raise funds for conserving bumblebees. BBCT actively advises on mitigation strategies to protect rare bumblebees as well as to promote populations of the more common species. BBCT is also considering an initiative to re-introduce *B. subterraneus* from New Zealand (where it was introduced from Britain), a species now considered extinct in Britain. Gardening to promote wildlife is a current fashion in Britain, and garden companies have used this opportunity to promote the sale of wild-flower mixtures that provide good nectar and pollen rewards, as well as wooden nest boxes to encourage bumblebees into the garden. However, the success of these boxes compared with existing garden features (compost heaps, bird boxes, etc.) remains to be seen (Gaston et al., 2005). There is also growing evidence to suggest that encouraging sensitive management of public parks and spaces will promote bumblebee diversity and abundance (Tommasi et al., 2004; McFrederick and LeBuhn, 2006).

## 7. CONCLUSIONS AND FUTURE NEEDS

Undoubtedly, more than one factor threatens bumblebees around the world. Species of

the subgenus *Subterraneobombus* may illustrate many of the characteristics associated with susceptibility in Europe, where all three European species are showing declines. They appear to have narrow climatic ranges, small colonies that start relatively late in the year, and their long tongues give them a tendency to visit deep flowers (for both nectar and pollen) like red clover that have become much scarcer with changes in land use in the last 50 years. Species of the subgenus *Bombus* show many of the opposite characteristics, but ironically some of them have also suffered even more in North America and in Asia, although probably from pathogens and from competition from one another. More research is needed to: (1) increase knowledge of the status and trends among bumblebee populations world-wide, although it would be appropriate to focus effort on Eastern Europe and Russia, which have the largest concentration of species categorized as ENDANGERED or worse (Fig. 4); (2) measure the effects of environmental factors on colony sizes and reproductive success (as opposed to just focusing on forager density and species richness) across species' geographical ranges in order to compare effects at the edges and centres of (climatic) ranges within and among species; (3) devote more effort to factors affecting mortality such as insecticide exposure, pathogens, predators and parasites, for which we have the least information on a global scale; (4) develop more effective management strategies for threat mitigation; and (5) find mechanisms by which these can be implemented in different regions of the world.

## ACKNOWLEDGEMENTS

Thanks for stimulating discussion to J. Ascher, R. Ayala, M. Brown, A. Byvaltsev, S. Cameron, S. Colla, L. Day, M. Edwards, P. Kennedy, D. Goulson, L. Manne, G. Melo, R. Paxton, P. Rasmont, F. Silveira, P. Schmid-Hempel, Y. Tang, R. Thorp, Z. Xie, J. Yao; to A. Brewer for access to data at the National Biodiversity Network and to the many BDMS and BWARS recorders, especially to M. Edwards, G. Else, M. Macdonald, S. Roberts; and to two anonymous referees for improvements to the manuscript.

**Vulnérabilité des bourdons et conservation au niveau mondial.**

***Bombus* / déclin population / menace / vulnérabilité / protection / utilisation des terres / pesticide / urbanisation / ressource alimentaire**

**Zusammenfassung – Weltweite Anfälligkeit und Erhaltung der Hummeln.** Wir geben eine weltweite Übersicht für Hummeln über den Rückgang der Vorkommenshäufigkeit oder der Verbreitungsgebiete bestimmter Arten, über den Zeitverlauf dieser Änderungen, über Gefährdungsfaktoren und Charakteristika der besonders gefährdungsanfälligen Arten und über die weltweit daher am meisten gefährdeten Arten, sowie über Maßnahmen zur Abschwächung der Gefährdung. Hiernach finden wir Belege, dass einige Hummelarten in Europa (Abb. 1, 2), Nordamerika und Asien auf dem Rückgang sind. Es wird allgemein angenommen, dass die Verminderung des Futterpflanzenangebots durch die Änderungen in der Landnutzung in vielen Teilen der Welt einen negativen Einfluss ausübt, allerdings könnten andere Faktoren wie Pathogene bei einigen Arten in einigen Regionen (insbesondere bei *Bombus* s. str. in Nordamerika) einen stärkeren und kurzfristiger wirksamen Effekt haben. Die bisherigen Anhaltspunkte weisen darauf hin, dass die weltweit anfälligsten Arten tendenziell in spezialisierten klimatischen Bereichen und nahe an den Grenzen dieser Bereiche vorkommen und spät beginnende aber lange Kolonieentwicklungszyklen haben. Zur Rolle von Pollenspezialisierung, Nistplätzen, Überwinterungsplätzen und Pestiziden werden noch mehr Angaben benötigt. Aus der derzeit verfügbaren begrenzten Information aus neueren Sammlungen um die Welt erstellen wir eine vorläufige Einschätzung, welche Arten wahrscheinlich am stärksten gefährdet sind (Tab. 1) und wo diese vorkommen (Abb. 4). Es ist noch zu früh, um den Erfolg von Maßnahmen zur Verbesserung des Futterangebots in landwirtschaftlichen oder Erhaltungsgebieten zu beurteilen. Allerdings waren Maßnahmen zur Verbesserung der öffentlichen Wahrnehmung sehr erfolgreich.

**Hummeln / *Bombus* / Gefährdung / Anfälligkeit / Erhaltung**

**REFERENCES**

- Alford D.V. (1975) Bumblebees, Davis-Poynter, London.
- Alford D.V. (1980) Atlas of the bumblebees of the British Isles, Institute of Terrestrial Ecology, Cambridge.
- Anonymous (1994) Biodiversity: The UK Action Plan, HMSO, London.
- Barnett E.A., Charlton A.J., Fletcher M.R. (2007) Incidents of bee poisoning with pesticides in the United Kingdom, 1994–2003, *Pest Manage. Sci.* 63, 1051–1057.
- Benton T. (2000) The bumblebees of Essex, Lopinga Books, Wimbish.
- Benton T. (2006) Bumblebees, the natural history & identification of the species found in Britain, Collins, London.
- Berenbaum M., Bernhardt P., Buchmann S., Calderone N., Goldstein P., Inouye D.W., Kevan P., Kremen C., Medellin R.A., Ricketts T., Robinson G.E., Snow A.A., Swinton S.M., Thein L.B., Thompson F.C. (2007) Status of Pollinators in North America, The National Academies Press, Washington, DC.
- Berezin M.V., Beiko V.B., Berezina N.V. (1996) Analysis of structural changes in the bumblebee (*Bombus*, Apidae) population of Moscow Oblast over the last forty years, *Entomol. Rev.* 76, 115–123.
- Bowers M.A. (1985) Bumble bee colonization, extinction, and reproduction in subalpine meadows in northeastern Utah, *Ecology* 66, 914–927.
- Brasse D. (2003) Poisoning incidents involving honeybees in Germany (1999–2002) and new problems for beekeeping, *Bull. Insectol.* 56, 199.
- Buchmann S., Kevan P.G., Adams L., Dalsimer A. (2008) Birds, bees, and bases: how military natural resource managers can help local pollinators and why they should care, *Natural Selections* 4, 5–6.
- Carvell C. (2002) Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes, *Biol. Conserv.* 103, 33–49.
- Carvell C., Meek W.R., Pywell R.F., Nowakowski M. (2004) The response of foraging bumblebees to successional change in newly created arable field margins, *Biol. Conserv.* 118, 327–339.
- Carvell C., Roy D.B., Smart S.M., Pywell R.F., Preston C.D., Goulson D. (2006a) Declines in forage availability for bumblebees at a national scale, *Biol. Conserv.* 132, 481–489.
- Carvell C., Meek W.R., Pywell R.F., Nowakowski M. (2006b) Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis, *Apidologie* 37, 326–340.
- Carvell C., Meek W.R., Pywell R.F., Goulson D., Nowakowski M. (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins, *J. Appl. Ecol.* 44, 29–40.



- Carvell C., Rothery P., Pywell R.F., Heard M.S. (2008) Effects of resource availability and social parasite invasion on field colonies of *Bombus terrestris*, *Ecol. Entomol.* 33, 321–327.
- Chapman R.E., Wang J., Bourke A.F.G. (2003) Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators, *Mol. Ecol.* 12, 2801–2808.
- Colla S.R., Packer L. (2008) Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson, *Biodiv. Conserv.* 17, 1379–1391.
- Colla S.R., Otterstatter M.C., Gegear R.J., Thomson J.D. (2006) Plight of the bumble bee: pathogen spillover from commercial to wild populations, *Biol. Conserv.* 129, 461–467.
- Corbet S.A., Saville N.M., Osborne J.L. (1994) Farmland as a habitat for bumble bees, in: Matheson A. (Ed.), *Forage for bees in an agricultural landscape*, IBRA, Cardiff, pp. 35–46.
- Cumber R.A. (1949) The biology of humble-bees, with special reference to the production of the worker caste, *Trans. R. Entomol. Soc. Lond.* 100, 1–45.
- Darvill B., Ellis J.S., Lye G.C., Goulson D. (2006) Population structure and inbreeding in a rare and declining bumblebee, *Bombus muscorum* (Hymenoptera: Apidae), *Mol. Ecol.* 15, 601–611.
- De La Rúa P., Jaffé R., Dall'Olio R., Muñoz I., Serrano J. (2009) Biodiversity, conservation and current threats to European honeybees, *Apidologie* 40, 263–284.
- Dias B.S.F., Raw A., Imperatriz-Fonseca V.L. (1999) International Pollinators Initiative: the São Paulo declaration on pollinators. Report on the recommendations of the workshop on the conservation and sustainable use of pollinators in agriculture with emphasis on bees, p. 79, Brazilian Ministry of the Environment, Brasília.
- Dornhaus A., Chittka L. (2001) Food alert in bumblebees (*Bombus terrestris*): possible mechanisms and evolutionary implications, *Behav. Ecol. Sociobiol.* 50, 570–576.
- Durrer S., Schmid-Hempel P. (1995) Parasites and the regional distribution of bumblebee species, *Ecography* 18, 114–122.
- Edwards M. (1999) U.K. B.A.P. Bumblebee Working Group report, 1999, p. 81, Privately published, Midhurst.
- Edwards M. (2003) U.K. B.A.P. Bumblebee Working Group Report, 2002, p. 45, [online] <http://hymettus.org.uk/reports.htm> (accessed 30 January 2009).
- Edwards M., Williams P.H. (2004) Where have all the bumblebees gone, and could they ever return? *Brit. Wildl. June*, 305–312.
- Ellis J.S., Knight M.E., Darvill B., Goulson D. (2006) Extremely low effective population sizes, genetic structuring and reduced genetic diversity in a threatened bumblebee species, *Bombus sylvarum* (Hymenoptera: Apidae), *Mol. Ecol.* 15, 4375–4386.
- Else G.R. (2000) Observations on *Bombus soroensis* (F.) *B. humilis* Illiger and *B. muscorum* (L.) on Salisbury Plain, Wiltshire, in 1998–2000, BWARS Newsletter Autumn 2000, 5–6.
- Fitzpatrick Ú., Murray T.E., Byrne A., Paxton R.J., Brown M.J.F. (2006) Regional Red Data list of Irish bees, [online] <http://www.npws.ie/en/media/Media,4860,en.pdf> (accessed 30 January 2009).
- Fitzpatrick Ú., Murray T.E., Paxton R.J., Breen J., Cotton D., Santorum V., Brown M.J.F. (2007) Rarity and decline in bumblebees – a test of causes and correlates in the Irish fauna, *Biol. Conserv.* 136, 185–194.
- Free J.B., Butler C.G. (1959) *Bumblebees*, New Naturalist Series, Collins, London.
- Fussell M., Corbet S.A. (1992) The nesting places of some British bumble bees, *J. Apicult. Res.* 31, 32–41.
- Fye R.E., Medler J.T. (1954) Field domiciles for bumblebees, *J. Econ. Entomol.* 47, 672–676.
- Gaston K.J., Warren P.H., Thompson K., Smith R.M. (2005) Urban domestic gardens (IV): The extent of the resource and its associated features, *Biodiv. Conserv.* 14, 3327–3349.
- Genersch E., Yue C., Fries I., de Miranda J.R. (2006) Detection of deformed wing virus, a honey bee viral pathogen, in bumble bees (*Bombus terrestris* and *Bombus pascuorum*) with wing deformities, *J. Invertebr. Pathol.* 91, 61–63.
- Génissel A., Aupinel P., Bressac C., Tasei J.-N., Chevrier C. (2002) Influence of pollen origin on performance of *Bombus terrestris* micro-colonies, *Entomol. Exp. Appl.* 104, 329–336.
- Goulson D. (2003) *Bumblebees, their behaviour and ecology*, Oxford University Press, Oxford.
- Goulson D. (2007) Places to see bumblebees: Poland, *Buzzword* 2007, 5–7.
- Goulson D., Osborne J.L. (in press) Foraging range and the spatial distribution of worker bumblebees, in: Jarau S., Hrncir M. (Eds.), *Food exploitation by social insects: an ecological, behavioral and theoretical approach*, CRC Press.
- 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., Hughes W.O.H., Derwent L.C., Stout J.C. (2002) Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats, *Oecologia* 130, 267–273.

- Goulson D., Hanley M.E., Darvill B., Ellis J.S., Knight M.E. (2005) Causes of rarity in bumblebees, *Biol. Conserv.* 122, 1–8.
- Goulson D., Hanley M.E., Darvill B., Ellis J.S. (2006) Biotope associations and the decline of bumblebees (*Bombus* spp.), *J. Insect Conserv.* 10, 95–103.
- Goulson D., Lye G.C., Darvill B. (2008) Decline and conservation of bumble bees, *Annu. Rev. Ent.* 53, 11.1–11.18.
- Grixti J.C., Wong L.T., Cameron S.A., Favret C. (2009) Decline of bumble bees (*Bombus*) in the North American Midwest, *Biol. Conserv.* 142, 75–84.
- Hanley M.E., Franco M., Pichon S., Darvill B., Goulson D. (2008) Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants, *Funct. Ecol.* 22, 592–598.
- Harder L.D. (1986) Influences on the density and dispersion of bumble bee nests (Hymenoptera: Apidae), *Holarct. Ecol.* 9, 99–103.
- Hatfield R.G., LeBuhn G. (2007) Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera, Apidae), in montane meadows, *Biol. Conserv.* 139, 150–158.
- Haughton A.J., Champion G., Hawes C., Heard M., Brooks D.R., Bohan D.A., Clark S.A., Dewar A., Firbank L.G., Osborne J.L., Perry J.N., Rothery P., Roy D.B., Scott R., Woiwod I.P., Birchall C., Skellern M.P., Walker J., Baker P., Browne E., Dewar A.J.G., Garner B., Haylock L., Horne S., Mason N., Sands R., Walker M.J. (2003) Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. II. Within-field epigeal and aerial arthropods, *Philos. Trans. R. Soc. B-Biol.* 358, 1863–1877.
- Hawes C., Haughton A., Osborne J.L., Roy D., Clark S., Perry J., Rothery P., Bohan D., Brooks D., Champion G., Dewar A., Heard M., Woiwod I., Daniels R., Young M., Parish A., Scott R., Firbank L., Squire G. (2003) Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops, *Philos. Trans. R. Soc. B-Biol.* 358, 1899–1913.
- Heard M.S., Carvell C., Carreck N.L., Rothery P., Osborne J.L., Bourke A.F.G. (2007) Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes, *Biol. Lett.* 3, 638–641.
- Hines H.M., Hendrix S.D. (2005) Bumble bee (Hymenoptera: Apidae) diversity and abundance in tallgrass prairie patches: effects of local and landscape floral resources, *Environ. Entomol.* 34, 1477–1484.
- Inouye D.W. (1977) Species structure of bumblebee communities in North America and Europe, in: Mattson W.J. (Ed.), *The role of arthropods in forest ecosystems*, Springer Verlag, New York, pp. 35–40.
- Inoue M.N., Yokoyama J., Washitani I. (2008) Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae), *J. Insect Conserv.* 12, 135–146.
- IUCN (2001) IUCN Red List categories and criteria: version 3.1, IUCN Species Survival Commission, Gland and Cambridge.
- IUCN (2008) Guidelines for using the IUCN Red List categories and criteria. Version 7.0, Standards and Petitions Working Group of the IUCN SSC Biodiversity Assessments Sub-Committee.
- IUCN (2008) IUCN red list of threatened species: *Bombus franklini*, IUCN [online] <http://www.iucnredlist.org/details/135295> (accessed 30 January 2009).
- Kearns C.A., Thomson J.D. (2001) *The natural history of bumblebees, a sourcebook for investigations*, University Press of Colorado, Boulder.
- Kells A.R., Goulson D. (2003) Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK, *Biol. Conserv.* 109, 165–174.
- Kevan P.G., Plowright R.C. (1989) Fenitrothion and insect pollinators, in: Ernst W.R., Pearce P.A., Pollock T.L. (Eds.), *Environmental effects of fenitrothion use in forestry*, Environment Canada, Conservation and Protection, Atlantic Region, p. 166.
- Kevan P.G., Greco C.F., Belausoff S. (1997) Log-normality of biodiversity and abundance in diagnosis and measuring of ecosystemic health: pesticide stress on pollinators on blueberry heaths, *J. Appl. Ecol.* 34, 1122–1136.
- Kleijn D., Raemakers I. (2008) A retrospective analysis of pollen host plant use by stable and declining bumble bee species, *Ecology* 89, 1811–1823.
- Kleijn D., Sutherland W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* 40, 947–969.
- Kosior A., Celary W., Olejniczak P., Fijał J., Król W., Solarz W., Plonka P. (2007) The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of western and central Europe, *Oryx* 41, 79–88.
- Kwak M.M. (1996) Bumble bees at home and at school, in: Matheson, A. (Ed.), *Bumble bees for pleasure and profit*, International Bee Research Association, Cardiff, UK, pp. 12–23.
- Lewis G., Thompson H., Smaghe G. (2007) In focus: Pesticides and honeybees – the work of the ICP-BR bee protection group editorial, *Pest Manage. Sci.* 63, 1047–1050.
- Løken A. (1961) *Bombus consobrinus* Dahlb., an oligolectic bumble bee (Hymenoptera, Apidae), *Trans. XI Int. Congr. Ent. Vienna* 1, 598–603.

- Løken A. (1973) Studies on Scandinavian bumble bees (Hymenoptera, Apidae), Norsk Entomol. Tidsskr. 20, 1–218.
- 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, Entomol. Mon. Mag. 137, 1–13.
- Marshall E.J.P., West T.M., Kleijn D. (2006) Impacts of an agri-environment field margin prescription on the flora and fauna of arable farmland in different landscapes, Agr. Ecosyst. Environ. 113, 36–44.
- Matheson A., Ed. (1994) Forage for bees in an agricultural landscape, IBRA, Cardiff.
- Matsumura C., Yokoyama J., Washitani I. (2004) Invasion status and potential impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) naturalized in southern Hokkaido, Japan, Global Environ. Res. 8, 51–66.
- McFrederick Q.S., LeBuhn G. (2006) Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? Biol. Conserv. 129, 372–382.
- McKinney M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views, Annu. Rev. Ecol. Syst. 28, 495–516.
- Milne A.A. (1926) Winnie-the-Pooh, Methuen, London.
- Murray T.E., Fitzpatrick U., Brown M.J.F., Paxton R.J. (2008) Cryptic species diversity in a widespread bumble bee complex revealed using mitochondrial DNA RFLPs, Conserv. Genet. 9, 653–666.
- Nagamitsu T., Kenta T., Inari N., Kato E., Hiura T. (2006) Abundance, body size, and morphology of bumblebees in an area where an exotic species, *Bombus terrestris*, has colonized in Japan, Ecol. Res. 22, 331–341.
- Osborne J.L., Williams I.H. (2001) Site constancy of bumble bees in an experimentally patchy habitat, Agr. Ecosyst. Environ. 83, 129–141.
- Osborne J.L., Clark S.J., Morris R.J., Williams I.H., Riley J.R., Smith A.D., Reynolds D.R., Edwards A.S. (1999) A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar, J. Appl. Ecol. 36, 519–533.
- Osborne J.L., Martin A.P., Shortall C.R., Todd A.D., Goulson D., Knight M.E., Hale R.J., Sanderson R.A. (2008a) Quantifying and comparing bumblebee nest densities in gardens and countryside habitats, J. Appl. Ecol. 45, 784–792.
- Osborne J.L., Martin A.P., Carreck N.L., Swain A.L., Knight M.E., Goulson D., Hale R.J., Sanderson R.A. (2008b) Bumblebee flight distances in relation to the forage landscape, J. Anim. Ecol. 77, 406–415.
- Otterstatter M.C., Thomson J.D. (2008) Does pathogen spillover from commercially reared bumble bees threaten wild pollinators? PLoS ONE 3, e2771.
- Plowright R.C. (1977) Nest architecture and the biosystematics of bumble bees, Proc. 8th Int. Congr. IUSSI, 183–185.
- Pywell R.F., Warman E.A., Hulmes L., Hulmes S., Nuttall P., Sparks T.H., Critchley C.N.R., Sherwood A. (2006) Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes, Biol. Conserv. 129, 192–206.
- Ranta E. (1982) Species structure of North European bumblebee communities, Oikos 38, 202–209.
- Rasmont P. (1988) Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae), pages 309+lxii, Faculté des Sciences agronomiques de l'État, Gembloux.
- Rasmont P., Mersch P. (1988) Première estimation de la dérive faunique chez les bourdons de la Belgique (Hymenoptera, Apidae), Ann. Soc. R. Zool. Belg. 118, 141–147.
- Rasmont P., Pauly A., Terzo M., Patiny S., Michez D., Iserbyt S., Barbier Y., Haubruge, E. (2005) The survey of wild bees (Hymenoptera, Apoidea) in Belgium and France, p. 18, Food and Agriculture Organisation, Rome.
- Richards K.W. (1978) Nest site selection by bumble bees (Hymenoptera: Apidae) in southern Alberta, Can. Entomol. 110, 301–318.
- Rodrigues A.S.L., Pilgrim J.D., Lamoreux J.F., Hoffman M., Brooks T.M. (2006) The value of the IUCN Red List for conservation, Trends Ecol. Evol. 21, 71–76.
- Rosenkranz P., Wallner K. (2008) The chronology of honey bee losses in the Rhine Valley during spring 2008: an example of a worst case scenario, pages 94–95 in Teal J., Osborne J.L., Paxton R.J. (Eds.), Eurbee3; 3rd European Conference of Apidology, Queen's University, Belfast.
- Rundlof M., Nilsson H., Smith H.G. (2008) Interacting effects of farming practice and landscape context on bumblebees, Biol. Conserv. 141, 417–426.
- Rural Development Service (2005) Environmental Stewardship: Look after your land and be rewarded, p. 12, Defra, UK.
- Sárospataki M., Novák J., Molnár V. (2005) Assessing the threatened status of bumble bee species (Hymenoptera: Apidae) in Hungary, Central Europe, Biodiv. Conserv. 14, 2437–2446.
- Schmid-Hempel P., Loosli R. (1998) A contribution to the knowledge of *Nosema* infections in bumble bees, *Bombus* spp., Apidologie 29, 525–535.
- Simberloff D., Boecklen W. (1981) Santa Rosalia reconsidered: size ratios and competition, Evolution 35, 1206–1228.
- Skovgaard O.S. (1936) Rødkløverens bestøvning, humlebieer og humleboer. [Pollination of red

- clover, bumblebees and bumblebee nests], Kgl. Danske Videnskab. Selskab Nat.- og Mat., Afd. 9. 6, 1–140.
- Sladen F.W.L. (1912) The humble-bee, its life history and how to domesticate it, with descriptions of all the British species of *Bombus* and *Psithyrus*, MacMillan, London.
- Spiewok S., Neumann P. (2006) Infestation of commercial bumblebee (*Bombus impatiens*) field colonies by small hive beetles (*Aethina tumida*), Ecol. Entomol. 31, 623–628.
- Stephen W.P. (1955) Alfalfa pollination in Manitoba, J. Econ. Entomol. 48, 543–549.
- Stout J.C., Morales C.L. (2009) Ecological impacts of invasive alien species on bees, Apidologie 40, 388–409.
- Svensson B.G. (1979) Patrolling behaviour of bumble bee males (Hymenoptera, Apidae) in a sub-alpine/alpine area, Swedish Lapland, Zoon 7, 67–94.
- Svensson B., Lagerlof J., Svensson B.G. (2000) Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape, Agr. Ecosyst. Environ. 77, 247–255.
- Thomas C.D., Franco A.M.A., Hill J.K. (2006) Range retractions and extinction in the face of climate warming, Trends Ecol. Evol. 21, 415–416.
- Thompson H.M. (2001) Assessing the exposure and toxicity of pesticides to bumblebees (*Bombus* sp.), Apidologie 32, 305–321.
- Thompson H.M., Hunt L.V. (1999) Extrapolating from honeybees to bumblebees in pesticide risk assessment, Ecotoxicology 8, 147–166.
- Thompson H.M., Maus C. (2007) The relevance of sublethal effects in honey bee testing for pesticide risk assessment, Pest Manage. Sci. 63, 1058–1061.
- Thorp R.W. (2003) Bumble bees (Hymenoptera: Apidae): commercial use and environmental concerns, in: Strickler K., Cane J.H. (Eds.), For non-native crops, whence pollinators of the future? Entomological Society of America, Lanham MD, pp. 21–40.
- Thorp R.W. (2005) Profile: *Bombus franklini* Frison, 1921, Franklin's bumble bee (Hymenoptera: Apidae: Apinae: Bombini). in: Shepherd M.D., Vaughan D.M., Black S.H. (Eds.), Red list of pollinator insects of North America, The Xerces Society for Invertebrate Conservation, Portland (Oregon), p. 8.
- Thorp R.W., Shepherd M.D. (2005) Profile: Subgenus *Bombus* Latreille, 1802 (Apidae: Apinae: Bombini), in: Shepherd M.D., Vaughan D.M., Black S.H. (Eds.), Red list of pollinator insects of North America, The Xerces Society for Invertebrate Conservation, Portland (Oregon), p. 5.
- Thorp R.W., Horning D.S., Dunning L.L. (1983) Bumble bees and cuckoo bumble bees of California (Hymenoptera: Apidae), Bull. Calif. Insect Surv. 23, viii+79.
- Tommasi D., Miro A., Higo H.A., Winston M.L. (2004) Bee diversity and abundance in an urban setting, Can. Entomol. 136, 851–869.
- Vaughan M., Shepard M., Kremen C., Black S. (2004) Farming for bees: Guidelines for providing native bee habitat on farms, The Xerces Society for Invertebrate Conservation, Portland, USA.
- Westphal C., Steffan-Dewenter I., Tscharntke T. (2003) Mass flowering crops enhance pollinator densities at a landscape scale, Ecol. Lett. 6, 961–965.
- Westphal C., Steffan-Dewenter I., Tscharntke T. (2006) Bumblebees experience landscapes at different spatial scales: possible implications for coexistence, Oecologia 149, 289–300.
- Westrich P. (1989) Die Wildbienen Baden-Wuerttembergs, Eugen Ulmer, Stuttgart.
- Williams I.H., Carreck N.L. (1994) Land use changes and honey bee forage plants, in: Matheson A. (Ed.), Forage for bees in an agricultural landscape, IBRA, Cardiff, pp. 7–20.
- Williams P.H. (1982) The distribution and decline of British bumble bees (*Bombus* Latr.), J. Apic. Res. 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. (1986) Environmental change and the distributions of British bumble bees (*Bombus* Latr.), Bee World 67, 50–61.
- Williams P.H. (1988) Habitat use by bumble bees (*Bombus* spp.), Ecol. Entomol. 13, 223–237.
- Williams P.H. (1989a) Bumble bees – and their decline in Britain, Central Association of Bee-Keeper, Ilford.
- Williams P.H. (1989b) Why are there so many species of bumble bees at Dungeness? Bot. J. Linn. Soc. 101, 31–44.
- Williams P.H. (1991) The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini), Bull. Br. Mus. Nat. Hist. (Entomol.) 60, 1–204.
- Williams P.H. (1998) An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini), Bull. Nat. Hist. Mus. Lond. (Entomol.) 67, 79–152 [updated at <<http://www.nhm.ac.uk/research-curation/projects/bombus/>>] (accessed 30 January 2009).
- Williams P.H. (2000) Some properties of rarity scores used in site quality assessment, Brit. J. Entomol. Nat. Hist. 13, 73–86.

- Williams P.H. (2005) Does specialization explain rarity and decline among British bumblebees? A response to Goulson et al., *Biol. Conserv.* 122, 33–43.
- Williams P.H., Araújo M.B., Rasmont P. (2007) Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? *Biol. Conserv.* 138, 493–505.
- Williams P.H., Colla S.R., Xie Z. (2009a) Bumblebee vulnerability: common correlates of winners and losers across three continents, *Conserv. Biol.* 23, in press.
- Williams P.H., Tang Y., Yao J., Cameron S. (2009b) The bumblebees of Sichuan (Hymenoptera: Apidae, Bombini), *Syst. Biodiv.* 7, 101–190.
- Winter K., Adams L., Thorp R.W., Inouye D.W., Day L., Ascher J., Buchmann S. (2006) Importation of non-native bumble bees into North America: potential consequences of using *Bombus terrestris* and other non-native bumble bees for greenhouse crop pollination in Canada, Mexico, and the United States, p. 33, A White Paper of the North American Pollinator Protection Campaign (NAPCC), San Francisco.
- Xie Z., Williams P.H., Tang Y. (2008) The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan, *J. Insect Conserv.* 12, 695–703.
- Yang D.-R. (1999) The status of species diversity and conservation strategy of bumble bees, a pollination insect in Lancang River Basin of Yunnan, China, *Chinese Biodiv.* 7, 170–174.
- Zayed A. (2009) Bee genetics and conservation, *Apidologie* 40, 237–262.