Decline and Conservation of Bumble Bees

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Hymenoptera, *Bombus*, rarity, population structure, habitat loss

Abstract

Declines in bumble bee species in the past 60 years are well documented in Europe, where they are driven primarily by habitat loss and declines in floral abundance and diversity resulting from agricultural intensification. Impacts of habitat degradation and fragmentation are likely to be compounded by the social nature of bumble bees and their largely monogamous breeding system, which renders their effective population size low. Hence, populations are susceptible to stochastic extinction events and inbreeding. In North America, catastrophic declines of some bumble bee species since the 1990s are probably attributable to the accidental introduction of a nonnative parasite from Europe, a result of global trade in domesticated bumble bee colonies used for pollination of greenhouse crops. Given the importance of bumble bees as pollinators of crops and wildflowers, steps must be taken to prevent further declines. Suggested measures include tight regulation of commercial bumble bee use and targeted use of environmentally comparable schemes to enhance floristic diversity in agricultural landscapes.

INTRODUCTION

The world bumble bee (*Bombus*) fauna consists of approximately 250 known species, largely confined to temperate, alpine, and arctic zones of the Northern Hemisphere (101). There is mounting evidence that many bumble bee species have declined in recent decades, particularly in developed regions such as western Europe and North America (34, 55, 89). The most comprehensive records available are from the United Kingdom, where between 1970 and 1974 data were collected from most of the British Isles at a resolution of 10 × 10 km squares (1). These records have been compared with a considerable body of pre-1960 records (100). The comparison revealed a dramatic decline in the distributions of many species. More recent data suggest that this decline has continued, with 3 of the 25 U.K. species having gone extinct and an additional 8 species having undergone major range declines (34). The most severely affected species tend to be those with long tongues associated with deep perennial flowers (40). Similar patterns are evident in Europe. In a review of declines in bumble bees of 11 central and western European countries, Kosior et al. (55) describe extinctions of 13 species in at least one European country between 1950 and 2000. Four species (*B. armeniacus*, *B. cullumanus*, *B. serrisquama*, *and B. sidemii*) went extinct throughout the entire region.

There are no equivalent baseline data for bumble bees in North America and there is debate whether they are suffering similar long-term declines. For example, Golick & Ellis (33) found little variation in the Nebraska bumble bee fauna between 1962 and 2000. In contrast, there is strong evidence for precipitous declines of some North American bumble bee species. *B. franklini* is endemic to a small area in western United States (California and Oregon) and has declined rapidly since 1998. Recent searches found no indication of this species at many former strongholds, and it is now thought to be extinct at many or all of them (88). *B. occidentalis* is native to western North America and was once the commonest bumble bee to that area, but since the late 1990s it has declined dramatically and is now rare (89, 90). *B. affinis* and *B. terricola*, both eastern North American species, are suffering similar declines, as have *B. sonorus* and *B. pennsylvanicus* (89). *B. ashtoni*, a social parasite of *B. affinis* and *B. terricola*, also appears to be suffering losses, presumably in response to decline of its hosts (102).

CONSEQUENCES OF DECLINES IN BUMBLE BEE POPULATIONS

A large number of wild plants are pollinated predominantly or exclusively by bumble bees, sometimes by particular species of bumble bee (34). Most bumble bees are generalist pollinators and most insect-pollinated plants use multiple pollinators (92), so it could be argued that pollination networks are buffered against the loss of a few pollinator species. However, a recent study simulating the effects of removal of individual pollinators from pollination networks demonstrated that removal of highly linked pollinators such as bumble bees produced the greatest rate of decline in plant species diversity (60). Reduced pollination services can be particularly detrimental when plants are already scarce and threatened directly by the same changes in land use that threaten the bees (34).

Aside from the implications for conservation, there are economic reasons for conserving bumble bees. The yields of many field, fruit, and seed crops are enhanced by bumble bee visitation (35). For example, field beans in Europe are pollinated largely by longer-tongued species such as *B. pascuorum* and *B. hortorum*, without which yields are poor (28). In the United States, there is an ongoing decline in managed honey bee (*Apis mellifera*) populations due to disease, misuse of pesticides, loss of subsidies, and dangers associated with invading Africanized honey bees (56).

The value of crop pollination by honey bees in the United States has been estimated at between $5 and $14 billion per year, but beekeeping has diminished by around 50% over the past 50 years (56). This decline has given rise to concerns over the future of insect-pollinated crops such as cucumber, pumpkin, watermelon, blueberry, and cranberry (18, 56, 74). At sufficient densities, bumble bees pollinate many of these crops efficiently, often more so than honey bees (82). However, the impoverished bumble bee communities often associated with agricultural landscapes may be insufficient to replace the services currently provided by honey bees.

CAUSES OF BUMBLE BEE DECLINES

Reductions in Floral Resources

The primary cause of bumble bee declines in western Europe is the intensification of farming practices, particularly during the latter half of the twentieth century (34, 37). In the United Kingdom, a self-sufficiency drive in the wake of World War II led to a number of major changes. Permanent unimproved grassland was once highly valued for grazing and hay production, but the development of cheap artificial fertilizers and new fast-growing grass varieties meant that farmers could improve productivity by ploughing up ancient grasslands. Hay meadows gave way to monocultures of grasses that are grazed or cut for silage. Between 1932 and 1984 over 90% of unimproved lowland grassland was lost in the United Kingdom (47). Grants were introduced to grub out hedgerows, to plough and reseed pasture, and to drain marshy areas. This led to a steady decline in the area of unfarmed land and of unimproved farmland.

In some regions of North America, agricultural intensification has caused similar loss and fragmentation of natural and seminatural habitat and an associated loss in biodiversity (98). For example, in Iowa, 85% of the land area was once prairie grassland, which provides good bumble bee habitat, but less than 0.1% now remains. The remainder of the land is covered largely with monocultures of crops or by urban areas (45).

There is evidence to suggest that bumble bee forage plants have suffered disproportionate declines. A recent study in the United Kingdom found that of 97 preferred bumble bee forage species, 71% have suffered range restrictions, and 76% have declined in abundance over the past 80 years, exceeding declines of nonforaging species (11).

On farmland, the crops themselves may provide an abundance of food during their brief flowering periods. Leguminous crops (notably clovers, *Trifolium* spp.) were an important part of crop rotations in much of Europe, and these are highly preferred food sources, particularly for long-tongued bumble bee species (40). Since the introduction of cheap artificial fertilizers, rotations involving legumes have been abandoned almost entirely, which may be one of the primary factors driving the decline of long-tongued bumble bees (38, 73). Flowering crops such as oilseed rape may contribute substantially to supporting bumble bee populations in arable landscapes (93). However, in order for bumble bee colonies to thrive, a continuous succession of flowers is required from April until August, and crops alone are unlikely to provide this succession.

Uncropped areas of farmland, such as hedgerows, field margins, and borders of streams, may provide flowers throughout the season and therefore support greater numbers of foraging bumble bees than cultivated areas (3, 57) provided they are numerous and have not been degraded by drift of herbicides and fertilizers. Insufficient flower-rich uncropped areas may lead to gaps in the succession of flowering plants during which bumble bee colonies may starve and die. With a decline in bees, the plants that they pollinate set less seed, resulting in less forage for the bees in subsequent years (64). The process by which mutually dependent species drive each other

Extinction vortex: a process of positive feedback whereby declines in abundance render a species less viable, leading to accelerated declines

to extinction is known as an extinction vortex. We do not know whether this process is really occurring, but it is clear that farmland provides less food for bees than it once would have done.

Loss of Nest Sites

In addition to floral resources, bumble bees need suitable nesting sites, the precise requirements for which vary among species (51). The carder bees (*Thoracobombus*) such as *B. pascuorum* tend to nest in dense grassy tussocks and other species such as *B. terrestris* nest underground in cavities. Both groups often use abandoned rodent nests. The loss of hedgerows and of unimproved pastures is likely to have reduced the availability of nest sites for both aboveground and belowground nesting bumble bee species (3). Those species that nest above ground frequently have their nests destroyed by farm machinery, particularly by cutting for hay or silage (34). The scarcity of weeds and field-margin flowers on modern intensive farms means that there are fewer seeds and therefore less food for voles and mice. Lower populations of these mammals will lead to fewer nest sites for both aboveground and belowground nesting bumble bee species.

In California, even on organically managed farms, the presence of bumble bees, in this case *B. vosnesenskii* and *B. californicus*, depends on proximity to areas of natural habitat in which the bees can nest (56). A study in Sweden found that field boundaries within 100 m of a seminatural grassland area contained a greater abundance and diversity of foraging bumble bees than did similar sites >1 km from such habitats. However, bumble bee abundance was significantly lower in the seminatural grasslands themselves, suggesting that these sites were used primarily for nesting (63). Similarly, Greenleaf & Kremen (42) found that tomato fields in northern California obtain high visitation rates from *B. vosnesenskii* only when they were positioned within 300 m of a patch of natural habitat and if at least 40% of the land within a 2100-m radius of the farm was natural habitat.

There is some evidence for a paucity of suitable nest sites in urban areas. Bumble bee abundance in urban parks in San Francisco was positively correlated with the number of rodent holes (59), suggesting that nest sites may be a limiting factor.

Pesticides

Pesticide risk assessments are routinely carried out for honey bees, but the results of these are probably not directly applicable to bumble bees (85). For example, to avoid honey bees, pyrethroids are commonly applied to flowering oilseed rape in the early morning or evening, when bumble bees are often active. Laboratory- and field-based bioassays appropriate to bumble bees have been developed in response to the growing use of bumble bees for the pollination of greenhouse crops, but these are not widely used and few toxicological data are available (84). Almost all tests conducted so far have been on *B. terrestris* and suggest that toxicity is similar to that found in honey bees. There are three possible routes for exposure: direct contact with sprays (on flowering crops or adjacent wild flowers), contact with contaminated foliage, and uptake of chemicals in nectar. The last route is most likely with systemic insecticides. Tests with dimethoate and carbofuran suggest that these chemicals are selectively transported into the nectar, where they can reach high concentrations (17). Given the large volume of nectar consumed by bumble bees, this could prove to be the most important route of exposure.

When colonies are large, they can tolerate the loss of some of their workers. However, in the spring, when queens are foraging and subsequently when nests are small and contain just a few workers, mortality may have a more significant effect (84). Thus, spring applications of pesticides may have disproportionate impacts.

Despite risk assessments, widespread poisoning of honey bees has been reported (27, 43). Such effects are obvious in domestic hives in which dead bees are ejected and form piles near the nest. Similar effects on bumble bees, which are not sprayed, are unlikely to be noticed in most situations. In Canada, the use of the insecticide fenitrothion in forests led to a decline in yield of nearby *Vaccinium* crops due to a reduction in the abundance of bumble bee pollinators (21). In the United Kingdom, bumble bee deaths have been reported following applications of dimethoate or α-cypermethrin to flowering oilseed rape and of λ-cyhalothrin to field beans (84, 85).

A growing appreciation of the damaging effects of broad-spectrum pesticides has led to the development of a new generation of more target-specific compounds. E.U., U.S., and Canadian law now demand that oral and acute toxicity tests are carried out on honey bees prior to the registration of any new pesticide (62). However, there is no obligation to study sublethal effects on any bees or to look at specific effects on bumble bees. Some of these substances cause no mortality in bumble bees if used appropriately (26, 77), but nonlethal effects may be overlooked. For example, spinosad is a commonly used insect neurotoxin that, based on studies of honey bees, has been deemed harmless to bees. However, it has recently been shown that bumble bee larvae fed with pollen containing this pesticide give rise to workers with reduced foraging efficiency (62). Mommaerts et al. (61) screened eight chitin synthesis inhibitors currently registered as pesticides and found that although no lethal effect could be found on adults, the use of these pesticides has strong effects on colony growth and larvae development. Diflubenzuron and teflubenzuron were the most harmful to bumble bees, greatly reducing reproductive output at concentrations far below the recommended field concentrations. In summary, it is likely that many pesticides currently in use do affect bumble bee populations, but hard data are largely lacking.

Impacts of Nonnative Bees

The most immediate threat to bumble bees in the United States, unlike in western Europe, may be the spread of disease due to widespread trafficking of commercial bumble bee hives (89). Commercial bumble bee hives are used for greenhouse pollination all over the world, including Israel, Korea, Japan, North America, and Europe (36). In the United States, colonies of *B. impatiens* and *B. occidentalis* have been commercially reared since the early 1990s for the pollination of greenhouse crops such as tomatoes (94) and sweet peppers (79). These colonies have a greater parasite load than wild colonies, with an elevated prevalence of the bumble bee–specific protozoan pathogens *Crithidia bombi* and *Nosema bombi*, and of the tracheal mite *Locustacarus buchneri* (12). These parasites have detrimental effects on colony survival and reproduction and/or the foraging efficiency of individual workers (5, 29, 65).

Greenhouse escapes occur. In Japan, feral colonies of the nonnative *B. terrestris* are now common (48), and a recent study in Canada found that 73% of pollen carried by workers returning to commercial colonies originated from plants outside the greenhouse (95). Consequently, there is a high likelihood of interaction between wild and commercially reared bees at flowers, providing conditions for pathogen spillover from the commercial population to wild populations. Significant increases in the prevalence of *C. bombi* and *N. bombi* have been found in wild bumble bee populations near commercial greenhouses, compared with wild populations elsewhere (12). In 1998, an *N. bombi* outbreak was reported in bumble bee production facilities in North America, perhaps a result of the importation of infected European *B. terrestris* colonies into Mexico in 1995 and 1996 (102). Similarly, *C. bombi* has been detected in the United States only since the use of commercially reared bumble bees began, and this parasite may not be native to the United States (102). The introduction may have occurred as a result of the shipment of *B. occidentalis* queens to Europe for commercial rearing before reimportation into the United States in the early 1990s (12, 102). Exposure to a nonnative pathogen is a likely cause of the catastrophic declines in *B. terricola*, *B. affinis*, *B. franklini*, and *B. occidentalis* (88, 89, 94). However, we have a poor understanding of the relative susceptibilities of bumble bee species to parasites, or of the natural distributions of these parasites, and work is urgently needed in this area. Tight controls are needed on transport of domesticated bumble bee hives.

There are other risks associated with commercial trafficking of bumble bees. *B. terrestris* is now naturalized in Japan and there are concerns regarding possible competitive effects of this species on native bumble bees. Studies have shown that *B. terrestris* has four times the reproductive output of native species (58) and that there are considerable overlaps in forage use and timing of foraging (48). There are similar concerns in the United Kingdom, where approximately 10,000 colonies of a southeastern European subspecies *Bombus terrestris dalmatinus* are imported each year (50). Britain has an endemic subspecies of this bee, *Bombus terrestris audax*. Evidence suggests that there are dangers to the British subspecies in the form of parasite transmission (49) or outcompetition, particularly because the introduced subspecies has superior foraging efficiency and reproductive rate (50). Also, *B. terrestris dalmatinus* and *B. terrestris audax* readily interbreed; therefore the native subspecies could be lost through introgression (49).

In addition to nonnative bumble bee species, native pollinator communities in many parts of the globe also have to contend with honey bees. These natives of Europe, Africa, and the Middle East have been introduced by humans to almost every country in the world. Their impacts are reviewed by Goulson (36). Recent studies suggest that honey bees can have negative effects on bumble bees. Walther-Hellwig et al. (91) found that short-tongued bumble bees avoided areas of forage close to honey bee hives, whereas carder bumble bees switched to foraging later in the day and were displaced from their preferred foodplant. Thomson (86) experimentally introduced honey bees and found that proximity to hives significantly reduced the foraging rates and reproductive success of *B. occidentalis* colonies. In the eastern United States, Thomson (87) found a strong overlap between the foraging preferences of bumble bees and honey bees, which peaked at the end of the season when floral resources were scarce, corresponding with a negative relationship between honey bee and bumble bee abundance.

There is increasing evidence that the spread of natural enemies of bumble bee colonies is aided by honey bees. Honey bees can act as vectors for the bumble bee–specific *C. bombi* via flowers (75). The African honey bee pest *Aethina tumida* (small hive beetle) recently invaded North America, Egypt, Australia, and Europe, and attacks on *B. impatiens* colonies cause considerable damage (80). Deformed wing virus, a viral honey bee pathogen, has been found in commercial colonies of *B. terrestris*, transmitted between the two species as a result of the widespread practice among commercial bumble bee rearers of placing newly eclosed honey bee workers with bumble bee queens to help induce colony founding (30). However, it has also been found in a wild colony of *B. pascuorum* that had been robbing a managed honey bee hive (30). This virus appears to have higher virulence to bumble bees than to honey bees, and the findings raise important questions about transmission and cross-infectivity between bumble bees and honey bees.

Habitat Fragmentation and Population Structure

As a consequence of the various factors discussed, populations of a number of bumble bee species have become increasingly small, fragmented, and separated from one another by large distances. In the United Kingdom, where distributions are best known, declines appear to have followed a characteristic pattern. *B. subterraneus*, the last bumble bee species to disappear from the United Kingdom, was once widespread across southern England but declined rapidly in the years after World War II. By the 1980s the few remaining populations were small and isolated, surviving on habitat islands (nature reserves) that had escaped agricultural intensification. However, these populations subsequently disappeared despite the apparent suitability and protected status of the remaining habitat (34). The species was last recorded at Dungeness National Nature Reserve in 1988. Several other U.K. species such as *B. distinguendus* and *B. sylvarum* are in the late stages of a similar process and are likely to go extinct in the near future. Understanding the consequences of the fragmentation of remnant populations of bumble bees is of great importance to conservationists, given the current distributions of many rare species.

Small populations of all taxa are inherently more vulnerable to local extinctions because of environmental and demographic stochasticity (25). If these populations form part of a broader metapopulation, then regional extinctions can be balanced by subsequent recolonization, but if fragmentation is severe, then extinct patches may never be repopulated. In addition, a functioning metapopulation ensures that dispersal maintains genetic cohesion. However, if habitat fragmentation results in the isolation of populations, then they may face an additional extinction threat through inbreeding (25). Bumble bees may be particularly badly affected by habitat fragmentation for several reasons. It is the effective population size (N_e) rather than the census population size (N_c) that determines the rate of genetic drift in a population, and N_e may be several orders of magnitude lower than N_c. In bumble bees, as in many other social insects, N_e depends on the number of successful colonies. N_e contributed by an individual colony depends on the number of egg-laying queens and the number of males they have mated with, but (unlike many other hymenopterans) bumble bee colonies are all founded by a single queen, and most species are monoandrous (22, 76). Furthermore, as a result of haplodiploidy, their N_e is equal to the number of successful nests times 1.5, not times 2 as would be the case for a diploid-diploid organism. It seems therefore that population sizes of bumble bees may be low, even relative to other social insects, making them particularly susceptible to the loss of genetic diversity.

To date, relatively few studies have attempted to determine the consequences of inbreeding in bumble bees. Gerloff & Schmid-Hempel (32) found significant reductions in colony foundation and hibernation success in response to brother-sister mating. Little evidence of inbreeding depression was found for reproductive output or cumulative fitness, as was the case for Duchateau et al. (19), but in both studies nests were reared in the laboratory and fed ad libitum. However, Beekman et al. (4) found that inbred queens laid fewer eggs. Gerloff et al. (31) found no evidence for a reduced encapsulation (immune) response. A recent meta-analysis concluded that, although haplodiploid insects suffer less from inbreeding than diploid insects [perhaps due to purging of nonsex-limited recessive alleles in haploid males (67)], substantial inbreeding depression does occur (44).

An additional cost may be imposed on inbred populations of many hymenopteran species as a result of their haplodiploid sex-determination mechanism. The mechanism centers on a polyallelic sex-determining locus and has important consequences for small populations (13). Individuals heterozygous at this locus develop into females, and homozygous (or hemizygous) individuals develop into males. As populations diminish in size, genetic drift will lead to a reduction in the number of sex alleles in the population, increasing the probability of a matched mating. A queen that mates with a male who shares one of her sex-determining alleles will produce a colony in which 50% of her workforce are diploid

Inbreeding: an increase in the frequency of individuals that are homozygous for alleles identical by descent relative to another or the ancestral population

Inbreeding depression: reduced fitness that can result from inbreeding

Diploid male: in inbred populations, bees that are genetically female may instead develop into sterile males if they are homozygous at the sex-determining locus males. In honey bees and ants, diploid male larvae are consumed by the workers, which minimizes their cost, but in bumble bees they are reared to adulthood (19). Bumble bee diploid males are viable but largely sterile (but see Reference 2 for evidence that diploid males do occasionally manage to produce triploid offspring) and therefore represent a considerable cost to the colony best viewed as 50% worker mortality (67).

Diploid males represent a clear example of inbreeding depression and have been detected in numerous wild populations of hymenopterans (81, 103). Their frequency has been proposed as an indicator of population fitness (105), and recent modeling work has shown that diploid male production, where present, may initiate a rapid extinction vortex (104). However, until recently, diploid male production had not been detected in naturally occurring populations of bumble bees.

Given the potentially serious consequences of inbreeding in bumble bees, it is essential that we understand its prevalence within wild bumble bee populations. The development of several highly variable microsatellite markers for bumble bees (24) has facilitated the assessment of their population structure. Initial studies focused largely on two abundant and widespread European species, *B. terrestris* and *B. pascuorum*. In *B. terrestris*, there appears to be little population substructuring within mainland Europe, suggesting that dispersal is frequent and that there are no substantial isolating barriers between populations (23). However, populations on various Mediterranean islands and Tenerife (Canary Islands) were distinct (23, 97). In *B. pascuorum*, populations throughout most of mainland Europe are similar, but these populations differ markedly from those found south of the Alps in Italy (69, 96). More recently, Shao et al. (78) compared seven mainland and island populations of *B. ignitus* in Asia and similarly found that mainland populations were genetically similar but that distant offshore populations had significantly differentiated. Genetic structuring is thus observed when populations are separated by appreciable barriers such as mountain ranges or large stretches of water.

Until recently, studying the population genetics of rare bee species was difficult, as lethal sampling was necessary. Work in this area was greatly aided by the development of a nonlethal DNA sampling technique (46), which has recently been applied to studies of fragmented populations of rare species: *B. muscorum* (15), *B. sylvarum* (20), and *B. distinguendus* (6). All three studies revealed significant population structuring. For example, in *B. muscorum*, all populations greater than 10 km apart were significantly differentiated, as were some populations just 3 km apart. Low frequencies of diploid males were found in 3 of the 16 populations studied. Ellis et al. (20) used microsatellite markers to group workers into sisterhoods and so estimated the number of colonies (and hence N_e) in populations of *B. sylvarum*, a species that is highly endangered in the United Kingdom. Estimates of N_e were low (range 21–72), suggesting that, if isolated, these populations are vulnerable to loss of genetic diversity through drift. Indeed, significant differentiation was found between all populations, suggesting that they are genetically isolated. Diploid males were found at one of the six sample sites. It is important to exercise caution when making comparisons among species based on a small number of microsatellite markers. However, in all three rare species, genetic diversity (as measured by allelic richness and heterozygosity) was reduced compared with common species, and island populations showed further reductions (**Table 1**).

We do not yet have unequivocal evidence that inbreeding plays a major role in driving small, isolated populations of bumble bees to extinction, but it seems likely. If reductions in the genetic diversity of neutral markers found in rare species are indicative of reductions in the diversity of functional genes, then there will be concomitant consequences for population fitness and evolutionary potential. Management strategies in vertebrates

Table 1 Genetic diversity estimates for populations of a number of *Bombus* species (mean ± SE)

***Bombus* species**	**Population**	**Sample size**	**Allelic richness**	**H_E**	**Reference**
B. ignitus	Beijing, China	33	12.2 ± 1.53[a]	0.85 ± 0.02	78
B. ignitus	Nagano, Japan	26	8.22 ± 0.72[a]	0.83 ± 0.03	78
B. pascuorum	Landford, U.K.	183	6.22 ± 1.19[a]	0.52 ± 0.15	16
B. pascuorum	Rothamsted, U.K.	125	5.71 ± 1.01	0.52 ± 0.11	54
B. pascuorum	Continental Europe	22.7 average	5.49 ± 0.16[a]	0.56 ± 0.01	96
B. terrestris	Continental Europe	37.5 average	5.96 ± 0.12[a]	0.61 ± 0.01	23
B. lucorum	Bern, Switzerland	40	7.00 ± 2.00[a]	0.60 ± 0.12	23
B. hypnorum	Various locations, Sweden	10	6.75 ± 1.03[a]	0.72 ± 0.14[b]	68
B. sylvarum	Southern U.K.	25.6 average	3.12 ± 0.10	0.39 ± 0.02	20
B. sylvarum	Epenede, France	10	4.00 ± 0.85	0.53 ± 0.09	20
B. muscorum	Outer Hebrides, U.K.	43.8 average	3.22 ± 0.12	0.39 ± 0.01	15
B. muscorum	Inner Hebrides, U.K.	62.7 average	3.21 ± 0.07	0.47 ± 0.01	15
B. muscorum	Southern U.K.	35.5 average	4.01 ± 0.06	0.51 ± 0.01	15
B. distinguendus	Scotland, U.K.	7.75 average	2.63 ± 0.23*	0.42 ± 0.01[b]	6

[a] Allelic richness was not available, and the average number of alleles per locus is presented. Allelic richness is a normalized measure that takes account of differing sample sizes to give a comparable figure for all populations.

[b] Expected heterozygosity was not available, and observed heterozygosity is given. These measures are expected to be similar for populations that are in Hardy-Weinberg equilibrium.

routinely consider genetic factors, and similar measures may prove necessary in the management of rare bumble bee populations.

Why Do Some Bumble Bee Species Remain Common?

Some bumble bee species are largely unaffected by habitat loss, fragmentation, and degradation. In much of Europe, six species are widespread and common (*B. terrestris*, *B. lucorum*, *B. lapidarius*, *B. pratorum*, *B. hortorum*, and *B. pascuorum*). How do these species differ from those that have declined? On the basis of studies of forage use, Goulson et al. (39, 40) argue that the rare species tend to be long tongued and have narrower diets; a large proportion of the pollen they collect is from Fabaceae, many of which have deep flowers. These bumble bee species are associated with Fabaceae-rich unimproved grasslands, a habitat that has been largely eradicated in western Europe. In contrast, the common species tend to have broad foraging preferences and readily encompass nonnative garden plants and mass-flowering crop plants in their diets (41). Williams (99) recently showed that rare and declining species in Britain tend to have small geographic ranges within Europe. He suggests that these species may have more specific habitat associations or climatic requirements, which render them more susceptible to environmental change. These two explanations are mutually compatible because a species with a narrow diet is also likely to have specific habitat requirements. However, current data suggest that most bumble bee species are not strongly associated with particular habitat types (39). For example, prior to its extinction in Britain, *B. subterraneus* occurred in habitats as diverse as shingle, salt marshes, sand dunes, and calcareous and neutral unimproved meadows. Although some of the rarer species do appear to exist in specific habitats, historical records show that most once existed across a much wider range of habitats (39).

In the United Kingdom there is a broad correlation between rarity and emergence time, with rare species tending to emerge later (40). The time of year at which queens emerge from hibernation differ greatly among species; the earliest species emerge in

February, whereas other species do not appear until late May. Where nesting habitat is scarce, those species in which queens emerge early in the season may be able to monopolize available nest sites, reducing the chances of colony founding for queens emerging later. In urban parks in San Francisco, *B. vosnesenskii* is the most abundant species and is also the earliest emerging of the community of bumble bees found there (59). Rodent holes limit bumble bee abundance, and the earliest emerging species may monopolize nest sites.

In recent years it has become apparent that there are major differences among bumble bee species in their foraging range (16, 54). Species such as *B. terrestris* and *B. lapidarius* forage farther afield than so-called doorstep foragers such as *B. pascuorum*, *B. sylvarum*, *B. ruderarius*, and *B. muscorum*. It is perhaps significant that the former two species remain ubiquitous in much of Europe, whereas three of the four doorstep foragers have declined. In theory, a larger foraging range gives a greater chance of colony survival in areas where the average density of floral resources is low or where resources are highly patchy. Intensively farmed arable landscapes with occasional fields of mass-flowering crops provide just such a landscape, and it is probably no coincidence that *B. terrestris* and *B. lapidarius* are among the species most commonly recruited in large numbers to such crops (39).

CONSERVING BUMBLE BEES

Enhancing Bumble Bee Diversity in Farmland

A major cause of bumble bee declines is loss of habitat to intensive farming. However, there are moves to reverse this trend in Europe and North America, where there is a growing emphasis on combining the goals of agriculture and conservation (53, 66). Subsidies are currently available in many countries for agri-environment schemes that promote biodiversity, including replanting of hedgerows, leaving land fallow, sowing wildflower strips, and restoring flower-rich grassland. Most of the management options promote floral abundance and diversity. A 6-m-wide field margin kept free of crops and agrochemicals may contain 6 times as many flowering plants and 10 times as many flowers as the equivalent cropped area (52). The effects of U.K. field margin management options on bumble bee communities have been the focus of many studies in recent years.

The most valuable form of field margin management for bumble bees is the sowing of either wildflowers or a pollen and nectar mix consisting of agricultural cultivars of legume species (7, 9, 10, 71, 72). Carvell et al. (9) found that the pollen and nectar mixture produced the highest flower abundance with a succession of forage plants flowering over the three-year trial period. The wildflower mixture produced few flowers in the first year, but flower abundance increased over the three years as the mixture became established. Both treatments led to an increase in bumble bee species richness and abundance, and in the third year the wildflower mix maintained as diverse a pollinator community as the pollen and nectar mixture. Once established, the wildflower mix persists for up to 10 years, while the agricultural cultivars in the pollen and nectar mix need resowing within 5 years (70).

Long-term set-aside (i.e., fallow, uncropped land) lasting five years or more can also produce the mid-successional communities preferred by bumble bees (64). However, the perennial plants vital to such communities are poorly represented in the seed banks in agricultural land, and therefore establishment of such species may be slow. To maintain mid-successional communities, intermediate levels of disturbance such as mowing, cutting, or seasonal grazing may be required. Carvell (8) conducted a study to assess the benefits of different grassland management regimes on bumble bee populations in the United Kingdom. Grazing during the autumn and winter months provided excellent bumble bee habitat, but without it coarse grasses became dominant. However, heavy grazing during the spring and summer is detrimental because most flowers are eaten. An alternative is rotational grazing through the spring and summer so that there are always some parts of the farm providing forage for bees. In general, grazing by cattle seems more favorable to bumble bees than grazing by sheep, and low summer grazing densities are preferable (8).

Studies of forage use by bumble bees suggest that it is not necessarily important to provide a great diversity of flowers (38, 40). In coastal scrubland in California, five plant species accounted for 80% to 93% of bumble bee visits over a three-year study period (87). Similarly, in studies of 15 bumble bee species across a broad range of habitats in the United Kingdom, 80% of all pollen-collecting visits were to just 11 plant species (40). Carvell et al. (9) found that 92% of visits were to only six flowering plants in managed field margins and that a diverse sown wildflower field margin option consisting of 18 herb species was no more beneficial than a simple sown wildflower option consisting of only 3 herbaceous species. A small number of well-chosen forage species provide suitable resources for a diverse bumble bee community.

Bumble bees require not only a suitable source of forage, but also nest and hibernation sites. A popular agri-environment scheme in the United Kingdom is the sowing of field margins with tussocky grasses (72). These habitats attract the small mammals whose abandoned holes are used by bumble bees for nest sites (83), so it is likely that this form of management is of value to bumble bees. Carvell et al. (10) found that field margins sown with a split treatment consisting of a mixture of tussocky grasses and wildflowers attracted almost as many bumble bees as margins sown solely with the wildflower seed, suggesting that it is possible to provide both forage and nesting habitats in small areas.

The Importance of Urban Areas

In the United States, 2.2 million acres of farmland and open space are converted into urban areas every year (59). There is evidence that gardens and urban parks are particular strongholds for some bumble bee species. Urban parks in San Francisco had higher mean abundances and equal diversities of bumble bees compared with nearby wilder areas. Abundance of bumble bees was explained partly by the openness of the matrix surrounding the park, suggesting that suburban gardens also played a role (59). In the United Kingdom, young nests of *B. terrestris* placed in suburban gardens grew more quickly and attained a larger size than nests placed in arable farmland (41). It is likely that gardens provide favorable habitat for several bumble bee species as a result of the density, variety, and continuity of flowers that they provide (41). However, many commonly used garden plants are unsuitable for bumble bees. Artificial selection has often resulted in modern flower varieties that provide little or no reward, or which are inaccessible to insects (14). Similarly, some exotic plants, such as those pollinated by hummingbirds, provide rewards that are inaccessible to native bee species. It is clear that urban gardens can provide a refuge for several bumble bee species, but encouraging gardeners to choose their plants appropriately could be particularly beneficial.

CONCLUSIONS

Widespread declines of bumble bee species threaten pollination services to both wildflowers and crops. It is clear from studies of population structure that most bumble bee species cannot be conserved by managing small protected islands of habitat within a sea of unsuitable, intensively farmed land (15, 20). Large areas of suitable habitat are needed to support viable populations in the long term. Also, studies of foraging range indicate that bumble bees exploit forage patches at a landscape scale (16, 54); therefore the scale of management must be appropriate. An integrated approach across large areas or several farms is more likely to succeed than localized efforts. Where small isolated populations of rare species remain in habitat fragments, targeting the adjacent farms for uptake of suitable agri-environment schemes could increase the population size and thus reduce the likelihood of stochastic extinction events and inbreeding. Similarly, such schemes could be used to provide linkage between habitat islands.

Unimproved flower-rich grassland is one of the most important habitats for bumble bees but has been lost largely to agriculture in western Europe and North America. Restoration of areas of this habitat can boost bumble bee populations and provide improved pollination services on nearby farmed land (8, 9). Substantial benefits could also be obtained by reintroducing clover (e.g., *Trifolium pratense*) lea crops into rotations, because this is a key forage source for many declining bumble bee species. This would also reduce dependency on artificial fertilizers.

Pesticide poisoning is likely to have contributed to bumble bee declines (84, 85), and the current risk assessments of the dangers of pesticides to honey bees are inadequate for bumble bees (85). In addition there is a clear need to assess sublethal effects of pesticides on bumble bees.

In the United States, recent declines in several bumble bee species have been linked to increases in the commercialization of bumble bees for greenhouse pollination and associated introductions of parasites (102). There are already restrictions in place on the importation and movement of bumble bees in North America, but there are calls for increased restrictions on transportation of bees and for stricter quarantine and monitoring systems (102).

Finally, long-term monitoring of bumble bee populations is required to gain a better understanding of the current status of bumble bee species and to establish baselines to which future studies can refer. This is particularly important in areas such as North America, where declines of some species have been documented but the extent is poorly quantified.

SUMMARY POINTS

1. Many bumble bee species have declined in western Europe and North America.
2. Declines are attributable largely to agricultural intensification and in North America probably to introduction of parasites into commercial bumble bee nests.
3. Bumble bees have a low effective population size, rendering them prone to stochastic extinctions and inbreeding.
4. Conservation measures must be coordinated and deployed at a landscape scale to be effective.
5. Improved safety testing of pesticides is needed.
6. Tight controls on the international trade in commercial bumble bee colonies are required to prevent further introductions of nonnative parasites.

FUTURE ISSUES

1. Baseline surveys of bumble bee abundance and distributions are lacking for most countries, such that quantifying population change is difficult.
2. It is not yet clear whether inbreeding depression plays a major role in bumble bee declines.

3. Agricultural intensification continues apace in developing countries in eastern Europe and Asia, and unless lessons are learned from developed countries, further declines in bumble bees are inevitable.
4. Basic aspects of the ecology of many species are not known, such that conservation measures are poorly informed.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

1. Alford DV. 1980. *Atlas of the Bumblebees of the British Isles*. Cambridge, UK: Inst. Terr. Ecol. Publ. No. 30
2. Ayabe T, Hoshiba H, Ono M. 2004. Cytological evidence for triploid males and females in the bumblebee, *Bombus terrestris*. *Chromosome Res.* 12:215–23
3. Banaszak J. 1992. Strategy for conservation of wild bees in an agricultural landscape. *Agric. Ecosyst. Environ.* 40:179–92
4. Beekman M, van Stratum P, Veerman A. 1999. Selection for nondiapause in the bumblebee *Bombus terrestris*, with notes on the effect of inbreeding. *Entomol. Exp. Appl.* 93:69–75
5. Brown MJF, Schmid-Hempel R, Schmid-Hempel P. 2003. Strong context-dependent virulence in a host-parasite system: reconciling genetic evidence with theory. *J. Anim. Ecol.* 72:994–1002
6. Bourke AFG, Hammond RL. 2002. *Genetics of the scarce bumble bee*, Bombus distinguendus, *and nonlethal sampling of DNA from bumble bees*. Rep. R. Soc. Prot. Birds (RSPB), Jan.
7. Carreck NL, Williams IH. 2002. Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *J. Insect Conserv.* 6:13–23
8. Carvell C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biol. Conserv.* 103:33–49
9. **Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M. 2007. Comparing the efficiency of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J. Appl. Ecol.* 44:29–40**

9. A long-term study of the relative merits of different field-margins management techniques for bumble bees.

10. Carvell C, Meek WR, Pywell RF, Nowakowski M. 2004. The response of bumblebees to successional change in newly created arable field margins. *Biol. Conserv.* 118:327–39
11. Carvell C, Roy DB, Smart SM, Pywell RF, Preston CD, Goulson D. 2006. Declines in forage availability for bumblebees at a national scale. *Biol. Conserv.* 132:481–89
12. **Colla SR, Otterstatter MC, Gegear RJ, Thomson JD. 2006. Plight of the bumble bee: pathogen spillover from commercial to wild populations. *Biol. Conserv.* 129:461–67**

12. Highlights the potentially devastating effects of pathogen spillover from commercial colonies.

13. Cook JM, Crozier RH. 1995. Sex determination and population biology in the Hymenoptera. *Trends Ecol. Evol.* 10:281–86
14. Corbet SA, Bee J, Dasmahapatra K, Gale S, Gorringe E, et al. 2001. Native or exotic? Double or single? Evaluating plants for pollinator-friendly gardens. *Ann. Bot.* 87:219–32

15. The first study of the population structure of a rare bumble bee species persisting in fragmented habitat islands.

15. **Darvill B, Ellis JS, Lye GC, Goulson D. 2006. Population structure and inbreeding in a rare and declining bumblebee, *Bombus muscorum* (Hymenoptera: Apidae). *Mol. Ecol.* 15:601–11**
16. Darvill B, Knight ME, Goulson D. 2004. Use of genetic markers to quantify bumblebee foraging range and nest density. *Oikos* 107:471–78
17. Davis AR, Shuel RW. 1988. Distribution of carbofuran and dimethoate in flowers and their secretion in nectar as related to nectary vascular supply. *Can. J. Bot.* 66:1248–55
18. Delaplane KS, Mayer DF. 2000. *Crop Pollination by Bees*. Wallingford, UK: CABI
19. Duchateau MJ, Hishiba H, Velthuis HHW. 1994. Diploid males in the bumble bee *Bombus terrestris*. *Entomol. Exp. Appl.* 71:263–69
20. Ellis JS, Knight ME, 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.* 15:4375–86
21. Ernst WR, Pearce PA, Pollock TL, eds. 1989. *Environmental Effects of Fenitrothion Use in Forestry: Impacts on Insect Pollinators, Songbirds, and Aquatic Organisms*. Halifax: Conserv. Prot., Environ. Can., Atlantic Reg.
22. Estoup A, Scholl A, Pouvreau A, Solignac M. 1995. Monandry and polyandry in bumble bees (Hymenoptera, Bombinae) as evidenced by highly variable microsatellites. *Mol. Ecol.* 4:89–93
23. Estoup A, Slignac M, Cornuet J-M, Goudet J, Scholl A. 1996. Genetic differentiation of continental and island populations of *Bombus terrestris* (Hymenoptera: Apidae) in Europe. *Mol. Ecol.* 5:19–31
24. Estoup A, Solignac M, Harry M, Cornuet JM. 1993. Characterization of (GT)n and (CT)n microsatellites in 2 insect species: *Apis mellifera* and *Bombus terrestris*. *Nucleic Acids Res.* 21:1427–31
25. Frankham R, Ballou JD, Briscoe DA. 2002. *Introduction to Conservation Genetics*. Cambridge, UK: Cambridge Univ. Press. 617 pp.
26. Franklin MT, Winston ML, Morandin LA. 2004. Effects of clothianidin on *Bombus impatiens* (Hymenoptera: Apidae) colony health and foraging ability. *Ecotoxicology* 97:369–73
27. Free JB, Ferguson AW. 1986. Foraging of bees on oil-seed rape (*Brassica napus* L.) in relation to the flowering of the crop and pest control. *J. Agric. Sci.* 94:151–54
28. Free JB, Williams IH. 1976. Pollination as a factor limiting the yield of field beans (*Vicia faba* L.). *J. Agric. Sci.* 87:395–99
29. Gegear RJ, Otterstatter MC, Thomson JD. 2005. Does parasitic infection impair the ability of bumblebees to learn flower-handling techniques? *Anim. Behav.* 70:209–15
30. Genersch E, Yue C, Fries I, de Miranda JR. 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
31. Gerloff CU, Ottmer BK, Schmid-Hempel P. 2003. Effects of inbreeding on immune response and body size in a social insect, *Bombus terrestris*. *Funct. Ecol.* 17:582–89
32. Gerloff CU, Schmid-Hempel P. 2005. Inbreeding depression and family variation in a social insect, *Bombus terrestris* (Hymenoptera: Apidae). *Oikos* 111:67–80
33. Golick DA, Ellis MD. 2006. An update on the distribution and diversity of *Bombus* in Nebraska (Hymenoptera: Apidae). *J. Kans. Entomol. Soc.* 79:341–47
34. Goulson D. 2003. *Bumblebees: Behaviour and Ecology*. Oxford, UK: Oxford Univ. Press
35. Goulson D. 2003. Conserving wild bees for crop pollination. *Int. J. Food Agric. Environ.* 1:142–44

36. **Goulson D. 2003. Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 34:1–26**
37. Goulson D. 2003. The conservation of bumblebees. *Bee World* 84:105–6
38. 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
39. Goulson D, Hanley ME, Darvill B, Ellis JS. 2006. Biotope associations and the decline of bumblebees (*Bombus* spp.). *J. Insect Conserv.* 10:95–103
40. Goulson D, Hanley ME, Darvill B, Ellis JS, Knight ME. 2005. Causes of rarity in bumblebees. *Biol. Conserv.* 122:1–8
41. Goulson D, Hughes WOH, Derwent LC, Stout JC. 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia* 130:267–73
42. Greenleaf SS, Kremen C. 2006. Wild bee species increase tomato production and respond differently to surrounding land use in northern California. *Biol. Conserv.* 133:81–87
43. Greigsmith PW, Thompson HMN, Hardy AR, Bew MH, Findlay E, Stevenson JH. 1994. Incidents of poisoning of honeybees (*Apis mellifera*) by agricultural pesticides in Great Britain, 1981–1991. *Crop Prot.* 13:567–81
44. Henter HJ. 2003. Inbreeding depression and haplodiploidy: experimental measures in a parasitoid and comparisons across diploid and haplodiploid insect taxa. *Evolution* 57:1793–803
45. Hines HM, Hendrix SD. 2005. Bumble bee (Hymenoptera: Apidae) diversity and abundance in tallgrass prairie patches: effects of local and landscape floral resources. *Environ. Entomol.* 34:1477–84
46. Holehouse KA, Hammond RL, Bourke AFG. 2003. Non-lethal sampling of DNA from bumble bees for conservation genetics. *Insectes Soc.* 50:277–85
47. Howard DC, Watkins JW, Clarke RT, Barnett CL, Stark GJ. 2003. Estimating the extent and change in broad habitats in Great Britain. *J. Environ. Manag.* 67:219–27
48. Inari N, Nagamitsu T, Kenta T, Goka K, Hiura T. 2005. Spatial and temporal pattern of introduced *Bombus terrestris* abundance in Hokkaido, Japan, and its potential impact on native bumblebees. *Popul. Ecol.* 47:77–82
49. Ings TC, Raine NE, Chittka L. 2005. Mating preference of commercially imported bumblebees (*Bombus terrestris*) in Britain (Hymenoptera: Apidae). *Entomol. Gen.* 28:233–38
50. Ings TC, Wards NL, Chittka L. 2006. Can commercially imported bumble bees outcompete their native conspecifics? *J. Appl. Ecol.* 43:940–48
51. Kells AR, Goulson D. 2003. Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biol. Conserv.* 109:165–74
52. Kells AR, Holland JM, Goulson D. 2001. The value of uncropped field margins for foraging bumblebees. *J. Insect Conserv.* 5:283–91
53. Kleijn D, Sutherland WJ. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* 40:947–69
54. Knight ME, Martin AP, Bishop S, Osborne JL, Hale RJ, et al. 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Mol. Ecol.* 14:1811–20
55. Kosior A, Celary W, Olejnikzak P, Fijal J, Krol W, et al. 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of western and central Europe. *Oryx* 41:79–88

36. A comprehensive review of the sometimes conflicting evidence concerning the impacts of nonnative bees on native ecosystems.

56. Kremen C, Williams NM, Thorp RW. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. USA* 99:16812–16
57. Mänd M, Mänd R, Williams IH. 2002. Bumblebees in the agricultural landscape of Estonia. *Agric. Ecosyst. Environ.* 89:69–76
58. Matsumara C, Nakajima M, Yokoyama J, Waishitini I. 2004. High reproductive ability of an alien bumblebee invader, *Bombus terrestris*, L., in the Hidaka region of southern Hokkaido, Japan. *Jpn. J. Conserv. Ecol.* 9:93–102
59. McFrederick QS, LeBuhn G. 2006. Are urban parks refuges for bumble bees? *Biol. Conserv.* 129:372–82
60. Memmott J, Waser NM, Price MV. 2004. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. London Sci. Ser. B* 271:2605–11
61. Mommaerts V, Sterk G, Smagghe G. 2006. Hazards and uptake of chitin synthesis inhibitors in bumblebees *Bombus terrestris*. *Pest Manag. Sci.* 62:752–58
62. Morandin LA, Winston ML, Franklin MT, Abbott VA. 2005. Lethal and sublethal effects of spinosad on bumble bees (*Bombus impatiens* Cresson). *Pest Manag. Sci.* 61:619–26
63. Ockinger E, Smith HG. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *J. Appl. Ecol.* 44:50–59
64. Osborne JL, Corbet SA. 1994. Managing habitats for pollinators in farmland. *Asp. Appl. Biol.* 40:207–15
65. Otterstatter MC, Gegear RJ, Colla S, Thompson JD. 2005. Effects of parasitic mites and protozoa on the flower constancy and foraging rate of bumble bees. *Behav. Ecol. Sociobiol.* 58:383–89
66. Ovenden GN, Swash ARH, Smallshire D. 1998. Agri-environment schemes and their contribution to the conservation of biodiversity in England. *J. Appl. Ecol.* 35:955–60
67. Packer L, Owen R. 2001. Population genetic aspects of pollinator decline. *Conserv. Ecol.* 5:4
68. Paxton RJ, Thorén PA, Estoup A, Tengö J. 2001. Queen-worker conflict over male production and sex ratio in a facultatively polyandrous bumble bee, *Bombus hypnorum*: the consequences of nest usurpation. *Mol. Ecol.* 10:2489–98
69. Pirounakis K, Koulianos S, Schmid-Hempel P. 1998. Genetic variation among European populations of *Bombus pascuorum* (Hymenoptera, Apidae) using mitochondrial DNA sequence data. *Eur. J. Entomol.* 95:27–33
70. Pywell RF, Bullock JM, Hopkins A, Walker KJ, Sparks TH, et al. 2002. Restoration of a species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *J. Appl. Ecol.* 39:294–309
71. Pywell RF, Warman EA, Carvell C, Sparks TH, Dicks LV, et al. 2005. Providing forage resources for bumblebees in intensively farmed landscapes. *Biol. Conserv.* 121:479–94
72. Pywell RF, Warman EA, Hulmes L, Hulmes S, Nuttall P, et al. 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biol. Conserv.* 129:192–206
73. Rasmont P, Mersch P. 1988. Première estimation de la dérive faunique chez les bourdons de la Belgique (Hymenoptera, Apidae). *Ann. Soc. R. Zool. Belg.* 118:141–47
74. Richards AJ. 2001. Does low biodiversity resulting from modern agricultural practice affect crop pollination and yield? *Ann. Bot.* 88:165–72
75. Ruiz-Gonzalez MX, Brown MJF. 2006. Honey bee and bumblebee trypanosomatids: specificity and potential for transmission. *Ecol. Entomol.* 31:616–22
76. Schmid-Hempel R, Schmid-Hempel P. 2000. Female mating frequencies in *Bombus* spp. from Central Europe. *Insectes Soc.* 47:36–41

77. Sechser B, Freuler J. 2003. The impact of thiomethoxam on bumble bee broods (*Bombus terrestris* L.) following drip application in covered tomato crops. *J. Pest Sci.* 76:74–77

78. Shao ZY, Mao HX, Fu WJ. 2004. Genetic structure of Asian populations of *Bombus ignitus* (Hymenoptera: Apidae). *J. Hered.* 95:46–52

79. Shipp JL, Whitfield GH, Papadopoulos AP. 1994. Effectiveness of the bumble bee *Bombus impatiens* Cr. (Hymenoptera: Apidae), as a pollinator of greenhouse sweet pepper. *Sci. Hortic.* 57:29–39

80. Spiewok S, Neumann P. 2006. Infestation of the commercial bumblebee (*Bombus impatiens*) field colonies by small hive beetles (*Aethina tumida*). *Ecol. Entomol.* 31:623–28

81. Stahlhut JK, Cowan DP. 2004. Inbreeding in a natural population of *Euodynerus foraminatus* (Hymenoptera: Vespidae), a solitary wasp with single-locus complementary sex determination. *Mol. Ecol.* 13:631–38

82. Stubbs CS, Drummond FA. 2001. *Bombus impatiens* (Hymenoptera: Apidae): an alternative to *Apis mellifera* (Hymenoptera: Apidae) for lowbush blueberry pollination. *J. Econ. Entomol.* 94:609–16

83. Svensson B, Lagerlöf J, Svensson BG. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agric. Ecosyst. Environ.* 77:247–55

84. Thompson HM. 2001. Assessing the exposure and toxicity of pesticides to bumblebees (*Bombus* sp.). *Apidologie* 32:305–21

85. Thompson HM, Hunt LV. 1999. Extrapolating from honeybees to bumblebees in pesticide risk assessment. *Ecotoxicology* 8:147–66

86. Thomson DM. 2004. Detecting the effects of introduced species: a case study of competition between *Apis* and *Bombus*. *Oikos* 114:407–18

87. Thomson DM. 2006. Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology* 85:458–70

87. The first convincing demonstration of the negative effects of nonnative honey bees on the reproduction of native bumble bees.

88. Thorp RW. 2005. Species profile: *Bombus franklini*. In *Red List of Pollinator Insects of North America*, ed. MD Shepherd, DM Vaughan, SH Black. Portland, OR: Xerces Soc. Invertebr. Conserv.

89. Thorp RW, Shepherd MD. 2005. Profile: subgenus *Bombus*. In *Red List of Pollinator Insects of North America*, ed. MD Shepherd, DM Vaughan, SH Black. Portland, OR: Xerces Soc. Invertebr. Conserv.

90. Tommasi D, Miro A, Higo HA, Winston ML. 2004. Bee diversity and abundance in an urban setting. *Can. Entomol.* 136:851–69

91. Walther-Hellwig K, Fokul G, Frankl R, Buechler R, Ekschmitt K, Wolters V. 2006. Increased density of honeybee colonies affects foraging bumblebees. *Apidologie* 37:517–32

92. Waser NM, Chittka L, Price MV, Williams N, Ollerton J. 1996. Generalization in pollinator systems and why it matters. *Ecology* 77:1043–60

93. Westphal C, Steffen-Dewenter I, Tsharntke T. 2003. Mass-flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* 6:961–65

94. Whittington R, Winston ML. 2004. Comparison and examination of *Bombus occidentalis* and *Bombus impatiens* (Hymenoptera: Apidae) in tomato greenhouses. *J. Econ. Entomol.* 97:1384–89

95. Whittington R, Winston ML, Tucker C, Parachnowitsch AL. 2004. Plant-species identity of pollen collected by bumblebees placed in greenhouse for tomato pollination. *Can. J. Plant Sci.* 84:599–602

96. Widmer A, Schmid-Hempel P. 1999. The population genetic structure of a large temperate pollinator species, *Bombus pascuorum* (Scopoli) (Hymenoptera: Apidae). *Mol. Ecol.* 8:387–98
97. Widmer A, Schmid-Hempel P, Estoup A, Scholl A. 1998. Population genetic structure and colonisation history of *Bombus terrestris* s.l. (Hymenoptera: Apidae) from the Canary Islands and Madeira. *Heredity* 81:563–72
98. Wilcove DS, Rothstein D, Dubrow J, Phillips A, Losos E. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48:607–15
99. Williams P. 2005. Does specialization explain rarity and decline among British bumblebees? A response to Goulson et al. *Biol. Conserv.* 122:33–43
100. Williams PH. 1982. The distribution and decline of British bumble bees (*Bombus* Latr.). *J. Apic. Res.* 21:236–45
101. Williams PH. 1994. Phylogenetic relationships among bumble bees (*Bombus* Latr.): a reappraisal of morphological evidence. *Syst. Entomol.* 19:327–44
102. Winter K, Adams L, Thorp R, Inouye D, Day L, et al. 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. *A White Pap. No. Am. Pollinator Prot. Campaign (NAPPC)*, *Aug.*
103. Zayed A, Packer L. 2001. High levels of diploid male production in a primitively eusocial bee (Hymenoptera: Halictidae). *Heredity* 87:631–36
104. Zayed A, Packer L. 2005. Complementary sex determination substantially increases extinction proneness of haplodiploid populations. *Proc. Natl. Acad. Sci. USA* 102:10742–46
105. Zayed A, Roubik DW, Packer L. 2004. Use of diploid male frequency data as an indicator of pollinator decline. *Proc. R. Soc. London Ser. B* 271:S9–S12

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