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Conservation of bumblebees

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ABSTRACT
Declines in bumblebee species in the last 60 years are well documented in Europe, where they are primarily driven by habitat loss and declines in floral abundance and diversity, in turn driven by changing agricultural practices. Amongst the most significant of these for bumblebees has been the loss of species-rich unimproved grasslands (haymeadows, chalk downland, machair etc.). Evidence suggests that the species which have declined most are specialists in collecting pollen from Fabaceae, especially red clovers, and loss of unimproved grasslands and abandonment of red clover leys have greatly reduced the abundance of red clover across western Europe. High densities of commercial honeybee hives may also impact upon bumblebees in some areas. Effects of habitat degradation and fragmentation on bumblebees are likely to be compounded by the social nature of bumblebees and their largely monogamous breeding system (queens mate only once) which renders their effective population size low. Recent studies suggest that surviving populations of some rare species consist of <30 breeding females, and such populations are susceptible to chance extinction events and inbreeding. Conservation measures must be implemented at the landscape-scale if they are to be effective, for small patches of habitat on nature reserves do not support viable bumblebee populations in the long term. Given the importance of bumblebees as pollinators of crops and wildflowers, it is vital that adequate steps be taken to prevent further declines. Suggested measures include careful management of surviving species-rich grasslands such as machair.

Many bumblebee species have declined in recent decades, particularly in developed regions such as Western Europe and North America (Goulson 2003a, Thorp & Shepherd 2005, Kosior et al. 2007, Goulson et al. 2008a). In the UK, three of the 25 native species have gone extinct and a further eight species having undergone major range declines (Goulson 2003a). The most severely affected species tend to be those with long tongues associated with deep perennial flowers (Goulson et al. 2005). Similar patterns are evident in Europe. In a review of declines in bumblebees of 11 central and western European countries, Kosior et al. (2007) describe extinctions of 13 species in at least one country between 1950 and 2000. Four species (*B. armeniacus, B. cullumanus, B. serrisquama, B. sidemii*) went extinct throughout the entire region.
Most researchers agree that the main cause of bumblebee declines in Western Europe and North America is the intensification of farming practices, particularly during the latter half of the 20th century (Goulson 2003a,c). 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 has meant that farmers could improve productivity by ploughing up ancient grasslands. Thus hay meadows gave way to monocultures of grasses which are grazed or cut for silage. Between 1932 and 1984 over 90% of unimproved lowland grassland was lost in the UK (Howard et al. 2003).

There is evidence to suggest that bumblebee forage plants have suffered disproportionate declines. A recent study in the UK found that of 97 preferred bumblebee forage species, 71% have suffered range restrictions, and 76% have declined in abundance over the past eighty years, exceeding declines of non-forage species (Carvell et al. 2006). Leguminous crops (notably clovers, *Trifolium* spp.) used to be an important part of crop rotations in much of Europe, and these are highly preferred food sources, particularly for long-tongued bumblebee species (Goulson et al. 2005). Since the introduction of cheap artificial fertilizers, rotations involving legumes have been almost entirely abandoned, and it has been argued that this is one of the primary factors driving the decline of many bumblebees (Goulson & Darvill 2004, Rasmont & Mersch 1988).

In addition to floral resources, bumblebees need suitable nesting sites, the precise requirements for which vary between species (Kells & Goulson 2003). The carder bees (*Thoracobombus*) such as *B. muscorum* tend to nest in dense grassy tussocks while other species such as *B. distinguendus* nest underground in cavities. Both groups often use abandoned rodent nests. The loss of hedgerows and of unimproved pastures is likely to have reduced availability of nest sites for both above and below-ground nesting bumblebee species (Banaszak 1992). Those species that nest above ground frequently have their nests destroyed by farm machinery, particularly by cutting for hay or silage. The scarcity of weeds and field-margin flowers on modern intensive farms means that there are less seeds, and therefore less food for voles and mice. Lower populations of these mammals will lead to fewer nest sites for both above and below-ground nesting bumblebee species.

One further potential threat to bumblebees is that they have to contend with commercial honeybees (*Apis mellifera*). Their potential impacts are reviewed by Goulson (2003b). Although honeybees are thought to be native to the UK (although probably not to the Western Isles), commercial beekeeping maintains much higher honeybee densities than could occur naturally. Recent studies suggest that honeybees have negative effects on native bumblebees. Walther-Hellwig *et al.* (2006) found that short-tongued bumblebees avoided areas of forage close to honeybee hives, while carder bumblebees switched to foraging later in the day and were displaced from their preferred foodplant. Thomson (2004) experimentally introduced honeybees and found that proximity to hives significantly reduced the foraging rates and reproductive success of *B. occidentalis* colonies. Thomson (2006) found a strong overlap between the foraging preferences of the two species, which peaked at the end of the season when floral resources were scarce, corresponding with a negative relationship between honeybee and bumblebee abundance. In Scotland, Goulson and Sparrow (in press) found that workers of four common bumblebee species were all significantly smaller in areas where honeybees were present. There is also evidence that honeybees can act as vectors for the bumblebee specific disease *Crithidia bombi* via flowers (Ruiz-Gonzalez & Brown 2006). Deformed wing virus, a viral honeybee pathogen, has been found in wild bumblebee nests (Genersch et al. 2006), and appears to have higher virulence to bumblebees than to honeybees.

As a consequence of the various factors discussed above, populations of a number of bumblebee species have become increasingly small, fragmented and separated from one another by large distances. In the UK, where distributions are best known, declines appear to have followed a characteristic pattern. The last bumblebee species to disappear from the UK (*B. subterraneus*, the sister species of *B. distinguendus*), was once widespread across southern England, but declined rapidly in the years after World War II. By the 1980's 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 (Goulson 2003a). The species was last recorded at Dungeness National Nature Reserve in 1988. Several other UK 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. Why do isolated populations go extinct? Understanding the consequences of the fragmentation of remnant populations of bumblebees 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 due to environmental and demographic stochasticity (Frankham et al. 2002). If these populations form part of a broader metapopulation then regional extinctions can be balanced by subsequent recolonisation, 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 (Frankham et al. 2002). There are a number of reasons why bumblebees may be particularly badly affected by habitat fragmentation. It is the effective population size (N_e) which determines the rate of genetic drift in a population. In bumblebees, as in many other social insects, N_e depends on the number of successful colonies, not the number of bees in the population. Each bumblebee colony contains just one breeding female, and in most bumblebees she will have mated with a single male (Estoup et al. 1995, Schmid-Hempel & Schmid-Hempel 2000). Therefore, it seems that population sizes of bumblebees may be low, making them particularly susceptible to the loss of genetic diversity.

Given the potentially serious consequences of inbreeding in bumblebees, it is essential that we understand its prevalence within wild bumblebee populations. Until recently, studying the population genetics of rare bee species was extremely difficult, as lethal sampling was necessary. Work in this area was greatly aided by the development of a non-lethal DNA sampling technique (Holehouse et al. 2003), and this has recently been applied to studies of fragmented populations of rare species: *B. muscorum* (Darvill et al. 2006), *B. sylvarum* (Ellis et al. 2006) and *B. distinguendus* (Bourke & Hammond 2002). All three studies found significant population structuring. For example in *B. muscorum,* all populations >10 km apart were significantly differentiated, as were some populations just 3km apart, suggesting that this species has very limited dispersal abilities. Ellis *et al.* (2006) 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 which is highly endangered in the UK. Estimates of N_e were very low (range 21-72) suggesting that these populations are very vulnerable to loss of genetic diversity through drift. In all rare species studied to date, genetic diversity (allelic richness and heterozygosity) is low compared to common species (Darvill 2007). If fragmented populations of rare bumblebee species are suffering from reduced fitness through inbreeding then we must take steps to conserve what genetic diversity remains. Management strategies in vertebrates routinely consider genetic factors, and we may need to adopt similar measures in the management of rare bumblebee populations.

An interesting aspect of bumblebee declines is that a small number of species have remained relatively abundant. What is the difference between the species that have declined (and in some cases gone extinct) and those that have not? It seems that the rare and declining species tend to be long tongued and have narrower diets, with a very large proportion of the pollen they collect being from Fabaceae (many of which have deep flowers) (Goulson and Darvill 2004; Goulson et al. 2005, 2006, 2008b). This is supported by a substantial data set of bumblebee foraging records gathered from throughout the UK, and separated according to whether they were collecting pollen, nectar, or both. Some species tend to get 90-100% of their pollen from Fabaceae (for example *B. hortorum, B. ruderatus, B. subterraneus* and *B. humilis*), and these tend to be long-tongued and, with the exception of *B. hortorum*, they are all declining species. It should be noted that *B. distinguendus* almost certainly falls within this group. Parallel studies of more diverse bumblebee communities in Poland confirm similar patterns (Goulson et al. 2008b). Studies of the nutritional quality of pollen reveal that Fabaceae pollen is unusually high in protein and essential amino acids (Hanley et al. 2008). Fabaceae tend to dominate species-rich grasslands such as machair, because their ability to fix nitrogen gives them a competitive edge in nutrient-poor soils. Hence the massive loss of species-rich grasslands throughout the UK has had a disproportionate effect on those bumblebee species that favour Fabaceae as their pollen source.

CONCLUSIONS

It is clear from studies of population structure that most bumblebee species cannot be conserved by managing small protected 'islands' of habitat within a 'sea' of unsuitable, intensively farmed land. Large areas of suitable habitat are needed to support viable populations in the long term. Unimproved flower-rich grassland is one of the most important habitats for bumblebees, but has been largely lost to agriculture in Western Europe and North America. Many of the bumblebee species that have declined most are specialized on collecting pollen from Fabaceae, especially *Trifolium pratense*, and Fabaceae tend to dominate species-rich grasslands. This explains why machair supports substantial populations of rare bumblebees; large areas survive (although much has been lost), and it can be exceptionally rich in Fabaceae. Restoration of areas of this habitat will boost bumblebee populations. Substantial benefits for bumblebee conservation could also be obtained by reintroducing clover (e.g. *Trifolium pratense*) ley crops into rotations, reducing dependency on artificial fertilizers.

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