Special Feature for Ecological Risk Assessment of Introduced Bumblebees

Impacts of non-native bumblebees in Western Europe and North America

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Abstract

The earliest deliberate introductions of bumblebees to areas outside of their native range occurred over 100 years ago. Transportation of bumblebees accelerated in the late 1980s following the development of techniques for mass rearing them, and their widespread adoption as the preferred pollinator for a range of glasshouse crops, primarily tomatoes. There is now a worldwide trade in one species, Bombus terrestris dalmatinus, originating from south east Europe. Within North America, which does not allow the importation of *B. terrestris*, the trade is primarily in *Bombus impa*tiens. Trade in B. t. dalmatinus threatens the integrity of other subspecies within Europe, such as B. t. audax which is endemic to Britain and Ireland. However, there is a conspicuous absence of data as to whether B. t. dalmatinus has established in the wild outside its native range, and whether it interbreeds with native subspecies. Perhaps a more significant risk associated with trade in bumblebees is the accidental spread of parasites, and the subsequent risk that native bumblebee species may be exposed to parasites for which they have little resistance. There is circumstantial evidence that catastrophic declines of several North American bumblebee species may have been triggered by the accidental introduction of pathogens from Europe. Even if commercial bumblebee colonies are reared locally, the high densities at which they are kept mean that glasshouse nests are likely to act as reservoirs for spread of disease to wild bumblebee populations nearby. There is clearly the need for tight quarantining of bee colonies before transportation, and a moratorium should be placed on the transport of bumblebees in cases where native species suitable for commercial rearing are readily available.

Key words: Bombus; competition; introgression; parasites; pathogens

INTRODUCTION

The devastating impacts which exotic organisms can have on ecosystems are well known, and surely ought to have taught us a lesson as to the perils of allowing release of alien species. Yet bumblebees (*Bombus*) and a range of other bee species continue to be deliberately transported around the world (Goulson, 2003a). Of course bees are widely perceived to be beneficial for their role in the pollination of crops and wildflowers, and for the production of honey. Perhaps for this reason, there seems to be reluctance to regard bees as potentially damaging in environments to which they are not native (Goulson, 2003a, b).

The natural range of bumblebees is largely confined to the temperate northern hemisphere

and the mountains of Central and South America

⁽Williams, 1994). Various Bombus species have been deliberately introduced to new countries to enhance crop pollination. The earliest deliberate and successful introduction specifically for pollination was of bumblebees to New Zealand. In 1885 and 1906, 93 and 143 queens, respectively, were caught in Britain and released in New Zealand (Hopkins, 1914; MacFarlane and Griffin, 1990). The intention was to improve seed set of red clover, Trifolium pratense, widely used as a fodder crop. Four bumblebee species became established, B. hortorum, B. terrestris, B. subterraneus and B. ruderatus. That these introductions were not well thought through is clear from the introduction of B. terrestris, which is not effective as a pollinator of red clover but acts as a nectar robber (Gurr, 1957).

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All four species have survived to this day; *B. hortorum* and *B. subterraneous* have restricted distributions within New Zealand, while *B. terrestris* and *B. ruderatus* have become ubiquitous (MacFarlane and Gurr, 1995).

The main period of bumblebee transportation began in the late 1980s with the commercialization of bumblebee rearing for crop pollination in glasshouses. For the last 20 years, colonies of B. terrestris of south eastern European origin have been transported in large numbers around the globe, throughout Europe and to countries as distant as Japan, Korea and Chile. During the 1990s B. terrestris became established in the wild in Japan following escapes from glasshouses (Dafni, 1998; Goka, 1998). In 1992 B. terrestris arrived in Hobart in south eastern Tasmania (it is not known how it got there), and it has since spread out to occupy much of the island (Stout and Goulson, 2000; Hingston, 2006). More recently, B. terrestris was introduced to Chile. This is the second UK species to arrive in Chile, for B. ruderatus was previously introduced in 1982 and 1983 for pollination of red clover (Arretz and MacFarlane, 1986). B. ruderatus had spread over the Andes to Argentina by 1993 (Abrahamovich et al., 2001). The spread of B. terrestris is likely to continue. Because of its efficacy as a pollinator of glasshouse tomatoes, recent applications have been lodged for deliberate release in mainland Australia, South Africa and Argentina.

Interestingly, the most recently recorded range expansion in bumblebees is in *B. hypnorum*, a species not used commercially. This species has been expanding its range and becoming more numerous in urban areas in mainland Europe, and was recorded for the first time in the UK in 2001 (Goulson and Williams, 2001). It has since spread \sim 300 km northwards, with strong and well established populations in a number of areas (D.G., unpublished data).

So why should these introductions be a cause for concern? There are a number of possible undesirable effects of non-native bumblebees (Goulson, 2003b), including:

- I. Competition with native bees
- II. Introgression with related species
- III. Transmission of parasites or pathogens to native organisms
- IV. Changes in seed set of native plants (either increases or decreases)

V. Pollination of exotic weeds

The majority of studies to date have focused on the impacts of non-native honeybees (notably in the Americas and Australia) and on impacts of bumblebees in regions where bumblebees are not native (for example in Tasmania). Only relatively recently has realization dawned that translocation of bumblebees between parts of the globe where bumblebees naturally occur also has inherent dangers. This review focuses on impacts of introduced bumblebees in Europe and North America where bumblebees naturally occur, and in these circumstances the first three possible impacts of non-native bumblebees mentioned above seem most probable. Affects on plant pollination are less likely since in these regions there are already bumblebee pollinators with a range of tongue lengths (an exception to this may be B. ruderatus in South America, since this species has a much longer tongue than any native American bumblebee species). A more general overview of the impacts of non-native bees on plants via pollination is provided by Cresswell (2010).

COMPETITION WITH NATIVE BEES

B. terrestris exists in Europe as a number of named subspecies. The main trade in commercial bumblebees is in B. terrestris dalmatinus, from Greece and Turkey. In much of western Europe the subspecies is *B. terrestris terrestris*, whereas Britain and Ireland have an endemic subspecies, B. terrestris audax. The widespread transportation of B. terrestris dalmatinus to regions where it does not naturally occur may result in competitive displacement of native subspecies. It is certain that commercial bees escape from glasshouses. In Japan, feral colonies of the non-native *B. terrestris* are now common (Inari et al., 2005), and a recent study in Canada found that 73% of pollen carried by workers returning to commercial colonies originated from plants outside the greenhouse (Whittington et al., 2004). In the UK there are no regulations regarding netting of doors or windows as there are now in Japan (Yoneda et al., 2007). From 2007, commercial bumblebee nests imported to the UK have been fitted with entrance holes that are too small to allow queens to escape (D.G., pers. obs.), but since they have been imported in large numbers for approximately 20 years, it is likely

that if they were going to escape into the wild that they have already done so. Also, these entrance holes do not restrict the escape of males, and it is very likely that some queens continue to find their way out of boxes (if the entrance is closed, the bees are capable of chewing through the sides of the box to escape, D.G., pers. obs.). We do not know whether *B. terrestris dalmatinus* has become established in the wild in parts of Europe where it is not native because the subspecies are hard to reliably distinguish on morphological grounds, and no molecular markers have been developed to separate the subspecies.

If B. terrestris dalmatinus has become established in the UK or elsewhere, what threat might it pose? Perhaps the most obvious is that it might compete with native bumblebees, particularly B. terrestris audax with which it presumably shares a similar niche. Unfortunately, competition is notoriously difficult to demonstrate. The only way to test unequivocally whether floral resources are limiting and competition is in operation is to conduct experiments in which the abundance of the introduced bee species is artificially manipulated, and the population size of native species is then monitored. If populations are significantly higher in the absence of the introduced bee, then competition is occurring. Although in principle a simple procedure, such experiments have proved to be exceedingly hard to accomplish. Bumblebees are highly mobile, foraging up to a kilometer or more from their nests (Knight et al., 2005; Osborne et al., 2008). Thus excluding them from an area is difficult. Within and between-season variation is likely to be large, so such experiments need to be well replicated, with replicates situated many kilometers apart, and conducted over several years. No such study has been carried out.

The only indication we have as to whether competition might occur between *B. terrestris dalmatinus* and *B. terrestris audax* comes from the work of Ings et al. (2006). They compared the performance of paired nests of these two subspecies when placed in the field in the UK, and found that *B. t. dalmatinus* produced larger workers which brought back more nectar per unit time, and that *B. t. dalmatinus* nests produced significantly more gynes than those of *B. t. audax*. Overall, their conclusion was that *B. t. dalmatinus* may outcompete *B. t. audax*. However, this work can be criticized on the grounds that all experimental colonies were initially reared in captivity, and the *B. t. dalmatinus* strain has been in captivity for many generations and therefore perhaps responds better to rearing under artificial conditions. Being adapted to a Mediterranean climate, *B. t. dalmatinus* has shorter hair than *B. t. audax* (Peat et al., 2005) and so we might expect it to struggle in the cool and wet conditions in the UK.

INTROGRESSION WITH RELATED SPE-CIES

An alternative potential threat from the commercial trade in bumblebees is the loss of genetic diversity at the sub-specific level. If B. t. dalmatinus interbreeds with local subspecies such as B. t. audax, then the integrity of B. t. audax will be lost and eventually all B. terrestris subspecies may become merged into a single homogenous population. We have no idea if this is happening. In cage choice tests, B. t. audax and B. t. dalmatinus readily interbreed and produce viable offspring, although they do prefer to mate assortatively (Ings et al., 2005). Given the choice, 71% of B. t. dalmatinus queens mated with B. t. dalmatinus males, the remainder with B. t. audax males. This low level of assortative mating would be insufficient to prevent rapid introgression between the two species. However, cage experiments may not be representative of natural situations and are more likely to break down barriers to introgression that exist in natural situations, such as use of pheromones to locate mates. It may be that introgression has been occurring since the trade in B. t. dalmatinus began in the late 1980s, and that no pure B. t. audax or B. terrestris terrestris remain. It may be possible to establish whether this is the case by extracting DNA from museum specimens collected before the commercialization of bumblebees occurred, or in the case of audax by using samples from New Zealand. Clearly more research is urgently needed to establish whether B. t. dalmatinus is established in the wild outside its native range, and whether it is competing or introgressing with native species/ subspecies.

TRANSMISSION OF PARASITES OR PATHO-GENS TO NATIVE ORGANISMS

Bees and their nests support a diverse microflora including both pathogenic, commensal and mutualistic organisms (Gilliam and Taber, 1991; Goerzen, 1991; Gilliam, 1997). Many pathogens are likely to have been transported to new regions with their hosts, particularly where introductions were made many years ago when awareness of bee natural enemies was low. Thus for example the honeybee disease chalkbrood, caused by the fungus Ascosphaera apis; foulbrood, caused by the bacteria Paenibacillus larvae; the microsporidian Nosema apis; and the mite Varroa destructor now occur throughout much of the world. Similarly, bumblebees in New Zealand are host to a parasitic nematode and three mite species, all of which are thought to have come from the UK with the original introduction of bees (Donovan, 1980). Recent studies in Japan have demonstrated that B. terrestris imported from the Netherlands are frequently infested with the tracheal mite Locustacarus buchneri (Goka et al., 2001, 2006), and that commercial colonies can act as reservoirs from which the parasite spreads into wild bee populations (Yoneda et al., 2008). Although this mite also occurs in Japan, the European race is genetically distinct (Goka et al., 2001, 2006).

We are very largely ignorant of the natural enemies of most bee species, particularly their pathogens. We do not know what species infect them, or what the host ranges of these pathogens are. Thus very little is known of the susceptibility of native organisms to the parasites and pathogens that have been introduced with exotic bees. Indeed the natural geographic range of bee pathogens is almost wholly unknown.

In the US, colonies of *B. impatiens* and *B. occidentalis* have been commercially reared since the early 1990s for the pollination of greenhouse crops such as tomatoes (Whittington and Winston, 2004) and sweet peppers (Shipp et al., 1994). These colonies have been found to have a greater parasite load than wild colonies with an elevated prevalence of the bumblebee specific protozoan pathogens *Crithidia bombi* and *Nosema bombi*, and of the tracheal mite *Locustacarus buchneri* (Colla et al., 2006). These parasites have detrimental effects on colony survival and reproduction and/or the forag-

ing efficiency of individual workers (Brown et al., 2003; Gegear et al., 2005; Otterstatter et al., 2005). Since a large proportion of workers in glasshouse colonies forage outside the glasshouse (Whittington et al., 2004), 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 bumblebee populations near to commercial greenhouses, compared to wild populations elsewhere (Colla et al., 2006). In 1998, a N. bombi outbreak was reported in bumblebee production facilities in North America. This was thought to be a result of the importation of infected European *B. terrestris* colonies into Mexico in 1995 and 1996 (Winter et al., 2006). Similarly, C. bombi has only been detected in the US since use of commercially reared bumblebees began and it is suspected that this parasite is not native to the US (Winter et al., 2006). The introduction may have occurred as a result of the shipment of queens of B. occidentalis to Europe for commercial rearing before re-importation into the US in the early 1990s (Colla et al., 2006; Winter et al., 2006). Exposure to a non-native pathogen is a likely cause of recent catastrophic declines in B. terricola, B. affinis, B. occidentalis and B. franklini, the latter of which is probably now extinct and if so, represents the first known bumblebee extinction event (Whittington and Winston, 2004; Thorp, 2005; Thorp and Shepherd, 2005).

There is increasing evidence that the spread of natural enemies of bumblebee colonies is also being aided by honeybees, and visa versa. Honeybees can act as vectors for the bumblebee-specific C. bombi via flowers (Ruiz-Gonzalez and Brown, 2006). The African honeybee parasite Aethina tumida (small hive beetle) recently invaded North America, Egypt, Australia and Europe, and attacks commercial B. impatiens colonies where it causes considerable damage (Spiewok and Neumann, 2006). Deformed wing virus, a viral honeybee pathogen, has been found in commercial colonies of B. terrestris, transmitted between the two species as a result of the practice of placing honeybees with queens to induce colony founding (Genersch et al., 2006). However it has also been found in a wild colony of B. pascuorum which had been robbing a managed honeybee hive (Genersch et al.,

2006). This virus appears to have higher virulence to bumblebees than to honeybees and the findings raise important questions about transmission and cross-infectivity between bumblebees and honeybees. In most countries importation of honeybees is carefully monitored to avoid accidental transport of honeybee diseases, but bumblebees are often not screened adequately or at all.

It seems likely that these few recorded instances of exotic bee pathogens infecting native species are just the tip of the iceberg, since so few studies have been carried out. As to whether these pathogens have had, or are having, a significant impact on native bee species (bumblebees or other bee species), in general we do not know. Studies of the incidence and identity of pathogen and parasite infestations of wild populations of native bees are urgently needed. In the meantime, legislation to enforce strict quarantine of bees prior to transportation would seem to be necessary.

CONCLUSIONS

Commercially-reared bumblebees provide substantial benefits to man in terms of pollination of crops. Ideally these quantifiable benefits should be weighed against the likely risks. There are ways in which the risks associated with commercial use of bumblebees could be greatly reduced. In many parts of the world which currently import bumblebees there are native bee species that could be exploited. For example a ban on the importation of *B*. terrestris to North America led to the swift development of *B. impatiens* as an alternative pollinator for tomatoes. The use of B. t. dalmatinus for pollination in parts of Europe where it is not native is entirely unnecessary. The other B. terrestris subspecies can readily be reared, so that it would for example be perfectly possible to rear B. t. audax for use in the UK, and B. t. terrestris for use in France, avoiding the need to import *B. t. dalmatinus* altogether. In the absence of any studies of competitive effects or introgression, the precautionary principle suggests that this would be by far the most sensible option. At present there is no legislation in North America or Europe to force growers to contain commercial bumblebees within glasshouses using netted vents and doors in the way that is now standard practice in Japan. Although this can never be 100% effective at preventing escape

of bees, it would greatly reduce pathogen spillover and would go some way to reducing the other risks associated with commercial use of bumblebees.

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