

Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size

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Abstract Numerous studies suggest that honeybees may compete with native pollinators where introduced as non-native insects. Here we examine evidence for competition between honeybees and four bumblebee species in Scotland, a region that may be within the natural range of honeybees, but where domestication greatly increases the honeybee population. We examined mean thorax widths (a reliable measure of body size) of workers of *Bombus pascuorum*, *B. lucorum*, *B. lapidarius* and *B. terrestris* at sites with and without honeybees. Workers of all four species were significantly smaller in areas with honeybees. We suggest that reduced worker size is likely to have implications for bumblebee colony success. These results imply that, for conservation purposes, some restrictions should be considered with regard to placing honeybee hives in or near areas where populations of rare bumblebee species persist.

Keywords *Bombus* · *Apis mellifera* · Floral resources · Foraging · Resource limitation

Introduction

The honeybee *Apis mellifera* L. (Apidae: Hymenoptera) is probably native to Africa and Eurasia (Michener 1974), although its association with humans is so ancient that it is hard to be certain of its origins and precise natural range. It has certainly been domesticated for at least 4,000 years (Crane 1990a), and has been introduced to more-or-less

every country in the world. It is now amongst the most widespread and abundant insects on earth.

Bees are widely perceived to be beneficial, for their role in the pollination of crops and wildflowers and, in the case of the honeybee, for the production of honey. Because of these economic benefits there is reluctance to regard bees as potentially damaging to the environment. However, there is a considerable body of evidence suggesting that non-native bee species such as the honeybee can have negative impacts on native pollinators and may facilitate the spread of non-native weeds through pollination (Goulson 2003a; Goulson and Derwent 2004).

Honeybees are highly polylectic, usually visit a hundred or more different species of plant within any one geographic region (e.g. Butz Huryn 1997; Coffey and Breen 1997), and in total they have been recorded visiting nearly 40,000 different plant species (Crane 1990b). There is thus the potential for them to compete with a large number of other flower-visiting organisms. It is well documented that honeybees can displace native organisms from preferred forage sources through disturbance and suppression of resource levels, but few studies have found evidence for impacts at the population level (Goulson 2003a).

In Europe, honeybees are widely viewed as native. However, in northern Europe, it is unlikely that honeybees would be able to persist without human intervention, or would at best occur at low density. Feeding of colonies in the winter, and general care and maintenance of domesticated colonies almost certainly results in far higher densities of honeybees than would occur naturally (Goulson 2004). Thus, regardless of whether honeybees are native in northern Europe or not, there is the potential for them to have human-mediated negative impacts on populations of other flower-visiting insects, but to our knowledge this has never been studied.

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Bumblebees (*Bombus* spp.) are among the most abundant natural pollinators in temperate regions of the northern hemisphere. There is substantial evidence that many bumblebee species have suffered major range declines in the last 60 years, across both western Europe and North America (reviewed in Goulson 2003b; Goulson et al. in press). Most authorities agree that these declines are primarily driven by agricultural intensification, but there is evidence that honeybees can also have negative effects on bumblebees. In western USA, Thomson (2004) experimentally introduced honeybees and found that proximity to hives significantly reduced the foraging rates and reproductive success of *B. occidentalis* colonies. Similarly, Thomson (2006) found a strong overlap between the foraging preferences of honeybees and bumblebees which peaked at the end of the season when floral resources were scarce, corresponding with a negative relationship between honeybee and bumblebee abundance. To our knowledge the only study performed in Europe, by Walther-Hellwig et al. (2006), found that short-tongued bumblebees avoided areas of forage close to honeybee hives, while carder (*Thoracobombus*) bumblebees switched to foraging later in the day and were displaced from their preferred foodplant. However, displacement of this sort may not result in any impact at the population level (Thomson 2006).

Here we examine whether domesticated honeybee colonies impact upon native bumblebees in central Scotland, a region in which it is unknown whether honeybees are native. We examine effects on foraging worker body size, which provides a readily measurable indicator of resource availability during the larval stage.

Methods

The study was carried out between June and August 2006. As part of a larger survey (to be published elsewhere), bumblebee and honeybee abundance was quantified using 1 h searches at 100 sites spaced at 4 km intervals in a 40×40 km² (north-eastern corner at N49°:46':09'' W7°:32':59''; ordnance survey grid reference NN 525 215). Of these sites, 10 of those with honeybees present and 10 without honeybees were randomly selected, excluding sites at >200 m altitude. All sites consisted predominantly of lowland pasture/arable land. At each site, the search was restricted to a circle of approximately 100 m radius.

Bumblebee worker size can vary during the season, although no consistent patterns are evident (Knee and Medler 1965; Plowright and Jay 1968). To minimise seasonal effects, the 20 sites were revisited in as short a time window as possible, between 1 and 22 August, to sample bumblebees. Foraging workers of the four most abundant bumblebee species were studied, *Bombus terrestris* (L.),

Bombus lucorum (L.), *Bombus pascuorum* (Scopoli) and *Bombus lapidarius* (L.). At each site, up to approximately 10 workers of *B. lapidarius* and *B. pascuorum* were caught, and a total of 20 of the other two species (*B. terrestris* and *B. lucorum* are difficult to distinguish in the field) (Table 1). The flower each bumblebee was found foraging on was recorded. Bees were freeze killed, and the thorax width measured at the widest point using Vernier callipers. The thorax width is proportional to the overall size of the bee (Peat et al. 2005a, b). Weight is less useful and it is heavily influenced by the contents of the honey stomach.

Differences in worker size according to the presence or absence of honeybees was examined using General Linear Modelling (GLM) in SPSS 15.0. Two tests were carried out, both using thorax widths as the dependent variable. The first treated individual bees as replicates, and included the flower on which the bees were feeding as an explanatory factor.

Flowers were grouped into one of three categories, *Chamaenerion angustifolium*, *Centaurea nigra* and 'others'. This analysis also included site as an explanatory factor. The second test was more conservative, treating sites as replicates, and using a single mean size for workers of each species at each site (ignoring possible differences in bee size according to the flower on which they were caught), since bees within sites may be sisters and thus not truly independent (Darvill et al. 2004; Knight et al. 2005).

Results

A total of 538 bumblebees were sampled (277 from sites with honeybees present and 261 from sites without honeybees) (Table 1). At the time of year of the study, forage resources were few and bees were foraging on a small number of plant species. *C. angustifolium* was the most frequently used forage source (on which 46.0% of bumblebees were caught), followed by *C. nigra* (26.6%). The remaining visits were to a wide variety of more scarce flowers.

Treating individual bees as replicates, there were significant differences between bumblebee species in the mean size of workers ($F_{3,507} = 85.0$, $P < 0.001$), with mean size declining in the order *B. terrestris* > *B. lapidarius* > *B. lucorum* > *B. pascuorum* (Fig. 1). There was no significant effect of the flower species on which a bee was caught ($F_{2,507} = 0.93$, n.s.) and no bee species \times flower species interaction ($F_{6,507} = 1.10$, n.s.). The most powerful explanatory variable was the presence or absence of honeybees, with all bumblebee species having a smaller mean thorax width in sites where honeybees were present than in sites where they were absent ($F_{1,507} = 190$,

Table 1 Numbers of each bumblebee species caught at each study site, and numbers of honeybees observed in 1 h

Site	NGR		<i>Apis</i>	<i>B. terrestris</i>	<i>B. lucorum</i>	<i>B. pascuorum</i>	<i>B. lapidaries</i>	Total bumblebees
1	NN685055	Honey bees absent	0	12	7	13	1	33
2	NN565015		0	9	5	9	3	26
3	NN605015		0	1	0	10	11	22
4	NS885975		0	4	2	10	10	26
5	NS685935		0	10	10	11	2	33
6	NS885935		0	1	10	9	0	20
7	NS525895		0	7	14	11	0	33
8	NS805895		0	11	7	10	11	39
9	NS885895		0	0	0	9	0	9
10	NS885855		0	3	0	12	6	21
11	NN565175	Honey bees present	75	14	6	10	10	40
12	NN525015		22	0	5	12	0	17
13	NS525975		35	2	10	12	0	24
14	NS765975		49	14	5	11	1	31
15	NS525935		67	8	6	10	10	34
16	NS565935		31	0	0	4	10	14
17	NS525855		31	8	8	11	0	27
18	NS685855		19	3	17	0	0	20
19	NS815965		52	14	4	11	8	37
20	NN785015		50	8	5	10	10	33
Total			431	129	121	195	93	538

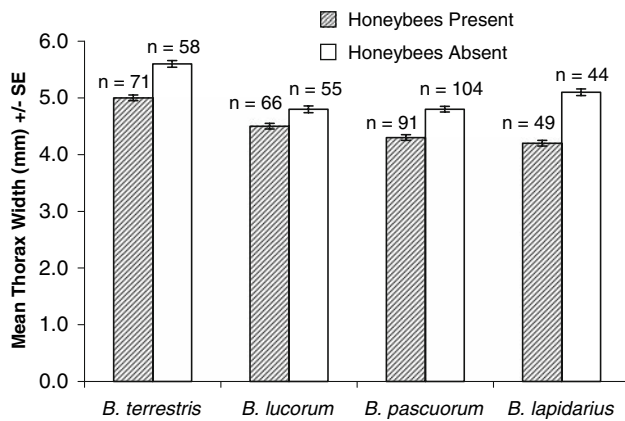


Fig. 1 Mean thorax widths (\pm SE) of workers of four bumblebee species in sites with and without honeybees

$P < 0.001$, Fig. 1). There was no significant interaction between bumblebee species and the presence/absence of honeybees ($F_{3,507} = 1.38$, n.s.).

Treating sites as replicates (a more conservative approach), the results remain unchanged. Differences in size between bumblebee species remain significant ($F_{3,57} = 35.4$, $P < 0.001$), and bumblebee species were significantly smaller in the presence of honeybees ($F_{1,57} = 93.6$, $P < 0.001$). There was no significant interaction between these factors ($F_{3,57} = 2.44$, n.s.).

Discussion

Our data clearly demonstrate that workers of these four common bumblebee species tend to be smaller in areas where they co-occur with honeybees. Worker size is highly variable in bumblebees, notably more so than in other social bee species (Goulson et al. 2002). Smaller workers tend to carry out within-nest tasks while the larger ones collect pollen and nectar. Only when forage is scarce or if the large workers are lost from the colony do the smaller ones leave the nest to forage (Goulson 2003b). Thus the smaller size of bumblebees at sites where honeybees were present might reflect depression of resource levels, forcing smaller bees to forage and so reducing the average worker size. Alternatively and perhaps more likely, worker size may be smaller in areas where honeybees are present due to reduced food availability as larvae; adult size in bumblebees is determined by the amount they are fed during the larval stage (Sutcliffe and Plowright 1988; Ribeiro 1994). Either explanation suggests a direct and significant impact of honeybees on bumblebees. Our data are not able to demonstrate a population-level effect, but it seems probable that if worker size is reduced that there would be effects on nest reproduction. Large workers collect more food per unit time than do their smaller sisters (Goulson et al. 2002; Peat and Goulson 2005), in part because large workers have higher visual acuity and so are better able to swiftly

locate floral resources (Spaethe and Weidenmuller 2002), and perhaps also because they are better able to forage in cool weather (Peat et al. 2005b). Hence a nest with smaller workers is likely to have a reduced food supply and so produce fewer or smaller reproductives. Gynes (new queens) depend on a plentiful supply of pollen to lay down fat reserves for hibernation, and gyne size is strongly linked to hibernation survival (Beekman et al. 1998).

Our data suggest that all four bumblebee species were approximately equally affected by the presence of honeybees. Honeybees are a relatively short-tongued species, and so we might predict greatest competition with the shorter-tongued bumblebee species such as *B. lucorum* and *B. terrestris*, compared to the longer tongued *B. pascuorum* (*B. lapidarius* is intermediate in tongue length). No such pattern is evident (Fig. 1). However, floral resources at the time of our study (late summer) were scarce, and all four bumblebee species and honeybees were foraging on the same small selection of flower species. Thomson (2006) observed a decrease in floral resources as the season progresses and an increasingly strong negative relationship between the number of honeybees and bumblebees later in the season. In more diverse floral landscapes or earlier in the year one might expect greater niche differentiation between species.

The majority of previous studies of impacts of honeybees on native bee species rely upon correlating abundance of honeybees and native bees. The problems with interpreting such data are considerable; displacement of native bees from favoured flower species or areas does not necessarily indicate that their population is reduced (reviewed by Goulson 2003a; Paine 2004; Thomson 2006). It is conceivable that the link between honeybee presence and small bumblebee worker size found in the present study is not causative, but that both are driven by some other, unidentified factor. For example, sites that are attractive to honeybees might be in some way less suitable for bumblebees, or only attract small bumblebees. We argue that this is unlikely. The presence of honeybees is controlled by two factors; the availability of suitable forage, and the presence of honeybee hives within foraging range. Since both honeybees and bumblebees were feeding on the same small number of forage plants at all sites, differences in forage availability or type are unlikely to be causing this effect. Indeed, honeybees are well known to target high-quality forage patches and to recruit nestmates to these patches, so we would expect honeybees to be present in sites that are also best for bumblebees. Wild honeybee colonies are scarce in the UK due to parasites, particularly the introduced mite *Varroa destructor*, so the distribution of honeybee hives is very largely controlled by humans. We would expect them to be placed preferentially in places with good forage availability, which ought also to be high

quality sites for bumblebees. Hence there is no obvious reason to expect honeybees to occur preferentially in sites that are poor for bumblebees; quite the reverse. However, manipulation of honeybee densities would certainly be desirable, rather than relying on their existing distribution, but is exceedingly hard to do at the landscape-scale required when hives are owned and managed by numerous individuals (as was the case in this study).

It would be informative to examine nest survival and reproduction in areas with and without honeybees (following Thomson 2004), to examine whether small worker size does impact on nest reproduction. Nonetheless our data strongly suggest a direct competitive effect of honeybees on bumblebees, and are the first to do so in northern Europe. Our data are in accordance with those of Thomson (2004) from the USA, who found that colonies of *B. occidentalis* near honeybee hives produced fewer and smaller gynes than those further away.

The bumblebee species studied here remain widespread and abundant, but many other species have declined in recent decades and are of conservation concern. If honeybees do impact on bumblebees as our data suggest, then care should be taken when positioning hives; for example it would seem sensible to avoid positioning large numbers of hives near or in sites where rare bumblebee species survive. At present there is no central register of honeybee hive locations in most countries, including the UK, and there are no controls on where hives are placed. It is thus extremely difficult to monitor or manage this potential threat to native bee species.

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