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Impacts of the Use of Nonnative Commercial Bumble Bees for Pollinator Supplementation in Raspberry

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ABSTRACT Evidence for pollinator declines has led to concern that inadequate pollination services may limit crop yields. The global trade in commercial bumble bee (*Bombus* spp.) colonies provides pollination services for both glasshouse and open-field crops. For example, in the United Kingdom, commercial colonies of nonnative subspecies of the bumble bee *Bombus terrestris* L. imported from mainland Europe are widely used for the pollination of raspberries, *Rubus idaeus* L. The extent to which these commercial colonies supplement the services provided by wild pollinators has not been formally quantified and the impact of commercial bumble bees on native bees visiting the crop is unknown. Here, the impacts of allowing commercially available bumble bee colonies to forage on raspberry canes are assessed in terms of the yield of marketable fruit produced and the pollinator communities found foraging on raspberry flowers. No differences were found in the abundance, diversity, or composition of social bee species observed visiting raspberry flowers when commercial bumble bees were deployed compared with when they were absent. However, weight of marketable raspberries produced increased when commercial bees were present, indicating that wild pollinator services alone are inadequate for attaining maximum yields. The findings of the study suggests that proportional yield increases associated with deployment of commercial colonies may be small, but that nevertheless, investment in commercial colonies for raspberry pollination could produce very significant increases in net profit for the grower. Given potential environmental risks associated with the importation of nonnative bumble bees, the development of alternative solutions to the pollination deficit in raspberry crops in the United Kingdom may be beneficial.

KEY WORDS *Rubus idaeus*, *Bombus terrestris*, pollination limitation, Scotland, agriculture

A potential pollinator deficit for the production of entomophilous crops is an increasing global concern as a result of apparent declines in a range of pollinator species worldwide (Allen-Wardell et al. 1998, Steffan-Dewenter et al. 2005). Although long-term trends in crop production reveal no current global pollination problem (Aizen et al. 2008), there is an increasing dependence on animal-pollinated plants that is not being met by increases in pollinator populations (Aizen and Harder 2009). Bumble bees (*Bombus* spp.) provide a superior pollination service for many flowering crop plant species (Free and Williams 1976, Stanghellini et al. 1997, Thomson and Goodell 2001), but declines in these insects have been occurring throughout their range (Kosior et al. 2007, Colla and Packer 2008, Xie et al. 2008, Grixti et al. 2009). Bumble bee declines in Europe have largely been attributed to changes in land management associated with the rise of intensive agriculture which has resulted in the reduction of floral abundance and diversity in the rural environment (Goulson et al. 2008, Williams and Osborne 2009). In the United Kingdom at least, it seems that those plant species that provide forage resources for bumble bees have been disproportionately affected by these changes (Carvell et al. 2006). As a result, bumble bee declines are particularly apparent in the agricultural environment and evidence suggests that rural areas now support lower densities of bumble bee colonies that do urban areas (Goulson et al. 2002, Osborne et al. 2008b).

In response to an apparent or perceived insufficiency of natural pollinators, it has become increasingly common for farmers of certain entomophilous crops to buy commercially available bumble bee colonies for field use to supplement the pollination service provided to their crops. Currently, ≈30–60,000 colonies per yr are imported into the United Kingdom for the pollination of greenhouse or field crop plants. However, this practice may be associated with detrimental ecological consequences, including pathogen spillover from commercial colonies to wild bumble bee populations, competitive interactions between introduced bumble bees and local pollinators, and introgression of native and nonnative subspecies of *B. terrestris* (Goulson et al. 2008).

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Although the import of commercially reared bumble bee colonies for field crop pollination is a huge industry, little research has been carried out to determine the need for pollinator supplementation for these crops in the United Kingdom. Although growers are unlikely to undertake this practice if yield loss by pollinator limitation is not significant, the effectiveness of current populations of native bees for producing good yields of high-quality crop, and the capacity of commercial colonies to supplement this have not been independently quantified. Soft fruit production is a significant proportion of the market for commercially reared bumble bee colonies in the United Kingdom, and one such example is raspberry, *Rubus idaeus* L. Raspberry production in Europe has been estimated at 316,000 metric tons per yr (www.fruitgateway.co.uk). Raspberry plants produce aggregate fruit consisting of several single drupelets, each of which must be individually fertilized to develop. Commercial raspberry cultivars are self-compatible (Colbert and de Oliveira 1990, Willmer et al. 1994) and the exclusion of pollinators is generally found to have no negative effect on fruit set (Couston 1963, Szklanowska and Wienlarska 1993, Cane 2005 but see Shanks 1969). This is because raspberry flowers often autopollinate as a result of contact between the stamens and the outermost ring of pistils (Cane 2005). However, the innermost pistils are generally not fertilized in the absence of insect pollinators, and this results in a terminal tuft of undeveloped drupelets (Shanks 1969, Szklanowska and Wienlarska 1993) rendering the fruit unsuitable for marketing. Insect visitation to raspberry flowers has been found to result in increased drupelet number and fruit weight (Couston 1963, Shanks 1969, Chagnon et al. 1991, Szklanowska and Wienlarska 1993, Cane 2005), and there is also evidence that some raspberry cultivars may demonstrate metaxenia (an enhanced development of maternal tissues as a result of fertilization by pollens of other varieties) giving rise to heavier fruit as a result of pollen transfer among cultivars (Colbert and de Oliveira 1990). Therefore, insect-mediated cross-pollination may provide economically important yield increases for raspberry production.

Raspberry flowers produce large quantities of nectar (Whitney 1984, Willmer et al. 1994) and are known to be highly attractive to bees (Free 1968). Attributes of this species are thought to be especially well suited to promoting visitation by bumble bees (Whitney 1984), which are extremely effective pollinators of this species due to their particular foraging behavior, morphology, and ability to forage in adverse environmental conditions (Gyan and Woodell 1987, Willmer et al. 1994). Many soft fruit growers in the United Kingdom now buy commercially reared bumble bee colonies for use in fields of raspberries to boost local pollinator availability. However, because many of the bee species native to the United Kingdom are highly attracted to raspberries (Willmer et al. 1994), it is possible that pollinator limitation for this crop is low.

Here, the effect of the use of commercially available bumble bee colonies on raspberry yields in central Scotland is assessed. The effect of the presence of these colonies on the natural pollinator communities foraging on the raspberry flowers also is examined to look for evidence of competitive interactions between commercial bumble bees and native social bees.

Materials and Methods

Fieldwork. Fieldwork was carried out at the Scottish Crop Research Institute (SCRI) in Invergowrie, central Scotland. The experimental site consisted of ≈0.5 ha of land planted with rows of raspberry canes of mixed genotypes. Replicate plots consisted of five canes of a single genotype planted in close proximity to one another along a portion of a row. All plots were uncovered during the first three weeks of the study, but open-ended polytunnels were erected over these at the end of the third week of recording, following normal commercial practice. Raspberry plants were provided with water and nutrients through an irrigation system which allowed the precise delivery of quantities of water and liquid feed calculated to maximize raspberry yields and ensure that these resources do not limit fruit production. Four commercially reared colonies of *B. terrestris* (Koppert Biological Systems, Berkel en Rodenrijs, The Netherlands) were placed at one end of the rows of raspberries, so that the density of colonies was consistent with that recommended by the retailers (six to nine colonies per ha). These colonies were opened or closed on alternate weeks of the study such that during 1 wk the imported bees were free to forage, but during the following week, they were contained within their colonies. This approach continued for 6 wk (three open, three closed), commencing on the 24 May, starting with the colonies open. During the weeks when the colonies were closed, colonies were provided with sugar solution ad libitum and ≈20 g of pollen per week (collected from honey bee hives by using pollen traps). Access to sugar solution was maintained during periods when colonies were open because this is standard practice by commercial growers when using colonies for pollination of field crops. When colonies were closed, an entrance containing a one-way valve allowing traffic into the colony but not out remained open to allow access to any foragers spending the night away from the colony.

Fifty replicate plots of five plants (distributed across three rows of canes) were selected for inclusion in the study. These included twenty-nine different novel genotypes (developed as part of the SCRI *Rubus* breeding and genetic research program; Harrison et al. 1996) ranging in representation from one to five plots each. (Each plot contained plants belonging to just one of these genotypes). Plots were visited twice a week at 1000 hours between 26 May and 3 July. During each visit, a 100-m transect was walked at a slow and constant pace along the length of each of the three rows and the number of insects visiting flowers were recorded for each plot of five plants. Each transect took ≈15 min to complete. because the majority of observations were of social bees (*Apis mellifera* L. or those belonging to the genus *Bombus*), only these species were classified to species level. Native *Bombus terrestris audax* Harris, commercial *Bombus terrestris dalmatinus* Dalla Torre, and bees belonging to the *Bombus lucorum* L. complex (Murray et al. 2008) were combined in a single group due to difficulties in reliably distinguishing workers of these taxa in the field. After observations of insect visitation, the number of receptive flowers per plot of five plants was recorded, and 10 randomly selected flowers were marked with a small twist of colored wire around the pedicel. Where fewer than 10 flowers were present, all flowers were marked in this way. The color of the wire was indicative of the day upon which the flower was marked.

Ripe fruit present on raspberry canes was hand-picked twice weekly between 1 July and 10 August. After each picking, the weight of marketable fruit produced from each plot was recorded. Wires also were collected to allow assessment of the time taken for flowers to develop into fruit. The number of unfertilized flowers and crumbly fruit (in which several drupelets failed to develop giving rise to a deformed fruit) marked with each wire color were recorded allowing assessment of fruit quality between the two treatments.

Weather data for the duration of the study period were obtained from the UK Met Office weather station in Leuchars, Fife.

Statistical Analysis. All analyses were carried out using SPSS, version 16.0 (SPSS Inc., Chicago, IL). Five plots were removed from the experimental site during the course of the investigation as a result of poor plant health and these were excluded from all analyses.

The number of social bee visits observed per raspberry flower recorded was calculated for each recording day. In addition, the ratios of *B. terrestris*/*B. lucorum* visits to the sum of all other social bee visits and a Simpson's index of diversity for social bee visits also were calculated. Mann–Whitney *U* tests were used to compare these measures between days when imported colonies were free to forage (colonies open) and days when the imported bees were contained within their colonies (colonies closed).

For each genotype, the time taken for each tagged flower to develop into a ripe fruit was calculated and a mean taken across all tagged fruit. This value was taken to be representative of the approximate time taken for all flowers belonging to that genotype to develop into fruit such that data collected during the first recording period could be paired with appropriate yield data. The proportion of total tagged flowers that failed to develop into marketable fruit either because flowers did not develop or because the number of drupelets that developed was low giving rise to "crumbly" fruit was calculated per day of tagging, and Mann–Whitney *U* tests were used to look for differences in these depending on colony status (open versus closed).

A linear mixed-effects model was built to assess the effect of colony status on the weight of fruit produced per five plant plot. The response variable was total weight of ripe marketable fruit harvested per plot per time point (log transformed). The repeated measures and nested elements of the experimental design were incorporated into the model by specifying plot and date as random effects (with plot included as the subject variable). Fixed effects included in the initial model were plant genotype, distance from the nearest commercial colony, flower number counted during the initial recording period (log transformed) and colony status during the initial recording period (open or closed). An interaction effect between colony status and distance from the nearest colony and between colony status and genotype also were tested for in this study. Yield scores with a value of 0 were excluded from the analysis because raspberries were only harvested when a significant number of fruit had become ripe, thus observations of 0 did not represent yield of 0 g but simply the lack of raspberry harvesting on that day. Calculating yield-to-flower ratios exposed six obvious outliers. Because all outliers were associated with low flower counts, these outliers are likely to have resulted from overestimation of yield per flower as a result of the inclusion of fruit derived from flowers from one or more of the previous flower counts in the corresponding yield measurement. Analyses were conducted with and without these outliers. Because removal of outliers did not affect the qualitative patterns observed results presented here exclude outlying data. The final model was created by stepwise removal of factors.

We used *t*-tests to compare daily averages of temperature and daily rainfall in weeks when colonies were open versus closed.

Table 1. Total number and percentage contribution of different insect taxa observed visiting raspberry flowers

Pollinator taxon	No. visits	% total visits
A. mellifera	102	5.1
B. hortorum	1	0.1
B. lapidarius	16	0.8
B. monticola	43	2.2
B. pascuorum	73	3.7
B. pratorum	299	15.1
B. terrestris/*B. lucorum*	1,427	72.0
B. bohemicus	1	0.1
Other (non-*Bombus*/*Apis*)	20	1.0
Total	1,982	100.0

Results

Many taxa were observed feeding on raspberry flowers, including several solitary bee and syrphid fly species. However, 99% of individuals observed belonged to *A. mellifera* or a *Bombus* species. At least nine species of social bee were represented, but just three species categories (*B. terrestris*/*B. lucorum, B. pratorum,* and *A. mellifera*) constituted the majority of observations (Table 1).

Abundance of social bee visits per raspberry flower was not affected by colony status ($U = 13$, $P = 0.49$) nor was the ratio of *B. terrestris*/*B. lucorum* to other social bee species ($U = 13$, $P = 0.49$). Social bee

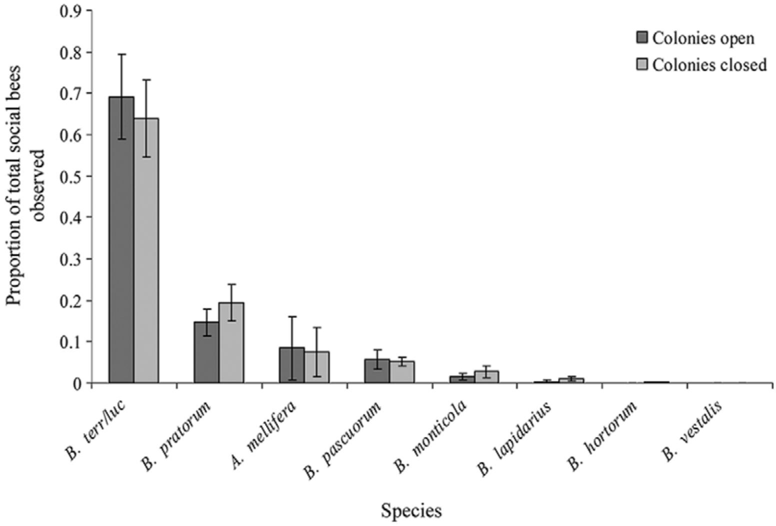

Fig. 1. Mean proportion contribution of different species to observed social bee visits to raspberries per day when commercially reared bumble bee colonies were open (free to forage) versus closed (foragers contained) ± SE. *B. terr/luc* refers to all individuals belonging to wild or commercial *B. terrestris* or any of the *B. lucorum* species complex.

diversity on raspberry flowers (as measured by Simpson's index of diversity) was the same regardless of colony status ($U = 14, P = 0.59$). Overall, there was no apparent effect of allowing commercially reared colonies to forage on the species composition of social bees foraging on raspberry flowers (Fig. 1).

Three thousand seven hundred and forty four tags were reclaimed from ripe raspberry fruit. The average time taken for tagged raspberry flowers to develop into ripe fruit varied among genotypes and ranged from 34 to 41 d. Based on their means, genotypes were assigned to one of three groups for which the mean times from flower to fruit were 35 d (SE ±0.22, $N = 493$), 37 d (SE ±0.13, $N = 1905$), and 40 d (SE ±0.14, $N = 1346$). Recording period pairs based on these data were 34, 38, and 41 d (±1) apart, respectively. Failure rate of marked fruit due to undeveloped flowers or crumbly fruit was low (1.7% marked flowers), and there was no difference in failure rates between proportions of failed fruit due to undeveloped flowers or proportions of crumbly fruit per recording period when colonies were open or closed ($U = 10.5, P = 0.24$ and $U = 9.5$, $P = 0.18$, respectively).

As would be predicted, number of flowers counted in the initial recording period was strongly positively correlated with weight of marketable fruit picked on the corresponding date in the second recording period ($F = 594.34$; df = 1, 309; $P < 0.001$), and yield of marketable fruit also differed significantly among genotypes ($F = 14.87$; df = 28, 289; $P < 0.001$). When other factors were taken into account, a greater weight of marketable raspberries was picked in time periods corresponding to weeks in which colonies were open compared with weeks in which they were closed ($F = 6.75$; df = 1, 336; $P = 0.010$). This was reflected by clear differences in raw yield (when divided by corresponding flower number) during the first 4 wk of the study but was not clear in the final 2 wk (Fig. 2). When yield was standardized by division by number of receptive flowers open during the corresponding recording period, the increase in average yield associated with allowing the commercial bumble bee colonies to for-

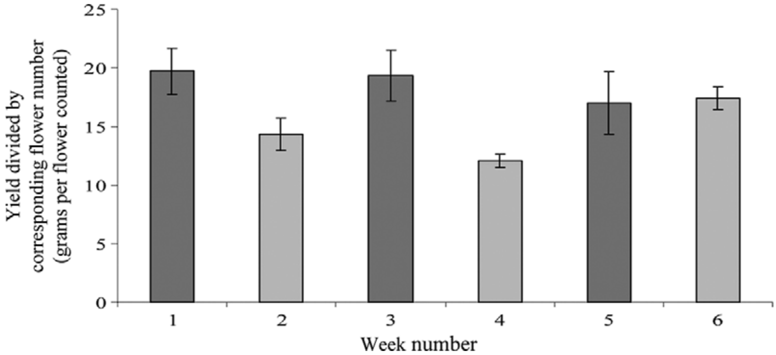

Fig. 2. Average yield of raspberries per flower counted in the corresponding recording period ± SE.

age was 27.93%. Distance of plots from colonies did not affect the total yield of fruit ($F = 2.13$; df = 1, 320; $P = 0.145$), nor was there any interaction effect between distance of plots from colonies and colony status ($F = 0.97$; df = 1, 282; $P = 0.681$) or genotype and colony status ($F = 1.43$, df = 28, 226; $P = 0.081$).

Average weekly weather was found to be similar throughout the duration of the study (data not shown), and no significant difference was found in daily averages of temperature or daily rainfall in weeks when colonies were open versus weeks when they were closed ($t = 0.41$; df = 41; $P = 0.68$ and $t = 0.57$, df = 41, $P = 0.57$, respectively).

The parameter estimate for colony status obtained from the model described above was used to calculate the change in yield associated with the presence of commercial colonies in the hypothetical situation in which the log(yield) value per plot per harvesting date in the absence of commercial colonies was 3.11 (the mean value when nests were closed) and all other factors remain constant. In this case, raspberry yield increases from 1,286.4 to 1,393.7 g per plot per harvesting date, an increase of 107 g or 8.3% (95% confidence intervals, 6.7%/10.3%). At the density at which canes were planted at SCRI (≈780 plots per ha), this translates to a yield increase of 83.7 kg/ha per time point. Because the average number of recording dates for which yield was greater than zero for each plot was nine, the total yield increase across the 6 wk of the study would be 753.3 kg. At a market value of ≈£6/kg of first class (for sale as fresh) raspberries in 2010, this could translate into an increase in gross profit of £4520/ha. The cost of providing bumble bee colonies at the density used here is £336/ha (Koppert Biological Systems, in 2009) giving an increase in net profit of £4,184/ha (95% CI, −£1392/+£7841). If raspberries are sold for pulp or for sale as frozen, market values are much lower (≈£0.7/kg and £2/kg, respectively), reducing the estimated increase in net profit associated with the use of commercial bees to £191/ha (95% CI, −£459/+£618) or £1,170/ha (95% CI, −£690/+£2,387), respectively.

Discussion

The observed yield increase in fruit produced from flowers receptive when commercial bumble bee colonies were allowed to forage compared with those receptive when the colonies were contained suggests that in the absence of commercial bumble bee colonies, pollination service does limit the yield of raspberry crops, at least at this site.

Despite the uniformity of the pollinator community observed on the raspberry flowers, the effect of commercial colony status on yield suggests that individuals of the commercial colonies did visit the raspberry flowers during periods when they were allowed to forage. It is therefore surprising that the relative contribution of *B. terrestris*/*B. lucorum* to other social bee species observed foraging on raspberry flowers did not increase during these weeks. This observation could either indicate that *B. terrestris* from commercial colonies were displacing native *B. terrestris, B. lucorum* complex species, or both or that some aspect of the experimental design resulted in undersampling of individuals from commercial colonies, for example, if individuals from commercial colonies were active at times of day other than that at which sampling took place. The latter may be more likely because there was no evidence for an impact of colony status on any social bee species visiting raspberry, and it seems improbable that negative effects of competition from commercial colonies should be restricted to wild *B. terrestris*/*lucorum.*

The increase in raspberry yield associated with the activity of commercially reared bumble bees in the absence of any significant difference in the rate of flower failure suggests that yield differences were the result of an increase in the weight of individual fruit rather than in the number of marketable fruit produced. Drupelet number in fruit produced was not counted, but it is likely that the increased weight of raspberries that developed from flowers pollinated when commercial bees were free to forage was the result of increased drupelet number due to more complete fertilization of ovules. However, because some raspberry cultivars have been shown to demonstrate metaxenic effects (Colbert and de Oliveira 1990), greater rates of cross-pollination among genotypes also may have contributed to this effect. Differences in yield may represent a greater frequency of visits to individual flowers as a result of increased pollinator numbers during periods when commercial colonies were allowed to forage. However, it also is possible that these differences could be partly attributable to the differing characteristics of imported versus native *B. terrestris.* Studies have shown that commercial colonies of *B. terrestris* demonstrate greater nectar-foraging efficiency compared with laboratory reared wild-caught *B. terrestris audax* (Ings et al. 2006), presumably the result of an increased rate of floral visitation per bee. Commercial *B. terrestris* also were found to have a larger body size than native *B. terrestris* (Ings et al. 2006), so it may be that they transfer more pollen grains per floral visit. Therefore, on an individual basis, commercial bees might be expected to provide a more effective pollination service than native British bumble bees. In addition to this, it has been shown that workers from commercial bumblebee colonies provided with nectar tend to focus on pollen collection to a greater extent than those that are not (Plowright et al. 1993). Because pollen-collecting bees have been shown previously to transfer larger quantities of pollen than nectar collectors (Goodell and Thomson 2007), it is possible that the availability of nectar within commercially reared colonies may increase pollen transfer by commercial bees compared with wild bees simply as a result of differences in foraging behavior.

Although differences in yield due to colony status were clearly evident during the first 4 wk of the study, there was no observable yield difference during the final 2 wk (Fig. 2). This may reflect an increase in the abundance of native bees as a result of seasonal colony growth, although it also may be partly due to a deterioration in vigor of the commercial colonies toward the end of the study (G.C.L., unpublished data).

A comparison of observations of bees visiting raspberry flowers in this study (summer 2009) with those reported in a study carried out at the same site (SCRI) in the summers of 1990 and 1992 (Willmer et al. 1994) suggests dramatic alterations in the local community of social bees between these years. In the current study, observations included at least seven bumble bee species (*B. terrestris*/*B. lucorum* included as a single species) as well as *A. mellifera*, whereas Willmer et al. (1994) recorded just five bumble bee species (*B. terrestris* and *B. lucorum* recorded separately) and *A. mellifera.* Regardless of commercial colony status (open or closed) the *B. terrestris*/*B. lucorum* species group contributed a much greater proportion to overall bee sightings in the current study (72%) than did the *B. terrestris* and *B. lucorum* categories from Willmer et al. (1994) (≈30%), and *B. pratorum* also was observed proportionately more commonly (15% in this study versus ≈8% by Willmer et al. (1994). Conversely, *A. mellifera* and *Bombus lapidarius* L. were far less well represented in the current study (5.1 and 0.8%, respectively) than in 1990 and 1992, in which they made up ≈34 and ≈23% of observations. Willmer et al. (1994) note that *B. lapidarius* was the commonest bumble bee species observed at Invergowrie despite its rarity in this region before the 1980s, but in the current study this species was poorly represented and has been relatively uncommon in central Scotland in the summers of 2007 and 2008 (G.C.L., unpublished data). The reduced number of *A. mellifera* observed may indicate a similar drop in abundance of this species but because the positioning of domestic hives during the studies is unknown, these differences may simply reflect differences in local hive density. The presence of *Bombus monticola* Smith visiting raspberry flowers in the current study is notable because this species is usually associated with upland bog and heath lands and also has shown range restrictions in the United Kingdom over the past 60 yr (Goulson 2010). The presence of this montane species at SCRI is surprising because Invergowrie is low lying, and the majority of the land surrounding this area comprises urban space or arable agricultural land.

Willmer et al. (1994) also note differences in attributes between bee visitors observed in their study, suggesting that some species might provide a more effective pollination service for raspberries than others. *B. lapidarius* demonstrated particularly fast handling times of raspberry flowers compared with other *Bombus* species, and *B. terrestris* and *B. lapidarius* were shown to transport more pollen grains between flowers than *Bombus pascuorum* Scopoli and *Bombus pratorum* L., mainly as a result of their larger body sizes. All species of *Bombus* were found to transport more pollen grains than did *A. mellifera.* These findings demonstrate that pollinator community composition may be as important in determining pollination service as pollinator abundance and also suggest that a decrease in proportion of visits by *B. lapidarius* could potentially result in less effective pollination of raspberry flowers.

Although this study demonstrates the value of commercial *B. terrestris* colonies for boosting raspberry yields, there are ecological concerns associated with the importation of these colonies into the United Kingdom (Goulson 2003, Ings et al. 2005, Ings et al. 2006). Although *B. terrestris* has been demonstrated to pollinate raspberries very effectively (Willmer et al. 1994), studies have shown that other species also can provide a high-quality pollination service for this plant species. For example, the solitary bee species *Osmia aglaia* Sandhouse is a superior pollinator of raspberry flowers in the United States (Cane 2005), and attributes of *B. lapidarius* suggest that it also can provide a very effective pollination service for this species in Europe (Willmer et al. 1994). At times of year when native bumble bees are flying, it is possible that measures targeted toward promoting populations of those native bee species known to provide an efficient pollination service for raspberries may be able to achieve similar increases in yield to bumble bee importation. Such measures might include the planting of targeted flower strips or the provision of nesting sites for solitary bees. This approach could, in principle, reduce the economic costs associated with the importation of bumble bees and also eliminate any ecological risks associated with the use of commercial colonies. The inclusion of subsidies for such measures into appropriate agri-environment schemes also might be beneficial, providing an additional incentive for farmers to consider these alternatives. Because the model presented in this study suggests that between 90 and 93% of total yield is achieved in the absence of commercial bumble bee colonies, the contribution by native pollinators is likely to be high, such that small increases in their population sizes may be enough to negate the effect of the commercial colonies. However, it must be borne in mind that growers are able to extend the fruiting period of raspberries with the use of hardy varieties, polytunnels, and glasshouses such that timing of flowering may not always correspond to pollinator phenology. In these situations, artificially reared colonies may be required to maximize yield in which case, the use of native *B. terrestris audax* (newly available from Biobest Biological Systems in 2010) or the rearing of *B. lapidarius* may provide an alternative solution if the ecological risks of introducing nonnative subspecies are considered to be great.

In conclusion, this study suggests that yields of marketable raspberries can be increased by the presence of commercially reared colonies of the bumble bee *B. terrestris.* No evidence was found to suggest that commercial bees had any negative effects on species abundance or composition of other social bee pollinators, although more thorough investigation would be required to satisfactorily exclude the possibility of competition between commercial bumble bees and wild pollinator species. Although this study provides an important insight into the use of commercially reared bumble bee colonies for soft fruit pollination, much of its value lies in highlighting the necessity for further study into a range of areas relating to this work. First, the mechanisms behind yield differences remain unclear because there was no evidence that deployment of commercial bumble bee colonies resulted in a greater density of bees on the crop plant. Further work is required to assess the propensity of commercially reared bumble bees to forage on local crop plants and any displacement of native bees of the same or closely related species by individuals from imported colonies. This could be achieved using a combination of mass-marking individuals from commercially reared colonies (as in Osborne et al. 2008a) and analyzing pollen loads coming into the colony to asses use of resources (as in Whittington and Winston 2004). Secondly, the pollination requirements of other soft fruit crops should also be considered, because different plant species will have differing pollination requirements and may be differentially attractive to commercial or native bees. Third, more research will be required to elucidate the reality of the perceived environmental risks associated with the importation of commercial bumble bees into the United Kingdom. If these risks are considered to be high, there is a need to develop viable alternatives to the use of these colonies. This could include both the development of methods of boosting natural pollinator populations in soft fruit growing regions, for example by the sowing of targeted flower mixes and/or provision of nesting sites, as well as use of native bumble bee species for use at times when natural pollinators are not active. In addition, a comparison of observations made during this study with those made at the same site in 1990 and 1992 demonstrates that we know little about the changing community structure of pollinator populations. Whether the observed differences reflect yearly fluctuations or ongoing trends in species composition, these differences are likely to have important implications for crop pollination and pollinator conservation into the future.

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