

Exploitative competition alters bee foraging and flower choice

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Abstract In this field experiment, we test and support the hypothesis that exploitative competition between bees can influence several aspects of their foraging behaviour. Three treatments of lavender patches were set out: bumble bees excluded, honey bees excluded, control. Bumble bees are known to handle lavender flowers more rapidly than honey bees, partly due to their longer tongues. As predicted, excluding these superior competitors consistently ($n=4$ trials) and greatly increased honey bee numbers per patch (14-fold increase; $P<0.001$). The exclusion of bumble bee also caused multiple changes to honey bee foraging behaviour: time spent on a patch (+857 %; $P<0.001$), flower handling time (+16 %, $P=0.040$), interval between probed flowers (−27 %, $P=0.012$), proportion of interflower flights (−26 %, $P<0.001$) and flowers rejected (−12 %, $P<0.001$). Conversely, and also as predicted, excluding honey bees had no effect on bumble bee numbers or foraging behaviour. A key consequence of bumble bee exclusion was to increase the mean flower nectar content from 0.007 to 0.019 μl (+171 %). By constructing an energy budget, we find that this leads to honey bees making a substantial, rather than a marginal, energetic profit per flower visited. Our results show the foraging behaviour of individual

bees is extremely flexible and greatly influenced by the effects of interspecific competition on nectar rewards. Collectively, these individual decisions can have rapid and important consequences at the community level, including competitive exclusion.

Keywords Competitive exclusion · Exploitative competition · Foraging behaviour · Interspecific competition · Niche partitioning · Foraging energetics

Introduction

Exploitative competition, where multiple species share a limited resource, is considered the most common form of competition amongst terrestrial animals (Schoener 1983). However, it is challenging to determine its influence on foraging behaviour and ecology as it often co-occurs with interference competition, in which there is direct inhibition, such as aggression, amongst individuals (e.g. Persson 1985; Hart 1987; Eccard and Ylönen 2002; Ward et al. 2007; Segers and Taborsky 2012).

Bee foraging is an excellent system to investigate the consequences of exploitative competition. Bees are diverse, with many species typically foraging in the same area and visiting the same flower species. Foraging bees compete for two largely generic resources, nectar and pollen, which are often scarce. Indeed, the majority (>90 %, Heinrich 1976) of the ‘standing crop’ of nectar produced by plants attractive to bees is consumed each day, leaving many flowers either empty of nectar or containing only small volumes (c. 0.1 μl , Wetherwax 1986; Williams 1998; Herrera 1989; Balfour et al. 2013). Consequently, both honey bee (*Apis mellifera*) and bumble bee (*Bombus* spp.) workers often need to visit hundreds of flowers per foraging trip (e.g. Ribbands 1949; Heinrich

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1979). Although some species defend patches of flowers from potential competitors (see Severinghaus et al. 1981; Biesmeijer and Slaa 2006), bees generally forage without physically interacting (e.g. Inouye 1978; Schaffer et al. 1979). In addition, bees are highly mobile and very sensitive to changes in floral rewards (e.g. Free 1965; Heinrich 1979; Seeley 1995). As such, they have the potential to respond quickly to resource depletion resulting from competition.

The fundamentals of interspecific competition and resource partitioning between bee species are thought to be reasonably well understood (e.g. Kevan and Baker 1983). Virtually all of this understanding, however, is from studies of different bumble bee species (e.g. Brian 1957; Inouye 1978; Harder 1983). As such, the frequency and scope of competition between honey bees and bumble bees remains largely unknown, even though they frequently co-occur (e.g. Herrera 1989; Goulson and Sparrow 2009; Balfour et al. 2013) and in spite of indirect evidence for competitive effects (Thomson 2004; Goulson and Sparrow 2009). Further understanding these interactions is relevant to recent concerns regarding their conservation (Goulson et al. 2008; Potts et al. 2010), the colonisation of honey bees and bumble bees to areas where they are not native (e.g. Paine 2004; Ishii et al. 2008) and their pollination services (e.g. Greenleaf et al. 2006; Brittain et al. 2013). There is evidence that competition between *A. mellifera* and *Bombus* negatively impacts the latter (Thomson 2004; Goulson and Sparrow 2009). Presumably, the opposite can also occur. Bumble bees are known to handle flowers faster than honey bees (Free 1968; Heinrich 1979; Kevan and Baker 1983) and also have longer tongues, both of which may provide a competitive advantage. Recent research has shown that *Bombus* visit lavender (*Lavandula x intermedia* ‘Grosso’) flowers over three times faster than honey bees (Balfour et al. 2013). Experimental shortening of lavender corolla tubes (from c. 7 to c. 3 mm) showed that this was partly due to the longer tongues of bumble bees (7.8–8.9 mm vs 6.6 mm in honey bees) which allows them easy access to Grosso’s concealed nectar, the main reward being sought by lavender visitors (Herrera 1989; Balfour et al. 2013). Bumble bees were c. 10 times as common as honey bees on lavender flowers (Balfour et al. 2013; Garbuzov and Ratnieks 2013) despite an abundance of honey bees on nearby patches of borage (*Borago officinalis*) suggesting that bumble bees were outcompeting honey bees on lavender.

In this study, we test the hypothesis that bumble bees are deterring honey bees from foraging on lavender via exploitative competition. We predicted that excluding bumble bees would increase standing nectar rewards and, in turn, the number of honey bee foragers. Conversely, we predicted that honey bee exclusion would not affect bumble bee numbers, because the few *A. mellifera* normally present on the lavender flowers would little affect nectar availability.

Materials and methods

Study site, species and experimental setup

In August 2012 and July–August 2014, we studied honey bees and bumble bees foraging on three experimental 2.0×1.1 m patches of lavender, variety Grosso (*Lavandula x intermedia*). Each patch comprised 66 plants, each in a 3 l pot. Plants were in full flower, each with 8–23 inflorescences of 3–16 open flowers (sometime called florets).

The patches were 100 m apart on the University of Sussex campus, southern England, in a sheltered, grassy area with full sun. Grosso is the most widely grown lavender variety for oil production (Upson and Andrews 2004) and has blue flowers with petals fused basally to form a long (average depth 7.2 mm) narrow corolla tube with basal nectaries.

We studied bee foraging on Grosso as our previous research (Balfour et al. 2013) on this variety had directly led to the hypothesis that exploitative competition between bumble bees and honey bees was deterring honey bees from foraging on this plant.

We excluded bumble bees from one lavender patch (BBE) and honey bees from another (HBE). No insects were excluded from a third, control (CON), patch. All insects were excluded overnight, 1800–0900 h, by covering all patches with 4 mm mesh netting. Between 0900–1800 h when foraging data were collected, we excluded bees foraging in the ‘wrong’ patch (e.g. bumble bees on BBE patch) by gently tapping them with a bamboo cane. Care was taken not to disturb bees foraging in the ‘correct’ patches. Results (Fig. 2) show that this method was highly effective, i.e. the mean numbers of bumble bees in the BBE patches were <0.1 per count. The few bees recorded foraging in the ‘wrong patch’ were due to the difficulty of differentiating, without close inspection, smaller *Bombus pascuorum* from honey bees, both of which were approximately the same size and colour. In 2012, a single five-day trial was made. In 2014, three trials were made by switching treatments at the start of Days 4 and 7 (3 and 6 August 2014) so that each patch was studied under all three treatments (BBE, HBE and CON).

Quantifying flower-visitor numbers and bee behaviour

To determine the overall effect of bumble bee exclusion on the number of honey bee foragers per patch, and vice versa, we quantified the number of all insects foraging on the lavender flowers at each patch once every 30 min from 1000–1800 h by making a near instantaneous count (see Garbuzov and Ratnieks 2013). Foraging insects were identified to species, except for *Bombus terrestris* and *B. lucorum* (as these species cannot be distinguished in the field) and non-Syrphidae Diptera. For analysis, insects were placed into four categories: (i) honey bees, (ii) bumble bees, (iii) butterflies and (iv)

hoverflies. Although several other species were observed in the vicinity, the only bees recorded visiting Grosso during the course of the experiment were honey bees, bumble bees and the wool carder bee *Anthidium manicatum*. Lavender flowers begin producing nectar before 6.00, and foraging can continue until after 19.00 (*L. latifolia*, Spain, Herrera 1990). Observations were made during between peak foraging hours (10.00–18.00; Herrera 1990).

Several aspects of the foraging behaviour of individual honey bees and bumble bees (see Table 1 and Balfour et al. 2013), on all three patch types, were quantified by watching videos frame by frame on Streamclip software (Streamclip 2014). Videos were made using a Sony HDR-CX115 camcorder during ideal foraging weather (>20C, wind <5kph) on days 3 and 4 (2012) when bee numbers per patch had stabilised. Individual bees were located opportunistically and videoed while they foraged on 20 consecutive flowers, then captured, placed in a honey bee queen marking cage and paint marked. Data were not used from bees that were already marked, evaded capture, or followed for <20 flowers.

Quantifying nectar volume and sugar concentration

To assess the impact of bee exclusions on nectar volumes, we collect nectar samples on days 3 and 4 (2012) and 3, 6 and 10 (2014) on each of our experimental patches. Thirty nectar samples, per day, were taken 1200–1400 h, the period of peak nectar production (Herrera 1989) from 30 flowers (10 each from upper, middle and lower locations) of randomly selected inflorescences of randomly chosen plants in each patch. Nectar volumes were quantified to $\pm 0.008 \mu\text{l}$ by measuring the length of liquid ($\pm 0.5 \text{ mm}$) in a 64 mm long, $1 \mu\text{l}$ micro-pipette (Drummond Microcaps).

In order to calculate the potential energy profits to bees foraging on lavender, we evaluated the sugar content of

Grosso. To gather sufficient volume of nectar to make a reliable measure of sugar content (c. $1 \mu\text{l}$) from uncovered Grosso plants would involve probing c. 100 flowers (the average volume per flower being c. $0.01 \mu\text{l}$) during which time the evaporation of the nectar within the capillary tube would increase the sugar concentrations and in turn compromise our results. Therefore, 30 flowers were emptied of nectar with a micro-pipette on 29 August 2012 at 1200 h. Flowers were then covered with a fine mesh ($0.2 \times 0.2 \text{ mm}$) to exclude all insects. After 2 h, the accumulated nectar was collected with a micro-pipette and the sugar concentration (degrees Brix) determined using a hand-held refractometer (Kruss HR 25/800). By restricting the data collection to 12.00 and 14.00, we reduced any potential biases caused by daily fluctuations in nectar production or concentration.

Determining the energetic returns per flower visited

We predicted that the exclusion of bumble bees would greatly affect the energetic profitability of lavender flowers to honey bees but not vice versa. To test this, we constructed an energy budget (see *ESM*) per lavender flower visited. These calculations use the foraging data collected in this study (Table 1), the sugar content of Grosso (described above), data from Balfour et al. (2013) and data on bee respiration rates (O_2 consumption or CO_2 production of resting, walking and flying bumble bees and honey bees) taken from 17 previous studies. We made our energy budget per flower as this is the key measure of overall energetic profitability, which would also include the energetic flights to and from the nest, etc. In particular, if foraging is not energetically profitable per flower, then it will not be profitable when additional energy expenditures are included.

To calculate the energy gain (in joules, J) of a foraging bee per Grosso flower, we first calculated the mean energy available (N) in the nectar of one flower. This is given by the

Table 1 Foraging behaviour of honey bees (*A. mellifera*) and bumble bees (*B. terrestris/lucorum*)

Bee and patch type	<i>n</i> , bees	Interflower time (s)	Orientation time (s)	Extraction time (s)	Search time (s)	Flower rejection (%)	Interflower flights (%)	Time on patch (s)
Honey bees, BBE	21	0.59±0.15 <i>P</i> =0.449	0.69±0.17 <i>P</i> =0.434	1.44±0.37 <i>*P</i> =0.040	1.07±0.46 <i>*P</i> =0.012	43 <i>*P</i> <0.001	38 <i>*P</i> <0.001	1111±547 <i>*P</i> <0.001
Honey bees, CON	21	0.64±0.25	0.65±0.18	1.24±0.38	1.48±0.55	55	64	117±61
Bumble bees, HBE	12	0.41±0.15 <i>P</i> =0.533	0.38±0.07 <i>P</i> =0.293	0.43±0.08 <i>P</i> =0.718	0.34±0.06 <i>P</i> =0.643	14 <i>P</i> =0.834	16 <i>P</i> =0.382	649±469 <i>P</i> =0.848
Bumble bees, CON	12	0.38±0.10	0.32±0.03	0.45±0.13	0.35±0.08	13	19	684±389

Bees foraged on Grosso lavender in patches from which bumble bees (BBE) or honey bees (HBE) had been excluded and a control patch (CON) without exclusion. Based on video footage, a bee's foraging sequence across 20 flowers was divided into four identifiable components: (a) interflower time: travelling between flowers; (b) orientation time: once landed, orientating body and inserting tongue into corolla tube; (c) Extraction time: imbibing nectar at the flower; (d) search time: travel between probed flowers, including any time spent on rejected flowers. Interflower flights are the proportion of movements between flowers made by flying (vs walking). *P* values show comparison of exclusion patch with control (ANOVA or GLMM). Data are presented as mean±1 standard deviation.

* Significant difference (*P*<0.05)

product of the mean volume (v in ml) of nectar per lavender flower, the sugar concentration (s) of nectar lavender (39 %; see “Results”), the specific gravity (g) of a solution which is 39 % sugar (1.148 Brix) and the energy content of sucrose (c ; 16480 J/g):

$$N = vsgc \quad (1)$$

From this, we subtracted the energy expended in all activities (flying, walking, handling) by a nectar collecting bee, per flower. The energy expended flying per flower (f), for example, is given by the product of the metabolic rate (r) of activity in J/g/s, the mean bee weight (b , in grams, g) and the mean duration (t) used in this activity per lavender flower:

$$f = rbt \quad (2)$$

Statistical analysis

All analyses use data collected during days 3 and 4 (2012) and 3, 6 and 10 (2014), during which bee numbers per patch had stabilised, unless stated otherwise. When quantifying the number of Grosso flower visitors, we undoubtedly counted the same insect on more than one occasion. Therefore, to average away the pseudoreplication in the data (Crawley 2014), ‘patch’ ($n=4$) was considered as the experimental unit in our count data analysis, i.e. prior to analysis, counts were averaged across four days: day 3 (2012) and 3, 6, 10 (2014). Statistical analyses were conducted using ‘R’ software (R-Project 2012). We used Generalized Linear Mixed-effect Models (GLMM R package lme4, version 1.1–7) or one-way ANOVA. ‘Day’ or patch was held as a random effect in GLMM analysis (R command: glmer (response variable~treatment+(1 day/patch), family=binomial). Delta Akaike information criterion (Δ AIC) is given by the AIC of the null model minus the AIC of the alternative model. Tukey’s Honestly Significant Differences tests (HSD, R package multcomp, version 1.3–6) followed significant ($P<0.05$) ANOVA. All values are presented as mean \pm 1 standard error.

Results

Honey bees (*A. mellifera*: 34 %) and bumble bees (60 %: *B. terrestris* and *B. lucorum*: 42 % [these species cannot be distinguished in the field], *B. pascuorum*: 17 %, *B. lapidarius*: <1 %, *B. hortorum*: <1 %, *B. hypnorum*: <1 %, *B. vestalis*: <1 %) comprised 94 % of all insects counted on all lavender flowers in the three patch types in 2012 and 2014 combined. The other 7 % were butterflies (4 %), hoverflies (2 %), other Diptera (<1 %) and wool carder bees (*A. manicatum*, <1 %). No aggressive or otherwise antagonistic interactions between foraging insects were observed with the exception of male

wool carder bees, which are known to aggressively defend flower patches (Severinghaus et al. 1981). When seen on our experimental patches, they were removed. We repeated the experiment in 2014 to confirm the 2012 result and to show that consistent effects resulted from bumble bee and honey bee exclusions.

As predicted, bumble bee exclusion greatly increased honey bee numbers. Across the four trials, the same trend was always observed, with the mean number of honey bees on the bumble bee-excluded patches (BBE) being 14 times greater than on the control patches (Fig. 1 and 2; 8.4 ± 0.67 vs 0.6 ± 0.23 ; GLMM; Δ AIC=73.41, $df=1$, $\chi^2=75.41$, $P<0.001$). However, the number of bumble bees on the honey bee-excluded patches (HBE), was not different from the control patches (7.1 ± 0.4 vs 7.3 ± 0.4 ; GLMM; Δ AIC=0.51, $df=1$, $\chi^2=2.26$, $P=0.107$).

Five measures of honey bee foraging behaviour were affected by bumble bee exclusion (BBE vs control), Table 1: (i) time between consecutively probed flowers (search time) was significantly less (–27 %; 1.07 vs 1.48 s; ANOVA; $df=40$, $F=6.924$, $P=0.012$); (ii) extraction time, the time spent imbibing nectar from a single flower, was significantly greater (+16 %; 1.44 vs 1.24 s; ANOVA; $df=40$, $F=4.502$, $P=0.040$); (iii) significantly fewer flowers were rejected (43 vs 55 %; GLMM; Δ AIC=10.51, $df=1$, $\chi^2=12.51$, $P<0.001$); (iv) the proportion of flights between flowers, vs the alternative of walking, was reduced (flying 38 vs 64 %; GLMM; Δ AIC=154.80, $df=1$, $\chi^2=156.77$, $P<0.001$) and (v) individuals spent ten times as long foraging in a patch after arriving (1111 vs 117 s; ANOVA; $df=18$, $F=35.54$, $P<0.001$).

Conversely, the same measures of bumble bee foraging behaviour were unaffected by honey bee exclusion (HBE vs control): (i) search time (0.34 vs 0.35 s; ANOVA; $df=22$, $F=0.221$, $P=0.643$); (ii) extraction time (0.43 vs 0.45 s; ANOVA; $df=22$, $F=0.134$, $P=0.718$); (iii) proportion of flowers rejected (14 vs 13 %; GLMM; Δ AIC=–1.34, $df=1$, $\chi^2=0.05$, $P=0.834$) and (iv) mode of locomotion between flowers (flying: 16 vs 19 %; GLMM; Δ AIC=1.24, $df=1$, $\chi^2=0.76$, $P=0.382$), (v) time spent foraging in a patch (649 vs 684 s; ANOVA; $df=22$, $F=0.038$, $P=0.848$).

Hoverfly and butterfly counts did not differ significantly between treatments (hoverflies: BBE: 0.16, HBE: 0.24, control: 0.08; ANOVA; $df=11$, $F=1$, $P=0.405$; butterflies: BBE: 0.33, HBE: 0.35, control: 0.44; ANOVA; $df=11$, $F=0.083$, $P=0.921$).

Mean nectar volumes per flower were greater in the absence of bumble bees (GLMM; BBE: 0.019 ± 0.036 μ l vs control: 0.007 ± 0.013 μ l; HSD; $P<0.001$). In contrast, the exclusion of honey bees did not affect nectar volume (GLMM; HBE: 0.007 ± 0.013 μ l vs control; HSD; $P=0.719$). The proportion of flowers without detectable nectar was also significantly lower with bumble bee exclusion (BBE: 44 % vs control: 60 %; two-sample proportion test, $\chi^2=7.065$, $df=1$, $P=$

Fig. 1 Numbers of honey bees (*Apis mellifera*) and bumble bees (*Bombus* spp.) present on three patches of lavender (*Lavandula x intermedia* ‘Grosso’) with and without bee exclusion from counts made every 30 min (data points) and the moving average of four consecutive counts (lines). The shaded area indicates the period of bee exclusion on the two treatment patches. Bees were not excluded from any patches on day 5. Bees were excluded from all patches overnight (1800–0900 h) using 4 mm mesh. Day 1=16 August 2012. Bumble bee counts are for all species combined

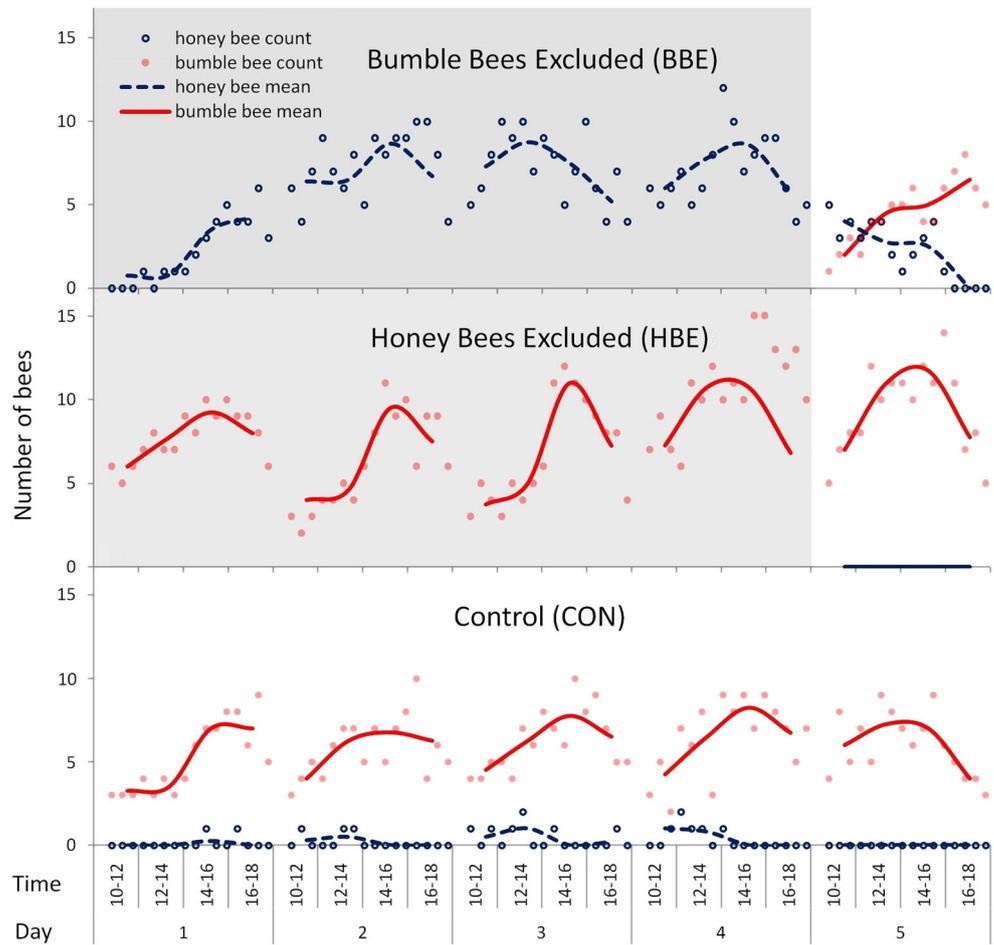
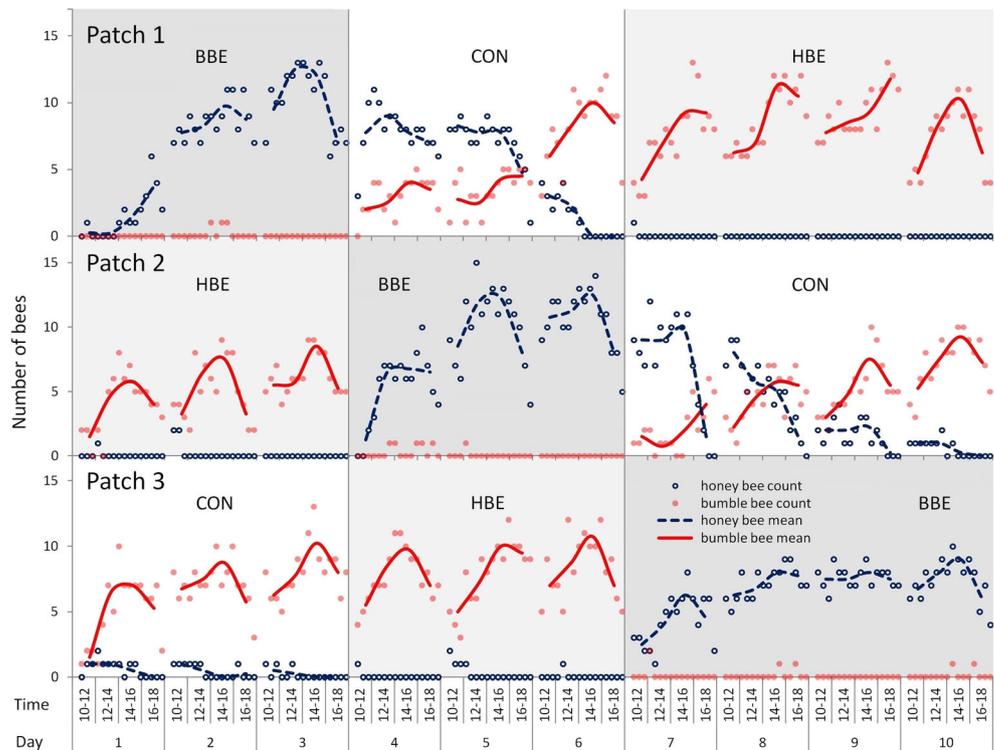


Fig. 2 Numbers of honey bees (*Apis mellifera*) and bumble bees (*Bombus* spp.) present on three patches of lavender (*Lavandula x intermedia* ‘Grosso’) with and without bee exclusion from counts made every 30 min (data points) and the moving average of four consecutive counts (lines). The shaded area indicates the period of bee exclusion (BBE bumble bees excluded, HBE honey bees excluded, CON control). The vertical black lines separating days 3 from 4 and 6 from 7 indicate the switching of treatments between the three patches. Bees were excluded from all patches overnight (1800–0900 h) using 4 mm mesh. Day 1=30 July 2014. Due to rain, data were not collected on day 4 and patches were left covered with nets. Bumble bee counts are for all species combined



0.008) but was not reduced significantly by honey bee exclusion (HBE: 55 % vs control; two-sample proportion test; $\chi^2=0.492$, $df=1$, $P=0.483$). Grosse nectar sugar concentration was $39\pm 3.3\%$ ($n=30$).

At first glance, it is perhaps surprising that a nectar volume increase of only 0.01 μl per flower would be sufficient to cause such a large increase in honey bee visitation. However, this corresponds to a 171 % increase and our energy budget calculations (see *ESM*) shows that, for honey bees, this turns a marginal net energy gain per flower in the control patches into a substantial ‘profit’ in the bumble bee-excluded patches (CON vs BBE), Fig. 3. Parallel calculations show that the energetic gains of bumble bees (*B. terrestris/lucorum*) are approximately the same per lavender flower whether honey bees are present or not (HBE vs CON, Fig. 3). Although we did observe a few honey bees foraging on the control patches, these stayed only a short time compared to those foraging on the bumble bee-excluded patch (1111s vs 117 s). This suggests that these honey bees were scouts sampling and then rejecting the patch as unprofitable.

Discussion

Our results clearly show that excluding bumble bees has a major effect on lavender flower visitation by honey bees. Indeed, honey bees effectively experienced competitive

displacement by bumble bees as they were virtually absent from the control patches but were consistently much more numerous, on average 14 times more, on patches from which bumble bees were excluded (Fig. 1 and 2). Although predicted by ecological theory, competitive displacement has rarely been documented in the field (Simberloff et al. 1997; Reitz and Trumble 2002).

Our results, like those of others (e.g. Inouye 1978; Schaffer et al. 1979), suggest that flower selection by generalist bees is often determined through ongoing competition rather than by the ‘ghost of competition past’. This is not surprising as there is very strong selective pressure on bees to respond quickly to changes in floral rewards whether from competition or other factors. Indeed, our data show considerable plasticity in the structure of flower-pollinator communities in response to exploitative competition.

Ecological release from interspecific competition has long been thought to allow niche expansion (e.g. Van Valen 1965), and this phenomenon has been observed in a variety of animal groups. Ocelots, for example, consume larger prey in areas where jaguars, which are much larger, are absent (Moreno et al. 2006). Comparable responses to reduced competition have also been documented in bird (Diamond 1970), fish (Persson and Hansson 1999) and lizard (Lister 1976) communities. Competition for resources can be considered a reduction in habitat quality and at the individual level has been shown to reduce survival and reproductive success (e.g. Eccard and Ylönen 2002).

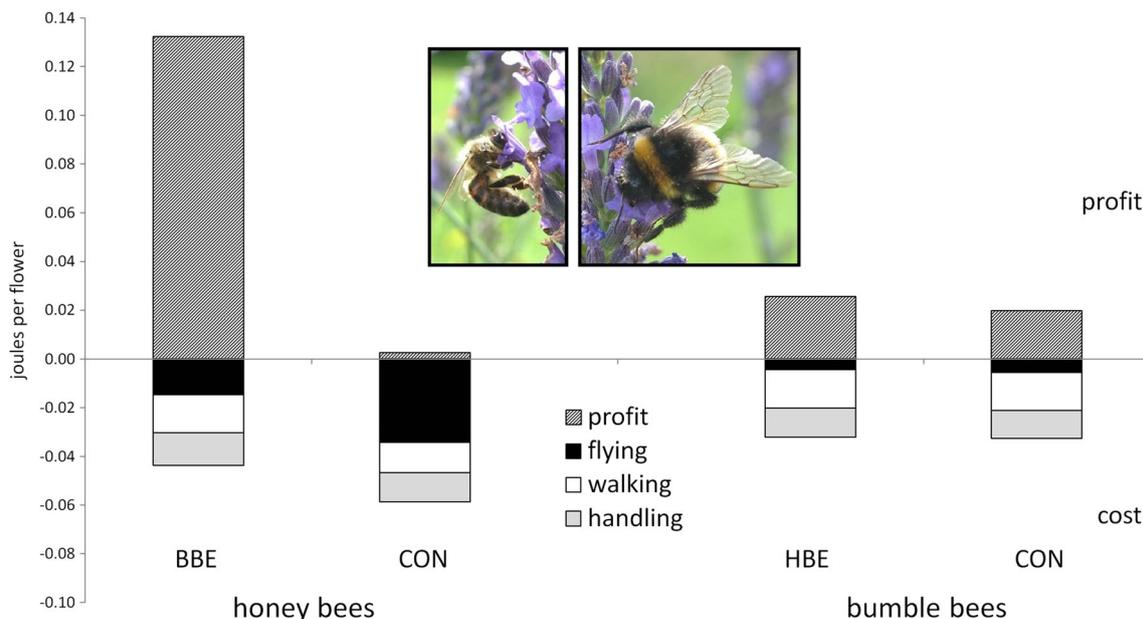


Fig. 3 Energy budgets of honey bees (*Apis mellifera*) and bumble bees (*Bombus terrestris/lucorum*) per lavender (*Lavandula x intermedia* ‘Grosso’) flower in our three experimental patch types (BBE bumble bees excluded, HBE honey bees excluded, CON control). Each bar represents the total energy value of nectar in an average lavender flower on each patch type. The hatched area at the top of each bar represents the mean energy gained (profit) per lavender flower. The black, white and

grey areas below the line represent the mean energy expended (cost) per flower. See *ESM* for calculations. The energy used for flying is greater for honey bees than bumble bees because honey bees usually fly (64 %) between flowers while bumble bees usually walk (81 %). In addition, bumble bees visit lavender flowers at three times the rate of honey bees. Therefore, bumble bee profit per flower would need to be multiplied by three to compare profits per unit time

At the start of each of the two field trials (Day 1, 2012 and 2014) honey bee numbers took longer to plateau than did bumble bee numbers: approximately 1.5 days for honey bees in the bumble bee-excluded patch vs <1 day for bumble bees in the honey bee-excluded and control patches (Figs. 1 and 2). This may be a result of their contrasting scouting strategies. Whereas each bumble bee forager acts as its own scout (Heinrich 1979), only c. 10 % of honey bee foragers scout, with most new foragers being recruited to flower patches via waggle dances (Seeley 1995).

Competition for resources between honey bees and bumble bees may be beneficial to pollination services. Our results show that exploitative competition with bumble bees reduces the amount of time spent in a patch by honey bees from 2 to 20 min. The increased movement of foragers between patches would give greater cross pollination per honey bee, although there would be fewer bees in total. Our results hint at the mechanisms underlying recent studies showing that wild bees increase the pollination efficiency of honey bees on almond flowers (Brittain et al. 2013) and sunflowers (Greenleaf and Kremen 2006) through causing more movements amongst patches.

Hoverfly and butterfly numbers were not significantly affected by bumble bee or honey bee exclusion. This may have been due to the lack of statistical power because of their relatively low numbers on our lavender patches (6 % of all insects, respectively 0.2 and 0.4 per count). However, we predict that nectarivores, such as hoverflies and butterflies, may not be as readily affected by exploitative competition as bees. Unlike female bees which collect resources not only to provision themselves, but also nestmates and their colony, butterflies and most other insects feed only to fuel their own activities. As a result, they are not under the same constraints to forage efficiently.

When faced with two alternative forage resources with differing rewards, optimal foraging theory predicts that an animal should focus on the more rewarding alternative (Stephens and Krebs 1986). In theory, this can lead to a ‘step’ function in which the less rewarding resource is abandoned. Fig. S1 shows how this step function may be operating for bees foraging for lavender nectar in this study. Nectar is the primary reward sought by bees from lavender (Herrera 1989; Balfour et al. 2013). Because bumble bees forage more efficiently than honey bees, they can profitably forage at a nectar content of 0.007 μl per flower in the control patch (Fig. 2). Because honey bees cannot make a significant net energy profit at this level (Fig. 3), we would expect them to reject the patch. Indeed, our data show that honey bees stayed, on average, less than 2 min foraging in these patches. However, in the bumble bee-excluded patches, nectar levels were higher (0.019 μl) and honey bees could make a considerable energy profit (Fig. 3). Many more honey bees were present in these patches and stayed ten times longer. Other nectarivores, such as

butterflies, are predicted to continue foraging at lower reward rates than bees. As such, the butterfly curve would be to the left of the bumble bee curve in ESM Fig. S1.

Our results show that exploitative competition can play a hidden but powerful role in shaping flower-visitor communities. Without experimental manipulation, an obvious inference from observational data alone (Garbuzov and Ratnieks 2013) would be that lavender is inherently much less attractive to honey bees than to bumble bees. But this would be an erroneous conclusion. In the absence of bumble bees, numerous honey bees forage on lavender. As illustrated in box A, our data show that a foraging advantage in one common competitor can have an important effect at the community level, leading to the complete, voluntary exclusion of another species via exploitative competition.

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Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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