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Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats

Abstract Many bumblebee species are declining at a rapid rate in the United Kingdom and elsewhere. This is commonly attributed to the decline in floral resources that has resulted from an intensification in farming practices. Here we assess growth of nests of the bumblebee, *Bombus terrestris*, in habitats providing different levels of floral resources. Experimental nests were placed out in conventional farmland, in farmland with flower-rich conservation measures and in suburban areas. Nests gained weight more quickly and attained a larger final size in suburban areas compared to elsewhere. The diversity of pollens gathered by bees was highest in suburban areas, and lowest in conventional farmland. Nests in suburban areas were also more prone to attack by the specialist bumblebee parasite *Aphomia sociella*, suggesting that this moth is more abundant in suburban areas than elsewhere. Overall, our results demonstrate that gardens provide a greater density and diversity of floral resources than farmland, and probably support larger populations of *B. terrestris*. Contrary to expectation, schemes deployed to enhance farmland biodiversity appear to have little measurable impact on nest growth of this bumblebee species. We argue that *B. terrestris* probably forage over a larger scale than that on which farms are managed, so that nest growth is determined by the management of a large number of neighbouring farms, not just that in which the nest is located.

Keywords Floral resources · Farm management · Set-aside · Foraging · Apidae

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Introduction

Bumblebees have declined considerably in recent decades in Europe and North America (Williams 1986; Rasmont 1995; Banaszak 1996; Buchmann and Nabhan 1996). In the United Kingdom, two species became extinct during the 20th century, and many others have become extremely rare (Edwards 1999). The reasons for this are unclear, but are probably linked to an intensification of farming practices which has resulted in a decline in the area of unfarmed land. In particular, loss of hedgerows and unimproved herb-rich grassland, and increased use of pesticides and fertilisers have resulted in a reduction in botanical species richness on farmland (Williams 1982; Greaves and Marshall 1987; Muir and Muir 1987; Corbet et al. 1991). This has led to a reduced availability of forage and perhaps also of suitable hibernation and nesting sites for bumblebees (Banaszak 1983; von Hagen 1994).

Whatever the causes, this decline in bumblebee populations is likely to have profound consequences. A large number of wild plants are pollinated predominantly or exclusively by bumblebees, sometimes by particular species of bumblebee (Corbet et al. 1991). Reduced pollinator services will result in reductions in outcrossing and seed set that can potentially lead to declines in the abundance of plant species. This can be particularly detrimental when plants are already scarce and threatened directly by habitat loss (Jennersten et al. 1992; Kwak et al. 1996; Young et al. 1996; Fischer and Matthies 1997; Steffan-Dewenter and Tscharntke 1997, 1999; Cunningham 2000). Negative effects upon plant populations may have further implications for plant community dynamics, associated herbivores, and other animals dependent on plant resources. Bumblebees also support a diverse array of symbiotic organisms (Alford 1975). Bumblebees fit the criteria for designation as keystone species (Power and Mills 1995), and so their loss may have disproportionate effects upon ecosystems. Aside from the implications for conservation, the yields of many field, fruit and seed crops are greatly enhanced by bumblebee visitation

(Crane and Walker 1984; Corbet et al. 1991; Free 1993; Osborne and Williams 1996; Carreck and Williams 1998). Hence there are also direct economic costs to the decline in bumblebee abundance.

In the last 20 years various farmland management techniques have been devised to counteract the general decline in farmland wildlife. These include new hedge-planting, repair of existing hedgerows, conservation headlands (unsprayed field margins), beetlebanks, uncropped field margins, and set-aside (Kaule and Krebs 1989; Marshall et al. 1994; Sotherton 1995; Kleijn et al. 1998). Such schemes have been found to provide over-wintering sites for invertebrate predators of crop pests, corridors for vertebrate and invertebrate population dispersal, game bird shelter and reproduction sites, and temporary and permanent habitats for an extensive number of organisms (Boatman and Wilson 1988; Boatman 1992; Aebischer et al. 1994). It seems probable that these schemes also benefit bumblebees, but there is a lack of quantitative evidence to support this.

Bumblebee nests vary in size according to their growth rate during the season, and thus produce variable numbers of reproductives at the end of the season. The growth rate of nests presumably depends largely upon the suitability of the local habitat for the bumblebee species – specifically, the availability of an abundant and predictable supply of appropriate flowers. Here we quantify the growth rate of nests of the bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) when sited in three different habitats in southern England. We examine whether schemes intended to promote farmland biodiversity are of benefit to this bumblebee species, and we also compare suburban and rural habitats.

Materials and methods

Thirty nests of *B. terrestris terrestris* were purchased from Koppert UK. This subspecies is widespread in Europe but is not native to the United Kingdom; nests of the UK species, *B. t. audax*, are not available commercially. The nests were small and even-aged, consisting of the founding queen and approximately 40 workers. Ten nests were placed out between 7 and 14 June 2000 in each of three habitats:

1. Suburban gardens.
2. Conventional arable farmland.
3. Arable farmland incorporating conservation headlands, areas of set-aside, and minimal use of pesticides.

The distinction between treatments 2 and 3 is blurred, since most farms have at least some set-aside, and few if any summer insecticide applications are needed on most arable crops in the United Kingdom. However, farmers were interviewed and the farms inspected, and sites allocated to treatment 3 only if it was clear that substantial measures were being implemented to encourage farmland biodiversity. To quantify differences between habitat types, the area within 500 m of each nest was surveyed to quantify the proportion of non-cropped land. This approach assumes that non-cropped areas are the main source of forage. This is largely true, since the predominant crops in the region are cereals. However, one nest in treatment 2 was situated within 500 m of a flowering field of spring rape (*Brassica napus*), a source of both nectar and pollen.

All sites were situated in Hampshire, Dorset or Wiltshire, UK. Suburban sites were located in a number of towns and villages to avoid pseudoreplication (Southampton, Salisbury, Bishopstoke, Fordingbridge, Romsey and Alderbury). All nest locations were separated by at least 2 km to minimise interference effects.

The nest box in which the bees were supplied consisted of a ventilated plastic inner box surrounded by an insulated layer of polystyrene, contained within a cardboard box. These nests were supplied with an in-built supply of honey solution which was removed when the nests were placed in the experimental sites. To protect them from rain the nest boxes were covered with a plastic lid. The boxes were placed on top of two house bricks to raise them off the ground, and a further brick was placed on top to prevent them from blowing over. The nests were sited under a hedge or shrub to shade them from direct sunlight; *B. terrestris* usually nests in such sites (Alford 1975). Once in position the entrance to the nests was opened. Nests were allocated to treatments at random and then placed out in experimental sites in random order.

Nests were weighed immediately before opening the entrance, and at 1-week intervals thereafter. Empty nest boxes were subsequently weighed so that the biomass of each nest could be calculated. Each week the nest traffic (number of foragers leaving and returning) during a 10-min period was recorded prior to weighing. During the 3rd week of the experiment two replicate nests (one each from treatments 2 and 3) were destroyed by badgers (*Meles meles*). After 4 weeks the first males and new queens were observed in nests, and the experiment was terminated in order to minimise the escape of reproductives. The inner plastic nest box was removed and replaced with an empty one. The nest entrance to these boxes is equipped with an optional valve which allows bees in but prevents them from leaving. This was put into operation, and the empty box left in place for 24 h to capture returning foragers.

The inner box containing the nest was sealed in a plastic bag with a piece of tissue soaked in ethyl acetate, and placed in a –30°C freezer to kill and preserve the nest. Subsequently, each nest was dissected, and the number of each of the following recorded: workers, queens and males; eggs; larvae; healthy pupal cells; hatched pupal cells; damaged or dead pupal cells; nectar pots; pollen pots. The thorax width of all adult bees was measured. Numbers of wax moth larvae (*Aphomia sociella*), and of any other symbiotic species were estimated. The nectar concentration in each of five nectar pots per nest was measured with a refractometer modified for small volumes (Bellingham and Stanley).

In addition, at the time that each nest was sealed, any returning foragers carrying pollen were captured (127 in total). Their pollen sacs were removed, and the diversity of pollens present was examined. The two pollen sacs from each bee were crushed and mixed up with a needle, and three samples of 50 pollen grains each were taken. Pollen samples were stained with safronin, and types were categorised and scored under a microscope. (They were not identified to species, and since some plant species have very similar pollen this will underestimate the true number of types present.) A Shannon–Weiner diversity index was calculated for each pollen sample, and a mean calculated from the three samples to give a single value for the diversity of pollen carried per bee.

Statistical analysis

The weight of nests in each successive week and nest traffic were examined by one-way repeated-measures analysis of variance. Differences between treatments in the numbers of workers, queens, etc. at the end of the experiment were compared using univariate one-way ANOVAs. Most of the data conformed to the assumptions of ANOVA, but the numbers of dead pupal cells required log transformation before analysis. Differences between treatments in the numbers of wax moths were examined with a Kruskal–Wallis test. To examine relationships between nest variables, Pearson product-moment correlation coefficients were calculated where the data conformed to the assumptions of a parametric test. Relationships between numbers of wax moth larvae and other nest variables were examined using Spearman's rank correlation coefficients. The diversity of pollen carried by incoming foragers was compared between habitats using a one-way analysis of variance.

Results

Differences between habitats

There were significant differences between habitats in terms of the proportion of non-cropped land within 500 m of each nest (one-way ANOVA, $F_{2,27}$=65.7, P<0.001). Predictably, suburban areas consisted predominantly of non-crop land (mean ±SE, 85.5±5.24%). In contrast, conventional farmland contained little non-cropped land (20.0±2.36%). Farmland with conservation measures was intermediate between the two (44.0±4.14%), with much of the difference being due to areas of set-aside. A Tukey's post hoc test indicated that the difference between the two farming types was significant (P=0.001).

Changes in nest weight

At the beginning of the experiment the biomass of the nests was 130±8.2 g (mean ± SE; including all bees). Once placed out in the field most nests gained weight rapidly, so that by the end of the 1st week they had on average nearly doubled in weight (Fig. 1). This is a slight underestimate of the true difference since when weighed in the field many workers would have been absent from the nests. Overall, nests in gardens gained weight more quickly than nests in either of the farmland treatments ($F_{2,25}$=4.68, P=0.019). However, during the final week of the study, weight gain tailed off and was similar in all treatments (Fig. 1.). After the 4 weeks, nests in gardens attained a biomass of 692±30.9 g, compared to 527±34.5 g in conventional farmland and 532±24.6 g on farms with conservation measures. Throughout the study there was no detectable difference in weight gain between nests sited on conventional farmland versus those on farms with conservation measures. Notably, on one conventional farm a field of spring rape came into flower during the experimental period, and during the week of peak flowering the nearby bumblebee
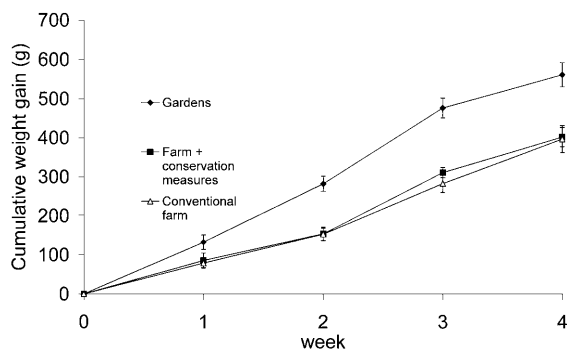

Fig. 1 Change in mass of bumblebee nests situated in three different habitat types (± SE). It should be noted that nests in gardens suffered from high infestation rates of the parasite *Aphomia sociella*, while those on farmland were rarely affected. This may have adversely affected the weights of these nests

nest experienced the largest weekly weight gain of any nest (305 g). However, exclusion of this nest from the analysis does not change the outcome.

Nest traffic

Nest traffic was extremely variable, ranging from 1 to 93 workers per 10 min. Overall, there was no significant differences in the traffic observed in the different habitat types ($F_{2,24}$=0.578, P=0.57). Nest traffic increased significantly during the 4 weeks ($F_{3,72}$=4.34, P=0.007). The highest nest traffic was observed at the nest on conventional farmland during the week of flowering of a nearby field of rape.

Measures of final nest size

By the end of the experiment all nests had produced substantial numbers of workers (the mean surviving number of workers per nest was 160). Production of new queens and males was extremely variable between nests, with some nests producing only queens and others only males. The maximum number of new queens produced in any one nest was 111, and the maximum number of males was 122. Overall there were slightly more males produced than queens (in total 1,009 versus 868, respectively). There were no significant differences between treatments in the number or size of queens, males or workers produced, although nests in gardens did produce more and larger queens and males than nests in farmland (Table 1). Interestingly, the final weight of nests was strongly correlated with the size of each caste, with queens, males and workers all being larger in heavy nests (r =0.56, P<0.01; r =0.50, P<0.01; r =0.59, P<0.01, respectively). Heavy nests also tended to contain more honey pots (r =0.68, P<0.001), and the honey tended to be more concentrated (r =0.47, P<0.001).

Apart from nest weight, most of the nest attributes that were measured did not differ significantly between treatments, with two notable exceptions. The number of damaged and dead pupal cells was far higher in nests in gardens than elsewhere (Fig. 2). Nests in gardens also contained significantly more larvae of the moth *A. sociella* compared to nests in farmland (Fig. 2). These larvae clearly inflicted serious damage on the nests that they infested, since they burrowed through the nest structure and through bee larvae and pupal cells. The number of *A. sociella* larvae within a nest was strongly correlated with the number of dead pupal cells (Spearman's rho =0.715, P<0.001), and negatively correlated with the number of larvae (Spearman's rho =–0.418, P=0.027) and the number of hatched pupal cells (Spearman's rho =–0.460, P=0.014). Only 3 of the 18 nests situated in farmland contained any larvae of *A. sociella*, compared to 8 of the 10 nests in gardens. The only other species found in any abundance were larvae of the fly *Fannia canicularis*, a nest commensal.

Table 1 Mean numbers of adult bees and immature stages in nests situated in each of the three habitat types. Degrees of freedom for analysis of variance are all 2 and 25. n =10 for gardens, and 9 for the other two treatments. *Other parasites/commensals* were predominantly dipteran larvae which scavenge faecal material and apparently do little damage. Differences between treatments were analysed by ANOVA, except for numbers of *Aphomia sociella* larvae which were examined using a Kruskal–Wallis test. Numbers of dead cells were log-transformed before analysis (*n.s.* not significant)

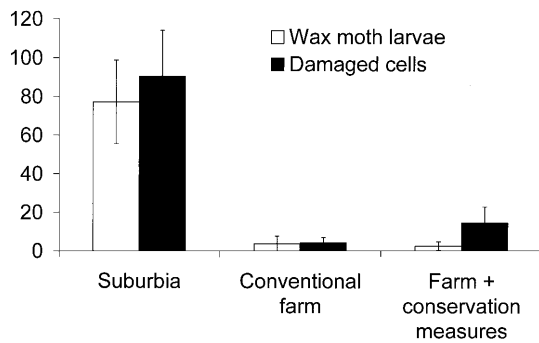|	Gardens		Conventional farm		Farm + conservation measures		Analysis	
	Mean	SE	Mean	SE	Mean	SE	F	P
No. of queens	35.9	11.5	21.0	9.4	35.6	12.7	0.55	n.s.
No. of males	52.3	11.8	25.4	12.9	28.6	4.6	1.98	n.s.
No. of workers	156.5	20.0	167.0	29.1	160.0	23.4	0.05	n.s.
Size of queens	7.94	0.07	7.60	0.08	7.78	0.12	3.26	n.s.
Size of males	5.68	1.80	5.47	0.06	5.52	0.10	2.02	n.s.
Size of workers	4.47	0.09	4.43	0.04	4.53	0.09	0.31	n.s.
No. of eggs	95.9	27.7	97.6	24.4	118.4	21.5	0.25	n.s.
No. of larvae	103.7	28.0	166.0	45.0	195.3	43.8	1.48	n.s.
No. of live pupal cells	209.3	29.4	253.0	43.7	231.4	77.1	0.45	n.s.
No. of dead pupal cells	90.6	23.5	4.67	7.68	14.8	8.3	8.33	0.004
No. of open pupal cells	142.2	37.3	114.1	13.7	174.9	22.2	1.20	n.s.
No. of nectar pots	110.1	35.8	92.2	30.1	49.0	18.9	1.12	n.s.
Nectar conc. (%)	77.9	0.58	58.3	19.5	72.8	3.27	1.85	n.s.
No. of pollen pots	13.7	4.15	15.9	3.87	12.6	2.73	0.20	n.s.
No. of A. sociella larvae	77.2	21.6	3.89	3.89	2.78	2.22	χ^2_2=8.33	0.001
No. of other parasites/commensals	61.5	30.4	26.3	8.75	45.1	27.1	0.52	n.s.

Fig. 2 Mean numbers of wax moth, *Aphomia sociella,* larvae per nest, and of dead pupal cells per nest, in each of the three habitats (± SE)

Diversity of pollen loads

Twenty-three distinct pollen types were identified from the 127 foragers that were examined. Bees varied greatly in the diversity of pollens they had collected, with some individuals being constant to just one flower type while others were carrying pollen from up to seven different plant species. Overall, the diversity of pollens brought back by foragers differed greatly between habitats ($F_{2,124}$=20.0, P<0.001). Pollen loads were most diverse for bees foraging in gardens, and lowest for bees foraging in conventional farmland (diversities ± SE: gardens, 0.86±0.06, n =51; farmland with conservation measures, 0.46±0.06, n =30; conventional farmland, 0.31±0.07, n =46). A Tukey's post hoc test revealed no significant difference between the two farmland habitat types (P=0.29).

Discussion

Contrary to expectation, the presence of schemes intended to promote farmland biodiversity appeared to have no significant influence on nest growth of *B. terrestris*, when compared to conventional farms. These schemes certainly appear to increase populations of zoophilous flowers (Kells et al., in press), and the diversity of pollens collected by foragers on farms with conservation measures was greater than on conventional farms. However, this did not translate into any measurable benefit to the growth rate of nests of *B. terrestris* in this study. There are a number of possible explanations. Firstly, many of these schemes encourage only annual flowers, since the soil is regularly tilled. Those schemes that allow land to be sequestered from crop production in the long-term are fairly new (introduced in the United Kingdom in 1992), and development of a mid-successional community dominated by perennials is likely to take a long time, particularly where the seed bank is depauperate due to years of intensive farming. As mid-successional communities are favoured by most bumblebee species (Fussell and Corbet 1991, 1992; Saville 1993; Steffan-Dewenter and Tscharntke 2001), it may be some years before these schemes fully benefit bumblebees (Corbet 1995). Secondly, the range of bumblebee foraging is probably far greater than the size of individual farms. It had long been thought that bumblebees forage close to their nests (Brian 1954; Alford 1975; Heinrich 1976; Teräs 1976; Bowers 1985; Rotenberry 1990), but recent calculations based on the energetics of foraging suggest that bumblebees could travel up to 8 km from their nest and return with a net profit (Cresswell et al. 2000). Using harmonic radar, Osborne et al. (1999)

found that *B. terrestris* regularly flew further than was necessary to find patches of forage, and many flew beyond the 500-m range of the radar. Other studies have found that *B. terrestris* regularly forage over more than 2 km (Witte et al. 1989; Dramstad 1996; Hedtke 1996; Walther-Hellwig and Frankl 2000a, b). Thus their foraging range may extend far beyond the farm on which the nest is located. If this were so, the management regimes of neighbouring farms and availability of flower-rich areas such as nature reserves or gardens may greatly influence nest growth rate and obscure any effects of local management. None of our farmland sites were more than 8 km from a town or village (usually much less), so all colonies may have had access to gardens. Similarly, it is probable that flowering crops such as spring rape provide vast resources which enable rapid nest growth for a short period of time. Availability of such crops within foraging range of nests could be a major source of variation within treatments.

Nests of *B. terrestris* gained weight more quickly and attained a larger size when placed in suburban gardens than when in farmland. Gardens undoubtedly provide a greater density and diversity of flowering plants than occur in most farmland, and this presumably explains why foragers gathering pollen in gardens visited a more diverse range of flowers than foragers in farmland. Modern flower cultivars are often less rewarding to pollinators than their wild counterparts (Comba et al. 1999), but nonetheless it seems that gardens provide good habitat for bumblebees. *B. terrestris* is one of six *Bombus* spp. that are abundant in suburban areas throughout the United Kingdom. We suggest that this explains the higher frequency of infestation of nests with larvae of the moth, *A. sociella*, in gardens compared to farmland; presumably the moth is more common in areas where its prey are abundant. *A. sociella* is a specialist predator of bumblebees (Alford 1975), and was considered by Hoffer (1982–83) to be their most important natural enemy. In heavily infested nests most of the bumblebee pupal cells had been destroyed, and much of the nest biomass consisted of moth larvae and their associated webs and frass. The heavier garden nests failed to produce more workers or reproductives compared to smaller nests on farmland, and this is probably due to the predations of this moth. However, when excavating wild *B. terrestris* nests we have rarely found *A. sociella*, even in suburban nests (D. Goulson, unpublished data). The experimental nest boxes are probably more easily detected by *A. sociella* than natural *B. terrestris* nests which are usually underground (Alford 1975). Thus it is likely that the high levels of infestation that we recorded may be an artefact of using artificial nest boxes. If the generally large suburban nests had not nearly all been attacked by *A. sociella*, it is reasonable to suppose that they would have produced more queens and males than farmland nests.

One limitation of our study was that the nests were destructively sampled before the end of their development; all contained larvae and pupae, and so we cannot know what the final reproductive output of the nests would have been. Also, some queens and males may have left the nests before they were destroyed. It would be exceedingly difficult to quantify precisely how many males and queens a nest produced in a field situation without constant monitoring over several weeks. We also used a non-native race of bumblebee, which may not be well adapted to local conditions. It also poses a potential threat to the native race, *B. terrestris audax*, through introgression or competition. The short duration of the experiment was intended to minimise escape of reproductives into the environment, but it is likely that some males escaped (queens take longer to leave the natal nest and return at night for some weeks, so most were probably captured). The advisability of experiments such as ours is thus debatable; they may provide useful information on bumblebee ecology while simultaneously having a detrimental effect. The decision to proceed was taken largely because many hundreds of nests are imported to the United Kingdom every year for commercial use, and in general all reproductives are allowed to escape. After careful consideration we felt that the additional impact of our experiment was likely to be negligible. Nonetheless, molecular studies to determine if this alien race is established in the wild and whether it is interbreeding with the native subspecies would be valuable.

To our knowledge, this approach for assessing the suitability of habitat in providing forage for bumblebees has not previously been used, and it seems to have great potential. However, the experiment described here examined only a small portion of the annual cycle, albeit the main period of foraging and nest growth. The nest establishment phase in early spring when the queen has to gather sufficient forage to provision her first batch of offspring may be the time when differences in availability of floral resources between habitats is most vital (Bohart and Knowelton 1953; Alford 1975). This could be examined in the same way, but using newly founded nests placed out earlier in the year. It is also important to note that bumblebee populations may be limited by availability of nest sites or hibernation sites rather than forage; the relative importance of these factors has not been investigated. The schemes that have been introduced to enhance farmland biodiversity primarily target floral diversity. It is not known if they also improve availability of nest or hibernation sites, although this seems likely.

Much of the research that has been carried out on bumblebees in recent years has focused on *B. terrestris*. This is in some respects not ideal since this is one of the most abundant and generalist bumblebee species, and it may not be representative of all bumblebees. For example it seems that bumblebee species vary greatly in their natural foraging range. Mark-recapture experiments and anecdotal observations suggest that species such as *B. pascuorum*, *B. sylvarum*, *B. ruderarius* and *B. muscorum* are "doorstep foragers", mostly remaining within 500 m of their nests whilst *B. lapidarius* forages further afield

(mostly <1,500 m), and *B. terrestris* regularly forage over 2 km (Witte et al. 1989; Dramstad 1996; Hedtke 1996; Walther-Hellwig and Frankl 2000a, b). Thus *B. terrestris* is likely to be less sensitive to local management regimes than other bumblebee species. Similar experiments to those described here but using some of the rarer long-tongued bumblebee species would provide an important insight into this subject.

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