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Does intraspecific size variation in bumblebees allow colonies to efficiently exploit different flowers?

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Abstract. 1. It has long been known that foraging bumblebee workers vary greatly in size, within species, and within single nests. This phenomenon has not been adequately explained. Workers of their relatives within the Apidae exhibit much less size variation.

2. For the bumblebee *Bombus terrestris* size, as measured by thorax width, was found to correspond closely with tongue length, so that larger bees are equipped to feed from deeper flowers.

3. The mean size of worker bees attracted to flowers was found to differ between plant species, and larger bees with longer tongues tended to visit deeper flowers.

4. Finally, handling time depended on the match between corolla depth and tongue length: large bees were slower than small bees when handling shallow flowers, but quicker than small bees when handling deep flowers.

5. Size variation within bumblebees may be adaptive, since it enables the colony as a whole to efficiently exploit a range of different flowers. Possible explanations for the marked differences in size variation exhibited by bumblebees compared with *Apis* species and stingless bees (Meliponinae) are discussed.

Key words. Apidae, *Bombus*, corolla depth, flower choice, polyethism, size.

Introduction

Bumblebee (*Bombus* spp.) workers exhibit an approximately 10-fold variation in mass within species and even within single nests (Alford, 1975; Goulson *et al*., 2002). In contrast, other eusocial bee species generally exhibit less than a two-fold variation in worker mass within nests (Waddington *et al*., 1986; Ramalho *et al*., 1998; Roulston & Cane, 2000).

What causes size variation in bumblebee workers? In species such as *Bombus terrestris*, larvae spend most of their development in individual cells, and are fed directly by the adults (Alford, 1975). Therefore the size attained by each larva is probably determined by the adults (Ribeiro, 1994). Why do the adults rear workers of greatly varying size? In part the explanation may relate to division of labour according to size, known as alloethism. In a range of bumblebee species, foragers have been found to be larger, on average, than bees that remain in the nest (Colville, 1890; Sladen, 1912; Richards, 1946; Cumber, 1949; Brian, 1952; Free, 1955; Goulson *et al*., 2002). In honeybees (*Apis mellifera*) all workers are approximately the same size. They begin life by working within the nest, and then all switch to foraging. It would thus not be possible for foragers to be larger than nest bees. By contrast, in bumblebees large workers tend to switch from within-nest tasks to foraging at an earlier age than small workers, and the smallest workers may remain within the nest for their entire lives (Pouvreau, 1989). Thus, on average, foragers are larger than nest bees.

A number of adaptive explanations have been proposed as to why foragers should be larger than nest bees. Large bees visit more flowers per unit time, compared with small bees (Spaethe & Weidenmuller, 2002). They can also carry more nectar and pollen, and when collecting nectar (but not pollen) they bring back more forage per unit time (Goulson *et al*., 2002). Their greater foraging efficiency may in part be because larger bees have greater visual acuity (Spaethe & Chittka, 2003), and visual acuity is likely to affect search times for flowers (Spaethe *et al*., 2001). Larger bees may be able to forage further from the nest (Cresswell *et al*., 2000).

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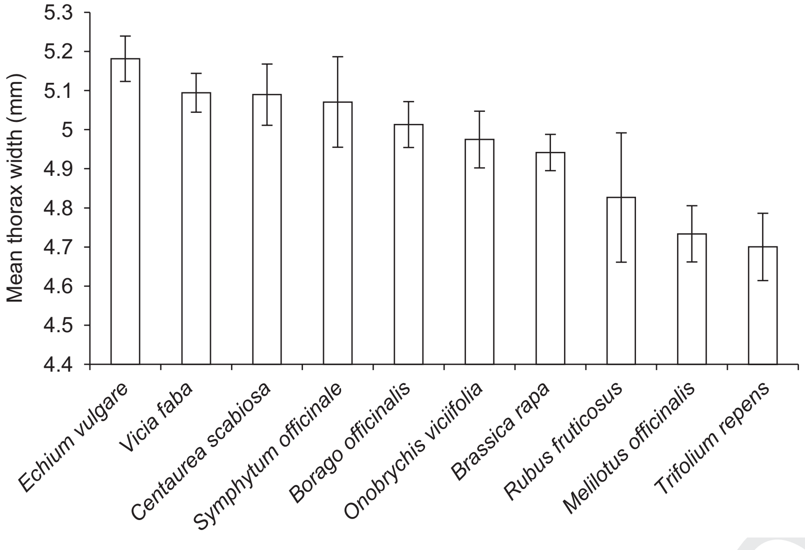

Fig. 1. The mean thorax width (± SE) of foraging *Bombus terrestris* workers visiting flowers of each of 10 different plant species. Differences were significant ($F_{9,247} = 5.53$, $P < 0.001$).

It would also be expected that large bees would be better able to maintain an adequate body temperature for activity in the sometimes inclement conditions they encounter outside the nest, although they will also be more prone to overheating in warm weather (Free & Butler, 1959; Heinrich, 1979). Rather than asking why foragers are large, Free and Butler (1959) reverse the question and discuss why nest bees are small. They suggest that there may be advantages to rearing small bees for within-nest tasks, other than the cheap cost of rearing them. Bumblebee nest structure is irregular and often crowded, and it seems likely that small bees may be better able to manoeuvre within these cramped confines.

Whatever the explanation as to why nest bees are smaller than foragers, it is notable that even among the larger forager class, there is still considerable size variation. In *B. terrestris*, thorax widths of all workers vary from 2.3 to 6.8 mm, with foragers varying from 3.3 to 6.8 mm (Goulson *et al.*, 2002). Bumblebee species belonging to the section *Odontobombus* vary even more in size (*B. terrestris* belongs to the *Anodontobombus*) (Alford, 1975). It has been suggested that having foragers of a range of sizes is an advantage since each specialises in flower types appropriate to their morphology, so improving overall foraging efficiency of the colony while minimising intra-colony competition (Goulson, 2003). It has long been known that *interspecific* differences in tongue length between bumblebee species explain differences in foraging preferences, with long-tongued bees tending to visit flowers with deep corollae (Inouye, 1978, 1980; Pyke, 1982; Barrow & Pickard, 1984; Harder, 1985; Johnson, 1986; Graham & Jones, 1996). This study examines whether *intraspecific* size variation also corresponds with floral choice; do bees tend to visit flowers that match their size? It also tests whether the choices made by bees influence their foraging efficiency, by comparing the handling time of large vs. small foragers on plant species varying in corolla depth.

Methods

All studies were carried out in southern U.K. during July and August of 2001–2003. To establish the relationship between tongue length and bee size, the thorax width and tongue lengths (glossa + prementum) of 34 *B. terrestris* workers were measured. These workers were sampled from a large wild population at Chilworth, Hampshire.

To examine whether bees of different size tended to visit different flowers, in 2001 and 2002 the proportion of *large* vs. *small* bees visiting each of eight plant species was quantified by walking a transect through patches of each flower species. *Bombus terrestris* workers were recorded as either large or small by reference to a pinned bee of average size (4.9 mm thorax width, Goulson *et al.*, 2002). Bees that were indistinguishable in size from the reference specimen were not included in the analysis. Each bee was observed for several consecutive flower visits to determine whether it was collecting nectar or pollen (or both). Pollen collection is evident from brushing of anthers with the legs, or grooming of pollen from the body into the corbiculae. Bees that were collecting pollen were not included in the analysis. During observation of each bee, care was taken to check whether the bee was *B. terrestris* or the morphologically similar *Bombus lucorum*. Recent molecular studies of *B. terrestris* and *B. lucorum* in the same area suggest that the field classifications used for these species are > 95% accurate (Darvill *et al.*, in press). Fifty bees classified as 2 large and 50 classified as small were captured and their thorax width measured.

In 2003 an additional measure of the size of workers visiting 10 different plant species was gathered by catching foragers visiting flowers (mean sample size 25.7 bees per plant species). The thorax width of each bee was measured using Vernier callipers. This method has the advantage that no bee could be counted more than once, and captured bees could be closely examined to preclude the possibility that any of them were *B. lucorum*.

During 2001–2002, the handling time of large and small bees on each of 10 flower species was recorded using a stopwatch. Each bee was observed visiting at least five florets, and the mean time per floret was used in subsequent analyses. A minimum of 30 bees were observed per bee size/flower species combination. For each flower species, corolla depth was measured for 15 florets randomly chosen from different plants.

Anova was used to compare the size of foragers recorded visiting each plant species. To examine whether bee size was related to flower depth, the ratio of large to small bees observed on each flower species was regressed against mean corolla depth. To examine how the relative handling time of large vs. small bees was affected by corolla depth, the ratio of mean handling time for large bees : mean handling time for small bees was calculated and regressed against corolla depth. All analyses were carried out in SPSS 12.0.

Results

In *B. terrestris* workers, tongue length was strongly and linearly related to thorax width [$F_{1,32} = 225$, $P < 0.001$, $r^2 = 0.876$, tongue length = 1.34(thorax width) + 1.73], confirming that larger bees do indeed have longer tongues. Tongue lengths varied from 4.9 to 7.9 mm.

Mean thorax width of foragers differed markedly between the 10 plant species ($F_{9,247} = 5.53$, $P < 0.001$; Fig. 1). On average *Echium vulgare* and *Vicia faba* were visited by the largest workers, while *Trifolium repens* and *Melilotus officinalis* attracted the smallest bees. Similarly, the proportion of large and small bees varied significantly between the eight plant species for which this was recorded ($\chi^2_7 = 26.9$, $P < 0.001$) (Table 1). No relationship was found between thorax width and sampling date (linear regression, $F_{1,254} = 0.36$, NS). The mean thorax width of bees classified as large and small was 5.33 ± 0.028 and 4.38 ± 0.035 respectively (mm ± SE).

The ratio of large to small bees visiting each plant species was significantly positively related to corolla depth ($r^2 = 0.672$, $F_{1,6} = 12.29$, $P = 0.013$; Fig. 2). In other words, flowers with deep corollae were mostly visited by large bees, while flowers with shallow corollae tended to be visited by small bees. The ratio of the handling time of large bees to the handling time of small bees was also significantly related to corolla depth ($r^2 = 0.445$, $F_{1,7} = 6.41$, $P = 0.035$; Fig. 3). Large bees tended to be slower than small bees when handling flowers with short corollae, but were faster than small bees when handling flowers with deep corollae.

Discussion

This study demonstrates that the distribution of foraging *B. terrestris* workers among flower species are not random with respect to their size; large bees tend to visit different flowers to small bees (although there is considerable variation in bee size on any one flower species). Secondly, larger bees had longer tongues, in accordance with earlier work (Harder, 1985; Prys-Jones & Corbet, 1991). Thirdly, large foragers tend to visit flowers with deeper corollae than do small foragers. Fourthly, these flower visitation patterns appear to correspond with handling time; large bees are faster than small bees at handling flowers with deep corollae, and vice versa.

Previous studies have noted a tendency for workers of different sizes to visit different flowers (Cumber, 1949; Morse, 1978; Inouye, 1980; Barrow & Pickard, 1984; Harder, 1985; Johnson, 1986). For example, Cumber (1949) found that large workers of *B. pascuorum* tended to visit *Lamium album*, which has a deep corolla, while the smaller workers visited *Lamiastrum galeobdolon*, which has a substantially shallower corolla. Harder (1985) observed that *B. vagans* sampled from woodland were larger than those foraging in nearby fields, which he attributed to

Table 1. Worker size and handling time when visiting flowers of 10 different plant species. Handling times per floret are means of means (at least five observations per bee and 30 bees). Corolla depths are means of 30 florets. –, data not collected.

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Plant species	Mean (± SE) handling time of large bees (s)	n	Mean (± SE) handling time of small bees (s)	n	Mean (± SE) corolla depth (mm)	Ratio of visits by large vs. small bees	n	Ratio of handling time for large vs. small bees
Borago officinalis	2.79 ± 0.31	30	2.93 ± 0.21	30	1.74 ± 0.08	1.43	51	0.95
Rubus fruticosus	4.22 ± 0.52	31	3.02 ± 0.27	33	0.00 ± 0.00	0.53	48	1.40
Trifolium repens	1.29 ± 0.05	30	1.14 ± 0.04	30	2.57 ± 0.07	0.25	37	1.13
Symphytum officinale	1.49 ± 0.05	30	1.55 ± 0.05	30	4.47 ± 0.39	0.92	61	0.96
Echium vulgare	1.32 ± 0.11	30	1.74 ± 0.09	31	6.73 ± 0.20	–	55	0.76
Centaurea scabiosa	1.25 ± 0.04	30	1.66 ± 0.07	30	13.6 ± 0.18	3.50	49	0.75
Melilotus officinalis	3.64 ± 0.31	30	3.74 ± 0.27	30	1.63 ± 0.06	–	46	0.97
Onobrychis viciifolia	2.25 ± 0.14	31	2.36 ± 0.14	33	4.3 ± 0.08	0.88	53	0.95
Knautia arvensis	1.14 ± 0.04	30	1.13 ± 0.03	30	5.99 ± 0.20	3.25	45	1.01
Cirsium vulgare	1.00 ± 0.04	30	1.05 ± 0.04	30	11.2 ± 0.22	2.67	39	0.96

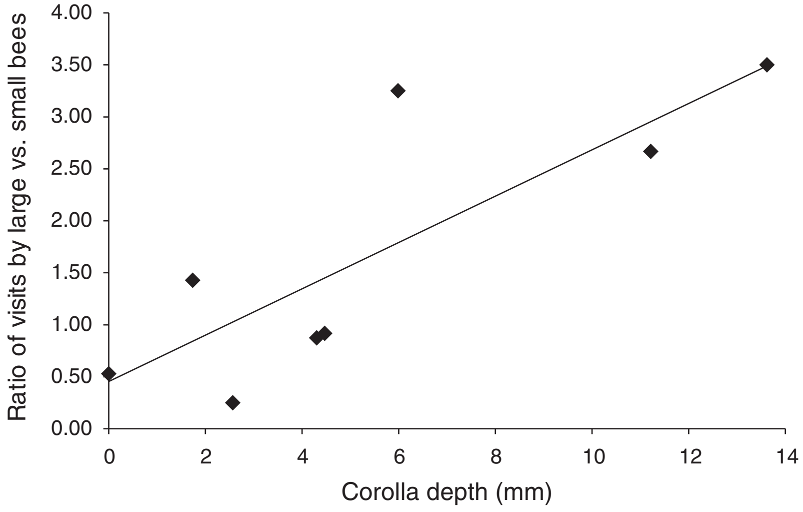

Fig. 2. The ratio of large to small *Bombus terrestris* workers recorded visiting each of eight plant species, plotted against the corolla depths of the plants [linear regression, $r^2 = 0.672$, $F_{1,6} = 12.29$, $P = 0.013$, ratio $= 0.454 + 0.223$ (corolla depth)].

differences in the forage plants that were available in the two habitats. However, previous studies have not demonstrated that *intraspecific* differences in choices correlate with corolla depth, or that the choices made by bees of different sizes minimise their handling times.

When comparing different bumblebee species, Plowright and Plowright (1997) found that bees with long tongues fed more slowly on shallow flowers than bees with shorter tongues. Presumably a long tongue is unwieldy for drinking from a shallow flower, but has obvious advantages when drinking from a deep one. Harder (1983) demonstrated that the rate of nectar uptake declines greatly as the nectar level approaches the limit of reach of the bee's tongue. Thus it would be expected for small bees to have longer handling times than larger bees when extracting nectar from deep flowers. By producing foragers of a range of sizes with a range of tongue lengths a bumblebee colony is presumably more able to efficiently exploit a range of different flower species of varying structure and corolla depth.

Why then do other social bees not show similar size variation? The coefficient of variation in size of *Apis mellifera* is less than one tenth of that found in *B. terrestris* (Waddington *et al.*, 1986; Goulson *et al.*, 2002). Tropical stingless bees (Meliponinae) exhibit slightly more size variation than honeybees, but much less than bumblebees (Waddington *et al.*, 1986). Honeybees and stingless bees probably evolved in tropical forests feeding primarily on mass-flowering trees. They use recruitment of nestmates to specific sites so that a large proportion of the colony is simultaneously exploiting the same large resource. In this situation size variation would not be advantageous. In contrast, temperate bumblebees feed on scattered, mainly herbaceous plants, and many different plant species flower at the same time. They do not recruit to particular flower patches, probably because most patches are so small that one bee can exploit them (Dornhaus & Chittka 1999). Instead, workers each specialise in visiting one or two flower species, and it seems that they choose flowers that are most suited to their own size. It would be interesting to

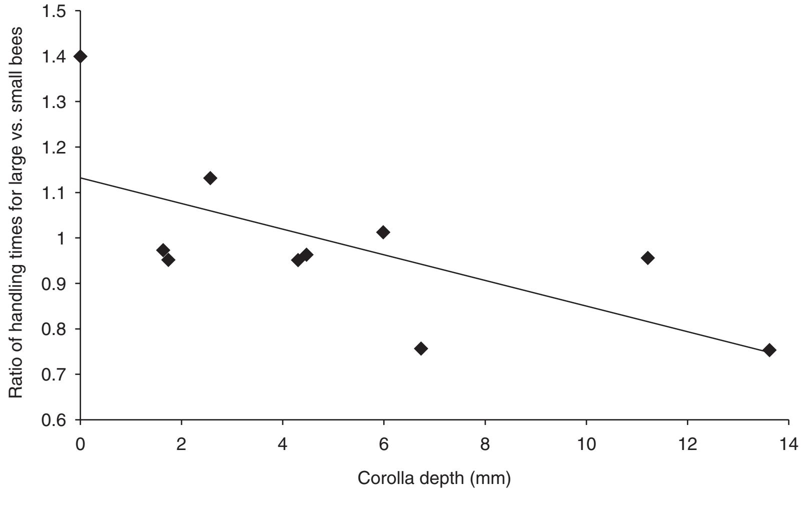

Fig. 3. The ratio of the handling time per floret for large bees vs. small bees when visiting nine different flower species, plotted against the corolla depths of the plants [linear regression, $r^2 = 0.445$, $F_{1,7} = 6.41$, $P = 0.035$, ratio $= 1.13 - 0.0282$(corolla depth)].

examine size variation in the small number of tropical bumblebee species for comparison.

One criticism of this study is that the different flower species were not all studied at the same place and time (which would be exceedingly difficult since the plants flower at different times). If mean worker size changes through the season, this could influence the results. Knee and Medler (1965) found an increase in worker size for three American species late in the season. Plowright and Jay (1968) found an increase in worker size as the season progressed in some species but not in others. Röseler (1970) describes an initial decline in the mean size followed by a general increase in *B. terrestris*. All agree that the change in mean size is small compared with variation found within broods. The study was not designed to examine this, but no significant change in forager size over the season was found.

Corolla depth and bee tongue length are clearly not the only factors that influence handling time. The flowers studied differed greatly in structure, in availability of nectar, and in distance to the next floret, all of which might be expected to influence handling time. For example, handling time of *Rubus fruticosus* was long for both large and small bees despite the very simple flower structure, probably reflecting the high levels of nectar that this species contains. Observation of foraging bees suggests that bee size has an influence on the flower types to which a bee is physically suited beyond its relationship with tongue length. *Trifolium repens* was visited mostly by small foragers, but occasionally by large ones. When this occurred the stalk of the inflorescence was unable to support the weight of the bee and it would collapse to the ground, making flower handling more difficult for the bee. The flowers preferred by large bees, such as *E. vulgare*, tend to have sturdier stalks. Flower constancy is a well-known characteristic of bumblebee behaviour for which there is not an entirely satisfactory explanation (reviewed in Goulson, 2003). If many of the flower species available to a bee (and apparently suitable as judged by visitation from conspecifics) are poorly suited to its morphology because of its particular size relative to the flower, then this will tend to favour constancy.

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