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Can alloethism in workers of the bumblebee, *Bombus terrestris*, be explained in terms of foraging efficiency?

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Bumblebee workers vary greatly in size, unlike workers of most other social bees. This variability has not been adequately explained. In many social insects, size variation is adaptive, with different-sized workers performing different tasks (alloethism). Here we established whether workers of the bumblebee, *Bombus terrestris* (L.) (Hymenoptera; Apidae), exhibit alloethism. We quantified the size of workers engaging in foraging compared to those that remain in the nest, and confirmed that it is the larger bees that tend to forage ($\bar{X} \pm \mathrm{SE}$ thorax widths 4.34 ± 0.01 mm for nest bees and 4.93 ± 0.02 mm for foragers). We then investigated whether large bees are better suited to foraging because they are able to transport heavier loads of food back to the nest. Both pollen and nectar loads of returning foragers were measured, demonstrating that larger bees do return with a heavier mass of forage. Foraging trip times were inversely related to bee size when collecting nectar, but were unrelated to bee size for bees collecting pollen. Overall, large bees brought back more nectar per unit time than small bees, but the rate of pollen collection appeared to be unrelated to size. The smallest foragers had a nectar foraging rate close to zero, presumably explaining why foragers tend to be large. Why might larger bees be better at foraging? Various explanations are considered: larger bees are able to forage in cooler conditions, may be able to forage over larger distances, and are perhaps also less vulnerable to predation. Conversely, small workers are presumably cheaper to produce and may be more nimble at within-nest tasks. Further research is needed to assess these possibilities.

Bumblebees (*Bombus* spp.) exhibit an approximately 10-fold variation in mass within the worker caste, even within single nests (Alford 1975). Other bee species that have been studied show far less variation in size, with generally less than a two-fold variation in worker mass within nests (Waddington et al. 1986; Ramalho et al. 1998; Roulston & Cane 2000). The most obvious comparable instance of size variation in social insects occurs in some ant species. Here, the size distribution is polymodal and size is related to behaviour, with individuals of particular sizes specializing in particular tasks, a phenomenon known as alloethism. For example, in *Atta* leaf-cutting ants, the largest workers have enlarged mandibular muscles, and specialize in nest defence, medium-sized workers forage for food, and the smallest workers are adapted by their small size for working within the fungus garden (Wilson 1980). The greatest known size variation occurs in the Asian marauder ant, *Pheidologeton diversus,* in which the largest workers have a mass 500 times greater than the smallest (Hölldobler & Wilson 1990).

Our aim in the present study was to establish whether size variation in bumblebee workers has a similar adaptive explanation. Polyethism, the division of tasks among workers, is thought to be the key feature underlying the phenomenal ecological success of the eusocial insects (Wilson 1990).

What causes size variation in bumblebee workers? In pollen-storing species such as *B. terrestris*, larvae spend most of their development in individual silk cells, and are fed directly on nectar and pollen mixes regurgitated by the adults (Alford 1975). Thus, adults probably determine the size attained by each larva (Ribeiro 1994). Some studies have shown that worker size increases through the season, but the change in mean size is small compared to

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variation found within broods (reviewed in Alford 1975). Bumblebee larval cells are not as neatly organized as are those of honeybees, *Apis mellifera*, and larvae at the periphery of the brood may receive less care than those in the centre. However, it seems implausible that a 10-fold variation in worker mass results from the accidental neglect of some larvae at the expense of others. Given that larvae are reared in a controlled environment by a team of specialized nest workers (Alford 1975; Sutcliffe & Plowright 1988, 1990), it seems more likely that this size variation has an adaptive function, and that colonies benefit from rearing workers of a range of sizes.

What might this function be? Bumblebees exhibit polyethism. Young adults perform only within-nest tasks and are more likely to become foragers as they become older (Pouvreau 1989; O'Donnell et al. 2000). Young foragers generally collect nectar, and tend to switch to collecting pollen as they age (Free 1955a). Bumblebees also exhibit behavioural plasticity. Individuals can switch between tasks in response to colony requirements; for example, nest bees will switch to foraging if the foragers are experimentally removed (Free 1955a; Pendrel & Plowright 1981). Individual bees differ in the threshold level of resources within the nest at which they respond by switching between tasks (van Doorn 1987; Cartar 1992). Specialized foragers bring most food to the nest, but other specialists carry out the majority of within-nest tasks (O'Donnell et al. 2000). Specialists are probably more efficient at their tasks; workers that are primarily foragers occasionally do within-nest tasks, but they do them more slowly than nest bees (Sakagami & Zucchi 1965; Cartar 1992; O'Donnell & Jeanne 1992).

There is evidence that polyethism in bumblebees is linked to size; that is they exhibit alloethism. Many studies have noted that foragers of a range of bumblebee species appear to be larger, on average, than bees that remain in the nest, although the evidence is predominantly anecdotal (Colville 1890; Sladen 1912; Meidell 1934; Richards 1946; Cumber 1949; Brian 1952; Free 1955a). Large workers tend to switch from within-nest tasks to foraging at an earlier age, and the smaller bees may never switch to foraging (Pouvreau 1989). As yet we do not know why large workers tend to forage while smaller bees tend to stay in the nest. We quantified the range of sizes of workers involved in foraging versus nest tasks in the bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae). We examined whether larger bees possess morphological adaptations for foraging. We then determined the relationships between forager size, the load of nectar or pollen that they bring back to the nest, and the rate at which forage is gathered, to assess whether alloethism can be explained in terms of foraging efficiency.

METHODS

Size of Queens, Males, Nest Workers and Foragers

We purchased 30 nests of *B. terrestris* from Koppert U.K. Ltd (Haverhill, Suffolk, U.K.). The nests were small and even-aged, consisting of the queen and up to 40 workers. These nests are supplied with a bag of nectar to feed the bees while in transit. This was removed, and nests were placed outside between 7 and 14 June 2000 at sites in south Hampshire, Dorset and Wiltshire, U.K. Subsequently the bees were allowed to forage naturally. Nests were situated at least 2 km apart, and were placed in sheltered sites (usually under a hedge). Two of the 30 nests were destroyed during the experiment, probably by badgers. We sealed each nest 4 weeks after placing it in the field. Bees returning to the nest during the next 30 min were captured in a butterfly net. These commercial nests consist of an outer cardboard box with a ventilated plastic inner box. The inner box containing the nest was removed and replaced with an empty inner box. The nest entrance to these boxes is equipped with an optional valve, which allows bees in but prevents them from leaving. This valve was put into operation, and the empty box left in place for 24 h to capture any more bees that returned. All bees that were collected were killed using a combination of ethyl acetate and freezing. We then dissected the nests and measured the thorax width of all bees (including males and gynes). All bees that were not in the nest at the time that it was sealed were classified as foragers. We examined differences in thorax width between bees in the nest and foragers by analysis of variance, including nest as a factor.

Allometry of Worker Morphology

We examined the relationships between worker mass, thorax width, tongue length, wing length and the maximum height of the corbicular hairs (which form the pollen basket) by weighing and measuring 100 unladen workers selected to span the full range of worker sizes. Tongue length was measured as the length of the glossa plus prementum. The height of the corbicular hairs was measured perpendicular to the posterior margin of the hind tibia.

The shape of the relationships between each morphological variable and thorax width was explored with log–log regressions. Departure from isometry is indicated by a slope differing significantly from 1.

Worker Size and Mass of Forage

As described above, 436 foragers were captured by hand as they returned to their nests, with the number caught per nest depending on nest activity. For each bee we recorded the following: thorax width, mass of pollen in the pollen baskets, and mass of nectar in the honey stomach. To obtain the latter, we first thawed each bee and fully extended the proboscis. We then squeezed the contents of the honey stomach from the mouth of the bee into a container by manually compressing the abdomen towards the thorax. Three bees were found to be carrying neither pollen nor nectar, and were excluded from further analysis.

Worker Size and Foraging Efficiency

In summer 2001, we purchased three nests from Koppert U.K. Ltd. We marked all bees individually by

Table 1. Summary of the number of experimental observations obtained per nest in the study examining the relationship between worker size and foraging efficiency

	No. marked bees	No. days observed	No. hours observed	Dates
Nest 1	154	12	81	15 June–3 July
Nest 2	169	13	100.5	10–31 July
Nest 3	150	12	100	6–24 August

gluing queen-marking discs to their thorax. The thorax width of each bee was recorded. The nests were kept in the laboratory with the nest entrance connected to the window by a clear plastic tube 16 mm × 1 m, allowing bees to forage freely outside. Approximately half-way along the tube, it opened out into a cylindrical arena over the pan of an electronic balance. The arena had solid sides and a red acetate filter ceiling.

The bag of nectar was removed from each nest, and bees were allowed to forage for 2 days before observations were taken. Observations consisted of recording the time, weight and identity of outgoing and incoming bees and the presence or absence of pollen in the corbicula of returning bees. Each nest was observed for as many daylight hours as was practically possible, over about 3 weeks (Table 1). Any unmarked bees that emerged were tagged as they appeared.

For the analysis, we treated individual bees as the unit of replication. For each bee, the mean weight on return from foraging and the mean duration of foraging trips were calculated separately for trips in which pollen was brought back (‘pollen trips’) and trips where no pollen was gathered (‘nectar trips’) (bees that brought back pollen undoubtedly often also brought back nectar). The mean amount of forage brought back by each bee was calculated from the difference between outgoing and incoming weights. Foraging efficiency could then be calculated as the amount of forage brought back per time spent foraging. It became apparent that rain greatly extended foraging times, presumably because bees ceased foraging and sheltered in the field, so any foraging trips that included periods of rain were excluded from the analysis. In addition, we used only bees for which we obtained data on at least five complete foraging trips. Four bees regularly left the nests but returned with no forage. These were excluded from the analysis.

The difference in mass between the outgoing and incoming bee is a measure of net foraging efficiency. Bees lose mass during foraging as they respire, and the rate of loss is greater in larger bees (Heinrich 1979). This loss is offset against gains accrued. However, we cannot be certain that the concentration of nectar in the honey stomach of returning bees is independent of size.

The amount of forage brought back, the duration of foraging trips and the foraging efficiency per unit time were each analysed separately for pollen and nectar trips, using a general linear model in SPSS. Bee thorax width and nest were included as potential explanatory factors.

RESULTS

Size of Queens, Males, Nest Workers and Foragers

In the 28 nests placed out in the field in summer 2000, 3077 workers were found (868 gynes and 1009 males). We recovered a further 1417 foragers either by catching them by hand as they returned, or by trapping them in the dummy nestboxes. Thus, a mean ± SE of 31.6 ± 2.5% of workers were foraging at the point at which the experiment was terminated. Workers were significantly more variable in thorax width ($\bar{X}\pm$SD=4.50 ± 0.79 mm) than were gynes (7.92 ± 0.39 mm) or males (5.63 ± 0.32 mm; Hartley's $F_{\max}$ test: $F_{3,1008}$=6.12, P<0.001). The thorax width of workers varied from 2.3 to 6.9 mm, with an overall coefficient of variation (CV) of 0.173, after taking into account differences between nests. CV values for gynes and males were 0.049 and 0.056, respectively. Workers in the nest were significantly smaller than foragers ($\bar{X}\pm$SE thorax widths=4.34 ± 0.01 and 4.93 ± 0.02 mm, respectively; $F_{1,4411}$=720, P<0.001; Fig. 1). There were also significant differences between nests in worker size ($F_{27,4411}$=18.6, P<0.001). The smallest workers, those with thorax widths between 2.3 and 3.2 mm, were rarely found outside the nests (Fig. 1).

Allometry of Worker Morphology

The relationship between the height of the corbicular hairs and thorax width appeared to be isometric, since the gradient of the log–log plot was approximately 1 (Table 2). Tongue length and wing length were both proportionally smaller in larger bees (as measured by the thorax width), with gradients of the log–log plots significantly less than 1 (Table 2). The relationship between the mass of workers and their thorax width was best described by the equation: ln (mass (g))=0.552 (thorax width (mm)) − 4.09; r^2=0.856, P<0.001.

Worker Size and Mass of Forage

Foragers that were netted on their return to the nest were classified into four categories: (1) nectar gatherers, bees that were carrying <1 mg of pollen and >10 mg of nectar; (2) pollen gatherers, bees that were carrying ⩾1 mg of pollen and <10 mg of nectar; (3) pollen and nectar gatherers, bees carrying ⩾1 mg of pollen and >10 mg nectar; (4) bees carrying <1 mg of pollen and <10 mg of nectar.

The largest category comprised nectar gatherers (203 bees) followed by pollen and nectar gatherers (160 bees). Specialist pollen gatherers were comparatively rare (52 bees), and 18 bees returned with little of either. There was a significant difference in the mean thorax width of bees in these categories (ANOVA: $F_{3,429}$=5.08, P=0.002, all nests combined). Tukey's post hoc tests were used to determine which differences were significant. Nectar gatherers were largest ($\bar{X}\pm$SE=5.05 ± 0.04 mm), and were significantly larger than pollen gatherers (4.81 ± 0.09 mm; P=0.020). Foragers that gathered both were of intermediate size (5.03 ± 0.05 mm), and did not

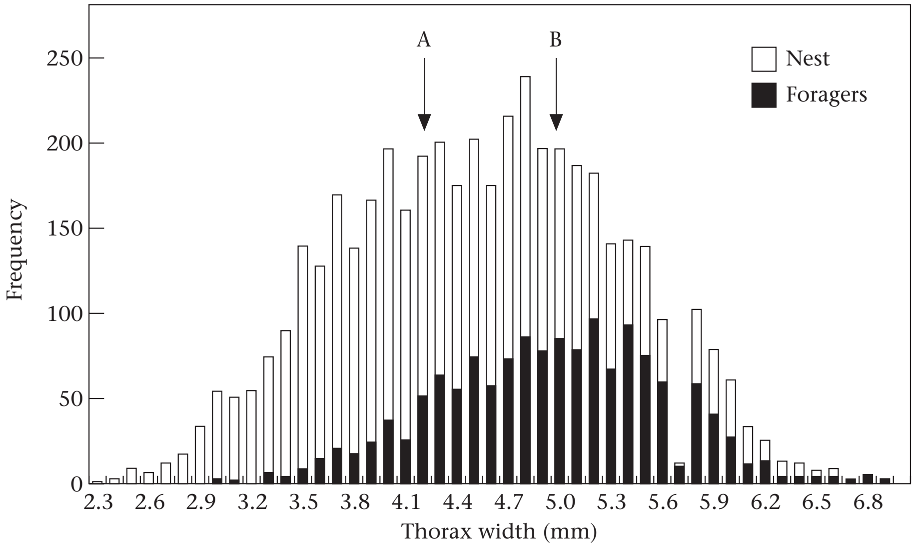

Figure 1. Frequency histogram of numbers of worker bees grouped by thorax width. Frequencies for bees caught in the nest (N=3.077) are stacked on top of those for foragers (N=1.417). Mean thorax widths of nest bees (A) and foragers (B) are indicated by arrows.

Table 2. Lines of best fit for the relationships between log (thorax width) and logs of tongue length, wing length and height of the corbicular hairs ($y=a+b$ log (thorax width))

	a	*b*	SE of *b*	95% confidence interval of *b*	Mean (mm)	SE	Range
Wing length	0.55	0.84	0.036	0.76–0.91	7.9	0.12	5.4–10.7
Tongue length	0.45	0.70	0.041	0.62–0.78	12.2	0.20	7.8–17.4
Height of corbicular hairs	0.52	0.97	0.108	0.75–1.2	0.65	0.03	0.65–1.90

Summary statistics are included for each variable.

differ significantly from either. The bees that collected very little were the smallest (4.67 ± 0.012 mm), and were significantly smaller than nectar gatherers (P=0.022) and bees that collected both nectar and pollen (P=0.045).

Bees carried a mean ± SE of 47.90 ± 1.42 mg of forage. Those that gathered both pollen and nectar carried more (59.6 ± 2.37 mg) than nectar gatherers (47.1 ± 1.80 mg) or pollen gatherers (26.3 ± 3.47 mg; $F_{2,411}$=30.3, P<0.001). Tukey's post hoc tests revealed that all three groups differed significantly from each other (P<0.001).

There was a significant positive relationship between the total mass of forage gathered (nectar and pollen) and the thorax width of the forager (Fig. 2a). Fitting of higher order equations increased the r^2 value very little, indicating that this relationship is essentially linear. When nectar gatherers and pollen gatherers were examined separately, similar linear relationships were apparent (Fig. 2b, c). The 433 foragers carried a mean ± SE mass of pollen and/or nectar equivalent to 23.10+0.01% of their unladen body mass. The heaviest load carried amounted to 77.1% of the bee's body mass. There was no relationship between the mass of forage expressed as a proportion of the bees' unladen mass and laden mass, for either nectar or pollen collectors (linear regression: $F_{1,201}$=0.13, P=0.72, and $F_{1,50}$=1.67, P=0.20, respectively), indicating that the relationship between mass of the bee and mass of forage is approximately proportional.

Worker Size and Foraging Efficiency

From the experiment conducted in 2001, a measure of foraging efficiency was obtained for 98 bees collecting nectar (based on an average of 14.1 trips per bee), and coincidentally for 98 bees collecting pollen (with an average of 10.9 trips per bee). There was no significant difference between the size of nectar and pollen collectors (t_{195}=1.23, P=0.22). Some individuals switched between collecting pollen and nectar, and so occur in both data sets. As before, the mass of forage brought back varied significantly according to thorax width, with larger bees returning with more nectar and pollen (Table 3). When collecting nectar, the duration of foraging trips was shorter for larger bees, even though they collected more nectar (Table 3, Fig. 3a). This pattern was not evident when collecting pollen (Table 3, Fig. 3b). Thus larger bees collected significantly more nectar per unit time than small bees, but this relationship was not significant when collecting pollen (Table 3, Fig. 4).

The efficiency of foraging varied greatly between the three nests, presumably reflecting changing abundance of

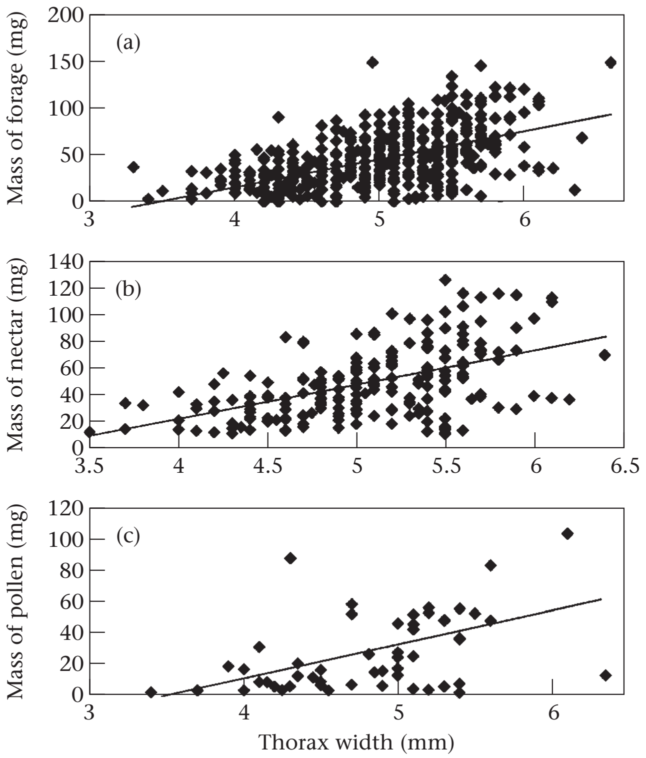

Figure 2. The total mass of forage carried by foragers in relation to their thorax width. (a) All foragers. Mass of forage (mg)=26.7 (thorax width (mm))−86, $r^2=0.26$, $N=433$, $F_{1,431}=151$, $P<0.001$. (b) Nectar gatherers. Mass of forage (mg)=24.0 (thorax width (mm))−74, $r^2=0.25$, $N=203$, $F_{1,201}=67.4$, $P<0.001$. (c) Pollen gatherers. Mass of forage (mg)=19.1 (thorax width (mm))−65, $r^2=0.22$, $N=52$, $F_{1,50}=14.3$, $P<0.001$.

Table 3. Relationships between thorax width and mass of forage, duration of foraging trips and forage obtained per unit time

Dependent variable	$F_{1,94}$	P
Nectar		
Mass of forage brought back	22.9	<0.001
Duration of foraging trip	11.0	0.001
Forage/time	11.0	0.001
Pollen		
Mass of forage brought back	27.7	<0.001
Duration of foraging trip	0.95	NS
Forage/time	2.10	NS

Data were analysed using a general linear model in SPSS.

resources during the season, or perhaps changes in the weather. Bees foraging in June (the first nest) gathered both nectar and pollen more rapidly than bees foraging in July (Nest 2) or August (Nest 3; Table 4).

DISCUSSION

Workers varied in size from a thorax width of 2.3 to 6.9 mm and their mass from 68 to 754 mg. The coefficient of variation of thorax width was 0.173. In contrast, Waddington et al. (1986) obtained CV values of 0.011–0.033 for 11 stingless bee species. Roulston & Cane (2000) found that the CV of females of 31 bee species varied from 0.018 to 0.117, with workers of the highly social *A. mellifera* varying least in size. They concluded that size variation in social bees seems to be less than that of solitary species, perhaps because the highly controlled nest conditions of social species enable rearing of uniform offspring. It seems, then, that worker bumblebees are exceptionally variable in size for social bees.

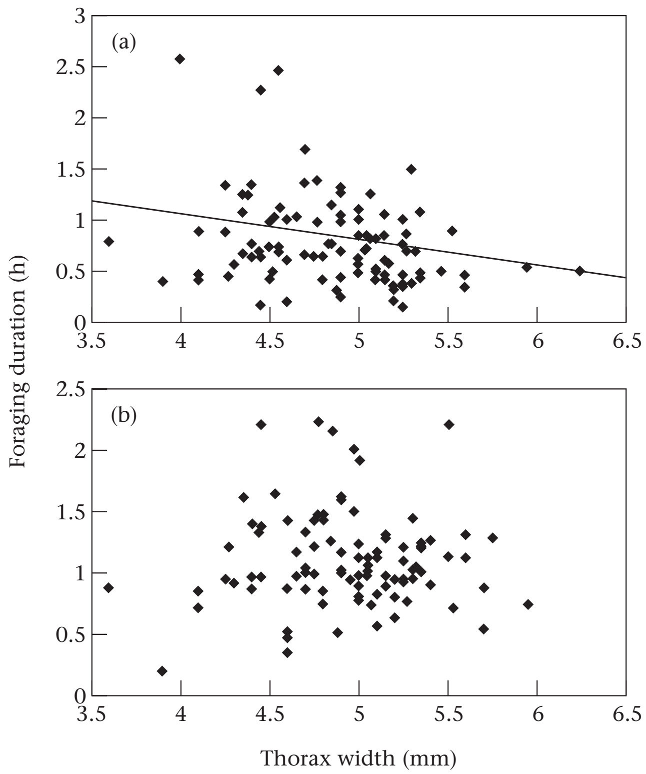

Figure 3. The mean duration of foraging trips in relation to forager thorax width. Data are combined for three nests. (a) Nectar gatherers. Line of best fit is: time=−0.28 (thorax width)+2.16, $r^2=0.08$, $N=98$, $F_{1,94}=11.0$, $P=0.001$. (b) Pollen gatherers (which may also have collected nectar), $N=98$, $r^2<0.001$, $F_{1,94}=0.95$, $P=0.33$.

The CV of worker sizes in our study was more than three times that of either gynes or males. We suggest that this is further evidence that worker size variation is adaptive. On the other hand, gynes and males are reared at the end of colony development when there are more workers to tend them, which could also explain their greater uniformity in size.

Our results show that foragers are, on average, larger than workers that remain within the nest. This finding is in accordance with those of previous studies (Colville 1890; Sladen 1912; Meidell 1934; Richards 1946; Cumber 1949; Brian 1952; Free 1955a). Furthermore, at least some foragers would have been in the nest at the time of sampling. Since larger foragers appear to go on shorter foraging trips (Fig. 3), they were more likely to have been in the nest at the time of sampling than smaller foragers. Thus, our estimate of the difference in size of foragers and nest bees (0.59 mm) is an underestimate of the true value.

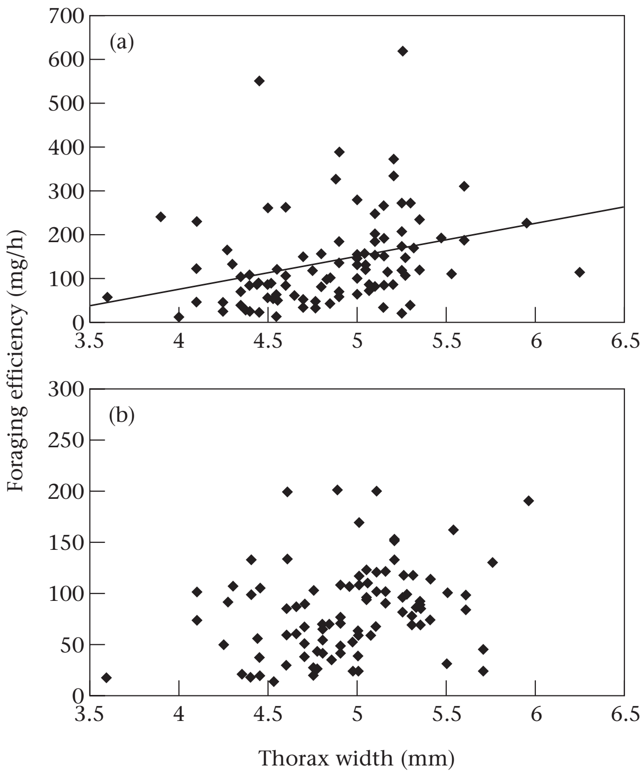

Figure 4. The mean efficiency of foraging trips (forage per unit time) in relation to forager thorax width. Data are combined for three nests. N=98 for both nectar and pollen gatherers. (a) Nectar gatherers. Line of best fit is efficiency=66.9 (thorax width)−197, r^2=0.61. (b) Pollen gatherers (which may also have collected nectar).

Why might large workers be more suited to foraging, and small workers to within-nest tasks? In many social insect species, different-sized individuals are adapted to their roles by having task-related body parts that are disproportionately large or small. For example, Ramalho et al. (1998) found such a pattern in the pollen baskets of stingless bees (*Melipona* spp.). However, in *B. terrestris* we found that although the size of pollen baskets was isometrically related to body size (as measured by thorax width), both wing length and tongue length were proportionally smaller in larger bees. This result is contrary to expectation, and suggests that the morphology of foragers is not especially suited to their task.

Free & Butler (1959) proposed that large workers tend to be foragers simply because they can carry more forage. We found that large foragers did indeed bring back more forage. When collecting nectar, they also did so more quickly, so that larger bees returned with significantly more food per unit time. This is a remarkable finding, suggesting that larger bees are able to forage at a much greater rate, either by visiting more flowers per unit time or by extracting more nectar per flower. The line of best fit between nectar foraging efficiency and thorax width (Fig. 4a) suggests that bees with a thorax width of less than about 3.5 mm have a low foraging efficiency. Although many of the workers were below this size, few of these bees were foragers.

The results for foraging efficiency of pollen collectors were less clear. Although large foragers brought back more forage, they were not significantly more efficient in terms of forage gathered per unit time. However, many of these bees were undoubtedly also collecting nectar. Our previous experiment, in which we captured returning bees and weighed their pollen and nectar loads separately, revealed that bees collecting both nectar and pollen returned with more than twice the mass of forage (mean 59.6 mg) than did bees that had gathered only pollen (26.3 mg). It seems likely that the efficiency of collecting both is higher (in terms of mass per time) than that of collecting only pollen, so combining these two groups of bees in our analysis may have obscured relationships between size and efficiency.

There are few data on the relationship between foraging rates and size in bumblebees, and what there is provides conflicting evidence. In a comparison of two bumblebee species feeding on *Aconitum columbianum*, Pyke (1978) found that the larger bee species travelled more rapidly between inflorescences. He used these data to predict an optimum body size for foragers, based on energetic efficiency, of 0.24 g, which was close to the observed size of the larger species. However, these calculations are of dubious validity, since they assume that differences in flight time between species are purely a function of size. No attempt was made to quantify differences in flight speed between different-sized workers of each species. As noted earlier, Stout (2000) found that smaller workers of *B. terrestris* and *B. lapidarius* were faster than large workers at handling flowers of *C. scoparius* (a source of pollen). Morse (1978b) found no difference in the foraging speed of large versus small workers of *B. vagans* foraging on *Vicia cracca*. If large bees moved faster between flowers than small bees, we would expect them to gather both pollen and nectar more quickly, but this is not the case. The pollen collection rate did not vary significantly with size. Perhaps the longer tongues of larger bees enabled them to extract more nectar per flower (although we found that large bees have proportionally shorter tongues than small bees, in absolute terms their tongues are longer). Pouvreau (1989) suggested that larger workers are at an advantage in foraging because they have longer tongues and so are able to feed on deeper flowers (long tongues would give them no advantage in pollen collection). However, having a long tongue is not necessarily an advantage (Harder 1986, 1988). Bees with short tongues can forage more quickly on shallow flowers (Plowright & Plowright 1997). In fact, the most common bumblebee species in the U.K., including *B. terrestris,* are all relatively short-tongued species. Studies of foraging rates on flowers, the amount of nectar removed per flower, and floral choices of large versus small foragers are required to shed light on the differences we observed.

Size may also affect other aspects of foraging. Morse (1978a) suggested that large workers may be able to forage over greater distances, and thus are more likely to have access to better forage. Large bumblebee species tend to go on longer foraging trips than smaller species, and thus may cover larger distances (Free 1955b), but since they

Table 4. Differences in mean±SE foraging efficiency (forage gathered per bee hour of foraging) between three nests operating at different times during the season

	Nest 1	Nest 2	Nest 3	$F_{3,92}$	P
Dates	15 Jun–3 Jul	10–31 Jul	6–24 Aug		
Nectar (g)/bee hour	0.202±0.018	0.068±0.008	0.103±0.009	20.6	<0.001
Pollen (g)/bee hour	0.126±0.012	0.062±0.005	0.062±0.010	11.7	<0.001

collect more forage this alone could account for the difference. There have been no studies of the distance or duration of foraging trips in relation to size variation within species, but the shorter nectar-foraging trips of large bees suggests that they do not travel greater distances.

Free & Butler (1959) pointed out that larger workers would be better able to forage in adverse weather. All bees are limited to foraging within a particular temperature range and, in general, the lower limit of this range shifts downwards as body size increases (Stone & Willmer 1989). For example, queens of *B. vosnesenskii* and *B. edwardsii* can sustain continuous flight in ambient temperatures ranging from 2 to 35°C, but workers are unable to maintain an adequate body temperature for flight below 10°C (Heinrich 1975). It seems that all conspecifics, from the smallest workers to queens, have to maintain their thoracic temperature within the range 31–42°C to be able to fly (Heinrich & Heinrich 1983a, b). Thus, larger foragers are presumably able to become active at lower ambient temperatures than small foragers, but conversely, they are more prone to overheating in warm weather (Heinrich 1975, 1979). The longer nectar-foraging trips made by small bees in our study may have occurred because the body temperature of these bees more frequently fell below that required for activity.

A final possible explanation for alloethism in bumblebees relates to predation. Foraging is a dangerous task that probably increases worker mortality (van Doorn 1987; O'Donnell & Jeanne 1995; O'Donnell et al. 2000). It seems likely that larger bees are less prone to predation, particularly by spiders, than small bees. Conversely, the conopid fly *Sicus ferrugineus*, which attacks bees while they are foraging on flowers, preferentially parasitizes large workers (Schmid-Hempel & Schmid-Hempel 1996). If large bees have a longer life expectancy as foragers, having large bees foraging may be the safest option for the colony. No data are available on the longevity of foragers in relation to size, and this would be an interesting and relatively straightforward area for study.

Demonstrating that large bees are more efficient foragers does not in itself explain size variation in bumblebees, for it does not take into account the cost of rearing bumblebees of different sizes. Presumably large bees are more costly to produce, but we do not yet know whether this relationship is linear. To calculate the optimum strategy for the colony, the rate at which forage is gathered should be offset against the rearing costs.

An alternative to asking why large bees tend to be foragers is to ask why small bees tend to perform within-nest tasks. Presumably small workers are cheaper to rear. Free & Butler (1959) suggested that small workers are better able to manoeuvre within the cramped confines of the nest. By experimental manipulation of the size of nest workers of *B. terrestris*, Cnaani & Hefetz (1994) showed that colonies with only large workers reared more larvae than colonies with an equal number of small workers. However, this result does not fully refute the hypothesis. A fairer comparison would be between larvae tended by an equal biomass consisting of either a few large workers or many small ones.

Bloch & Hefetz (1999) showed that the first cohort of workers within a colony of *B. terrestris* are behaviourally dominant. These workers also tend to be smaller than those of subsequent cohorts (reviewed in Alford 1975). It is possible that these older, smaller workers remain in the nest to maximize their reproductive prospects, and force their younger, larger siblings to become foragers. However, this hypothesis does not explain why size variation occurs in the first place, and particularly why most size variation occurs within cohorts (see Alford 1975).

None of the explanations that we have considered for size variation in bumblebees explains why bumblebees exhibit more size variation than other bee species. If size variation in bumblebees is adaptive, why do other bees not show it? Bumblebees are unusual in that they are very large (for bees), and are adapted for foraging in cooler weather than most smaller species. The temperature in the nest is often many degrees warmer than the air temperature in which foragers operate. Perhaps these conditions have favoured evolution of a large caste that specializes in foraging.

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