

# Size variation and foraging rate in bumblebees (*Bombus terrestris*)

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**Summary.** Size polymorphism is an important life history trait in bumblebees with strong impact on individual behavior and colony organization. Within a colony larger workers tend to serve as foragers, while smaller workers fulfill in-hive tasks. It is often assumed that size-dependent division of labor relates to differences in task performance. In this study we examined size-dependent interindividual variability in foraging, i.e. whether foraging behavior and foraging capability of bumblebee workers are affected by their size. We observed two freely foraging *Bombus terrestris* colonies and measured i) trip number, ii) trip time, iii) proportion of nectar trips, and iv) nectar foraging rate of different sized foragers. In all observation periods large foragers exhibited a significantly higher foraging rate than small foragers. None of the other three foraging parameters was affected by worker size. Thus, large foragers contributed disproportionately more to the current nectar influx of their colony. We provide a detailed discussion of the possible proximate mechanisms underlying the differences in foraging rate.

*Key words:* Bumblebees, size polymorphism, foraging behavior, nectar loads, division of labor, interindividual variability.

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## Introduction

Intra-colonial worker size variation is weak in honeybees and most stingless bee species, but pronounced in bumblebees (Garófalo, 1978; Inouye and Kato, 1992; Knee and Medler, 1965). *Bombus* workers of various sizes are produced throughout the colony life cycle, and body mass differences between small and large workers can reach up to a factor of seven (Cumber, 1949).

The size of a bumblebee worker affects her physiological abilities, including thermoregulation (Bishop and Armbruster, 1999; Heinrich and Heinrich, 1983), flight speed (Spaethe, unpublished data; Pyke, 1978), or nectar ingestion

rate (Harder, 1983 b). Comparing large and small individuals, most investigations reveal a superior performance of larger bees. Larger individuals, for instance, are better adjusted to regulate their body temperature and are therefore able to forage at lower ambient temperatures (Heinrich and Heinrich, 1983).

Body size is also known to affect task preferences of workers. While in bumblebee colonies only weak age-related division of labor occurs (Cameron, 1989), several studies have revealed a correlation between a worker's size and the probability of performing a certain task. Large workers were found to have a higher probability of foraging for nectar and pollen, whereas small workers tended to stay inside the nest and attend to nest duties (Cumber, 1949; Free, 1955 b; Garófalo, 1978).

As the survival, growth and reproduction of a colony depend strongly upon the influx of nectar and pollen, selection is expected to maximize energy influx into the colony by efficient allocation of the available workforce to the necessary tasks. This assumption together with the finding that larger bumblebees perform better in several physiological demands during foraging provoked some authors to suggest that size-related division of labor between within-nest tasks and foraging is caused by a superior foraging performance of large workers: "...it is doubtless more economical that larger individuals should forage, and that the smaller ones should do the 'housework'" (Cumber, 1949, p. 16). Although this assertion appears intuitively convincing, we do not know of any investigation which clearly shows that larger workers are more efficient in collecting nectar or pollen, or that smaller workers are better in nursing the brood. Here, we address the question whether workers of different size differ in their foraging success. Although several authors found a positive correlation between a forager's body size and the amount of nectar or pollen she brought back to the nest (Allen et al., 1978; Free, 1955a), it has not been ruled out that a small forager counterbalances her smaller loads by completing more collecting trips per unit time. In order to evaluate the relative contribution of small and large workers to the colony's food

influx, we need to compare foraging rates (amount of pollen or nectar per time) rather than absolute load sizes of foragers. This is the approach we have taken in the present study.

## Material and methods

### Study animals

We studied two colonies of *Bombus terrestris* (L.) (Colony A: approximately 100 individuals; colony B: approximately 200 individuals). Both colonies were housed in small wooden boxes (15×28×11 cm) inside a lab at the bee station of the University of Würzburg, Germany. A Plexiglas tunnel (7×45×4 cm) between the nest and the outside allowed the bees free outdoor access for foraging.

### Data collecting

In each colony, we randomly marked 100 workers with numbered 'Opalithplättchen'. We collected data during four observation periods, one six-day period in colony A in 1999 (A1, six intermittent days between 11 August and 3 September) and three three-day periods in colony B in 2000 (B2: 07–09 June; B3: 14–16 June; B4: 19–21 June).

In 1999 our daily observations lasted from 10:00 to 17:00, in 2000 from 05:00 to 15:00 and from 19:00 to 22:00, resulting in a total of 159 hours of observation. For all marked workers we recorded i) departure time, ii) mass at departure, iii) arrival time, iv) mass at arrival, v) and presence of pollen loads. In 1999 we measured the mass of a worker by catching her at the entrance of the tunnel with a small plastic cap while leaving or returning, weighing her on an electric scale (Sartorius BA 61, Göttingen, Germany) and releasing her at the entrance. However, this method did not allow us to record the masses of all marked bees during times of high flight activity. In 2000 we therefore refined the method. We placed the electric scale under a small opening (5×3 cm) in the floor of the entrance tunnel, so that all leaving and returning bees walked on the scale while passing through the tunnel. This allowed us to take mass data of every exiting and entering worker while leaving the colony completely undisturbed. The applied method provides highly repeatable measurements: ten successive measurements of the same individual resulted in very low standard deviations of between 1.6 and 3.7 %.

### Foraging parameters

All bees returning to the nest without pollen loads were defined as nectar foragers. Bees returning with pollen loads were classified as pollen foragers. This group contained individuals which collected pollen only or both pollen and nectar.

We analyzed the following foraging parameters: The net nectar load of a worker was calculated as the difference between departure mass and arrival mass. The foraging rate of a worker was then computed as the quotient of net nectar load divided by trip time. For each observation period we calculated the mean foraging rate of each worker, including only foragers that performed at least three nectar foraging trips during the observation period. Only trips longer than 10 minutes were considered in order to exclude orientation or defaecation flights (Capaldi and Dyer, 1999; Capaldi et al., 2000).

For colony B, we also calculated the mean daily trip number and trip time of each worker that performed at least three nectar trips per observation period. Furthermore, for each worker with a minimum of three foraging trips per observation period (irrespective of the kind of collected food) we analyzed the proportion of nectar trips by dividing the number of nectar trips through the total number of foraging trips. The value ranged from 0 (only trips with pollen) to 1 (only nectar trips).

As a measure of size we used the bees' mean body mass at departure. Empty body mass correlates very well with a multitude of morphometric measures like forewing length, head capsule width or intertegular span (Spaethe, unpubl. data; Bullock, 1999). Further, mass

measured at departure seems to be a good estimate of empty body mass because foragers take only very small nectar provisions with them when leaving their colony (Allen et al., 1978).

### Data analysis

We tested correlations between each of the measured foraging parameters and body size by a nonparametric test for association (Spearman's rank order test). All p-values above 0.05 were considered not statistically significant. We treated each group of data obtained from each observation period in colony B independently because only two individuals (2.3%) foraged in all three periods and more than 80% of all bees in period B2 and B3 were not observed in any other observation period. Since we performed multiple significance tests on data from colony B we adjusted p-values using the sequential Bonferroni procedure to control for Type I error (Rice, 1989).

## Results

### Trip time, number of trips and probability of nectar foraging

The first workers started foraging between 05:00 and 05:42 in the morning. Foraging trips of bees which spent the night outside the nest and brought back nectar or pollen very early were excluded from our analysis. The last foragers entered the hive between 20:47 and 21:42, when daylight began to decline. The mean trip number per worker (nectar and pollen trips) in each observation period ranged from 3.3 to 5.8 trips per daily observation time, the mean trip time from 57 to 75 minutes (Table 1).

In all observation periods roughly one-fourth of the observed foragers collected nectar and were never seen with pollen loads (B2: N = 10 (15%); B3: N = 14 (26%); B4: N = 14 (29%)). On average, two thirds of all trips were nectar trips (Table 1). Between 10 and 18% of all foragers in each period collected pollen on more than 75% of their trips (B2: N = 12 (18%); B3: N = 5 (9%); B4: N = 5 (10%)), but only one or no forager always carried pollen when returning to the colony (B2: N = 1 (2%); B3: N = 1 (2%); B4: N = 0). For none of the three parameters (trip time, trip number, and proportion of nectar trips) did we find a significant correlation with body mass.

For reasons explained above, we did not take into account trips shorter than 10 minutes. One could argue that very small (or large) bees may perform a disproportionately high number of short foraging trips (<10 minutes) and that this possible correlation between trip time and size went undetected in our study. However, since we did not observe a single forager that made at least three foraging trips (heavier on return than at departure) shorter than 10 minutes during one observation period, and since those workers that did show one or two occasional foraging trips of less than 10 minutes did not differ significantly in mass from the foragers with foraging trips of more than 10 minutes, this can be ruled out.

### Nectar foraging rate

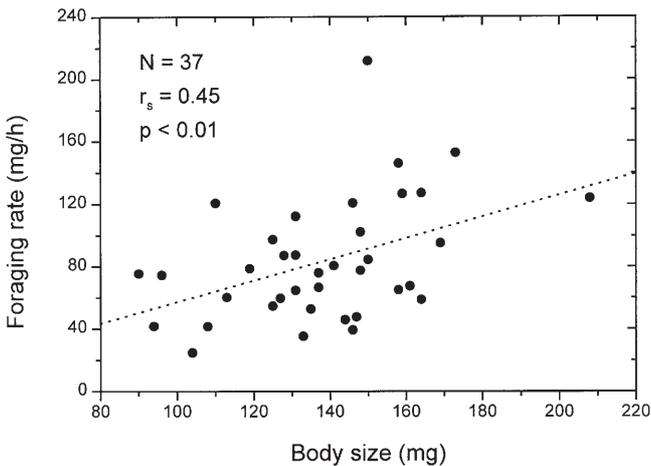
In each observation period we analyzed between 30 and 38 foragers with at least 3 nectar foraging trips. The mean for-

**Table 1.** Mean daily trip number, mean trip time and proportion of nectar foraging trips of all foragers of colony B with a minimum of three nectar foraging trips per observation period (for the proportion of nectar foraging trips we used foragers with a minimum of three foraging trips). None of the three parameters showed a significant correlation with body size ( $r_s$ , Spearman-rank correlation coefficient, all p-values > 0.05)

Observation period (d.m)	Trip number				Trip time				Proportion of nectar trips			
	Mean daily trip number [max]	$r_s$	p-value	$N$	Mean trip time (min) [min; max]	$r_s$	p-value	$N$	Ratio nectar trips/all foraging trips [min; max]	$r_s$	p-value	$N$
B2 (07. – 09.06.)	4.8 [10]	-0.10	> 0.05	34	57 [24; 103]	-0.22	> 0.05	34	0.59 [0;1]	0.17	> 0.05	66
B3 (14. – 16.06.)	3.3 [8]	-0.03	> 0.05	38	75 [29; 129]	-0.10	> 0.05	38	0.69 [0;1]	-0.10	> 0.05	53
B4 (19. – 21.06.)	5.8 [12]	-0.16	> 0.05	37	72 [27; 139]	0.04	> 0.05	37	0.71 [0.07;1]	-0.01	> 0.05	48

**Table 2.** Mean nectar foraging rate and mean empty body mass of foragers in the four observation periods;  $N$ , number of observed nectar foragers;  $r_s$ , Spearman's rank correlation coefficient for nectar foraging rate and body mass. All correlations were significant

Colony	Observation period (d.m.y)	Mean foraging rate ( $\text{mg} \cdot \text{h}^{-1}$ ) [min; max]	Mean body mass (mg) [min; max]	$r_s$	p-value	$N$
A	A1 (11.8.–3.9.1999; 6 observation days)	54.9 [1.4; 222.9]	140.4 [98; 210]	0.41	<b>0.02</b>	30
B	B2 (7.–9.6.2000)	86.9 [22.6; 215.3]	149.3 [104; 245]	0.36	<b>0.03</b>	34
B	B3 (14.–16.6.2000)	58.3 [16.6; 149.3]	142.1 [96; 213]	0.38	<b>0.02</b>	38
B	B4 (19.–21.6.2000)	83.3 [24.8; 211.8]	138.1 [90; 208]	0.45	<b>0.006</b>	37



**Figure 1.** Nectar foraging rate as a function of body size (observation period: B4 (19–21 June)). Equation for the regression line:  $y = -11.4 + 0.69x$

aging rate per observation period ranged from 54.9 to 86.9 mg nectar per hour. The mean empty body mass per observation period ranged from 138.1 to 149.3 mg (Table 2), the smallest and largest forager differed more than two-fold in mass. In all four observation periods we found a significant correla-

tion between body mass and nectar foraging rate (Fig. 1 and Table 2). Larger foragers had higher nectar returns to the colony per time compared to their smaller nestmates. Since small and large workers did not differ in their trip time, this was caused by the ability of large worker to collect more nectar during the same time period compared to their smaller nestmates.

## Discussion

The aim of this study was to test whether bumblebee workers of different size differ in their foraging success. Our data reveal a clear size effect on nectar foraging rate. Previous studies reported that larger foragers return to their colony with larger loads (Spaethe and Weidenmüller, unpubl. data; Allen et al., 1978; Fisher, 1987). We have now shown that larger foragers collect their loads in the same amount of time as their smaller nestmates and thus contribute disproportionately to the total nectar influx of their colony. Thus, our data support the hypothesis that larger foragers are superior in nectar foraging. These results are consistent with findings published in a methodological paper on *B. griseocollis* (DeGeer) (Fisher, 1987); the only other study that reports foraging rates of differently sized workers.

### *Trip time, trip number and probability of pollen foraging*

In contrast to foraging rate, the other foraging parameters measured, trip time, trip number and probability of collecting pollen, respectively, were unaffected by forager size. Foraging trips lasted on average between 57 and 75 minutes (Table 1) and were longer compared to results of most earlier studies (Cartar, 1992: 25 to 30 minutes; Brian, 1952: 18 minutes). This might be due to differences in species and habitats and in applied methods. For example, the observation periods in Brian's study lasted no more than one hour thus excluding trips longer than one hour (Brian, 1952). Brian also included trip times shorter than 10 minutes which are usually non-foraging flights (see above). Both factors may lead to an underestimation of foraging times. The only other study in which observational methods are comparable to ours reports very similar trip times (Allen et al., 1978). On average, foragers made between 3 and 6 trips per daily observation time (Table 1). Number of trips varied substantially among foragers, but was not affected by forager size. Likewise, we found no correlation between proportion of pollen trips and size (Table 2). This finding is in contrast to earlier observations, which showed that the proportion of pollen trips was higher in larger foragers (Brian, 1952; Free, 1955b; Fisher, 1987). Again, different results might arise from fundamental differences in the life history of the observed species (Cartar, 1992; Heinrich, 1979), from varying observational methods or because colonies were observed at different stages of their life cycle (Cartar, 1992).

### *Why do large foragers have higher nectar foraging rates?*

Which factors are responsible for the size-dependent differences in foraging rate? First of all, flight speed presumably has strong impact on foraging rate. Bumblebees visit several patches with hundreds to thousands of flowers during one foraging trip (Michener, 1974), and flight time between flowers and patches constitutes up to 80% of total foraging time (Heinrich, 1979). Additionally, the distance between the nest and a forage site can reach 1 to 4 kilometers in *B. terrestris* (Hedtke, 1996; Walther-Hellwig and Frankl, 2000). By increasing flight speed only slightly, a forager can substantially economize her trip time expenditure. When foragers increase their flight speed, their fuel expenditure per trip length does not increase, because for an individual bumblebee the per-meter costs of flying remain constant over a wide range of her flight speed (Ellington et al., 1990). Thus larger foragers may have higher foraging rates because they spend less time flying to and between flowers.

A second factor which can vary with size is handling time at flowers. In order to exploit the nectar in a flower the bees first have to reach the nectaries, which is sometimes rendered difficult by a long corolla tube or a narrow entrance, and then ingest the nectar. Larger bees may reach the nectaries more easily and extract the nectar faster because of their longer tongues and stronger sucking related muscles (Harder, 1983b; Winston, 1979). Indeed, several authors discovered that bees with longer tongues spend less probing time per

flower (Harder, 1983a; Heinrich, 1979). In a study investigating the distribution of long- and short-tongued bumblebee foragers of *B. vagans* (Smith) among cow vetch (*Vicia cracca*) flowers, Morse (1978) found a correlation between proboscis length and floret depth of visited flowers but no differences in handling time (Morse, 1978). However, assuming that larger flowers provide more nectar (Cohen and Shmida, 1993 and citations therein) and that larger bees are able to ingest nectar more rapidly (see above), we would expect larger bees to extract more nectar at each flower per time even when handling times do not differ. Thus, the nectar foraging rate of larger workers may be higher because they spend less time per flower for the same amount of nectar compared to their smaller nestmates.

Finally, an often overlooked factor influencing foraging behavior of bumblebee workers is a size-dependent constraint imposed by the bees' sensory system. In a recent study, Spaethe et al. (2001) showed that bumblebees searching for artificial flowers of varying sizes and colors are strongly constrained by their visual abilities. Small flowers evoked a substantial increase in search time because the spatial resolution of a bee's eye is poor and a small decrease of floral size at a critical value considerably lowers the probability of detecting the flower (Spaethe et al., 2001). We predict that a similar increase in search time will occur when small bees with smaller eyes (and thus lower spatial resolution) search for a certain floral size. Due to their poorer resolving power they can detect a flower only from a shorter distance than larger bees (Spaethe, 2001). Thus, larger foragers may have shorter search times than their smaller nestmates due to their superior ability in detecting flowers, again resulting in higher foraging rates.

In summary, various size-dependent factors are known to influence the foraging abilities of bumblebees and may lead to the observed differences in foraging rates between large and small workers of a colony.

### *Worker size variation – constraint or adaptation?*

Our data reveal a clear size effect on nectar foraging rate. Larger foragers contribute disproportionately to the total nectar influx of their colony. Clearly, by allocating its largest workers to foraging a colony will maximize its nectar influx. And indeed, others found that larger workers are more prone to adopt foraging tasks than within-nest duties (Cumber, 1949; Free, 1955b; Garófalo, 1978). So why do bumblebee colonies produce small workers at all?

Some of the factors responsible for worker size variation at the proximate level have been identified. The primary factor seems to be unequal food provisioning during the larval stage (Plowright and Pendrel, 1977; Sutcliffe and Plowright, 1988). Bumblebee nests consist of a more or less irregular conglomerate of egg clumps, larval cells and nectar and pollen cells. The larvae positioned at the border and at the bottom of the nest are visited less often by nurse bees and thus receive less food during their development than central larvae (Sladen, 1912, cited in Cumber, 1949). Further factors may be competition among the larvae from one egg clump

(Cumber, 1949; Michener, 1974) and differences in temperature conditions depending on position in the nest.

The ultimate reasons, if any, for the production of workers of different sizes are much harder to assess. Is size variation among workers of a bumblebee colony an adaptive feature or is it caused by some constraint? In other words, does selection promote behavior which leads to unequal food provisioning of the larvae, or does some unknown constraint prevent bumblebees from building regular layers of larvae cells, which seems to be a prerequisite for producing monomorphic workers? Here we can only offer some speculative thoughts. One important step in answering this question would be to know whether polymorphism in bumblebees arose secondarily from monomorphism or whether it represents the ancestral state. If the pronounced size polymorphism in *Bombus* is indeed a derived feature, it will be interesting to find out more about the functional significance of a size related division of labor, that is, the benefits of having workers of different sizes under different conditions. To this aim, future studies will need to identify the size related capability of workers at within-nest tasks such as brood care and nest climate control.

Further, it will be important to identify the costs for the colony of small vs. large workers (i.e. costs of production and costs caused by factors such as different life expectancy or different parasitation rates (Müller et al., 1996) and to test whether the occurrence of size polymorphic workers increase colony fitness. The latter can be done by comparing the reproductive output of colonies which are artificially assembled and comprise equally 'expensive' monomorphic and polymorphic worker groups respectively.

In summary, our results show that size affects foraging success in bumblebee workers. How this size dependent interindividual variability relates to colony organization and colony fitness remains to be investigated.

## Acknowledgments

We thank Lars Chittka and Jürgen Tautz for valuable comments on the manuscript and Laura Bollwahn, Petra Frauenstein, Tonja Schamberger, Katja Soer and Karin Weinmann for help with data collecting. Financial support was provided by the 'Deutsche Forschungsgemeinschaft' (Ch 147/2-1, Ta 82/7-2 and SFB 554).

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