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Original Article

Effects of experience and weather on foraging rate and pollen versus nectar collection in the bumblebee, *Bombus terrestris*

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Abstract This study examines factors that affect foraging rate of free-flying bumblebees, *Bombus terrestris*, when collecting nectar, and also what factors determine whether they collect pollen or nectar. We show that nectar foraging rate (mass gathered per unit time) is positively correlated with worker size, in accordance with previous studies. It has been suggested that the greater foraging rate of large bees is due to their higher thermoregulatory capacity in cool conditions, but our data suggest that this is not so. Workers differing in size were not differentially affected by the weather. Regardless of size, naïve bees were poor foragers, often using more resources than they gathered. Foraging rate was not maximised until at least 30 trips had been made from the nest. Foraging rates were positively correlated with humidity, perhaps because nectar secretion rates were higher or evaporation of nectar lower at high humidity. Temperature, wind speed and cloud cover did not significantly influence foraging rate, within the summertime range that occurred during the study. Weather greatly influenced whether bees collected pollen or nectar. Pollen was preferably collected when it was warm, windy, and particularly when humidity was low; and preferably during the middle of the day. We suggest that bees collect pollen in dry conditions, and

avoid collecting pollen when there is dew or rain-water droplets on the vegetation, which would make grooming pollen into the corbiculae difficult. Availability of sufficient dry days for pollen collection may be an important factor determining the success of bumblebee colonies.

Keywords Humidity · Size variation · Temperature · Thermoregulation · Wind

Communicated by M. Giurfa

Introduction

Bumblebees have been widely used as model organisms for studies of foraging behaviour and have become popular vehicles for examining the assumptions and predictions of foraging models and the interplay between learning, memory constraints and foraging rate in a complex and unpredictable environment (e.g. Heinrich 1979; Cresswell 1990; Dukas and Real 1993a, 1993b, 1993c; Goulson 1994, 1999, 2000a, 2000b; Dreisig 1995; Cresswell et al. 2000). Much of this work has focussed on individual behaviour on flowers, but little is known of the overall cumulative effect of learning on foraging rate.

Bumblebees are also of interest because, uniquely among the social bees, they exhibit great size variation within the worker caste and workers of different sizes engage in different tasks (alloethism). Larger workers tend to engage in foraging, while smaller workers tend to carry out within-nest tasks (reviewed in Goulson 2003). Large workers bring back more forage per unit time (Goulson et al 2002; Spaethe and Weidenmuller 2002), but it is not known how they do so. It has been argued that larger workers are better able to keep warm under cool conditions, and that it is this that gives them an advantage in foraging. Bumblebees were among the first insects in which endothermy was described, and it has since been studied in some detail (reviewed in Heinrich 1979; Goulson 2003). To generate the power needed for flight, bumblebees need to raise the temperature of their flight muscles to above 30°C (Heinrich 1979), and to do so they generate heat through shivering the flight muscles. Because heat production is proportional to muscle mass, but heat loss is proportional to the surface area, small bees are at a disadvantage in warming up, and should have a higher minimum ambient temperature for activity. Queens of *Bombus vosnesenskii* and *B. edwardsii* can sustain continuous flight in ambient temperatures as low as 2°C, while workers are considerably smaller and are unable to maintain an adequate body temperature for flight below 10°C (Heinrich 1975). It thus seems likely that small workers may struggle to maintain

a sufficient thoracic temperature at cooler temperatures and that this may explain why they gather nectar more slowly. However, the comparative foraging rate of large versus small bees under varying weather conditions has not previously been examined.

Here, we quantify the foraging rate of nectar-gathering workers of *B. terrestris* under natural conditions, and examine how foraging experience and forager size affect rate. We also assess how weather conditions affect foraging rate, and whether small or large bees are differentially affected by adverse weather conditions. Finally, we examine how weather affects the tendency of bees to collect nectar versus pollen.

Methods

The experiment was carried out from early June to late August 2001. Three nests of *B. terrestris* were purchased from Koppert UK (Haverhill, Suffolk). For each nest, all workers were labelled with numbered honeybee queen marker discs (purchased from E.H. Thorne, Wragby, Lincs.) glued to the thorax. Thorax widths were measured as an indicator of bee size. Water-filtered CO₂ was used to anaesthetise each bee for labelling and measurement. Each nest was housed in an unheated building, located on the University campus in suburban Southampton. The nests were connected to clear plastic tubing linking the nest entrance to the outdoors via a balance (accurate to 0.01 g), over which the bees walked. The balance was enclosed with a card wall topped with a clear, red light filter to discourage individuals from flying above the balance but enable viewing. A white plastic funnel was used as a recognisable landing platform at the end of the tube. A trap door was cut into the tubing to allow the removal of new individuals for labelling, measuring and reintroduction during the experimental period. A digital thermo-hygrometer placed beneath the funnel was used to record outside temperature and relative humidity.

Nests were bought and set up for observation consecutively, so that only one nest was in operation at any one time (Table 1). The nectar bag provided with each nest by the manufacturers was removed and the bees were allowed to forage freely. Two people observed the outgoing and incoming bees regularly for approximately 3 weeks per nest. When possible, observations were continuous during each day. For each bee that left or entered the nest the following was recorded: date, time, bee number, direction of travel (in/out), bee mass, presence of pollen in corbiculae, temperature, relative humidity, estimated wind strength, estimated cloud cover, and whether it was raining. Wind speed was scored on a scale of 0 to 3, 0 representing still air, 1 a gentle breeze when leaves were observed to move, 2 a stronger breeze when small branches were seen to be in

motion and 3 anything stronger than that. Commonly the two people observed the nest at once, so perceptions of wind speed were quickly calibrated.

[Table 1 will appear here. See end of document.]

Nectar-foraging rate for each trip was calculated by pairing appropriate outgoings and incomings then dividing the difference between in and out mass by the time taken for that trip. For any one trip, the number of previous trips recorded defined experience. Bees that left the nest five or less times in total were excluded from the analyses since these were presumably not primarily foragers. Data recorded 30 min prior, during and up to 30 min after periods of rain were excluded, as rain appeared to disrupt foraging trips. Trips of less than 10-min duration were excluded as these may not have been foraging trips (Capaldi and Dyer 1999; Spaethe and Weidenmuller 2002). Only foraging trips to gather nectar alone were included in this analysis. Bees often gather both nectar and pollen during the same trip (Goulson et al. 2002). From the weight of the returning bee it was not possible to determine how much forage was composed of nectar and how much of pollen. It seems probable that the rate of pollen collection differs greatly from that of nectar collection, so it would not be meaningful to examine foraging rate in bees with mixed loads. Hence all trips in which the bees returned with pollen were excluded. However, for calculation of foraging experience, all trips were included, because trips to collect pollen will contribute to the navigational experience of the bee and, as previously noted, most trips to collect pollen also involve some nectar collection.

Factors affecting foraging rate were analysed using univariate general linear models fitted in SPSS 11.0. Both linear and quadratic relationships between foraging rate and explanatory variables were examined, with stepwise removal of factors that did not contribute significantly to the model.

To examine what factors determine whether bees collect nectar or pollen, the presence or absence of pollen in the corbiculae of returning bees was analysed as a binomial variable in GLIM (Crawley 1993). Explanatory factors included in the model were previous foraging experience, thorax width, time of day, temperature, humidity, wind speed and cloud cover.

Results

In total, 473 workers were marked in the three nests, of which 199 were recorded making one or more complete foraging trips. The three nests were observed for a total of 281 h. During this time, 2,356 complete trips (where both outgoing and incoming measurements obtained) were recorded.

Foraging rate

Foraging rate was positively related to bee thorax width (Table 2). It also varied with experience, although the relationship was not linear (Fig. 1). Foraging rate was low for the first few trips from the nest, and many bees returned weighing less than when they left the nest. Foraging rate increased with experience, but the increases became smaller as experience increased so that after approximately 30 trips from the nest there was little further improvement.

[Table 2 will appear here. See end of document.]

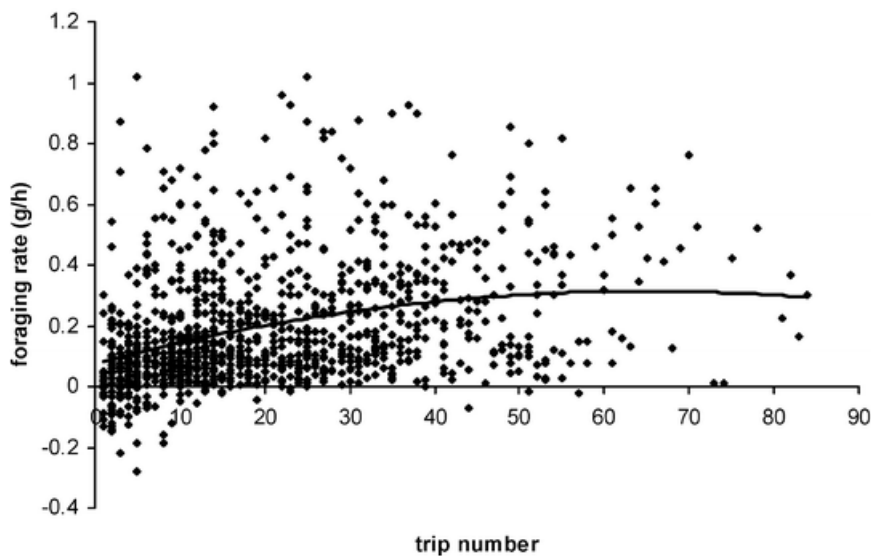


Fig. 1 The effect of experience, measured as the number of previous foraging trips recorded for each bumblebee, *Bombus terrestris*, on foraging efficiency when collecting nectar

The only weather variable that significantly influenced foraging rate was humidity, which was linearly and positively related to rate (Table 2). There was no significant interaction between thorax width and any weather variable ($F_{1,1035}=0.819, 0.246, 1.000$ and 1.05 for temperature, cloud cover, wind speed and humidity, respectively). Time of day had no significant influence on foraging rate (Table 2). Foraging rate varied significantly between the three nests (Table 2).

Nectar versus pollen collection

The number of previous foraging trips did not affect the likelihood of a bee collecting pollen ($\chi^2_1=0.2, P>0.05$), suggesting that the predilection for collecting pollen does not vary with age or experience of the forager. All other explanatory variables examined significantly affected pollen versus nectar collection (Table 3), with the sole exception of cloud cover ($\chi^2_1=0.2, P>0.05$). On average, bees collecting pollen were larger than those collecting nectar. Of the weather variables,

humidity had the greatest effect, with bees tending to collect pollen at low humidity and nectar at high humidity. They also collected with preference pollen on warmer and windier days, compared to nectar. The relationship between time of day and pollen collection was more complex, being best described by a quadratic equation. Bees tended to collect nectar early and late in the day, and pollen during the middle of the day (Fig. 2).

[Table 3 will appear here. See end of document.]

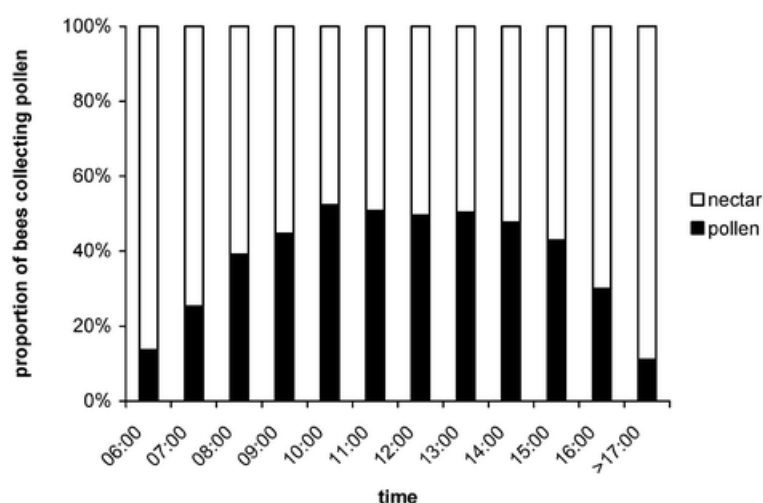


Fig. 2 Proportions of pollen versus nectar collecting visits according to time of day of departure of the bee from the nest

Discussion

We demonstrate that nectar collection rate, measured as the mass of forage gathered per unit time, is higher in larger bees and increases with experience. That foraging rate is greater in larger workers has been found before (Goulson et al. 2002; Spaethe and Weidenmuller 2002). It has long been known that foragers are, on average, larger than nest bees (reviewed in: Goulson 2003). One of the most promising explanations for alloethism in bumblebees is that larger bees are better able to forage in adverse weather conditions and, in particular, that they are better able to maintain an adequate thoracic temperature for flight in cool or windy conditions (Goulson et al. 2002). We might thus predict that the difference in foraging rate between large and small foragers would be greatest at low temperatures, or at high wind speeds. However, we found no significant interaction between the effects of bee size and weather conditions on foraging rate. It seems that, within the size range of foragers in our experiment, bees of different sizes were not differentially affected by the weather. It is possible that the range of temperatures that occurred during our study (13–29°C)

was not sufficient to reveal differences in thermoregulatory ability according to size. Presumably the lowest temperatures recorded in our study did not challenge the thermoregulatory ability of even the smallest foragers (3.6 mm thorax width). Repetition of the experiment in cooler conditions (at higher latitudes or earlier in the year) may be revealing.

If the greater foraging rate of large bees cannot be explained by greater thermoregulatory capacity, then other explanations must be considered. It seems plausible that larger bees may be less prone to predation (for example by being caught in spider's webs), although experimental evidence is lacking (Goulson et al. 2002; Goulson 2003). Larger *B. terrestris* workers have larger eyes and larger ommatidia than smaller workers, giving them superior sensitivity and image resolution (Spaethe and Chittka 2003). This allows them to detect single targets, such as flowers, with greater precision. They may also have greater neural capacity which would aid them in navigation and learning of flower handling skills; it seems likely that within-nest tasks are less demanding in this respect. This would be an interesting area for further investigation.

Increasing foraging rate with experience is to be expected, but has never previously been examined in this way. Previous studies have shown that bumblebees and other flower-visiting insects exhibit rapid sensory learning, and can use scent, colour, shape or a combination of all three to identify flower species which previously provided a reward (Menzel 1999). Learning to extract rewards efficiently from within the structure of a flower takes a number of visits to that flower species, resulting in a decline in handling time on successive visits (Lavery 1980; Lewis 1986; Lavery and Plowright 1988; Goulson and Cory 1993; Keasar et al. 1996). Thus, when a naïve bee first leaves the nest, it must learn which flowers provide rewards, and where to find them. It must also learn how best to extract those rewards. These processes take considerable time. In their first few departures from the nest some bees registered a negative foraging rate, meaning that they lost more weight (as water and metabolised sugars) than they gathered. Foraging by naïve bees may place an overall burden on the colony, since on their return to the nest these bees must stock up from honey stores in the nest before attempting to forage once more. Our data suggest that overall foraging rate is not maximised until approximately 30 trips have been made from the nest. This is probably an underestimate since recording at the nest entrance was not continuous, so some departures must have gone unnoticed.

Our data suggest that the weather had limited effects on foraging rate (when collecting nectar); rate was higher during conditions of high humidity, but was otherwise not influenced by weather conditions. So far as we are aware, little is known as to how weather conditions affect nectar secretion rates by plants. It seems likely that low humidity may place plants under water stress,

so that nectar production is reduced. Alternatively, these conditions will lead to rapid evaporation of nectar, increasing its concentration. This may mean that the weight of returning bees is less, but that the sugar concentration of their honey stomach contents is greater. To take this into account when measuring foraging rate, each returning bee could be caught and squeezed to eject the stomach content and quantify nectar concentration, but clearly this would be time consuming and likely to affect subsequent foraging behaviour.

Our approach measures foraging rate, in terms of mass gained per unit time, but further work is needed to determine how this correlates with foraging efficiency. We would expect foraging bees of differing sizes to use different amounts of energy per unit time, and we might also expect weather conditions to affect energy expenditure when foraging (Wolf et al. 1999). Respiration will result in some loss of mass as CO₂ and water, which will affect the net rate at which overall mass increases while foraging. To gain an accurate measure of foraging efficiency, and how this is influenced by body size and weather, direct measurement of metabolic rate as well as accrual of nectar is needed. Metabolic rate can be measured in free-flying bees using doubly labelled water (Wolf et al. 1996, 1999)

Weather strongly determined whether the bees collected pollen, with pollen mainly being collected on warm, windy days with low humidity, and particularly during the middle of the day. We suggest that these patterns may have a common explanation. Pollen is likely to be difficult to gather when there are water droplets on the flower or on the bee, such a morning dew or following rainfall. The middle of warm, windy days with low humidity is likely to be the driest time, and thus most suitable for pollen collection. Dry conditions also favour anther dehiscence, meaning that more pollen is likely to be available. Given that pollen is a vital resource without which bumblebees can rear no offspring, the availability of suitable dry conditions for pollen collection may be a critical factor affecting the success of bumblebee nests, particularly in wet climates such as are found in western Europe.

References

- Capaldi EA, Dyer FC (1999) The role of orientation flights on homing performance in honeybees. *J Exp Biol* 202:1655–1666
- Crawley MJ (1993) *GLIM for ecologists*. Blackwell, Oxford
- Cresswell JE (1990) How and why do nectar-foraging bumblebees initiate movements between inflorescences of wild bergamot *Monarda fistulosa* (Lamiaceae). *Oecologia* 82:450–460
- Cresswell JE, Osborne JL, Goulson D (2000) An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Ecol Entomol* 25:249–255
- Dreisig H (1995) Ideal free distributions of nectar foraging bumblebees. *Oikos* 72:161–172

- Dukas R, Real LA (1993a) Learning constraints and floral choice behaviour in bumblebees. *Anim Behav* 46:637–644
- Dukas R, Real LA (1993b) Effects of recent experience on foraging decisions by bumblebees. *Oecologia* 94:244–246
- Dukas R, Real LA (1993c) Effects of nectar variance on learning by bumblebees. *Anim Behav* 45:37–41
- Goulson D (1994) A model to predict the role of flower constancy in inter-specific competition between insect pollinated flowers. *J Theor Biol* 168:309–314
- Goulson D (1999) Foraging strategies for gathering nectar and pollen in insects. *Perspect Plant Ecol Evol Syst* 2:185–209
- Goulson D (2000a) Are insects flower constant because they use search images to find flowers? *Oikos* 88:547–552
- Goulson D (2000b) Why do pollinators visit proportionally fewer flowers in large patches? *Oikos* 91:485–492
- Goulson D (2003) *Bumblebees; their behaviour and ecology*. Oxford University Press, Oxford
- Goulson D, Cory JS (1993) Flower constancy and learning in the foraging behaviour of the green-veined white butterfly, *Pieris napi*. *Ecol Entomol* 18:315–320
- Goulson D, Peat J, Stout JC, Tucker J, Darvill B, Derwent LC, Hughes WOH (2002) Can alloethism in workers of the bumblebee *Bombus terrestris* be explained in terms of foraging efficiency? *Anim Behav* 64:123–130
- Heinrich B (1975) Thermoregulation in bumblebees. II. Energetics of warmup and free flight. *J Comp Physiol* 96:155–166
- Heinrich B (1979) *Bumblebee economics*. Harvard University Press, Cambridge, Mass.
- Keasar T, Motro U, Shur Y, Shmida A (1996) Overnight memory retention of foraging skills by bumblebees is imperfect. *Anim Behav* 52:95–104
- Laverty TM (1980) Bumble bee foraging: floral complexity and learning. *Can J Zool* 58:1324–1335
- Laverty TM, Plowright RC (1988) Flower handling by bumblebees—a comparison of specialists and generalists. *Anim Behav* 36:733–740
- Lewis AC (1986) Memory constraints and flower choice in *Pieris rapae*. *Science* 232:863–865
- Menzel R (1999) Memory dynamics in the honeybee. *J Comp Physiol* 185:323–340
- Spaethe J, Chittka L (2003) Interindividual variation of eye optics and single object resolution in bumblebees. *J Exp Biol* 206:3447–3453
- Spaethe J, Weidenmuller A (2002) Size variation and foraging rate in bumblebees (*Bombus terrestris*). *Insect Soc* 49:142–146
- Wolf TJ, Ellington CP, Davis S, Fletham MJ (1996) Validation of the doubly labelled water technique for bumblebees *Bombus terrestris* (L.). *J Exp Biol* 199:959–972
- Wolf TJ, Ellington CP, Begley IS (1999) Foraging costs in bumblebees: field conditions cause large individual differences. *Insect Soc* 46:291–295

Table 1 Summary of the number of experimental observations obtained per bumblebee, *Bombus terrestris*, 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

Table 2 Effects of weather and previous foraging experience on foraging efficiency (mass of nectar/h). Factors that did not contribute significantly to the model have been removed. $r^2=0.282$. The minimum adequate model to predict foraging efficiency was: efficiency (g/h) = $-0.451 + 0.055$ thorax width (mm) $+0.003$ humidity (%) $+0.006$ experience -0.456×10^{-4} experience²

Explanatory factor	Type III Sum of Squares	df	MS	F	P
Intercept	1.000	1	1.00	33.9	<0.001
Bee size	0.585	1	0.585	19.9	<0.001
Humidity	0.944	1	0.944	32.0	<0.001
Experience	1.23	1	1.23	41.9	<0.001
Experience ²	0.346	1	0.346	11.7	0.001
Nest	6.14	2	3.07	104	<0.001
Error	30.6	1038			
Total	42.6	1045			
Factors removed from model					
Time of day	0.042	1	0.042	1.42	0.235
Temperature	0.091	1	0.091	3.10	0.079
Cloud cover	0.035	1	0.035	1.21	0.271
Wind speed	0.010	1	0.010	0.35	0.552

Table 3 Effects of weather, time of day and bee size on whether bees collect pollen or nectar

	Mean±SE		<i>df</i>	χ^2	<i>P</i>
	Nectar trips	Pollen trips			
Thorax width	4.913±0.012	4.973±0.013	1	16.1	<0.001
Time of day	11:26±0:04	11:43±0:03	1	21.6	<0.001
Time of day ²	-	-	1	25.7	<0.001
Temperature (°C)	20.46±0.085	20.51±0.096	1	12.8	<0.001
Humidity (%)	68.73±0.31	64.09±0.29	1	65.7	<0.001
Wind speed	1.041±0.018	1.058±0.018	3	9.2	<0.05