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SHORT COMMUNICATION

Pollen foraging: learning a complex motor skill by bumblebees (*Bombus terrestris*)

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Abstract To investigate how bumblebees (*Bombus terrestris*) learn the complex motor skills involved in pollen foraging, we observed naïve workers foraging on arrays of nectarless poppy flowers (*Papaver rhoeas*) in a greenhouse. Foraging skills were quantified by measuring the pollen load collected during each foraging bout and relating this to the number of flowers visited and bout duration on two consecutive days. The pollen standing crop (PSC) in each flower decreased drastically from 0530 to 0900 hours. Therefore, we related foraging performance to the changing levels of pollen available (per flower) and found that collection rate increased over the course of four consecutive foraging bouts (comprising between 277 and 354 individual flower visits), suggesting that learning to forage for pollen represents a substantial time investment for individual foragers. The pollen collection rate and size of pollen loads collected at the start of day 2 were markedly lower than at the end of day 1, suggesting that components of pollen foraging behaviour could be subject to imperfect overnight retention. Our results suggest that learning the necessary motor skills to collect pollen effectively from morphologically simple flowers takes three times as many visits as learning how to handle the most morphologically complex flowers to extract nectar, potentially explaining why bees are more specialised in their choice of pollen flowers.

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Introduction

To understand whether animals should specialise on a particular task or remain as generalists, it is important to know how much an animal must invest to learn it. When learning a skill requires a large investment (e.g., time), we expect selective pressures to favour task specialisation. Such pressures can act at the species (so that hard-to-learn tasks become increasingly genetically preprogrammed: Strickler 1979; Laverty and Plowright 1988) or the individual level (so that animals from generalist species will forage more efficiently if they stick with a foraging skill they have already developed: Heinrich 1976; Waser 1986; Chittka et al. 1999).

In general, bees invest relatively little time in learning how to handle flowers to extract nectar in comparison with the duration of their foraging career, which can last several weeks or months. Indeed, bees will typically take less than 100 visits (equivalent to about 1 h of foraging) to achieve saturation performance when learning the motor patterns required to extract nectar from the most morphologically complex flowers (Laverty and Plowright 1988; Laverty 1994; Chittka et al. 1997). Correspondingly, we often find little specialisation in nectar foragers. Social bees will often visit several flower species during a single foraging bout (Chittka et al. 1997; Raine and Chittka 2005, 2007 in press), and numerous solitary bee species known as obligate specialists are, in fact, only specialised in terms of pollen foraging (Strickler 1979; Westrich 1989). Pollen foraging appears to be a much more complex skill than nectar collection (Ribbands 1949; Heinrich 1976; Harder 1990). Effective pollen collection requires the bee to remove powdery pollen from the anthers, aggregate these pollen grains by meticulously grooming their entire body, before packing it into specialised structures (scopae) for transport to their nest (Heinrich 1976; Michener et al. 1978; Thorp 1979, 2000). The optimal techniques to remove pollen from flowers will differ widely across species depending on many factors including floral structure, anther morphology and pollen properties (Thorp 2000; Stone et al. 2003; Willmer and Stone 2004). For these reasons, it is unlikely that pollen foraging in generalist species, such as the bumblebee, *Bombus terrestris* (L.), involves fully genetically preprogrammed, stereotyped motor skills.

To examine whether pollen collection rate of bumblebee foragers increases with experience, i.e., whether they learn how to collect pollen, we monitored the pollen harvesting behaviour of naïve *B. terrestris* workers from their first flower visit. We allowed them to collect pollen from corn poppy flowers (*Papaver rhoeas* L.), which produce large quantities of pollen but no nectar (Pohl 1937; Kugler 1970); therefore, any observed foraging behaviour was motivated solely by pollen collection.

Materials and methods

B. terrestris workers, with no pollen foraging experience, were allowed to forage individually for pollen from 94 poppy flowers in a greenhouse. We observed the behaviour of six individuals within this array, recording the number of flowers visited and the duration of each foraging bout (all bees were marked with unique numbered, coloured tags: Opalith tags, Christian Graze KG, Germany). As the bee returned to the colony at the end of each bout, we removed and weighed one randomly chosen pollen load. Only one load was removed as preliminary tests showed removing both caused bees to stop foraging. Bumblebees have been reported to add nectar to pollen they collect (Michener et al. 1978; Thorp 2000). Presumably, the use of nectar as a binding agent depends on its availability and the physical properties of pollen collected. As *Papaver* pollen is highly adhesive and tends to clump (Pacini and Franchi 1999) and its flowers are nectarless, there is minimal need to use nectar as a binding agent, or opportunity to obtain it, when foraging exclusively on poppies. Therefore, we infer that the weight of pollen loads is directly proportional to the number of grains collected. Before starting experiments, bees had ad libitum access to pollen inside the nest (pollen-honey paste). Bees were also allowed to perform orientation flights and collect sucrose solution (50% w/w) from a gravity feeder within the greenhouse, but were not exposed to flowers or pollen outside the nest.

Before each foraging bout, we collected 94 fresh flowers from the field beside the greenhouse. Cut flowers were presented to the test bee in pairs, with each pair placed upright in a clean, water-filled 330 ml bottle (n=47), set out in a hexagonal arrangement (25 cm between bottles) on the greenhouse floor (2.4 m×1.2 m). We observed the foraging performance of each individual bee for four consecutive foraging bouts during day 1, 0600–0930 hours (although one of six bees completed only three bouts), and rechecked their performance again the next morning (only one forager was tested per day). Collection rate was measured by relating the pollen mass collected per bout to the number of flowers visited and bout duration, as follows: $\text{collection rate} = \text{pollen load(mg)} \ / \ \text{number of pollen grains available per flower} \times \text{number of flowers visited per bout} \times \text{bout duration(s)}$.

To relate collection rate to the pollen standing crop (PSC) available, we quantified the pollen presentation schedule in the field. Pollen is released from anthers before poppy flowers open (Rogers 1969) and is progressively removed by flower visitors once it becomes available: the flowers open around dawn (Heß 1990, p.217) and can be emptied of pollen within 3–4 h (Ribbands 1949). To obtain accurate PSC measurements, we took repeated anther samples from ten marked flowers every 30 min (0530–0900 h) on two consecutive days before behavioural experiments (Fig. 1). Pollen was collected from anthers using an ultrasonic cleaning bath (Sonorex GT250) and counted with a haemocytometer (Wolfe and Barrett 1989). These data were used to calculate collection rates by assigning all flowers per bout with the PSC of the 30-min period in which they were picked. We also quantified the amount of pollen removed by a bee during a single flower visit. Anther samples were taken from focal flowers before and after a bee visit (pollen was collected from anthers and counted as above). Samples were taken for naïve (bout 1) and experienced (bout 5) foragers when the PSC per flower was directly comparable.

Results

The amount of pollen available in poppy flowers in the field decreased very markedly, but steadily, from 0530–0900 hours (Fig. 1). On average, each flower contained 2.25 million pollen grains when it opened (0530 hours), falling to 313,000 by 0900 hours as pollen was removed by insects including wild bumblebees. Thus, PSC per flower varied across foraging bouts 1–4 (day 1), but was directly comparable between bouts 1 and 5 for each bee tested. Relating the foraging success of each worker to the steadily decreasing levels of pollen available in each flower over time, we found that pollen collection rates of all foragers

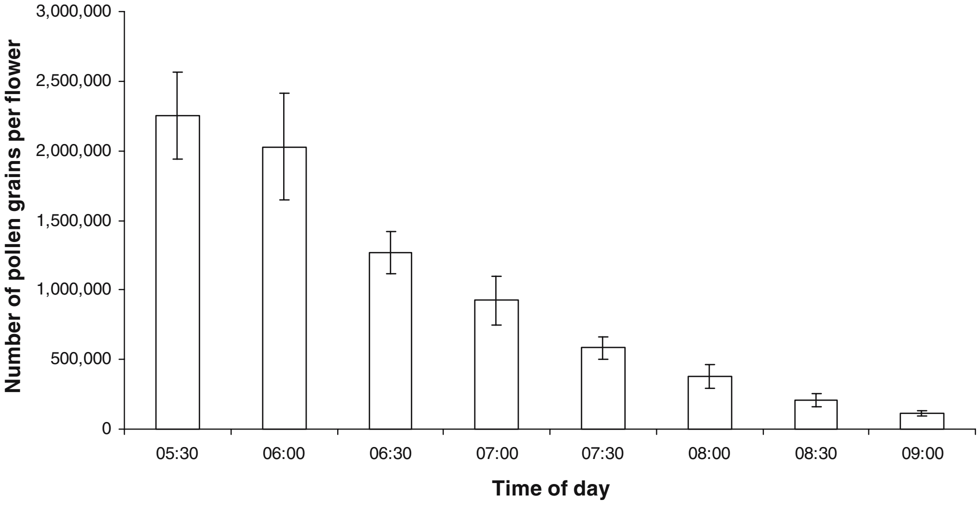

Fig. 1 Pollen availability in each poppy flower (*P. rhoeas*) decreases markedly and steadily during the early morning (0530–0900 hours). Data presented represent the mean number of pollen grains (±1 SE) per flower at each time interval, i.e., pollen standing crop (*PSC*). Anther samples were taken in the field on two consecutive mornings from a total of 20 plants (2×10 plants per day)

increased across their first four consecutive foraging bouts (Fig. 2), during the course of which each bee made 277–354 flower visits. During bout 4, bees made significantly more flower visits than in bout 1 (t_4=−6.034, p=0.004: Table 1). However, this increase could not be explained by the drop in PSC per flower over this time period, as bees collected significantly larger pollen loads (t_4=−9.213, p=0.001: Table 1) and harvested more pollen from each flower visited in bout 4 compared to bout 1 (t_4=−3.095, p=0.036: Table 1). Thus, all bees became more effective pollen collectors with increasing foraging experience on poppy flowers.

The next morning, when PSC in each flower was directly comparable to the previous morning, experienced foragers collected pollen at a higher rate (bout 5 vs 1: t_4=−2.26, p=0.043: Fig. 2) and also collected larger pollen loads (t_4=−6.79, p=0.002: Table 1) than as naïve bees. Bees also collected significantly more pollen grains per flower visit during bout 5 than in bout 1 (means±1 SE: bout 1: 8,809±4,247, n=8; bout 5: 41,134±15,311, n=9: Mann–Whitney U=13, p=0.027). Thus, learnt foraging skills were, at least in part, retained in memory overnight. However, comparing the foraging performance during the first bout of day 2 (bout 5) with that of the last on day 1

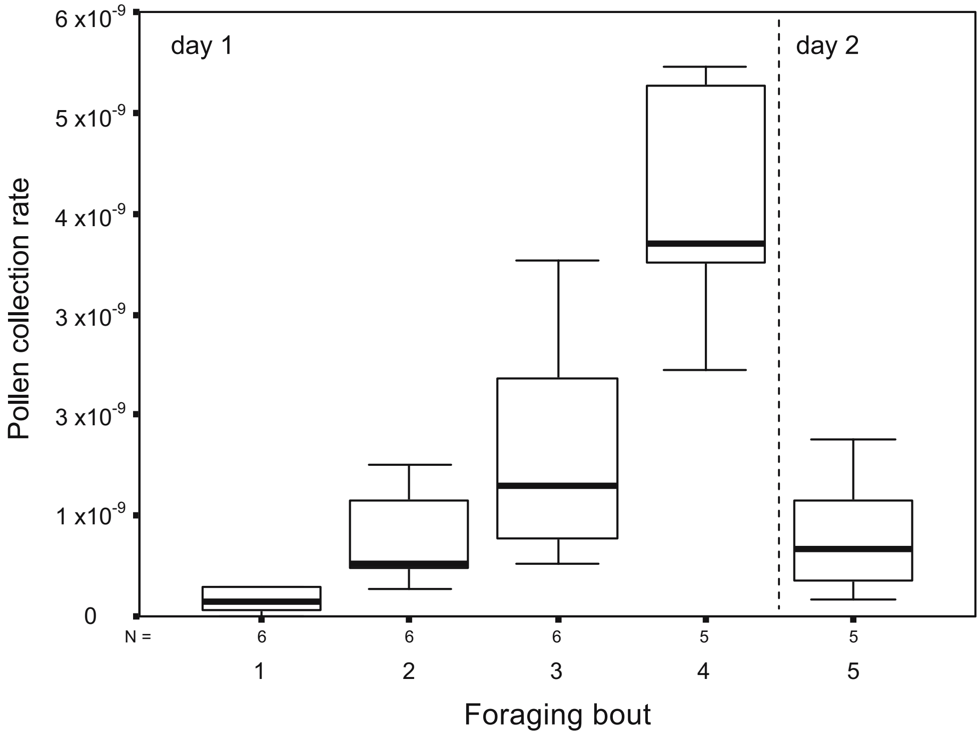

Fig. 2 The pollen collection rate of bumblebee (*B. terrestris*) workers foraging on poppy flowers (*P. rhoeas*) across five consecutive foraging bouts. Foraging bouts 1–4 occurred on the first morning (day 1), and bout 5 was observed the following morning (day 2): change of day is indicated by the *dashed vertical line*. In each *box* the *thick horizontal bar* is the colony median, whilst the *lower and upper edges* represent the 25% and 75% quartiles, respectively. *Whiskers* indicate the maximum and minimum values. The number of bees tested in each bout (*N*) is displayed along the *x*-axis

Table 1 Foraging behaviour of *B. terrestris* workers in their first, fourth (day 1) and fifth (day 2) foraging bouts on poppy flowers

Table 1	Day 1		Day 2
Measures of foraging performance	Bout 1 (n=6)	Bout 4 (n=5)	Bout 5 (n=5)
Number of flowers visited	40.17±4.78	79.33±7.45**	54.40±10.74
Pollen load per bout/ mg	4.45±1.56	28.66±3.13**	13.98±1.93**
Pollen collected per flower visit/ mg	0.11±0.04	0.31±0.05 *	0.31±0.09
Mean flight time between flowers/ s	7.67±1.38	4.96±0.29	5.30±0.57
Mean flower handling time/ s	4.45±0.73	4.78±0.54	3.94±0.38

Data presented represent the: number of flowers visited per foraging bout, amount of pollen load collected per foraging bout (mg), average amount of pollen collected per flower visit (mg), average flight time between flowers and average time spent inside (handling) a poppy flower for each foraging bout. Data presented are mean (±1 SE) values for each bout, or flower visit, for the number of bees (n) indicated by the column headings. Asterisks indicate significant differences in performance either over the course of day 1 (bout 1 vs 4) or between the first foraging bout of each consecutive day (bout 1 vs 5)

*$p<0.05$

**$p<0.01$ respectively

(bout 4), we observed a large drop in both the pollen collection rate (Fig. 2) and the average size of pollen load collected (Table 1). So, although pollen foraging improves with experience during each day, a decrease in performance occurs overnight.

Bee behaviour inside each poppy flower also changed with increasing experience. During their first few visits, all bees were surprisingly clumsy, one bee even failed to collect any pollen during its first foraging bout despite making 56 flower visits. In the early stages of their foraging career, bees were observed to collect pollen loads that fell apart, or were so large that they fell from the bee’s corbiculae (pollen baskets) before reaching the nest. As each bee gained foraging experience, the frequency of such events rapidly declined. Bees also changed how they used ‘buzzing’, a technique of holding the anthers in their mandibles while vibrating their flight muscles, to facilitate pollen collection (Thorp 1979; Buchmann 1983). While naïve bees typically buzzed either all or no flowers, skilled foragers would selectively ‘buzz’ flowers containing less pollen.

Discussion

Pollen collection rate of bees improved continually across the four consecutive foraging bouts during day 1 (Fig. 2), even though the PSC per flower decreased dramatically over the same time frame (Fig. 1). During these four bouts, each bee made 277–354 flower visits, suggesting that learning to forage for pollen takes a substantial amount of time. Indeed, 277 visits represents a conservative estimate of the time investment required to master pollen collection from poppy flowers as there is no indication that the collection rate in bout 4 represents task saturation performance. So, whilst bees can take 100 visits to master the motor skills required to harvest nectar effectively from morphologically complex flowers (Laverty 1994; Chittka and Thomson 1997), it appears that they take around 300 visits (perhaps considerably more) to learn to collect pollen effectively from flowers with simple morphology like *P. rhoeas*. This is, perhaps, not surprising when we consider that the task of pollen foraging is more complex than collecting nectar. All foraging bees, whether collecting pollen or nectar, must learn how best to handle and extract rewards from each new flower type they encounter. Nectar foragers need only to learn how best to get into the flower to access the nectar, after which they simply suck it up and fly on to the next flower. In contrast, pollen foragers face several additional challenges when learning how to collect, aggregate and pack pollen for transport back to their nest (Heinrich 1976; Michener et al. 1978; Thorp 2000).

Bees must adapt their collection and packing strategies depending on the floral structure and anther morphology of the flowers visited and the characteristics of pollen (e.g., grain size and adhesiveness) collected (Thorp 2000; Stone et al. 2003; Willmer and Stone 2004). We observed several incidences during the earliest stages of the bees’ foraging careers (predominantly during bout 1) when they lost partial or complete loads from their corbiculae, presumably the result of poor or over-packing. Bees rapidly mastered the skills required to pack their corbiculae: despite a continued reduction in PSC over time, they managed to collect equally large pollen loads during bouts 2–4, and increased their rate of pollen collection across the four bouts on day 1. In addition to a reduction in PSC, the remaining pollen in each flower becomes drier over time. Such desiccation makes pollen less sticky and harder for bees to collect. If pollen desiccation was responsible for the change in foraging performance, we would predict that foraging efficiency would decrease with successive foraging bouts. However, in spite of pollen becoming harder to collect over time, we see a continued improvement in foraging performance during day 1.

Changes in foraging performance could also be explained by bees becoming warmer or more motivated to forage (across bouts 1–4) or due to individual maturation during the experiment. Under natural conditions, bumblebees are typically among the first bees to be observed foraging in spring months, when they will forage at temperatures above 5°C (Heinrich 1979). Given these adaptation to cold and the warm test conditions (overnight greenhouse temperatures in July remain high), it seems unlikely that any foraging improvement could be due to thermal constraints. Similarly, bumblebees typically begin foraging as soon as it becomes light, thus, our testing period (0600–0930 hours) falls within an intense period of foraging activity for *B. terrestris* colonies under natural conditions (Ings et al. 2005, 2006). Pollen availability could also potentially affect bee's motivational state. However, as PSC (per flower) decreased over the testing period, bees were exposed to the highest pollen levels during their first bout when they were least efficient at collecting it. It also seems unlikely that bees could become highly motivated by the pollen levels in individual flowers having already been exposed to ad libitum pollen in the nest. Foraging performance could also potentially improve irrespective of increasing levels of foraging experience. It seems more likely over the short time frame of our experiment (about 24 h of the bee's lifespan lasting several weeks or months: Raine et al. 2006b) that changes are due to increasing experience (learning) rather than other, unrelated ontogenetic processes.

Whilst the continual improvement in foraging efficiency across bouts 1–4 could be due to bees learning how to collect pollen more effectively, efficiency might also increase because bees behave according to the marginal value theorem (MVT: Charnov 1976), such that they 'deliberately' change foraging strategy in accordance with pollen levels available in particular flowers (Harder 1990). MVT predicts that bees would leave substantial amounts of pollen behind in pollen-rich flowers because switching to new pollen-rich flowers is more efficient than harvesting all the pollen remaining in the current flower. Conversely, when PSC is low, emptying each flower entirely may be the more efficient tactic. However, comparing the performance of naïve and experienced foragers when the PSC per flower was comparable (i.e., bout 1 vs 5), we found that bees with more foraging experience collected pollen at a higher rate over the timescale of a bout (Fig. 2) and collected more pollen grains from a single flower visit. These results demonstrate a strong effect of learning on pollen foraging success, which cannot be explained by MVT. However, we cannot be sure how much of the increase in foraging efficiency during day 1 (bouts 1–4) is attributable to learning and how much to MVT. Conducting a further experiment where PSC per flower is kept constant across subsequent foraging bouts on the same day would enable us to tease the effects of learning and MVT apart.

Comparing the final levels of foraging performance on day 1 (bout 4) with initial levels on day 2 (bout 5), we saw marked reductions in both pollen load size (Table 1) and collection rate per bout (Fig. 2). Similar reductions in performance have been reported for nectar foraging bumblebees tested on the same task overnight (Keasar et al. 1996) or several weeks later (Chittka 1998). Whilst this overnight drop in foraging performance could reflect changes in behavioural strategy as a response to PSC at different times of day (i.e., MVT), it could also be explained by imperfect memory retention of learned skills. If some components of foraging behaviour must regularly be relearned, such partial loss of skills may be adaptive in allowing individual foragers to react quickly to changes in resource profitability by modifying flower choices and handling techniques (Keasar et al. 1996; Raine et al. 2006a,b).

Pollen and nectar are the most important nutrient sources for bees, so differences in their ability to collect either resource could have very significant effects on potential survival and fecundity. However, almost all the extensive literature regarding bee foraging and learning is focused on nectar foraging (e.g., Menzel 1985; Seeley 1995; Chittka et al. 2004; Raine et al. 2006a,b). This is perhaps unsurprising given the ease with which the quantity and quality of artificial nectar can be controlled under experimental conditions. Whilst pollen foraging behaviour is undoubtedly harder to study, it clearly deserves more attention. The results of this study suggest that learning to forage for pollen takes a substantially larger time investment than learning to handle even highly complex flowers to extract nectar. Potentially, this provides some insight into why bees are typically more specialised in their choices of pollen flowers compared to the decisions made when collecting nectar (Heinrich 1976; Strickler 1979; Chittka and Thomson 1997).

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