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Evidence for Handedness in Bumblebees

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We describe a simple study of how bumblebees (Bombus *spp.) behave when visiting florets which are arranged in a circle around a vertical inflorescence. In four species of bees, individuals showed a tendency for rotation in the same direction around each inflorescence on successive visits, i.e., each individual tended to go either clockwise or anticlockwise. Similar behavior has also been observed in mammals including humans. The implications of this tendency to repeat tasks in the same way are discussed, particularly in relation to our understanding of the phenomenon known as flower constancy. In humans, the tendency for individuals to turn in a particular direction is strongly related to handedness. In three of the four bee species there was a significant overall tendency for the bees to rotate in a preferred direction, suggesting that they too may exhibit handedness.*

KEY WORDS: *Bombus*; rotation; foraging; nectar; handling; flower constancy.

INTRODUCTION

Bee foraging behavior has proved to be a fruitful and popular area of research, and studies in this area have greatly improved our understanding of the learning and memory capacities of insects (Menzel *et al.*, 1993; Chittka, 1998; Menzel, 1999). Bees have the ability to learn associations between sensory stimuli, such as visual and olfactory cues, and rewards, so that they can recognize rewarding flowers (Menzel and Erber, 1978). They learn

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appropriate motor skills for handling often complex floral structures (Laverty, 1980, 1994). New associations and motor skills can be learned when needed (Woodward and Laverty, 1992; Chittka and Thomson, 1997). Bees can distinguish and avoid recently visited flowers using traces of odor deposited by the previous visitor (Goulson *et al.*, 1998; Stout *et al.*, 1998). They learn the relative spatial positions of landmarks and use these to navigate complex routes to and from their nest (Southwick and Buchmann, 1995; Menzel *et al.*, 1996, 1997).

One aspect of bee foraging, that of flower constancy (which is also found in other flower-visiting insects), has not yet been adequately explained, it is one of the few areas in which bee behavior appears to be less than optimal. The various explanations for flower constancy that have been suggested all tend to argue that foraging is constrained by some aspect(s) of the capacity and temporal dynamics of the bumblebee brain (reviews by Chittka *et al.*, 1999; Goulson, 1999a). For example, bees may be unable to remember motor skills for several flowers at the same time, or they may be unable to recall quickly a succession of different motor skills from their long-term memory. They may simply not be aware of the rewards offered by many of the flower types present. Recently Chittka *et al.* (1999) argued that bees have a large long-term memory and that the most probable limitation is the stability and capacity of short-term memory; cues for recognition of a rewarding flower or for motor skills to handle that flower can be down-graded from the short- to the long-term memory if replaced by other information. This is rather similar to an hypothesis proposed by Goulson (1999b), that constancy may reflect use of a search image to find a rewarding flower type: search images are thought to occur due to a limited ability to recognize several "prey" types at once. This "nonadaptive behavioral persistence" also appears evident in the phenomena of site-fidelity and traplining (Thomson *et al.*, 1982, 1987).

In this study we examine the behavior of bumblebees (*Bombus* spp.) when foraging on vertical inflorescences of *Onobrychis viciifolia* (Fabaceae), in which the florets that are open at any one time form a circle around the raceme. Bumblebees may forage by visiting florets in a clockwise or an anticlockwise sequence. We demonstrate that bees tend to use the same direction of rotation on successive inflorescences, revealing that bees have in innate tendency to repeat tasks in the same way even when the rewards provided by alternative behaviors are exactly the same.

METHODS

The study was carried out during June 1999 in Hampshire, UK, in a field of *O. viciifolia* planted to provide forage for bees. Four species of bumblebee

Table I. Mean Numbers of Anticlockwise (A) and Clockwise (C) Visits Made by Each Bee Species[a]

				Monte Carlo simulation value			
Bee species	N	Anticlockwise	Clockwise	0.05	0.01	0.001	P
B. lapidarius	17	4.18	5.82	5.70	5.94	6.24	<0.05C
B. terrestris	11	4.91	5.09	5.91	6.09	6.46	n.s.
B. lucorum	11	6.09	3.91	5.91	6.09	6.46	0.01 A
B. pascuorum	13	6.46	3.62	5.77	6.08	6.39	0.001 A

[a] Our null hypothesis predicts that the direction of rotation on each visit is random. A simple Monte Carlo simulation was used to determine whether observed values deviated significantly from random (two-tailed test).

were present in abundance: *B. lapidarius* (L.), *B. terrestris* (L.), *B. lucorum* (L.), and *B. pascuorum* (Scopoli). *B. terrestris* and *B. lucorum* were distinguished on the basis of color, which is not absolutely reliable. Between 11 and 17 individuals of each bee species (Table I) were selected at random and observed as they foraged on 10 successive inflorescences. The direction in which they rotated around each inflorescence was recorded. A different bee species was chosen each time to minimize the likelihood of observing the same bee twice, but the bee population was so large that this is likely to have occurred very rarely if at all. The observer also moved around the field when making observations, so risk of pseudo-replication was minimal. Where a bee probed fewer than three florets on an inflorescence, or was forced to alter direction due to obstacle (leaves, stem of another flower, interference from another pollinator), that individual was excluded from the data set. For the duration of the data collection period, weather conditions were approximately uniform (temperature 23.5 ± 0.5°C; relative humidity, 35 ± 5%).

Analysis

Our null hypothesis is that the direction of rotation on each flower is random, so that we expect equal numbers of clockwise and anticlockwise visits. The mean numbers of anticlockwise and clockwise visits made by each bee species were compared with critical values obtained from a simple Monte Carlo simulation model. This simulation was used to calculate threshold values for significant departures from random.

To determine whether the four bee species, differed in the frequency at which individual bees switched between clockwise and anticlockwise visits, the proportion of switches made by each bee was analyzed according to species in GLIM with binomial errors (Crawley, 1991).

Since bee species did not differ in the frequency at which they switched between clockwise and anticlockwise foraging, the four species were combined for subsequent analysis. To examine whether the frequency of switches was significantly lower than would be expected from a random forager (i.e., 50%), a paired t test was conducted on the number of switches made by each bee versus the number of times the bee rotated around an inflorescence in the same direction as on its previous visit. The GLIM analysis was also used to estimate the overall mean and standard error of the frequency of switching.

To examine whether there were differences between individual bees in their propensity to switch between clockwise and anticlockwise foraging, the number of switches made on the first four transitions between inflorescences was correlated with the number of transitions made in the following five transitions. If some bees tended to switch, while others consistently exhibited either clockwise or anticlockwise foraging, we would expect a positive correlation.

RESULTS

Comparing average numbers of anticlockwise versus clockwise visits for each species against the values expected if this was random indicates significant overall handedness for three of the four species studied (Table I). Two species preferentially foraged in an anticlockwise direction, while *B. lapidarius* displayed a significant tendency to visit flowers in a clockwise direction. Only *B. terrestris* did not exhibit a tendency to handedness in either direction.

The GLIM analysis of the proportion of switches between clockwise and anticlockwise visits exhibited by each bee indicated no differences among the four bee species ($\chi^2 = 4.86$, df $= 3$, $P > 0.05$). Overall, bees tended to forage on consecutive inflorescences by rotating in the same direction. The number of switches between directions was significantly lower than the number of times a bee continued to forage by rotating in the same direction ($t = 3.34$, df $= 51$, $P > 0.001$). This is clearly illustrated by comparing the frequency distribution of switches which that which would be expected if the direction of foraging was random on each visit to an inflorescence (Fig. 1). Overall, bees rotated around inflorescences in the same direction as on their previous visit on 68.6% of visits (all bee species combined; SE = 9.34).

There was no indication that some individual bees were more likely to switch than others. No correlation was apparent between the number of switches made in the first four transitions between inflorescences and the number of switches made in the following five transitions ($r = -0.046$, df $=$ 51, $P > 0.05$).

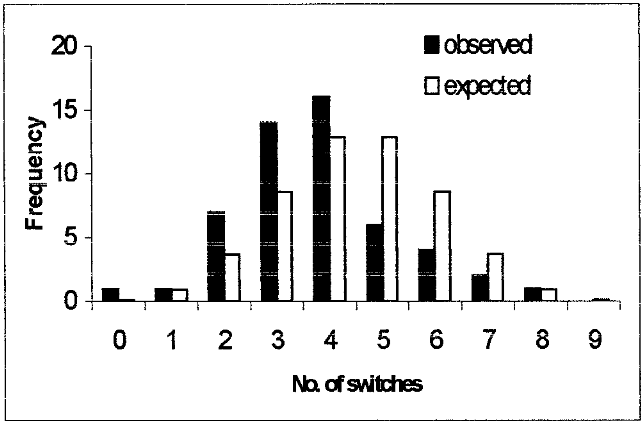

Fig. 1. The frequency of switches between clockwise and anticlockwise rotation of inflorescences, based on 10 visits to inflorescences. The expected distribution is calculated assuming random foraging, so that the probability of switching between directions is 0.5. Data are for 52 bees (all four species combined).

DISCUSSION

When faced with a choice of two possible ways of handling an inflorescence, individual bees tended to move repeatedly in the same direction around successive inflorescences. Presumably, a bee which exhibited random rotation would receive the same rate of reward, and hence just as much reinforcement of its behavior, as a bee with a fixed direction of rotation. Ecologically, the direction of rotation is trivial, since it has no consequence for either the bee or the plant.

There are several possible causes of the observed tendency for bees to rotate in the same direction on successive inflorescences. First, there could be an asymmetry of the flower which may have induced the directionality of the rotation. If flowers visited in succession were located in close proximity, they may have been exposed to similar asymmetries of environmental factors (e.g., shade, illumination), to which the bees were merely responding. However, that asymmetry is the reason behind the observed directionality of rotation here is unlikely. It was common to observe two bees of the same species foraging in opposite directions around the same flower, which implies that if there are asymmetries in flowers, these do not influence directionality. Observations were carried out in a large field, surrounded by low hedges, which had a slight south-facing aspect. The similarity of sward height and density, and the number of florets on each plant (A.R.K., unpublished data), tends to indicate that drainage, soil fertility, and other environmental factors were similar across the crop.

Second, the direction in which a naïve bee turns on the first inflorescence it encounters may be random, but the bee may then simply repeat this behavior since it has proved to be successful. If this is so, then flower constancy too could result from a bee simply repeating whatever was previously successful. In a sense, this is equivalent to the "costly information" hypothesis (Chittka *et al.*, 1999), which argues that if information as to the profitability of other strategies is costly to obtain, and so long as the forager is gaining at least a moderate rate of return, then the forager should continue with its current strategy. Menzel (1999) found with sensory learning that learned handling abilities can fade from short-term memory if not frequently reinforced. It is likely that this phenomenon could apply to motor learning. The direction in which an individual tends to rotate could depend on its earliest foraging experiences or could be relearned every day if motor skills are lost from the memory overnight. Either way, we would expect the observed frequencies of rotation in either direction to be approximately equal in the population on any given day. However, three of the four species exhibited an overall tendency for rotation in a particular direction, which would seem to discredit this hypothesis in this instance.

Corbet *et al.* (1981) suggested that insect posture during a visit to a floret may influence directionality. Subsequent movement in one direction requires less time and energy than movement in the other, hence directionality within an inflorescence may act to decrease foraging costs. If the initial posture of the bee on the first floret of an inflorescence influences the direction it moves in around that inflorescence, we would expect rotation on subsequent inflorescences to be random and related to the initial posture of the bee on the floret. Even if there were reinforcement of this behavior, resulting in a bias in the direction of rotation of individuals, we would still expect an equal distribution of individuals following either strategy within the population.

Another possible explanation for the phenomenon of individual bees exhibiting constancy to rotation in one direction is that they are exhibiting something akin to "handedness" in humans, i.e., individuals have an innate preference for rotation in one direction or another. It may be possible to distinguish between these possibilities by examining behavior over longer periods. If, for example, it was found that there is no correlation between the preferred direction used by an individual bee on different days, this would suggest that they do not exhibit handedness but, rather, just tend to repeat the direction of rotation that was tried initially on that day.

Giurfa *et al.* (1995), working on color choice in *A. mellifera*, concluded that evaluation of a floral signal in this instance is jointly controlled by innate and experience-dependent processes. If motor memory functions in a similar way, it could be that a naive forager is innately programmed for "handedness" but, with experience (encountering an obstacle, interference from another forager), learns that there is no difference in reward if flowers are visited in the opposite direction. Therefore the age of the forager could at least partly explain the varying degrees of stereotype found between individual foragers, although this does not account for a species exhibiting an overall preference for rotation in one direction or another.

The history of the flower may also affect the direction the forager moves around the flower. It is known that both honeybees and bumblebees deposit volatile repellent scent marks when visiting flowers (Williams, 1998; Stout *et al.*, 1998). It could be that the direction of rotation is influenced by the relative strength of the scent mark on either side of the forager when it lands; this is more likely to be of importance in those flowers where many florets make up an inflorescence. However, this explanation fails to explain why bees tend to rotate in the same direction around successive flowers.

Three of the four species observed displayed an overall tendency for individuals of that species to rotate in one direction as opposed to the other. Individuals of *B. pascuorum* and *B. lucorum* tended to exhibit a preference for left-handed movement around an inflorescence, while those of *B. lapidarius* displayed a right-handed preference. It would appear that the most likely explanation for such behavior is that it is the result of nonadaptive behavioral persistence, although why *B. terrestris* did not exhibit this is unclear. Parallels toward a tendency for rotation in a given direction are also evident in higher organisms. In behaviors which require body rotation, children exhibit a tendency to turn in one direction or another, and just as in two of the bee species here, most children tend to rotate anticlockwise. This tendency becomes more pronounced with the child's age (Day and Day, 1997). Preferred directions are correlated with handedness (Yangzen *et al.*, 1996). Similar rotational preferences have been found in other mammals including capuchin monkeys (Westergaard and Suomi, 1996) and mice (Nielsen *et al.*, 1997), but apparently these do not occur in goats (Ganskopp, 1995).

To our knowledge, these data represent the first study into constancy in turning direction in an insect. Further studies are needed, chiefly the marking of emergent foragers, to establish if age affects the degree of stereotypy, and records of how the visitation history of the plant affects subsequent foragers. Observations of bees foraging on more plant species may also be useful in helping to establish the generality of this phenomenon. Its existence suggests that there is an innate constancy in bee foraging behavior which need not relate to memory constraints or to rewards.

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