



How do solitary bees forage in patches with a fixed number of food items?

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ARTICLE INFO

Article history:

Received 20 April 2011

Initial acceptance 16 May 2011

Final acceptance 7 September 2011

Available online 24 October 2011

MS. number: 11-00333

Keywords:

cognition

counting

Eucera

foraging

numerical competence

solitary bee

Efficient foragers avoid returning to food sources that they had previously depleted. *Bombus terrestris* bumblebees use a counting-like strategy to leave *Alcea setosa* flowers just after visiting all of their five nectaries. We tested whether a similar strategy is employed by solitary *Eucera* sp. bees that also forage on *A. setosa*. Analyses of 261 videorecorded flower visits showed that the bees probed five nectaries in 26% of visits, which was the most common case. However, this proportion did not differ significantly from that of six-nectary visits. Probe durations that preceded flower departures were generally shorter than those followed by an additional nectary visit in the same flower. Assuming that probe durations correlate with nectar volumes, this suggests that flower departure frequencies increased after probing of low-rewarding nectaries. The flowers' spatial attributes were not used as departure cues, but the bees may have left flowers in response to scent marks on previously visited nectaries in a small fraction (<14%) of visits. These findings suggest that a combination of a reward-based patch-leaving rule and scent marking contribute to *Eucera*'s efficient foraging. While a counting-like strategy cannot be completely ruled out for *Eucera*, it seems less exact than in *Bombus*, and may be mediated by different cognitive processes. Thus, *Eucera* resemble bumblebees in avoiding most revisits to already visited nectaries, but probably use different foraging strategies to do so. This difference may reflect lower learning capabilities of solitary bee species compared to social ones.

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To forage efficiently, animals should exploit all the available profitable food sources, and avoid returning to food sources that they had previously depleted. Behavioural mechanisms that involve systematic movement, and reduce the likelihood of revisits to exploited food patches, are therefore expected to be selected. Several such mechanisms have been described in bees, which are popular models for foraging studies. They include bottom-to-top movement along vertical inflorescences (Pyke 1979; Waddington & Heinrich 1979), foraging along a fixed route (trap lining; Ohashi & Thomson 2009; Lihoreau et al. 2010) and scent marking of visited flowers (Giurfa & Núñez 1992; Giurfa 1993; Goulson et al. 2001).

Recently, we explored whether bees exploit regularities in the number of food sources in a patch as an additional source of information to increase foraging efficiency (Bar-Shai et al. 2011). Flowers with a fixed number of nectaries occur in several plant families, including the Malvaceae, Brassicaceae, Ranunculaceae, Oxalidaceae, Asclepiadaceae and Liliaceae. Bees that forage on such

flowers can benefit from visiting all nectaries in a flower once, and then departing the flower. They may implement this foraging pattern if they are able to count the nectaries, or estimate other variables that covary with nectary number, that is, time spent in the flower and the volume of nectar collected. *Bombus terrestris* bumblebee workers indeed usually visit all of *Alcea setosa*'s (Malvaceae) five nectaries before leaving for another flower. Two lines of evidence suggest that the bumblebees have numerical capabilities that account for this foraging pattern. First, analyses of the bees' behaviour demonstrated that the bees visit five nectaries per flower even when they do not use the following alternative flower-leaving strategies: spending a constant time on each flower, following a fixed route along nectaries and scent marking of visited nectaries. Second, bumblebees can be trained to depart three-feeder patches after visiting two rewarding feeders under laboratory conditions, that is, to use the number of recent rewards as a patch departure cue. Patch visit duration, nectar volume, scent marks and recurring visit sequences in a patch were ruled out as possible sources of patch-leaving information in this experiment (Bar-Shai et al. 2011). This evidence for counting-like abilities in foraging complements previous reports on the use of numerical information by honeybees, *Apis mellifera*, in navigation tasks (Chittka & Geiger 1995; Dacke & Srinivasan 2008). Additionally,

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honeybees succeeded in a discrimination task based on the number of simultaneously displayed items (Gross et al. 2009).

The counting-like foraging strategy used by *B. terrestris* is not necessarily shared by other bee species. Social bees, such as bumblebees, live in a much more complex social environment than solitary species. This was hypothesized to promote improved learning and memory skills in social bees, which possibly include numerical capabilities (Dukas & Real 1991; Willmer & Stone 2004). A correlation between social structure and learning abilities is supported by two experiments that subjected social and solitary bees to identical tasks. In one study, social bumblebees, *Bombus bimaculatus*, learned a colour discrimination task more quickly than the solitary carpenter bee, *Xylocopa virginica* (Dukas & Real 1991). In the second, honeybees outperformed the solitary leafcutter bee, *Megachile rotundata*, in a shape discrimination task (Campan & Lehrer 2002).

In the present study we investigated how females of the solitary genus *Eucera* (Anthophoridae) forage for nectar on *A. setosa*'s five-nectary flowers. These large (11–18 mm) ground-nesting bees, which are active between February and May, are important pollinators in the Mediterranean and desert habitats of Israel (Michener 2000). Having confirmed that the bees forage efficiently by frequently visiting five nectaries per flower, we examined whether this foraging pattern is based on the use of numerical information as in bumblebees or whether it could result from other behavioural strategies. We also considered the possibility that bees of both species use numerical information while foraging, but with different degrees of precision.

METHODS

Study Site and Species

A wild population of *A. setosa* was observed in the Judaeen Hills of Israel (altitude 500 m) during 6 days in May 2009. Seventy to 100 flowers were in bloom during the days of observation. *Alcea setosa* is an herbaceous perennial that grows mainly in mountain areas of the Mediterranean region and blooms during April and May. The flowers are shaped as wide funnels, 8–13 cm in diameter, are situated vertically on tall (1–2 m) stalks, and produce large amounts of nectar and pollen. The nectar is secreted from five nectaries located behind the petals and is accessible through five slits situated between the petals (Endress 1994). The flowers' size and shape do not allow insects to see the entire flower while visiting it, nor the surrounding area. The most common visitors to the flowers were workers and young queens of *B. terrestris*, followed by females of solitary bees (*Eucera* of unidentified species) and honeybee workers.

Data Recording

The bees' visits were recorded with a hand-held video camera. Each individual was followed from the time it was first observed on a flower until it disappeared from view. We took note of the following variables for each flower visit when analysing the video sequences: (1) the date and hour of visit, (2) the number of nectaries probed, (3) the location of the first and last nectaries visited, relative to the horizontal plane, (4) the direction of movement within the flower (clockwise or anticlockwise), (5) the time spent in each nectary and the duration of the whole flower visit (previously shown to correlate with nectar reward; Zimmerman 1988; Milet-Pinheiro & Schlindwein 2009), and (6) whether the bee turned towards a nectary without visiting it before leaving the flower, which may indicate rejection because of scent marks. Corbet et al. (1984) interpreted approaches to a distance of <1 cm of food sources that are not followed by landing and feeding as

inspection for scent marks. This approach was adopted by several later studies (Schmitt & Bertsch 1990; Goulson et al. 2001; Yokoi & Fujisaki 2009), as well as in the present project.

We sampled nectar standing crops (the amounts of nectar available in flowers exposed to visitors) at 0530, 0630, 0930 and 1300 hours on one observation day. The 0530 hours sample was taken before the onset of bee activity, and the 0630 hours sample was taken shortly after the bees started foraging. Each sample was based on two flowers from each of five to seven plants. Nectar was collected separately from each nectary, using 5 µl micropipettes. Sucrose concentration was determined in samples with sufficient volume (<0.33 µl) with a Bellingham and Stanley hand-held refractometer, modified for nectar.

Data Analysis

One-way analysis of variance (ANOVA) followed by post hoc tests was used for testing the effects of sampling hour on *A. setosa*'s nectar standing crops. We combined observations of foraging sequences conducted by *Eucera* between 0700–0900, 0900–1200 and 1200–1600 hours on all observation days. We then tested for the effect of foraging hour on the time spent per flower, time spent per nectary and the number of nectaries visited per flower, using one-way ANOVAs followed by Tukey's post hoc tests. We compared, with *t* tests, the durations of probing *N* nectaries (*N* = 1–6) and then departing the flower, and the durations of probing the same number of nectaries but not departing the flower thereafter.

To characterize the bees' movement patterns within flowers, we assigned numbers from 1 to 5 to the nectaries within each flower. The topmost nectary relative to the horizontal plane was designated as no. 1 and the remaining nectaries received consecutive numbers, clockwise, starting at no. 1. Nectaries 1 and 5 were thus always located at the top half of the flowers, whereas 3 (and usually also 4) occupied the bottom half. Each foraging path within a flower, in visits that involved two or more probes, was characterized by a three-character string. The first two characters (range 1–5) designated the first and last nectaries probed within the flower, respectively. The third character was defined as '+' or '-' for clockwise or anticlockwise movement, respectively. Using a chi-square test, we assessed whether the bees' choices of the first nectary probed conformed to a uniform distribution. Similarly, we tested whether the bees had any preference for certain nectaries as a point to end the visit in a flower. We used the binomial test to find whether the frequencies of '+' and '-' path directions deviated from a random 1:1 distribution. Binomial tests were also used to check whether individual bees were more likely to retain their starting position and movement direction, in two consecutive flower visits, than expected at random.

The random expected probability for probing two consecutive flowers at the same starting position was estimated as:

$$\sum_{N=1}^5 (p_N)^2$$

where p_N is the observed frequency of the *N*th nectary being used as the starting position within a flower. Based on the data set of *Eucera* observations, the random expected probability for retaining the starting position in two consecutive flowers was 0.40. The random expected probability for keeping the same movement direction in two consecutive flowers was calculated as $p(+)^2 + p(-)^2$. $p(+)$ and $p(-)$ are the frequencies for clockwise and anticlockwise movement, estimated from the data. Based on these estimates, the expected probability that a bee would take the same direction of movement in two consecutive flowers, under a random null model, was 0.50.

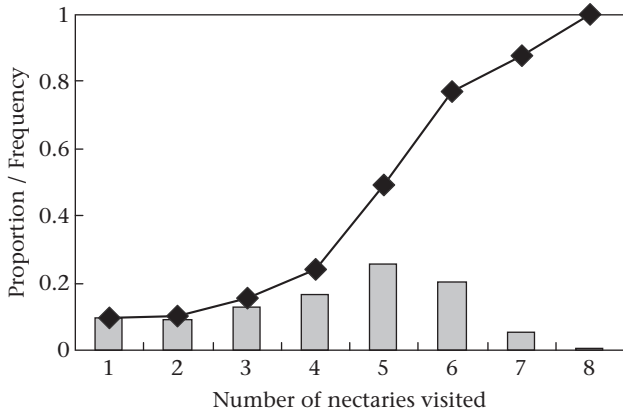


Figure 1. The relative frequency of probing one to eight nectaries in *A. setosa* flowers by *Eucera* females (bars), and the conditional probability for departing the flowers after varying numbers of probes (line). Conditional probabilities were calculated as the ratio of the number of flower departures after the *N*th nectary and the number of probes of this nectary. Sample size was 261 flower visits, which included 1111 nectary visits.

We calculated the expected probabilities for probing one to eight nectaries per flower under a logarithmic null model. The frequency of leaving (p_i) a flower after probing one nectary was estimated from the data. The predicted probability of leaving after probing two nectaries is $p_1(1-p_1)$, the leaving probability after three nectaries is $p_1(1-p_1)(1-p_1)$, etc. We compared the observed and expected distributions of visits of one to eight and more than eight nectaries per flower using a chi-square test with 7 degrees of freedom, because the parameter of the expected distribution was estimated from the observed data.

RESULTS

Number of Nectaries Visited per Flower

The bees most frequently (in 25.6% of the cases) visited five nectaries per flower. Five-nectary visits were significantly more common than four-nectary visits (binomial test: $P < 0.01$), but did not differ significantly in frequency from six-nectary visits

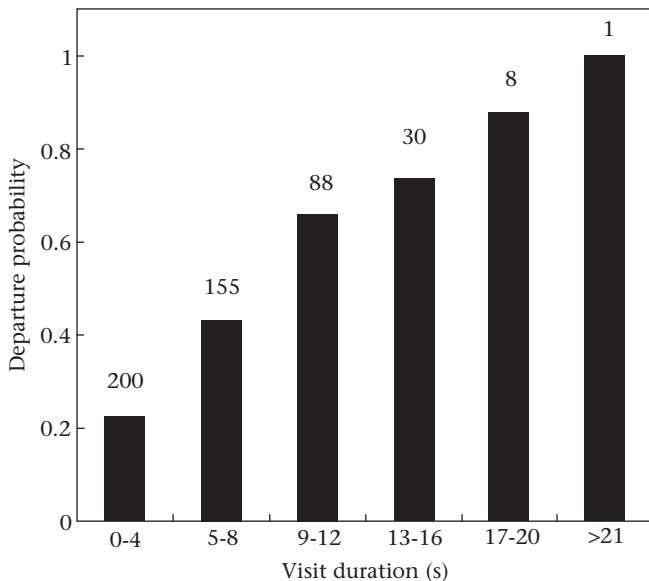


Figure 2. Frequencies of flower departures as a function of the duration of visit to the flower. Sample sizes are indicated at the top of each bar.

($P = 0.11$). Flower visits that involved probing an already visited nectary (when six, seven or eight nectaries were visited) occurred in 26.4% of the cases. This corresponds to 7.8% of the nectary probes involving a revisit by the same forager. The conditional probability of departing a flower after *N* nectary probes was calculated by dividing the number of flower departures after the *N*th nectary by the number of probes of this nectary. This calculation shows that the frequency of flower departure increased monotonically with increasing number of nectaries probed, with the general shape of a sigmoid function (Fig. 1). The frequency of flower departure also increased monotonically with time at the flower (Fig. 2).

The bees foraged differently in early morning compared with later hours. During early hours (0700–0900 hours) they visited fewer nectaries per flower, but spent a longer time per nectary and per flower than later on (Fig. 3). The longer visit times could be due to the flowers' higher nectar standing crops in early morning (Fig. 4), because the nectar was more viscous and took longer to imbibe during the cool morning hours, and/or because the bees moved more slowly at low temperatures (Bar-Shai et al. 2011). To avoid possible confounding effects of these variables, we excluded observations recorded before 0900 hours from further analyses of visit durations. Within the remaining data set ($N = 200$ visits), we tested for possible foraging patterns that could account for the high frequency of five- and six-nectary visits.

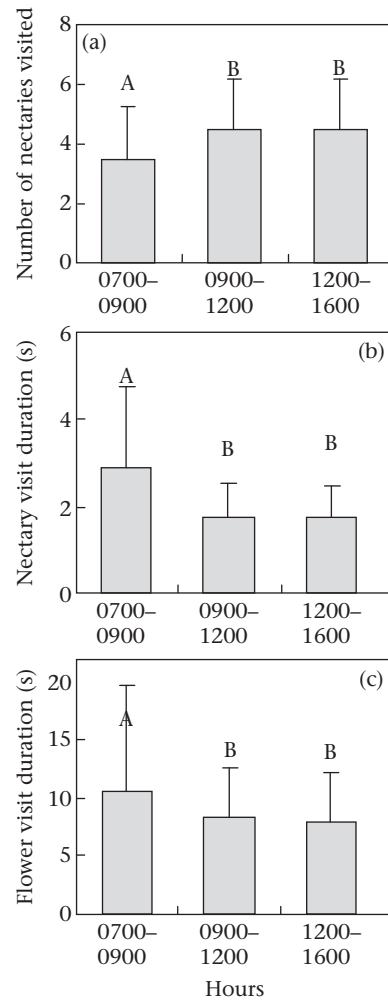


Figure 3. Means + SD of (a) the number of nectaries visited per flower, (b) the duration of a nectary visit and (c) the duration of a flower visit at different times of day. Different letters indicate significant differences in Tukey's post hoc tests. Sample size was 261 flower visits.

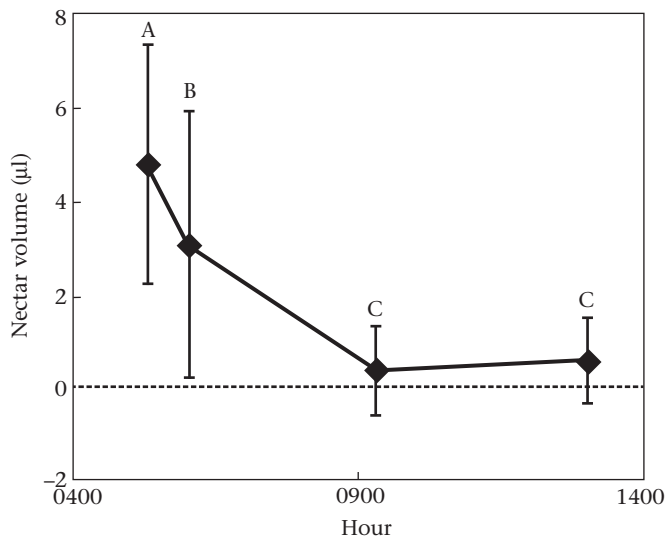


Figure 4. Mean \pm SD nectar volumes in *A. setosa* flowers at different hours ($N = 10$ – 14 flowers per sample, totalling 50 flowers). Different letters indicate significantly different means in Tukey's post hoc tests. The figure is reproduced from Bar-Shai et al. (2011) with permission from Oxford University Press and the International Society for Behavioral Ecology.

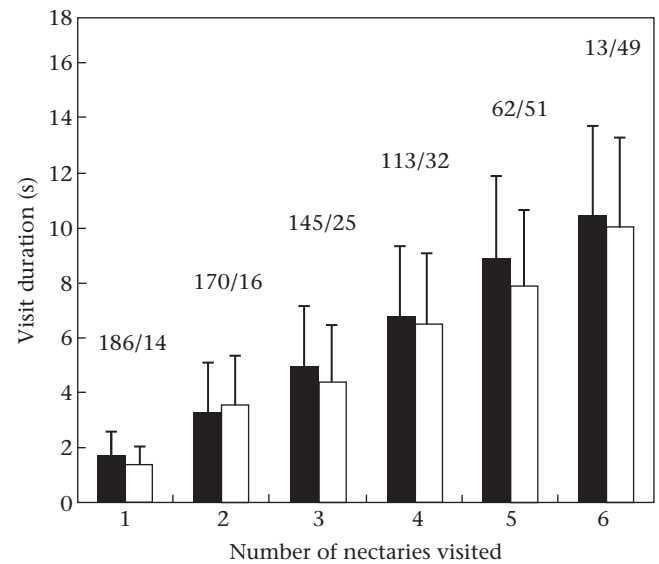


Figure 5. Mean \pm SD time spent by *Eucera* females on *A. setosa* flowers while probing one to six nectaries, prior to staying on a flower (black bars) or departing it (white bars). Flower visits that involved probing of more than one nectary contribute more than one data point to this figure. For example, probing of five nectaries in a flower generated time records regarding staying decisions after nectaries 1, 2, 3 and 4, and a departure decision after nectary 5. Sample sizes are indicated at the top of each bar.

Do Eucera Bees Use a Time-based Flower Departure Rule?

The use of a time-based departure rule would motivate bees to leave a flower after probing it for more than some threshold duration. If bees use this rule, they are expected to depart flowers at higher frequencies after long visits than after short ones, because long visits are more likely to surpass the threshold. We tested this prediction by comparing the durations of probing N nectaries ($N = 1$ – 6) and then departing the flower, and the durations of probing the same number of nectaries but not departing thereafter. Contrary to the predicted trend, probes that preceded flower departures were shorter than probes that were not followed by departures (Fig. 5). This difference was significant for five-nectary visits ($t_{111} = 1.99$, $P = 0.024$) and marginally significant for one-nectary ($t_{17} = 1.65$, $P = 0.06$) and three-nectary visits ($t_{35} = 1.59$, $P = 0.06$). In other words, after spending a longer time in a flower's first N nectaries, the bees were more likely to visit nectary $N + 1$ as well. We conclude that flower departures were not driven by a simple time-based rule that restricts flower foraging durations.

Do Bees Leave after Completing a Fixed Foraging Path?

We tested whether bees tend to use the flowers' spatial characteristics to follow fixed foraging paths of five or six nectaries. The distribution of the starting points of flower visits deviated significantly from uniform ($\chi^2_4 = 278$, $P < 0.001$): 56% of the visits started in nectary 1, 29% in nectary 5 and only 15% in one of the three other nectaries. Thus the bees strongly tended to land on the top part of *A. setosa*'s flowers. They were equally likely to move clockwise (52% of visits) and anticlockwise (48% of visits) on the flowers ($P = 0.26$). Landing position and movement direction were independent of each other ($\chi^2_4 = 4.14$, $P = 0.39$). The distribution of flower departure positions did not differ significantly from uniform ($\chi^2_4 = 2.58$, $P = 0.63$).

We next tested the possibility that, although no particular foraging path could be identified at the population level, individual bees may have their own favourite foraging paths. By consistently following their preferred paths, foragers may leave the flowers after five or six nectaries. To evaluate this hypothesis, we first checked

whether individuals tended to keep their landing positions and movement directions in consecutive flower visits. Landing position was retained in 45 of 79 observed pairs of consecutive visits, significantly more often than expected at random (binomial test: $P = 0.028$), and movement direction was retained in 51 of 87 cases (binomial test: $P = 0.051$). Thus, individual bees indeed tended to forage repeatedly along the same path. Next we examined whether five-nectary flower visits were more likely when the bees retained the movement path of the previous flower visit than when they changed their route. Five-nectary visits occurred in 0.23 of cases when the previous visit's landing point was retained ($N = 81$), and in 0.28 of cases when it was changed ($N = 75$). The frequency of five-nectary visits was 0.22 when the movement direction was retained between consecutive visits ($N = 96$), and 0.32 when it was changed ($N = 60$). Overall, the frequency of five-nectary visits did not depend on whether or not a forager kept the same path in consecutive visits ($\chi^2_1 = 0.32$, $P = 0.57$ for landing position; $\chi^2_1 = 1.36$, $P = 0.24$ for movement direction). This suggests that the bees did not rely on spatial attributes in the flowers to follow five-nectary movement trajectories.

Are Self-scent Marks Used as Departure Cues?

Bees turned towards a nectary (without probing it), before leaving a flower, in 32 of 225 cases. Such turns may allow the bees to inspect nectaries for scent marks, thereby identifying nectaries that they had already visited. While the turns could serve other functions, flower departures that were not preceded by turns were surely not performed in response to self-scent marks. We therefore compared the number of nectaries probed in visits that involved turns versus visits that did not. The proportion of turns was highest at the end of five-nectary visits (Fig. 6). This proportion was significantly higher (binomial test: $P = 0.028$) than the overall frequency of turns in the data set ($32/225 = 0.142$). When visits that did not involve turns were considered separately, six-nectary sequences became the most common. As in the entire data set, the differences between the frequencies of four-, five- and six-nectary visits were

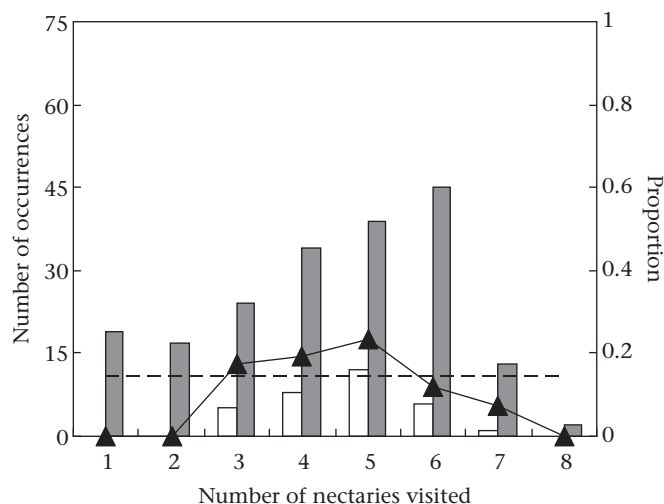


Figure 6. The number of probes of one to eight nectaries in *A. setosa* flowers by *Eucera* females (out of 225 observed flower visits) that were followed (light bars) or not followed (dark bars) by turns towards an additional nectary. Such turns potentially indicate inspection for scent marks, as a means of detecting previously visited nectaries. The triangles with solid line show, for each number of nectaries probed, the proportion of visits that were followed by a turn. The dashed line indicates the mean proportion of visits followed by turns in the whole data set. The values of the proportions are indicated on the right-hand Y-axis.

not statistically significant (binomial tests). These results are compatible with the possibility that ‘footprint’ scent marks allowed the bees to detect nectaries that they had already visited, and to avoid revisiting them.

DISCUSSION

Claims for complex cognitive abilities in animals are widely debated (Davis & Péruce 1988; Seibt 1988; Gallistel 1989; Capaldi 1993), and very little is known about such capabilities in insects. We asked whether bees employ one such skill, numerical ability, to forage efficiently in the field. *Eucera* bees most commonly foraged on all of *A. setosa*'s five nectaries, and avoided returns to nectaries they had previously probed. The conditional probability of flower departure increased with the number of visited nectaries. These features also characterize *B. terrestris*' foraging on *A. setosa*. However, the two bee species apparently differ in the flower departure rules that underlie their foraging choices. *Bombus terrestris* workers seem to use the number of visited nectaries as their flower-leaving signal. They do not base flower departure decisions on the time spent in the flower and the volume of reward obtained. Moreover, they very rarely revisit depleted nectaries even when cues such as the flowers' spatial characteristics or pheromonal scent marks are not available to them (Bar-Shai et al. 2011). The flower-leaving behaviour of *Eucera*, on the other hand, may involve time-, reward- and odour-based mechanisms that do not require numerical abilities:

The frequency of flower departures by *Eucera* foragers increased with time in the flowers (Fig. 2), suggesting that flower probing time could provide the bees with a leaving cue. On the other hand, flower departures generally followed shorter probe durations per nectary (presumably because the bees imbibed smaller nectar volumes, Hodges 1985; Zimmerman 1988; Manetas & Petropoulos 2000) than nondepartures (Fig. 5). Thus, the bees' patch-leaving patterns may also respond to the food reward obtained.

Waage (1979), who studied the patch departure choices of the parasitoid *Nemeritis canescens* searching for larval hosts, suggested that foragers enter food patches with an initial level of motivation (or ‘responsiveness’) that reflects their expectation of patch

profitability. The motivation to remain in the patch decreases with time, but increases when a prey item is discovered. The foragers leave the patch when their motivation drops below some threshold. This mechanism predicts longer searching times of rich patches compared to poor ones, and leaving of depleted patches after their prey densities have been reduced. Waage's (1979) model successfully explained patch departure behaviour in additional parasitoid wasps (reviewed by van Alphen et al. 2003), and in two *Bombus* species foraging for patchily distributed nectar (Lefebvre et al. 2007; Biernaskie et al. 2009).

Nectar foraging by *Eucera* in the present study resembled host searching in parasitoids in two important respects. First, *Eucera* may form prior expectations about reward levels in its foraging patches (flowers) based on previous visits to *A. setosa*. Similarly, the levels of host kairomones enable parasitoids to estimate patch profitability before they start foraging. Second, both nectar availability (for bees) and host suitability (for parasitoids) cannot be assessed from a distance, so that foragers need to check each potential food item. Indeed, *Eucera*'s foraging behaviour in the present study is compatible with Waage's mechanism in that the frequency of departure increased with time at the flower, and decreased with long per nectary foraging durations. However, the frequencies of flower departures by *Eucera* were a sigmoid function of the visit duration (Fig. 1), while Waage's model assumes a linear relationship. Additional source of patch-leaving information could contribute to this nonlinear function.

Eucera foragers may also rely on ‘footprint’ scent traces that they had deposited on previously visited nectaries, and which may be detected during inspection turns, to avoid revisits. This possibility is supported by the observation that the proportion of flower departures following inspection turns was highest after five-nectary visits (i.e. when a previously visited nectary was inspected). Moreover, when only visits that did not involve inspection turns were considered, six-nectary visits were more common than five-nectary visits; thus the frequency of nectary revisits increased. Once a forager visited the fifth nectary, the probability of departure without turning to the next nectary was only 0.37 (Fig. 6, sum of the three rightmost data points). This suggests that, when scent marks were not in use, being the fifth visit in a sequence of nectary visits was not a significant cue for leaving the flower. *Eucera* foragers performed turns rather infrequently (in 14.2% of visits, compared with 25.2% of visits in *B. terrestris*). However, if we also consider visits that included six nectaries and more, where scent marks could be detected while standing at the nectary, the percentage increases to a significant 40.9% of all visits (Fig. 1, sum of the four rightmost bars). This suggests that scent marks may have played a major role in guiding *Eucera*'s flower-leaving decisions.

A few other potential sources of information did not affect *Eucera*'s flower-leaving decisions. The bees did not depart flowers after a fixed foraging time. The large variation in nectar standing crop among flowers and sampling hours suggests that they did not leave flowers after imbibing a fixed nectar volume either. Although bees usually started foraging at the top of the flowers, they did not have a preferred movement direction or departure point. In addition, five-nectary visits were equally frequent, whether foragers used the same movement path in the flower in two consecutive visits or not. These observations suggest that the flowers' spatial characteristics did not guide the bees' departure decisions.

The use of non-numerical patch-leaving cues provides a more parsimonious explanation for *Eucera*'s flower departure behaviour than counting-like ability. This interpretation is supported by *Eucera*'s relatively weak preference for five-nectary visits: the difference in frequency between five- and six-nectary visits was not significant; the increase in departure probability from the fourth to the fifth nectary (0.25) was lower than the increase from the fifth to

the sixth (0.28; Fig. 1); and five-nectary visits were not the most common case, when only visits not followed by a turn were considered. However, the use of numerical information (i.e. the ordinal position of a nectary in a sequence of nectary visits in a flower) by *Eucera* is not categorically ruled out by our observations. This possibility is supported by previous reports of numerical competence in honeybees (Chittka & Geiger 1995; Dacke & Srinivasan 2008) and bumblebees (Bar-Shai et al. 2011). In particular, it is not certain that Waage's patch departure rule, combined with reliance on scent marking, is sufficient to explain the observed high frequency of five-nectary visits. When considering possible numerical competence in *Eucera*, it is interesting to speculate how it relates to numerical abilities in other species. Studies on untrained rhesus macaques, *Macaca mulatta*, and human infants demonstrate the use of two 'core systems' for representing numbers: a precise representation of a small number of individual objects and an approximate representation of larger quantities (Hauser et al. 2000; Feigenson et al. 2004). The inexact core system is assumed to involve one cumulative representation of all encountered items, which is prone to measurement error. When applied to foraging bees, this 'accumulator model' predicts that nerve signals are generated upon each encounter with a nectary. The signals are summed and compared to a threshold value, and the forager leaves the flower when the accumulated signal exceeds the threshold (Meck & Church 1983). Such an inexact system is compatible with the rather high proportion of four- and six-nectary visits observed in *Eucera*. In bumblebees, on the other hand, the frequency of five-nectary visits is significantly higher than visits of any other number of nectaries (Bar-Shai et al. 2011). This could hint that, if *Eucera* bees do process numerical information while foraging, they may use a less exact representation of number than *Bombus*.

Manipulative experiments under precisely controlled laboratory conditions would have allowed more detailed testing of the bees' numerical skills, as previously done with bumblebees (Bar-Shai et al. 2011). However, such experiments require bees of known and controlled foraging experience (ideally, laboratory-reared naïve foragers) that successfully feed from artificial feeders. *Eucera* bees are not reared in captivity, and their abilities for navigating and foraging indoors have not yet been characterized. These constraints limit their use in laboratory experiments and hence our conclusions as to their numerical competence and its cognitive basis.

Eucera bees were less efficient than bumblebees in exploiting *A. setosa*'s nectar. Bumblebees probed exactly five nectaries in 48% of all flower visits, and only 1.1% of all visits to nectaries were returns to nectaries that the same individual had just probed (Bar-Shai et al. 2011). In *Eucera*, on the other hand, the frequency of five-nectary visits was only 25.6%, and 7.8% of the nectary probes were revisits. Thus the use of numerical information in foraging, as in *B. terrestris*, is probably selectively beneficial. Our observations, which suggest reduced or no reliance on numerical information by foraging *Eucera*, may reflect limitations on these bees' learning abilities. The need to deal with a complex social environment has been proposed to favour the evolution of complex cognitive skills in social bees more than in solitary ones (Dukas & Real 1991; Campan & Lehrer 2002). Additional ecological differences between species, such as in body size, flight range or longevity, may further account for differences in learning capabilities.

Acknowledgments

We are grateful to Guy Bloch and Michael Ben-Or for helpful discussions. This work was supported by the Center for Rationality and Interactive Decisions at the Hebrew University.

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