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DO SOLITARY BEES COUNT TO FIVE?

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Do solitary bees count to five?

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ABSTRACT

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 video-recorded flower visits showed that the bees most commonly probed five nectaries, but occasionally (in 7.8% of visits) continued to a nectary they had already visited. Probing durations that preceded flower departures were generally shorter than probings that were followed by an additional nectary visit in the same flower. Assuming that probing 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. We conclude that *Eucera* females do not exhibit numerical competence as a mechanism for efficient patch use, but rather a combination of a reward-based leaving rule and scent-marking. The bees' foraging pattern is compatible with Waage's (1979, *Journal of Animal Ecology*, **48**, 353-371) patch departure rule, which states that the tendency to leave a foraging patch increases with time, and decreases when food items are encountered. Thus, *Eucera* resemble bumblebees in avoiding most revisits to already-visited nectaries, but use a different foraging strategy to do so. This difference may reflect lower learning capabilities of solitary bee species compared to social ones.

KEYWORDS: cognition, counting, foraging, numerical competence, solitary bee.

INTRODUCTION

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 were described in bees, popular models for foraging studies. They include bottom-to-top movement along vertical inflorescences (Pyke 1979; Waddington and Heinrich 1979), foraging along a fixed route (traplining) (Ohashi and Thomson 2009, Lihoreau et al., 2010), and scent marking of visited flowers (Giurfa and Nunez 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 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. *Bombus terrestris* (L.) 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 excluded the following alternative possible flower-leaving cues: 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, i.e. 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 and bumblebees in navigation tasks (Chittka & Geiger, 1995, Dacke & Srinivasan, 2008).

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. 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 color-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 describe how females of the solitary genus *Eucera* (Fam. 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). We first show that the bees forage efficiently by frequently visiting five nectaries per flower. We then ask whether this foraging pattern is based on the use of numerical information as in bumblebees, or whether it could result from other behavioural strategies.

METHODS

Study Site and Species

A wild population of *A. setosa* (Boiss.) was observed in the Judaeian Hills of Israel (altitude 500 m) during 6 days in May 2009. Seventy to 100 flowers were in bloom during the days of observation. *A. 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 5 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 bumblebees (*Bombus terrestris* L.), 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 analyzing 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 counter-clockwise), 5) the time spent in each nectary and the duration of the whole flower visit (previously shown to correlate with nectar reward (Zimmerman 1988, Millet-Pinheiro & Schindwein 2009)), and 6) whether the bee turned toward a nectary without visiting it before leaving the flower, which may indicate rejection because of scent marks. Corbet (1984) interpreted

approaches to a distance of <1 cm of food sources, which 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.

Nectar standing crops (the amounts of nectar available in flowers exposed to visitors) were sampled at 0530, 0630, 0930, and 1300 h on one observation day. The 0530-h sample was taken before the onset of bee activity, and the 0630-h sample was taken shortly after the bees started foraging. Each sample was based on 2 flowers from each of 5–7 plants. Nectar was collected separately from each nectary, using 5- μ l micropipettes. Sucrose concentration was determined in samples with sufficient volume (<1/3 μ l) 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 h 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 used t-tests to compare the times spent in flower until departure versus the time spent for visiting the same number of nectaries in cases when the bees did not depart 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 #1 and the remaining nectaries received consecutive numbers, clockwise, starting at #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 2 or more probings, was characterized by a 3-character string. The first 2 characters (which ranged 1–5) designated the first and last nectaries probed within the flower, respectively. The third character was defined as “+” or “-” for clockwise or counter-clockwise 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 there was any preference to 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 2 consecutive flower visits, than expected at random.

The random expected probability for probing 2 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 2 consecutive flowers was 0.40. The random expected probability for keeping the same movement direction in 2 consecutive flowers was calculated as $p(+)^2 + p(-)^2$. $p(+)$ and $p(-)$ are the frequencies for clockwise and counter-clockwise movement, estimated from the data. Based on these estimates, the expected probability that a bee would take the same direction of movement in 2 consecutive flowers, under a random null model, was 0.50.

We calculated the expected probabilities for probing 1–8 nectaries per flower under a logarithmic null model. The frequency of leaving (p_1) a flower after probing 1 nectary was estimated from the data. The predicted probability of leaving after probing 2 nectaries is $p_1(1-p_1)$, the leaving probability after 3 nectaries is $p_1(1-p_1)(1-p_1)$, etc. We compared the observed and expected distributions of visits of 1–8 and >8 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

The Number of Nectaries Visited per Flower

The bees most frequently (in 26% of the cases) visited five nectaries per flower. 5-nectary visits were significantly more common than 4-nectary visits (binomial test, $p < 0.001$), but did not significantly differ in frequency from 6-nectary visits ($p = 0.11$). 6-nectary visits involved probing of an already-visited nectary, which occurred in 7.8% of the cases. The conditional probability of departing a flower after n nectary probings was calculated by dividing the number of flower departures after the n th nectary by the number of probings of this nectary. This calculation shows that the frequency of flower departure increased monotonously with increasing number of nectaries probed (Fig. 1).

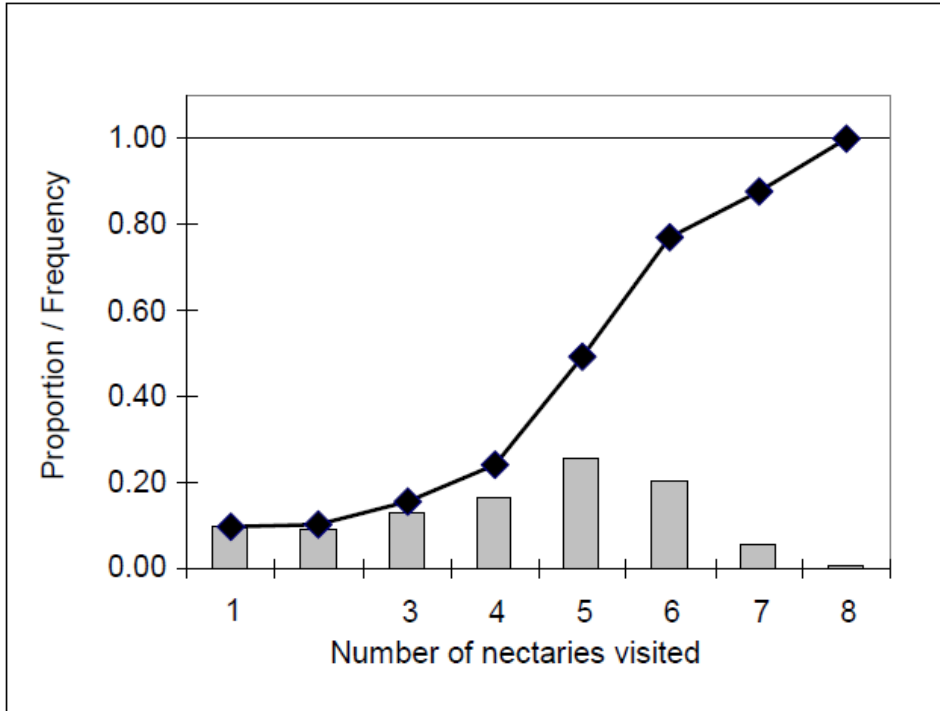


Fig. 1: The relative frequency of probing 1-8 nectaries in *A. setosa* flowers by *Eucera* females (bars), and the conditional probability for departing the flowers after varying numbers of probings (line). Conditional probabilities were calculated as the ratio of the number of flower departures after the n th nectary and the number of probings of this nectary.

The bees foraged differently in early morning compared with later hours. During early hours (9-11 am) they visited fewer nectaries per flower, but spent a longer time per nectary and per flower than later on (Fig. 2). The longer visit times could be due to the flowers' higher nectar standing crops in early morning (Fig. 3), 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. To avoid possible confounding effects of these variables, we excluded observations recorded before 9 am from further analyses of

visit durations. Within the remaining dataset (n=200 visits), we tested for possible foraging patterns that could account for the high frequency of 5- and 6-nectary visits.

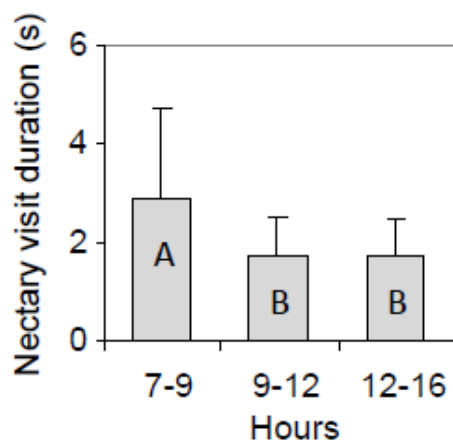
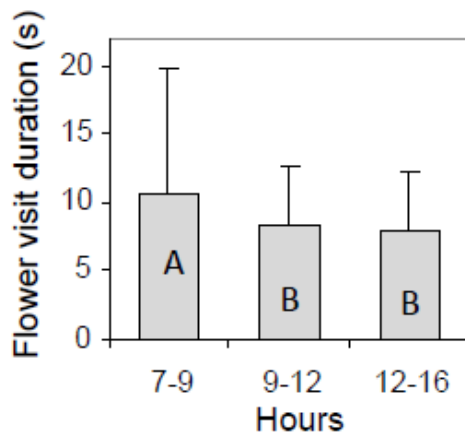
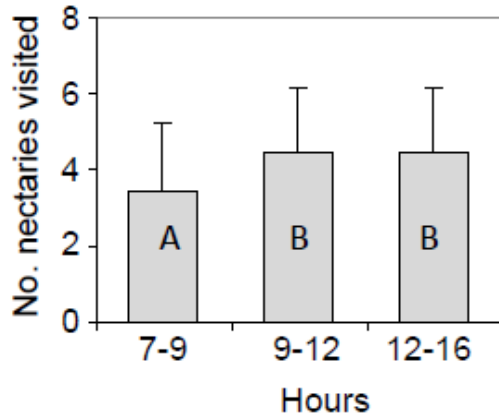


Fig. 2: The number of nectaries visited per flower (a), the durations of a nectary visit (b) and of a visit flower (c) at different times of day. Means are shown with their standard deviations. Different letters indicate significant differences in Tukey's post-hoc tests.

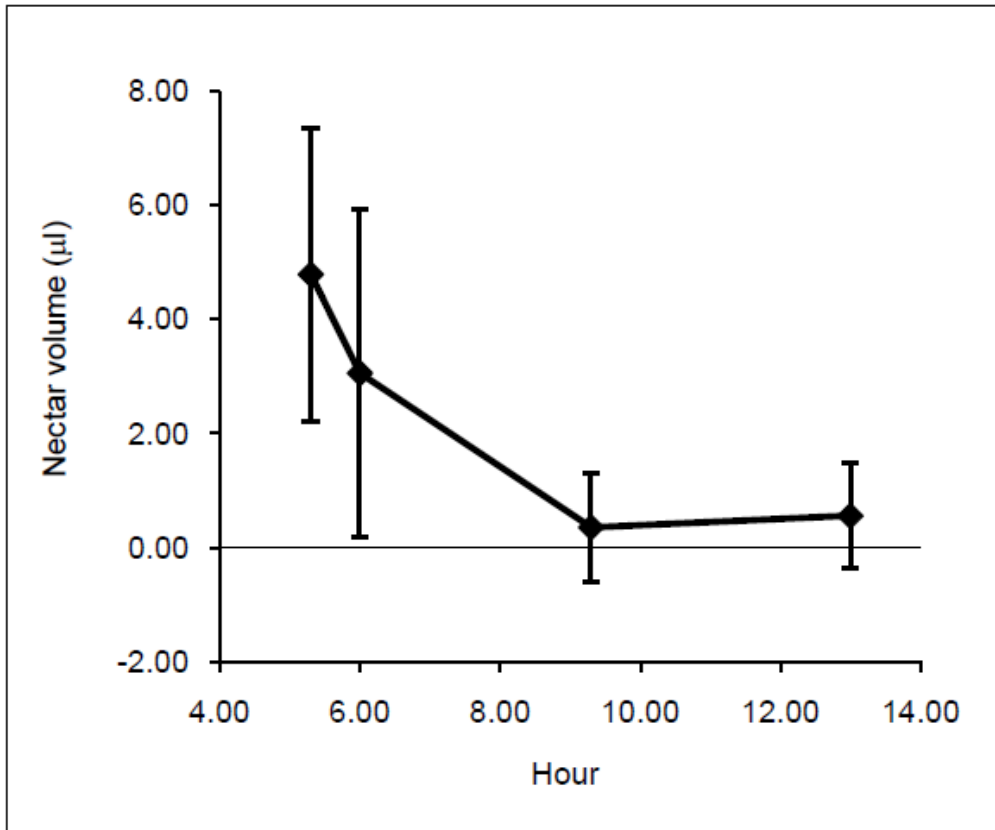


Fig. 3: Mean \pm SD nectar volumes in *A. setosa* flowers at different hours. Different letters indicate significantly different means in Tukey's post-hoc tests. The figure is reproduced from Bar-Shai et al., 2011.

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. We tested this prediction by comparing the duration of visits that preceded flower departures vs. non-departures, separately for visits of 1-6 nectaries. Contrary to the predicted trend, visits that preceded flower departures had shorter durations than visits that were not followed by

departures (Fig. 4). This difference was significant for 5-nectary visits ($t_{111}=1.99$, $p=0.024$) and marginally significant for 1-nectary ($t_{17}=1.65$, $p=0.06$) and 3-nectary visits ($t_{35}=1.59$, $p=0.06$). We conclude that flower departures were not driven by a simple time-based rule that restricts flower foraging durations.

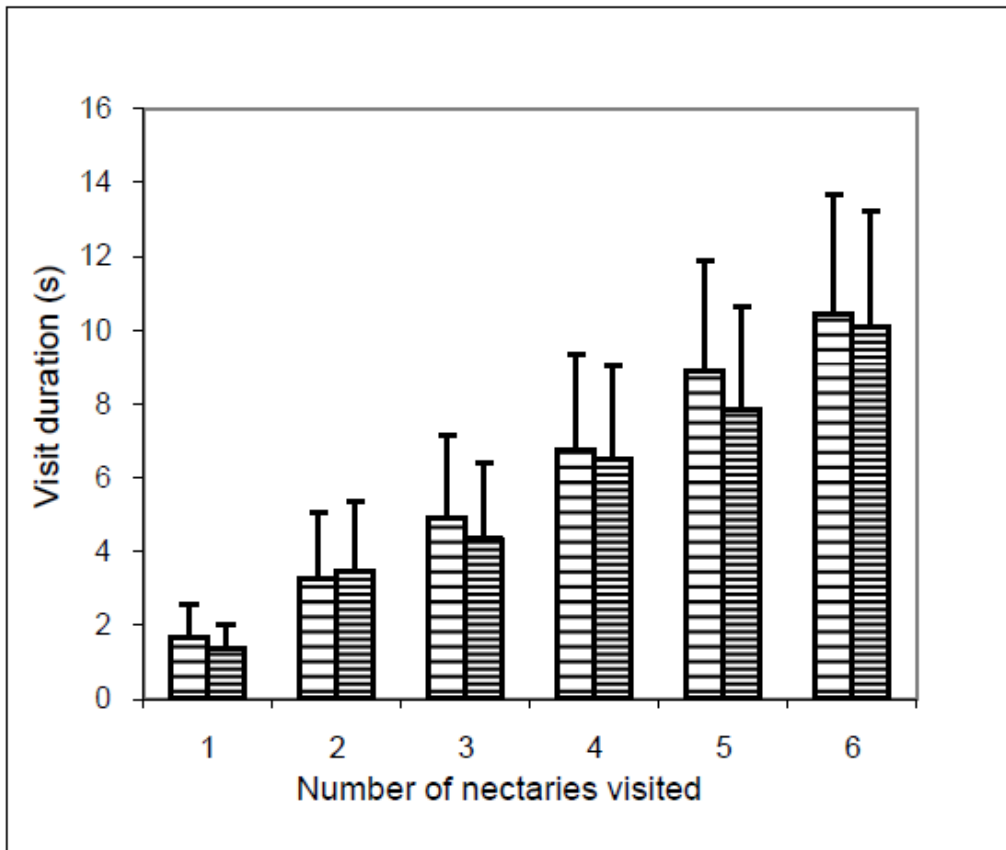


Fig. 4: Mean \pm SD time spent by *Eucera* females on *A. setosa* flowers while probing 1-6 nectaries, prior to staying on a flower (light bars) or departing it (dark bars). Flower visits that involved probing of more than one nectary contribute more than one data point to this figure. For example, probing 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.

Do Eucera Bees Leave Flowers after Completing a Fixed Foraging Path?

We tested whether bees tend to use the flowers' spatial characteristics to follow fixed foraging paths in the flowers, which are 5-6 nectaries long. The distribution of the starting points of flower visits significantly deviated from uniform ($\chi^2 = 278$, $p < 0.001$). 56% of the visits started in nectary #1, 29% started in nectary #5, and only 15% of the visits started 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 counterclockwise (48% of visits) on the flowers ($p = 0.26$). Landing position and movement direction were independent of each other ($\chi^2 = 4.14$, $p = 0.39$). The distribution of flower departure positions did not significantly differ from uniform ($\chi^2 = 2.58$, $p = 0.63$).

We next tested the possibility that, although no particular foraging path could be identified at the population level, individual bees may have varying favorite foraging paths. By consistently following their preferred paths, foragers may leave the flowers after 5-6 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 out 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 out of 87 cases (binomial test, $p = 0.051$). Thus, individual bees indeed tended to forage repeatedly along the same path. Next we examined whether 5-nectary flower visits were more likely when the bees retained the movement path of the previous flower visit than when they changed their route. 5-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 5-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 5-nectary visits did not depend on whether or

not a forager kept the same path in consecutive visits ($\chi_1^2 = 0.32$, $p = 0.57$ for landing position, $\chi_1^2 = 1.36$, $p = 0.24$ for movement direction). This suggests that the bees did not rely on spatial attributes in the flowers to follow 5-nectary movement trajectories.

Do Eucera Bees Leave Flowers when they Detect their own Scent Marks?

Bees turned towards a nectary (without probing it), before leaving a flower, in 32 out 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 vs. visits that did not. The proportion of turns was highest at the end of 5-nectary visits (Fig. 5). This proportion was significantly higher (binomial test, $p = 0.028$) than the overall frequency of turns in the dataset ($32/225 = 0.142$). When visits that did not involve turns were considered separately, 6-nectary sequences became the most common. As in the entire data set, the differences between the frequencies of 4-, 5- and 6-nectary visits were 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.

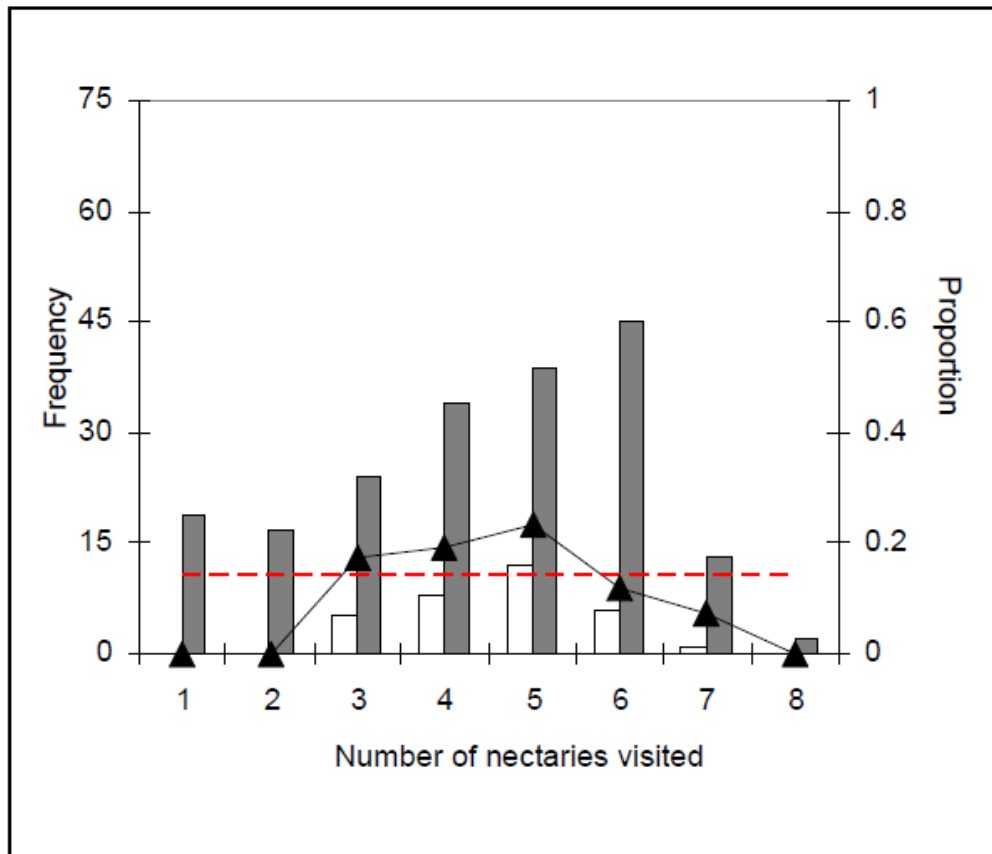


Fig. 5: The number of probings of 1-8 *A. setosa* nectaries that were followed (light bars) or not followed (dark bars) by turns towards an additional nectary. Such turns possibly indicate inspection of scent marks, as a means of detecting previously visited nectaries. The solid line shows the proportion of turns towards an additional nectary after varying numbers of nectary probings. The dashed line indicates the mean frequency of inspection turns in the whole dataset.

DISCUSSION

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. *B. 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, the volume of reward obtained, the flowers' spatial characteristics or on pheromonal scent marks (Bar-Shai et al., 2011). The flower-leaving behaviour of *Eucera*, on the other hand, can be explained using the following decision mechanisms, which do not require numerical abilities:

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 resembles 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 increases monotonously with time at the flower. Moreover, long probing durations of nectaries, presumably due to imbibing of large nectar volumes (Hodges, 1985, Manetas & Petropootou 2000, Zimmermann, 1988) increase patch tenure, similar to host encounters by parasitoids. The frequencies of flower departures by *Eucera* are an accelerating function of the visit duration (Fig. 1), while the basic version of Waage's model assumed a linear relationship. However, the decrease in responsiveness to patch cues that eventually leads to the foragers' departure was suggested to reflect a habituation process (Waage, 1979). Such a habituation response, which builds up logarithmically rather than linearly with time, agrees with the observed patterns of departure frequencies in *Eucera*.

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 5-nectary visits (i.e., when a previously-visited nectary was inspected). Moreover, when only visits that did not involve inspection turns were considered, 6-nectary visits were most common than 5-nectary visits, thus the frequency of nectary revisits increased. Nevertheless, *Eucera* foragers performed potential inspection actions rather infrequently (in 14.2% of visits, compared with 25.2% of visits in *B. terrestris*). This suggests that their role in guiding flower-leaving decisions in *Eucera* is probably secondary.

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, 5-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.

Eucera bees were less efficient than bumblebees in exploiting *A. setosa*'s nectar. The frequency of revisits to depleted nectaries was 1.1% in bumblebees (Bar-Shai et al., 2011), compared to 7.8% in *Eucera*. Thus the use of numerical information in foraging, as in *B. terrestris*, is probably selectively beneficial for bees. Our observations, which suggest 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 was proposed to favor 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 difference in learning capabilities.

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