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Assessment of nectar flow rate and memory for patch quality in the ant *Camponotus rufipes*

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Ants as central place foragers are known to visit repeatedly renewable patches such as extrafloral nectaries, yet the criteria workers use to evaluate their quality, as well as the rules used to decide when to leave the patch, have not been identified. We examined the assessment of nectar flow rate by nectar-feeding ants, *Camponotus rufipes*. Single workers from a laboratory colony were trained to visit an artificial feeder providing 20% sucrose solution either ad libitum or at controlled flow rates (0.118–2.36 $\mu\text{l}/\text{min}$). These flow rates simulate the conditions faced by workers when visiting plant extrafloral nectaries. Ants adjusted their visit times to the different flow rates, so that the time spent at the feeder decreased with increasing nectar flow rates. The volume of nectar collected increased with increasing nectar flow rates, and workers were observed to return to the nest with partially filled crops. To investigate the rules used by ants to decide when to depart from the patch, we confronted experienced workers on their fifth visit with a depleted patch, and recorded the time spent there before leaving. The time depended on the previously experienced flow rate, even though ants always found a depleted patch, indicating that ants arrive at the patch with an expectation about the nectar flow rate, and use as a departure rule an estimate of time that depends on the flow rate previously experienced.

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To understand the decision rules of foraging animals from an adaptive standpoint, we often assume that individuals have evolved to maximize rate of food intake (Krebs 1981). This implies that animals are able to evaluate the quality of a food source not only by assessing its energy content, but also by considering the time invested in food intake. Time allocation both within and between patches may be particularly relevant for animals that forage on renewable, predictable resources such as nectar (Cruden et al. 1983). This could be why, among insects, the ability to learn the time and location of a food source has been found in honeybees, *Apis mellifera* (Wahl 1932), and in nectar-feeding ant species such as *Paraponera clavata* (Harrison & Breed 1987) and *Ectatomma ruidum* (Schatz et al. 1994, 1999), but not in ant species that do not forage on nectar (Reichle 1943; Dobrzanski 1956).

Nectar-feeding ants repeatedly visit renewable resources such as extrafloral nectaries or aphid colonies, yet the criteria workers use to evaluate resource quality, as well as the rules they use to decide when to leave the patch, have not been identified. Such renewable resources

usually offer nectar at flow rates very much lower than the maximal intake rate of individual ants. This means that ants have to wait for the nectar to be produced. Under such conditions, it may be relevant for ants to adjust their foraging efforts at a patch to its quality. Rates of extrafloral nectar secretion are very low. For instance, maximal rates of 0.12 $\mu\text{l}/\text{min}$ per plant have been measured in species regularly visited by ants (Dreisig 2000). The maximal crop capacity of an ant worker belonging to a typical nectar-feeding ant species such as *Camponotus mus* averages, for instance, 5 μl (Josens et al. 1998); therefore, to fill its crop, an ant should spend about 40 min on a plant.

Ants may leave a patch by using the simplest rule of collecting nectar until the crop is filled, but even under ad libitum conditions, workers often return to the nest with partially filled crops (Josens & Roces 2000; Mailleux et al. 2000), with the extent of filling being a function of food quality (Josens et al. 1998). Workers of the species *Camponotus sericeus* and *C. compressus*, which forage on extrafloral nectar or on honeydew secreted by aphids, decide about the quality of a food source by sampling only a part of it, so that they abandon plants if food of poor quality is found in the sampled region, or they continue foraging upon finding food of good quality (Ganeshaiah & Veena 1988; Veena & Ganeshaiah 1991).

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Local search strategies and residence times have been investigated quantitatively in workers of the ant *P. clavata* (Breed et al. 1996a, b) at artificial patches that provided discrete nectar droplets with volumes below the maximal loading capacity of the individuals and which did not require the ants to wait for the nectar secretion. These conditions, however, do not represent the natural situation in which nectar is provided at a given flow rate. Under such conditions, a worker needs to wait for the nectar to be produced, so that the longer the worker waits, the more it collects. Hence, quantitative studies that manipulate nectar production rate in the natural range of nectar flows, and investigate the rules ants use to assess patch quality and to decide when to leave the patch, are lacking.

We investigated patch departure rules in workers of the nectar-feeding ant *Camponotus rufipes* as a function of nectar flow rate. Workers of this species regularly feed on arthropods and collect nectar from extrafloral sources (Jaffé & Sánchez 1984). In independent laboratory assays, single naïve workers were given access to an artificial 'nectary' providing different flow rates of sucrose solution, and both the time spent collecting and the amount collected were recorded. To examine the rules governing patch departure in foragers, we investigated whether previous experience with a given nectar flow rate leads to the development of reward expectations, and therefore affects the time foragers spend at a depleted patch on the subsequent visit. Ants may, for instance, decide to search for longer at those patches that had the highest rewards on previous visits. To investigate these hypotheses, we presented individually marked ants, which had collected at the patch over four consecutive visits, with a depleted nectary on the fifth visit, and recorded their time allocation and the rate of their feeding attempts.

METHODS

Study Animals

We used a colony of *C. rufipes* consisting of one queen, approximately 500 workers and abundant brood. The founding queen was collected in November 1994 in Misiones, Argentina. The colony was reared in a plaster nest and kept in an open-top Plexiglas container (37 × 57 cm and 27 cm high) with fluon-coated walls to prevent escape, maintained at 25°C, 50% relative humidity and a 12:12 h light:dark regime (lights on at 0730 hours). Because we used only one colony, we had to use the number of workers instead of the number of colonies as the sample size for statistical analysis. We used a single colony to control for potential differences in nutritional state between colonies, which may affect the behavioural responses under investigation (Josens & Roces 2000).

The colony had free access to water and pieces of cockroaches but was deprived of sugar solution for 3–7 days before measurements to ensure high foraging motivation by the ants. Carbohydrate deprivation over

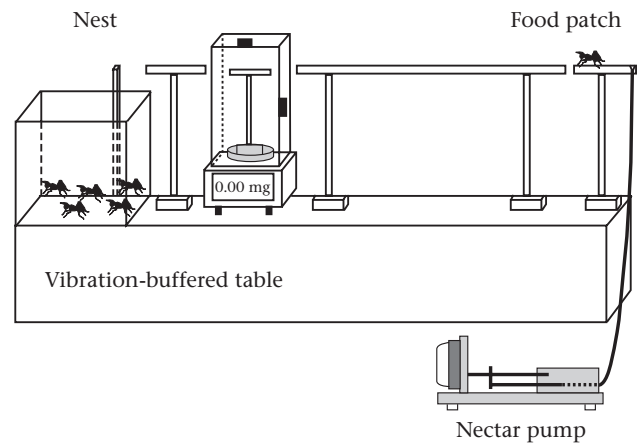


Figure 1. The apparatus used in all experiments.

this period does not significantly modify foraging behaviour (unpublished data).

Food Sources

We used a sucrose solution of 20% (w/w) concentration provided, in different experiments, either ad libitum or at continuous and controlled flow rates. The ad libitum source consisted of a 1-ml droplet of the 20% sucrose solution. A nectar pump that simulated the secretion provided by an extrafloral nectary delivered the different flow rates. Fluid flow rates of 0.118, 0.236, 0.59, 1.18 or 2.36 $\mu\text{l}/\text{min}$ were assayed, which span the natural range of extrafloral nectar secretion for plants regularly visited by ants (e.g. 0.005 $\mu\text{l}/\text{min}$ per leaf of *Ochroma pyramidale*, with a carbohydrate concentration of 64%: O'Dowd 1979; 0.075–0.21 mg/min per plant for various plant species: Dreisig 1988; 0.039–0.116 $\mu\text{l}/\text{min}$ per *Urena lobata* plant, with a carbohydrate concentration of 18.5%: Dreisig 2000). Workers of *C. rufipes* are ubiquitous visitors of extrafloral nectaries, but are opportunistic and are not associated with any particular plant species.

Experimental Procedure

We began each assay by connecting the laboratory nest to the food patch with a 1-m-long wooden bridge (Fig. 1). The patch consisted of a single feeding capillary (0.5 mm internal diameter) at the bottom of a small plastic cup connected to the pump tube. A single ant was able to introduce its mouthparts inside the cup, and, if it stopped feeding briefly, the fluid provided by the pump accumulated in the cup, so that no drops of solution could fall off.

Only a single worker was allowed to enter the bridge and to reach the patch. At the first attempt of the ant to introduce its mouthparts into the feeding capillary, we manually switched on the nectar pump and the ant began feeding. When the ant had finished feeding and ran back to the nest, we gently marked it with coloured powder (yellow pigment from Lukas-Farbe Würzburg, Germany) on its way over the bridge. We used the

pumping time (min), multiplied by the offered flow rate ($\mu\text{l}/\text{min}$), to calculate the volume collected by the ant. However, ants were able, at the end of the visit, to collect a small extra volume by introducing their glossa deep into the feeding capillary (individuals collected no more than $0.5 \mu\text{l}$ in this way, i.e. less than 10% of their maximal crop capacity), which needs to be considered as part of the total volume collected. To quantify this extra volume, we let the pump run for a short period after the ant left, until the meniscus of the sucrose solution reached the initial level (before feeding), and we measured the elapsed time. We could then calculate the extra volume collected and add it to the volume already obtained. The level of the meniscus at the capillary was easily controlled visually with the help of a CCD-Video camera aimed at the feeder. Upon arrival at the nest, the marked worker was allowed to enter and to unload the collected fluid via trophallaxis with nestmates. Immediately after unloading, which took about 1 min, the marked ant searched for the bridge to return to the food patch, and was therefore free to decide when to enter the bridge and to run again to the patch to feed.

At the patch we measured visit time (the time a forager spent at the feeder collecting the sucrose solution) and pump time (the time for which the nectar pump was switched on). A third variable, the crop load, expressed in volumetric units, was calculated by multiplying the pump time (min) by the assayed flow rate ($\mu\text{l}/\text{min}$). For workers in the ad libitum treatment, we calculated the crop load by weighing the ant before and after feeding to the nearest 0.01 mg using an analytical balance (Mettler UMT5), and by dividing the weight difference, which corresponds to the collected fluid mass, by the density of a 20% sucrose solution (Wolf et al. 1984). The balance placed between two parts of the bridge (Fig. 1) enabled undisturbed weighing when the ant passed.

To investigate the rules ant workers use to decide when to leave the patch, we confronted experienced workers, that is, those that had collected nectar at the same flow rate over four visits, with a depleted patch on the fifth visit. The time spent at the depleted patch and the rate of feeding attempts were measured and compared with the values obtained on the fourth visit. For this, we monitored the behaviour of ants that were presented with one of four nectar flows (0.59 , 1.18 , $2.36 \mu\text{l}/\text{min}$, and ad libitum) over four consecutive visits. On the fifth visit, the pump remained switched off so that the ants found a depleted patch, and could collect only the small volume of $0.5 \mu\text{l}$ accessible at the end of the feeding capillary as mentioned above. This tiny amount represents less than 10% of the maximal crop capacity.

RESULTS

The crop load increased and the visit time decreased with increasing flow rates (Fig. 2), showing that the decision to stop collecting was not based on a fixed period or a fixed crop volume. The highest crop loads averaged $6 \mu\text{l}$ and were obtained for ants feeding ad libitum. The mean intake rate of ants collecting solution ad libitum $\pm \text{SE}$ was $4.1 \pm 0.2 \mu\text{l}/\text{min}$ ($N=13$; brief feeding interruptions were

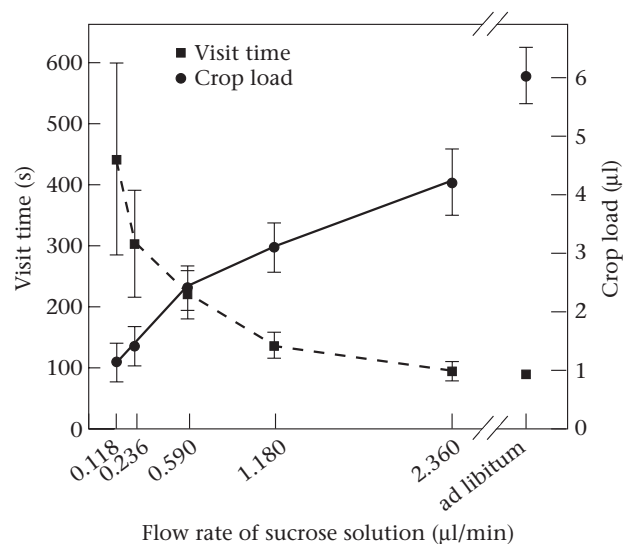


Figure 2. Visit time (s) and crop load (μl) of foragers as a function of the flow rate of the sucrose solution at their first visit to the patch. The number of ants assayed per condition varied from 10 to 14. Means are shown $\pm \text{SE}$.

not included as feeding time). This is almost twice as high as the highest flow rate ($2.36 \mu\text{l}/\text{min}$) and about 35 times higher than the lowest rate ($0.118 \mu\text{l}/\text{min}$).

Over the initial four visits, in which the flow rate was invariant, the visit time of the ants was independent of the visit number, with the exception of ants collecting at $0.59 \mu\text{l}/\text{min}$ (ANOVA: ad libitum: $F_{3,12}=0.347$, NS; $2.36 \mu\text{l}/\text{min}$: $F_{3,11}=0.726$, NS; $1.18 \mu\text{l}/\text{min}$: $F_{3,12}=0.985$, NS; $0.59 \mu\text{l}/\text{min}$: $F_{3,13}=4.651$, $P<0.01$; Fig. 3). For these ants, there was a significant difference between the first and each of the following three visits (after Tukey comparisons: $P<0.05$).

The time spent by the ants during the fifth visit at the depleted patch depended on their previously experienced flow rate (Kruskal–Wallis test: $H_{14,13,12,13}=17.567$, $P<0.001$). Significant differences were found between 0.59 and $2.36 \mu\text{l}/\text{min}$ (Dunn's test: $Q_4=3.052$, $P<0.02$) and between 0.59 and the ad libitum group (Dunn's test: $Q_4=3.966$, $P<0.001$). At the extremes of the nectar flow range assayed, workers collecting fluid ad libitum, with the shortest visit time during the rewarded visits (ca. 85 s), showed the shortest visit time at the depleted patch (ca. 79 s). Similarly, workers collecting fluid at the lowest flow rate ($0.59 \mu\text{l}/\text{min}$), with the longest visit time during the rewarded visits (ca. 5.5 min), showed the longest visit time at the depleted patch before leaving (ca. 4.0 min). The times spent at the depleted patch were not significantly different from the time spent in the previous, rewarded visit, with the exception of the group collecting at $0.59 \mu\text{l}/\text{min}$ (Friedman test: ad libitum group: $\chi^2_{4,12}=4.741$, NS; $2.36 \mu\text{l}/\text{min}$: $\chi^2_{4,11}=2.200$, NS; $1.18 \mu\text{l}/\text{min}$: $\chi^2_{4,12}=4.985$, NS; $0.59 \mu\text{l}/\text{min}$: $\chi^2_{4,13}=9.486$, $P=0.05$).

During their residence at the depleted patch, workers were observed repeatedly to attempt to feed by introducing the mouthparts into the feeding capillary and to walk around the source for a while in between these attempts.

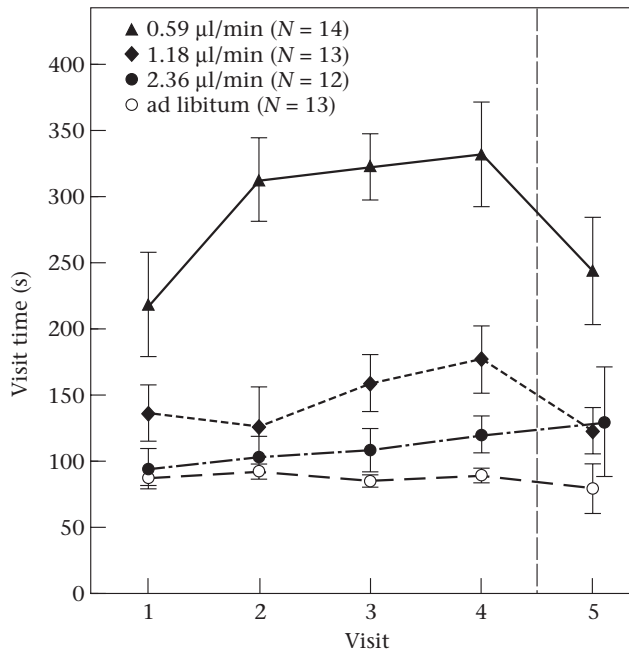


Figure 3. Visit time (s) over five consecutive visits at the patch, for different patch qualities. On the fifth visit, workers found a depleted patch. Means are shown \pm SE. The vertical dashed line separates the first four visits (with nectar provided at a given flow rate) from the fifth visit, which corresponds to a depleted patch.

Even during feeding, ants were regularly observed spontaneously to interrupt collecting the fluid. During these brief interruptions, ants moved back on the bridge a few centimetres and then returned, or just ran around the source. These movements were clearly distinguished from the decision to return to the nest, when an ant showed conspicuous trail-marking behaviour by bending its gaster downward and dragging the tip over the ground. These interruptions were more frequent at lower nectar flow rates, but still occurred at ad libitum sources.

We used the occurrence of feeding attempts on the fifth visit as a measure of foraging expectancies of workers finding a depleted patch. Both the number and rate of feeding attempts under such 'open-loop' conditions, under which only a little sucrose solution inside the capillary was available, were compared with the same variables measured on the fourth visit, with sucrose solution available, i.e. 'closed-loop' conditions in which ants were able to feed.

For both the fourth and fifth visits, the number of feeding or attempted feeding events depended on the flow rate of sucrose solution (fourth visit: Kruskal-Wallis test: $H_{14,13,12,13}=21.123$, $P<0.0001$; fifth visit: $H_{14,13,12,13}=10.977$, $P<0.015$; Fig. 4a). This relationship was brought about by the differences between the ad libitum group and each of the others on the fourth visit (Dunn's test: ad libitum versus 0.59 $\mu\text{l}/\text{min}$: $Q_4=4.247$, $P<0.001$; ad libitum versus 1.18 $\mu\text{l}/\text{min}$: $Q_4=3.533$, $P<0.01$; ad libitum versus 2.36 $\mu\text{l}/\text{min}$: $Q_4=2.939$, $P<0.05$). On the fifth visit, significant differences were found between ad libitum and 0.59 $\mu\text{l}/\text{min}$ (Dunn's test: $Q_4=3.177$, $P<0.05$).

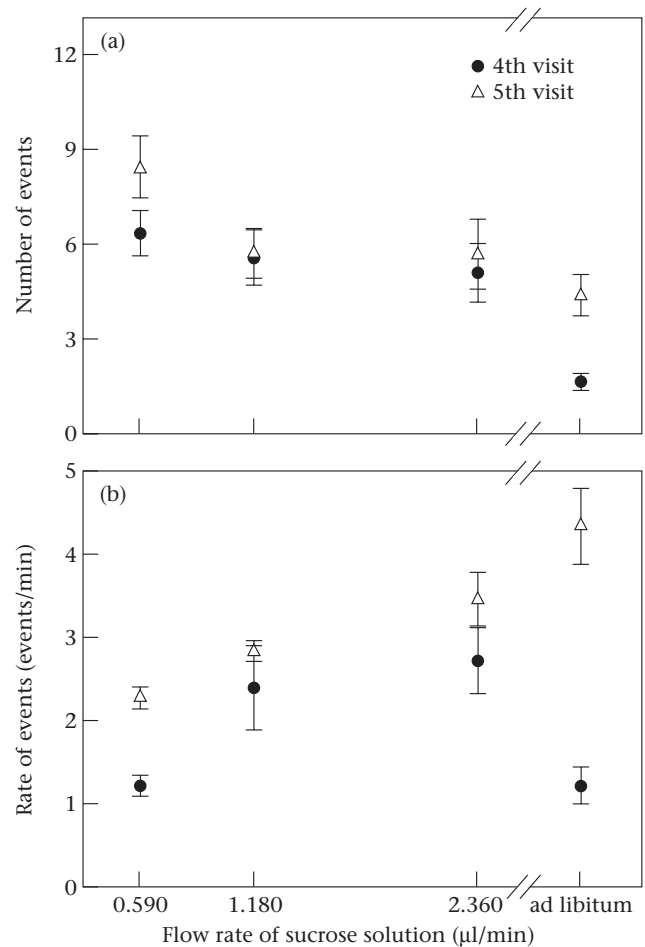


Figure 4. (a) Number of feeding events and (b) rate of feeding events as a function of the nectar flow rate experienced by workers at their fourth or fifth visit to the patch. On the fifth visit, workers found a depleted patch, and so their feeding attempts are shown.

The number of feeding events on the fourth visit and feeding attempts on the fifth visit were similar in most cases and independent of patch quality, with the exception of the ad libitum group (Wilcoxon paired-samples test: $T_+=9$, $T_-=-82$, $N=13$, $P<0.01$ for the ad libitum group, otherwise NS; Fig. 4a).

The rate of both feeding events (fourth visit) and feeding attempts (fifth visit) depended on patch quality (Kruskal-Wallis test: fourth visit: $H_{14,13,12,13}=19.346$, $P<0.001$; fifth visit: $H_{14,13,12,13}=18.887$, $P<0.001$; Fig. 4b). Differences in feeding events (fourth visit) were found between 0.59 and 2.36 $\mu\text{l}/\text{min}$ (Dunn's test: $Q_4=3.191$, $P<0.01$), between 1.18 $\mu\text{l}/\text{min}$ and ad libitum ($Q_4=2.950$, $P<0.05$), and between 2.36 $\mu\text{l}/\text{min}$ and ad libitum ($Q_4=3.603$, $P<0.01$). For the fifth visit, significant differences were found between 0.59 and 2.36 $\mu\text{l}/\text{min}$ ($Q_4=3.051$, $P<0.05$) and between 0.59 $\mu\text{l}/\text{min}$ and ad libitum ($Q_4=4.114$, $P<0.001$). Even though ants feeding ad libitum had a low rate of feeding events (fourth visit), they attempted to feed at the depleted patch very often (fifth visit; Wilcoxon paired-samples test: $T_+=1$, $T_-=-90$, $N=13$, $P<0.001$), with a rate that was significantly different and about twice as large as that observed

for the lowest flow rate. The rate of feeding attempts (fifth visit) followed a positive trend with increasing patch quality (Fig. 4b).

Finally, none of the behavioural differences indicated above could be explained by differences in body size between groups (Kruskal–Wallis test: ants in Fig. 2: $H_{10,14,14,13,12,13}=10.205$, NS; ants in Fig. 3: $H_{14,13,12,13}=5.422$, NS).

DISCUSSION

Our results indicate that ants respond quantitatively to differences in nectar flow rate, thus extending previous findings for honeybees (Núñez 1966, 1982) and wasps (Pflumm 1986). Assessment of nectar flow rates in ants is also suggested from field studies in *C. sericius* and *C. compressus*, where correlations between the number of ants and the sucrose production rate of an inflorescence, and between ant number and number of aphids on a branch, were found (Ganeshiah & Veena 1988; Veena & Ganeshiah 1991). Assessment of nectar flow rate implies that individuals may be able to measure the volume collected over the time spent in this activity, or to integrate information about both variables during the feeding event. Workers were able to assess the nectar flow rate and adjust their visit times very rapidly, within one or two visits (Fig. 3).

Whatever the underlying mechanisms involved in the assessment of nectar flow rates, the ability to measure time intervals is needed. Two phenomena underlie behavioural timing in animals: a phase sense, which refers to the ability of animals to anticipate events that recur at a fixed time of the day (at a fixed phase of the day–night cycle), and an interval sense, which refers to the ability to respond to something that comes a fixed time after an event that occurs at varying points in the day–night cycle (Gallistel 1990). Studies on temporal learning reported for honeybees (Wahl 1932) and nectar-feeding ants (Harrison & Breed 1987; Schatz et al. 1994, 1999; reviewed by Fourcassié et al. 1999), which have focused on the finding of food at a certain time of day, dealt with the phase sense. In contrast, being able to assess nectar flow rates needs measurement of time intervals independent of the time of day. The ability to measure time intervals has already been implicitly acknowledged in studies on honeybee feeding behaviour (Núñez 1966, 1982), and proposed for honeybees in the context of food unloading (Seeley 1989; Farina 2000; Wainelboim et al. 2002, 2003) but the mechanisms involved remain to be elucidated.

Our results under open-loop conditions, under which ants found a depleted patch and had to decide how long to stay on it, clearly showed that ants have quantitative expectations about the resource quality to be found upon arrival. Even though ants that collected at different flow rates always found a depleted patch on the fifth visit, the time spent at it depended on the flow rate previously experienced. This suggests that ants may use as a departure rule an estimate of time that depends on the flow rate previously experienced, that is, a foraging rule

that involves the use of experience to generate resource expectations in current food patches. The observation of an increased rate of feeding attempts at the depleted patch with increasing patch quality (Fig. 4b) indicates that ants do not simply repeat their previous feeding pattern at the depleted patch (feeding events followed by interruptions), but qualitatively respond to the patch quality experienced in the previous visit. This memory for reward is unlikely to result, for instance, from odours learned at the food patch, since the visit frequency of ants at the patch was similar in all groups. Also unlikely are differences in the internal state of the individuals assayed that may account for the observed effects, since all of them unloaded the collected nectar after feeding, and belonged to the same colony.

Assessment of nectar flow rate at a nectar source and memory for nectar flow rates would allow ants to visit nectar sources at a rate proportional to the nectar production, as observed in field studies (Pascal & Belin-Depoux 1991; Dreisig 2000), and to arrive at a patch with expectations about the resource quality to be found. If the expectations upon arrival at a patch are not fulfilled, a worker may decide to abandon the patch prematurely. Subsequent foraging experiences would update the existing expectations, thus leading to a more accurate tracking of changing resources. For instance, workers of the ants *C. sericius* and *C. compressus* are able to assess the resource quality of a patch by sampling part of it, and use this to decide to abandon or continue foraging in this patch (Ganeshiah & Veena 1988; Veena & Ganeshiah 1991). A similar phenomenon was described for bumblebees foraging on inflorescences (Pyke 1978; Hodges 1985).

In our study, *C. rufipes* workers spent longer at a depleted patch, the lower the nectar flow rate they previously experienced. What is the adaptive value of waiting when no food is forthcoming? Longer giving-up times at poorer sources may reflect the searching behaviour of ants, which often circled the source and kept on searching for additional food. Such a phenomenon has been described in the ants *P. clavata* (Breed et al. 1996a) and *Lasius niger* (Mailleux et al. 2000), for workers that found small discrete nectar volumes below their maximal loading capacity, which could be readily collected without waiting. In our study, however, the patches found by experienced foragers were depleted. We argue that longer visit times at the depleted patches after the ants experienced low nectar flows may reflect both the kind of sensory mechanisms involved in the assessment of nectar flows by ants, and how workers use this information to make foraging decisions. Assessment of nectar flow, as mentioned above, implies the evaluation of the rate of fluid collection, that is, the integration of information about the level of crop filling over the elapsed time. There are no physiological studies on the control of crop filling in ants. In honeybees, information about the level of crop filling is provided not only by stretch receptors on the crop wall, as intuitively expected, but also by receptors on the body wall, thus representing a complex integration of feedback loops that monitor body volume (Núñez 1966; Rau 1970). While this information, integrated over time, may be needed during the

initial visits at a patch to evaluate the nectar flow, individuals that have experience with predictable patches may instead rely only on an estimate of time to decide when to stop feeding, without the need for a recurrent processing of feedback information from the crop every time they arrive at a recently visited patch. Such a scenario is speculative, but it is experimentally testable, for instance by recording the responses of experienced workers provided with nectar flows that change within the feeding event. Wainelboim et al. (2002, 2003) used this approach to investigate the assessment of nectar flows and the control of trophallactic behaviour in honeybees.

If the collection of partial crop loads requires a complex integration of sensory information over time, the question arises why ant foragers do not completely fill their crops when collecting nectar provided at lower rates. Ants could simply stay longer at the source to fill their crops, but they did not, so that they apparently do not maximize their gross energy gain per trip. This apparent disadvantage of spending less time at a source is, however, associated with two potential, but not yet investigated advantages, one at the individual and the other at the colony level: (1) reducing foraging time will decrease the probability of being predated or of desiccation at the foraging site; (2) reducing foraging time at good sites would allow workers to return earlier to the colony, so that information about the discovery could be transferred earlier to nestmates. In fact, *C. rufipes* foragers are known to recruit more intensively, the higher the quality of the resource found (Jaffé & Sánchez 1984). In addition to information transfer via recruitment, information about alternative food sources exploited by nestmates could be obtained earlier, as suggested for honeybees (Núñez 1982). Since the probability of obtaining or passing on information would depend on the frequency of contacts among workers in the colony (Farina 1996), it may be adaptive to leave low-rewarding sources with partial loads to return earlier to the nest, even at the expense of a reduced performance as an individual forager (Roces & Núñez 1993; Roces & Hölldobler 1994; Roces 2002). However, the question whether the observed partial loading in *Camponotus* ants, with a concomitant reduction in visit time, contributes to increasing the rate of exchanging information at the nest, remains to be investigated.

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