Abstract The recruitment of honeybee foragers individually exploiting a low-flow rate-feeder that presented different temporal reward programs was experimentally analyzed. By capturing hive bees that landed at the feeder in a 2-h period, the arrival rate of incoming bees could be obtained. With this procedure we quantitatively analyzed the maximum number of hive bees that can be brought to the feeding station by single foragers. Test bees collected sucrose solution during 12 visits to a rate-feeder located 160 m from the hive. The constant programs offered 0.6, 1.2, or 2.4 M sugar for all 12 visits, while the variable programs delivered either 0.6, 1.2, or 0.6 M or 0.6, 2.4, or 0.6 M, with four visits for each modality. Results showed that the sucrose concentration exploited by single foragers increased the arrival rate. Moreover, there was a linear relationship within this range of sucrose concentrations that presented a slope of 1.58. Since the sugar solutions were provided at the same flow rate (5 µl/min) in all the programs, the arrival rate expressed in terms of sucrose flow rate (milligrams of sucrose/minute) shows that one additional incoming bee per hour arrived when the single forager assessed an increase in the sucrose flow rate of 0.75 mg sucrose/min at the rate-feeder. The absence of differences in the frequency of visits of the single foragers during the constant programs suggests that the differences observed in the arrival rate can mainly be explained by a more intensive display of the recruitment mechanisms performed per foraging trip instead of by their iterativeness throughout different foraging cycles. Variable reward programs showed that arrival rate is rapidly adjusted according to the reward change and is independent of its magnitude.

Keywords Apis mellifera · Honeybee · Recruitment · Foraging

Introduction

Recruitment has been defined as a type of communication that brings nest-mates to a place where work is required (Wilson 1971). Among social insects, recruitment coordinates several activities, such as nest defense, colony emigration, and food gathering (Wilson 1971). In this last case, the profitability (expressed in terms of sugar flow rate or concentration) gathered by individual honeybees at the food source affects the number of newcomer hive-mates that arrive at the source (von Frisch 1965; Núñez 1971a; Seeley 1986).

Many studies have investigated how a complex pattern such as colony-level exploitation of nectar sources emerges from the behavior of individual colony members. For instance, studies from Seeley et al. (1991) have shown how honeybees grade their rates of recruitment and abandonment of nectar sources in accordance with the concentration of the sugar solution offered in ad libitum food sources. Under these experimental conditions, bees attain maximal crop loads and remain for only brief periods at the source, and the sugar solution flow gathered is only limited by their own intake rate (Núñez 1966; Wells and Giacchino 1968). However, flowers deliver nectar at very low rates; thus, bees spend much longer times on flowers. For example, an average feeding time of 52 min was reported by Istomina-Tsvetkova (1960) when bees exploited natural nectar sources. As a consequence, bees return to the hive far less frequently than in the experimental studies that use ad libitum feeders.

Bees partially load their crops when collecting at low-nectar flows, such as those produced by flowers (Núñez 1977). Thus, rate-feeders allow experimental modifica-
tion of the flow rate of the delivered solution, simulating natural nectar flow by flowers and manipulating the intake rate below the honeybee’s maximal capacity to ingest nectar. Under these conditions, Núñez (1966, 1982) found that the crop load and the duration of the round trip of foraging bees depend on solution flow rate. He observed that for a 50% w/w sucrose solution provided at a flow rate below 10 µl/min, the crop load attained by foraging bees was not maximal. However, recruitment at these low-flow rate-feeders could also be observed (Núñez 1971a). Contrary to the situation observed with ad libitum feeders, when a foraging bee recruits hive-mates at a rate-feeder, the flow rate obtained by each forager per feeding visit decreases, leading to a reduction in the crop load carried to the hive. For instance, with an increasing number of foragers, the flow of solution received per bee diminishes. This fact acts as a negative feedback mechanism, stabilizing the number of bees that exploit a floral patch (Núñez 1973).

At the colony level, the number of bees exploiting a floral patch would thus be the output of a complex system. It may depend on the level of food reserves in the hive, the nectar influx, the size and characteristics of the bee population, the time of year and time of day, the weather conditions, and so on (Seeley 1995). At the individual level, the number of bees that exploit a flower patch depends on the information exchange in the hive about energetic aspects of the food source and the flow of solution received per bee once the recruitment activity has begun. From the interaction of the different communication channels involved in nectar-foraging activity, a graded recruitment as a function of the reward rate at the food source would be expected (Núñez 1971a).

With the aim of understanding the honeybee recruitment system under conditions of low-flow-rate delivery, we focused this study on single trained foragers. As a result, our study examined the relationship between single foragers and the incoming bees that arrive at a known food source. Bees were trained to a feeding station that offered sucrose solution at a low flow rate. Experiments were conducted during a period in which natural nectar sources were scarce to minimize the effect of different environmental variables. In this way, it was possible to analyze quantitatively the maximum number of hive bees that can be recruited and/or reactivated by a single forager that forages at a feeding station with variable profitability. The use of low flow rates of sugar solution and the absence of intraspecific competition at the feeding station facilitated the study of recruitment rate in relation to flow of energy carried to the colony by a single forager.

Previous results showed that sudden changes in food source profitability affect the display of recruitment mechanisms: the number of waggle runs, the trophallactic behavior, and the quantity of scent marks released by the Nasonov gland (Free 1968; Núñez 1971a; Raveret-Ritcher and Waddington 1993; De Marco and Farina 2001; Fernández and Farina 2001). Accordingly, we expected that changes in the current profitability offered to a single forager would lead to instantaneous differences in the recruitment rate. This was analyzed by means of the presentation of variable reward programs.

On the other hand, it is well known that the reward expectation that bees acquire throughout successive foraging visits may affect the estimation of food source profitability (Greggers and Menzel 1993). For example, bees elicit different dance and trophallactic behaviors according to their previous foraging experience at the feeding site (Raveret-Ritcher and Waddington 1993; De Marco and Farina 2001; Wainselboim et al., in press). Thus, the individual recruitment rate may be modified according not only to the current food source profitability but also to the previous experience of the foraging bee. This issue was also analyzed by means of variable reward programs.

Methods

Experiments were performed at the experimental field of the University of Buenos Aires (34°32’S, 58°26’W) from March to April 1997 when competition with natural nectar sources was reduced. A colony of approximately 2,000 European bees (hybrid descents of Apis mellifera ligustica bees) was located in a single-frame observation hive (see von Frisch 1965).

Apparatus

The experimental food source was located 160 m from the hive in an open and shady place. It consisted of an artificial feeder delivering sucrose solution scented with almond oil (80 µl/l). Scented solutions were used during both training and assay. They were delivered at a constant rate of 5 µl/min through the center of a 40-mm-diameter disk of yellow paper. A synchromotor activated a pumping system, with a syringe delivering the sugar solution through a cannula (Núñez 1971b). The syringe containing the sucrose solution could be replaced when the bee was in the hive. In this way, the same “artificial flower” was able to offer different sucrose solutions (0.6, 1.2, or 2.4 M). Because these were provided at the same flow rate (5 µl/min), different amounts of sugar were delivered per unit time (1, 2, and 4 mg/min). The feeder was switched on when the bee arrived at the feeding area, and off when it left for the hive. Therefore, sucrose solution did not accumulate between foraging visits.

Procedure

Approximately 20–25 bees were individually labeled with a colored tag on the thorax and trained to collect sucrose solution from the artificial feeder. Each day, the apparatus switched on automatically at 0700 hours. Observations began at 1030 hours. At that time, several bees (approximately 5) were foraging at the feeder (i.e., the employed foragers) while the rest of the labeled foragers stayed in the hive (i.e., the unemployed foragers). During the experiment only one labeled bee was selected for observations (i.e., the test bee) while the other employed foragers were caged. The selected test bee was allowed to visit the feeder freely and was recorded during 12 successive visits. During the observation period, we recorded the number of hive bees (labeled or not) that arrived and landed at the feeding platform. We defined these bees as “in-coming bees.” We avoid the term “recruits” because scouts and recruits search for food sources unknown to them and inspector and reactivated foragers go to food sources they have visited previously (Biesmeijer and de Vries 2001). The term “incoming bees” includes all these kinds of bees. We captured all the incoming bees...