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SHORT COMMUNICATION

Selective recruitment for pollen and nectar sources in honeybees

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ABSTRACT

Honeybees (*Apis mellifera*) use cues and signals to recruit nestmates to profitable food sources. Here, we investigated whether the type of resource advertised within the colony (i.e. pollen or nectar) correlates with the choices of recruits at the feeding site. We observed that pollen recruits preferred to collect pollen once arrived for the first time at the feeding site, while nectar recruits preferred to forage sucrose solutions. Bees recruited by foragers carrying both resources showed intermediate preferences. Studying the plasticity of this response, we found that nectar recruits have a low probability of switching to pollen collection, yet pollen recruits were likely to switch to sucrose solution of increasing concentrations. Our results show that cues associated with the advertised resource type correlate with the foraging tendency of recruits for pollen and sucrose solution, a feature that would guarantee an efficient resource collection.

KEY WORDS: Foraging preferences, *Apis mellifera*, Task specialisation, Task switching

INTRODUCTION

Recruitment to food sources is a major feature of the foraging strategy of many social insects (von Frisch, 1967; Hölldobler and Wilson, 1990; Maschwitz and Steghaus-Kovac, 1991; Nieh, 2004; Dornhaus and Chittka, 2004). Such information gained from conspecifics enable more efficient foraging (von Frisch, 1967; Núñez, 1970; Seeley and Visscher, 1988). The honeybee uses a variety of mechanisms to recruit nestmates. Its most sophisticated recruitment behavior is the waggle dance, a multicomponent signal that encodes the distance and direction to the target in figure-eight runs (von Frisch, 1967; Gould et al., 1970; Riley et al., 2005; Seeley, 1995; Grüter and Farina, 2009) as well as the recruiter's subjective evaluation of the resource (Seeley et al., 1991; 2000). In addition, food-source-related cues are very important for recruitment. For example, incoming foragers could incidentally transfer tastes and odors diluted in the collected nectar (Wenner and Wells, 1990; Farina et al., 2005, 2007; Gil and De Marco, 2005; Grüter et al., 2006; Martinez and Farina, 2008) while they share the liquid food through mouth-to-mouth contact (trophallaxis). Similarly, they could inadvertently convey the source smell absorbed in their bodies by simple body contact (Balbuena et al., 2012).

In the honeybee, an efficient collection of food sources, mainly protein and carbohydrates, is achieved by the division of labor among pollen and nectar foragers. The regulation of this division of labor is still not well understood, but there is evidence that pollen and nectar foragers differ in how they perceive rewards: pollen foragers are more sensitivity to gustatory (Page et al., 1995; 1998; Pankiw and Page, 2000; Arenas and Farina, 2012; Nery et al., 2020) and olfactory stimuli (Scheiner et al., 2004; Latshaw and Smith, 2005) than nectar foragers. So far, whether and to what extent the type of resource advertised (i.e. pollen or nectar) correlates with the foraging preferences of recruits for resource type remains unknown. Díaz et al. (2007) observed that contacts of bees that followed dancers loaded with pollen were more focused on the hind legs than contacts of bees that followed dancers carrying nectar (positioned closer to the head), a distribution that suggests that followers discriminate the resource type during recruitment. We hypothesized that the transfer of odors, tastes and/or textures from the pollen carried by the incoming foragers bias recruitment towards pollen sources, while nectar odors and/or taste bias recruitment toward nectar sources. This selectivity of recruitment could be adaptive by guiding bees to sources according to their foraging tendency, thus contributing to a more efficient resource collection.

Here, we tested whether the type of resource advertised inside the hive (i.e. pollen or nectar) correlates with recruits' foraging preferences at the foraging site. To this end, we quantified the individual preferences for collecting pollen or sucrose solution of bees recruited by foragers that returned to the hive carrying sucrose solution, pollen or both. Second, we analyzed whether pollen and nectar recruits were sensitive to modifying their responses according to the foraging scenario they faced when first arriving at the foraging station. Just as foragers switch from nectar to pollen (and vice versa) in response to the decreasing or increasing profitability of pollen versus nectar sources (Arenas and Kohlmaier, 2019), we evaluated the extent to which the decisions of pollen and nectar recruits change or not when, in addition to the resource that led to recruitment, the bees were offered the alternative resource of low, intermediate or high quality.

MATERIALS AND METHODS

Study site and animals

Experiments were carried out during summer 2018 and 2019 in the Experimental Field of the Faculty of Exact and Natural Sciences of the University of Buenos Aires (34°32°S, 58°26°W). Free flying worker bees from colonies of European honeybees *Apis mellifera* Linnaeus 1758 from our apiary were used for the experiments. All experiments complied with the animal care guidelines of the National Institutes of Health (1985) and the current laws of Argentina.

Experiment 1: Recruitment selectivity according to the type of resource advertised

To test the selectivity of recruitment, we quantified the individual preferences for collecting pollen or sucrose solution of bees recruited by foraging nestmates that returned to the hive carrying sucrose solution (sucrose) or pollen (pollen). To deepen on the effect of resource cues on recruitment selectivity, we included two

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additional series with foragers that returned to the colony with cues of both resource types: foragers that, while they were collecting sucrose solution, were experimentally sprinkled with crushed pollen on their bodies (sucrose>pollen), and pollen foragers that were induced to ingest a drop of 40% w/w unscented sucrose solution (c.a. 7 µl) (pollen>sucrose) after touching their antennae with the same solution (Kuwabara, 1957). Pollen foragers were fed the sucrose solution shortly before they finished collecting pollen. The timing was estimated based on the size of the pollen loads packed in the corbiculae.

To this end, we individually trained foragers from three different two-frame observation hives to collect either sucrose solution or pollen at a mixed feeder located 80 m from the hives. At the beginning (training phase), the mixed feeder offered either pollen or sucrose solution, so that bees could be unambiguously trained to collect only one of the two resources. For the pollen treatment, crushed pollen (1 g of bee-collected multi-floral) was presented attached to the bristles of a pipe cleaner rolled on 10 ml plastic tube. For the sucrose treatment, the tube contained sucrose solution (8 ml, 15% w/w), which the bees accessed through a small opening on its base. To avoid interactions among bees, they were trained one at a time. Trained foragers were marked with acrylic paints of different colors to identify them at the feeder. If any bee other than the marked forager reached the station during training, it was captured and killed. Marked foragers were also followed into the hives (Fig. 1A) to check that they did interact with their colony mates by means of trophallaxis, dances or body contact. Because interactions were not quantified, we were not able to determine the contribution of each of them to the recruitment, yet we can confirm that all trained recruits displayed dances.

During the testing phase, the mixed feeder offered both pollen and sucrose solution simultaneously. Then, we quantified first foraging choices of any arriving bees according to the resource type collected and incorporated into the hive by the trained forager:

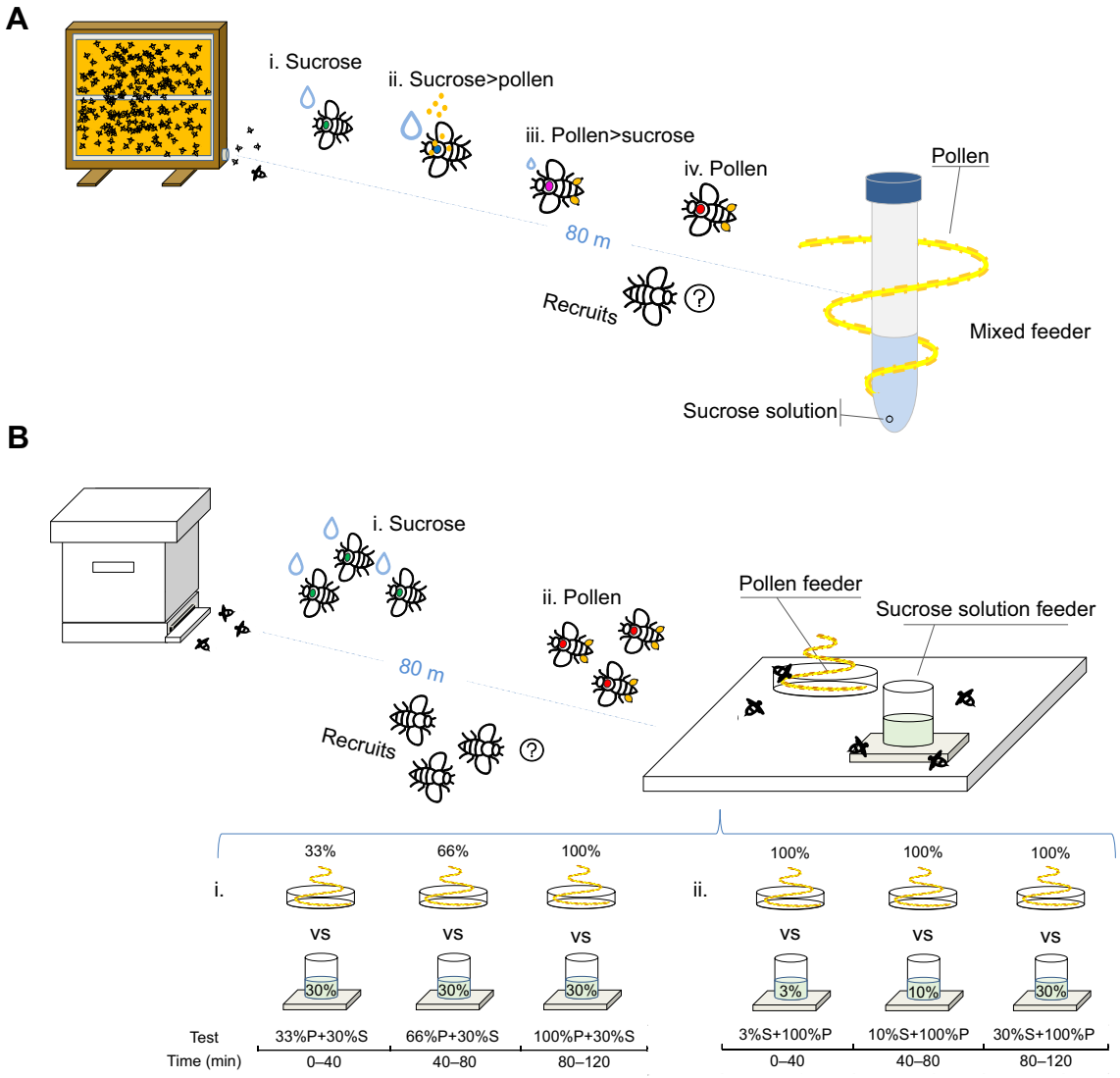

Fig. 1. Schematic description of the experimental procedures. (A) Experiment 1. Foragers were individually trained to visit the mixed feeder and manipulated (if necessary) to obtain recruiters carrying: (i) sucrose, (ii) sucrose>pollen, (iii) pollen>sucrose and (iv) pollen. Foraging preferences of recruits were quantified according to the type of resource advertised inside the hive. (B) Experiment 2. Foragers were trained in groups to visit (i) a feeder offering sucrose solution or (ii) a Petri dish offering pure pollen. In the meantime, the first choice of recruits was evaluated in three tests in which the relative quality of the resources (P, pollen; S, sucrose) changed (for the sucrose series: 33%P versus 30%S; 66%P versus 30%S and 100%P versus 30%S; and for the pollen series: 3%S versus 100%P; 10%S versus 100%P; 30%S versus 100%P). Experiments 1 and 2 were repeated many times with different bees.

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sucrose, pollen, sucrose>pollen or pollen>sucrose (Fig. 1A). We considered that arriving bees preferred to collect pollen if they landed on the pipe cleaner, chewed the pollen and loaded it into the corbicules; or that they preferred to collect 'nectar' if they managed to find the opening of the tube and ingested the sucrose solution. The reason we asked these bees to inspect the feeder to find the sucrose solution was to prevent incidental contacts with the energy-rich food that may have altered their perception, and hence their true decision. To what extent the access to the sucrose solution in the mixed feeder influenced the selectivity of the recruitment was evaluated in experiment 2.

Once the preference of the arriving bee was revealed, we marked it with paint and tracked it into the hive to confirm that it belonged to the same colony as the recruiter. Only those bees that we identified as nestmates of the focal recruiters were considered for the analysis. On its second visit to the feeder, the recruit was captured to avoid interference with the following observations. Although the mixed feeder offered both resources at testing, we observed that all recruiters continued foraging on their trained items for the whole period (~2 h), except for the pollen>sucrose treatment, where foragers were prone to switch to sucrose solution after the third or fourth time they received the solution. If any recruiter switched, the event was interrupted, and the bee was excluded.

Trained foragers were allowed to visit and recruit nestmates to the mixed feeder for 3 h in what we called the recruitment event. Thus, from a recruitment event (experimental unit) we obtained the number of bees and the foraging preferences of all recruited bees by one trained forager during the 3-h period. The trained foragers participated in only one recruitment event and recruited on average 10.9±5.7 bees (mean±s.d. of 296 individuals, of which 95 were recruited by pollen and 201 by nectar foragers). Whilst pollen foragers recruited 7.9±5.8 recruits per recruiter, nectar foragers recruited 13.4±4.4 recruits. From the preferences of bees recruited in a single recruitment event, we calculated the recruitment index (RI), defined as the ratio of recruits choosing the sucrose solution over the total number of recruits (those choosing the sucrose solution+those choosing pollen). RIs were compared among treatments (sucrose, sucrose>pollen, pollen>sucrose and pollen) as fixed effects by means of a generalized linear model (GLM) following a binomial error distribution in with R v.3.3.3 (https://www.r-project.org/) via RStudio (Rstudio Inc. 2019). Because treatments were replicated in the three hives, we include 'colony' as a random factor.

Experiment 2: Effect of the relative profitability of the pollen versus sugar source on recruit switching probability

Here, we evaluated whether and to what extent foragers recruited to a certain resource type modified their response based on the local assessment of the relative quality of the sources at the target. To compare recruitment selectivity among different rewarding conditions, we measured the choices of recruits along three successive tests during which the profitability of the non-advertised source increased while the profitability of the advertised source remained constant.

Foragers from three different hives were trained to collect either sucrose solution or pollen. Sucrose solution and pollen were offered in different *ad libitum* feeders (a 70 ml jar with solution inverted on a plate and a 20 cm pipe cleaner formed as a spiral on a 9 cm diameter Petri dish) located 15 cm apart from each other and 80 m from the hives (Fig. 1B). Unlike experiment 1, foragers were not trained alone but in groups of several bees (nine on average) all from the same colony. We allowed several recruiters to forage together to ensure a group of recruits large enough to be used in all three tests. The foragers of one hive were trained independently from the foragers of the other hives. Recruiters within a group were color-marked and monitored at the foraging station and at the entrance of the hive but not inside, as conventional 10-frame hives were used.

In the pollen series, decisions of recruits were quantified by offering the pollen feeder that induced recruitment (5 g of 100% crushed bee pollen) and a feeder that, during the first 40 min, offered a 3% sucrose solution (test 3%S versus 100%P, where S is sucrose solution and P is pollen), but then (between the 40 and 80 min) offered 10% (test 10%S versus 100%P) and finally (80–120 min) 30% sucrose solution (test 30%S versus 100%P). In the sucrose series, choices of nectar recruits were tested when the sucrose solution feeder remained unaltered (30% w/w) but the profitability of the pollen feeder steadily improved from an initial proportion of 33% pollen in inert cellulose (test 33%P versus 30%S) to 66% pollen (test 66%P versus 30%S) and finishing with the supply of pure pollen (test 100%P versus 30%S). Recruits were always captured immediately after they revealed their foraging preferences. It is worth mentioning that during the experiment (training and testing phase), no bees that had visited the feeders other than the recruiters could leave the station. In preliminary experiments, we measured the probability of spontaneous visits of honeybees to our feeding station and found that at times when the feeders were not frequented by trained foragers, there were no visits. We then reasoned that all, or at least most, of the bees arriving at the station during the experiment were the consequence of recruitment. As in experiment 1, if any recruiter changed the type of resource collected during testing phase, it was captured and excluded from the experiment.

The effect of changing rewarding conditions on recruit switching probability was analyzed by comparing RIs among tests within the pollen and sucrose solution series by means of GLMM (McCullagh et al., 1989; Crawley, 2007) with a binomial distribution (https://CRAN.R-project.org/package=lme4). The test was considered as a fixed effect and recruitment event as a random effect, specified via the model formula. Because only one hive participated in each recruitment event, we assume that most of the variation caused by colony differences was already explained by the random effect recruitment event. We checked for overdispersion (Zuur et al., 2009). We used the glmer function of the lme4 package (Length, 2016) that uses Wald Z-tests to approximate P-values for GLMMs.

RESULTS AND DISCUSSION

We found that honeybee recruitment is selective for the type of resource advertised, as food-source-related cues introduced into the hive correlated with the foraging choices of recruits for pollen or sucrose solution at the foraging site. Then, pollen foragers were prone to recruit bees with predisposition to collect pollen while 'nectar' recruits preferred foraging on the sucrose solution (experiment 1, sucrose versus pollen: T=7.879; P<0.0001; Fig. 2; Table S1). Preferences of nectar recruits also differed from those of bees recruited by pollen foragers carrying a small volume of sucrose solution (experiment 1, sucrose versus pollen>sucrose: T=5.432; P=0.0001) and from those of nectar recruits with pollen particles (experiment 1, sucrose versus sucrose>pollen: T=3.771, P=0.0054; Fig. 2). Similarly, responses of pollen recruits differed from those of individuals recruited by nectar foragers with pollen particles (experiment 1, pollen versus sucrose>pollen: T=6.222; P<0.0001; Fig. 2). Interestingly, groups recruited by bees carrying both resources (sucrose>pollen and pollen>sucrose) also differed in their choices (experiment 1, T=3.362; P=0.0139; Fig. 2), suggesting

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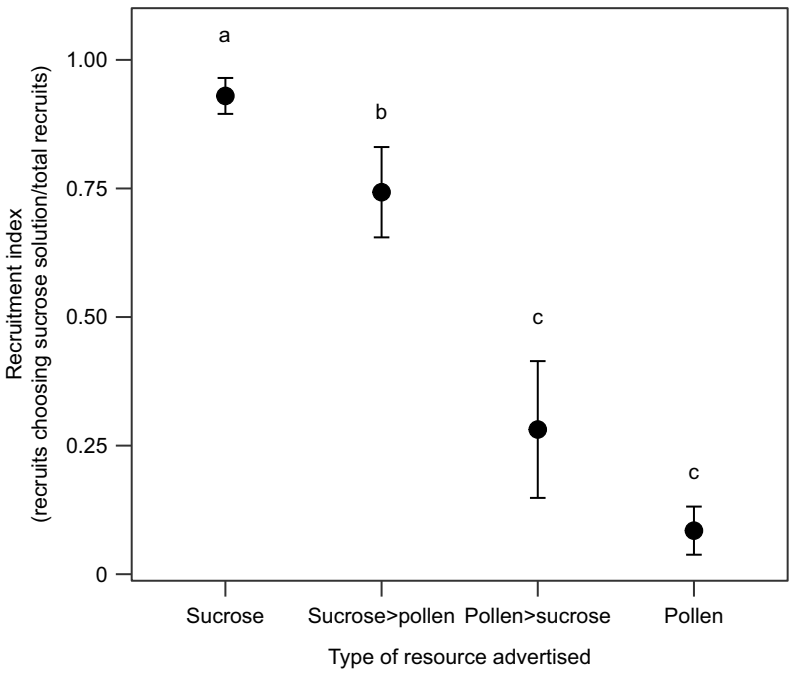

Fig. 2. Recruitment index for honeybees recruited by foragers carrying the different resources: sucrose solution (i.e. nectar foragers), sucrose>pollen (i.e. nectar foragers with pollen particles), pollen>sucrose (i.e. pollen foragers that ingested sucrose solution) or pollen (i.e. pollen foragers). Black circles indicate the mean values and bars show the 95% confidence intervals from 7, 7, 3 and 10 recruitment events. Different letters indicate statistically significant differences among resources advertised during recruitment (P<0.05).

that the presence of pollen or nectar traces introduced by the incoming forager are perceived by recruits, affecting their recruitment.

For recruitment selectivity to occur, we assume that information advertised into the colony (e.g. through the display of dances) was not all equally attended by the potential recruits. In line with the differences in sensitivity to the reward (Page et al., 1995, 1998; Scheiner et al., 2004; Nery et al., 2020), our results suggest that pollen information is mainly gained by highly sensitive recruits that become attracted to the cues released by pollen (Arenas and Farina, 2014). On the contrary, information about the sucrose solution might be gained by less sensitive recruits that, restricted to perceive pollen-related cues as reinforcement (Nery et al., 2020), might require strong sensory inputs, such as the taste of concentrated sugar solutions, to respond. Then, differences in response thresholds might be functional in the recruitment context, enabling the transference of nectar- and pollen-related cues among recruiters and recruits with similar foraging tendencies.

Furthermore, some interactions are expected to be more efficient than others in transferring cues associated with pollen or nectar. Trophallaxis, the mouth-to-mouth exchange of liquid food among honeybee nestmates (Farina, 1996), seems to be highly suitable for the characterization of a nectar source by providing unequivocal information on nectar quality and source profitability (Farina, 1996; Farina and Núñez, 1991). In contrast, and because in many cases pollen foragers return with no nectar, we expect body

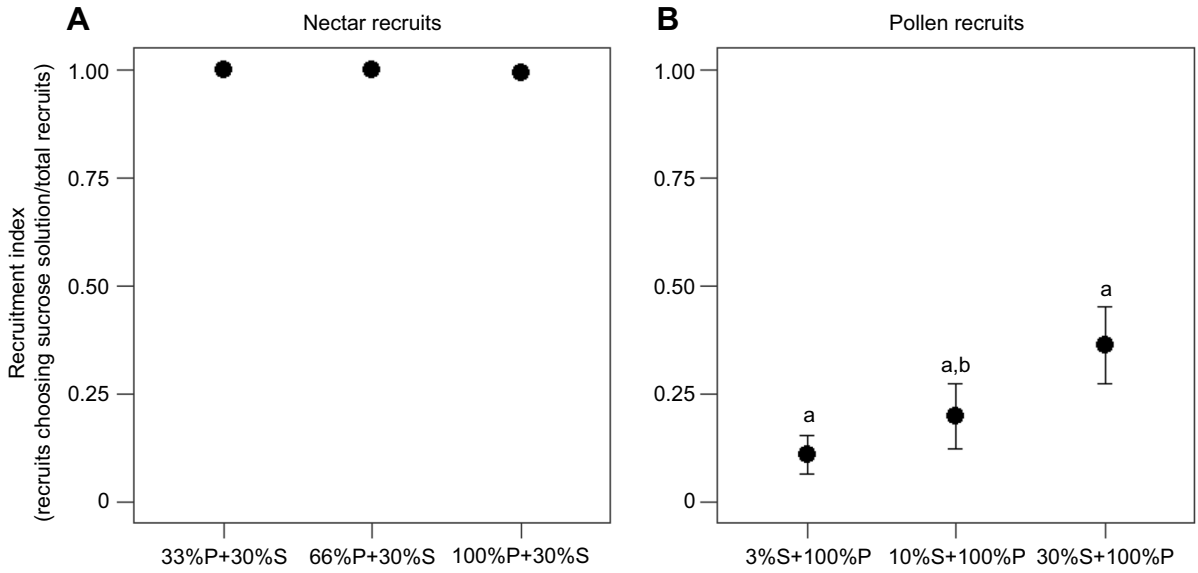

Fig. 3. Recruitment index for bees recruited by foragers carrying sucrose solution or pollen during three tests, in which the relative quality (% w/w concentration) of the sources changed. (A) Sucrose solution. (B) Pollen. Black circles indicate the mean values and bars show the 95% confidence intervals from six pollen and six nectar recruitment events. Different letters in B indicate statistically significant differences among resources advertised during recruitment (P<0.05).

contact, especially with pollen-loaded corbicula of the incoming bee, to be relevant in recruitment to pollen sources (Díaz et al., 2007).

In addition, body and corbicula contact might mediate learning of pollen-related cues, as we recently observed that contact of the antennae with pollen could act as an appetite reinforcement for pollen foragers, but not for nectar foragers (Nery et al., 2020). Thus, although recruits with low chemosensory response thresholds might learn the features of pollen sources in the complete absence of food intake, recruits with higher response thresholds might require inputs such as taste or ingestion of small samples of sugar to learn cues (Farina et al., 2005; 2007). In experiment 1, we confirmed that all trained recruiters displayed dances. Acquisition of both pollen- and nectar-related cues might be greatly improved by the display of dances that facilitate the transmission and propagation of the incidental cues among the bees that congregate around the dancer (Grüter and Farina, 2009).

Despite the high selectivity of recruitment, the decision about which resource to collect was influenced by the relative profitability of the available resources. Results of experiment 2 indicate that choices of pollen recruits, but not nectar recruits, were affected by the relative quality of the advertised versus the non-advertised feeder (χ^2=9.7684, d.f.=2, P=0.0075; Fig. 3). In the pollen series, preference for the pollen source was high (i.e. low RIs) when the foraging station offered a poor-quality sucrose solution (3%), but decreased as the concentration of the solution rose to 30% (experiment 2, 3%S+100%P versus 30%S+100%P: Z=3.074, P=0.006; Fig. 3B, Table S3). Then, most pollen recruits focused on collecting pollen if the sucrose solution was of low quality or difficult to access, such as in experiment 1 (bees collected 30% sucrose solution through a small opening), but turned to the sucrose solution when it was concentrated enough and/or easily accessible. This suggests that recruits could perceive and integrate information of both resource types to get the most profit out of their foraging visit (Arenas and Kohlmaier, 2019). Thus, while collecting pollen, recruits might sample and/or smell the sucrose solution to assess whether it is worth switching. Even with response thresholds being primarily responsible for driving the choices of recruits, we cannot rule out that to some extent, the presence of conspecifics at the source may have attracted recruits, e.g. by means of local enhancement (D'Adamo et al., 2000; Chittka and Leadbeater, 2005; Kawaguchi et al., 2006; Avarguès-Weber and Chittka, 2014). On the contrary, we found that honeybees have a very low probability of switching to pollen collection after being recruited to a sugar source (Fig. 3A). In all cases, bees preferred to visit the sucrose solution irrespective of the quality of the pollen source (because the RIs varied very little, a statistical analysis could not be performed; Table S2). This lack of plasticity exhibited by some bees allows us to speculate that in a scenario where bee recruitment is not selective, recruited individuals would leave the targeted source without exploiting it. On the contrary, the observed selectivity of the honeybee recruitment towards pollen or sucrose solution could be adaptive by guiding bees to sources according to their foraging predisposition, thus improving the chances of successfully completing their foraging bout.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: A.A.; Methodology: A.A., R.L.; Formal analysis: A.A., R.L.; Investigation: A.A., R.L., W.F.; Resources: A.A., W.F.; Writing - original draft: A.A.; Supervision: A.A.; Project administration: A.A.; Funding acquisition: A.A.

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