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ORIGINAL PAPER

What makes a honeybee scout?

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Abstract A honeybee colony needs to divide its workforce so that each of the many tasks it performs has an appropriate number of workers assigned to it. This task allocation system needs to be flexible enough to allow the colony to quickly adapt to an ever-changing environment. In this study, we examined possible mechanisms by which a honeybee colony regulates the division of labor between scouts (foragers that search for new food sources without having been guided to them) and recruits (foragers that were guided via recruitment dances toward food sources). Specifically, we examined the roles that the availability of recruitment dances and worker genotype has in the colony-level regulation of the number of workers engaged in scouting. Our approach was threefold. We first developed a mathematical model to demonstrate that the decision to become a scout or a recruit could be regulated by whether a potential forager can find a recruitment dance within a certain time period. We then tested this model by investigating the effect of dance availability on the regulation of scouts in the field. Lastly, we investigated if the probability of being a scout has a genetic basis. Our field data supported the hypothesis that scouts are those foragers that have failed to locate a recruitment dance as predicted by our model, but we found no effect of genotype on the propensity of foragers to become scouts.

Keywords *Apis* · Division of labor · Foraging · Honeybees · Scouting

Introduction

The food sources exploited by social insects are often ephemeral, widely scattered, or both. One benefit of social life is that nest mates can direct each other to known food sources and can recruit additional foragers to patches of such exceptional profitability that an individual acting alone could not fully exploit the resource. Although the recruitment mechanisms differ greatly among species, an insect colony's global foraging behavior results from the decisions made by individual foragers and their interactions with colony members and the foraging environment. The outcome is a complex colony-level foraging pattern typical of insect societies (e.g., Seeley et al. 1991; Biesmeijer and Ermers 1999; Brown and Gordon 2000; Beekman et al. 2001; Sumpter and Beekman 2003).

Honeybees have a unique way of directing nest mates to food sources, the waggle dance (von Frisch 1967). Waggle dances are performed by individual foragers on returning to the nest and convey information about the direction and distance of the forage site visited by the dancing bee. The information encoded in the symbolic language is then used by unemployed foragers to locate the forage site. Because a returning forager will only perform a recruitment dance when she was foraging at a highly profitable food source, the honeybee dance language helps the colony to focus its foraging effort on the most profitable sites known to the colony (Seeley et al. 1991). However, a colony also needs a

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mechanism to explore the environment and collect information on alternative and possibly superior forage sites to those which it currently has knowledge of.

Little is known about how a honeybee colony regulates the number of workers involved in scouting: the exploration of the surroundings for new sites. Even though the early work of von Frisch (1923, 1967), later followed by Seeley (summarized in Seeley 1995), on the dance language of the honeybee has revolutionized our understanding of how a colony recruits a sufficient number of individuals to each site, the division of labor between scouts and those that are guided to known sites by recruitment dances (recruits) has barely been studied (Oettingen-Spielberg 1949; Lindauer 1952; Seeley 1983). A honeybee colony utilizes these different individuals (scouts and recruits) to obtain a continuous flow of current information regarding their surroundings and the available forage.

Before 1923, a distinction was made between individual social insects that search for food and those that collect the food. Searching individuals were referred to as “searchers” while the collecting individuals were referred to as “collectors” (summarized in Biesmeijer and Vries de 2001). von Frisch (1923) also recognized this difference in behavior but suggested that these were not different classes of individuals but rather different tasks performed by the same class of individuals. Von Frisch later termed workers engaged in foraging as “primary” and “secondary” searchers. Primary searchers were defined as those individuals that search for food independently and secondary searchers were defined as those individuals that search for food using the information obtained from nest mates.

Dreller (1998) suggested that the propensity of a forager to scout has a strong genetic basis such that some subfamilies-workers that share the same father due to the honeybee queen mating with a large number of males (Palmer and Oldroyd 2000) —will preferentially scout rather than follow recruitment dances. Similar effects of worker genotype on the propensity of an individual to perform certain subtasks were found previously between foragers collecting pollen and those collecting nectar (Calderone and Page 1988, 1992; Dreller et al. 1995; Page et al. 1995, 1998).

Downplaying purely genetic determination, other studies have concentrated on determining how the organization of work in an insect society may determine a forager’s role (Seeley 1995; Theraulaz et al. 1998). A deeper understanding of how the propensity of individual workers to perform tasks arising from a response to differing levels of stimuli has led researchers away from looking for classes of individuals and toward studying the mechanisms that regulate task allocation and division of labor (e.g., Deneubourg et al. 1983, 1987; Seeley 1983; Pasteels et al. 1987; Fewell and Bertram 1999). In the light of such an understanding, a strict division between scout and recruit is thought to be unlikely (Biesmeijer and Vries de 2001). Rather, the role of individual foragers is thought to be the outcome of a response to differing levels of stimuli for independent or directed searching. Such a mechanism does not exclude an effect of genetics, as the response threshold of an individual may well be influenced by its genotype (see Jones et al. 2004).

An experimental observation that argues against a purely genetic basis for scouting (e.g., not based on genetic differences in response threshold but assuming a fixed genetic propensity to scout) is the negative correlation between the available forage and the proportion of foragers engaged in scouting (Seeley 1983). Thus, the regulation of the proportion of scouts is somehow controlled by the availability of recruitment dances to potential recruits, as the abundance of forage directly affects the abundance of recruitment dances. One possible regulatory mechanism could be that scouts are unemployed foragers that have failed to find a recruitment dance (Sumpter 2000). When forage availability is high, so too is the number of recruitment dances, and most potential foragers will be able to find a dance resulting in a low number of scouts. The reverse is true when forage is sparse. Hence, under this hypothesis scouts are “failed followers.” We therefore refer to this hypothesis as the failed follower mechanism.

In this study, we formalize the failed follower mechanism and investigate whether it regulates scouting in honeybee colonies. Our approach was threefold. We first developed a mathematical model to investigate in more detail whether the failed follower mechanism is a feasible mechanism by which scouting could be regulated. We then tested some of our model predictions in the field using real honeybees foraging for natural forage and under conditions where we could manipulate the availability of forage. Even if the failed follower hypothesis is true, this does not imply that there is no role of genetics in determining whether a particular subfamily scouts. Indeed, propensity to scout may still differ between subfamilies. To test the possible role of genetics we, in the final part of our study, examined whether some subfamilies were more likely to become scouts than others, using more powerful genetic markers than those used by Dreller (1998).

Materials and methods

Mathematical model

To investigate the failed follower mechanism we developed a differential equation model of how scouting could be regulated. We use the framework, and follow the notation of Sumpter and Pratt (2003). In the model, individual honeybee foragers can be in one of five behavioral states as described below.

Unemployed foragers

Unemployed foragers (*W*) are individuals who are not engaged in any task and are available to begin foraging with the right motivation. All unemployed foragers begin as novices, having no prior foraging experience. Unemployed foragers go to the dance floor with rate λ and become potential dance followers. We assume that the *D* dancing bees dance at random points on the dance floor, and on average, a potential follower searches an area, *a*, of a dance floor with total area *A*. Then the probability that the follower finds at least one dancing bee is $1-(1-a/A)^D$. Under the failed follower hypothesis we assume that those bees that do not find a dance leave the colony and become scouts, and those that do find a dance search for the advertised site.

Recruits

Recruits (*F*) are those individuals that have followed a dance and are now looking for the forage site advertised by the dance. They find a site at a rate β and become exploiting foragers. If they fail to find a site they give up foraging and become unemployed at rate θ.

Scouts

Scouts (*S*) search independently after failing to locate a recruitment dance. They find a forage site and become exploiting foragers at a rate $\alpha<\beta$. Likewise, if they fail to find a site they give up foraging and become unemployed at rate θ.

Exploiting foragers

Exploiting foragers (*E*) collect food at their visited sites regardless of whether the site was advertised or not. They switch to dancing with rate ρ, proportional to the quality of the available nectar, and retire from foraging with rate σ, inversely proportional to the quality of nectar. In the model, the time during which a bee is an exploiting forager includes all the time the bee is outside the hive and time inside the hive but is unloading nectar or resting (i.e., not dancing).

Dancers

Dancers (*D*) dance and then return to exploiting at a rate δ, inversely proportional to the quality of nectar.

These assumptions give rise to the following set of differential equations for unemployed foragers, recruits, scouts, exploiting foragers, and dancers.

$$\frac{\mathrm{dW}}{\mathrm{dt}}=\sigma E+\theta(S+F)-\lambda W$$
$$\frac{\mathrm{dF}}{\mathrm{dt}}=\lambda\left(1-(1-a/A)^D\right)W-\theta F-\beta F$$
$$\frac{\mathrm{dS}}{\mathrm{dt}}=\lambda(1-a/A)^D W-\theta S-\alpha S$$
$$\frac{\mathrm{dE}}{\mathrm{dt}}=\beta F+\alpha S-\sigma E-\rho E+\delta D$$
$$\frac{\mathrm{dD}}{\mathrm{dt}}=\rho E-\delta D$$

The model is illustrated as a flow diagram in Fig. 1.

Numerical solution

We considered a population of $N=1{,}500$ honeybee foragers. Initially, we assumed that all individuals were unemployed foragers. Sumpter and Pratt (2003) and Seeley et al. (1991) provide baseline estimates for the model's parameters. We were interested in how profitability affected scouting, so we performed numerical simulations of the equations under two different foraging scenarios: "high profitability" (scenario I) and "low profitability" (scenario II). For simplicity, we do not model separate forage sites, but instead, set the parameters ρ, σ, and δ on the basis of the average quality of the available nectar and pollen (see Camazine and Sneyd 1991 for an extension of our model for different quality forager sites). Parameter values for these two different scenarios are given in Table 1. Once parameterized, the model was solved using a differential equation solver package in Matlab version 6 (Sumpter and Pratt 2003).

Field experiments

To test some of the model's predictions in the field, we investigated the individual behavior of scouts using honeybee colonies foraging under natural conditions, once in summer and once in autumn. We were particularly interested in investigating if a scout had been following a dance before leaving the colony for her scouting trip. In addition, we wanted to determine the relationship between the number of dances performed in the colony and the number of scouts. We therefore constructed colonies of which all the bees (first experiment $N=5{,}000$, second experiment $N=8{,}000$) were individually marked using a combination of paint marks and colored number plates. For a description of techniques used in bee labeling, see Seeley (1995) and Beekman et al. (2006). Once all the bees were

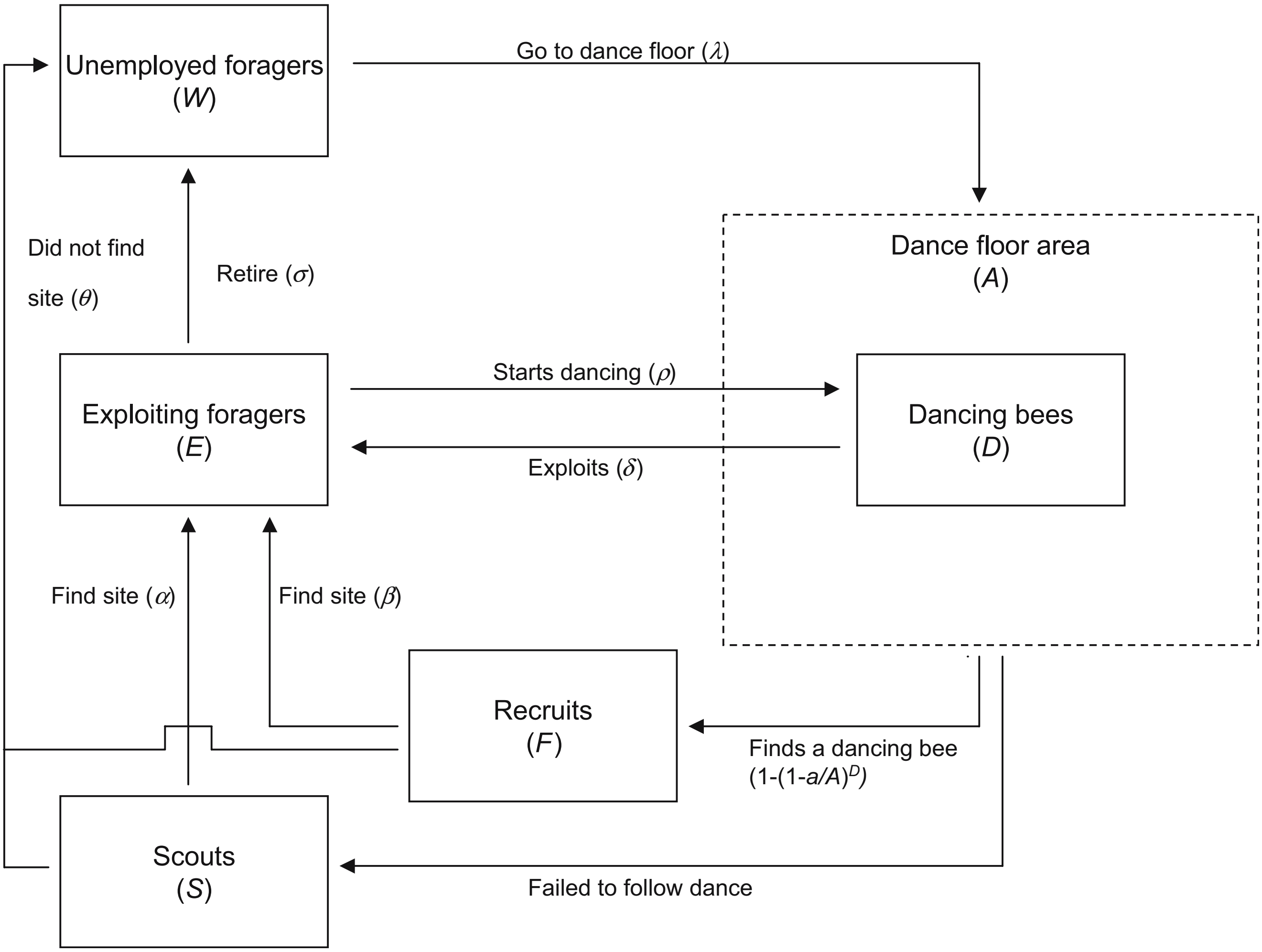


Fig. 1 Flow diagram of the model. Bees can be in five different states represented by *boxes*; *lines* represent the rate of flow of bees between states. Unemployed foragers will search an area α of the total dance floor A. The chance of locating a forage site is higher for dance followers (recruits) then it is for scouts, i.e., $\beta > \alpha$. See text for further details

labeled, the queen and the workers were transferred to a two-frame nucleus box containing two brood combs with only eggs and young larvae. After being allowed to settle on the combs overnight, the combs and adhering paint-marked and numbered bees were then placed into a two-frame observation hive. The colonies used were of standard commercial type headed by an open-mated commercial queen.

Table 1 Parameter values for scenario I (high profitability) and II (low profitability)

Parameter	Symbol	Parameter value	Source
Rate at going to dance floor (bee per minute)	λ	0.05	Seeley et al. (1991)
Proportion of dance floor searched for dance	a/A	0.1	
Rate that recruits find food (bee per minute)	β	0.0167	
Rate that scouts find food (bee per minute)	α	0.0083	
Rate that recruits/scouts fail to find a site (bee per minute)	θ	0.067	Seeley et al. (1991)
Rate that exploiting foragers switch to dancing (bee per minute)	ρ	0.2857 (scenario I) 0.1220 (scenario II)	Seeley et al. (1991)
Rate that dancers switch to exploiting (bee per minute)	δ	0.6667 (scenario I) 3.3333 (scenario II)	Seeley et al. (1991)
Rate that exploiting foragers retire (bee per minute)	σ	0.01 (scenario I) 0.04 (scenario II)	Seeley et al. (1991)

See text for details.

Experimental design

The first field experiment was conducted at the School of Biological Science's Crommelin Research Station ("Warrah") during January 2005. During this period we experienced a honey flow that made the manipulation of the number of dances difficult. We therefore conducted a second experiment in May 2006 when natural forage was much lower. This experiment took place on the Hawkesbury campus of the University of Western Sydney. We placed the observation hives inside a tent (first experiment) or a purpose-made "bee hut" (second experiment).

Our main aims were to determine if foragers that locate a forage site previously unknown to the colony had followed a dance before arriving at the new location and if the number of scouts is inversely related to the number of dances in the colony. To monitor the number of scouts we offered the colony a bait feeder and monitored the arrival of foragers. Each day we placed the bait feeder away from the entrance of the hive, either next to or behind the tent (first experiment), or to either side of the bee hut (second experiment). The assumption was that this bait feeder could only be discovered by scouts, as we did not allow any bees to dance for this feeder (see below). The bait feeder comprised of a large tray containing ground bee-collected pollen (first experiment) or a petri dish with pollen plus a feeder containing peppermint scented sugar solution (second experiment). In the first experiment we used ground pollen instead of the more commonly used sugar solution because natural forage for pollen was scarce and foragers were highly motivated to forage and scout for pollen. During the second experiment bees were equally motivated to dance and scout for pollen and nectar, so we offered them both. The bait dish was removed as soon as data collection was concluded on a particular day to prevent recruitment to it either by the experimental bees or by feral colonies.

The first experiment was conducted for 8 days and each day we continually recorded the identity of the bees that were dancing and of those that were following dances. We also recorded the time at which each dancer and dance follower was observed. Scouts caught at the bait feeder (see below) were placed in ethanol for microsatellite analysis.

The main aim of our second experiment was to manipulate the number of dances performed in the colony as this was not feasible in the first experiment. We therefore trained foragers to feed of a feeder filled with unscented sugar solution placed approximately 100 m from the colony. By offering a sugar solution of 1 M we obtained a low number of dances. When we filled the feeder with a 2.5 M sugar solution, many dances took place in the colony. We had 2 days on which dances were low (May 2 and 8) and 2 with high number of dances (May 5 and 9). Data were collected until no or only a small number of bees followed dances. Bees normally lost interest in dances around 14:00 because of the lateness of the season. On the 2 days when we had high number of dances, we only kept track of the identity of bees performing dances, as we were unable to also identify dance followers.

In both experiments, bees that arrived at the bait feeder, scouts, were caught and their identity recorded. Hence, no recruitment could take place to the bait feeder. Individuals were captured by placing an open zip-lock bag over them, forcing them to fly upward, after which the bag was inverted and sealed. Scouts caught were then cross-referenced with bees recorded dancing or following dances (where possible) on the day they were caught and the previous days.

DNA extraction and microsatellite analyses

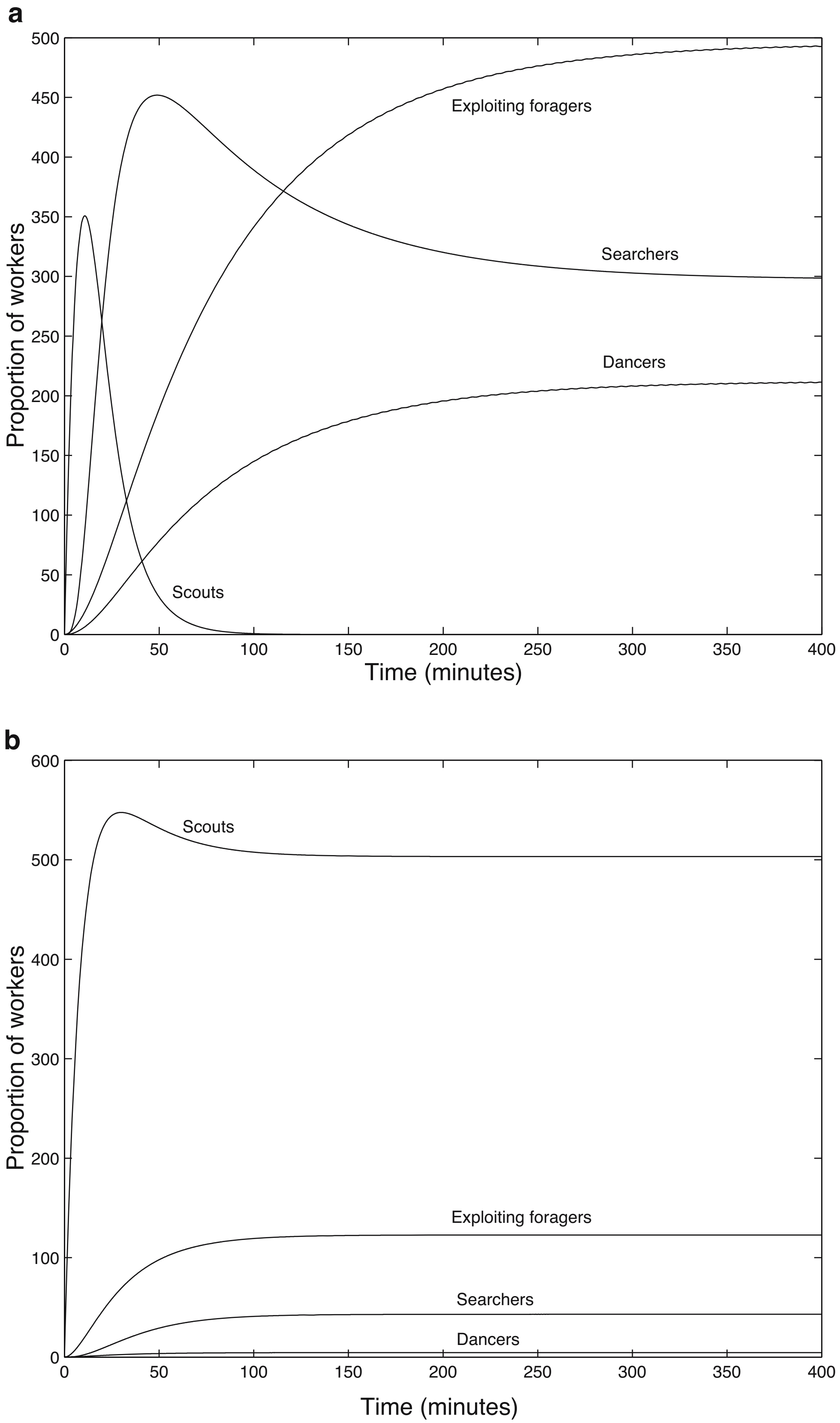
We were also interested in determining if our scouts belonged to a subset of the subfamilies present in the colony. At the conclusion of the first field experiment we killed the entire colony by placing it in a chest freezer. We then sampled 157 workers to determine the proportions of the different subfamilies present in the colony. We then determined the subfamily of the scouts caught at the bait feeder.

Chelex DNA extractions and amplifications were carried out using standard methods (Estoup et al. 1994). Three highly polymorphic microsatellite loci (A7, A29, and A107) (Estoup et al. 1994) were chosen to differentiate between patrilines in the colony. At each locus we determined the genotype of the queen heading the colony based on the distribution of alleles among workers (Oldroyd et al. 1996). Paternal alleles were then inferred by subtraction. By combining this information for all loci, each individual worker was assigned to a distinct subfamily (Oldroyd et al. 1996).

Statistical analyses

We compared the subfamily frequencies of the colony and scout samples to test whether the scouts belonged to a subset of subfamilies. This was achieved by constructing a $2\times N$ contingency table, where N is the number of subfamilies observed in each sample. Conventional contingency table analyses based on χ^2 tests or G tests would be biased due to low sample size because most of our samples contained rare subfamilies (Zar 1996). Consequently, we determined statistical significance using the computer program Monte Carlo RxC contingency table test, version 2.1 (Bill Engel, University of Wisconsin, Madison, WI, USA) to perform a modification of Fisher's exact test. This program provides an estimate of the probability of

Fig. 2 Number of scouts, recruits, and dancers through time when average forage profitable is high (**a**) and low (**b**)



observing a table with as much association as the observed table. It draws a large number (100,000) of random tables with the same marginal totals as those of the data, and compares these to the observed table.

Using the program G*Power 2.1.2 (Erdfelder et al. 1996), we determined the power at which to detect statistically significant results (Cohen 1992). This test was performed post hoc.

Results

Mathematical model

Our model produces a clear correlation between the number of scouts and the average forage profitability (Fig. 2). When the newly established area is defined to have on average high profitability (scenario I), the number of scouts increases quickly at first, but as forage sites are found this number falls and ultimately stabilizes at low levels. Under this scenario the number of exploiting foragers and dancers increases and remains high. When the profitability of the newly established area is set to have low profitability (scenario II) the number of scouts climbs to a high level and remains there, while the number of exploiting foragers and dancers remains low.

The model results can be understood by looking at how the probability with which a dance follower becomes either a recruit or a scout is affected by the number of dancing bees (Fig. 3). Under high profitability, exploiting foragers are motivated to not only forage but also to advertise their visited site, resulting in dances being readily available for unemployed foragers. Increased dancing leads in turn to decreased scouting and increased numbers of recruits. At low profitability exploiting foragers are far less motivated to advertise their visited site and, as a result, the number of available dances is low and scouting is more common than recruitment.

Field observations

Experiment 1

We caught a total of 43 individuals at the bait feeder during the time the experiment was conducted. Of these individuals, 22 were found to have never followed dances during the observations, 6 were found to have followed waggle dances on previous days but not the day of their capture, 9 were found to have followed round dances for a nearby source before being caught at the bait feeder (a round dance is a typical dance that sends recruits out in a random direction in search for a nearby site; von Frisch 1967), and 6 could not be identified as they had lost their colored number. In no case did we observe a bee that had followed a waggle dance that day arrive at the bait feeder.

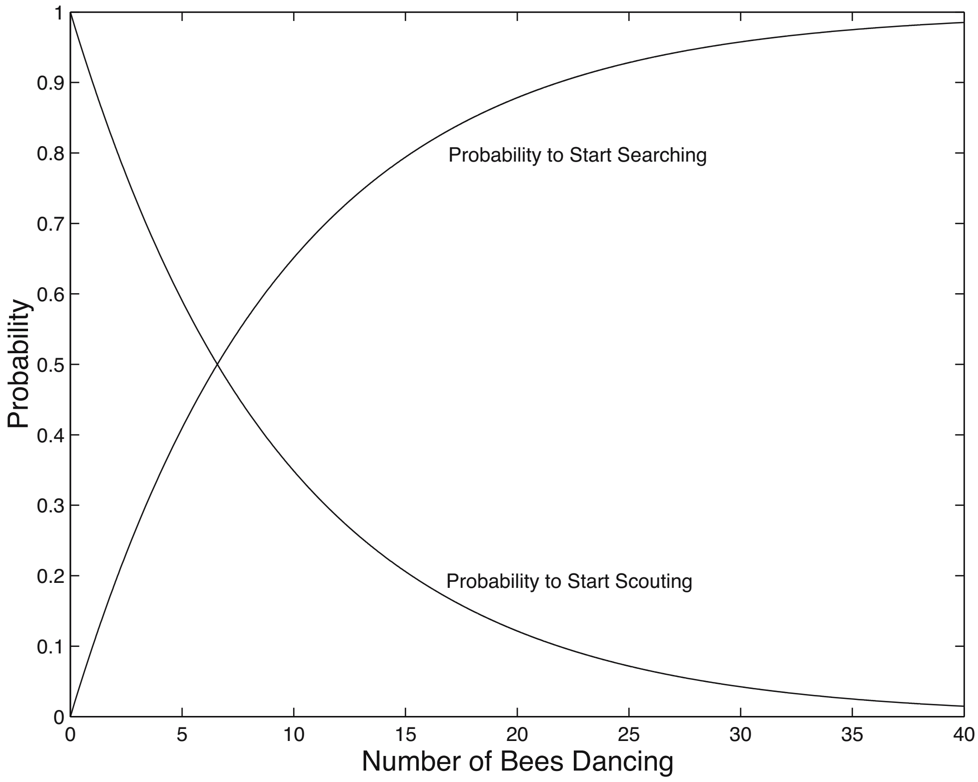


Fig. 3 Relationship between the probability of finding a dance (thus determining whether an individual becomes a scout or recruit) and the number of dancing bees. Here we plot the function $1-(1-a/A)^D$ for $a/A=1/10$ (i.e., a perspective dance follower samples one tenth of the total dance floor)

We also determined if there was a change in the availability of dances before a scout was caught at the bait feeder. We measured the number of dances available in the hive in the 45 min leading up to the capture of one or more scouts. Because a scout will spend at least 20 min searching before returning to the hive (Seeley 1983), we determined the number of dances 45, 30, and 15 min before a scout was caught at the bait feeder. Of the 18 separate occasions, when one or more scouts were found at the bait feeder, 5 of these occurred within 45 min of the start of our observations (data not shown). Of the other 13 occasions, the number of dancing bees in the 15 min before the scouts arrived at the bait feeder was lower than the average over the proceeding 30 min (Fig. 4). This result, however, was not statistically significant (binomial test, $P=0.13$).

Experiment 2

In this experiment we caught a total of 22 scouts, most of which were captured on the 2 days when the number of dances was low (Fig. 5). The number of scouts is significantly higher when the number of dances is low and vice versa, thereby supporting the failed follower hypothesis (*t* test $t=-5.06$, $df=2$, $P=0.037$).

Six scouts could not be conclusively identified because they had lost either their numbered disc or their paint color. Of the 14 scouts caught on the low dancing days that could be identified, none was seen following a dance on the day of its capture at the bait feeder. As we did not record dance followers on the high dancing days, we could not determine this for the two scouts that could be identified and that were caught on those 2 days. Five of our caught scouts were seen dancing on day(s) before being caught at the bait feeder.

Microsatellite analyses

We genotyped 26 bees caught at the bait feeder and 103 bees sampled from the colony after experiment 1 was finished. We excluded the bees that had followed round dances before being caught at the bait feeder and those of which the identity could not be determined. Not all bees identified at the bait feeder were kept in ethanol; hence, the number of genotyped bees is lower that the total number of bees caught.

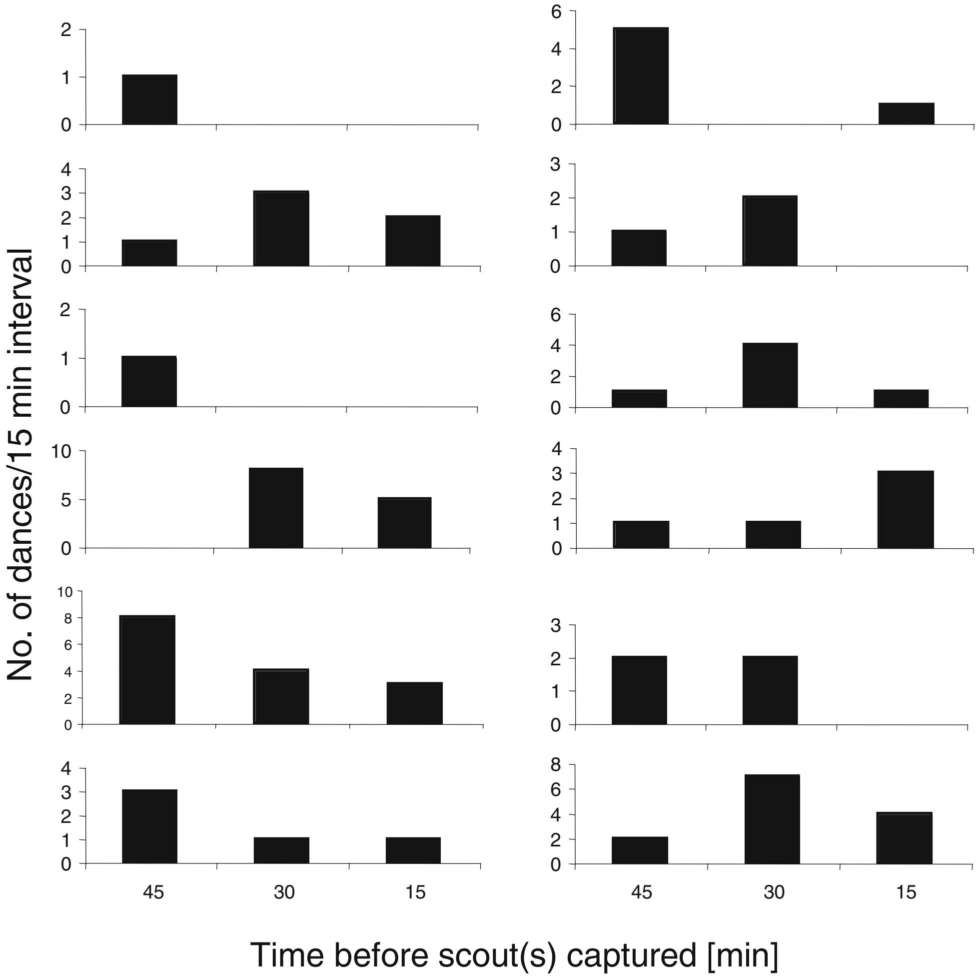


Fig. 4 Number of dances present in the hive up to 45 min before scouts being captured at the bait feeder for the 12 15-min intervals when scouts were caught. All scouts captured within a 15-min interval were lumped. Note that the *Y*-axes scales are different

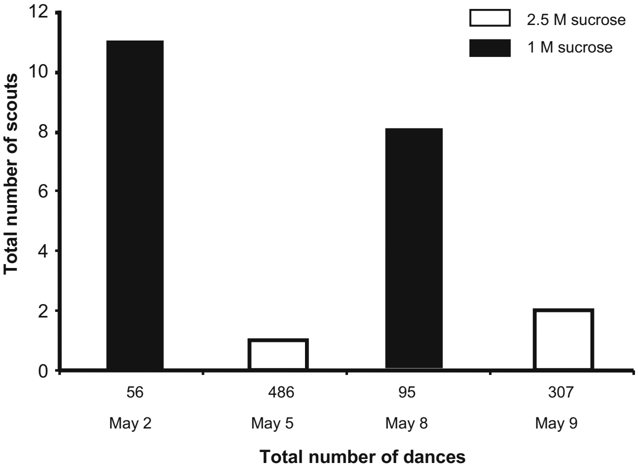


Fig. 5 Number of scouts vs the total number of dances performed in the colony in the second experiment for 2 days of low dancing (black bars) and 2 days of high dancing (white bars)

We found no significant difference in the distribution of subfamilies between the colony and scout samples (Fisher's exact test, P=0.83, Power=0.57; Fig. 6). These results suggest that, in our colony, no subfamily was more likely to scout than any other.

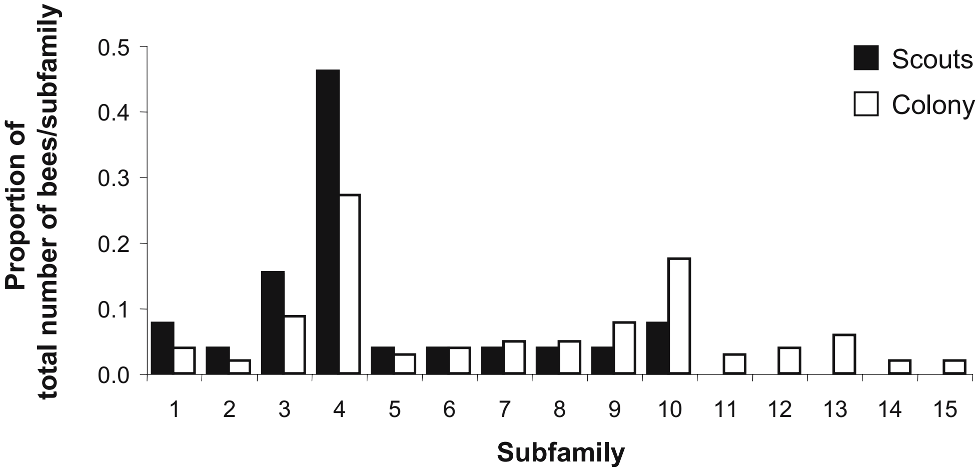
Discussion

In this study, we set out to determine the likely mechanism that regulates scouting in honeybee colonies. Our model suggests that individuals can use the availability of recruitment dances to decide to become a scout or a recruit. When dances are freely available, the chances that an unemployed forager encounters a dance are high. Hence, it will become a recruit. If the number of dances is low, an unemployed forager is less likely to find a dance. This individual is then more likely to become a scout. The model predicts a negative correlation between the available forage, and hence, the number of dances and the number of scouts. Our experimental observations support this prediction in two different contexts, in a natural foraging environment and in an experimentally manipulated environment, confirming previously published empirical observations (Seeley 1983).

Further support for this failed follower mechanism was obtained from our field observation that the majority of the scouts (foragers that located the bait feeder the location of which was not advertised in the colony) did not follow dances before being caught at the bait feeder. The only bees that had followed a dance before appearing at the bait feeder had followed nondirectional round dances that send recruits out into a random direction (von Frisch 1967). Therefore, these bees were most likely recruits and not scouts. Although the total number of scouts was most likely higher than the number caught at the bait feeder, this underestimation is not likely to have affected the generality of our conclusions, as it should not change with changing foraging profitability.

As we could not ascertain that our scouts indeed tried to locate a dance before leaving the hive, it could be argued that scouts are mostly novice foragers that do not even attempt to locate a dance on their first foraging trip. There are several reasons to doubt this alternative hypothesis. First, such a mechanism is not likely to result in a negative correlation between available forage (and hence dances) and the number of scouts found empirically and predicted by the failed follower mechanism, unless forage availability somehow directly affects the number of novices that become motivated to forage. Second, an earlier study by Biesmeijer and Seeley (2005) found that 60% of novices rely on information obtained from dances. Finally, six of the scouts collected at the bait feeder in the first experiment had followed dances on previous days, while five were seen dancing on previous days in the second experiment, suggesting that they were not novice bees. Our experiments do not completely rule out the existence of another, yet to

Fig. 6 Representation of each subfamily among scouts (N=26) (bees caught at the bait feeder) and bees sampled from the colony after the experiment was finished (N=103)



be determined, mechanism that produces a negative correlation between scouting and available forage, but the failed follower mechanism remains by far the most parsimonious and the only one yet proposed that is consistent with our experimental observations.

While genetic variation is important to honeybees in the generation of some stable group-level phenotypes, such as thermoregulation (Jones et al. 2004; Myerscough and Oldroyd 2004), it does not appear to be important in the regulation of scouting. Subfamily proportions did not differ significantly between scout and colony samples, suggesting that the subfamilies present in the experimental colony had similar tendencies to become scouts. This is in contrast to Dreller's (1998) observation of strong subfamilial variance in the willingness of foragers to engage in scouting. This may suggest that genetic variance for propensity to scout is perhaps less than Dreller's experiment indicated. For example, genotype could have an effect on the exact wait time before an individual of a certain patriline decides to become a scout, but this could be too subtle to have been picked up in our analysis. Our model did not incorporate individual differences in thresholds for scouting, and still resulted in model outcomes that were similar to those observed in the field. If genetic variation for propensity to scout does exist, its effect appears less important than that of the underlying behavioral mechanisms.

The failed follower mechanism provides the honeybee colony with the means to rapidly adjust its number of scouts depending on the amount of information available about profitable forage sites. Even when the colony is exploiting profitable patches, there may still be other, undiscovered, profitable sites that are not yet exploited. As soon as there is a reduction in the number of dances occurring in the colony, the probability that some unemployed foragers are unable to locate a dance increases, and the colony therefore sends out some scouts. Such fluctuations in the number of dances regularly occur in honeybee colonies, even when there is plenty of forage (Beekman et al. 2004).

Honeybees collect food over a vast area, often more that 100 km^2, changing their focus on a daily basis to adjust to the often rapid changes in foraging conditions (Visscher and Seeley 1982; Schneider 1989; Waddington et al. 1994; Beekman and Ratnieks 2000; Beekman et al. 2004). Their impressive colony level foraging behavior is the result of a sophisticated communication system in which foragers integrate a large amount of information about the conditions of the patch they themselves are exploiting, as well as information obtained both directly and indirectly from their nest mates. The failed follower mechanism is an elegant example of a regulatory feedback in this communication system (Seeley 1995; Fewell 2003; Sumpter 2005). Scouting is influenced by the amount of information, in the form of recruitment dances, being brought into the colony. When incoming information is low, the number of scouts is upregulated to gather more information. Potential scouts thus obtain a good estimate of the need to scout without leaving the colony. A similar mechanism could regulate scouting in other contexts. For example, Passino and Seeley (2006) and Janson et al. (2007) both incorporated the failed follower mechanism in an individual-based model of nest-site selection in honeybees. In all these situations, a simple change in the behavior of an individual in response to the failure to achieve some local goal can lead to a well-regulated group response to changing global conditions.

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