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From nonlinearity to optimality: pheromone trail foraging by ants

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Pheromone trails laid by foraging ants serve as a positive feedback mechanism for the sharing of information about food sources. This feedback is nonlinear, in that ants do not react in a proportionate manner to the amount of pheromone deposited. Instead, strong trails elicit disproportionately stronger responses than weak trails. Such nonlinearity has important implications for how a colony distributes its workforce, when confronted with a choice of food sources. We investigated how colonies of the Pharaoh's ant, *Monomorium pharaonis*, distribute their workforce when offered a choice of two food sources of differing energetic value. By developing a nonlinear differential equation model of trail foraging, and comparing model with experiments, we examined how the ants allocate their workforce between the two food sources. In this allocation, the most profitable feeder (i.e. the feeder with the highest concentration of sugar syrup) was usually exploited by the majority of ants. The particular form of the nonlinear feedback in trail foraging means that when we offered the ants a choice between two feeders of equal profitability, foraging was biased to the feeder with the highest initial number of visitors. Taken together, our experiments illuminate how pheromones provide a mechanism whereby ants can efficiently allocate their workforce among the available food sources without centralized control.

To survive, insect societies must organize their workforce efficiently. This organization involves making collective decisions that optimize the colony's fitness. For example, honeybee, *Apis mellifera*, colonies focus their foraging efforts on only the most profitable patches, ignoring those of inferior quality (Seeley 1995). Both ants and honeybees are capable of choosing the best of several possible new nest sites during migration or swarming (Mallon et al. 2001; Seeley & Buhrman 2001). Ants are capable of laying pheromone trails to food sources that maximize energy efficiency (Denny et al. 2001) and follow the shortest route to a food source (Goss et al. 1989). Such trails will preferentially lead to food sources with the strongest concentration of sucrose (Beckers et al. 1993) or with volumes larger than a single ant can carry (Mailleux et al. 2000) and towards places where there are prey that require collective transport (Detrain & Deneubourg 1997; Robson & Traniello 1998). Insect societies achieve such organization and collective decision making because they share information between workers in the colony. The collective success of social insects is thus achieved through feedback mechanisms arising as information is shared between individuals (Bonabeau et al. 1997; Pratt et al. 2002). Indeed, it is widely recognized that understanding these feedback mechanisms provides a key to understanding how insect societies organize their workforce efficiently (Camazine et al. 2001).

For the foraging of many species of ants, feedback mechanisms are in the form of pheromone trails, chemicals that are deposited by ants that have found a profitable food source and connect the nest with the food source (Hölldobler & Wilson 1990). These pheromone trails guide nestmates to discovered food sources and, upon finding the food, these recruited ants leave their own pheromone trail during their return to the nest. The trail is thus reinforced and the probability that other ants will follow the trail is further increased. The formation of such foraging trails allows nestmates to locate and exploit the source.

Although it is clear that pheromone trails involve a feedback mechanism through which ants can share information and increase their collective success, it is less clear precisely how this feedback produces an efficient

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distribution of ants between available food sources. For example, from the above description alone, it is not clear how pheromone trails will allow the colony to allocate its workforce to the better of two sources. The success of the pheromone trail mechanism is likely to be caused, at least in part, by the nonlinear response of ants to pheromone trails where, for example, the distance that an ant follows a trail before leaving it is a saturating function of the concentration of the pheromone (Pasteels et al. 1986). In other words, the probability that an ant will follow a trail is a function of trail strength (expressed as concentration of pheromone), but ants never have a zero probability of losing a trail, regardless of the strength of the trail. These observations can be modelled mathematically using differential equations to describe the rate at which ants join and leave trails (Sumpter & Pratt 2003). Mathematically, nonlinearity in response means an increase in the number and complexity of solutions of these differential equations (linear equations have only a single solution). Biologically, a solution to a differential equation corresponds to a distribution of ants between food sources and an increase in solutions implies more flexibility as the ants 'choose' between possible solutions.

By deriving nonlinear differential equations from laboratory experiments it is possible to predict the distribution of ants between feeders when offered a choice. In experiments where ant colonies were established in a foraging arena, within which the ants could explore freely and into which sugar feeders were placed at fixed distances from the nest, the equilibrium distribution of ants between feeders corresponded reasonably well to the solution of differential equation models (Pasteels et al. 1987; Beckers et al. 1990; De Biseau et al. 1991). Unfortunately, these experiments had few replicates: usually only three and at most seven for each experimental set-up. Other experiments, where ants on leaving the nest were forced to choose one or other branch of a Y-shaped bridge, rather than being allowed to explore freely in a foraging arena, did have sufficient replicates, 12–17 for each experimental set-up, to give a clear picture of how *Lasius niger* distributes it workforce between two feeders of differing or equal quality (Beckers et al. 1993). A differential equation model based on these experiments showed that pheromone trails can, although are not always guaranteed to, produce an allocation of ants to food sources such that a majority of the ants visit the feeder that maximizes energy efficiency (Nicolis & Deneubourg 1999). Based on the above experiments, theoretical speculation and mathematical modelling have proceeded at pace (see Camazine et al. 2001, chapter 13 for a review), although little experimental work has been done to confirm Beckers et al.'s (1993) results in other experimental set-ups and with other species. To understand the dynamics of pheromone trails and how ants are distributed between feeders, experimental evidence is needed both for a number of species and in experimental set-ups that more closely mimic foraging conditions close to those found in the ants' natural habitats.

We investigated how the Pharaoh's ant, *Monomorium pharaonis*, distributed its workforce between feeders in a foraging environment where ants were free to explore an arena in a relatively unconstrained manner. We used a differential equation model to examine how this allocation was made.

METHODS

The Pharaoh's ant exclusively uses pheromone trails, so-called mass recruitment, to communicate the location of food (Sudd 1960; Fourcassie & Deneubourg 1992). We chose it as a model species because the workers are small, 2 mm long, which facilitates laboratory study. In addition, colony size can easily be manipulated because Pharaoh's ants have multiple queens and lack nestmate recognition (Sudd 1960; Hölldobler & Wilson 1990). Study colonies, which were derived from a strain originally collected in 1968 from Bergnassau-Scheuern/Lahn, Germany, had several queens, brood (eggs, larvae and pupae) and 1000 workers. They were housed in a heated room kept at 20 ± 2°C and fed with egg yolk and dead insects. The colony was housed in a wooden nestbox (11×2 cm and 8 cm high) inside a plastic box (45×30 cm and 15 cm high) that acted as a foraging environment. Either one or two stands with plastic strips were kept permanently in the plastic box. Our basic experimental protocol was to place one or two droplets of syrup at the end of these strips and observe the build-up of a pheromone trail to the syrup droplets. The distance from the base of the stand to the droplet at the end of the strip was 50 cm. Before each experimental trial, the ants were deprived of syrup for 1–3 days. Earlier experiments have shown that, although the foraging response varies between colonies and between days, there is no correlation between the number of days for which a colony is deprived of syrup (provided it is between 1 and 3 days) and its foraging response, either in terms of the total number of foragers visiting feeders or the rate at which the colony responds to a feeder becoming available (Beekman et al. 2001).

Three experiments were performed. In single-feeder experiments (for convenience we use the term 'feeder' instead of 'droplet'), we provided a single droplet of either a 1-M sugar solution (33 trials) or a 0.1-M sugar solution (24 trials). Droplets were sufficiently large, 1.5 cm in diameter, to feed as many ants as arrived at them during the experiments. In two-feeder experiments, we provided two droplets. These droplets could either be of the same quality (i.e. same concentration of sugar, 1.0 M; 18 trials) or of different quality (1.0 and 0.1 M; 18 trials). When two feeders were offered, the stands with the plastic strip were placed at opposite sides of the nestbox, so that the distance between the two feeders was 111 cm.

During each experimental trial, we counted ants crossing a line 5 cm from the feeder for the minute after the first ant discovered the feeder (0 min), again for 1 min after 5 min, then subsequently for 1 min at intervals of 10 min. We made seven such measurements per trial. To obtain the maximum number of ants foraging at the feeder for each trial, we took the three consecutive measurements with the largest mean number of visiting ants over the three measurements (we refer to this

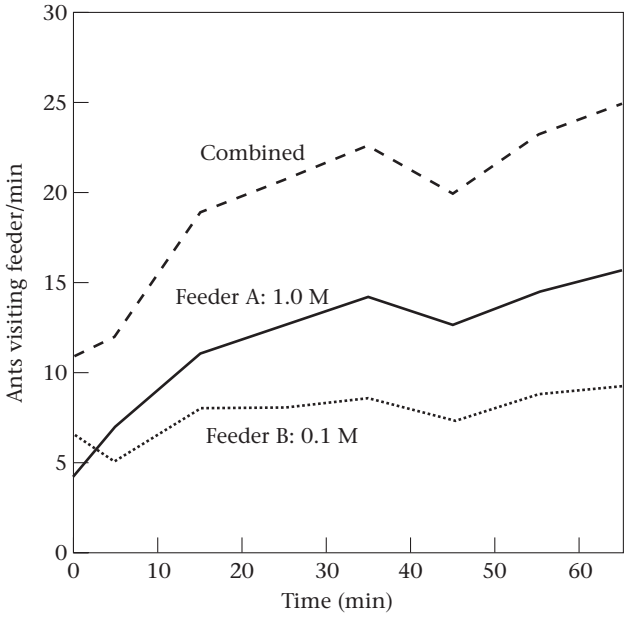

Figure 1. Change in feeder exploitation over time for the experiment with two unequal feeders: number of ants/min visiting feeder A and feeder B, averaged over all 18 experimental trials. 'Combined' is the total number of ants visiting both feeders.

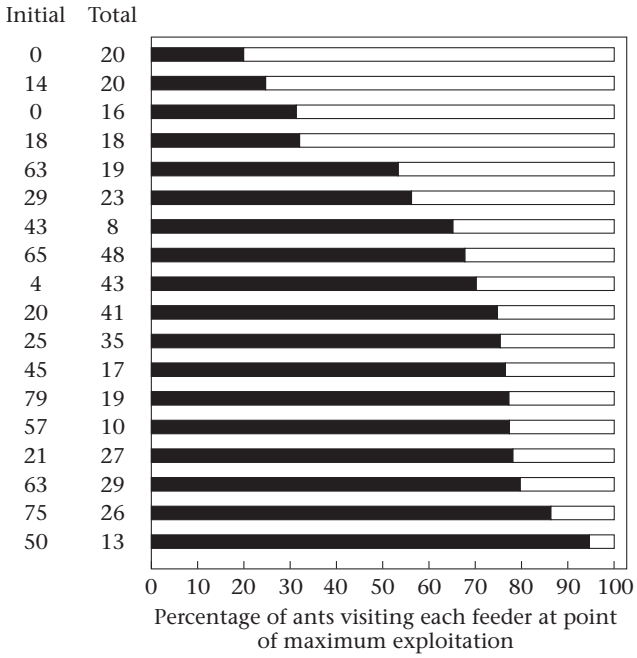

Figure 2. Percentage exploitation of each feeder (■: feeder A, 1.0 M; □: feeder B, 0.1 M at the point of maximum exploitation for each of the 18 trials in the experiment with two unequal feeders. The numbers to the left are the percentages of ants visiting feeder A before the experiment started (initial) and the combined total number of ants visiting both feeders/min at the point of maximum exploitation (total).

measurement as maximum exploitation). In the two-feeder experiments the point of maximum exploitation was that at which the sum of the ants visiting both feeders over three consecutive measurements was greatest. In this way we were sure of comparing the maximum foraging response in each trial. In particular, this measure eliminates the possibility that different delays in the onset of foraging in different trials cause anomalous differences in the results.

RESULTS AND MODEL

Feeders of Different Quality

When the ants were presented simultaneously with two feeders each of different quality (i.e. different concentration of sugar syrup), they exploited the better quality feeder significantly more often; 14 out of 18 trials had greater maximum exploitation at the 1.0-M feeder (sign test: P=0.009; Figs 1, 2). The average increase in ants visiting, at the point of maximum exploitation, the 0.1-M feeder was only 1.60 ± 5.20 ants/min compared with 9.24 ± 8.14 for the 1.0-M feeder. The mean time until maximum exploitation was 50.3 ± 14.5 min from the start of the experiment.

Model of Feeder Choice

How does the ant colony achieve this allocation of the majority of its workers to the most profitable feeder? Individual Pharaoh's ants leave pheromone trails to both 1.0-M and 0.1-M feeders (personal observation and see below), so it is not simply a failure to exploit weaker feeders that leads the workers to choose the better one. The speed of response would suggest that although some ants visit both feeders, few could have the opportunity to compare the feeders. Indeed, Beekman et al. (2001) found that the discovery rate for a foraging ant of a single sugar feeder 50 cm from the nest was only 0.0052 per min. Because the main mechanism by which Pharaoh's ants communicate about the location of food is through pheromone trails, it is by understanding the dynamics of trail laying and following that we can understand the allocation of workers to food sources.

To understand pheromone trail dynamics, we developed a simple mathematical model of a choice between two feeders, extended from Beekman et al.'s (2001) model of recruitment to a single feeder. We let N be the total number of ants available to forage, X_A the number of ants engaged in foraging at source A and X_B the number of ants engaged in foraging at source B. The model assumes that the rate at which the $(N - X_A - X_B)$ exploring ants begin foraging at a particular source depends both on random encounters with that source and on the number of ants depositing a trail to the source. The rate at which ants lose the pheromone trail is assumed to depend on the strength of the trail already laid to the food source (Deneubourg et al. 1983). If the strength of a pheromone trail is proportional to the number of ants foraging at a source, then the rates of change X_A and X_B are

$$dX_A/dt=(\alpha+\beta_A X_A)(N - X_A - X_B) - sX_A/(K+X_A) \quad (1)$$
$$dX_B/dt=(\alpha+\beta_B X_B)(N - X_A - X_B) - sX_B/(K+X_B) \quad (2)$$

where α is the rate at which ants randomly find the feeders, $sX/(K+X)$ is a saturating function which determines the rate at which individual ants lose the pheromone trail (Pasteels et al. 1987), s is the maximum rate at which ants lose the trail when the trail is saturated with ants and K is the number of ants on a trail that gives a rate of loss of $s/2$. β_A and β_B determine the strength of recruitment to sources A and B. The strength of recruitment is determined by the amount of pheromone that the ants deposit, which we assume depends on the strength of the food sources. α, s and K do not depend on the quality of the source, because in the experiments the feeders were equal distances from the nest site.

Our model was parameterized using data collected by Beekman et al. (2001) on single-feeder experiments. We set α=0.0052, which was measured directly as the rate of random discoveries of a single food source. We assumed N=100 as the maximum number of ants available to forage (10% of the colony). The other parameters, β_A=0.0015, K=10 and s=1, were set to reproduce both the rate of recruitment to a single 1.0-M feeder and the phase transition to trail-based foraging which occurs when the colony has roughly 700 ants (Beekman et al. 2001). We set β_B=0.0010 to give slower recruitment to the 0.1-M feeder.

Figure 3a shows a numerical solution of equations (1) and (2). As in the experiments, the simulated ants eventually chose the 1.0-M source (feeder A) and at equilibrium nearly all of the available ants foraged at that source. The mathematical model thus shows that the ants can make a collective choice as to which feeder to exploit simply by having a faster rate of recruitment to the superior food source, without requiring that individual ants compare the two food sources. The model assumes only simple behaviour on the part of the ants, but successfully generates the foraging pattern observed in our experiment.

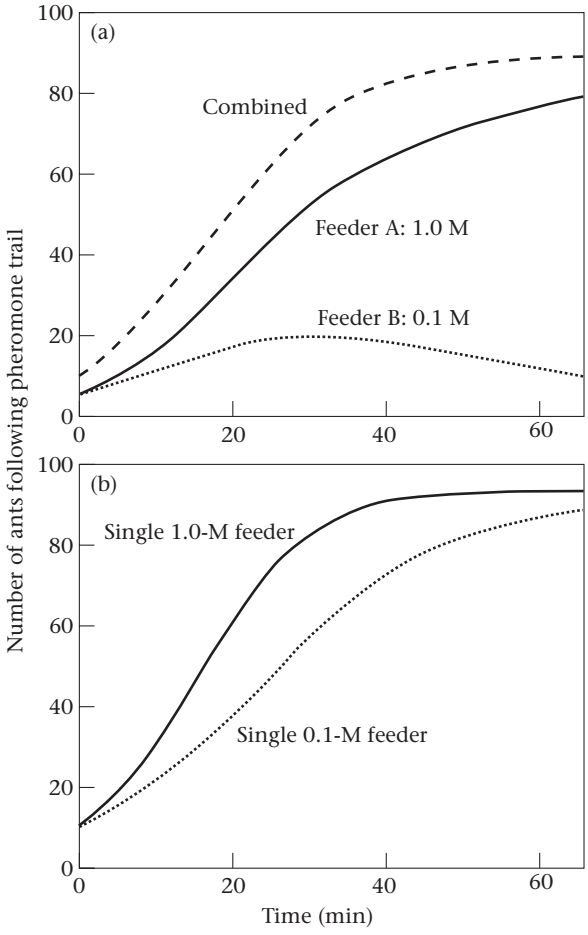

Figure 3. Numerical solution of the mathematical model of foraging when (a) two feeders of different quality are available simultaneously and (b) only a single feeder is available. Specifically, (a) is the solution of equations (1) and (2) with β_A=0.0015 and β_B=0.0010, and (b) is two separate solutions of equation (3), one with β_A=0.0015 and the other with β_A=0.0010, where β_A and β_B are the strengths of recruitment to feeders A and B, respectively. In all solutions the rate at which ants randomly find feeders (α) is 0.0052, N is 100, the maximum rate at which ants lose the trail when the trail is saturated with ants (s) is 1, and the number of ants on a trail that gives a rate of loss of $s/2$ (K) is 10. 'Combined' is the total number of ants visiting both feeders.

Recruitment to Single Feeder

The model suggests that either the ants lay weaker pheromone trails or individual ants have a lower propensity to lay trails when a food source is of lower quality, or a combination of both. In the model, when we have only a single feeder, A, then

$$dX_A/dt=(\alpha+\beta_A X_A)(N-X_A)-sX_A/(K+X_A) \qquad (3)$$

determines the number of ants visiting the feeder. Figure 3b gives theoretical predictions for the number of ants following trails to a single feeder for β_A=0.0015 (1.0-M feeder) and β_A=0.0010 (0.1-M feeder). The number of exploiting ants grows more rapidly at the 1.0-M feeder, but at equilibrium the number of ants exploiting both feeders is roughly equal (the equilibrium numbers are 93.8 for the 1.0-M feeder and 90.5 for the 0.1-M feeder).

Our model thus makes a strong prediction: a trail will build up faster to a single 1.0-M feeder than to a single 0.1-M feeder but, once a trail has reached equilibrium, approximately the same number of ants will forage at the feeder regardless of quality. The experimental results fit this prediction (Fig. 4). The mean time at which the maximum number of ants visited the feeder ± SD was 33.4 ± 13.0 min from the start of the experiment for the 1.0-M feeder and 55.2 ± 7.5 min for the 0.1-M feeder. The ants thus took longer to form a trail to a weaker food source. As in the model, the maximum level of exploitation was approximately the same for both feeders: the average maximum number of ants walking to the feeder ± SD was 26.39 ± 11.78 for the 1.0-M feeder and 25.90 ± 10.37 for the 0.1-M feeder. The maximum exploitation level did not differ significantly between the two feeders (two-sample chi-square test: χ^2_6=8.6, P=0.13) or between the single-feeder and the two unequal feeder experiments (single 1.0-M versus two unequal feeders: χ^2_6=6.5, P=0.26; single 0.1-M versus two unequal feeders: χ^2_6=4.8, P=0.44). As predicted by our

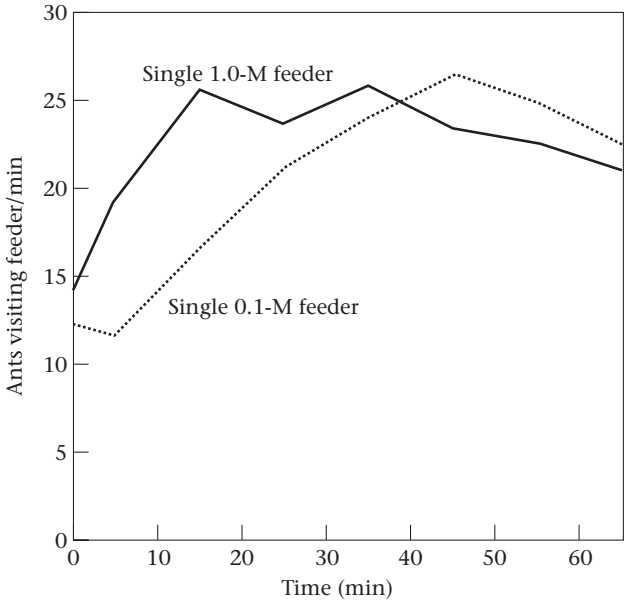

Figure 4. Change in feeder exploitation over time for single-feeder experiments. Number of ants/min visiting the 1.0-M feeder and 0.1-M feeder, averaged over 33 (1.0 M) and 24 (0.1 M) experimental trials.

model, when the ants were presented with only a single feeder, the quality of the feeder did not affect the eventual maximum level of feeder exploitation, but stronger positive feedback (i.e. recruitment) at the better quality source meant that the maximum level of exploitation was reached sooner.

Feeders of Equal Quality

How does the colony allocate its workforce when it is offered two equal-quality feeders? According to the model, when the numbers of foragers initially discovering the feeder are exactly equal for both feeders then the feeders are exploited equally (Fig. 5a). However, if there is a small difference in the initial level of discovery, the feeder with the most ants initially attracts a majority of the ants after 60 min (Fig. 5b). Ultimately, the model predicts that all ants will be recruited to the feeder with the highest initial number of visitors. We thus predict that the feeder with the most ants visiting it initially will be 'preferred' by the colony.

When the ants were presented with a choice of two 1.0-M feeders, the average combined maximum number of ants visiting both feeders did not differ from that of the single-feeder experiments, or the two-feeder experiments with different-quality feeders (two-sample chi-square test comparing two 1.0-M feeders with single 1.0-M feeder: χ^2_6=1.2, P=0.94). The fact that there were now two 1.0-M feeders available to the ants did not increase the total exploitation of the feeders. Furthermore, when presented with two equal-quality feeders, the ants showed no preference for either feeder (9 of 18 trials had greater maximum exploitation at feeder A; sign test: P=0.50; Fig. 6).

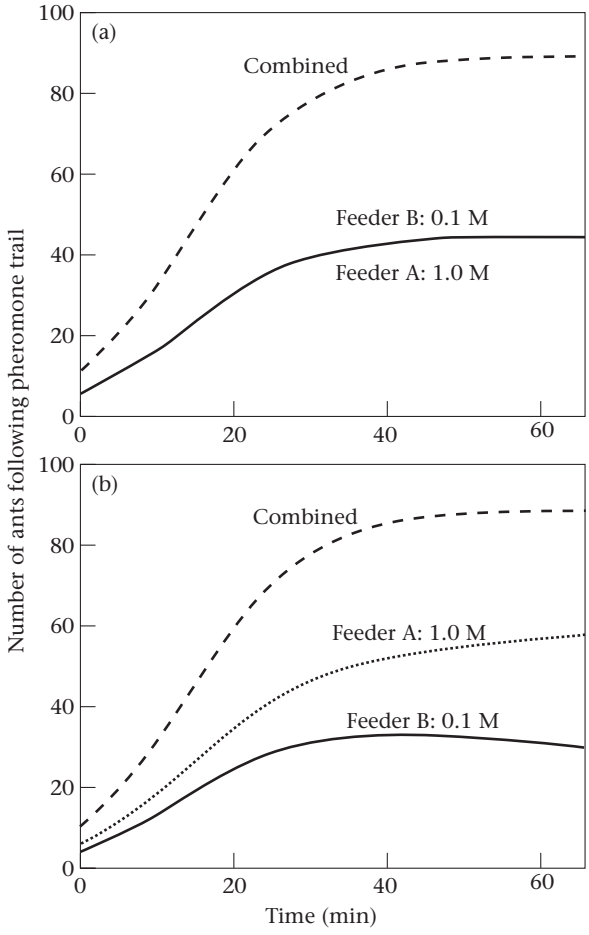

Figure 5. Numerical solution of mathematical model of foraging, equations (1) and (2), when two feeders of the same quality are available simultaneously. In (a) the initial number of ants visiting each feeder is equal, $X_A(0)=X_B(0)=5$, and in (b) the initial number of ants visiting each feeder is different, $X_A(0)=4$ and $X_B(0)=6$. In both solutions $\beta_A=\beta_B=0.0015$, $\alpha=0.0052$, $N=100$, $K=10$ and $s=1$ (see Fig. 3 legend for parameter definitions).

Although when averaged over all trials there was an equal number of ants visiting each feeder, we must look in detail at the results of each experimental trial to test the model's prediction that the majority of foraging ants will visit the feeder that has the most ants visiting it initially. For each trial we tested whether the probability that the number of ants visiting each feeder is consistent with a binomial distribution with N=number of ants foraging at the feeder at the point of maximum exploitation (Fig. 7a) and P=1/2; that is, for each trial we tested the null hypothesis that each visiting ant chooses a feeder at random, as if tossing a fair coin. Over all the experiments, the P values were significantly different from those expected if choice of feeder was made according to this binomial distribution (making a histogram of P values with boxes 0.5–0.6, 0.6–0.7, . . ., 0.9–1.0 and comparing it to the appropriate uniform distribution gives χ^2_4=11.33, P=0.01). Rather than having a single mode at 0.5, as would be predicted if each ant chose a feeder at random, the frequency distribution is bimodal (Fig. 7b).

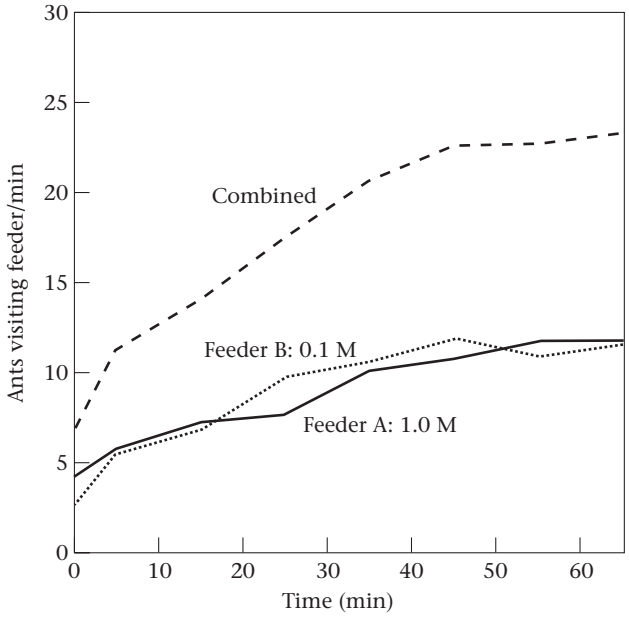

Figure 6. Change in feeder exploitation over time for two equal-quality feeder experiments. Number of ants/min visiting each of the 1.0-M feeders, averaged over all 18 experimental trials. 'Combined' is the total number of ants visiting the feeders.

Thus, when presented with two equal-quality food sources, the colony biased its foraging towards one or the other.

There is also statistical evidence of a relation between the feeder that received the most foragers at the point of maximum exploitation and the initial number of foragers at that feeder. Of the 15 trials where one feeder initially had more ants than the other, this feeder was ultimately exploited more in 11 trials (sign test: P=0.038; Fig. 7a). Taken as a whole, these results are consistent with the model's prediction that a small difference in the initial level of discovery produces a longer-term distribution of ants focused on the feeder with the most ants initially.

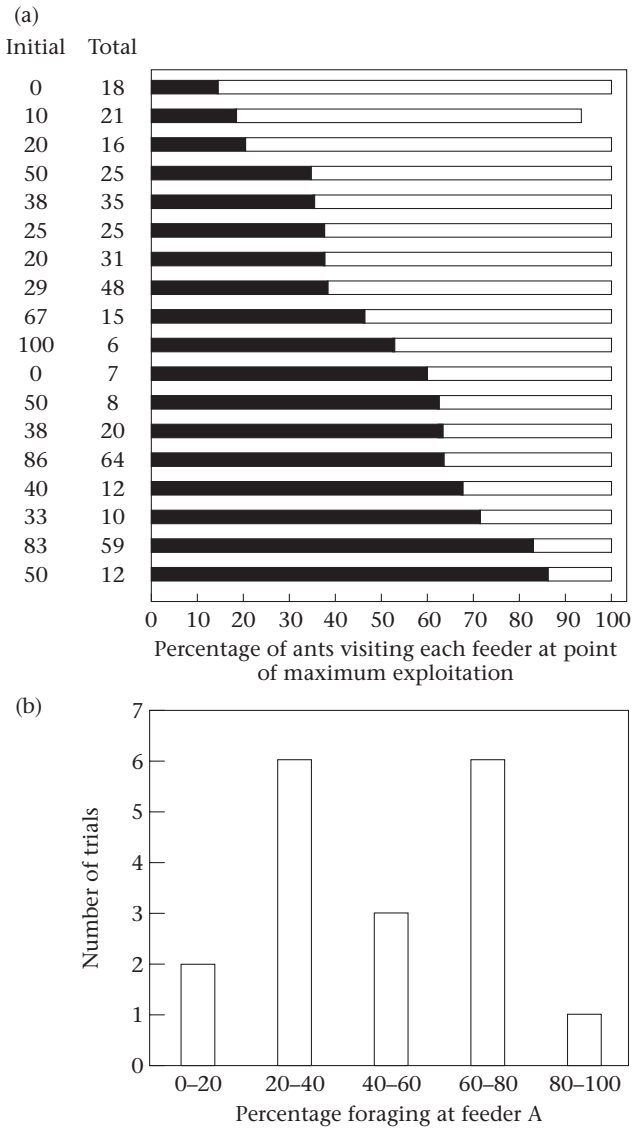

Figure 7. (a) Percentage exploitation of each of two feeders of equal quality at the point of maximum exploitation for each of the 18 trials in the two equal-feeder experiments (■: feeder A, 1.0 M; □: feeder B, 0.1 M). The numbers to the left are the percentages of ants visiting feeder A (1.0 M) before the experiment started (initial) and the combined total number of ants visiting both feeders/min at the point of maximum exploitation (total). (b) The same data plotted as a histogram of percentage of ants exploiting feeder A at the point of maximum exploitation for the 18 trials.

DISCUSSION

Our experiments show that the simple mechanism of regulating recruitment towards discovered food sources allows a Pharaoh's ant colony to allocate its workforce efficiently. When only a single food source was available, the colony exploited that source to the same degree, regardless of its quality. Furthermore, when two food sources were provided, the combined exploitation of the feeders remained equal to the exploitation of a single source. The ability of Pharaoh's ants to choose reliably the better of two food sources does not require individual ants to compare food sources, but is simply the result of a slower build-up of the pheromone, and thus slower recruitment, to the less profitable feeder. The resultant allocation of workers between food sources, which assigns nearly all-trail following foragers to the better food source, is optimal provided the food source has unlimited capacity. Our results agree with earlier experiments on several other ant species (Beckers et al. 1990; De Biseau et al. 1992). In particular, Beckers et al. (1993), using a Y-shaped bridge, showed that *L. niger* chose the branch to the 1.0-M feeder, when the other branch had a 0.1-M feeder, in 12 of 14 trials. Our experiments show that such results were not simply an artefact of the Y-shaped bridge set-up, and that feedback mechanisms are at work in the ants' natural foraging environment. There are also similarities between the pheromone trail recruitment of ants and the dance recruitment of bees. The same basic allocation pattern, of nearly all foragers at the better feeder, is seen in honeybees foraging for nectar (Seeley et al. 1991). The allocation is again due to differential recruitment towards more profitable food sources, with

individual honeybees increasing both the duration and the rate of waggle-run production with increasing profitability of the food source (Seeley et al. 2000).

In our study, we did not investigate the precise individual behaviours that underlie the regulation of recruitment: in experiments on other species individual ants adjusted the amount of pheromone they left, or the number of ants depositing pheromone changed, depending on the quality of the food source (Hangartner 1969; Breed et al. 1987; Beckers et al. 1992a; De Biseau et al. 1992). Such differences in the parameters governing individual behaviours will lead to differences in the precise form of equations (1) and (2). For example, in experiments where ants were offered a choice of a long and a short branch to a food source, the U-turns made by *L. niger* gave a stronger nonlinearity in their recruitment than for *Linepithema humile*, which did not make U-turns (Goss et al. 1989; Beckers et al. 1992b). While changing the specific functions used in equations (1) and (2), the incorporation of such individual-level behaviours will still produce the same pattern of nonlinear recruitment and saturating retirement. Indeed, provided the equations resulting from inclusion of specific behavioural details are at least cubic in form (so that when equation 1 is equated to zero and rearranged as a polynomial it includes a term X_A^3) the qualitative form of their solution will not differ greatly from those presented here. These mathematical observations suggest that similar patterns of forager allocation, as we have found in our experiments, are a generic property of mass-recruiting, pheromone-laying ant species, independent of the underlying individual recruitment mechanisms.

We do expect, however, differences between honeybee dance recruitment and pheromone trail recruitment. These are illuminated by our final experiment where the ants were offered a choice of two food sources of equal quality; the food source that received the most visiting ants early in the recruitment process was exploited disproportionately more. Such a distribution is not predicted from the differential equations that have been applied in the mathematical description of dance recruitment (Camazine & Sneyd 1991). Honeybees retire from foraging independently of the recruitment of other bees, whereas the loss of pheromone trails, and hence retirement, by ants depends on the saturating function $sX_A/(K+X_A)$, which implies that individual ants lose the trail faster when fewer ants are foraging at the feeder. If we replace this saturating function with a term rX_A, to represent independent retirement, in equations (1) and (2) they no longer have a cubic form. The resultant model then predicts that a colony presented with two equal-quality feeders will exploit the two feeders in the same proportion as the initial distribution. Unlike the distribution seen in Fig. 7b, the predicted distribution for the bees has a single mode at 0.5.

Neither the distribution generated by pheromone trails nor that generated by dance following is suboptimal in terms of energy intake. When information gathering is taken into account, however, it is possible that one or other of the mechanisms may be more efficient. For example, we may conclude that a dance-recruiting workforce is balanced between the two food sources, allowing the bees to change their allocation quickly to the single remaining source if one or other is depleted. Ants, on the other hand, must rebuild a trail to the remaining source. Such arguments are much harder to quantify without detailed knowledge of the insects' foraging environment. The differences in allocation between feeders occurred when nothing was to be gained in terms of optimizing energy intake. The two very different communication mechanisms both generate the same optimal energy intake distributions. Differences in those patterns can be detected only when nothing is to be gained or lost in terms of this optimality.

It has been argued that ants using pheromone trail recruitment alone may make suboptimal (again in terms of energy intake) choices of food source, if the ants first establish a trail to a low-energy source before a high-energy source is introduced (Beckers et al. 1990). The positive feedback to the low energy source may be too strong for the high energy source to compete and the ants become 'stuck' at the low-energy source. This argument is again supported by mathematical analysis of the models proposed by Nicolis & Deneubourg (1999) for ant foraging. There is some experimental evidence in our experiments to support this view: in the four of 18 experimental trials where the majority of foraging took place at the 0.1-M feeder (Fig. 2) all had more ants foraging at the 0.1-M feeder at the start of the experiment. Furthermore, in the seven trials where more ants foraged initially at the 1.0-M feeder, all preserved that majority. We are, however, wary of drawing the conclusion that in our experiments the ants were sometimes 'stuck' in a suboptimal solution. In all our experiments both feeders were visited regularly and large numbers of ants were seen exploring other areas of the foraging arena. Such variability allows the colony to find newly available food sources quickly and to reallocate its workforce to these sources. A future challenge, which must be addressed empirically as well as theoretically, is to determine how ants maintain a robust balance between intake of energy and information gathering (Detrain et al. 1999). Is the variation we see within replicates part of an adaptive search algorithm, or is it simply a physical limitation of pheromone trails as a means for transmitting information?

Despite the inherent variability in foraging patterns, our combined approach of mathematical modelling and experimentation has shown there are clear patterns that underlie Pharaoh ant foraging: (1) on average the colony allocates the same number of workers to foraging, regardless of whether there is a single feeder, two feeders of different quality, or two feeders of equal quality; (2) these workers are focused on the better food sources or on only one of two identical food sources; and (3) this pattern is consistent with a simple mechanism of regulating positive feedback to reflect the strength of a food source without comparison of food sources by individual ants. Such observations are important because they show that successful patterns of behaviour do not require complex individuals or centralized organization. Insect societies are ecologically successful, not necessarily because they

have evolved particularly complex or novel patterns of behaviour, but because haplodiploidy allows for co-operation and very simple forms of cooperation, such as depositing a chemical upon finding food, make colonies robust and highly adaptive.

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