Linear recruitment leads to allocation and flexibility in collective foraging by ants

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Positive feedback in communication is central to the emergence of collective behaviour in animal groups. The nonlinearity hypothesis predicts that group behaviour will be defined in large part by the degree of cooperative interaction in this feedback. Strong interactions mean that the effectiveness of communication grows nonlinearly with signal quantity, leading to robust spatial patterning and consensus decision making. These predictions have been supported in many experimental systems, but the corresponding behaviour of linear systems, where signal effectiveness is proportional to signal quantity, has not been well explored. We examined the consequences of tandem running, a linear method of recruitment, for collective decision making by foraging colonies of the ant *Temnothorax rugatulus*. We found that colonies collectively chose the better of two unequal feeders, but they allocated foragers equally when feeders were identical. This result accords with theoretical predictions and contrasts with symmetry breaking seen in species with highly nonlinear trail pheromone recruitment. Colonies were also able to reallocate foragers when the quality of two unequal feeders was switched, again in accord with theoretical expectations. We built a model based upon the behaviour of individual ants and found that colony-level qualities of choice, allocation and flexibility can be predicted by two behaviours: quality-dependent linear recruitment and quality-dependent attrition. These experiments are the first thorough investigation of the consequences of linear recruitment for collective animal behaviour.
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The collective behaviour of insect societies is a leading example of emergence in the biological sciences. Without leaders or central control, colonies build complex nest structures, regulate their internal environment, allocate workers across multiple tasks and respond adaptively to environmental changes (Seeley 1995; Hölldobler & Wilson 2008). The underlying mechanisms are not well understood, but some insights have been gained for collective decision making, when colonies choose the best among several nest sites or food sources. These decisions are not merely summations of individual choices, but complex outcomes of interactions among colony members, none of which possess global information about every option (Seeley 1986; Bonabeau et al. 1997; Sumpter 2010).

The central mechanism for decision making is positive feedback through recruitment (Detrain & Deneubourg 2008). Recruitment includes any behaviour by which a worker summons nestmates to a place of interest, such as a food source or nest site. It takes a variety of forms across the social insects, but one of the best-studied examples is mass recruitment by pheromone trails (Hölldobler & Wilson 2008). When a *Lasius niger* colony is presented with two unequal sources, scouts that find the better one have a higher likelihood of laying a trail than do scouts that find the weaker one (Beckers et al. 1993). Recruits further reinforce the trails, also with a quality-dependent probability. Over time this differential positive feedback generates more effective trails, and stronger exploitation, at the better source (Beckers et al. 1990, 1993).

While positive feedback can yield differences in exploitation, it does not necessarily result in true consensus, with all individuals choosing a single source. Consensus is vividly illustrated when a colony is given a choice between two identical options. Rather than exploit both equally, mass-recruiting ants tend to concentrate all of their foragers on only one of them, a phenomenon known as symmetry breaking (Beckers et al. 1990; Sumpter & Beekman 2003). The 'nonlinearity hypothesis' suggests that this outcome requires not only positive feedback but also a strongly nonlinear relationship between the effectiveness of recruitment and the number of recruiters (Detrain & Deneubourg 2008; Sumpter 2010). The idea can be represented in a simple model of an ant choosing between two trails to food sources A and B. The probability that she chooses the trail to A (P_A) is expressed as follows:

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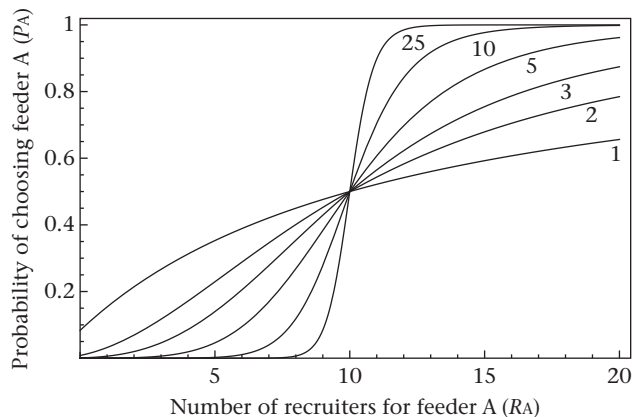 E-mail address: zshaffe@asu.edu (Z. Shaffer).

Figure 1. The effect of nonlinear recruitment on individual decision making between two options A and B, illustrated with plots of equation (1). Each plot gives the probability of an individual choosing A as a function of R_A, the number of nestmates already recruiting to A. In all plots $R_B = 20$ and $k = 1$, but each plot has a different value of the exponent n (shown under each plot). For low values, the relationship is nearly linear. Higher values yield an increasingly step-like function, leading to a clear preference for the option with the greater number of recruiters, even when the difference in recruitment is very small.

$$P_A = \frac{(k + R_A)^n}{(k + R_A)^n + (k + R_B)^n} \tag{1}$$

where R_A and R_B are the number of individuals recruiting to feeders A and B, respectively. The parameter n determines how steeply (or nonlinearly) recruitment effectiveness rises with recruiter number, while k determines the attractiveness of an option in the absence of any trail (Fig. 1). For sufficiently large n (roughly 1 or greater), colonies are predicted to make consensus choices even when presented with identical options. This is because a strongly nonlinear relationship magnifies small chance differences in exploitation, driving the ants toward exclusive use of only one option. Thus, even a tiny difference in pheromone concentration on competing trails leads to a clear preference for the stronger trail, at least for colonies of sufficient size (Beekman et al. 2001). Mass recruitment by ants exemplifies this consensus-building process, but many other examples are found in a variety of social animals including humans and bacteria (Saffre et al. 1999; Crespi 2001; Jeanson et al. 2005; Ame et al. 2006; Visscher & Seeley 2007; Ward et al. 2008; Clotuche et al. 2011; Kameda et al. 2012). The specific behavioural mechanisms vary widely, but they all have one feature in common: as the number of individuals supporting a given option increases, their per capita effectiveness at drawing new adherents grows.

Besides its role in consensus formation, nonlinear recruitment is also expected to yield some loss of decision-making flexibility. For mass-recruiting ants, models predict that a colony exploiting a food source will have difficulty switching to a better source that becomes available later (Detrain & Deneubourg 2008; Sumpter 2010). This is because positive feedback from the established trail overwhelms any nascent trail laid by discovers of the better source. Experimental evidence supports this prediction in mass-recruiting ants (Beckers et al. 1990) and stingless bees (Schmidt et al. 2006).

Not all recruitment is nonlinear, and very different outcomes are predicted for colonies using linear methods (Sumpter & Beekman 2003; Detrain & Deneubourg 2008; Sumpter 2010; Lanan et al. 2012). For example, honeybees recruit using the waggle dance, in which a successful forager advertises a food source using a series of dance circuits, with the number of circuits encoding food quality

(Seeley 1986; Couvillon 2012). Waggle dancing is linear because the effectiveness of an additional circuit is the same regardless of how many dancers are active (Seeley et al. 1991). A potential recruit attends to a single dance at a time, and other dances do not reinforce the recruitment signal (Seeley & Towne 1992). With linear recruitment, models predict that colonies offered two sources of different quality exploit both, but allocate more foragers to the better one (Camazine & Sneyd 1991). If the sources are identical, colonies are not expected to reach consensus, but instead to divide their foraging effort equally (Camazine & Sneyd 1991; Sumpter & Beekman 2003; Lanan et al. 2012). Finally, these colonies should flexibly redistribute foraging effort in response to changes in resource quality. Linear recruitment has not received much study, but the limited evidence is consistent with these predictions. Honeybee colonies allocate foragers according to feeder quality, and they quickly reallocate effort when relative feeder quality is altered (Seeley et al. 1991; Granovskiy et al. 2012). However, the most revealing test of the nonlinearity hypothesis (i.e. whether groups show symmetry breaking when given two equal options) has not been carried out with honeybees or any other species showing linear recruitment.

This study investigates the collective consequences of linear recruitment in an exceptionally tractable system: the ant *Temnothorax rugatulus*. *Temnothorax* is a Holarctic genus whose small colony size and robustness to laboratory conditions has made it a model system for collective decision making, especially nest site selection (Franks et al. 2002; Pratt et al. 2002). Colonies typically live in rock crevices, hollow nuts or other pre-formed cavities, and are adept at choosing the better of two or more sites, distinguishing them on the basis of cavity volume, interior dimness, entrance size and other features (Franks et al. 2003; Visscher & Seeley 2007). Decisions depend on active scouts that find and assess candidate sites, and then recruit to them with a probability that depends on site quality (Mallon et al. 2001). Recruitment is not by pheromone trails, but instead by tandem runs, in which a leader ant releasing an ephemeral pheromone directly guides a nestmate to the candidate site (Moglich et al. 1974; Franks & Richardson 2006; Franklin et al. 2011). Like the honeybee waggle dance, the effectiveness of tandem runs is linear in recruitment effort: as long as there is a pool of potential recruits at the old nest, each additional tandem run is expected to increase the arrival rate of new ants by the same amount (Pratt et al. 2002).

Temnothorax also use tandem runs when foraging, and this is the context that we examine here. Although their foraging behaviour in nature has only begun to be documented (Bengston & Dornhaus 2013), laboratory studies show that they recruit to sugary liquids (Franks & Richardson 2006), which they exploit and share through complex food exchange networks (Sendova-Franks et al. 2010). Unlike nest site selection, where tandem running is combined with a nonlinear quorum rule (Pratt et al. 2002), the simpler process of foraging appears to rely purely on tandem runs. This makes it a suitable context in which to test the effects of linear recruitment on collective decision making. Our approach was to present *T. rugatulus* colonies with three basic decision challenges as follows. (1) Can they discriminate between sucrose feeders of different concentration, allocating more foraging effort to the stronger feeder? (2) When given identical feeders, do colonies reach consensus on a single one, or do they instead allocate foragers equally to both? (3) If relative feeder quality is changed midway through a foraging bout, can colonies flexibly alter their foraging effort to track the better source? To link these colony-level properties to individual recruitment actions, we also developed a simple model of forager behaviour and tested whether it predicted the patterns of choice, allocation and flexibility demonstrated in our experiments.

METHODS

Experimental Subjects

Colonies of *T. rugatulus* were collected from rock crevice nests in the Pinal Mountains near Globe, Arizona, U.S.A. (33°19.000′N, 110°52.561′W) between April and June 2010. In the laboratory each colony was housed in an artificial nest made from a 2.4 mm thick balsa wood slat with a rectangular central cavity measuring 3.8 × 6.4 cm. The slat was sandwiched between 50 × 75 mm glass microscope slides that served as floor and ceiling. A 3 mm wide entrance was cut through the side of the slat. Each nest was placed in an 11 × 11 cm plastic box and kept in a Sheldon diurnal incubator on a 16:8 h day:night schedule, with a daytime temperature of 23 °C and a nighttime temperature of 15 °C. Colonies were provided weekly with water and an agar-based diet (Bhatkar & Whitcomb 1970). On completion of the study, colonies were maintained in similar conditions for use in other behavioural experiments. Colonies typically decline after 1–2 years and are then killed by placing them in a −20 °C freezer. No permits or licenses were required for this study.

Choosing between Unequal Feeders

In this experiment colonies were presented with two sucrose solution feeders of unequal quality. The 'good' (0.8 M) and the 'poor' (0.1 M) sources consisted of 0.1 ml droplets on the arena floor. Twelve replicates were run simultaneously, with observers rotating between arenas to collect data at approximately 5 min intervals for 2 h. At each observation we recorded recruitment (the number of tandem runs being led in the direction of each feeder) and exploitation (the number of ants drinking from each droplet). After the experiment, we calculated foraging effort in two ways: (1) we took the average number of exploiters at each feeder over all observations; (2) we took the number of exploiters at each feeder at the point of maximum exploitation (i.e. when the sum of ants at both feeders had reached its greatest value). We also measured recruitment effort as the average number of tandem runs to each feeder over all observations. We watched each tandem run until we could make a reasonable conclusion about which feeder it was aiming for. Because the exact number of observations varied between experiments, we performed most analyses on average recruitment and exploitation (per observation) to allow comparison between experiments.

To ensure strong motivation to forage, ants were starved for 14 days prior to the experiment. Colonies were placed into arenas (75 × 60 cm) 24 h before the start of the experiment. Feeders were placed 30 cm from the nest and 40 cm from each other. They were replenished once every 30 min with an additional 0.1 ml of sugar water. All colonies contained brood, and average colony population was 382 ± 40 (this and all other measures of variability are given as standard errors). This experiment was performed on 15 September 2010.

Choosing between Equal Feeders

In this experiment colonies were given a choice between two feeders of equal quality (0.8 M sucrose). Methods were otherwise the same as in the unequal choice experiment described above. We tested 14 colonies with an average population of 401 ± 46; all colonies contained brood. This experiment was performed on 29 August 2010.

Responding to a Switch in Feeder Quality

In these trials, colonies were initially presented with one poor and one good feeder (0.1 M and 0.8 M). Colonies were observed for just under 1 h, and then the quality of the two feeders was switched. To facilitate this change, the droplets were placed into depression well slides rather than directly on the arena floor. At the switch, each old slide was removed and immediately replaced with a fresh slide containing the new solution. The switch was made 50–57 min after initial introduction of the feeders. Average and peak exploitation, as well as average recruitment, were calculated both before and after the switch. All other details were the same as in the prior experiments. We tested 20 colonies with an average population size of 311 ± 33 individuals. This experiment was performed over 2 days (10 colonies per day) on 20 October and 22 October 2010.

Individual Behavioural Rules

To determine the individual behaviour leading to a colony-level decision, and to estimate parameter values for a mathematical model of the process, we replicated the unequal choice experiment with marked colonies of ants. In each of four colonies, every worker received a unique combination of paint dots on the head, thorax and abdomen using Pactra R/C Car Lacquer paint. With separate cameras trained on the nest, each feeder and the entire arena, the colonies were recorded for 4 h as they foraged.

From these videos, three behaviours were quantified: food discovery, recruitment and attrition. For discovery, we determined the number and identity of all ants that exploited any feeder at any time during the experiment. The independent discovery rate α was estimated via survival analysis of the discovery times of each of these active foragers. Specifically, we fitted an exponential distribution to the latencies between the start of the experiment and each forager's first appearance at a feeder, and estimated α as the parameter of this distribution. We restricted this analysis to the first 15 min of the experiment, before any tandem runs were observed, so that we could be certain that recruitment did not influence the rate of discovery. If a forager found neither feeder in this period, she was assigned a latency of 15 min and treated as censored data. We first calculated α separately for each feeder, but found no effect of feeder quality. We therefore estimated a common value for both feeders.

Attrition was defined as the rate λ_i at which exploiters of feeder i abandoned it. We used survival analysis to fit an exponential distribution to the intervals between each ant's discovery of a feeder and her abandonment of it. We did this separately for the good and poor feeders and estimated λ_{good} and λ_{poor} as the parameters of the fitted distributions. An ant was considered to have abandoned a feeder if she went back to the nest and never returned to that feeder, or if she switched to exploiting the other feeder. To minimize effects of colony satiation on attrition, data were analysed for only the first 60 min of the experiment. If an ant was still exploiting a feeder at the 60 min mark, she was treated as censored data and assigned an interval of 60 min minus her discovery time.

Recruitment to feeder i was quantified by the rate β_i at which ants exploiting the feeder led successful tandem runs to it. A run was deemed successful if the follower reached the feeder within 5 min of the run's breakup. To minimize effects of colony satiation, we analysed only the first 60 min of each trial. For each feeder, we calculated β as the total number of successful tandem runs to that feeder divided by the total number of ant-minutes of exploitation at that feeder. The latter was calculated by summing the total exploitation time of each ant that foraged at the feeder during the 60 min interval. Estimates of β and the other parameters were calculated using the statistical computing environment R (R Foundation for Statistical Computing, Vienna, Austria).

Only a fraction of each colony's workers forage. To estimate this fraction, we counted the number of workers that exploited a feeder

at least once in the first 2 h after introduction of sugar water. We then counted the entire colony population with the aid of still images from video recordings of the nest interior. The results showed that an average of $24 \pm 8\%$ of the total worker population foraged.

RESULTS AND MODEL

Choosing between Unequal Feeders

For 12 colonies presented with unequal feeders, the better feeder had a significantly higher average number of feeding visits per observation (Wilcoxon signed-ranks test: $Z = -3.1$, $N = 12$, $P = 0.002$; Fig. 2a). This preferential exploitation was mirrored by a greater average recruitment effort to the better feeder ($Z = -2.9$, $N = 12$, $P = 0.003$; Fig. 2b). At peak exploitation, most colonies allocated the majority of foragers to the better feeder (Fig. 2c).

Choosing between Equal Feeders

When 14 colonies were presented with two equal feeders (0.8 M sucrose) there was no significant difference in average number of feeders per observation (Wilcoxon signed-ranks test: $Z = -1.7$, $N = 14$, $P = 0.084$; Fig. 3a) or average recruitment per observation ($Z = -1.8$, $N = 14$, $P = 0.065$; Fig. 3b). At peak feeding, colonies showed equal allocation to both feeders, with few colonies making a clear choice in favour of one feeder (Fig. 3c).

Responding to a Switch in Feeder Quality

When 20 colonies were initially presented with unequal feeders they allocated more foragers to the better one, just as in the first experiment. Both the average number of ants feeding (Wilcoxon signed-ranks test: $Z = -2.240$, $N = 20$, $P = 0.025$; Fig. 4a) and the average recruitment effort ($Z = 3.052$, $N = 20$, $P = 0.001$; Fig. 4b) were significantly greater at the better feeder, and it had the larger number of foragers at peak exploitation (Fig. 4c). When feeder quality was switched at about the 50 min mark, recruitment and exploitation at the formerly good feeder initially remained high. Within 20–30 min, however, tandem runs faded there and began towards the other, now superior feeder (Fig. 5). Exploitation similarly shifted, so that the average number of ants feeding at the newly good feeder exceeded that at the newly poor one ($Z = -3.472$, $N = 20$, $P = 0.001$; Fig. 4d).

On the other hand, there was no significant difference in average recruitment effort between the two feeders after the switch (Wilcoxon signed-ranks test: $Z = -0.616$, $N = 20$, $P = 0.538$; Fig. 4e). This was due to the initial continuation of tandem runs to the formerly good feeder, including runs that were initiated before the switch. These faded as their leaders arrived at the feeder and discovered its reduced quality. When we excluded observations during this 30 min transitional phase from the analysis, average recruitment in the remaining post-switch period was significantly greater to the newly good feeder than to the newly poor feeder ($Z = -3.000$, $N = 20$, $P = 0.003$). In spite of the lag in rerouting of recruitment, most colonies were ultimately able to allocate the majority of their foragers to the new location of the better feeder, as measured by the allocation of foragers at the time of peak feeding after the switch (Fig. 4f).

Model of Foraging Dynamics

How do colonies of *Temnothorax* achieve the decision making, allocation and flexibility demonstrated in our experiments? To answer this, we developed a simple mathematical model of a choice between two feeders, A and B. The model assumes three possible behavioural states for each ant: uncommitted, committed to feeder A, or committed to feeder B (Fig. 6). The model assumes that the numbers of ants committed to each feeder (X_A and X_B) depend on random discoveries, recruitment and attrition. The rates of change of X_A and X_B can be represented by the following ordinary differential equations:

$$\frac{dX_A}{dt} = \alpha(N - X_A - X_B) + \beta_A X_A(N - X_A - X_B) - \lambda_A X_A \tag{2}$$

$$\frac{dX_B}{dt} = \alpha(N - X_A - X_B) + \beta_B X_B(N - X_A - X_B) - \lambda_B X_B \tag{3}$$

This model has four parameters: N is the total number of potential foragers, α is the rate at which uncommitted ants independently discover a feeder, β_A and β_B are the recruitment rates to each feeder, and λ_A and λ_B are the attrition rates at each feeder. Ants that abandon a source become uncommitted and can make further discoveries or be recruited. From our data on individually marked ants, we estimated the following parameter values: α equals 0.0125 discoveries per ant per minute and does not depend on feeder quality, β equals 0.015 and 0.006 recruits per committed ant per minute for good and poor feeders, respectively; λ equals 0.009 and 0.038 for the good and poor feeders, respectively. We assumed N equals 100 foragers, based on a colony size of 400 ants.

The model was integrated numerically, using MatLab's ode45 function (MatLab, Mathworks, Natick, MA, U.S.A.), to describe the expected time course of feeder exploitation for the three experiments. For each experiment, the model reproduced the basic pattern seen in the data: clear preference for the better of two unequal feeders (Fig. 7), equal allocation to two equivalent feeders
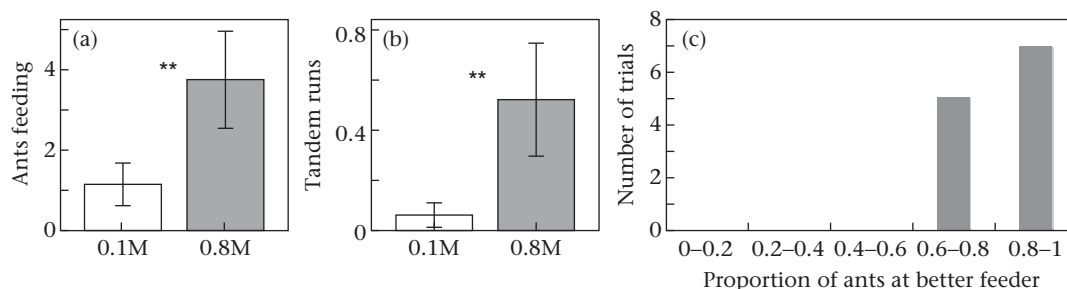
Figure 2. Collective choice by 12 ant colonies presented with unequal sucrose feeders. (a) Mean $\pm$ SE number of ants feeding per observation at a 0.1 M feeder (white) and a 0.8 M feeder (grey). (b) Mean $\pm$ SE number of tandem runs per observation. $**P < 0.01$. (c) Forager distribution at peak feeding time, defined as the observation with the highest total number of foragers at both feeders. Bars show the number of colonies with a given proportion of foragers at the better feeder. The skewed distribution shows strong preference for the better feeder.
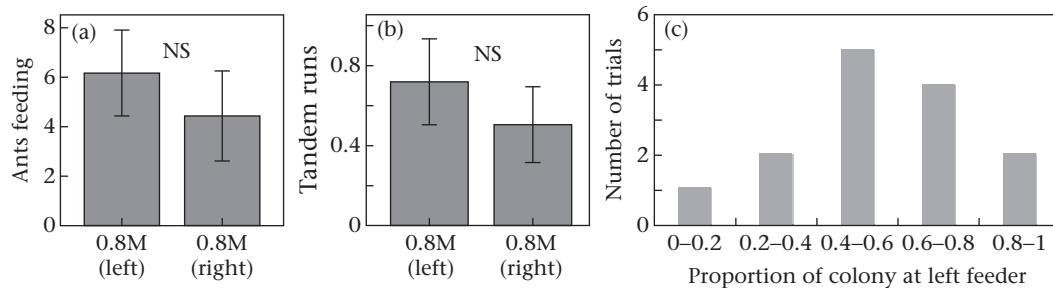
Figure 3. Collective choice by 14 ant colonies presented with identical 0.8 M sucrose feeders: (a) number of ants exploiting each feeder; (b) number of tandem runs to each feeder. (c) Forager distribution at the time of peak feeding. The single mode near 0.5 shows that colonies tended to allocate foragers equally between the feeders, rather than concentrating on only one of them.

(Fig. 8) and flexible reallocation when resources changed in quality (Fig. 9).

Because ordinary differential equation (ODE) models do not account for stochasticity and the discrete nature of individual ants, they might produce misleading results when forager number is low. To confirm the model's predictions, we therefore re-implemented it as an agent-based simulation, using the program NetLogo (Wilensky 1999). The model tracked 100 foragers, each of which could occupy the same three behavioural states used in the ODE. Transitions between states were governed by the same discovery, recruitment and attrition rules described above, implemented probabilistically at time steps representing 120 min. The results (not shown) closely matched those of the ODE model, except for the added noise expected in a stochastic simulation. The details and full implementation of this model are available in the OpenABM model library (http://www.openabm.org/models).

Recruitment Effort

The experimental results above showed more recruitment to good than to poor feeders, but they did not give actual numbers of tandem runs. This is because arenas were sampled intermittently, meaning that long runs might be counted more than once and short ones missed altogether. For accurate counts, we turned to the four trials with marked colonies used to estimate model parameters. During the first 60 min after food discovery, scouts initiated an average of 10.0 ± 2.7 tandem runs to the better feeder and 1.5 ± 0.9 tandem runs to the poor feeder. Tandem runs were usually initiated near the nest entrance, where the would-be recruiter stood still, apparently releasing a pheromone signal that attracted one or more interested followers. Often several ants would jostle to follow this leader, so that several short tandem run events might occur in a brief period. Usually, only a single follower would persist, but leaders sometimes led two ants concurrently to a feeder. Many tandem runs broke up before reaching their destination, but their followers often found the feeder soon after on their own. We therefore counted a run as successful if the follower discovered the feeder within 5 min of breakup. In the first 60 min after food discovery, we saw an average of 5.0 ± 2.7 successful runs to the better feeder and only 0.5 ± 0.5 successful runs to the poor feeder. This difference matches the pattern seen in the main experiments using a cruder measure of recruitment effort.

DISCUSSION

We have shown three important features of collective foraging behaviour by *T. rugatulus* colonies. First, they are effective decision-makers, readily choosing the better of two sucrose feeders. Second,
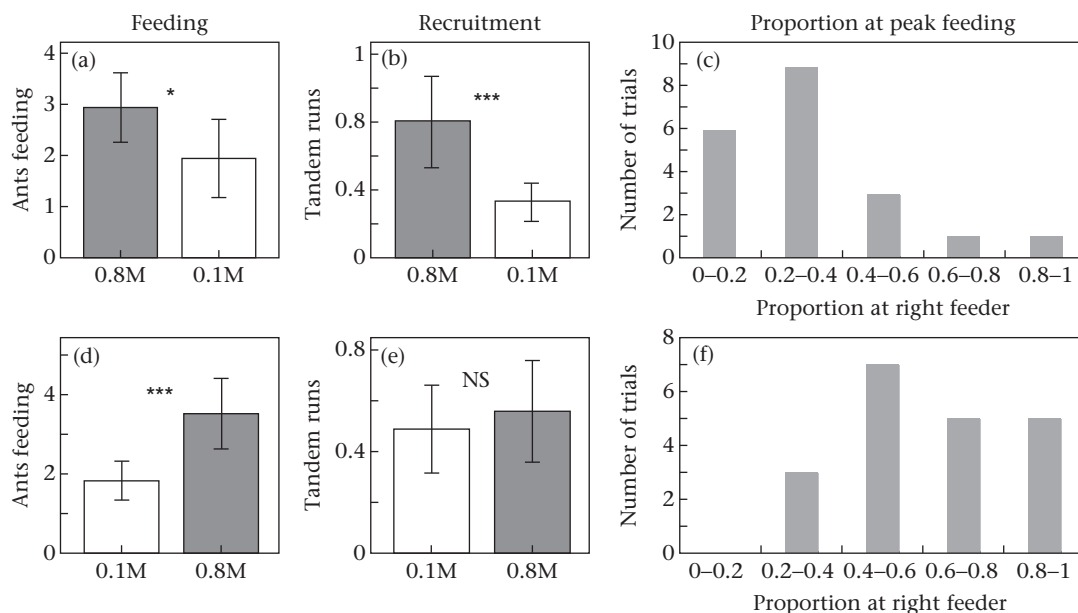

Figure 4. Response of 20 ant colonies to a change in relative quality of two feeders before and 60 min after the quality of the two feeders was switched, respectively: (a, d) numbers of ants feeding at each feeder; (b, e) number of tandem runs to each feeder; (c, f) forager distribution at the time of peak feeding. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
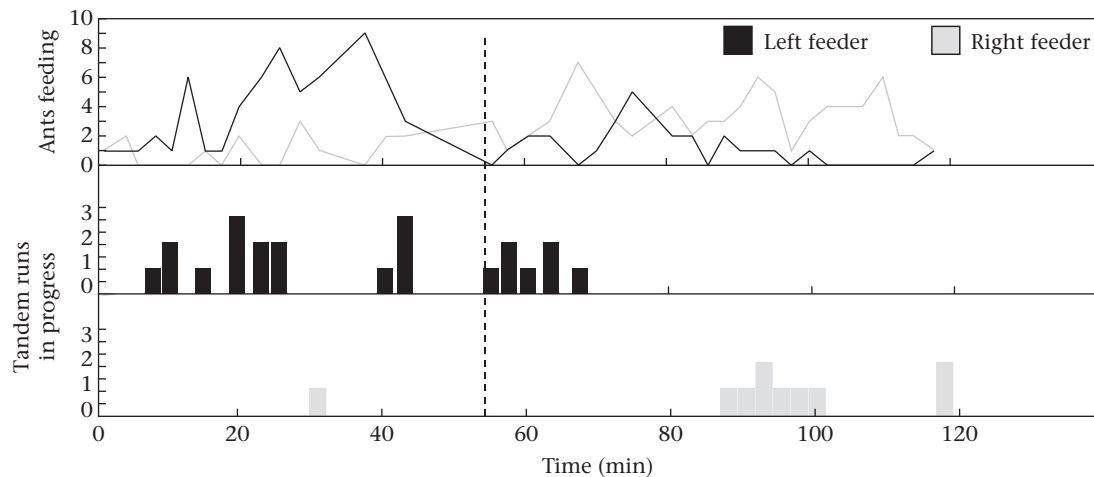
Figure 5. Detailed time course of feeder exploitation and recruitment by a single ant colony from the experiment presented in Fig. 4. The left feeder was initially better than the right one. When their quality was switched (dotted line), the relative number of ants exploiting each feeder was reversed. At first, tandem recruitment continued towards the left feeder, but was eventually replaced by recruitment to the newly superior right feeder.

they allocate foragers equally when presented with feeders of equal quality. Third, they flexibly reallocate exploitation following a change in feeder quality. Analysis of individual behaviour, combined with a mathematical model, shows that these features can be explained as an emergent property of simple individual rules. Foragers encounter feeders randomly and then make quality-dependent decisions about whether to exploit them and whether to recruit nestmates. By recruiting to good feeders with higher probability, and abandoning them with lower probability, they can collectively choose the better of two feeders, even without individual ants visiting both feeders and comparing them.

Our results confirm predictions of the nonlinearity hypothesis, which relates a group's collective behaviour to the mathematical relationship between recruitment effort and recruitment effectiveness. This hypothesis has yielded insights about the effects of highly nonlinear relationships, such as those found in mass

recruitment by pheromone trails (Beckers et al. 1990; Nicolis & Deneubourg 1999; Camazine et al. 2001; Detrain & Deneubourg 2008). Nonlinearity is expected to create consensus even when options do not vary, a prediction that has been confirmed many times (Beckers et al. 1990; Millor et al. 1999; Saffre et al. 1999; Sumpter & Beekman 2003). Our study expands this research by offering the first thorough analysis of a species with linear recruitment. Tandem runs summon recruits with an effectiveness that is directly proportional to recruitment effort. As a result, they should not create the strong information cascades that drive consensus in nonlinear systems. Our results confirm this prediction, finding equal allocation of foraging effort between equal options, rather than consensus on one. We further confirm two other predictions: (1) linear recruitment leads to differential exploitation of feeders of different quality, rather than exclusive focus on the better option; (2) linear recruitment allows colonies to track changes in relative option quality, rather than getting locked into an initial choice. The latter is a risk for species with highly nonlinear recruitment (Beckers et al. 1990; Detrain & Deneubourg 2008), although they may have other behavioural means to escape these traps (de Biseau et al. 1991; Dussutour et al. 2009a, b; Gruter et al. 2012; Latty & Beekman 2013).

Our results are consistent with previous work on honeybees, where waggle dance effectiveness also shows a linear relationship to recruitment effort (Seeley & Towne 1992; Sumpter 2010). Honeybees have not been subjected to a choice between two equal feeders, the most revealing test of the nonlinearity hypothesis. However, they do show both flexibility to changing conditions and forager allocation according to quality (Seeley et al. 1991; Seeley 1995). Both of these features have been argued to have adaptive value by allowing colonies to track patchy and ephemeral flower patches (Seeley 1995; Dornhaus & Chittka 2004; Donaldson-Matasci & Dornhaus 2012). The lack of strong consensus means that colonies can direct the bulk of their foragers to the best patches while continuing to monitor poorer ones. If these patches later improve, the colony can rapidly redirect foraging effort accordingly. Flower patches can have brief periods of maximum nectar productivity, making speedy reallocation particularly important to bees (Seeley 1985).

Temnothorax ants conceivably derive similar benefits, but too little is known of their foraging ecology to be sure. Alternatively, the emergent properties described above may not be selective drivers for the ants' reliance on linear recruitment. That is, they may use
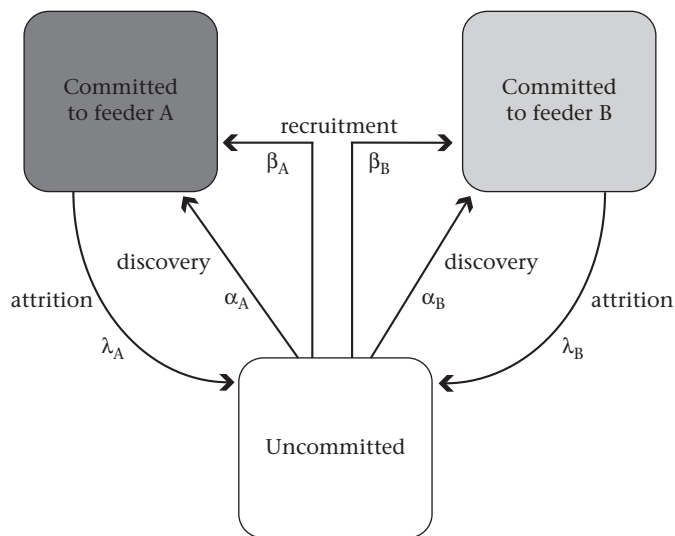

Figure 6. Model of ant foraging behaviour in the presence of two feeders. Boxes represent the three behavioural states that a forager can occupy: uncommitted, committed to feeder A, or committed to feeder B. Arrows indicate the ways that a forager can change state: uncommitted ants can discover a feeder at rate α, or be recruited by an already committed ant at rate β. Committed ants abandon their feeder at rate λ, returning to the uncommitted state. Both β and λ depend on feeder quality, but α does not.
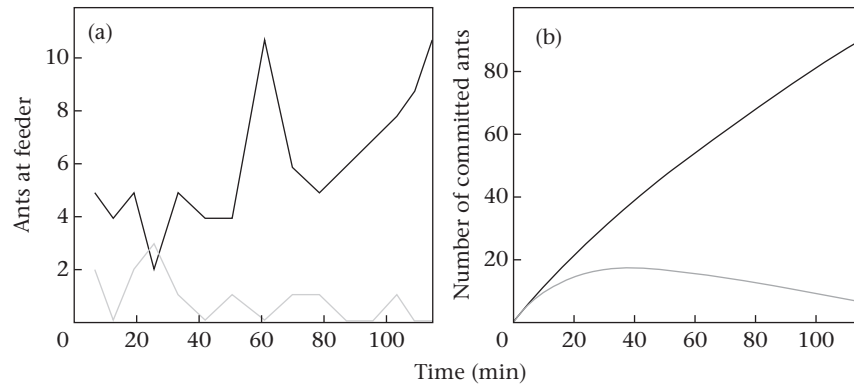
Figure 7. A simple behavioural model predicts colonies' choice of the better of two feeders. (a) Results for a single experimental colony presented with a good (0.8 M) and poor (0.1 M) sucrose feeder. Black and grey lines show numbers of ants feeding at the good and poor feeders, respectively. (b) An ordinary differential equation (ODE) implementation of the model in Fig. 6 predicted a similar predominance of exploitation at the better feeder. Absolute exploitation levels are higher for the model, because it measures the total number of ants committed to each feeder, while the data show only those ants that were currently at the feeder.

tandem runs not because of their linearity, but simply because they are an effective communication method for small colonies (Hölldobler & Wilson 2008; Dornhaus et al. 2012). Mass recruitment by pheromone trails can only be sustained with large populations (Beekman et al. 2001; Dornhaus et al. 2012), but *Temnothorax* colonies rarely number more than a few hundred workers, making tandem running a better way to share information about food sources. If tandem recruitment is primarily a result of small colony size, then the consequences of its linearity, including flexible reallocation of foragers, may be an epiphenomenon rather than an adaptation to unstable food resources.

Even for honeybees, allocation across multiple options is not always a desirable outcome. When a swarm chooses a site to build a new nest, consensus on a single option is vital to ensure an adequate workforce (Seeley 2010; Rangel & Seeley 2012). Like honeybees, *Temnothorax* are also cavity-nesters and face a similar need for consensus during house-hunting (Franks et al. 2002; Pratt et al. 2002; Visscher & Seeley 2007). Both groups have converged on a similar strategy to achieve consensus despite their linear recruitment: they add a nonlinear component in the form of a quorum rule (Pratt et al. 2002; Seeley & Visscher 2004). Scouts use waggle dances or tandem runs to attract more scouts to candidate sites. Once a site achieves a minimum number of adherents, its scouts switch to rapid movement of the passive bulk of the colony. This threshold effect mirrors the step-like growth in trail

attractiveness seen in mass-recruiting ants, and it has a similar consensus-building effect (Sumpter & Pratt 2009). The facultative use of a quorum may allow colonies to optimize their collective behaviour according to circumstances. Similar tunability is found in *L. niger*, where ants can adjust the degree of symmetry breaking by modulating the intensity of pheromone deposition (Portha et al. 2004).

The emergence of complex group patterns from nonlinear communication is one of the more revealing insights into collective behaviour of recent decades (Camazine et al. 2001; Sumpter 2010). A combination of theory and experiments has shown how nonlinear interactions between colony members are at the heart of self-organized phenomena including aggregation, collective decision making, nest construction and pattern formation (Camazine et al. 2001; Buhl et al. 2005; Jeanson et al. 2005; Detrain & Deneubourg 2008). Nonlinearity can generate rapid consensus on a single option, which may be advantageous when speed and unanimity are important, as in nest site selection by an exposed and vulnerable group. In other contexts, however, strong consensus may not be the most adaptive outcome. When, for example, a colony monitors many rapidly changing food sources, the greater flexibility and broader allocation given by linear interactions may be more beneficial. Even within the same society, linear and nonlinear recruitment can complement one another, each one adaptive in the appropriate circumstances.
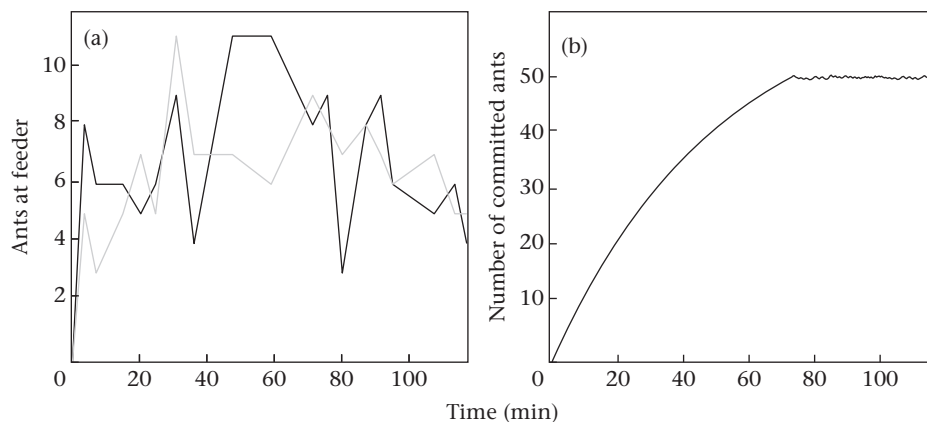

Figure 8. The behavioural model predicted equal forager allocation to feeders of equal quality. (a) Exploitation of two identical 0.8 M feeders by an experimental colony. (b) The ordinary differential equation (ODE) model predicted the observed pattern of equal exploitation (the two lines were identical and thus lie on top of one another).
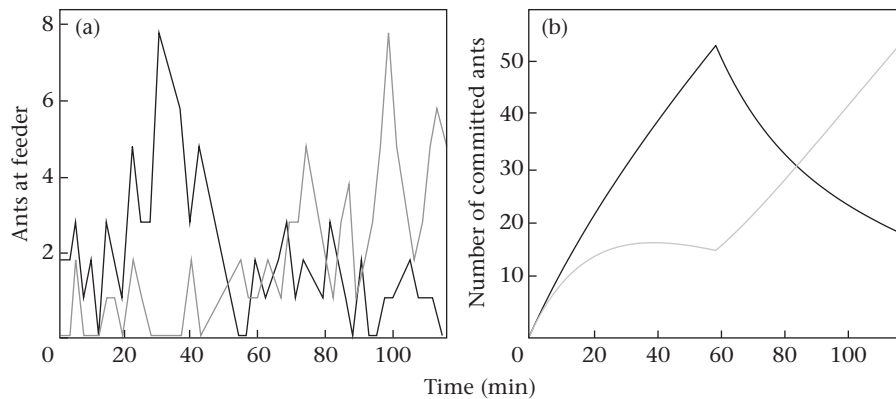
Figure 9. The behavioural model predicted the ability of ant colonies to track changes in resource quality. (a) Feeder exploitation by an experimental colony initially presented with a good feeder at the left (black line) and a poor one at the right (grey line). After the feeder qualities were reversed at 55 min, exploitation levels also reversed. (b) The ordinary differential equation (ODE) model predicted a similar switch.

Acknowledgments

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