REVIEW

D.J.T. Sumpter · S.C. Pratt

A modelling framework for understanding social insect foraging

Abstract The foraging of an insect society is a complex process involving large numbers of individuals collecting food from many different sources. Differential equation models have shown how quite simple communication mechanisms can produce complex and functional group-level foraging patterns. In this paper we review previous differential equation models for pheromone trails, honey bee dances and other methods of communication used during foraging. We develop a general framework for modelling social insect foraging systems that incorporates each of the previous models. This framework identifies the different behaviours that insects undertake while foraging, along with generalised rate functions that determine how the insects switch between behaviours. We describe how to tailor our framework to specific insect societies, by incorporating the details of specific behavioural mechanisms into appropriate expressions for rates of discovery of, recruitment to, and retirement from food sources. Our framework thus provides an experimental tool for improved understanding of the foraging behaviour of particular species, as well as a system for meaningful comparisons of foraging behaviour across species. We end this article by linking our framework to inclusive fitness theory. We demonstrate how understanding of the proximate mechanisms involved in social insect foraging ultimately furthers understanding, not only of how insect societies function, but also of how these mechanisms are used to optimise colony fitness and survival.

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Introduction

Many of the impressive examples of collective foraging seen in insect societies are self-organised, in that complex global patterns emerge from purely localised cues and signals among colony members (Bonabeau et al. 1997; Camazine et al. 2001; Seeley 1995). For example, although individual honey bee foragers follow only a small number of the waggle dances advertising flower patches, the colony can nonetheless focus its foraging effort on the most profitable patches (Seeley 1995). Similarly, certain ants deploy their foragers preferentially on the shorter of two paths, despite few if any individual insects directly comparing the paths (Beckers et al. 1992; Goss et al. 1989). How these adaptive colony-level patterns derive from local interactions between individuals is generally far from obvious.

Differential equations provide a promising tool for analysing the mechanisms underlying colony-level patterns, and they have frequently been applied to foraging by insect societies (Bartholdi et al. 1993; Beckers et al. 1990, 1993; Beekman et al. 2001; Bonabeau et al. 1997; Deneubourg et al. 1990; Goss and Deneubourg 1989; Goss et al. 1989; Nicolis and Deneubourg 1999; Seeley et al. 1991). The power of these models lies in their simple mathematical formalism for describing how populations change through time. The number of ants or bees foraging at a particular food source can be represented as a single variable that changes its value as the insects are recruited to and abandon the source. These recruitment and abandonment rates can be written as functions of the number of insects foraging at a source, waiting at the nest, or scouting for new sources. Different recruitment mechanisms – dances, pheromone trails, etc. – can be represented by appropriate rate functions to model the foraging system of a particular species.

Once specified, differential equation models can generate testable predictions about foraging systems. For example, a model predicted, and experiments confirmed, that honey bee colonies can switch their foraging effort to a good food source that is presented after foraging is

already well underway at another, inferior source (Camazine and Sneyd 1991; Seeley et al. 1991). When a similar experiment was performed on the ant *Lasius niger*, however, colonies remained trapped at the poor feeder (Beckers et al. 1990). A differential equation model was able to explain this inflexibility in terms of differences in the recruitment mechanisms used by the two species (Beckers et al. 1990). Because this result depended upon the different recruitment functions employed by ants and bees, purely verbal reasoning could not have yielded such non-intuitive experimental predictions.

In this paper we show how to derive differential equation models for the various types of foraging systems employed by social insects. We discuss critically how these derivations have been made previously and propose our own rate functions for recruitment mechanisms ranging from waggle dances to trail pheromones to tandem running to group recruitment. We place all of these mechanisms into a general modelling framework. This framework does not encompass every possible foraging system, although it does incorporate many of those currently known. Instead, we intend the framework as a guide to those researchers interested in modelling and understanding particular foraging systems. By providing a common framework, we allow for comparisons among many foraging systems, both those currently well understood, such as honey bees and *Lasius niger*, and those yet to be studied in detail.

While we concentrate here on the proximate understanding of social insect foraging, the use of our framework in comparing foraging systems will ultimately facilitate understanding of the function or survival value of group-level foraging strategies. Indeed, we conclude this paper with an example of how better understanding of the mechanisms underlying pheromone trail foraging by ants actually provides insight into the problem of optimising sexual reproduction. This example illustrates how mathematical models of proximate and ultimate causation complement each other and can be used together to further understanding of social foraging.

A state-based framework

Behavioural states

In our framework we define five different behavioural states. Colonies have access to n food sources (e.g. patches of flowers or sugar feeders). Each state has an associated variable, indexed by source where appropriate, representing the number of individuals in that state. The states (and corresponding variables) are:

1. Waiting (W) Waiting at the nest and available to start foraging. Examples include honey bees waiting on the dance floor to follow recruitment dances, or ants waiting near the nest entrance to be led to a food source.
2. Searching (S) Searching for food sources.

3. Exploiting (E_i) Exploiting food source i. Workers in this state do not directly recruit nestmates, although they may leave signals, such as pheromone trails, that increase the likelihood of other foragers finding the source.
4. Recruiting (R_i) Attempting to recruit nestmates to food source i. Recruitment in this sense involves actively leading one or more workers, or directly communicating to nestmates the location of a food source, rather than leaving chemical signals in the environment.
5. Following (F_i) Attempting to follow recruiters to food source i. This encompasses not only literal following of recruiters, but also independent search for a source advertised by a dance or other signal.

Foraging models may include other states, such as resting at the nest or transferring food from foragers to a storage area. We do not model these behaviours, but it should become clear how they could be incorporated.

Flow between behavioural states

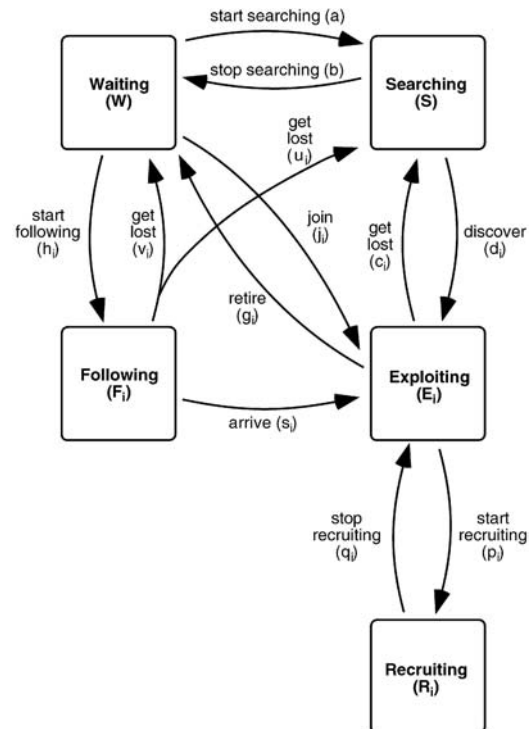We next describe the rates at which individuals change between states, as shown in Fig. 1. A waiting worker (W)

Fig. 1 Flow diagram for behavioural state variables. *Boxes* represent behavioural states, while *lines* connecting states indicate rate of flow of workers between states. *Arrows* indicate direction in which individuals change states. For example, a is the rate at which ants waiting at the nest become activated to search, j_i is the rate at which individuals become exploiters through indirect recruitment (e.g. following a pheromone trail), and h_i is the rate at which ants are recruited directly (e.g. through dances or tandem running)

can become an exploiting forager at source i (E_i) through three different routes. Firstly, she might be activated to search (through function a), and then discover the food source (through d_i). Secondly, she might be led toward the food source through direct contact or communication (h_i) with another worker, arriving (s_i) only if the communication is successful. Finally, she might reach a food source by following an indirect signal, such as a pheromone trail (through j_i).

The function j_i represents indirect recruitment, where successful foragers influence their environment in a manner that increases the chance of nestmates finding the food. The classic example is leaving a pheromone trail from the nest to a food source, (e.g. Hölldobler and Wilson 1978; Rickli and Leuthold 1986; Wilson 1962). Indirect recruitment also includes depositing or releasing volatile pheromones near the food source to attract searching workers, as in ants (Hölldobler et al. 1978), honey bees (Free and Williams 1970a, b) and some stingless bees (Kerr 1994). The function f_i represents direct recruitment, where successful foragers either physically lead nestmates to the food source or directly communicate, in the nest, the location of the source. Examples include tandem running in ants (Hölldobler et al. 1974; Moglich et al. 1974), and the waggle dance of the honey bee (Frisch 1967). Group recruitment in ants is also best described this way, even though it involves the laying of a pheromone trail. This is because the trail alone is insufficient to recruit nestmates, who will leave the nest only if led by the recruiting ant. Direct recruitment also includes less complex forms of communication, as when certain stingless bees convey the odour of a food source to their nestmates, who can then use this information to find the source (Kerr 1969).

In terms of flow between states, the difference between direct and indirect recruitment is subtle but important: workers recruited indirectly by a pheromone trail for the first time are largely indistinguishable from those following the same trail for a second or subsequent time. Workers recruited directly, in contrast, have need of the recruiter's information only when they are first being led to or searching for the source. Thus, models of direct recruitment require a distinct state (F_i) to represent this initial phase of following a leader or signal.

The population of workers in the nest, W, increases as searchers are deactivated (b), exploiters retire from foraging (g_i), and followers get lost and return to the nest (v_i). Conversely, the population decreases as nest workers are activated to search (a), as they are led by indirect recruitment signals to become exploiters (j_i), and as they begin to follow direct recruitment to various food sources (h_i). Combined, these give the following differential equation:

$$\frac{dW}{dt} = \text{stop searching} + \text{retire} + \text{get lost}$$
$$- \text{start searching} - \text{join exploiters} - \text{start following}$$
$$= b + \sum_{i=1}^{n} g_i + \sum_{i=1}^{n} v_i - a - \sum_{i=1}^{n} j_i - \sum_{i=1}^{n} h_i \qquad (1)$$

where the summations indicate the gain and loss from all n sites. The searching population increases as nest workers are activated (a) and as ants get lost while following direct recruitment to a site (u_i) or while exploiting a site (c_i). The population decreases as searchers deactivate (b) and as they discover sites (d_i). Thus

$$\frac{dS}{dt} = \text{start searching} + \text{get lost} - \text{stop searching} - \text{discover}$$
$$= a + \sum_{i=1}^{n} u_i + \sum_{i=1}^{n} c_i - b - \sum_{i=1}^{n} d_i \qquad (2)$$

The population of exploiting workers increases as workers arrive through direct recruitment (s_i), follow indirect signals from the nest (j_i) and discover the site (d_i). It decreases as workers retire (g_i) and get lost (c_i). Exploiting workers may spend a proportion of their time engaged in direct recruitment. This proportion is determined by the rates at which they begin direct recruitment (p_i) and stop recruiting to exploit again (q_i). The equations for exploiting and recruiting workers are thus

$$\frac{dE_i}{dt} = \text{arrive} + \text{join exploiters} + \text{discover} + \text{stop recruiting}$$
$$- \text{retire} - \text{get lost} - \text{start recruiting} \qquad (3)$$
$$= s_i + j_i + d_i + q_i - g_i - c_i - p_i \quad \text{for all } i \in \{1, \dots, n\}$$

$$\frac{dR_i}{dt} = \text{start recruiting} - \text{stop recruiting}$$
$$= p_i - q_i \text{ for all } i \in \{1, \dots, n\} \qquad (4)$$

The population of workers following a recruitment signal to a site increases with recruitment (h_i) but decreases as workers arrive at the food source (s_i) or get lost, either to begin searching (u_i) or to return to the nest (v_i):

$$\frac{dF_i}{dt} = \text{start following} - \text{get lost} - \text{arrive}$$
$$= h_i - v_i - u_i - s_i \quad \text{for all } i \in \{1, \dots, n\} \qquad (5)$$

Equations 1, 2, 3, 4, 5 express a very general model of social insect foraging. By determining the form of each of the functions – a, b, h_i, etc. – we can express models for particular species. In doing so, we will considerably simplify the equations, but by keeping each model in the context of the general framework we can better understand the functional similarities and differences among the mechanisms.

Activation and deactivation

We begin by considering the rate at which workers start searching for food. Each worker may start independently or may be influenced by her nestmates.

Self-activation

Self-activation (and deactivation) occurs when workers start (and stop) searching independently of the behaviour of other colony members. In this case, the rate of activation is a linear function of the number of workers waiting in the nest W

$$a(W) = \lambda W \tag{6}$$

where $1/\lambda$ is the average time an individual worker waits in the nest before searching. Similarly, the rate of deactivation is a linear function of the number of searching workers S:

$$b(S) = \gamma S \tag{7}$$

where $1/\gamma$ is the average time a worker spends searching before returning to the nest.

Arousal

In many species, including some wasps (Jeanne 1980), and many stingless bees (Kerr 1969), successful foragers perform a motor display that arouses nestmates but does not direct them to food sources. In this case the search rate depends on the number of recruiting foragers. For $n=2$ food sources, we have:

$$a(R_1, R_2, W) = (\mu_1 R_1 + \mu_2 R_2)W \tag{8}$$

where μ_i determines the rate of recruitment, and the R_is are the number of workers performing the calling display. The amount of arousal per individual (i.e. how effectively she arouses other workers) may depend on the strength of the food source – i.e. if food source 1 is better than food source 2 then $\mu_1 > \mu_2$.

Independent discovery

When searchers work independently of each other, without any kind of recruitment, as in desert ants of the genus *Cataglyphis* (Wehner et al. 1983), then the rate of discovery depends linearly upon the number of searchers. In general, if the mean time until an individual finds source i is $1/\alpha_i$ then the rate of discovery for the population as a whole is

$$d_i(S) = \alpha_i S \tag{9}$$

Since nearly every species of social insect engages in some form of independent search or scouting, this is an important term in foraging models. Independent discovery is of most interest, however, when it occurs in conjunction with recruitment.

How much recruitment effort does a forager make?

In Fig. 1 direct recruitment to site i is represented by the h_i function, which will usually depend on the number of recruiters R_i. The amount of time workers spend recruiting depends on the functions p and q, the rate at which workers switch between direct recruitment and exploitation. For example, a honey bee's foraging trip consists of a journey to the food source, a period of unloading, possibly rest, and a bout of dancing. The dancing part of this trip is considered the time performing direct recruitment.
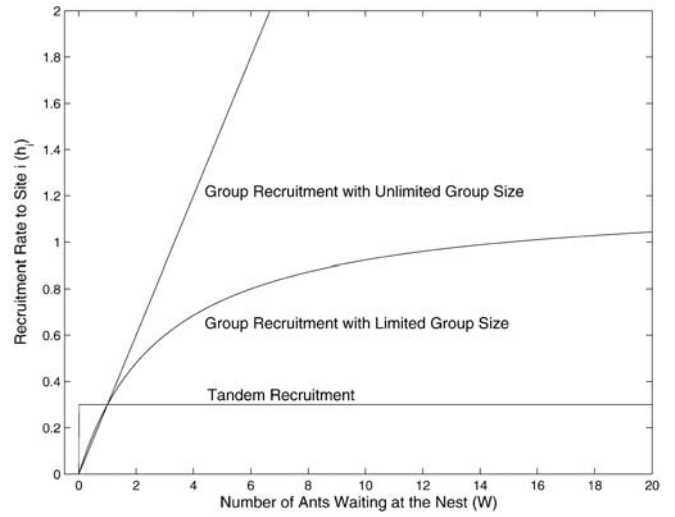

Fig. 2 Plots of tandem recruitment (Eq. 12), group recruitment with unlimited group size (Eq. 13) and group recruitment with limited group size (Eq. 14). The parameter and variable values for these plots are $R_i=3$, $\mu_i=0.1$, $k=3$ and $G=4$

If a bee dances for a proportion $\rho_i/(\rho_i+\delta_i)$ of each trip to site i, then

$$p_i(E_i) = \rho_i E_i \tag{10}$$

$$q_i(R_i) = \delta_i R_i \tag{11}$$

models the rate that the bees switch between direct recruitment and exploitation. This rate may depend on food source quality, with foragers at better sites spending more time recruiting. Species with no direct recruitment (e.g. those using only pheromone trails or independent scouting) have $p_i=q_i=0$.

Direct recruitment

Recruitment via leading

In many ants (Hölldobler and Wilson 1990) and stingless bees (Kerr 1969), successful foragers directly lead one to several nestmates from the nest to the food source. The simplest form for h_i assumes that workers in the nest are led to a site in proportion to the number of recruiters:

$$h_i(R_i, W) = \begin{cases} \mu_i R_i, & W > 0 \\ 0, & W = 0 \end{cases} \tag{12}$$

where μ_i is the rate of recruitment by each recruiter to site i. This functional form – plotted in Fig. 2 – models the tandem running behaviour of many ants, in which a single worker at a time is led to the food source, (e.g. Agbogba 1984 ; Hölldobler et al. 1974 ; Moglich et al. 1974). Provided there is a worker waiting at the nest, then a returning forager is able to lead a tandem run to the food source. Equation 12 thus assumes that the rate at which workers follow tandem runs is independent of the number of workers available to follow (provided

$W>0$). This assumption is based on observations of 'tandem calling' where the leader of a tandem run first attracts available nestmates by releasing a pheromone signal within the nest (Moglich 1979; Moglich et al. 1974). Such attraction ensures that, until the supply of foragers in the nest is depleted, it is the number of leaders that limits the rate at which they are followed.

The assumption that recruitment rate is mostly independent of W does not necessarily hold for group recruitment, where recruiters lead more than one worker from the nest (e.g. Hölldobler 1971). The size of the group of followers is likely to depend on the number of workers in the nest. In this case, Beckers et al. (1990) suggest that the functional form of h_i should be

$$h_i(R_i, W) = \mu_i R_i W \qquad (13)$$

where $\mu_i W$ is now the rate of recruitment by each recruiting worker. While this form of h_i does ensure that group size is correlated with the number of workers in the nest, it does not take into account practical limits on group size (see Fig. 2). An alternative model that includes such limits – and also has the mathematical advantage of being a continuous function – is

$$h_i(R_i, W) = \mu_i R_i \frac{W}{K + W} G \qquad (14)$$

where G is the mean recruited group size when the number of workers in the nest is large and K is the level of W which gives a group size of $\frac{1}{2} G$ (see Fig. 2). In general, the functional form of h_i should be determined experimentally. In particular, the relationship between recruited group size and the number of available workers in the nest should be established empirically, and an appropriate h_i chosen to fit the data.

Competition among food sources

Equations 12, 13, 14 all assume that the proportion of workers going to a particular site is not directly affected by recruitment to other sites – i.e. h_i is a function of R_i and W but not of R_j for any site $j \neq i$. As the number of sites is increased, so too is the rate at which workers are recruited from the nest. In many cases, however, recruiters for different sites compete for a limited number of potential followers. For example, most unemployed honey bee foragers wait on the dance floor to follow dances of returning foragers, and the rate of recruitment to a particular site depends both on the number of waiting bees (W) and the proportion of bees dancing for each of the various sites (R_i) (Seeley 1995). These elements are incorporated in the following extension of a model of bee foraging due to Camazine and Sneyd (1991) for two available forage sites ($n=2$):

$$h_1(R_1, R_2, W) = \lambda \frac{R_1}{R_1 + R_2 + K_0} W \qquad (15)$$

$$h_2(R_1, R_2, W) = \lambda \frac{R_2}{R_1 + R_2 + K_0} W \qquad (16)$$
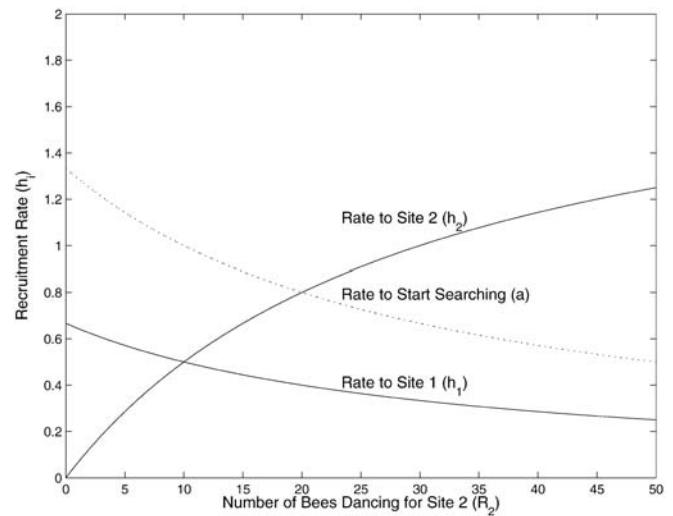

Fig. 3 Plots of rate of dance recruitment determined by Eqs. 15, 16, 17 with $W=20$, $\lambda=0.1$, $R_1=10$ and $K_0=20$

$$a(R_1, R_2, W) = \lambda \frac{K_0}{R_1 + R_2 + K_0} W \qquad (17)$$

where $\lambda>0$ is – as in Eq. 6 – the overall rate at which bees leave the nest, and is proportional to the number of bees in the nest (i.e. $a+h_1+h_2=\lambda W$). The constant K_0 determines how many bees search instead of following dances.

Equations 15, 16, 17 reflect the observation that bees on the dance floor randomly sample a single dance from those performed, then attempt to follow that dance to the food source (Seeley and Towne 1992). When there are few recruiting bees, unemployed bees are more likely to scout for food without following dances (Seeley 1995). Fig. 3 shows that, when R_1 and R_2 are small in comparison to K_0, then a is large and most unemployed bees will scout. As R_2 increases in magnitude, a decreases and the number of waiting bees following dances increases.

Recruitment via odour cues

Bee species in which workers respond to flower odours borne by returning foragers can also be considered direct recruiters. For example, bumble bees aroused by a successful forager fly preferentially to flowers which produce the odour carried by the forager (Dornhaus and Chittka 1999). This phenomenon can be modelled with a functional form similar to that of group recruitment – i.e., with Eq. 13 or 14.

Indirect recruitment

The most dramatic form of indirect recruitment is mass recruitment by trail pheromones in ants and termites. Trails can summon searchers already searching for food,
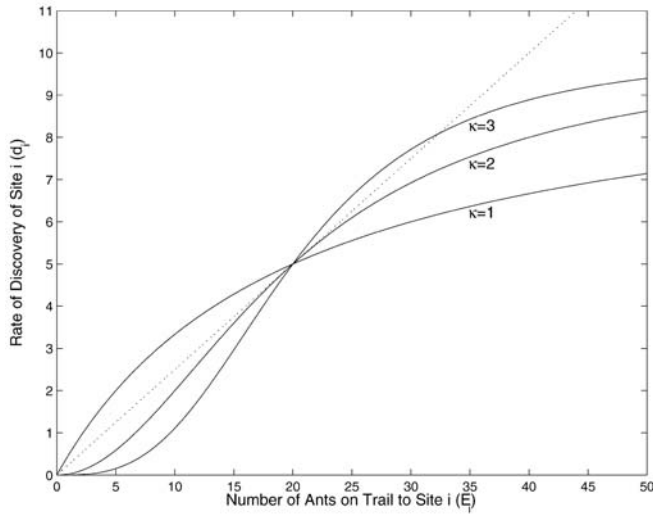
Fig. 4 The rate of site discovery as a function of the number of workers already foraging at (and hence depositing a trail to) a site. The relationship is given by Eq. 18, with $\beta_i=0.1$, $k_i=1$, $S=100$, $K_*=20$ and κ ranging between 1 and 3. The *dotted line* is the linear recruitment function given by equation 36, with $\beta=\beta_i/(2K_*)$

Fig. 5 The rate of joining one of two pheromone trails, or instead searching, as a function of the number of workers already foraging at site two. The relationship is given by Eqs. 20, 21, 22, with $\lambda=0.1$, $W=20$, $K_*=20$, $E_1=10$ and $\kappa=2$

as well as workers waiting at the nest. We consider each type of recruit in turn.

Effect of trails on searchers

The discovery of the food source by searchers (d_i) depends upon the amount of pheromone deposited on trails to site i. Most models of pheromone foraging assume that the concentration of a pheromone trail varies over the same time scale as the number of workers on the trail – in our case, E_i (Bonabeau 1997). We use a general sigmoidal curve to model how the number of workers discovering a site increases with the number of workers depositing a pheromone trail to the site (Fig. 4). This form easily allows the incorporation of non-linear effects, and also takes into account the likelihood that a trail's effectiveness saturates at higher pheromone concentrations.

$$d_i(E_i, S) = \beta_i \frac{(k_i E_i)^\kappa}{(k_i E_i)^\kappa + K_*^\kappa} S \qquad (18)$$

β_i is a constant determined by the rate at which searchers find the pheromone trail, while κ, k_i, and K_* determine the relationship between the number of workers on the trail and the probability that searchers join the trail which they have found. K_* determines the number of ants on the trail at which d_i reaches its midpoint; κ determines the nonlinearity of the response; k_i takes into account the different amount of pheromone a forager may add to a trail, depending on the quality of the food source she has visited (e.g. Beckers et al. 1993; Breed et al. 1987; Hangartner 1969). For any particular case, these parameters should be determined experimentally (e.g. Deneubourg et al. 1990).
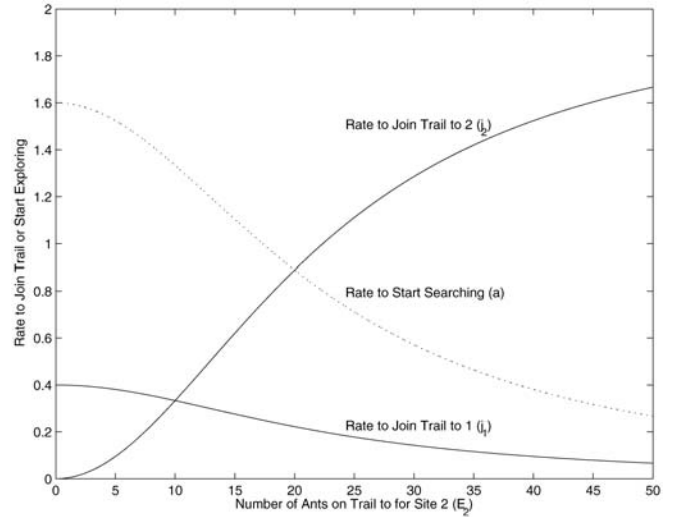
Effect of trails on ants at the nest

Unlike searchers, ants joining trails at the nest entrance may take any one of the trails currently active, because every trail leads back to the nest. In experiments where workers leaving the nest are forced to choose one of n paths to a food source – by offering the workers a choice of bridges to the source – the proportion of workers joining each path i has been modelled as

$$j_i(E_1, \ldots, E_n, W) = \lambda \frac{(k+E_i)^\kappa}{\sum_{j=1}^n (k+E_i)^\kappa} W \qquad (19)$$

where k and κ are constants and E_i is the number of workers already on route i (Deneubourg et al. 1990; Nicolis and Deneubourg 1999). This model has been successfully tested experimentally for *Tetramorium caespitum* (Pasteels et al. 1987) and *Myrmica sabuleti* (de Biseau et al. 1991).

In a natural setting, when workers are not forced by the topology of their foraging arena into choosing one trail or another, some of the workers leaving the nest will search instead of joining a trail. When there are two food sources,

$$j_1(E_1, E_2, W) = \lambda \frac{(k_1 E_1)^\kappa}{(k_1 E_1)^\kappa + (k_2 E_2)^\kappa + K_*^\kappa} W \qquad (20)$$

$$j_2(E_1, E_2, W) = \lambda \frac{(k_2 E_2)^\kappa}{(k_1 E_1)^\kappa + (k_2 E_2)^\kappa + K_*^\kappa} W \qquad (21)$$

$$a(E_1, E_2, W) = \lambda \frac{K_*^\kappa}{(k_1 E_1)^\kappa + (k_2 E_2)^\kappa + K_*^\kappa} W \qquad (22)$$

models the rate at which they join the two separate trails (j_1 and j_2) or instead search (a). These recruitment functions are plotted in Fig. 5. This situation is similar to that

modelled for direct recruitment by honey bees (Eqs. 15, 16, 17). Indeed, the honey bee model is identical to the trail model, with $\kappa=1$. (Compare the curves for j_2 etc. in Fig. 5 with those for h_2, etc. in Fig. 3) The ant model must include the possibility of $\kappa>1$, because, unlike the bees, who sample only a single dance, ants can potentially show a non-linear recruitment response. Deneubourg et al. (1990) provide empirical evidence that $\kappa=2$ for the Argentine ant, *Linepithema humile*.

Note that in Eqs. 20, 21, 22, when a large number of ants are on the two trails, recruitment becomes so strong that no workers will search – i.e. as $E_1+E_2\to\infty$ then $a\to0$. In many cases this does not accurately model real ants, where some ants will ignore even very strong trails and search by themselves. To model this we set

$$a(E_1, E_2, W) = \lambda \frac{K_*}{E_1^\kappa + E_2^\kappa + K_*} W + \lambda_* W$$

where λ_* is a small proportion of workers that never follow trails. This last term, which is biologically realistic and can greatly affect the structural stability of the equations, has often been omitted from models of ant foraging – see for example Bonabeau (1997).

Arousal Combined with Pheromone Trail

Equations 20, 21, 22 for pheromone trail recruitment from the nest assume that workers leave the nest and join trails at a constant rate. However, some ant species use a display or physical contact to alert nest members to the presence of a trail (e.g. Pratt 1989; Traniello 1977). This combined arousal and trail gives the recruitment model

$$j_1(E_1, E_2, R_1, R_2, W) = \mu \frac{k_1 E_1^\kappa}{k_1 E_1^\kappa + k_2 E_2^\kappa + K_*} (R_1 + R_2) W \quad (23)$$

$$j_2(E_1, E_2, R_1, R_2, W) = \mu \frac{k_2 E_2^\kappa}{k_1 E_1^\kappa + k_2 E_2^\kappa + K_*} (R_1 + R_2) W \quad (24)$$

$$a(E_1, E_2, R_1, R_2, W) = \mu \frac{K_*}{k_1 E_1^\kappa + k_2 E_2^\kappa + K_*} (R_1 + R_2) W \quad (25)$$

These equations may also apply to some stingless bees that similarly combine pheromone trails and arousal within the nest (Kerr 1969). For some ant species, such as *Solenopsis invicta* (Wilson 1962), the trail itself arouses the ants in the nest. This is modelled by replacing the R_is in Eqs. 23, 24, 25 with E_is, since arousal is dependent on trail strength rather than the number of recruiting workers.

Other indirect recruitment mechanisms

In the simplest forms of indirect recruitment, foragers deposit pheromone marks near the food source (e.g. Kerr 1969), or release a short-range chemical signal (e.g. Hölldobler et al. 1978). These can be modelled simply by adapting Eq. 9 to make the discovery rate d_i dependent on the number of ants exploiting a source, as well as the number of searchers:

$$d_i(S, E_i) = \beta_i E_i S \quad (26)$$

where β_i is a constant giving the rate at which searchers find a food source marked by one exploiter.

This kind of recruitment is often combined with arousal of nestmates, through motor displays, sounds, or short-lived trails (e.g. Kerr 1969; Moglich and Hölldobler 1975; Traniello 1977). These cases can be modelled by combining Eq. 26 with Eq. 8 describing the rate at which ants in the nest are aroused to search.

Failure and abandonment

Retirement

The simplest sort of abandonment of a forage site is retirement. Exploiting workers stop foraging independently of the actions of other workers and return to wait in the nest. This is modelled simply as

$$g_i(E_i) = \sigma_i E_i \quad (27)$$

where $1/\sigma_i$ is the average time until a worker decides to retire from site i. Retirement from sites is very important in the organisation of honey bee foraging, because foragers retire from low quality sites more rapidly than from higher quality sites (Seeley et al. 1991). Those retiring are then available to be recruited to the better quality sites.

Retirement is not always independent of the actions of other colony members. It also occurs, for example, when a food source becomes overcrowded. For a food source with capacity K_i

$$g_i(E_i) = \sigma_i \frac{E_i}{K_i - E_i} \quad (28)$$

describes a negative feedback loop ensuring that the population exploiting the feeder never exceeds K_i provided that initially $E_i < K_i$.

Success of direct recruitment

Social insects following recruitment signals do not always arrive at the advertised destination. For example, honey bees usually follow about four dances before successfully locating a forage patch (Seeley 1983; Seeley and Visscher 1988). Success or failure of direct recruitment is reflected in our model by the functions s_i and u_i (see Fig. 1). Typically,

$$u_i(F_i) = \theta_i F_i \quad (29)$$

$$s_i(F_i) = \phi_i F_i \quad (30)$$

where θ and ϕ are respectively the rates of getting lost and successfully finding source i. The proportion of successfully recruited workers is then $\phi_i/(\theta_i+\phi_i)$. Followers

which fail to reach their destination do not necessarily become searchers. For example, failed honey bee recruits will return to the nest to read further dances. In this case, $u_i=0$ and

$$v_i(F_i) = \theta_i F_i \tag{31}$$

instead. Bees do not always find the site advertised by the dance they have followed, but instead find another site. The model can take this into account by having u depend both on the advertised site, i, and the other site which may be found, j:

$$u_{ij}(F_i) = \theta_{ij} F_i \tag{32}$$

which is the rate at which bees searching for site i find site j.

Failure to follow pheromone trails

Experimental observations of *Myrmica rubra* showed that the average distance a forager travels along a pheromone trail before losing it first increases and then saturates as trail strength is increased (Pasteels et al. 1986, 1987). The probability that an individual worker leaves a pheromone trail is thus negatively correlated with the number of workers currently on the trail. Furthermore, the probability of leaving is independent of the time spent on the trail by the worker. The rate at which workers lose a trail to food source i is thus,

$$c_i(E_i) = \frac{\sigma_i E_i^{\upsilon}}{K^{\upsilon} + E_i^{\upsilon}} \tag{33}$$

where σ_i depends on the distance to i, and K and υ, which should be determined experimentally and may vary among species, measure how accurately the workers follow a trail. For any particular species, the values of K and υ are likely to equal those of K_* and κ (in Eq. 18), since both model reaction to trail strength.

Case studies

Ant pheromone trails

In an experimental setup where ants are forced to take one of two or more routes to a food source, Eq. 19, for trail joining, and Eq. 27 for retirement give

$$\frac{dE_i}{dt} = \lambda \frac{(k+E_i)^{\kappa}}{\sum_{j=1}^{n} (k+E_i)^{\kappa}} W - \sigma_i E_i \quad \text{for all } i \in \{1, \ldots, n\} \tag{34}$$

$$\frac{dW}{dt} = -\lambda W + \sum_{j=1}^{n} \sigma_j E_i \tag{35}$$

as recruitment equations for the number of ants foraging at the n sites. Analysis of this model, given in detail by Nicolis and Deneubourg (1999), leads to the prediction that some species of ants, when already foraging at a mediocre food source, will be unable to switch to a better

food source that is offered later, even if scouts discover the latter food source. This inflexibility depends on the respective rates of recruitment (λ) and retirement from the various sites (σ_i). A number of experiments have been performed to investigate how such inflexibility might manifest itself in real ant colonies (Beckers et al. 1990; Pasteels et al. 1987).

Often, in order to analyse a set of foraging equations, it is useful to simplify them. For example, Beekman et al. (2001) use the discovery function

$$d_1(E, S) = \beta E S \tag{36}$$

for ants directed to a single food source by pheromone trails. This simplification of Eq. 18 ignores the saturation which occurs for well attended trails in the rate of joining a trail. However, in nature trails seldom reach the point of saturation, and for a range of values the simplified function – shown as the dotted line in Fig. 4 – approximates Eq. 18. A model for search and discovery which combines the simplified function with random discovery of food sources and a simple non-linear term for losing the trail, is

$$\frac{dE}{dt} = (\alpha + \beta E) S - \frac{\sigma E}{K + E} \tag{37}$$

$$\frac{dS}{dt} = \frac{\sigma E}{K + E} - (\alpha + \beta E) S \tag{38}$$

In this model it is assumed that ants not on the trail are searching, so that the number of searching plus exploiting ants is constant. In the next section we will analyse this model and compare it to experiments on the effect of colony size in ants.

The waggle dance of the honey bee

Differential equations have also been successfully applied to the modelling of honey bee foraging (Camazine and Sneyd 1991; Seeley 1995; Seeley et al. 1991). In this work, a model was developed by first considering the different behaviours that constitute nectar foraging: the collection and unloading of nectar, and the performance and following of recruitment dances. The rates at which bees switched between these behaviours were established experimentally for two feeders containing sugar solution of differing strengths (Seeley et al. 1991). It was then possible to make reasonably accurate qualitative and quantitative predictions of how the distribution of bees between two feeders changed as the quality of the feeders was changed.

As with models of pheromone trail following, the Camazine and Sneyd (1991) model contains a number of simplifcations that facilitate mathematical analysis. For example, while they use Eqs. 15, 16, 17 to model dance recruitment, they assume that $K_0=0$ so that all bees follow dances and no bees scout. While it makes little difference to the qualitative behaviour of their model, this assumption increases the rate at which small numbers of

bees recruit to a food source, and may cause the model to predict faster growth in the number of bees at a good feeder than actually occurs in experiments (compare Figs. 2 and 5 in Seeley et al. 1991).

Another simplification made by Camazine and Sneyd (1991) is the omission of a behavioural state equivalent to our following to site i (F_i). They instead define a single state that includes both the time spent following dances at the nest, and the time spent searching for an advertised site. The combination of these states means that the site at which a bee arrives depends on the number of bees performing dances at the *end* of her search. In reality, however, this decision is made at the *start* of the search, when the bee reads a specific dance. A bee usually searches for more than 15 min before either arriving at a food source or returning to the nest to read another dance (Seeley 1995). In our framework this decision mechanism can be modelled by including the state F_i and the rates h_1 and h_2 defined in Eq. 15 and 16.

We take the above observations in to account when fitting Camazine and Sneyd's (1991) model into our general framework. The specific model for honey bee foraging in this framework is thus

$$\text{In the hive}: \frac{dW}{dt} = \sigma_1 E_1 + \sigma_2 E_2 + \theta_1 F_1 + \theta_2 F_2 - \lambda W + \gamma S \quad (39)$$

$$\text{Looking for site}: \frac{dF_1}{dt} = \lambda \frac{R_1}{R_1 + R_2 + K_0} W - \theta_1 F_1 - \phi_1 F_1 \quad (40)$$

$$\frac{dF_2}{dt} = \lambda \frac{R_2}{R_1 + R_2 + K_0} W - \theta_2 F_2 - \phi_2 F_2 \quad (41)$$

Independent scouts :

$$\frac{dS}{dt} = \lambda \frac{K_0}{R_1 + R_2 + K_0} W - (\alpha_1 + \alpha_2) S - \gamma S \quad (42)$$

$$\text{Exploiting site}: \frac{dE_1}{dt} = \phi_1 F_1 + \alpha_1 S - \sigma_1 E_1 - (\rho_1 E_1 - \delta_1 R_1) \quad (43)$$

$$\frac{dE_2}{dt} = \phi_2 F_2 + \alpha_2 S - \sigma_2 E_2 - (\rho_2 E_2 - \delta_2 R_2) \quad (44)$$

$$\text{Dancing for site}: \frac{dR_1}{dt} = \rho_1 E_1 - \delta_1 R_1 \quad (45)$$

$$\frac{dR_2}{dt} = \rho_2 E_2 - \delta_2 R_2 \quad (46)$$

In the next section we demonstrate a numerical simulation of this model for parameter values estimated from the literature.

Insight from the model

The purpose of mathematical models is to better understand and predict properties of the systems they model. While the design of a model often clarifies our thinking about the system, it is only by determining how it behaves that new insights into the model, and thus the system, can be obtained. There are two complementary approaches to understanding mathematical models: analysis and numerical simulation. Analysis is most often used to elicit general features of the model while numerical simulation is applied to determine more specific features; such as behaviour under experimentally determined parameters. Usually, both approaches should be pursued. Simulation without analysis can lead to results without understanding, while analysis without simulation is often insufficient for discovering the more interesting properties of a model.

Analysis

Analysis of differential equations is a massive research area in its own right. One of the most accessible accounts of the application of differential equations to biology is by Edelstein-Keshet (1988). Here, we discuss only the most basic techniques, which are sufficient to analyse our model of pheromone trail foraging in the section Ant pheromone trails (above).

Simplifying the equations

The first step of analysis is often to simplify the equations. This involves reducing both the number of different variables (e.g. the states E and S) and parameters (e.g. α and σ) to a minimum while not changing the behaviour of the model. Simplification may also involve ignoring parameters which have very small values relative to the other parameters. Our pheromone foraging model – given by Eqs. 37 and 38 – can be simplified both by noting that the number of ants $N=E+S$ remains constant and by *non-dimensionalisation* (see Edelstein-Keshet (1988) for details of this procedure). Non-dimensionalisation involves establishing new time and quantity scales. For Eqs. 37 and 38 the equivalent non-dimensional equation is

$$\frac{dx}{d\tau} = f(x) = a + bx - cx^2 - \frac{x}{1+x} \quad (47)$$

where

$$x = \frac{E}{K}, \ \tau = \frac{t}{\sigma}, \ a = \frac{\alpha N}{\sigma}, \ b = \frac{K(\beta N - \alpha)}{\sigma} \text{ and } c = \frac{\beta K^2}{\sigma}$$

This formulation shows there are three fundamental parameters governing the behaviour of our ant foraging model and illustrates how changes in our five parameters can produce equivalent behaviour from the model. For example, for fixed α, setting the parameters to $\beta=0.01$, $\sigma=0.1$, $K=10$ and $N=100$ is equivalent to setting $\beta=0.001$, $\sigma=1$, $K=100$ and $N=1,000$.
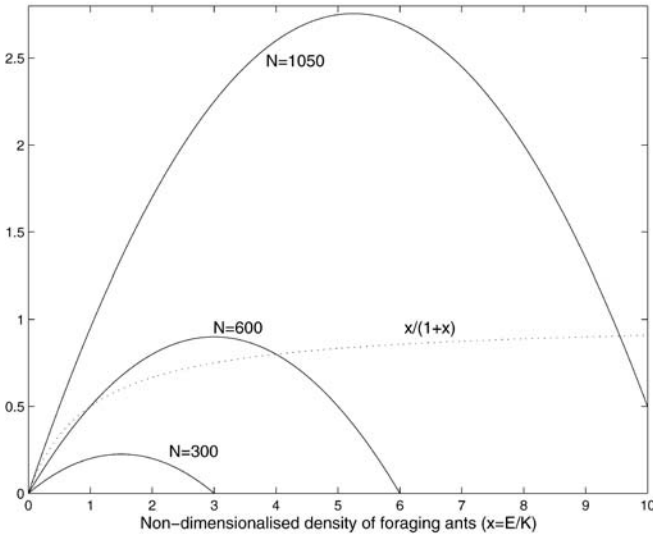
Fig. 6 Plots of quadratic function $a+bx-cx^2$ (*solid line*) for various values of N and the saturating function $x/(1+x)$ (*dotted line*). Where these two plots cross is a steady state of Eq. 47 governing the number of ants exploiting a given food source. The plots cross once for $N=300$ and $N=1,050$ and three times for $N=600$. For all plots, $\alpha=0.0$, $K=100$, $\sigma=1$ and $\beta=0.00001$

Fig. 7 Number and position of steady states of Eq. 47 as a function of N. *Solid lines* are stable steady states, while *dotted lines* are unstable steady states. At $N=\sqrt{4\sigma/\beta}-K$, Eq. 47 switches from having a single steady state at 0 to having three (two stable and one unstable). At $N=(\alpha+\sigma/K)/\beta$ the zero steady state becomes unstable. Parameters, other than N, are identical to those given in Fig. 6

Steady states and stability

We will answer the question "given the parameters and $x(0)$ ants foraging initially, will the ants form a strong pheromone trail to the feeder if given enough time?". The answer to this question is the *steady state* of a differential equation, which is reached when the variables no longer change – i.e. when

$$\frac{dx}{d\tau} = 0 \text{ or equivalently } a + bx - cx^2 = \frac{x}{1+x}$$

Figure 6 shows three qualitatively different solutions to this equality, depending on the parameter values: the point at which the solid and dotted lines cross is a steady state. In general, Eq. 47 has either one, two or three positive steady states. If we set $\alpha=0$, so that there are no random finds of the food source, then the steady state solutions, x_*, are determined by

$$bx_* - cx_*^2 = \frac{x_*}{1+x_*}$$

This gives steady states at $x_*=0$ and, in terms of our original parameters:

$$x_* = \frac{1}{2K}\left(N - K \pm \sqrt{(N+K)^2 - \frac{4\sigma}{\beta}}\right) \tag{48}$$

These non-zero steady states exist when
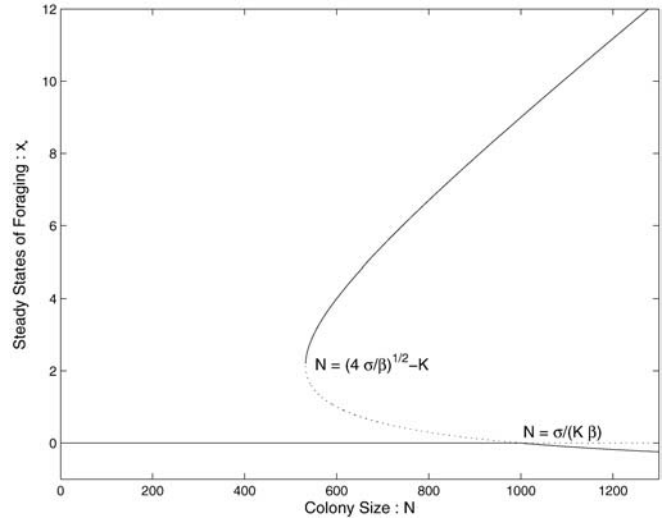
$$N > \sqrt{\frac{4\sigma}{\beta}} - K$$

The stability of a state is determined by considering whether small perturbations to a system resting in a particular steady state will shrink or grow. A steady state, x_* is stable (again see Edelstein-Keshet 1988 for details) if

$$\left.\frac{df}{dx}\right|_{x=x_*} < 0$$

i.e. we differentiate f, as defined in Eq. 47, and evaluate the resulting function with $x=x_*$. Thus, for our current example, $x_*=0$ is stable provided $N<(\alpha+\sigma/K)/\beta$.

We can now determine the stability of all the steady states. Figure 7 shows the steady states and their stability as a function of the colony size N. Note that Fig. 7 is essentially a plot of the values at which $a+bx-cx^2$ crosses $x/(1-x)$ found as we smoothly increase the value of N. In Fig. 7, $\beta=0.001$ and $\alpha=0$, so the steady state at which no ants forage at the feeder becomes unstable when the number of ants in the colony reaches $N=1/\beta=1,000$. According to our model, for colonies of more than 1,000 ants, discovery of the food source by a single ant will result in many ants foraging at the food source in the long term. For smaller colonies the same small perturbation will not ultimately result in an increase in foraging.

It is now possible to answer our original question regarding the long term dynamics of ant foraging. In particular, by drawing a diagram such as Fig. 7 we can determine a unique steady state number of ants foraging at the feeder for any given initial conditions: the population at the feeder will move directly up or down to the stable steady state through a trajectory which does not cross an unstable steady state.

One interesting feature of Fig. 7 is that for some parameter values – N between $\sqrt{4\sigma/\beta}-K$ and $\sigma/(K\beta)$ – the ultimate number of ants foraging at the feeder depends critically on the initial number of foragers. For example, if $x(0)$ is between the 0 steady state and the unstable steady state then the population will reach equilibrium at 0, while if $x(0)$ is above the unstable steady state the population will reach equilibrium at the upper stable steady state, corresponding to a large number of foragers exploiting the food source. This prediction has been confirmed experimentally for Pharaoh's ants by Beekman et al. (2001), who showed that while colonies of 700 ants were unable to create a trail to a food source, workers initially placed at the food could sustain a trail to the nest. Indeed, the foraging ability of Pharaoh's ant colonies has a relationship to colony size qualitatively similar to that shown in Fig. 7.

Numerical simulation

While differential equations have been fruitfully applied to understanding the qualitative aspects of social insect foraging, their application to quantifying changes in the behavioural states of foragers has been less successful. The main reason for this failure is the high level of accuracy required for a model to make quantitative predictions. While Eqs. 37 and 38 have been shown to capture the non-linear increase in foraging ability with colony size, they do not include enough detail to predict exactly how many ants will arrive at the feeder for any particular colony size. Creating a quantitative model requires careful experiments to determine the exact functional form and parameter values for all the mechanisms of recruitment, retirement, etc.

Camazine and Sneyd's (1991) model of honey bee foraging effectively captures many of the qualitative aspects of foraging. It shows, for example, that a law of competitive exclusion operates on food sources, with the best site ultimately attracting all of the foraging bees. Seeley et al. (1991) also use this model to make quantitative predictions about the outcome of switching the relative quality of two feeders, and thus the amount of time spent dancing for each by foragers from an experimental colony. The observed rapid change in the distribution of bees between the feeders is accurately predicted by the model.

The case study of honey bee foraging, presented in the previous section, is closely related to Camazine and Sneyd's (1991) model, but adjusted to fit into our general framework. The principle differences are that our model includes the terms S for scouting bees and F_1 and F_2 for bees using the information given in a dance to search for a source. Our revised model can be compared to Camazine and Sneyd's model and to the data through numerical simulations. Figure 8 shows such a simulation of our revised model – given by Eqs. 39, 40, 41, 42, 43, 44, 45, 46 – with parameter values taken from experimental data. These simulations were produced by the differential equation solver in Matlab (Pärt-Enander and Sjöberg 1999).
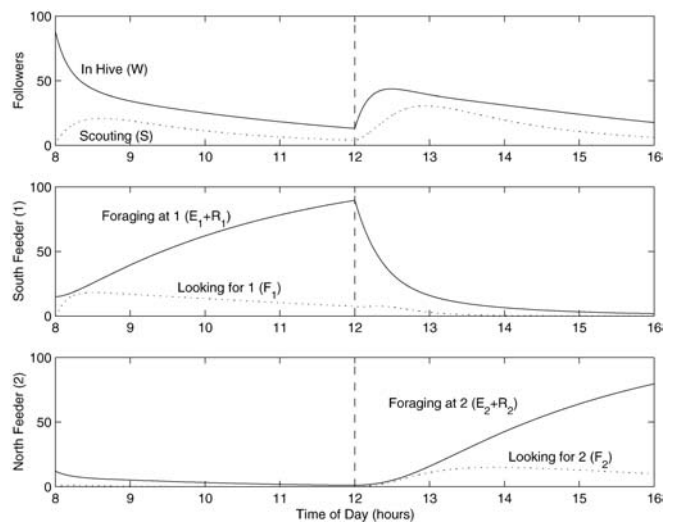

Fig. 8 Simulation of honey bee foraging. Numerical solution of Eqs. 39, 40, 41, 42, 43, 44, 45, 46. As in the Seeley et al. (1991) experiment the simulation begins with $E_1(0)=15$ and $E_2(0)=12$. We set $W(0)=125-15-12=98$ since 125 bees different bees visited the feeder throughout the duration of the experiment. Initially the south feeder is of highest quality, but at midday the quality of the two feeders is swapped. The parameter values are taken from the literature: $\sigma_1=0.000$, $\sigma_2=0.040$, $\rho_1=0.286$, $\rho_2=0.122$, $\delta_1=0.667$ and $\delta_2=3.333$ are derived from the parameter values presented in Seeley et al. (1991). $\theta_1=\theta_2=0.067$ and $\phi_1=\phi_2=0.0167$ to reflect the observation of Seeley (1995) that bouts of foraging last 15 min, and the observation that a bee takes, on average, 60 min to find a food source (Seeley et al. 1991). $\gamma=0.0083$ to reflect the longer search time of scouting bees (Seeley et al. 1991). We set $K_0=3$ to reflect Seeley's (1995) observation that colonies with only one dancing bee have 36% of bees scouting, while colonies with five dancing bees have only 5% scouts. Finally, $\lambda=0.050$, so that bees spend 20 min resting between foraging bouts. To reflect the changing of the feeder qualities at midday, each of the parameter values for the two sites are swapped (e.g. after midday, $\sigma_1=0.040$ and $\sigma_2=0.000$)

Although the results of our revised model largely mirror experimental observations and the predictions of Camazine and Sneyd's (1991) model, there are several important differences. In our revised model, the slow initial increase in bees visiting feeder 1 better matches observations (from Fig. 2 of Seeley et al. 1991) than Camazine and Sneyd's model. We can surmise that this slower, and more accurate, increase is due to the addition of a behavioural state S for scouting. Indeed, by setting $K_0=0$ and rerunning the simulations, we can restore the rapid increase given by the Seeley and Camazine model (Seeley et al. 1991). The revised model fails, however, to produce the same speed of response to changing feeder quality as found in experiments and in Camazine and Sneyd's model. This failure resulted from the addition of the terms F_1 and F_2 for following. Thus the addition of terms for greater realism has paradoxically reduced the accuracy of our model's predictions. This strongly suggests that the mechanism by which bees produce the response to changing conditions is not yet understood at a level that allows quantitative mathematical modelling.

The preceding discussion highlights an important advantage of developing a mathematical model in a frame-

work: particular states can be included or excluded, simulated and compared to the data in order to better understand the actual mechanisms at work. A recent review by Biesmeijer and de Vries (2001) correctly points out that there are a larger number of behavioural states involved in honey bee foraging than are captured by Eqs. 39, 40, 41, 42, 43, 44, 45, 46. Beismeijer and de Vries (2001) provide a flow chart for the behavioural control structure of a single forager which could easily be used to give a differential equation model of bee foraging. Indeed, Biesmeijer and de Vries (1998) used part of this flow chart as the basis of an individual-based computer simulation which they claim more accurately reproduces experimental results than Camazine and Sneyd's (1991) model. These results still require experimental verification, and once more data is available, the construction of appropriate differential equation and individual-based models will further advance our understanding of honey bee foraging. This may well involve the addition of further behavioural states to our framework to account for memory of foraging bees.

Optimal allocation of resources to foraging

The models that we discuss in this paper aim to understand the proximate mechanisms underlying a colony's foraging behaviour. It is important, however, to place our understanding of these proximate mechanisms in the context of the selective forces ultimately shaping colony behavior. Indeed, experiments and models of proximate mechanisms tell us only "how" a system works and not "why" it works. For example, while the experiments of Beekman et al. (2001) confirmed a prediction of our case study – that pheromone trail foraging ants require a minimum colony size to function efficiently – these experiments cannot in themselves explain the size distribution that has evolved in trail-laying ants. To find such an explanation, we must consider our experiments and proximate models in the light of inclusive fitness theory (Crozier and Pamilo 1996).

A recent paper by Reuter and Keller (2001) considered how workers and queen can maximise their inclusive fitness by investing in sexuals and workers. To this end they defined a productivity function $b(f,w)$ where f is the proportion of resources invested in females, and w is the proportion of those females that are workers (i.e. fw is the overall investment in workers). They then proposed the following inclusive fitness function for colony member X

$$V_X(f, w) = b(w, f) \left(g_{fX} \frac{f(1-w)}{F(1-W)} + 0.5 g_{mX} \frac{1-f}{1-F} \right) \quad (49)$$

where $F(1-W)$ and $1-F$ are the population biomass of gynes (queens) and males respectively, and g_{fX} and g_{mX} are the relatedness of X to females and males, respectively. The optimal strategy for member X is defined by the values of f and w which maximise V_X (Reuter and Keller 2001).

By combining the above inclusive fitness function with our earlier model of ant pheromone trails, we can estimate the optimal investment in workers by colonies
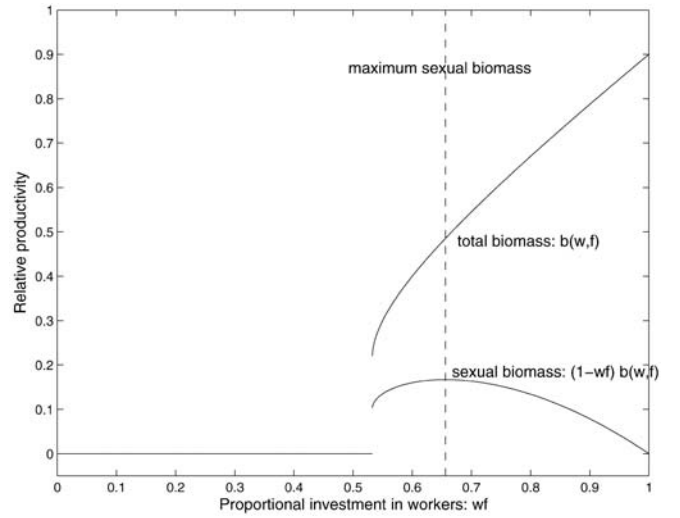

Fig. 9 Productivity as a function of investment in workers for ants foraging via trail pheromones, given by Eq. 50. Parameter values as in Fig. 7. *Solid lines* indicate total biomass and sexual biomass. The *vertical dashed line* indicates the value which maximises sexual biomass and is thus the evolutionarily stable strategy for single party control

that use this foraging mechanism. To achieve this we define a productivity function based on Eq. 48, which shows how foraging efficiency depends on x_*, the maximum number of ants foraging at a food source at stable equilibrium.

$$b(w, f) = \begin{cases} \frac{1}{2N} \left(wfN - K \pm \sqrt{(wfN + K)^2 - \frac{4\sigma}{\beta}} \right), \\ 0, \end{cases}$$
$$wfN\sqrt{\frac{4\sigma}{\beta}} - K \quad (50)$$
$$\text{otherwise}$$

Here we have assumed that intake of food is proportional to overall productivity. This assumption is speculative but allows us to investigate how the minimum colony size required by pheromone trail foraging ants might affect the fitness of different parties in the colony.

Maximising $V_X(f,w)$ with respect to f and w gives the optimal investment in workers, gynes and males for trail foraging colonies. The solid lines in Fig. 9 show how the colony's production of total biomass, $b(w,f)$ and sexual biomass, $(1-wf)b(w,f)$, change with investment in workers. The vertical dashed line indicates the evolutionary stable strategy (ESS), i.e. the maxima of $V_X(f,w)$ assuming that a single party (either the queen or the workers) controls both the primary sex ratio, f, and the proportion of females becoming workers, w. Since the maxima of $(1-wf)b(w,f)$ and $V_X(f,w)$ coincide, we conclude that single party control favours maximisation of sexual biomass. The outcome is quite different, however, if the queen controls f and the workers control w. In that case, the conflict over sex ratio generated by relatedness asymetries between queens and workers leads to an ESS investment in workers that is *less* than the value that maximises sexual biomass (Reuter and Keller 2001). The

dashed line thus shows the maximum possible investment by the colony in workers, under the assumption of no conflict. Any conflict will move the dashed line, and thus the investment in workers, to the left.

Unsurprisingly, optimal investment in workers is above the minimum level at which a colony can work efficiently. What is interesting, however, is how close to the minimum the optimum lies. If colony conflict is taken into account, the optimal investment would move nearer still to that critical minimum level. Thus, selection does not favour larger worker biomass per se. On the contrary, the evolutionary stable strategy is to optimise production of sexuals by generating a worker biomass sufficient to allow successful pheromone trail foraging.

Conclusions

We have presented a general framework for applying differential equations to the analysis of foraging by insect societies. Differential equations have proven quite useful in dissecting complex foraging systems where the behaviour of the whole colony is difficult to predict intuitively from the behaviour of individual insects. Still, detailed analyses have been carried out for very few species, and many groups with quite complex recruitment communication, such as stingless bees and termites, remain largely unstudied. We hope that our approach will facilitate the application of differential equation modelling to a broad range of species. Indeed, our approach is general enough to encompass many examples of social foraging in vertebrates, such as information centres in co-operatively breeding birds (Galef and Giraldeau 2001), and recruitment trails in rodents (Galef and Buckley 1996).

The study of proximate mechanisms in insect societies has sometimes been contrasted with optimality models that predict the foraging decisions animals should make in order to maximise their fitness (Beckers et al. 1990). A better description would see the two methods as complementary approaches. Indeed, mechanistic models have a potentially large role in guiding the development of better functional models. The study of optimal foraging has frequently been criticised for failing to take into account constraints imposed by morphology and physiology (Janetos and Cole 1981; Ward 1992). The importance of such constraints is now generally recognised in the study of foraging by individuals. For example, an expanding literature on the neurobiological basis of learning and memory in birds has helped to inform the study of the fitness consequences of their decision-making (Capaldi et al. 1999; Clayton 1998; Clayton and Soha 1999).

Analogous physiological constraints also matter in social foraging, but to them is added an entirely new level of mechanistic complexity: the colony-level behaviours that emerge from interactions among individual insects. We concluded this paper with a simple example in which such a physiological constraint, i.e. minimum colony size, has been identified by experiment, modelled as a proximate mechanism, and then incorporated into an inclusive fitness model. Building mathematical models which capture the working of insect societies thus gives a foundation for more realistic optimality models. Conversely, optimality models give a structure within which to interpret mechanistic studies of particular species. Models of ultimate and of proximate factors thus build on each other, ultimately connecting, rather than contradicting, one another.

Appendix 1

Notation

The notation for behavioural states and rates of flow between states can be seen in the flow diagram in Fig.1. Below we give a list of the specific parameters used in the models with their biological meaning.

- λ = rate at which workers leave the nest to search
- γ = rate at which searching workers return to the nest
- μ_i = rate of recruitment by workers recruiting to site i
- α_i = rate of independent discovery of site i
- ρ_i = rate at which exploiting workers start recruiting to site i
- δ_i = rate at which workers recruiting to site i start exploiting
- G = mean recruited group size when number of workers at nest is not limiting
- K = number of ants in nest at which half maximum group size is recruited
- K_0 = number of recruiters at which half departing foragers begin searching
- K_* = number of ants on trail to site i which will induce half departing foragers to follow trail to site i
- k_i = strength of pheromone deposited to site i
- κ = non-linearity in response to pheromone of ants following a trail
- β_i = rate at which searchers find trail to site i
- σ_i = rate of retirement of ants exploiting site i
- θ_i = rate of getting lost for ants following recruitment signal to site i
- ϕ_i = rate of finding site i for ants following recruitment signal
- υ = non-linearity in response to pheromone of ants following a trail

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