



A flexible model of foraging by a honey bee colony: the effects of individual behaviour on foraging success

Melissa D. Cox, Mary R. Myerscough*

School of Mathematics and Statistics, University of Sydney, NSW2006, Australia

Received 14 May 2001; received in revised form 16 January 2003; accepted 1 February 2003

Abstract

This paper develops and explores a model of foraging in honey bee colonies. The model may be applied to forage sources with various properties, and to colonies with different foraging-related parameters. In particular, we examine the effect of five foraging-related parameters on the foraging response and consequent nectar intake of a homogeneous colony. The parameters investigated affect different quantities critical to the foraging cycle—visit rate (affected by g), probability of dancing (m_{pd} and b_{pd}), duration of dancing (m_{circ}), or probability of abandonment (A). We show that one parameter, A , affects nectar intake in a nonlinear way. Further, we show that colonies with a midrange value of any foraging parameter perform better than the average of colonies with high- and low-range values, when profitable sources are available. Together these observations suggest that a heterogeneous colony, in which a range of parameter values are present, may perform better than a homogeneous colony. We modify the model to represent heterogeneous colonies and use it to show that the most important effect of heterogeneous foraging behaviour within the colony is to reduce the variance in the average quantity of nectar collected by heterogeneous colonies.

© 2003 Elsevier Science Ltd. All rights reserved.

Keywords: Genetic variance; Mathematical model; *Apis mellifera*; Polyandry

1. Introduction

Many social insect species are known to exhibit polyandry. Honeybees are the most profligate in this respect, with *Apis mellifera* mating approximately 10–20 times (Estoup et al., 1994) and *A. dorsata* up to an estimated 70 times (Oldroyd et al., 1996). This is despite some clear costs to multiple mating. Notably, polyandry decreases the average relatedness between workers, thus diminishing the genetic benefits of eusociality to the workers (Hamilton, 1972).

Polyandry must therefore imbue considerable benefits to offset these costs. Several possible benefits have been postulated (reviewed in Palmer and Oldroyd, 2000), the most plausible of which fall into the category of “genetic variance” hypotheses (Crozier and Page, 1985; Keller and Reeve, 1994). These argue that a genetically heterogeneous colony is either better protected against

misfortune (e.g. disease (Liersch and Schmid-Hempel, 1998), diploid brood (Page, 1980)) or better adapted to exploiting a wider range of environmental circumstances (e.g. type and availability of forage sources (Calderone and Page, 1988; Oldroyd et al., 1993)) than a homogeneous colony.

We wish to investigate the latter, in relation to the foraging response of a honey bee colony to a number of sources. To do this, we need to know which aspects of foraging behaviour may be genetically determined, and how much variation occurs between bees. Further, we must investigate how such genetically determined foraging parameters affect the colony-level foraging dynamics. In this paper, we identify key foraging parameters and construct a mathematical model to explore the impact of each parameter on foraging dynamics, and on the energy intake of colonies, under a range of foraging conditions. We extend the model to investigate the effect of multiple subfamilies.

The premise of this model is that different subfamilies (patrilines) vary in one or more parameters related to foraging. We assume here that this variance may be considered as a variance in response thresholds—for

*Corresponding author. Tel.: +61-2-9351-3724; fax: +61-2-9351-4534.

E-mail address: m.myerscough@maths.usyd.edu.au (M.R. Myerscough).

example, different subfamilies will dance for sources of lower or higher profitability, so may be considered to vary in thresholds related to dancing. Thus, this model may be considered to fall into the category of fixed threshold model that has been explored previously (Bonabeau et al., 1996, 1998). These studies have demonstrated that in combination with the concept of a task stimulus (that decreases in intensity the more a task is performed), differences in thresholds are sufficient to generate division of labour within an abstract “colony”.

In addition to the theoretical attention that response threshold models have received, there is a body of empirical evidence to support the existence of such thresholds and their effect on division of labour. In particular, response thresholds to sucrose have been measured by monitoring the honey bee’s proboscis-extension reflex (PER) (Page et al., 1998). This reflex occurs when a droplet of liquid is touched to the antennae of a restrained bee. Different bees respond at different sucrose concentrations, some responding to water alone. Using this test, an effect of genotype on response thresholds has been demonstrated: foragers from a high-pollen strain have a lower response threshold than foragers from a low-pollen strain, both before and after a foraging trip (Page et al., 1998). Further, these differences are evident in young bees that have not yet commenced foraging (Pankiw and Page, 1999), dismissing the possibility that the response thresholds are a consequence of foraging experience, rather than a cause of foraging behaviour. Finally, PER response thresholds of 1-week-old bees are correlated with observed foraging behaviour of the same bees 2–3 weeks later (Pankiw and Page, 2000): those with the lowest thresholds became water foragers, followed by pollen foragers then nectar foragers. Bees that returned empty after a foraging trip were without exception bees with the highest response threshold, suggesting that they had not encountered a nectar source of sufficiently high sucrose concentration to meet their threshold.

The current model investigates the effect of genotypic differences in the foraging rate or in various parameters of the dancing response, as functions of source profitability.

The model we explore is a system of nonlinear differential equations. Such a system has been used previously to model honey bee foraging behaviour (Camazine and Sneyd, 1991; Seeley et al., 1991), and Camazine and Sneyd’s model is the starting point for this model. Alternative approaches to modelling honey bee foraging dynamics have been used, notably the individual-oriented (i-o) model of de Vries and Biesmeijer (1998), which is a good choice of formalism for identifying the consequences of behaviour belonging to specific individuals. However, in this model we are concerned primarily with properties of the whole

colony, such as colony fitness. Thus, the differential equation approach is a suitable choice.

The model of Camazine and Sneyd (1991), as it stands, is not suitable for investigating the effects of environmental factors (such as appearance and disappearance of foraging sources) or colony factors (such as the existence of two or more subfamilies) on the dynamics of foraging; nor does it associate any measure of “fitness”, by which different distributions could be compared, with a particular distribution of foragers at forage sites. The first step, then, is to devise a differential equation model, inspired by Camazine and Sneyd’s model, but more suitable for exploring the effects of properties of the source (rate of nectar flow, sucrose concentration, distance from hive) and of the foragers’ behaviour (such as threshold at which they may dance for or abandon a source). We use this model first to explore the effect of different behaviour on a homogeneous population and then, in later sections, extend the model to examine the effects of heterogeneity in foragers’ behaviour.

2. The model

2.1. Fundamental differential equations

Let us consider a colony with a pool of n_f potential foragers. Out of this pool, there will be a number of bees F which will be actively foraging and a number U which will be unemployed foragers. If there are m sources of nectar which the colony can use, then we can indicate symbols which relate to activity at source j by using j as a superscript. Hence, F^j is the number of bees actively foraging at source j and

$$n_f = U + F^1 + F^2 + \dots + F^m. \quad (1)$$

We assume that n_f is constant and that U and F^j change with time, t .

Bees carry out a foraging cycle (flying to source, collecting nectar, returning to the hive, unloading and then dancing or resting) on a time-scale of minutes, but recruiting new foragers occurs on a time-scale of hours. Mathematically, this means that the proportion of bees in each phase of the foraging cycle is essentially at equilibrium on the recruitment time-scale. Consequently, it is only necessary to consider the total number of active foragers at a source without classifying them as collecting, unloading, dancing and so on. The time that bees spend in different parts of the cycle is important in parametrising the model but not in the model’s overall structure.

We assume that the total number of bees actively foraging at source j is affected only by the recruitment of unemployed bees to source j by active source j foragers; by active foragers abandoning source j ; and by

unemployed bees finding source j independently through scouting. This can be expressed as a differential equation

$$\frac{dF^j}{dt} = B_1^j U - B_2^j F^j + B_3^j U, \quad (2)$$

where B_1^j , B_2^j and B_3^j are mathematical expressions which model the behaviour of the bees and which are determined later on in this section. The first term on the right-hand side represents recruitment to source j by dancing. The second term models the rate that active foragers abandon source j . The final term represents the discovery of source j by scouting.

Bees are recruited to each source from the pool of unemployed foragers and return to that pool when they abandon a source. So, the change in the number of unemployed bees is

$$\frac{dU}{dt} = \sum_{j=1}^m B_2^j F^j - \sum_{j=1}^m B_1^j U - \sum_{j=1}^m B_3^j U. \quad (3)$$

Here the first term on the right-hand side gives the rate that abandoning bees become unemployed bees, the second term gives the rate that bees are recruited to sources by dances and the last term represents the rate that unemployed bees find nectar sources by scouting.

2.2. Modelling recruitment

The probability that a bee will follow a dance for source j is given by the probability p_f that it will follow any dance at all, multiplied by the probability p^j that the dance which it follows is for source j . We model the probability that a bee follows any dance as

$$p_f = \frac{1}{n_{df}} \sum_{k=1}^m D^k, \quad (4)$$

where n_{df} is the total number of bees on the dance floor and D^j is the number of bees dancing for source j . This assumes that the probability that a bee follows a dance reflects the probability that she will randomly come across a dancer on the dance floor. This is clearly a simplification of interactions on the dance floor but is adequate for our purposes. The number of bees dancing for source j is proportional to the number of bees actively foraging for source j , the probability p_d^j that a forager will dance for the source and the proportion of time in each foraging cycle given to dancing. So

$$D^j = F^j p_d^j T_d^j r^j, \quad (5)$$

where the proportion of time that a bee spends dancing is given by the absolute time spent dancing T_d^j divided by the total time spent in a foraging cycle which is $1/r^j$. Here r^j is the visit rate which is the time it takes for a bee to complete one foraging cycle to source j . Now the probability that a bee who chooses to follow a dance follows one for source j depends on the number of

dancers dancing for source j . The simplest relationship is

$$p^j = \frac{D^j}{\sum_{k=1}^m D^k},$$

which gives

$$B_1^j = p_f p^j = \frac{1}{n_{df}} F^j p_d^j T_d^j r^j. \quad (6)$$

2.3. Abandoning a source

We assume that bees who dance do not abandon the source that they are exploiting; bees who do not dance wait in the hive for time T_w^j and may abandon the source during that time. The second expression B_2^j , which governs the rate of abandonment of source j , can be written as

$$B_2^j = \frac{W^j p_x^j}{F^j T_w^j}, \quad (7)$$

where W^j/F^j is the proportion of active source j foragers who are waiting in the hive at any given time (W^j is the absolute number of waiting source j bees), p_x^j is the probability that an individual will abandon source j in a given foraging trip and T_w^j the length of time that bees wait in the hive between trips to the source. Since W^j is given by the total number of active foragers exploiting source j who do not dance but spend time waiting in the hive, multiplied by the proportion of the foraging cycle that each bee spends waiting in the hive, we have

$$W^j = (1 - p_d^j) F^j T_w^j r^j.$$

Hence

$$B_2^j = p_x^j (1 - p_d^j) r^j. \quad (8)$$

2.4. Finding a source by scouting

A bee that does not follow a dance may find a source of nectar by independent scouting. We assume that if a bee has not followed a dance in time T_ℓ she will become a scout and find a source. The probability that a bee does not follow a dance is $(1 - p_f)$ and so, using Eq. (4) we have

$$B_3^j = \frac{1}{m} \frac{1}{T_\ell} \left(1 - \frac{1}{n_{df}} \sum_{k=1}^m D^k \right), \quad (9)$$

where each of the m sources has an equal probability of being discovered by scouting.

3. The role of source profitability

Eqs. (2) and (3) together with the expressions B_1^j , B_2^j and B_3^j give a simple mathematical description of

foraging behaviour. Many of the parameters in this description, such as visit rate r^j and probability of dancing p_d^j are strongly influenced by the quality of the source. In this section we discuss a standard method of measuring the profitability of a nectar source and show how it can be incorporated into our model. For clarity, we will drop the superscript j , which indexes the nectar sources, for the time being and reintroduce it at the end of the next section.

3.1. Profitability and foraging costs

According to Seeley (1986, 1994), the most likely unit of profitability perceived by bees is the *energy efficiency* of the foraging trip, defined by

$$P = \frac{G - C}{C}, \quad (10)$$

where G is the gross gain in energy from the foraging trip (that is, the energy content of the nectar extracted on that trip), and C is the total energetic cost of the trip. It will be seen below that C depends on the length of time that a bee spends in the hive, which in turn depends on P . Therefore, C is a function of P , say $C(P)$, and the following equation must be solved for P :

$$P = \frac{G - C(P)}{C(P)}. \quad (11)$$

The energy gain, G , is completely described by the equation:

$$G = V \times \alpha \times 5.8, \quad (12)$$

where V is the volume (in μL) of nectar collected at the source, α is the concentration of sucrose ($\mu\text{mol } \mu\text{L}^{-1}$), and 5.8 is the standard value for the energetic equivalence of sucrose ($\text{J } \mu\text{mol}^{-1}$).

It has been demonstrated (Seeley, 1994) that the energy cost in fuel expenditure is sufficient for calculating the currency of profitability. Other non-fuel costs, such as wear and tear on the bee, risk of predation and so on, do not appear to influence a bee's perception of source quality.

The fuel costs can be thoroughly accounted for in the equation

$$C_{\text{fuel}} = \sum_{i=1}^4 t_i \rho_i, \quad (13)$$

where i denotes the segment of a foraging trip (1 = flight from hive to source, 2 = at source, 3 = flight from source to hive, 4 = at hive), t_i denotes the duration of segment i (in s) and ρ_i is the metabolic rate of the bee during segment i (in J s^{-1}) (Seeley, 1994). Seeley calculated that $\rho_i = 0.00287M^{0.629}$ for flying bees and $\rho_i = 0.00248M^{0.492}$ for resting or walking bees, where M is the mass of the bee (in mg, including any crop load). Seeley (1986) measured the weights of foragers arriving

at the feeder to be 77.2 ± 5.0 mg, and of foragers leaving the feeder to be 155.0 ± 5.5 mg (average ≈ 116 mg). In another experiment (Cox, 2000), unladen bees weighed approximately 90 mg, and the weight of imbibed sucrose could be calculated from the formula

$$\Delta M = V(0.1356\alpha + 1). \quad (14)$$

In this paper we use the latter.

3.2. Visit rate and time spent in the hive

Having considered the bees' metabolic rates during different phases of the foraging cycle, we will determine the time spent in each phase.

Foraging time consists of flight time from the hive to the source, time spent foraging at the source, and flight time from the source to the hive. The flight times to and from the source are linear functions of d , the distance between the hive and the source. Núñez (1982) suggests a constant flight speed of approximately $26.5 \text{ km h}^{-1} \approx 442 \text{ m min}^{-1}$, so that the time a bee takes to fly in one direction is $d/442 = 0.00226d$ measured in minutes. We assume that bees take 2 min to collect a cropful of nectar so that T_0 , the total time a forager spends out of the hive is

$$T_0 = 2 + 0.00452d. \quad (15)$$

The total duration of a single foraging cycle is $T_s + T_h$, where T_h is the time which a bee spends in the hive. Hence the visit rate r is

$$r = \frac{1}{T_h + T_s}. \quad (16)$$

It has been observed (Oldroyd et al., 1991a; Cox, 2000) that the rate of visits to a feeder by individual bees decreases as the concentration of the source decreases. In other words, total trip duration increases. This could be interpreted as either r depending on source profitability, or as T_h depending on source profitability, since $T_h = 1/r - T_s$ and T_s is approximately constant for a fixed distance.

Using experimentally determined visit rates (Oldroyd et al., 1991b; Cox, 2000) and Eq. (15) for T_s , P and T_h can be calculated under various conditions, using Eqs. (10) and (12). From this data we looked for a relationship between T_h and P , and found that time spent in the hive can be well approximated by the formula:

$$T_h = 1.2 \times P^{-g}, \quad (17)$$

where $g \approx 0.75$ is a parameter that may vary between colonies or between individuals. This relationship is depicted in Fig. 1. Based on the scatter of the data, we suggest investigating g in the range $0.65 \leq g \leq 0.85$. Visit

rate is consequently defined as

$$r = \frac{1}{1.2 \times P^{-g} + 1/60(2 + 0.00453d)}, \quad (18)$$

where r has units h^{-1} .

Clearly, Eq. (17) is not useful for very low profitabilities, as it suggests that T_h becomes infinitely large. In particular, T_h is undefined at $P = 0$. We note first that for such very low profitabilities, the probability of abandoning the source will be high—this is discussed later. Thus, the effect of most bees abandoning the source will override the effect of very large T_h . In fact, for low profitabilities we force $P \geq 0.095$ —this is sufficiently small to ensure that $p_x = 1$ without incurring the difficulties associated with $P = 0$.

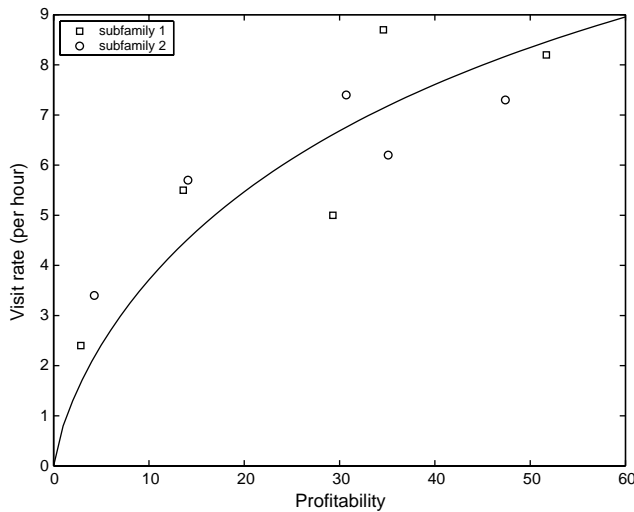


Fig. 1. Visit rate vs. profitability for data from Oldroyd et al. (1991b). Solid line is (3.17) with $g = 0.75$.

3.3. Solving for profitability

In the discussion above we have given the formula for profitability P as the solution of the transcendental equation (11). Now, using the parameter values and formulae determined in the previous subsections, we are in a position to calculate P for various values of d , α and g . This can be done, for example, using the Matlab (The MathsWorks, 1984) function `fzero()`. For $g = 0.75$, P is depicted in Fig. 2. As expected, it is highest for high α and low d , dropping off rapidly as these parameters decrease and increase, respectively.

3.4. Probability and duration of dancing

The probability (p_d) and duration (T_d) of dancing are quite distinct, as evidenced by an experiment conducted by Oldroyd et al. (1991a). They investigated dancing in a two-patriline colony, and demonstrated significant subfamily differences in both p_d and T_d —however, the subfamily with smaller p_d showed a higher T_d . Our model reflects this with two separate equations for these dancing parameters.

Experimental data from Oldroyd et al. (1993) and from Seeley (1986) suggest that either the slope (m_{pd}) or intercept (b_{pd}) of the dancing response may vary between different colonies, or between different subfamilies within a colony. Hence, we model the probability of dancing by

$$p_d = -b_{pd} + m_{pd}P. \quad (19)$$

The threshold value of P below which no dancing occurs is given by

$$P_{crit} = \frac{b_{pd}}{m_{pd}}.$$

As it stands, Eq. (19) does not take into account the observation that p_d is modulated by the rate of nectar

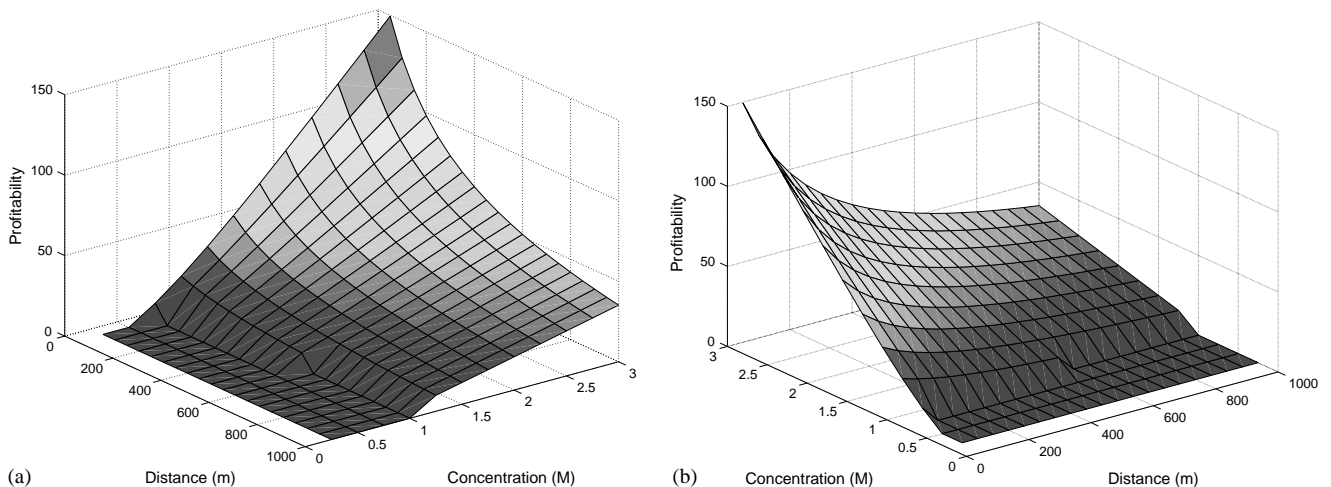


Fig. 2. Graph of P as a function of α and d ($g = 0.75$). Note that the actual surface is smooth. The fact that it does not appear completely smooth in the above representations (for example, where $d = 600$ and $\alpha = 1$ in (a)) is an artefact of the way the picture was produced.

intake (Seeley, 1995): when nectar influx is high, P_{crit} increases, so that dancing will cease for sources of relatively low profitability. This adjustment appears to be mediated by the interactions between returning foragers and food-storers on the dancefloor: waggle dancing, which recruits foragers, will only occur when the number of available food-storer bees is sufficiently high. When the number of available food-storer bees is very low, “tremble dancing”, which discourages foragers and inhibits further waggle dancing (Seeley, 1995), may be stimulated.

Seeley (1992) demonstrated how p_d depends on T_u , the time that a returning forager takes to find a food-storer bee who is able to receive her load of nectar for a particularly profitable source ($\alpha = 2.5M, d = 350$ m). Using the default value for g of 0.75, this source has a profitability of $P = 57.7$. The dancing response for increasing T_u was sigmoidal and is well approximated by the formula

$$p_d = \frac{20^3}{20^3 + T_u^3}. \quad (20)$$

Using Eq. (19) with $m_{pd} = 0.01$ and $b_{pd} = 0.2$ (reasonable values, based on Oldroyd et al.'s and Seeley's data), we arrive at $p_d = 0.365$ for this source. Substituting this value of p_d into Eq. (20), it follows that $T_u = 24$ s satisfies the relationship. Thus, Eq. (19) assumes that T_u is constantly 24 s. To adequately reflect the fluctuations in T_u as bees are recruited to new sources or abandon existing ones, a modification to Eq. (19) is required.

A formula that incorporates both the response to profitability and to T_u is

$$p_d = -b_{pd} + m_{pd}P \frac{s^3}{s^3 + T_u^3}, \quad (21)$$

where s is a scaling parameter.

In this equation, m_{pd} has been redefined; effectively, m_{pd} (but not b_{pd}) has been scaled by the term involving T_u , so that as T_u increases m_{pd} decreases, thus increasing P_{crit} . Explicitly, P_{crit} is now defined as

$$P_{crit} = \frac{b_{pd}}{m_{pd}} \left(1 + \left(\frac{T_u}{s} \right)^3 \right). \quad (22)$$

Appropriate values for m_{pd} , b_{pd} and s can be determined empirically from Seeley's data. He found $p_d \approx 0.95$ for his source of $P = 57.7$ when $T_u = 0$; also, $p_d = 0$ for $T_u \geq 60$. Hence,

$$s \approx 0.355, \quad (23)$$

$$m_{pd} \approx 0.0172, \quad (24)$$

$$b_{pd} \approx 0.0424. \quad (25)$$

Data from Seeley (1986, 1994) indicate that P_{crit} may range from 10 to 60 J J⁻¹ in a naturally mated colony. Hence, it is a plausible candidate for a parameter which

has a high degree of individual variability, due to genetic or other sources of variability. Using $m_{pd} = 0.017$, $b_{pd} = 0.042$ and $s = 0.36$ in Eq. (22) allows P_{crit} to range from 2.5 (when $T_u = 0$) to 9 (when $T_u = 30$ s) to 55 (when T_u reaches 1 min). This is in reasonable agreement with the observed range of P_{crit} , although it would be improved with a greater ratio $b_{pd} : m_{pd}$.

The duration of dancing T_d is an increasing function of the profitability of the source danced for (the number of dance circuits performed increases linearly with source profitability (Seeley, 1994)) and of the distance of the source (the duration of each circuit increases linearly with distance (von Frisch, 1967)). The following equation accounts for these observations:

$$T_d = n_{circuits} \times t_{circuit} \\ = m_{circ}(P - P_{crit})(0.0333 + 0.0000167d), \quad (26)$$

where $n_{circuits}$ is the number of circuits performed; $t_{circuit}$ is the duration of a single circuit in min; and m_{circ} is the slope of the response function. The relationship $t_{circuit} = 0.0333 + 0.0000167d$ is a linear approximation to data taken from von Frisch (1967, p. 100) and gives the time in min.

Data from Seeley (1986, 1994) indicate that m_{circ} may be (at least) in the range 0.01 to 1.2 runs J J⁻¹. Again, there is a large observed variability in this parameter.

3.5. Profitability and source abandonment

The probability of abandonment (p_x), measures the probability that a non-dancing (waiting) bee begins to follow dances by other bees rather than return to the food source. This will depend on the profitability of the food source, is likely to depend on the overall rate of nectar influx to the hive, and may also depend on genetic factors.

There is very little data available on probability of abandonment. Cox (2000) measured abandonment rates for bees visiting a food source that decreased in concentration progressively throughout one foraging day. A more comprehensive set of data has recently been obtained by Beekman et al. (2002) which is in quantitative agreement with that of Cox. A logarithmic line of best fit to the data of Cox is described by the equation

$$p_x = 0.610 - 0.168 \ln P, \quad (27)$$

($R^2 = -0.94$). In order to explore the effects of individual variation in abandonment behaviour we define p_x in terms of the parameter A (for abandonment):

$$p_x = A - 0.168 \ln P \quad (28)$$

and investigate the effect that varying A has on colony fitness.

4. Colony nectar quantity

We use the net quantity of nectar N (expressed as mg of sucrose) collected by foragers as a measure of colony fitness or colony foraging success. Then

$$\frac{dN}{dt} = R_{in} - R_{fuel}, \quad (29)$$

where R_{in} is the rate that nectar is brought into the hive by foragers and R_{fuel} is the rate of sucrose consumption and is equivalent to the rate that energy is used by the foragers in excess of resting metabolic rate. We assume R_{fuel} is the rate of energy consumption during flight during the foraging cycle and so R_{fuel} can be calculated by finding the total metabolic cost of a foraging trip (this is done when finding the profitability of a source) and subtracting the resting metabolism costs from that. The gross increase to the sucrose stores per foraging trip is $V \times \alpha \times 0.3423$ where 0.3423 is a factor converting μmol of sucrose to mg.

Overall then,

$$\frac{dN}{dt} = \sum_{j=1}^m (F^j r^j \times 0.3423 V^j \alpha^j - R_{fuel}^j), \quad (30)$$

where we have reintroduced the superscript j which indexes over all available nectar sources.

5. Implementing the model

The system of ODEs, Eqs. (2) and (3), was solved numerically, using Matlab's ode45 solver (The Maths-Works, 1984). The other variables are updated according to equations given in Sections 2 and 3. The parameters on which the model depends are summarized in Table 1. The detailed procedure used to solve the model is as follows:

1. A number (m) of nectar sources was described by assigning values for the parameters concentration (α^j) and distance (d^j).
2. The values of the other model parameters were set to default values (listed in Table 1).
3. A single parameter was selected for investigation.
4. The selected parameter was assigned from within the range indicated in Table 1.
5. The model was iterated for 600 simulated foraging minutes. The values of N , F^j and U were recorded.
6. When running the iterated trials described in Section 8, steps 4 and 5 were repeated 100 times for each value of n . The mean and standard deviation of the 100 recorded values of N , F^j and U were calculated.

Before carrying out experiments with the model, the model was “calibrated” by applying it to the two-source, single-subfamily system explored by Seeley et al. (1991) and Camazine and Sneyd (1991). The model was initialized with sources whose specifications matched those used in the experiment, and with the default parameter values given in Table 1. To verify that the chosen parameter values were reasonable, the settings were modified to find the best match between the modelled foraging response and the experimentally observed response. As it turned out, the original choices for each parameter provided the best fit to the data. This is a valuable justification of the original parameter choices. When doing the calibration we found some inconsistency between the speed of response to the second feeder in Seeley's experiments and our model results; more bees were observed at the second feeder in the experiment than was predicted by the model. However, this is probably due to more foragers entering the experiment as the day progressed.

Table 1
Parameter values for the model

Parameter	Description	Default value	Range explored
α^j	Concentration of source j ($\mu\text{mol } \mu\text{L}^{-1}$)	1	0.25 → 2.5
d^j	Distance of source j from hive (m)	250	100 → 1000
g	Parameter determining T_h and r^j	0.75	0.65 → 0.85
m_{circ}	Slope of dancing response (number of circuits) to changing $P^j - P_{crit}$	0.6	0 → 1.2
m_{pd}	Slope of dancing response (probability of dancing) to changing P^j	0.015	0.005 → 0.025
b_{pd}	Intercept of dancing response (probability of dancing)	0.045	-0.155 → 0.245
A	Intercept of probability of abandonment as a function of $\ln P^j$	0.61	0.46 → 0.76
T_ℓ	Time unemployed foragers spend following dancers before locating a source by scouting (min)	360	na
V^j	Volume collected from source j (μL)	55	na
t_{sim}	Number of simulated foraging minutes	600	na
n_f	Total number of foragers	125	na
n_{df}	Number of bees on dancefloor	750	na

6. Results for a homogeneous colony

6.1. Foraging at a single source

We investigated the response of a homogeneous colony to a single source, present throughout the day. The properties of the single source were varied to explore the effect of varying profitability on foraging behaviour. The foraging response of a homogeneous colony for three of these sources is illustrated in Fig. 3.

For sources with $P = 0.095$, the probability of dancing is $p_d = 0$, and the probability of abandonment is $p_x = 1$. Hence, there is no recruitment and no commitment to these sources, so the observed foraging response is a balance between discovery of the source due to scouting, and immediate abandonment. In each case, this balance is struck at approximately 20 foragers exploiting the source at any given moment.

As P increases, the response for the default parameter values (given in Table 1) increases steadily, due to p_d increasing and p_x decreasing. The responses to non-default parameter values are more varied. For values of

P less than 20 (Fig. 3(a)), the response for small values of A is strikingly greater than for the default parameter values, with nearly all foragers exploiting the source by the end of the day. This is because, for small values of A , p_x decreases extremely rapidly as P increases. When A takes on its minimum tested value of 0.41, $p_x = 0$ for $P \geq 11.5$, and when $A = 0.51$, $p_x = 0$ for $P \geq 20.8$. Thus, small decreases in A lead to big increases in the level of commitment to sources of relatively low profitability. In contrast, the response to non-default values of all other parameters remains close to the default response. This suggests that increases in the probability of dancing (mediated by increases in m_{pd} and decreases in b_{pd}), increases in perceived source profitability (mediated by increases in g) and increases in duration of dancing (mediated by increases in m_{circ}) have relatively less impact on the foraging response than decreases in the probability of abandonment.

For particularly high values of P (Fig. 3(c)), this situation is reversed: the response for large values of A is strikingly lower than for the default parameter values, whereas the response for non-default values of all other

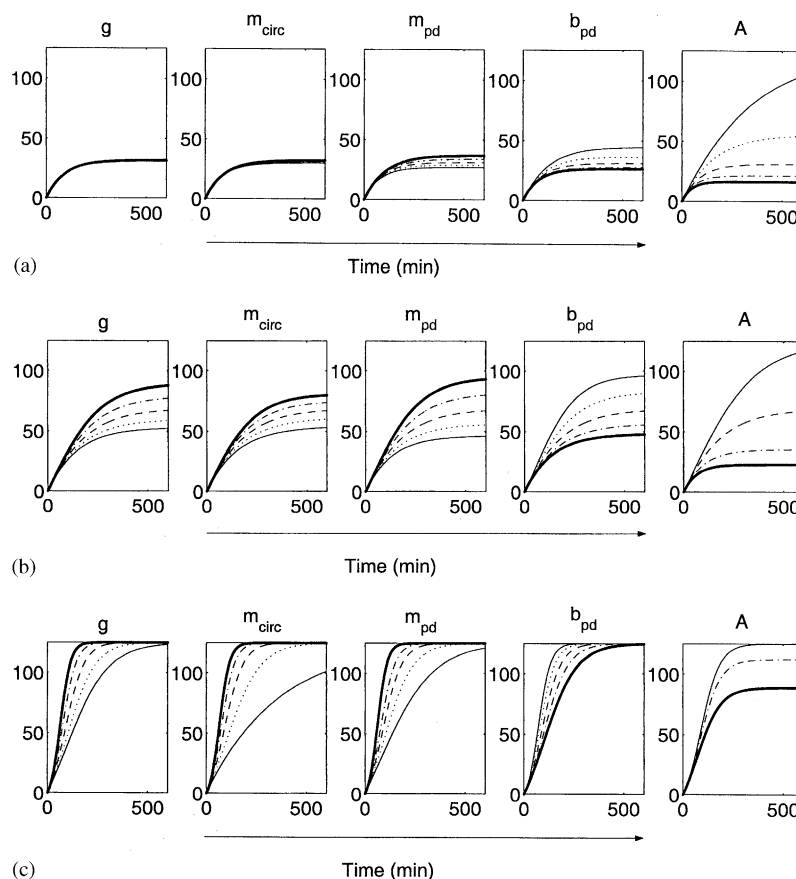


Fig. 3. Foraging response of a homogeneous colony to a single source. Responses to three sources of increasing profitability are illustrated. In each subplot, the abscissa is time and the ordinate is number of foragers at the source. The parameter being varied is indicated above the subplot. Different linestyles represent different parameter values: Thin solid line: range minimum; dotted line: intermediate between minimum and midrange; dashed line: midrange; dash-dotted line: intermediate between midrange and range maximum; thick solid line: range maximum. For (a) $P = 13.5$, $\alpha = 1.5M$, $d = 1000$ m; (b) $P = 25.7$, $\alpha = 2.0M$, $d = 750$ m; (c) $P = 50.4$, $\alpha = 2.0M$, $d = 250$ m.

parameters remains evenly spread about the (high) default response. For these highly profitable sources, $p_x \approx 0$ for the default value of A , meaning that all foragers are committed to the source. Small increases in A mean that p_x increases: at the most profitable source, $p_x = 0.15$ for the maximum tested value of A . This translates to less than 100% commitment to the source, so that the equilibrium number of foragers exploiting the source is significantly fewer than for the default parameter choice.

In summary, there is a range of low P (roughly, $P \in (10, 20)$) for which small values of A represent a distinct foraging advantage for this one-source case. There is a range of high P (roughly, $P > 30$) for which large values of A represent a distinct foraging disadvantage, for the one-source case. However, when more than one source is present, the relative advantage or disadvantage is likely to change. For example, if a poor source and a good source are present simultaneously, then the low values of A which allow foragers to commit to the poor source will be a disadvantage, as they will distract some foragers from the better source. Similarly, if a good source is present, and an even better source appears later, then the high values of A that cause some foragers to abandon the good source will be an advantage, as they will allow those foragers to exploit the even better source.

6.2. Foraging at four sources

We next examined the case where foragers have four different sources of varying profitabilities represented by the following source configurations:

SC1 $\alpha^j = 2M$ for all sources, $d^1 = 250$ m, $d^2 = 500$ m, $d^3 = 750$ m, $d^4 = 1000$ m.

SC2 $\alpha^j = 1.5M$ for all sources, $d^1 = 250$ m, $d^2 = 500$ m, $d^3 = 750$ m, $d^4 = 1000$ m.

SC3 $d^j = 250$ m for all sources, $\alpha^1 = 0.5M$, $\alpha^2 = 1M$, $\alpha^3 = 1.5M$, $\alpha^4 = 2M$.

SC4 $d^j = 1000$ m for all sources, $\alpha^1 = 0.5M$, $\alpha^2 = 1M$, $\alpha^3 = 1.5M$, $\alpha^4 = 2M$.

Fig. 4 shows results for the first two sets of sources. In each subfigure, each row represents the results for one parameter, indicated to the left of the row. Each set of axes shows the dynamic response of one variable over time: the first four columns show the number of foragers at each of the four sources, the fifth column shows the number of unemployed foragers, and the final column shows the net nectar intake.

The foraging response at the most profitable source in each configuration exhibited a monotonic increase (g, m_{circ}, m_{pd}) or decrease (b_{pd}) when four of the five parameters were increased. This translated to a monotonic increase (or decrease) in the net nectar intake to

the hive. That is, in both source configurations illustrated in Fig. 4, either the maximum (g, m_{circ}, m_{pd}) or minimum (b_{pd}) value of the parameter allowed the greatest intake of nectar by the homogeneous colony. The response to increasing A , however, was not always monotonic. For the second source configuration where all sources were fairly low in profitability, the nectar intake decreased monotonically as A increased. However, for the more profitable source configuration, the default value of A was associated with greatest nectar intake. That is, either increasing or decreasing the value of A from its default value led to a decrease in nectar intake for this source configuration. Similar results applied where profitability was decreased by increasing the distance from the hive for a fixed sucrose concentration.

The reason for this non-monotonic response to increasing A is as follows. For a fixed source configuration, the nectar intake is maximized when all foragers commit to the best available source, and none commit to any other sources. That is, the response is optimal when $p_x = 0$ for the most profitable source, and $p_x = 1$ for all others. To achieve this, the optimal value of A should be sufficiently high that foragers do not commit to any secondary sources present; but at the same time, should not be too high, or else foragers will not be completely committed to the best source. Indeed, the cost of $p_x > 0$ for the best source is high, since this results in a steady stream of foragers returning to the pool of unemployed foragers, from which the time required for re-recruitment to the source is long.

However, for a source configuration that varies throughout the day, values of $p_x = 0$ and 1 are undesirable, as they reflect an inflexible foraging population. When foragers commit completely to one source, the pool of unemployed foragers gradually decreases to zero. In contrast, intermediate values of p_x allow for the pool of unemployed foragers to be constantly replenished. Although this leads to suboptimal nectar intake for the fixed source configurations discussed above, it allows for greater flexibility when, for example, a new, more profitable source appears. In such situations, a large pool of unemployed foragers allows this new source to be discovered more rapidly than in the case where all foragers are already committed to other sources.

Although nectar intake increases monotonically for all parameters other than A , this increase (as measured by the final amount of nectar) is not linear. This can be seen most clearly for the parameters m_{circ} and m_{pd} , for the generally profitable source configuration, SC1. In this case, the increase in nectar that results when the parameter is increased from the range minimum to the midrange value is much greater than the increase in nectar that results when the parameter is increased from the midrange value to the range maximum. This

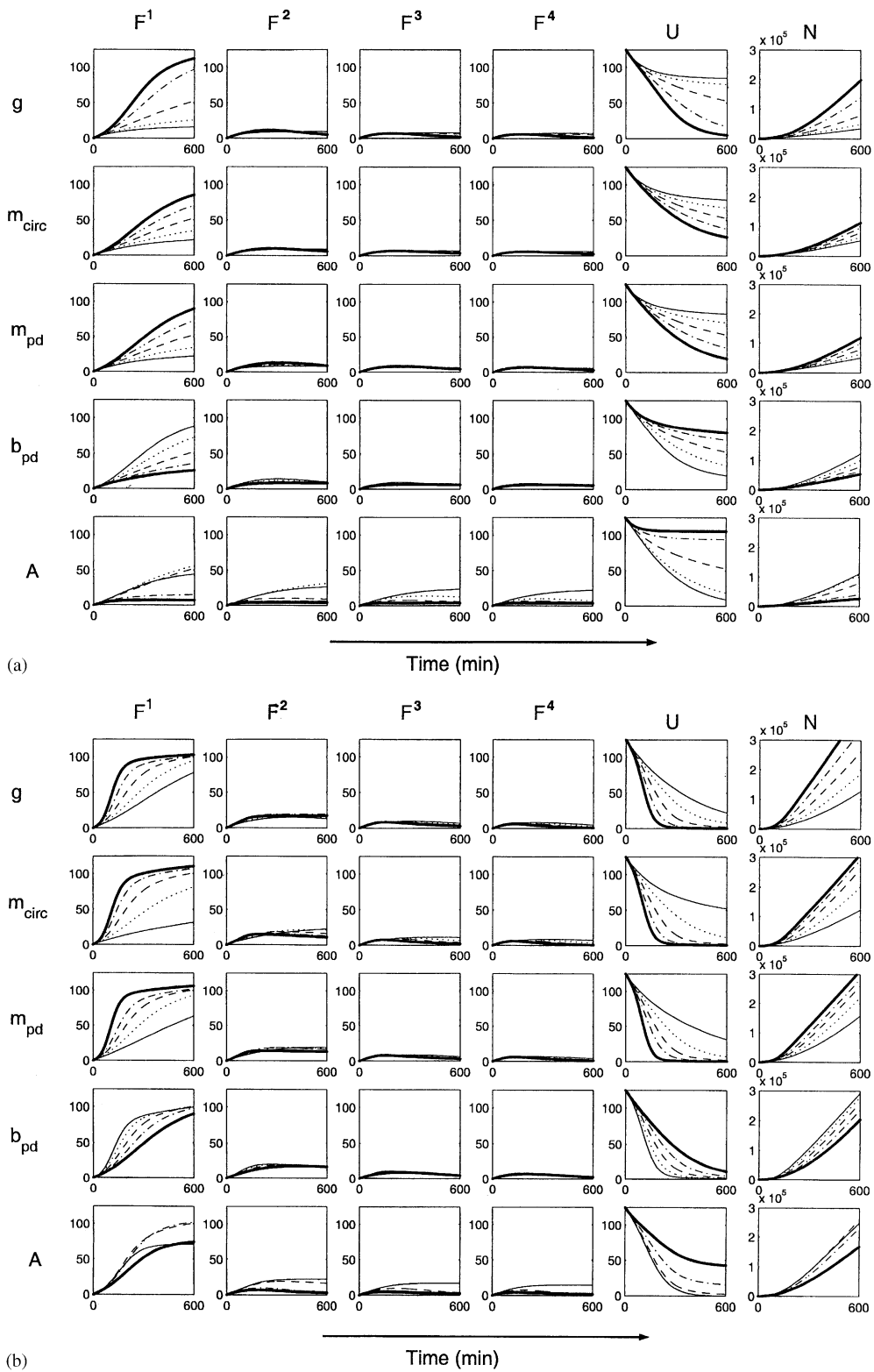


Fig. 4. Effect of varying each foraging parameter on the distribution of foragers in a homogeneous colony foraging at source SC1. In each set of axes, the abscissa is time (min), and the ordinate is the variable named at the side. (Thus, in this figure the first four columns represent number of foragers at each of the four sources, the fifth column represents number of unemployed foragers, and the sixth column represents net nectar intake.) Different linestyles represent different parameter values, as described in the caption to Fig. 3.

Table 2

Comparison of nectar intake for a homogeneous colony with the average parameter value (N_{av}) and the average nectar intake for homogeneous colonies across all parameter values (\bar{N})

		g	m_{circ}	m_{pd}	b_{pd}	A
N_{rel}	SC1	0.62	-9.56	-5.40	-2.39	-12.4
	SC2	20.9	2.64	3.56	5.79	-8.30
	SC3	-1.00	-12.6	-6.78	-3.07	-10.9
	SC4	2.48	0.66	2.82	7.58	12.8

The table shows the percentage difference between \bar{N} and N_c ; entries with absolute value greater than five are in bold. See text for further explanation.

indicates that the average amount of nectar produced by a homogeneous colony, when the parameter is selected at random from the allowed range, will be less than the amount of nectar produced by a homogeneous colony with the average value of that parameter.

This is illustrated further in Table 2. The nectar intake for a homogeneous colony with one of five values of each parameter was recorded. These five values were uniformly distributed across the range of each parameter given in Table 1. The average of all five nectar intakes (\bar{N}) was then compared to the nectar intake of the average parameter value (N_{av}) by calculating their percentage difference as $N_{rel} = (\bar{N} - N_{av})/\bar{N} \times 100$. If this percentage is negative it indicates that $N_{av} > \bar{N}$; that is, that a colony with the average parameter value ends up with more nectar than the average nectar intake over the entire parameter range. It is clear that this is generally the case for the two more profitable source configurations (SC1 and SC3), with m_{circ} , m_{pd} and A showing the greatest differences, and generally not the case for the two less profitable source configurations (SC2 and SC4). The exception is that varying A produces a negative relationship for SC2. This is probably because SC2 contains a more profitable source ($P = 32.2$) than SC4 ($P = 20.7$), with the result that colonies with the midrange A value are able to commit to this best source in SC2. In contrast, only colonies with the lowest two A values are able to commit to the best SC4 source. This increases the value of N_{av} for SC2 relative to the mean nectar value.

It is interesting that the parameters which have the greatest negative effect on N_{rel} for the profitable source configurations have the least positive effect on N_{rel} for the poor source configurations. (Again, A is the exception.) A striking example is g , which has negligible effect on N_{rel} for SC1, SC3 and SC4, but has a strong positive effect for SC2. This appears to be related to the amount of spread in the foraging response at the best source. For example, the most profitable source in SC1 is sufficiently profitable that, by the end of the foraging day, all colonies are able to achieve close to maximum foraging effort at that source (see Fig. 4). In contrast, at SC2, the foraging response is much more varied: the

foraging effort by the colony with the lowest value of g is markedly less than that with the greatest value of g (see Fig. 4). In SC4, all sources are so poor that there is equally little foraging effort at all of them.

6.3. Best source disappearing, or appearing later

Several source configurations were investigated in this category. The results of the following pair of experiments is typical of the range of observed responses:

SC5 $\alpha^j = 2M$ for all sources (1–4), $d^1 = 250$ m, $d^2 = 500$ m, $d^3 = 750$ m, $d^4 = 1000$ m. Source 1 (the most profitable) disappears after 300 min.

SC6 $\alpha^j = 2M$ for all sources (1–4), $d^1 = 1000$ m, $d^2 = 750$ m, $d^3 = 500$ m, $d^4 = 250$ m. Source 4 (the most profitable) does not appear until 300 min.

For source configurations SC5 and SC6, the effect on the distribution of a homogeneous colony of varying each of the foraging parameters is illustrated in Fig. 5. In general, the absolute nectar intake was slightly higher for the case where the best source disappeared than for the corresponding case where the best source appeared late. This is presumably a consequence of the fact that when a source appears late, foragers have meanwhile become committed to the second-most profitable source. Thus, when the best source appears, it cannot be fully exploited. In such cases, the greatest exploitation of the new source was achieved when the parameter A was varied. As illustrated in Fig. 5, by the end of the simulated foraging day up to 60 foragers were able to exploit the best source (source 4), for an intermediate value of A . For all other parameters, fewer than 50 foragers were able to exploit the new source, for any parameter value. As discussed earlier (in Section 6.2), this is because higher values of A ensure that the pool of unemployed foragers is constantly replenished. Therefore, when the new source appears, there is a large pool of potential foragers ready to exploit it.

7. Introducing variation between individuals

The model of Section 2 can easily be extended to incorporate a number of classes of individuals which differ in their behaviour. We assume here that these are genetic differences and so will refer to the classes as subfamilies. These individual differences could, of course, have other origins but this would make no difference to the equations.

Let us assume that there are n subfamilies and introduce another superscript i to index them; so, for example, F^{ij} is the number of foragers of subfamily i foraging at source j . The governing differential

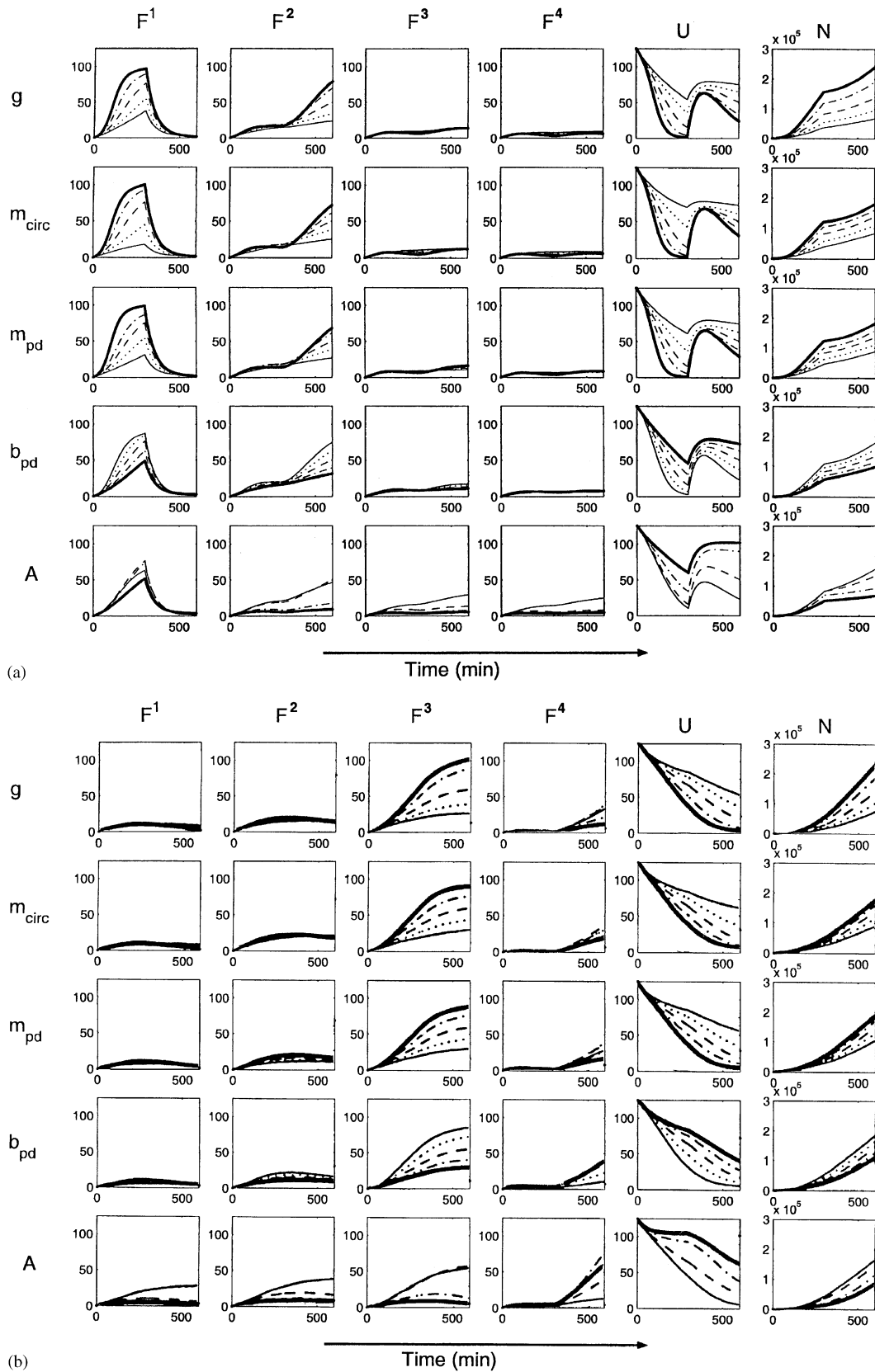


Fig. 5. Effect of varying each foraging parameter on the distribution of a homogeneous colony when the best source (a) disappears, or (b) does not appear until halfway through the day. See Fig. 3 for an explanation of plot symbols. Note that in (a) the sources are in decreasing order of profitability, in (b) they are in increasing order.

equations (2) and (3) then become:

$$\frac{dF^{ij}}{dt} = B_1^{ij}U^i - B_2^{ij}F^{ij} + B_3^{ij}U^i, \quad (31)$$

$$\frac{dU^i}{dt} = \sum_{j=1}^m B_2^{ij}F^{ij} - \sum_{j=1}^m B_1^{ij}U^i - \sum_{j=1}^m B_3^{ij}U^i. \quad (32)$$

Here U^i is the number of unemployed foragers of subfamily i . The expressions for B_1^j , B_2^j and B_3^j change to reflect the multiple subfamilies.

The probability that a bee will follow any dance now requires the number of dancers to be summed over both j and i :

$$p_f = \frac{1}{n_{df}} \sum_{i=1}^n \sum_{j=1}^m D^{ij}.$$

This assumes that the probability that a bee follows a dance is not dependent on the subfamily of either the dancer or the follower. The probability that a dancer who follows a dance will be following a dance for source j is therefore:

$$p^j = \frac{\sum_{i=1}^n D^{ij}}{\sum_{i=1}^n \sum_{j=1}^m D^{ij}},$$

where the number of dancers of subfamily i for source j is $D^{ij} = F^{ij}p_d^{ij}T_d^{ij}r^{ij}$ by analogy with Eq. (4). Hence

$$B_1^{ij} = \frac{1}{n_{df}} \left(\sum_{i=1}^k F^{ij}p_d^{ij}T_d^{ij}r^{ij} \right). \quad (33)$$

In fact B_1^{ij} depends only on the source j not on the subfamily i but we will keep the two superscript notation to emphasise that B_1^{ij} is different from B_1^j in Section 2.2. Subfamilies interact with one another *via* this dance recruitment term.

The abandonment term is relatively unchanged as bees do not interact with others when they abandon a source. From Eq. (7)

$$B_2^{ij} = p_a^{ij}(1 - p_d^{ij})r^{ij}. \quad (34)$$

Finally, the scouting term given in Eq. (8) requires additional summation similar to the dance recruitment term

$$B_3^{ij} = \frac{1}{m} \frac{1}{T_\ell} \left(1 - \frac{\sum_{i=1}^n \sum_{j=1}^m D^{ij}}{n_{df}} \right). \quad (35)$$

Several quantities in the above equations depend on source profitability P^j and parameters associated with the behaviour of individual bees. For example

r^{ij} depends on P^j and g^i ,

p_d^{ij} depends on P^j , b_{pd}^i and m_{pd}^i ,

T_d^{ij} depends on P^j and m_{cirs}^i ,

p_x^{ij} depends on P^j and A^i .

Profitability only has a source superscript as it depends solely on the nectar concentration of the source and the distance of the source from the hive. Other parameters only have a subfamily superscript as they describe differing individual behaviour and do not relate to the properties of the source. The augmented model seeks to explore how these individual behaviours affect nectar foraging for a variety of source distances d^j and concentrations α^j . As before we measure outcomes by determining the amount of nectar N collected by a colony where now:

$$\frac{dN}{dt} = \sum_{i=1}^n \sum_{j=1}^m (F^{ij}r^{ij} \times 0.3423V^j\alpha^j - R_{fuel}^j). \quad (36)$$

8. Investigations with multiple subfamilies

8.1. Single source and variable behaviour

We investigated the following source configurations:

SC1 $\alpha^j = 2M$ for all sources, $d^1 = 250$ m, $d^2 = 500$ m, $d^3 = 750$ m, $d^4 = 1000$ m.

SC2 $\alpha^j = 1.5M$ for all sources, $d^1 = 250$ m, $d^2 = 500$ m, $d^3 = 750$ m, $d^4 = 1000$ m.

SC3 $d^j = 250$ m for all sources, $\alpha^1 = 0.5M$, $\alpha^2 = 1M$, $\alpha^3 = 1.5M$, $\alpha^4 = 2M$.

SC4 $d^j = 1000$ m for all sources, $\alpha^1 = 0.5M$, $\alpha^2 = 1M$, $\alpha^3 = 1.5M$, $\alpha^4 = 2M$.

In Section 6 above we showed that, in a homogeneous colony, for profitable source configurations, $N_{rel} < 0$ for all foraging parameters. That is, a homogeneous colony with the average parameter value ends up with more nectar than the average intake for colonies across the entire parameter range. For unprofitable source configurations, the opposite is generally true (although the parameter A is an exception).

We now consider the case of a heterogeneous colony. The more subfamilies there are, the less likely it will be that all subfamilies have a very low or a very high parameter value, and the more likely it will be that the average parameter value of all subfamilies is close to the midrange value. Since the total amount of nectar produced by the colony is the sum of the amount produced by each subfamily, this suggests that as n increases, the amount of nectar produced may approach the amount that would be produced by a homogeneous colony with the average parameter value. If this is the case, then for the cases mentioned in the previous paper, where N_{rel} is negative, an increase in mean nectar intake might be observed as n increases.

To test whether the amount of nectar produced by a heterogeneous colony with average parameter value, say, λ is similar to the amount of nectar produced

Table 3

Deviations of the nectar intake of a heterogeneous colony from the nectar intake of a homogeneous colony. The average parameter value of the heterogeneous colony is equal to the parameter value of the corresponding homogeneous colony. Entries with absolute value greater than 1% are in bold. Deviation of zero indicates no difference between nectar intake of homogeneous and heterogeneous colonies; positive deviation means that the heterogeneous colony does better

		g	m_{circ}	m_{pd}	b_{pd}	A
N_{rel}	SC1	+0.60%	+0%	−0.061%	+0.18%	− 2.9%
	SC2	+ 4.9%	+0%	+0.43%	+ 1.2%	− 2.3%
	SC3	+0.56%	+0%	−0.050%	+0.20%	− 2.7%
	SC4	+0.35%	+0%	+0.37%	+ 1.2%	+ 11.7%

by a homogeneous colony with parameter value λ , we compared the amount of nectar produced by a homogeneous colony which had the midrange parameter value with the amount of nectar produced by a 10-subfamily colony whose average parameter value was the same. For each of the subfamilies, the selected parameter was assigned randomly (with a uniform distribution) from half the range indicated in Table 1, centred on the default value. The deviations of each heterogeneous colony nectar intake from the corresponding homogeneous colony nectar intake are presented in Table 3.

Clearly, for most parameters the deviations are close to zero—that is, the nectar intake of the heterogeneous colonies is very close to that of the corresponding homogeneous colony. For the parameter m_{circ} , the deviations are always zero—the nectar intake of a heterogeneous colony is exactly the same as the nectar intake for a homogeneous colony with the average parameter value. For the other parameters, the deviations are rarely greater than 1%. There are some notable exceptions. For the profitable source configurations (SC1 and SC3), the deviations are positive for high-range values of m_{pd} , which suggests that for high m_{pd} and profitable sources, the foraging response is more efficient when there are several subfamilies. Similarly, for the generally poor source configuration SC2, there is a tendency for a heterogeneous colony varying in g (and thus visit rate) to do better than the homogeneous colony.

Taking these observations together with the observations of Section 6, the following picture develops. For the parameter m_{circ} , we showed that for homogeneous colonies, the nectar intake for the midrange parameter value is greater than the average nectar intake over all parameter values, for the two profitable source configurations (SC1 and SC3). Table 3 shows that a heterogeneous colony produces the same amount of nectar as a homogeneous colony with the average parameter value. We know that as n increases the average parameter value will be increasingly close to the midrange value. It follows that as n increases, the

average nectar intake may increase for SC1 and SC3. Similarly, for m_{pd} and the same two source configurations, the midrange parameter value does better than the full range, and a heterogeneous colony produces at least as much nectar as a corresponding homogeneous colony, so again we might expect to see an increase in the average nectar intake as n increases. In contrast, in the study of homogeneous colonies we observed that for the poor source configuration SC2, the average value of g does worse than the full range, which might suggest that a decrease in nectar intake could result from increasing n . However, Table 3 shows that heterogeneous colonies tend to do better than the corresponding homogeneous colony. These two conflicting effects may cancel each other out. As far as A goes, it is impossible to predict the effect on nectar of increasing n , because heterogeneous colonies do both better and worse than homogeneous colonies depending on source configuration.

8.2. The effect of the number of subfamilies

To further investigate the effect on nectar intake of increasing numbers of subfamilies we performed the following numerical experiments. A single parameter was selected to vary between subfamilies and all other parameters were set to their default value given in Table 1. For each subfamily the selected parameter was assigned randomly from within the range given in Table 1, using a uniform distribution. The model was iterated for 600 simulated foraging minutes and the final values of N , F^{ij} and U^i were recorded. This process was repeated 100 times for each value of n . The mean and standard deviation of the 100 recorded values of N , F^{ij} and U^i were calculated.

The effect that increasing the number of subfamilies has on net nectar intake for the SC1 and SC2 source configurations is illustrated in Fig. 6. Each subfigure shows the mean \pm the standard deviation of 100 measurements of nectar intake for each parameter and for each number of subfamilies. Here parameters were chosen at random using a uniform distribution from the entire parameter range given in Table 1. In each case, the results have been scaled, relative to the mean and standard deviation of the homogeneous case—that is, of the 100 iterations of the case $n = 1$. A mean of 1 indicates a mean equal to that of the homogeneous case; similarly, a standard deviation of 1 indicates a standard deviation equal to that of the homogeneous case.

Clearly, increasing n had only a small effect on the mean nectar intake. In the majority of cases, there was no change in the mean, indicating that, on average, the colony was neither better off nor worse off for having more than one subfamily. In certain cases the mean increased—namely, when m_{circ} and m_{pd} were varied in SC1 (Fig. 6(a)) and when A was varied in SC2

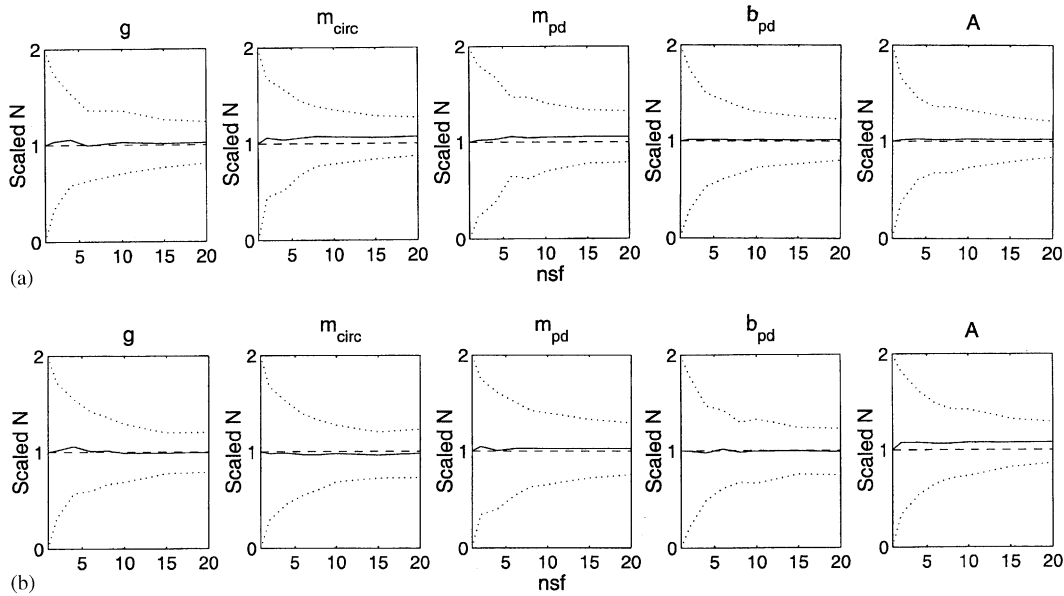


Fig. 6. Effect of increasing n on net nectar intake; (a) for source configuration SC1; (b) for source configuration SC2. In each subfigure, each smaller subfigure corresponds to varying one parameter, as indicated above that subfigure. In all cases, the abscissa is number of subfamilies, the ordinate is the nectar intake, scaled relative to the nectar intake for the homogeneous ($n = 1$) case. Solid line is scaled mean nectar intake, dotted lines are mean \pm variance, dashed line indicates where scaled nectar intake is equal to one.

(Fig. 6(b)). In these cases, the colony fared better, on average, with more than one subfamily. Two of these three cases—those involving m_{circ} and m_{pd} —are those cases where such an increase was predicted, above. In none of these cases was there any observed decrease in mean nectar; that is, the colony was never worse off for having more than one subfamily, although decreases were observed for other source configurations not illustrated here.

The more obvious effect of increasing the number of subfamilies is to decrease variance in the nectar intake. In effect, this means that the reliability of nectar foraging increases. With a homogeneous colony ($n = 1$), a single parameter is selected at random from the allowable range. This chosen parameter may be beneficial, leading to very high nectar intake. However, it may also be very bad, leading to very low nectar intake. As n increases, and the number of selected parameters increases, the probability that all these chosen parameters will fall into the extremely good or extremely bad range decreases, so that the probability of either very high or very low nectar intake decreases.

8.3. Random source configurations

In assigning the random sources, distance (d^j) was allowed to range between 100 and 1000 m; concentration (α^j) between $0.5M$ and $2M$; and start time (t_0^j) between 0 and 600 min. Finish time (t_f^j) was calculated by first assigning a duration for the source's appearance, which was allowed to range between 45 and 600 min.

Duration was added to t_0^j to calculate t_f^j , which was capped at 600 min.

The properties of two randomly generated source configurations are illustrated in Fig. 7. The figure indicates the relative incidence of the sources over time, and shows the concentration and distance of each source.

As in the previous experiments, the consistent characteristic of the nectar response was a decrease in the variance as n was increased. Again, deviations of the mean nectar response were small, sometimes positive and sometimes negative. There was no clear association between the time average of P for the source configuration and the direction of deviation of the mean. For example, the nectar response when b_{pd} was varied was observed to decrease slightly in the most profitable configuration, Fig. 7(a), but to increase slightly in another very profitable configuration (not illustrated). It seems likely that profitability P , averaged over time and sources is not per se a good indication of the foraging response. Rather, the dynamics of sources appearing and disappearing, and whether or not the best sources co-exist or are staggered, will have an important impact on the foraging dynamics and the resulting nectar intake.

9. General discussion and conclusions

In this paper, we have identified some key transition rates of foraging dynamics and suggested how they may

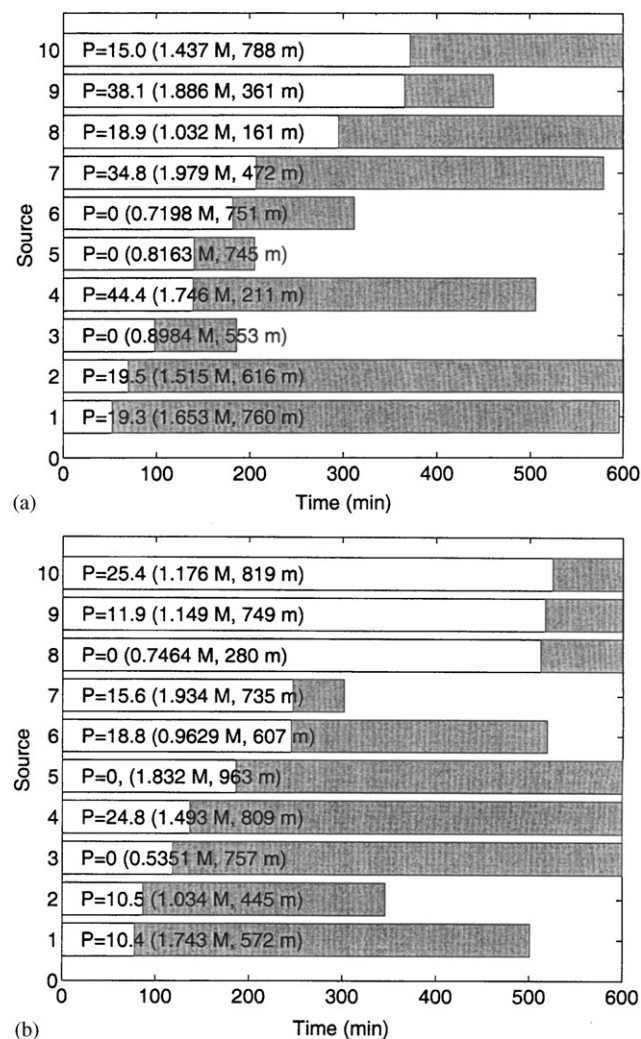


Fig. 7. Summary of two random source configurations; (a) is a highly profitable source configuration with average profitability $10.5 \text{ source}^{-1} \text{ min}^{-1}$ and (b) is a less profitable source configuration with average profitability of $5.30 \text{ source}^{-1} \text{ min}^{-1}$. In each subfigure, each horizontal bar represents one source. The shaded region of the bar denotes the time in which that source is "on". The profitability, concentration and distance of the source are indicated on the horizontal bar.

depend mathematically on five parameters: specifically, how the visit rate of a bee may depend on the activity parameter, g ; how rate and duration of dancing may depend on the three parameters m_{pd} , b_{pd} and m_{circ} ; and how rate of abandonment may depend on the single parameter, A . The relationships between these rates and the corresponding foraging parameters were defined to have good agreement with the available biological data while retaining mathematical simplicity. Clearly, these relationships may not be mediated in precisely the way suggested in this model. For example, dancing probability may be mediated by a single biological threshold, whereas we have modelled it using two mathematical parameters, m_{pd} and b_{pd} . Alternatively, where we have reduced the observed variance in visit rate to the effect

of the single parameter g , there may in reality be multiple thresholds acting together to produce this effect. Further, we have suggested that each parameter is independent of all the others, so that, for example, there may be an increase in m_{pd} (increasing the probability of dancing for a source) with no corresponding decrease in A (decreasing the probability of abandoning a source). In reality, it may be the case that such parameters are linked. Nevertheless, the model provides considerable insight into the way that colony-level foraging dynamics are tuned by variation in each of the key transition rates, and into how this translates to colony fitness.

The primary finding of the first part of this paper concerns the parameter A . Monotonically decreasing values of A do not correspond to monotonically increasing nectar intake. For certain source distributions, the smallest parameter value results in the highest nectar intake. However, for other source distributions, a midrange parameter value is the most beneficial in terms of nectar intake. For this parameter, then, it is likely to be beneficial to the colony to have a range of values represented by phenotypically different bees.

Although A is the only parameter for which a midrange value is optimum *per se*, there is some evidence that heterogeneity in other parameters' values may also be beneficial. This follows from the observation that a colony consisting of a single subfamily with the average parameter value will generally perform better than a heterogeneous colony whose parameter has the same average value under conditions of plentiful forage. That is, although increasing g , for example, will always increase nectar intake, this increase is not linear: a low value of g is relatively worse for a colony than a high value of g is beneficial. A colony may reduce its chances of having a low value of g by being heterogeneous. Thus, again, we might expect that colonies containing phenotypically different bees might perform better on average than homogeneous colonies. Here we have assumed that the phenotypic differences arise from genotypically different patrines observed in naturally mated colonies, but there are of course many other sources of variation between individuals.

The observation that increasing number of subfamilies reduces the variance in a colony-level response (here, in nectar intake) is in agreement with other studies. Experimentally, Page et al. (1995) demonstrated that multi-patriline colonies exhibit the "average" phenotype of corresponding genetically homogeneous colonies, so that extremely good or extremely bad phenotypes tended not to be observed in the heterogeneous colonies.

This model was able to examine the 'averaging' effect quite specifically. It confirms that, where the measure of phenotype is nectar foraging success, a heterogeneous colony acts like a homogeneous colony with the average parameter value for most of the parameters investigated.

Further, it shows that the nectar intake for the average parameter value can be better than the average nectar intake across the full range of possible parameter values, for certain source configurations.

The one consistent exception was the parameter A , for which a heterogeneous colony was observed to fare up to 12% better or worse than the corresponding average homogeneous colony, under different source configurations. However, the nectar intake for the average value of A also tended to be considerably better than the average nectar intake over the full range of the parameter, so that the net effect of increasing the number of subfamilies varying in this parameter was very similar to that of all other parameters—viz, the variance in nectar intake was greatly reduced.

The observation that the mean nectar intake varies very little with increasing number of subfamilies, in most parameter–source configurations, is interesting. It suggests that, on average, colonies with multiple patrilineages do just as well as homogeneous colonies. If we are to accept this, yet simultaneously to speculate that polyandry is so widespread because it is beneficial to the colony, it follows that we must attribute a benefit to the reduction in variance per se. That is, we must assert that the negative impact of extremely poor phenotypes outweighs the positive impact of extremely good phenotypes, so that a colony with mostly midrange phenotypes does better than a colony with extreme phenotypes.

It is easy to argue that this would be the case. In order to survive a winter, a colony must have acquired sufficient nectar resources during the spring and summer (Seeley and Visscher, 1985; Beauchamp, 1992). That is, there is some threshold amount of nectar which equates to colony survival. Any amount of nectar below this threshold means the colony will die. In contrast, any amount of nectar above the threshold simply means that the colony, which will survive anyway, has a headstart on foraging for the next season. Thus, the impact of the extremely poor phenotypes translates to the difference between survival and death, whereas the impact of the extremely good phenotypes simply translates to less foraging pressure in the next season.

The observation that variance is reduced when n increases thus offers an explanation for why polyandry may be beneficial, given that a spread of possible parameter values exists. However, it does not explain why a spread of possible parameter values should exist in the first place. For the parameter A , the results of the homogeneous modelling suggest a clear explanation. Monotonically decreasing values of A do not correspond to monotonically increasing nectar intake. Depending on the properties of the available sources, different values of A maximize nectar intake. Thus, it is beneficial to the colony to have a range of parameter values, represented by phenotypically different bees.

Although this will be a disadvantage for certain source distributions (for example, when there are some highly profitable sources present), it allows the colony to profit in a broader range of source distributions. This could be particularly important when sources are poor.

This is not the case for the other foraging parameters investigated. Since increasing g , for example, always results in a higher nectar yield, why would not low values of g be selected against? There are at least two responses to this. First, an increase in the biological thresholds represented by the modelled foraging parameters may indeed be occurring. To observe such an increase would require a wide sampling and measurement of these parameters over a long-time period. In any case, for such an increase to be possible implies that a range of parameter values must exist in the first place.

Second, the gain in nectar intake must be weighed against costs to the colony. It is very difficult to measure these costs. One example relates to subfamily differences in visit rate (Cox, 2000). Such differences in rate of foraging suggest that for a given profitability, one subfamily works harder than another. The increased visit rate would increase the non-fuel costs of a foraging bee, since there is a greater amount of wear and tear on the bee. Is it better for a colony to produce lots of bees that forage very quickly, then burn out and die quite soon, or to produce bees that forage less quickly but survive for longer? There is likely to be some upper limit to the parameter choices where a balance is struck. Thus, while high values of g produce greater nectar intake, leading to selection pressure in favour of increasing g , they may also produce higher turnover of bees, leading to an opposing selection pressure.

The model presented here offers some support to the fixed threshold models which demonstrate that division of labour can result from different thresholds existing within a colony (Bonabeau et al., 1996, 1998). The current model does not investigate a task distribution—it is concerned only with the forager subset of a colony, so that all modelled bees are either engaged in foraging activities, or are not. However, it does predict a division between active foragers and unemployed foragers, or between foragers at different sources, with some subfamilies actively exploiting sources that other subfamilies do not. Examples of this are illustrated in Fig. 8. In Fig. 8, the subfamily with the smallest value of g (represented by the thin solid line) does not exploit source 3 at all by the end of the day. Instead, this subfamily has the greatest foraging response to source 4. In Fig. 8, the subfamily with the smallest value of A is the only subfamily to exploit source 2. The subfamilies are divided at source 3, and also in the unemployed category, to which only two subfamilies contribute any foragers. Such separation of subfamilies at forage sources should be verifiable experimentally. Indeed, similar behaviour has already been observed in

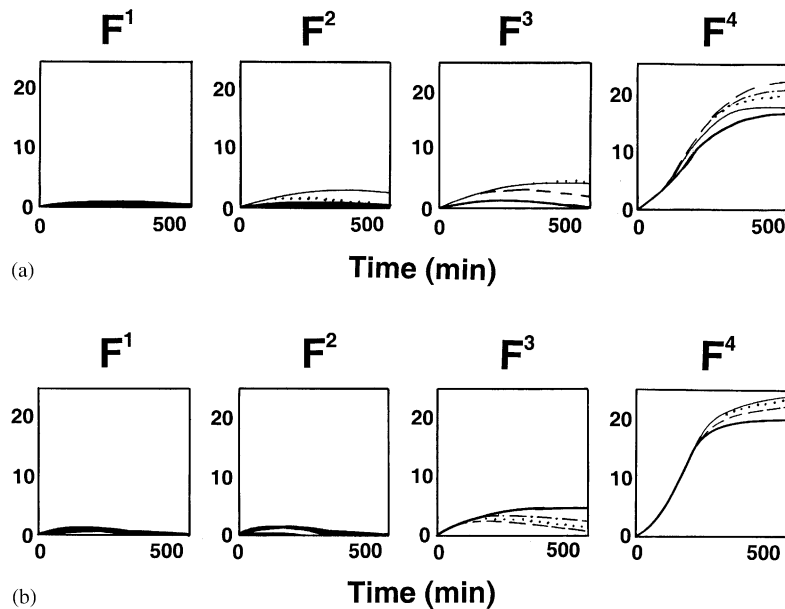


Fig. 8. Division of subfamilies between sources. The sources are those of source configuration 1 (see description at the beginning of Section 6.2). Each linestyle represents a different subfamily in a heterogeneous (five subfamily) colony. The subfamilies differ in the parameter (a) g , or (b) A . Different linestyles represent different parameter values: Thin solid line: range minimum; dotted line: intermediate between minimum and midrange; dashed line: midrange; dash-dotted line: intermediate between midrange and range maximum; thick solid line: range maximum.

experiments that monitored a division of subfamilies between nectar and pollen sources (Fewell and Page, 2000).

In this model, we investigated the effect of variation in parameters related to visit rate, probability and duration of dancing, and probability of abandonment. There are many other parameters that may be expected to vary between subfamilies. For example, it has been observed that subfamilies may differ in their propensity to scout (Dreller, 1998), or in the distance at which they prefer to forage (Oldroyd et al., 1993; Dreller, 1998). Such behaviours are likely to have an influence on colony fitness. For example, if some patrines specialize in near-scouting and others in far-scouting, a search for new sources will be more efficient when a greater number of subfamilies is present, and again we would expect increasing number of subfamilies to correlate to decreased variance in colony fitness. Such hypotheses could be tested with slight modifications to the current model.

In summary, this model has examined the effect of five foraging-related parameters on the foraging response and consequent nectar intake of a homogeneous or a heterogeneous colony. The parameters investigated affect different quantities critical to the foraging cycle—visit rate (affected by g), probability of dancing (m_{pd} and b_{pd}), duration of dancing (m_{circ}), or probability of abandonment (A). Each parameter affects its respective foraging quantity through widely differing mathematical definitions: probability of abandonment depends exponentially on A , probability of dancing depends

linearly on m_{pd} and b_{pd} , g affects visit rate through an inverse power relationship. Yet in all cases, the effect of increasing n is qualitatively similar: as the number of subfamilies increases, the mean nectar intake differs very little, and the variance in nectar intake decreases greatly. This result supports the “genetic variance” hypotheses (Crozier and Page, 1985; Keller and Reeve, 1994) that argue that genetically heterogeneous colonies are better protected against misfortune than homogeneous colonies. A colony that contains several patrines, differing in the biological equivalent of the foraging parameters explored in this model, is less likely to experience a particularly bad foraging season, and hence more likely to survive.

Acknowledgements

The authors wish to thank Ben Oldroyd and Andrew Barron for collaboration on the field experiments from which empirical data for this paper were drawn; Basil Panayotakos for technical assistance in the experiments; Jane Sexton for advice about Matlab; and two anonymous referees whose comments have much improved this paper.

References

- Beauchamp, G., 1992. Effects of energy requirements and worker mortality on colony growth and foraging in the honey bee. *Behav. Ecol. Sociobiol.* 31 (2), 123–132.

- Beekman, M., Oldroyd, B.O., Myerscough, M.R., 2002. Sticking to their choice—honey bees are reluctant to abandon low quality food sources. *J. Entomol. Ecol.*, in press.
- Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., 1996. Quantitative study of the fixed threshold model for the regulation of division of labour in insect societies. *Proc. R. Soc. London Ser. B* 263, 1565–1569.
- Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., 1998. The synchronization of recruitment-based activities in ants. *Biosystems* 45 (3), 195–211.
- Calderone, N.W., Page Jr., R.E., 1988. Genotypic variability in age polyethism and task specialization in the honey bee, *Apis mellifera* (Hymenoptera: Apidae). *Behav. Ecol. Sociobiol.* 22, 17–25.
- Camazine, S., Sneyd, J., 1991. A model of collective nectar source selection by honey bees: self-organization through simple rules. *J. Theor. Biol.* 149, 547–571.
- Cox, M.D., 2000. Models for self-organisation in insect societies. Ph.D. Thesis, University of Sydney, Sydney, NSW, Australia.
- Crozier, R.H., Page, R.E., 1985. On being the right size: male contributions and multiple mating in social hymenoptera. *Behav. Ecol. Sociobiol.* 18 (2), 105–116.
- de Vries, H., Biesmeijer, J.C., 1998. Modelling collective foraging by means of individual behaviour rules in honey-bees. *Behav. Ecol. Sociobiol.* 44, 109–124.
- Dreller, C., 1998. Division of labour between scouts and recruits: genetic influence and mechanisms. *Behav. Ecol. Sociobiol.* 43, 191–196.
- Estoup, A., Solignac, M., Cornuet, J.-M., 1994. Precise assessment of the number of patrines and of genetic relatedness in honey bee colonies. *Proc. R. Soc. London Ser. B* 258, 1–7.
- Fewell, J.H., Page Jr., R.E., 2000. Colony-level selection effects on individual and colony foraging task performance in honeybees, *Apis mellifera* L. *Behav. Ecol. Sociobiol.* 48 (3), 173–181.
- Hamilton, W.D., 1972. Altruism and related phenomena, mainly in social insects. *Ann. Rev. Ecol. Syst.* 3, 193–232.
- Keller, L., Reeve, H.K., 1994. Genetic variability, queen number and polyandry in social hymenoptera. *Evolution* 48 (3), 694–704.
- Liersch, S., Schmid-Hempel, P., 1998. Genetic variation within social insect colonies reduces parasite load. *Proc. R. Soc. London Ser. B* 265, 221–225.
- Núñez, J.A., 1982. Honeybee foraging strategies at a food source in relation to its distance from the hive and the rate of sugar flow. *J. Apic. Res.* 21 (3), 139–150.
- Oldroyd, B.P., Rinderer, T.E., Buco, S.M., 1991a. Honey bees dance with their supersisters. *Anim. Behav.* 42, 121–129.
- Oldroyd, B.P., Rinderer, T.E., Buco, S.M., 1991b. Intracolony variance in honey bee foraging behaviour: the effects of sucrose concentration. *J. Apic. Res.* 30 (3/4), 137–145.
- Oldroyd, B.P., Rinderer, T.E., Buco, S.M., Beaman, L.D., 1993. Genetic variance in honey bees for preferred foraging distance. *Anim. Behav.* 45, 323–332.
- Oldroyd, B.P., Smolenski, A.J., Cornuet, J.-M., Wongsiri, S., Estoup, A., Rinderer, T.E., Crozier, R.H., 1996. Levels of polyandry and intracolony genetic relationships in *Apis dorsata*. *Ann. Entomol. Soc. Am.* 89, 276–283.
- Page, R.E., 1980. The evolution of multiple mating behavior by honey bee queens (*Apis mellifera* L.). *Genetics* 96, 263–273.
- Page Jr., R.E., Erber, J., Fondrk, M.K., 1995. Effect of worker genotypic diversity of honey bee colony development and behavior (*Apis mellifera* L.). *Behav. Ecol. Sociobiol.* 36, 135–144.
- Page Jr., R.E., Erber, J., Fondrk, M.K., 1998. The effect of genotype on response thresholds to sucrose and foraging behaviour of honey bees (*Apis mellifera* L.). *J. Comp. Physiol. A* 182, 489–500.
- Palmer, K.A., Oldroyd, B.P., 2000. Evolution of multiple mating in the genus *Apis*. *Apidologie* 31, 235–248.
- Pankiw, T., Page Jr., R.E., 1999. The effect of genotype, age, sex, and caste on response thresholds to sucrose and foraging behavior of honeybees (*Apis mellifera* L.). *J. Comp. Physiol. A* 185, 207–213.
- Pankiw, T., Page Jr., R.E., 2000. Response thresholds to sucrose predict foraging division of labor in honeybees. *Behav. Ecol. Sociobiol.* 47, 265–267.
- Seeley, T.D., 1986. Social foraging by honeybees: how colonies allocate foragers among patches of flowers. *Behav. Ecol. Sociobiol.* 19, 343–354.
- Seeley, T.D., 1992. The tremble dance of the honey bee: message and meanings. *Behav. Ecol. Sociobiol.* 31, 375–383.
- Seeley, T.D., 1994. Honey bee foragers as sensory units of their colonies. *Behav. Ecol. Sociobiol.* 34, 51–62.
- Seeley, T.D., 1995. *The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies*. Harvard University Press, Cambridge, MA.
- Seeley, T.D., Visscher, P.K., 1985. Survival of honey bees in cold climates: the critical timing of colony growth and reproduction. *Ecol. Entomol.* 10, 81–88.
- Seeley, T.D., Camazine, S., Sneyd, J., 1991. Collective decision-making in honey bees: how colonies choose among nectar sources. *Behav. Ecol. Sociobiol.* 28, 277–290.
- The MathWorks Inc., 1984. *Matlab*. Version 5.3.1.29215a (R11.1).
- von Frisch, K., 1967. *The Dance Language and Orientation of Bees*. The Belknap Press of Harvard University Press, Cambridge, MA.