

Dancing for a Decision: A Matrix Model for Nest-Site Choice by Honeybees

Author(s): Mary R. Myer-scough

Source: *Proceedings: Biological Sciences*, Vol. 270, No. 1515 (Mar. 22, 2003), pp. 577-582

Published by: The Royal Society

Stable URL: <http://www.jstor.org/stable/3558704>

Accessed: 16/01/2009 02:42

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=rsl>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



The Royal Society is collaborating with JSTOR to digitize, preserve and extend access to *Proceedings: Biological Sciences*.

Dancing for a decision: a matrix model for nest-site choice by honeybees

Mary R. Myerscough

*School of Mathematics and Statistics, The University of Sydney, Sydney, NSW 2006, Australia
(m.myerscough@maths.usyd.edu.au)*

A mathematical model is formulated for decision making by honeybees during nest-site choice, using a population matrix model. This model explains how the observed dynamics of the nest-site scouts' dancing can reliably lead to a choice of the best nest site available.

Keywords: *Apis mellifera*; Leslie matrix; stationary swarm; self-organization

1. INTRODUCTION

In the spring a swarm of honeybees (*Apis mellifera*) may leave the hive and settle in a cluster nearby while scouts search for a suitable cavity for a new home. A scout that finds a suitable nest site returns to the swarm and seeks to recruit other scouts to visit the site. Scouts communicate the location and quality of the site by dancing (Lindauer 1961; Camazine *et al.* 1999; Seeley & Buhrman 1999, 2001) in a way similar to that by which foragers communicate the presence and quality of forage patches (see Seeley 1995; Seeley *et al.* 2000). While the colony is house hunting many scouts may be dancing on the swarm for many different sites, but eventually nearly all the dances are for a single site and the swarm sets off to settle in the chosen nest site.

Scouts' assessment of site quality covers several factors (Seeley 1977; Seeley & Morse 1978). Only 22% or fewer of individual scouts visit more than one site (Camazine *et al.* 1999; Seeley & Buhrman 1999) and it is highly unlikely that direct comparisons of sites by individual scouts play any part in the swarm's choice of a new home (Visscher & Camazine 1999). Even with most scouts visiting just one site, the dynamics of the dancing alone enables the swarm to choose a good site. Scouts that return from a high-quality site dance vigorously with faster return phases between waggle runs and with more waggle runs per dance than scouts returning from poorer sites (Seeley & Buhrman 2001). The number of waggle runs in each dance performed by each scout, generally speaking, declines with every successive return to the swarm, independently of the quality of the nest site (Seeley & Buhrman 1999) and each scout will eventually stop dancing, although she may continue to visit the nest site (Camazine *et al.* 1999). In almost every case the swarm is able to come to a decision on where to live and will choose the best site of those advertised by dancers on the swarm (Lindauer 1961; Seeley & Buhrman 2001).

This swarm decision-making process has previously been modelled by Britton *et al.* (2002), using a differential equation formulation, incorporating ideas from decision theory and epidemiology. The scouts are modelled as a population with individuals who switch from one site to another or from being committed to a choice to being uncommitted. The model does not explore how the mechanics of the dance communication reliably produces a

unanimous decision for a good site. In this paper, I explore the effects of observed dance behaviour during nest-site selection, by using a model that tracks both scout numbers and the number of dances for different sites. I present theory that explains how the scouts' dancing behaviour can reliably produce a good unanimous decision even though each scout only knows about a single site.

2. CONSTRUCTING A MODEL FOR SITE SELECTION BY DANCING

(a) *The general structure of the model*

To formulate a model for the dynamics of scout dancing and nest-site choice, I focus both on the dances and on number of the scouts and examine how the dances decay (or age) and propagate (or reproduce) on the swarm.

Seeley & Buhrman (1999) observed that, generally speaking, the number of waggle runs was less each time a particular scout returned from the nest site that she was advertising and that after some time a scout might stop dancing altogether, even if she was dancing for the site that was eventually chosen. Therefore, I assume in the model that the number of waggle runs in a scout's dance decreases after each successive visit to the nest site and ceases after a certain number of visits, denoted by v_f . Scouts may also abandon dancing for a site at any visit with the probability p_x . Here, I assume that p_x is constant. However, p_x may vary, depending on how many dances a scout has performed, without affecting the overall conclusions of the model. I also assume, following the observations of Seeley & Buhrman (2001), that the better the quality of the nest site, the higher the number of waggle runs that a scout performs at any given visit. Dances recruit other scouts to nest sites and these new recruits in turn come back to the swarm and dance. Therefore, in some sense, the dances reproduce themselves.

Given that dances can be considered to decay and to reproduce in this way, the whole process of information exchange through dancing can be recast in a population biology format with populations of dances for different sites. Within each population, different dances can age, as the scout repeatedly visits the site; die, if the scout stops dancing for the site; or reproduce when the scout recruits new dancers to the site. I track these dance populations by tracking the number of scouts performing dances of different ages for each site.

If I assume that all dances are synchronized with each other, then the dancing dynamics can be represented by using Leslie matrices. This is equivalent to saying that the dances are like populations that reproduce once per season rather than continuously throughout the year. The effect of this assumption is to standardize the time between dances; it eliminates the effects of travel times and delays owing to bad weather, night-time or other factors. Modelling dancing in this way, therefore, implicitly assumes that none of these factors are of primary importance in the process of choosing a nest site and that it makes no fundamental difference to swarm decision-making whether dances are distributed continuously in time or occur synchronously.

(b) Dancing behaviour of scouts

The observations of Seeley & Buhrman (1999, 2001) showed that the number of waggle runs that a scout performed on her return to the swarm depended on the quality of the site that she was advertising and the number of times that she had previously danced for that site. A scout dancing for a high-quality site performed more waggle runs per dance and performed more waggle runs per second than a scout dancing for a site of moderate quality (Seeley & Buhrman 2001). The number of waggle runs performed per dance also declined at each successive return to the swarm (Seeley & Buhrman 1999). The scouts can therefore be divided into different populations with each population dancing for a different site. For a given population, the number of waggle runs $W(m)$ in the m th dance that the scout performs could, for example, be modelled, mathematically by

$$W(m) = f(Q)\exp(-m/k), \tag{2.1}$$

where k is a constant and $f(Q)$ describes how the number of waggle runs depends on the quality of the site Q . As the number of waggle runs increases with site quality, $f(Q)$ must increase as Q increases. Equation (2.1) represents the number of waggle runs as decreasing exponentially with dance number until the final visit when $m = v_f$. This is irrespective of the quality of the site. Fig. 8 in Seeley & Buhrman (1999) indicates that this is a reasonable assumption.

Other expressions for $W(m)$ will work equally well provided that $W(m)$ increases with Q and, to reflect observations of dancing scouts, decreases with m .

(c) Recruiting new scouts

Visscher & Camazine (1999) observed that potential recruits choose at random which dance they will follow. In addition, I assume that there is a constant probability p_r , of a potential scout on the dance floor being recruited by a single waggle run. Then the number of scouts recruited to a particular site, say site i , is

$$\begin{aligned} & \text{total number} && \text{probability of} \\ & \text{of potential scouts on} \times \text{recruiting one scout} \\ & \text{the dance floor} && \text{per waggle run} \\ & \times \frac{\text{total number of waggle runs for site } i}{\text{total number of waggle runs for all sites}} \end{aligned}$$

This means that, in the model, new scouts are more likely to be recruited to good sites, as these dances contain more

waggle runs, and are more likely to be recruited to sites that are being advertised by more scouts as the total number of waggle runs for these sites is high. If we denote the number of scouts doing their m th dance for site i at time t by $b_i(m, t)$, the number of waggle runs in the m th dance for site i by $W_i(m)$, and the total number of potential scouts on the dance floor by n_{df} then we can write the number of scouts recruited to site i in each synchronized dance episode as

$$n_{df}p_r \frac{\sum_m W_i(m)b_i(m,t)}{\sum_i \sum_m (W_i(m)b_i(m,t))} = n_{df}p_r \frac{\sum_m W_i(m)b_i(m,t)}{W_{tot}(t)}, \tag{2.2}$$

where $W_{tot}(t) = \sum_i \sum_m (W_i(m)b_i(m,t))$.

(d) Putting it all together

If we assume that all dances are synchronized, we can construct a Leslie matrix model which will allow us to find the number of scouts for site i at time t , given that we know the number of scouts dancing for all the sites at the previous dancing episode at $t - 1$. As of the nature of the model, t is always an integer and denotes the number of the dance episode. So, we have

$$\begin{pmatrix} b_i(1,t) \\ b_i(2,t) \\ b_i(3,t) \\ \vdots \\ b_i(v_b,t) \end{pmatrix} = \begin{pmatrix} \frac{n_{df}p_r W_i(1)}{W_{tot}(t-1)} & \frac{n_{df}p_r W_i(2)}{W_{tot}(t-1)} & \frac{n_{df}p_r W_i(3)}{W_{tot}(t-1)} & \dots & \frac{n_{df}p_r W_i(v_b)}{W_{tot}(t-1)} \\ 1 - p_x & 0 & 0 & \dots & 0 \\ 0 & 1 - p_x & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 1 - p_x & 0 \end{pmatrix} \begin{pmatrix} b_i(1,t-1) \\ b_i(2,t-1) \\ b_i(3,t-1) \\ \vdots \\ b_i(v_b,t-1) \end{pmatrix}. \tag{2.3}$$

This describes the changes over time in the numbers of scouts dancing for each site. In principle this model could be used to perform simulations to explore how the populations of scouts dancing for different sources evolve. It is far more useful and illuminating, however, to perform a general analysis using tools from the mathematical theory of Leslie matrix models.

3. OUTCOMES OF THE MODEL

The total population $P_i(t)$ of scouts dancing for site i at time t is given by

$$\begin{aligned} P_i(t) &= b_i(1,t) + b_i(2,t) + b_i(3,t) + \dots + b_i(v_b,t) \\ &= \sum_m b_i(m,t). \end{aligned} \tag{3.1}$$

If the dominant eigenvalue λ_d of the matrix in equation (2.3) is greater than 1, this population will increase exponentially (at a rate proportional to λ_d). If the dominant eigenvalue is less than 1, the population of scouts dancing for site i will decrease exponentially. For the entire swarm the population of dancers for some sites might be decreasing while populations of dancers for other sites are increasing. At the end of the site-selection process Seeley & Buhrman (1999) observed that only one site was advertised. The populations of dancers for other sites had all declined to zero.

The eigenvalues, λ , of the matrix are given by the characteristic equation

$$\lambda^{v_r} - \frac{n_{df}}{W_{tot}(t)} W_i(1) \lambda^{(v_r-1)} - \frac{n_{df}}{W_{tot}(t)} (1-p_x) W_i(2) \lambda^{(v_r-2)} - \frac{n_{df}}{W_{tot}(t)} (1-p_x)^2 W_i(3) \lambda^{(v_r-3)} - \dots - \frac{n_{df}}{W_{tot}(t)} W_i(v_r) = 0 \quad (3.2)$$

(see Rorres & Anton 1977). This can be rewritten in terms of q_i , which is a function of λ

$$q_i(\lambda) = \frac{W_i(1)(1-p_x)}{\lambda} + \frac{W_i(2)(1-p_x)^2}{\lambda^2} + \frac{W_i(3)(1-p_x)^3}{\lambda^3} + \dots + \frac{W_i(v_r)(1-p_x)^{v_r}}{\lambda^{v_r}} = \frac{W_{tot}(t)}{n_{df}} \quad (3.3)$$

If p_x is not constant but varies between dance episodes, then the powers of $(1-p_x)$ in equation (3.3) will instead be products of terms of the form $(1-p_x(m))$ where p_x is a function of visit number m .

Every different site will have its own version of q_i but the expression on the right-hand side of the equation is the same for every site at any given time. This expression will change with time as the number of scouts at each site and the distribution of their dance ages changes with time. On the other hand, the expression for $q_i(\lambda)$ does not change with time but does depend on the quality of the site, because $W_i(m)$ is a function of site quality.

Figure 1 illustrates the $q_i(\lambda)$ curves for different sites. The time-varying quantity $W_{tot}(t)/n_{df}$ where $W_{tot}(t)$ is defined in equation (2.2), is represented by a straight horizontal line. The dominant eigenvalue for each site is given by the value of λ , where the q curve for that site intersects the $W_{tot}(t)/n_{df}$ line. If more than one site has a dominant eigenvalue greater than one, then the number of scouts dancing for each such site increases. Hence, with time, $W_{tot}(t)$ will increase and n_{df} may decrease as more scouts are recruited to these sites. (If there are lots of sites with $\lambda_d < 1$ then W_{tot} may initially decrease, but as time progresses it will start to increase.) This means that the W_{tot}/n_{df} line will move upwards as W_{tot} increases or n_{df} decreases, while the $q_i(\lambda)$ curves stay fixed. As a result the dominant eigenvalue λ_d for each site, that is the value of λ where the q_i curves and the line intersect, will decrease. So as W_{tot} increases, the dominant eigenvalue for some sites will move from being greater than 1 (with the number of scouts dancing for that site increasing) to less than 1 (when the number of scouts dancing for that site will decrease). Eventually, provided that the q_i curves are sufficiently well separated, there will only be one site left that has an increasing number of scouts dancing for it. This will become the chosen site. The positions of the q_i curves are determined by the number of waggles in each dance typically performed by returning scouts, that is W_i , with W_i greater the further right the curve.

If there is no site whose quality is high enough for its associated dominant eigenvalue to be greater than 1, then the numbers of scouts dancing for all sites will decline as the number of dancers at each site declines. This will lower W_{tot}/n_{df} until one site has $\lambda_d > 1$. The number of dances for this site will then increase while dances for other sites continue to decline. Hence, this analysis predicts that the site for which the scouts dance most vigorously should always be the chosen site, regardless of the

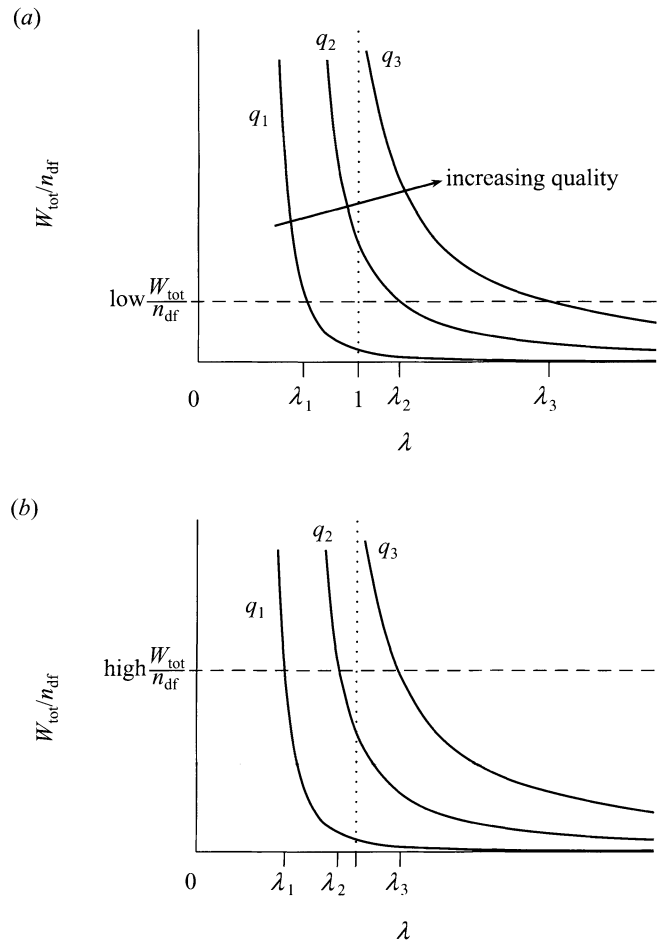


Figure 1. Diagram illustrating how the dominant eigenvalues change as W_{tot}/n_{df} increases. The q_i curves are independent of time and remain fixed. The dominant eigenvalues for each site are λ_1 , λ_2 and λ_3 , respectively, and are determined by the values of λ where the dashed line intersects the q_i curves. (a) For a low value of W_{tot}/n_{df} two sites have λ_d . (b) As W_{tot}/n_{df} increases, λ_2 becomes less than one for the lower quality site 2.

number or quality of alternative sites that the scouts are advertising.

4. COMMENTS AND CAVEATS

(a) The role of dance attrition

Both Camazine *et al.* (1999) and Seeley & Buhrman (1999, 2001) observed that scouts dance vigorously on first visiting a site but later the number of circuits in their dances declines until they cease dancing altogether. They may continue to visit the site but once dancing has stopped they have no role in propagating the dance. Is dance attrition necessary for this model and how does it operate within the model?

Ideas from population biology give insight into the effects of dance attrition. For a population to survive, each individual must, on average, at least replace itself, otherwise the population eventually becomes extinct. Here, scouts dancing for less favoured sites are not able to each recruit one or more new dancers to the site and so eventually the dance becomes extinct. Dancers for good sites, however, do, on average, recruit at least one new dancer

each and so the dance continues to exist. As the decision-making progresses it becomes harder to recruit dancers as the pool of potential scouts becomes smaller and so dances for all but the best site eventually become extinct.

From a more mathematical perspective, the expression for $q_i(\lambda)$ is, in mathematical terms, a polynomial in $1/\lambda$. The properties of this polynomial are dependent on the behaviour of the scouts advertising nest sites. If scouts continued dancing then this polynomial would be infinite; it would go on forever with higher and higher powers of $1/\lambda$. When $\lambda > 1$ then each succeeding term would get smaller and the polynomial would tend to a limit that can easily be graphed as the curve q_i . However, if $\lambda < 1$ then the polynomial would not sum to a finite limit unless $W_i(m)(1 - p_x)$ rapidly became smaller as m increased, to balance the increasing powers of $1/\lambda$. Hence, either there is a maximum number of times a scout dances or the number of circuits that a scout covers in each successive dance must drop off rapidly or there is a finite probability that a scout will abandon dancing after each visit. This argument is somewhat technical; however, the main point is that without dance attrition this model cannot be properly formulated or applied.

(b) *Randomness and start-up effects*

The model represents a highly simplified version of swarm decision making by dancing. In addition to the obvious assumption that dances occur synchronously, the model has the implicit assumptions that there are no random effects in the propagation of dances on the swarm and that the swarm's decision is only reached once the age-structure of the dances has settled down to its equilibrium structure (Caswell 1989), so that the balance of different aged dances for a particular site is not changing, only the total number of dances. Only at this stage is the dominant eigenvalue a guaranteed indicator of the outcome of the model. Clearly, the population of scouts dancing for a good site that is discovered late in the decision-making process may not reach this equilibrium before the decision is made. Hence, the results of the model may not apply in this case.

Random effects can be introduced into the decision-making process through individual differences in scouts' dancing; through different scouts assessing the quality of a site differently; or through random effects when bees on the swarm follow dances. In the model, such random effects would, broadly speaking, tend to smear out the q_i curves, making them fuzzy lines rather than sharp lines and hence reduce the clear-cut nature of the decision that the model predicts. This model, however, being based on discrete individuals, can be readily adapted to take account of various sources of random behaviour.

5. DISCUSSION

(a) *The model and observed bee behaviour*

The matrix formulation of this model predicts that once scouts have settled down to dance for a particular site then either the number of dancers for that site will be growing exponentially (for $\lambda_d > 1$) or be declining exponentially (for $\lambda_d < 1$). The model further predicts that the number of dancers for a particular site can grow and then decline as the total numbers of dancers increases. This exponential growth prediction agrees well with obser-

vations of Camazine *et al.* (1999) of a swarm, dancing for two similar sites that reached a point where dances for the favoured site increased exponentially while dances for the unsuccessful site levelled off. The model is also consonant with the diagrams of swarm dancing presented by Lindauer (1961) and Seeley & Buhrman (1999) where the number of dances for the successful site are observed to grow during most periods of observations while the number of dances for unsuccessful sites may grow initially but eventually declines until no dances are observed for those sites.

The model predicts that the single, best site will be chosen but swarms have been observed where the bees either cannot choose between sites (Lindauer 1961) or do not choose the best site that scouts have visited (Seeley & Buhrman 2001).

If we assume, in the first case, that the scouts have found two nest sites of very similar quality more or less simultaneously, then dances for both sites will settle down at about the same time and will have very similar $q_i(\lambda)$ curves. Hence, it would be highly likely that the number of scouts dancing for each of these sites would both be growing or both declining, given that randomness in real swarms would be likely to smear out the $q_i(\lambda)$ curves.

In the second case, where the bees chose the lower quality site over the high-quality site, the relative times of discovery of the sites and the vigour of the first few dancers may have had a significant impact on the swarm's choice. It is apparent from the data presented by Seeley & Buhrman (2001) that the high-quality site was discovered after the lower quality site and by the time that the number of scouts (and hence, I infer, the number of dances) for the lower quality site started to grow rapidly, recruitment to the high-quality site had barely begun and probably not settled down to the point where the age-structure of the dances had reached equilibrium. Seeley & Buhrman make the remark, in fact, that dancing for the high-quality site was noticeably weak.

This model indicates that the numbers of potential scouts on the swarm may influence the time that the colony needs to make a decision. If potential scouts are removed this reduces n_{df} in the model and raises the horizontal W_{tot}/n_{df} line in figure 1 and speeds up decision making. Alternatively, if scouts that are already dancing are removed then this will depress the W_{tot}/n_{df} line and decision making will take longer. In fact, if dancers are continually removed then the swarm may never come to a decision.

(b) *Comparison of dancing for nest sites with dancing for forage sites*

Advertising and recruiting foragers to forage sites appears to be similar to recruiting scouts to nest sites but has essentially different aims and outcomes. In selecting a nest site, the colony is making a single choice among resources that mostly do not vary over the time that the decision is being made; in foraging the colony distributes its foragers over several sites, whose properties may change significantly over a few days or during the course of a single day, in such a way as to maximize the amount of nectar brought into the hive (Seeley 1995). Therefore, the duration and liveliness of foragers' dances may change as the quality of the source changes (Seeley *et al.* 2000) or as the

number of available unloaders inside the hive varies (Seeley 1995). Hence, in a corresponding model for foraging, the polynomials $q_i(\lambda)$ would not be fixed but would be changing continually with time as the foragers dynamically assess the perceived quality of the source that they are advertising. As foragers continue dancing as long as their source is profitable and the nectar that they collect is in demand (Seeley 1994), the number of waggle runs $W(m)$ does not necessarily decline with each successive return to the hive. Hence, the nature of the $q_i(\lambda)$ polynomials will be quite different in a foraging model compared with the nest-site selection model.

(c) *Consensus versus quorum sensing*

This model implicitly assumes that a nest site is chosen by reaching a consensus among the dancing scouts although it could be adapted to model decision making by quorum sensing. Although it is known that the ant *Leptothorax albipennis* uses quorum sensing to select among nest sites (Pratt *et al.* 2002) the experimental evidence for bees is not yet available although experiments are underway (Seeley 2002). There is no obvious reason why ant and honeybee behaviour in nest-site choice should be the same—ants and bees use different methods to recruit foragers, for example. If bees are using consensus decision making rather than quorum sensing, it is easier to understand why dance attrition occurs. Dance attrition is vital for reaching consensus but not for reaching a quorum where the first site to attract a certain number of visitors would be selected, regardless of what is happening at other sites. In fact, dance attrition would tend to increase the time needed to reach a quorum. This may be useful in allowing time for scouts to find alternative sites, but will also increase the time that the swarm remains in an exposed position in the open air.

(d) *Formulating models for swarm decision making*

When constructing a model, the type of formulation that is chosen for the model should reflect the scale and nature of the process which is being modelled. Models for self-organization in social insects are rich and structurally diverse because social insect behaviour occurs mostly on intermediate spatial scales, where the effects of the individuals cannot be smoothly averaged out, but nor can every individual be modelled explicitly. Some insect behaviour can be well represented by differential equation models which give a smooth representation of the colony; for example the heat flow through a stationary swarm of bees (Myerscough 1993; Watmough & Camazine 1995) or forager recruitment in a large colony of small ants (Beekman *et al.* 2001). Other types of colonial behaviour have been successfully modelled by using two different types of formulation; for example honeybee foraging, where De Vries & Biesmeijer (1998) use individually oriented models whereas Camazine & Sneyd (1991) and Cox & Myerscough (2003) use differential-equation formulations. Some colony behaviours must be modelled at an individual level as the important behaviours are averaged away if a higher-level approach, such as differential equations, is used. Crowding-based models, where insects have finite size, is one example of this (O'Toole *et al.*

1999). Each approach emphasizes a different aspect of the actual system that is being modelled.

The model of Britton *et al.* (2002) for swarm decision making uses a differential-equation formulation to get a grand, overall perspective of the decision-making processes. This model is easy to formulate, easy to analyse and fits in well with previous work on decision making. The differential-equation formulation, however, makes it difficult to model aspects of the decision process that are specific to honeybees, such as the dynamics of the scout dances and the detailed mechanics of how the scouts use dances to convey and assess information. The differential-equation model predicts that there are regions in parameter space where a deadlock is reached with stable numbers of scouts dancing for each of two sites. It also predicts that under some circumstances support for all sites will die away when all sites are poor quality and then no decision will be made. These outcomes of the differential-equation model indicate that this model has not completely captured all the important mechanics of the bees' decision making. The emphasis on scouts switching allegiance from one site to another is also, perhaps, a little too strong, given that Visscher & Camazine (1999) conclude that removing switchers from the system makes no difference to either the speed or the accuracy of the bees' decision making.

I have chosen here to use a formulation that allows the individual scouts, and hence the number of waggle runs advertising each site, to be counted, although individuals are not tracked explicitly, as is done in many individual-based models. This allows the observed dance behaviour that is specific to scouts advertising nest sites to be incorporated into the model. This model also describes the flow of information that is contained in the waggle runs as the decision-making process proceeds and shows how the transmission of information on lower-quality sites decays while information on high-quality sites spreads increasingly rapidly. Scouts that continue to visit a site but do not dance also carry information. This model is flexible and could easily be extended to monitor information held by non-dancers. This formulation can also be readily adapted to model information flows during foraging for food.

Indeed, the combination of flexibility and robustness is a strength of this population-matrix model. It can easily represent many different groups of scouts, each dancing for a different source, but at the same time predicts that one site will always be chosen. This choice will be made regardless of the quality of the available sites; the swarm is able to choose the best of a bad lot as well as choosing from high-quality sites.

Finally, what insight does this modelling give into the nature and behaviour of individual honeybees? For the decision-making process to work as modelled it is essential that scouts' dances decline with each successive visit or cease altogether after a certain number of dances. Less obviously, each scout must also have an innate ability to accurately assess the quality of a site and tune her dancing appropriately. This assessment must be the same or very similar from bee to bee. Without this innate similarity between all the scouts, a decision process where each scout only has information about one site could not consistently agree on the best site.

The author thanks Madeleine Beekman, Ben Oldroyd, members of the Bee Laboratory at Sydney University, Glenda Wardle and Peter Myerscough for helpful comments on the manuscript.

REFERENCES

- Beekman, M., Sumpter, D. J. T. & Ratnieks, F. L. W. 2001 Phase transition between disordered and ordered foraging in Pharaoh's ants. *Proc. Natl Acad. Sci. USA* **98**, 9703–9706.
- Britton, N. F., Franks, N. R., Pratt, S. C. & Seeley, T. D. 2002 Deciding on a new home: how do honeybees agree? *Proc. R. Soc. Lond. B* **269**, 1383–1388. (DOI 10.1098/rspb.2002.2001.)
- Camazine, S. & Sneyd, J. 1991 A model of collective nectar source selection by honey bees: self-organisation through simple rules. *J. Theor. Biol.* **149**, 547–571.
- Camazine, S., Visscher, P. K., Finley, J. & Vetter, R. S. 1999 House-hunting by honey bee swarms: collective decisions and individual behaviors. *Insectes Soc.* **46**, 348–360.
- Caswell, H. 1989 *Matrix population models: construction, analysis, and interpretation*. Sunderland, MA: Sinauer.
- Cox, M. D. & Myerscough, M. R. 2003 A flexible model of foraging by a honey bee colony: the effects of individual behaviour on foraging success. *J. Theor. Biol.* (Submitted.)
- 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.
- Lindauer, M. 1961 *Communication among social bees*. Cambridge, MA: Harvard University Press.
- Myerscough, M. R. 1993 A simple model for temperature regulation in honeybee swarms. *J. Theor. Biol.* **162**, 381–393.
- O'Toole, D. V., Robinson, P. A. & Myerscough, M. R. 1999 Self-organized criticality in termite architecture: a role for crowding in ensuring ordered nest expansion. *J. Theor. Biol.* **198**, 305–327.
- Pratt, S. C., Mallon, E. B., Sumpter, D. J. T. & Franks, N. R. 2002 Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* **52**, 117–127.
- Rorres, C. & Anton, H. 1977 *Applications of linear algebra*. Chichester: Wiley.
- Seeley, T. D. 1977 Measurement of nest cavity volume by the honey bee (*Apis mellifera*). *Behav. Ecol. Sociobiol.* **2**, 201–227.
- 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*. Cambridge, MA: Harvard University Press.
- Seeley, T. D. 2002 Collective decision making in honey bee swarms: reaching a consensus or building a quorum? In *Proc. XIV Int. Congress IUSSI, Sapporo, Japan, 27 July–3 August 2002*, p. 216. Sapporo, Japan: Hokkaido University.
- Seeley, T. D. & Buhrman, S. C. 1999 Group decision making in swarms of honey bees. *Behav. Ecol. Sociobiol.* **45**, 19–31.
- Seeley, T. D. & Buhrman, S. C. 2001 Nest-site selection in honey bees: how well do swarms implement the 'best-of-N' decision rule? *Behav. Ecol. Sociobiol.* **49**, 416–427.
- Seeley, T. D. & Morse, R. A. 1978 Nest site selection by the honey bee (*Apis mellifera*). *Behav. Ecol. Sociobiol.* **25**, 323–337.
- Seeley, T. D., Mikheyev, A. S. & Pagano, G. J. 2000 Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. *J. Comp. Physiol. A* **168**, 813–819.
- Visscher, P. K. & Camazine, S. 1999 Collective decisions and cognition in bees. *Nature* **397**, 400.
- Watmough, J. & Camazine, S. 1995 Self-organized thermo-regulation of honeybee clusters. *J. Theor. Biol.* **176**, 391–402.