Deciding on a new home: how do honeybees agree?

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A swarm of honeybees (*Apis mellifera*) is capable of selecting one nest-site when faced with a choice of several. We adapt classical mathematical models of disease, information and competing beliefs to such decision-making processes. We show that the collective decision may be arrived at without the necessity for any bee to make any comparison between sites.

Keywords: collective decision-making; social insects; honeybees; *Apis mellifera*; nest-site choice

1. BIOLOGICAL INTRODUCTION: HONEYBEE BEHAVIOUR

A fundamental issue in biology, and especially in animal behaviour, is the evolution of decision-making systems. Organisms must make resource-allocation choices, throughout their lives, that are likely to determine their fitness. There are both strategic and tactical issues involved in decision-making: which is the best option and how is that option recognized and selected?

Social insects provide some of the most thoroughly studied examples in which both the strategy and the tactics of decision-making have been elucidated (Bourke & Franks 1995; Seeley 1995; Camazine *et al.* 2001). Most intriguingly, in many of the well-known cases in social insects the best strategy may be to keep several options open rather than to make an all-or-nothing decision. For example, honeybee colonies, through the dynamics of dance recruitment, can allocate the vast majority of their foragers to the most rewarding nectar-rich flower patches. Nevertheless, some foragers remain faithful to currently less rewarding food sources. This may represent strategic bet hedging. Flowers are ephemeral and a good patch now may be a poor one soon. By maintaining contact with, and knowledge of, several patches of flowers a honeybee colony should be able to reallocate its foragers more rapidly and effectively over fields of capricious blooms (Seeley 1995).

Similarly, certain ants can select the shortest paths to food sources. Indeed, where there is a short and a long path to the same food source, the decision-making mechanism can be surprisingly simple. Those ants that happen to take the shorter path get there and back more quickly than those ants that happen to take the longer path. All the ants lay trails of attractive pheromones and such pheromones get reinforced more rapidly on the shorter path, simply because that path is shorter and quicker. In such cases, individual ants do not directly compare the lengths of the two paths but the colony is able to choose the shorter one (Goss *et al.* 1989; Beckers *et al.* 1990, 1992).

In certain cases, the shorter path is used exclusively, whilst in others a small amount of traffic continues to use the longer path. Some traffic continuing to use the longer path may be costly in the short term, but it may represent a beneficial insurance policy if the shorter path becomes blocked or dangerous.

In the case of honeybee foragers or ant trail makers, decision-making mechanisms that are not all-or-nothing but retain the benefits of fuzzy logic can pay off. In these systems what might be thought of as errors—honeybees repeatedly going to the weaker nectar sources, ants stubbornly wasting energy on longer routes—can be adaptive in the long term.

By contrast, in some situations social insects need to make a dissent-free collective decision. For example, when a honeybee swarm is faced with a choice among several suitable nest-sites, it seems of paramount importance that the swarm as a whole selects only one. How honeybee swarms select a single new nest-site is the issue we will consider in this paper.

Colony propagation in honeybees (*Apis mellifera*) is described by Michener (1974), Seeley (1982) and Winston (1987). A swarm of bees, consisting of the old maternal queen and most of her workers, leaves the old hive and typically settles in a tree. Scouts leave the swarm and individually search for a tree hole or similar cavity as a suitable new home for the colony. If they find a potentially suitable nest-site, they measure a suite of its characteristics, and represent their overall enthusiasm for that site in the vigour of their dance back on the surface of the swarm (Lindauer 1955, 1961; Seeley & Buhrman 1999, 2001). Their dance not only advertises the quality of the nest-site, but also indicates its distance and direction to other potential scouts, who may also go to that site and in turn advertise its charms through vigorous dances. Different scouts may find different nest-sites and may advertise them concurrently. In other words, dances leading to further recruitment of scouts to different sites may occur simultaneously on the swarm. Nest-site choice by honeybees can therefore involve different positive feedback loops of recruitment by different scouts to different sites and can be a protracted process taking several days. Nevertheless, sooner or later the entire swarm takes off as a single cohes-
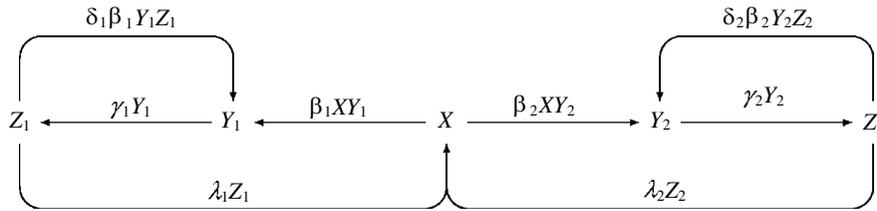
Figure 1. Diagram of the possible transitions between states in the indirect switching model. In the text, and for numerical simulations, we have made the simplifications $\gamma_1 = \gamma_2 = \gamma$, $\delta_1 = \delta_2 = \delta$, $\lambda_1 = \lambda_2 = \lambda$.
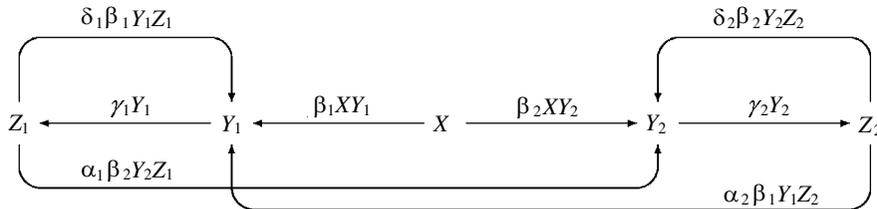

Figure 2. Diagram of the possible transitions between states in the direct switching model. In the text and for numerical simulations we have made the simplifications $\alpha_1 = \alpha_2 = \alpha$, $\gamma_1 = \gamma_2 = \gamma$, $\delta_1 = \delta_2 = \delta$.

ive entity and flies to only one new nest-site among the many that have been advertised. How this apparent unanimity is achieved is the subject of this paper.

Recent studies (Camazine *et al.* 1999; Seeley & Buhrman 1999; Visscher & Camazine 1999*a,b*) have recorded the behaviour through time (the time-lines) of all scouts dancing on the surface of swarms during the entire nest-choice process. Such studies show that

(i) the dances of individual scout bees tend to decrease in strength and eventually cease, and that
(ii) some scouts switch allegiance between sites.

Thus, in honeybees, as in our own societies, a crucial decision-making process involves competing advertisement, recruitment to different political parties, opinion polls, the growth of apathy and first-past-the-post elections. Here we review and extend classical mathematical models of the spread of infectious diseases, and the spread of infectious ideas, to elucidate what are likely to be the most important factors in the decision-making processes of house-hunting honeybees.

2. MATHEMATICAL INTRODUCTION: MODELS OF SPREAD OF INFORMATION OR BELIEF

The spread of information has been thought of as mathematically equivalent to the spread of an infectious disease. The analogy is drawn between those ignorant of the information and susceptibles, those spreading the information and infectives, and, in some models, those no longer spreading the information and those immune to the disease. Let us denote these states by X, Y and Z respectively. Individuals may move from the 'susceptible' X to the 'infective' Y state, and from the 'infective' Y to the 'immune' Z state. Diagrammatically, the possible transitions between states are

$$X \rightarrow Y \rightarrow Z.$$

The information is spread by contact between an ignorant individual and a spreader, so that the rate of 'infection'

is most simply modelled by βXY. The rate of 'recovery' is most simply modelled by γY, where it is assumed that any spreader stops spreading the information in the next interval of time δt with probability $\gamma \delta t$. The equations are from Kermack & McKendrick (1927).

$$\frac{\mathrm{d}X}{\mathrm{d}t} = -\beta XY, \quad \frac{\mathrm{d}Y}{\mathrm{d}t} = \beta XY - \gamma Y, \quad \frac{\mathrm{d}Z}{\mathrm{d}t} = \gamma Y.$$

Let $N = X + Y + Z$. The basic reproductive ratio $R_0 = \beta N / \gamma$ is the average number of individuals that a spreader, in an ignorant population, tells before ceasing to spread the information. It is straightforward to show that, if a small number of spreaders are introduced into an ignorant population, the information spreads if $R_0 > 1$. However, irrespective of how fast the information spreads, there will be some individuals who never hear it.

At least in human societies, the process of leaving the spreader class may be somewhat different. Daley & Kendall (1965) argued that spreaders will carry on spreading the information until they meet someone who already knows it, when, with some probability, they cease to spread it. People who have ceased to spread the information become 'stiflers'. In this case, the information always spreads if a small number of spreaders are introduced into an ignorant population, but again there are some who remain ignorant.

Things are different again if we model belief rather than information. Now the X class represents unbelievers and the Y class believers, who are assumed to be actively spreading the belief. The motion from X to Y is now conversion to the belief. The possibility that some believers lapse into unbelief might also be included. This has analogies with diseases that do not impart immunity, where recovered individuals return to the susceptible class.

Karmeshu & Pathria (1980) modelled the case of two conflicting beliefs. They assumed, for simplicity, that all believers are active spreaders, so that the population is split into neutrals X and believers in each of the two camps Y_1 and Y_2, and that the following transitions in state could occur:
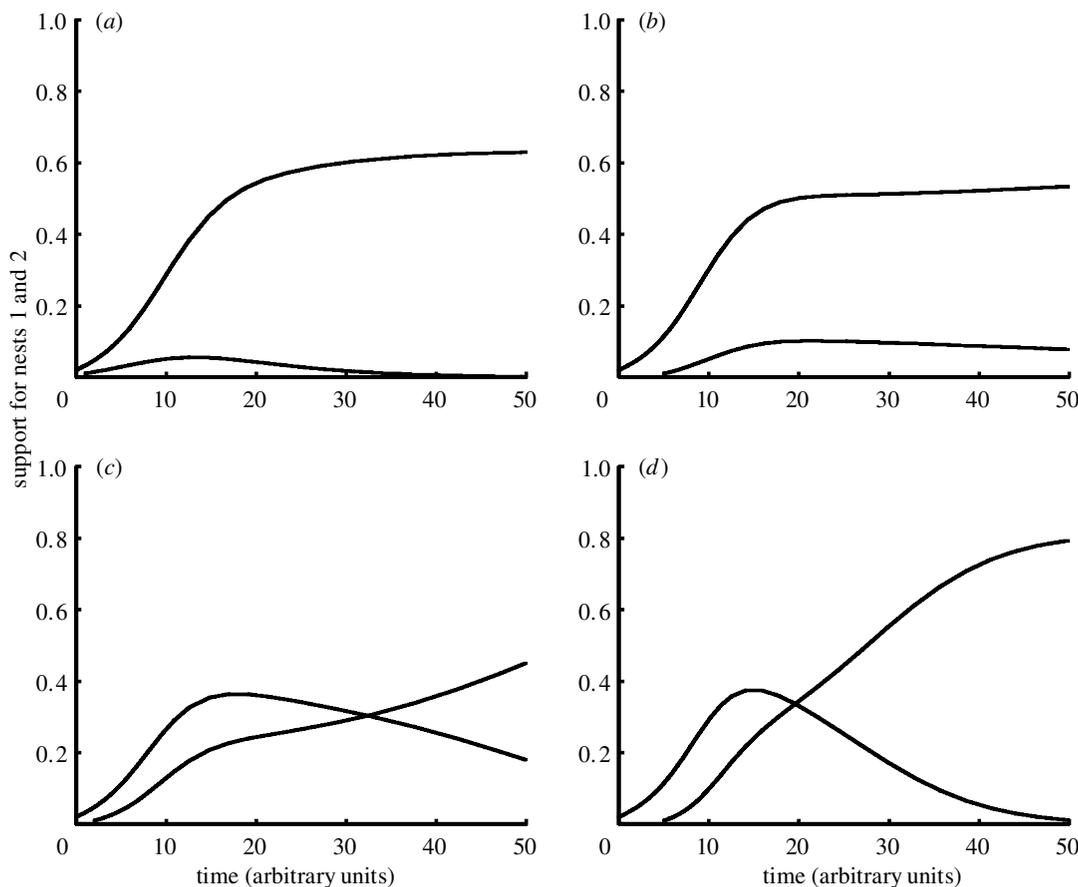
Figure 3. Indirect switching. The vertical axis represents total support for each site as a fraction of the total population, $(1/N)(Y_1 + Z_1)$ and $(1/N)(Y_2 + Z_2)$. In all four panels, $\beta_1 N = 0.6$, $\gamma = 0.3$, $\lambda = 0.3$, $\delta = 0.5$. In (*a*), $\beta_2 N = 0.5$, so that the second site is of inferior quality and fails to win support. In (*b*), $\beta_2 N = 0.7$, so that the second site is of marginally superior quality, but news of it arrives at $t = 5$, too late to change the consensus. Over a longer time-scale, support for it dies away to zero. In (*c*), $\beta_2 N = 0.7$, news of the second site arrives at $t = 2$, and the colony consensus switches to it. In (*d*), $\beta_2 N = 0.9$, so that the second site is of much better quality than the first. A switch will take place however late the news arrives, and we have taken $t = 5$ as an illustration.

(i) a believer in camp i converts a neutral, at rate $\beta_i XY_i$;

(ii) a believer in camp i lapses to neutrality, at rate λ_i;

(iii) a believer in camp i proselytizes a believer in another camp j, at rate $\epsilon_{ji} Y_i Y_j$. The equations become

$$\frac{dX}{dt} = \lambda_1 Y_1 + \lambda_2 Y_2 - \beta_1 XY_1 - \beta_2 XY_2,$$

$$\frac{dY_1}{dt} = \beta_1 XY_1 - \lambda_1 Y_1 - \epsilon Y_1 Y_2,$$

$$\frac{dY_2}{dt} = \beta_2 XY_2 - \lambda_2 Y_2 + \epsilon Y_1 Y_2,$$

where $\epsilon = \epsilon_{12} - \epsilon_{21}$. This parameter is proportional to the net rate of flow from belief 1 to belief 2 as a result of proselytization. If belief 2 is more credible than belief 1 then this net flow is positive, i.e. $\epsilon > 0$.

There are four possible steady states for these equations:

(i) naive (all neutrals);

(ii) all either belief 1 or neutral;

(iii) all either belief 2 or neutral;

(iv) no consensus, with both $Y_1 > 0$ and $Y_2 > 0$.

We shall refer to the second and third of these as the *dissent-free* states.

One may also include non-evangelical believers Z_1 and Z_2, who believe in one of the two beliefs but who are not actively spreading the word. These might, on occasion, return to the evangelical classes Y_1 and Y_2. The equations depend on the detailed assumptions made about the mechanisms by which conversions and lapses occur.

3. MODELLING NEST-SITE CHOICE IN HONEYBEES

Potential nest-sites are only visited and evaluated by a sub-population of bees in the swarm, the scouts (Lindauer 1955, 1961). We shall assume that a decision has been made by the colony as a whole when a consensus has been reached by the scouts, and will therefore model scouts only.

We adapt the model of Karmeshu & Pathria (1980). Since bees do not dance constantly for a particular site, but often take up dancing again for the same site they previously advertised (Camazine *et al.* 1999; Seeley & Buhrman 1999; Visscher & Camazine 1999*a,b*) we included non-evangelical believers Z. We assumed that they take up dancing again when stimulated to do so by an evangelist (a dancer) Y, although they could do so spontaneously without altering the results qualitatively.

The recruitment process is begun by dancers converting neutrals. There is no evidence in individual bee time-lines

(Camazine *et al.* 1999; Seeley & Buhrman 1999; Visscher & Camazine 1999*b*) for dancers suddenly switching allegiance from one site to another (a direct switch from Y_i to Y_j), and we shall assume that this never occurs. Two possibilities remain: (i) conversion from Z_i to Y_j (direct switching of allegiance) and (ii) lapsing from Y_i to X, possibly via Z_i (ceasing to dance and becoming neutral), and then being recruited to Y_j (indirect switching). Empirically, it may be impossible to differentiate between these possibilities, since a bee in state X may be indistinguishable from one in state Z, but the two possibilities lead to somewhat different outcomes. We modelled both situations to decide whether direct switching is important. To clarify the situation as much as possible, we compared one model with direct switching *only* with one with indirect switching *only*.

We assumed that no stifling process takes place, so that bees do not stop dancing for a particular site when some or many of those they meet already support that site.

We tested the hypothesis that no direct comparison of sites is necessary. We further assumed that any decision by a bee to support a site is made on the basis of information about that site alone. The rate of switching allegiance from site i to site j depends only on the quality of site j and on how strongly it is being advertised, and not on the quality of site i. Similarly, we shall assume that the rate of lapsing from support for site i to neutrality is independent of site i. Relaxation of these assumptions could produce a more efficient decision process, but we show that efficient decisions can be made even under these conditions.

(a) Indirect switching model

A diagram of the transitions in this model is shown in figure 2. Let β_1 and β_2 be measures of how vigorously the bees dance for sites 1 and 2, and hence of their quality. For the utmost simplicity, these are assumed to be the only parameters that differ between bees supporting sites 1 and 2, either actively or inactively. The analogue of the epidemiological *force of infection*, which we shall call the *force of persuasion*, is the product $\beta_i Y_i$ of the *persuasion parameter* β_i and the number of bees dancing for i. The per capita rates at which the bees leave the naive X class and the non-dancing Z_i class for the dancing Y_i class are proportional to the force of persuasion, with constants of proportionality 1 and δ respectively, where δ is independent of the site supported. The per capita rates of ceasing to dance and lapsing from the non-dancing class to the naive class are taken to be constants, independent of the site supported, and given by γ and λ respectively. The equations are

$$\frac{dX}{dt} = -\beta_1 XY_1 - \beta_2 XY_2 + \lambda Z_1 + \lambda Z_2,$$

$$\frac{dY_1}{dt} = \beta_1 XY_1 - \gamma Y_1 + \delta\beta_1 Y_1 Z_1,$$

$$\frac{dY_2}{dt} = \beta_2 XY_2 - \gamma Y_2 + \delta\beta_2 Y_2 Z_2,$$

$$\frac{dZ_1}{dt} = \gamma Y_1 - \lambda Z_1 - \delta\beta_1 Y_1 Z_1,$$

$$\frac{dZ_2}{dt} = \gamma Y_2 - \lambda Z_2 - \delta\beta_2 Y_2 Z_2.$$

(b) Direct switching model

A diagram of the transitions in this model is shown in figure 1. The equations are

$$\frac{dX}{dt} = -\beta_1 XY_1 - \beta_2 XY_2,$$

$$\frac{dY_1}{dt} = \beta_1 XY_1 - \gamma Y_1 + \delta\beta_1 Y_1 Z_1 + \alpha\beta_1 Y_1 Z_2,$$

$$\frac{dY_2}{dt} = \beta_2 XY_2 - \gamma Y_2 + \delta\beta_2 Y_2 Z_2 + \alpha\beta_2 Y_2 Z_1,$$

$$\frac{dZ_1}{dt} = \gamma Y_1 - \delta\beta_1 Y_1 Z_1 - \alpha\beta_2 Y_2 Z_1,$$

$$\frac{dZ_2}{dt} = \gamma Y_2 - \delta\beta_2 Y_2 Z_2 - \alpha\beta_1 Y_1 Z_2.$$

There is now no return to the naive state, and hence no indirect switching, but direct switching takes place at a per capita rate proportional to the force of persuasion, with the constant of proportionality α independent of the site supported. This assumes that the bees do not make a direct comparison between sites and are converted to a new site at a rate that depends only on its quality and how strongly it is being advertised.

4. RESULTS

(a) Indirect switching model

Naive, dissent-free and no-consensus steady states are possible. For belief i to grow in a naive population of size N, we require that the basic reproductive ratio $R_i = \beta_i N/\gamma > 1$. We shall always assume this to be the case, otherwise support for site i can never grow and we can immediately eliminate it from consideration. Under these conditions, the naive steady state is unstable, and news of a single site results in a dissent-free choice of that site. Can such a verdict be overturned by news of a second site? There are three cases.

(i) If the second site is less good than the first, $\beta_2 < \beta_1$, the verdict remains unchanged.
(ii) If the second site is very much better than the first, the consensus switches to the second site.
(iii) If the second site is marginally better than the first, the verdict will be changed only if the news comes in sufficiently early in the process. If the news arrives too late then the verdict will remain fixed on the less good first site.

These results are summarized in figure 3.

(b) Direct switching model

Naive, dissent-free and no-consensus steady states are again possible. The naive steady state is always unstable, and news of site 1 only will lead to a dissent-free state (Y_1^*, Z_1^*) for site 1. However, the character of this steady state is quite different, depending on the quality parameter β_1. If this is high enough, $\beta_1 N > \gamma/\delta$, then $Y_1^* > 0$, but if it is lower than this, then $Y_1^* = 0$. In the first case, the site is danced for indefinitely, but in the second case dancing ceases after a time, and support for the site only comes
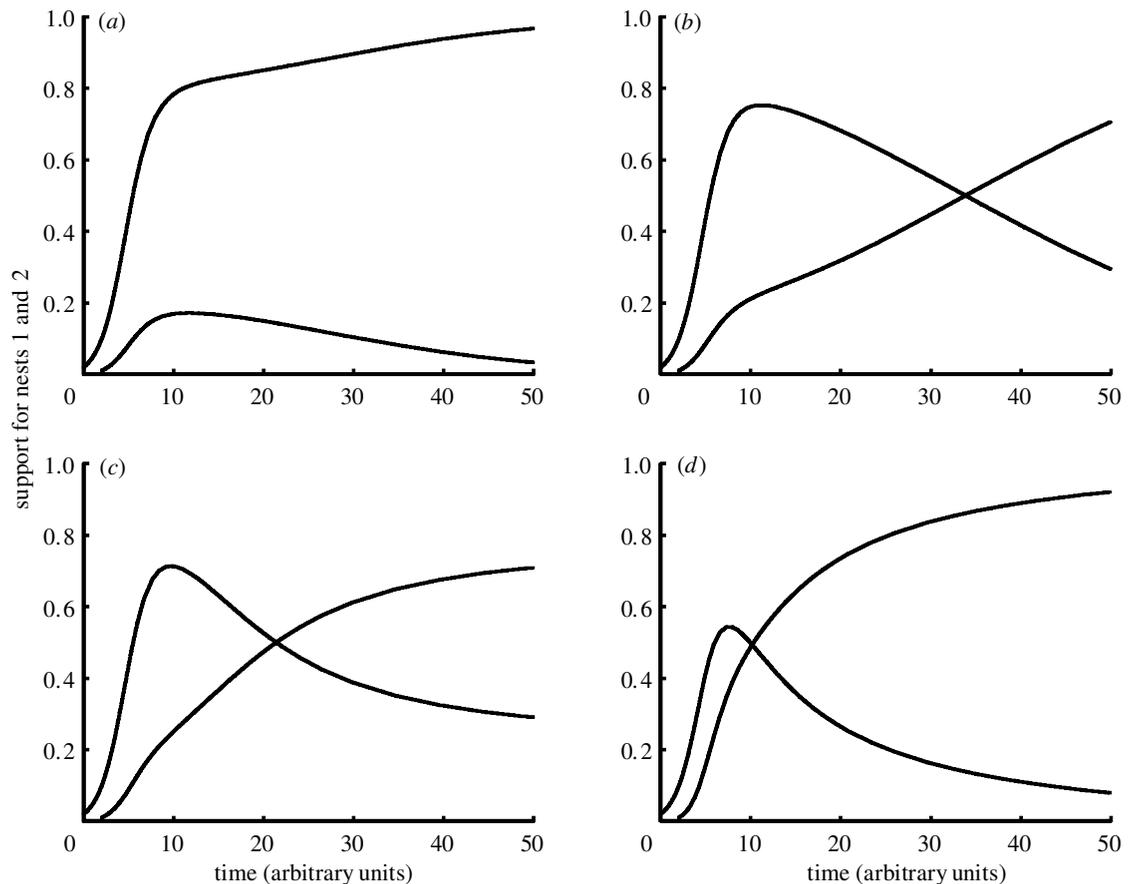
Figure 4. Direct switching. The vertical axis represents total support for each site as a fraction of the total population, $(1/N)(Y_1 + Z_1)$ and $(1/N)(Y_2 + Z_2)$. In the first three panels, $\beta_1 N = 1.0$, $\beta_2 N = 1.2$, $\gamma = 0.3$, $\delta = 0.5$, so that the second site is marginally superior to the first. In (*a*), $\alpha = 0.2 < \delta$, news of the second site arrives too late and fails to win support. In (*b*), $\alpha = \delta = 0.5$, the colony consensus always switches to site 2, however late the news arrives. In (*c*), $\alpha = 0.7$, and no consensus is reached. Over a longer time-scale, the system tends to a steady state with positive support for each site. In (*d*), $\alpha = 0.7$ again, but $\beta_2 N = 1.5$, so that the second site is much better than the first. The colony consensus switches to site 2.

from non-dancers Z_1^*. Since these non-dancers presumably cannot rouse the whole colony, then this may be interpreted as saying that a site of such low quality will never be chosen. It may, however, prevent consensus from being reached on a site of slightly higher quality.

Now let us assume that news of site 1 arrives first. What effect does the later arrival of news of an alternative site 2 have? The consequences depend on the relative sizes of α and δ, and there are three cases.

(i) If $\alpha < \delta$, the situation is similar to the indirect switching model; site 2 is chosen if it is much better, or if it is marginally better and the news arrives early.
(ii) If $\alpha = \delta$, site 2 is chosen if and only if it is better.
(iii) If $\alpha > \delta$, site 2 is chosen if it is much better. However, if it is marginally better, no consensus is reached.

These results are summarized in figure 4.

5. DISCUSSION

Very similar results to ours have been observed and analysed in decision-making in other societies. For example, ant colonies presented with two foraging sites will generally choose the better of them, but may become fixed on

the worse if it is discovered sooner (Pasteels *et al.* 1987; Deneubourg & Goss 1989). In this case, the decision is encoded in pheromone trails leading to each site rather than in the individuals in the colony.

We have assumed that scouts recruit more strongly to a better site because a measure of the quality of the site is encoded in their dance, possibly through its vigour (Seeley & Buhrman 2001). Alternatively, only a fraction of scouts returning from a site may dance at all, as Seeley *et al.* (1991) found in their study on nectar sources, with this fraction depending on the site quality. Either alternative may be modelled by taking the persuasion parameter β to be larger for better sites. Dances for better sites are also longer (Seeley & Buhrman 2001). This may be modelled by taking the parameter γ, the probability of ceasing to dance per unit time, to be smaller for a better site; such a modification makes no qualitative difference to the results.

In their study on recruitment to foraging sites, Seeley *et al.* (1991) use a force of persuasion proportional to $(\tau_i D_i)/(\tau_i D_i + \tau_j D_j)$, whereas ours is simply proportional to Y_i. Here D_i includes both those bees dancing for i and those that have ceased dancing for i but are still in the dancing compartment, and is therefore equivalent to our $Y_i + Z_i$. The parameter τ_i represents the time spent dancing for site i, and so corrects from $Y_i + Z_i$ to Y_i. Their

force of persuasion therefore depends on the *fraction* of dancers that are dancing for site i, whereas ours depends on the *numbers* dancing for site i. We have chosen our form for simplicity and because it seems reasonable that if the total number of dancing bees is reduced, while keeping the proportions dancing for each site the same, then recruitment will also be reduced. The alternative form does not change the results qualitatively.

We have not taken into account in this paper the time taken by scouts to find and evaluate nest-sites and return to the swarm. It is straightforward to do so, and results in a slower build-up of support for any given site. However, the results are qualitatively unchanged, and we have therefore neglected these effects for the sake of simplicity.

Both indirect and direct switching models seem to work well. Direct switching allows a greater number of possible behaviours, due to the difference between the parameters α and δ. In the particular case $\alpha = \delta$, the best site is always chosen, whereas in the indirect switching model a marginally inferior site is chosen if the news of the superior site does not arrive in time. This may be a shortcoming of the indirect switching process, or it may be that the benefits of a quick decision outweigh the costs of choosing a marginally worse site.

The possibility of no consensus in the direct switching model is presumably non-adaptive, although it does allow the colony to wait for news of a third better site. It can occur if $\alpha > \delta$, i.e. if it is easier to stimulate believers in an alternative site to dance than believers in your own site. If $\alpha \leqslant \delta$, which may be more realistic, then consensus is always reached. The results of Visscher & Camazine (1999a) suggest that $\alpha = \delta$. They found that dancers who followed other dances on the swarm chose them at random from those available, rather than preferentially following dancers for their own site (as might be expected if $\alpha < \delta$) or dancers for other sites (as might be expected if $\alpha > \delta$).

It is not known whether bees are capable of the cognitive processing required to make a direct comparison between nest-sites. This paper shows that there is no need for any individual bee to make such a direct comparison in either the indirect or the direct switching model, she needs only to judge the quality of one site at a time. A decision between sites is then made at the colony level.

Recently, the importance of information flow in social insect colonies has been emphasized (Detrain *et al.* 1999). Information flow between individuals in many other social animals is also of great interest (Giraldeau 1997). We have shown that the classical model of Karmeshu & Pathria (1980) in human societies can illuminate decision-making in other animal societies.

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