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Animal behaviour

Making good choices with variable information: a stochastic model for nest-site selection by honeybees

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A density-dependent Markov process model is constructed for information transfer among scouts during nest-site selection by honeybees (*Apis mellifera*). The effects of site quality, competition between sites and delays in site discovery are investigated. The model predicts that bees choose the better of two sites more reliably when both sites are of low quality than when both sites are of high quality and that delay in finding a second site has most effect on the final choice when both sites are of high quality. The model suggests that stochastic effects in honeybee nest-site selection confer no advantage on the swarm.

Keywords: *Apis mellifera*; stationary swarm; Monte Carlo simulations; mathematical model

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1. INTRODUCTION

When a swarm of honeybees (*Apis mellifera*) leaves the hive, it settles in a hanging cluster while scouts search for a suitable new home. Scouts communicate information to the nestmates about locations and quality of sites by performing waggle dances (Camazine *et al.* 1999; Seeley & Buhrman 1999, 2001) in the same way that foragers communicate about forage patches (Seeley 1995). Newly recruited scouts visit the site, return to dance and recruit others. When the number of scouts visiting a particular site reaches a quorum, the swarm takes off and occupies that nest (Seeley & Visscher 2003).

Scouts' dances follow a characteristic pattern (Seeley & Buhrmann 1999, 2001). A scout's dance on each subsequent return contains fewer waggle runs than on previous returns and she ceases dancing after several visits to the site. High-quality sites stimulate longer and more vigorous dancing on each return than low-quality sites. Scouts cease to dance sooner for a poor site than for a good site. The collective effect is that more scouts are recruited to good quality sites than to poor quality sites.

Mathematical models formulated to describe this process include an ordinary differential equation model (Britton *et al.* 2002), a matrix model where dances age, die and reproduce (Myerscough 2003), and an individual-based model (Passino & Seeley 2006). While these models help in understanding the role of dance attrition, duration and vigour in decision making, they give little substantial indication of the effects of random variation on decision making.

Random events have been observed to decisively influence bees' decision making (Seeley & Burhmann 2001). When a swarm has a choice between a good nest site and mediocre nest sites, it may still choose a mediocre one due to when various sites are discovered, the relative vigour of the scouts' dances, inaccuracies in the presentation of information by dancers (Tanner & Visscher 2006) or in potential scouts' interpretation of this information.

So, how robust is the nest-site selection process to random events? How do random events affect the speed of nest-site selection? Is stochasticity a help or hindrance in selecting the best available nest site? We use a simple model here to explore the effect of randomness on nest-site selection in honeybees.

2. THE MODEL

We construct a very simple model for decision making, which includes only the aspects of nest-site selection that are directly relevant to the questions we address. Fundamentally, nest-site selection in honeybees is driven by the propagation and loss of information about potential new homes. Informed scouts visit the nest site and return to advertise it on the swarm. Information is lost when a scout ceases to dance for a site.

Let $S(t)$ be a random variable representing the number of uncommitted potential scouts. Let $D_j(t)$ be the number of scouts dancing for site j. Potential scouts are workers who are not dancing but may be recruited to become scouts. 'Scout' refers to workers who are dancing to advertise a site's location and quality. We assume that the maximum number of potential scouts, N, is constant during each nest-site selection. Then, for m sites, since $S(t)+D_1(t)+D_2(T)+D_3(t)+\cdots+D_m(t)=N$, we need to consider only the number of scouts that are dancing for each site. We assume that when numbers for one site, say $D_j(t)$, reach a quorum, the jth site is chosen.

We model scout recruitment and loss as a density-dependent Markov process in discrete time. In other words, in any single sufficiently small period of time Δt, for any given site, exactly one of three events occurs: either a new scout is recruited or a scout ceases to dance and again becomes a potential scout or nothing happens.

We assume that growth in scout numbers is proportional to the number of scouts already advertising a site and the number of potential scouts available for recruitment. Then the probability of recruiting a scout to site j in a single time-interval is

$$\Pr\{D_j(t+\Delta t) = d_j + 1 | D_j(t) = d_j\}$$

$$= \frac{\alpha_j d_j}{N}\left(N - \sum_{k=1}^{m} d_k\right)\Delta t, \qquad (2.1)$$

where $N-\sum_{k=1}^{m} d_k$ is the number of potential scouts at time t. The parameter α_j indicates how strongly scouts are supporting site j. If α_j is large, scouts' dances advertising the site have many waggle runs. If α_j is small, scouts produce few waggle runs on each return to the swarm.

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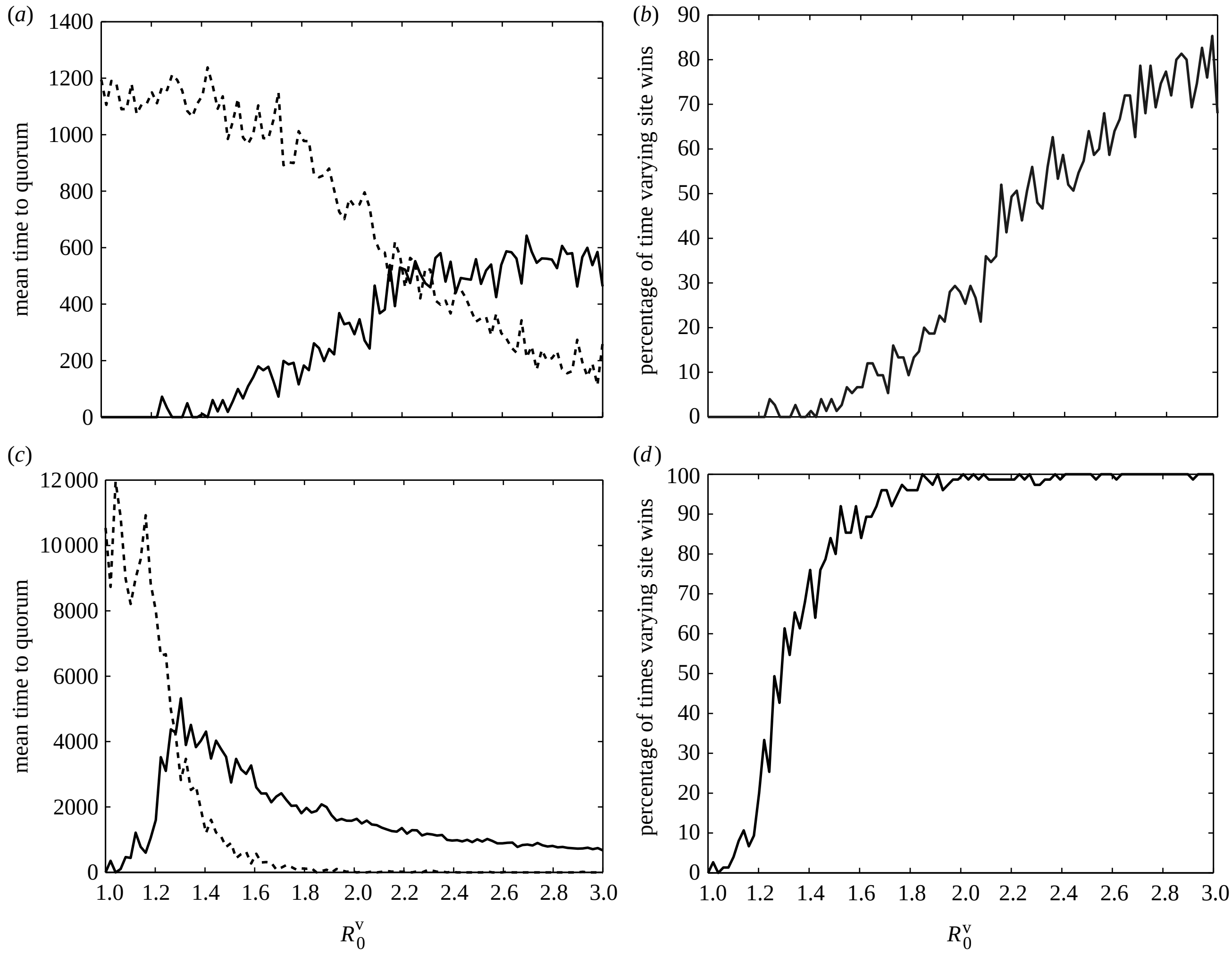

Figure 1. Results for two competitions between two sites, one of fixed quality and another with quality given on the horizontal axis. The fixed site has (*a*) and (*b*) $R_0^f=2.3$, $\alpha=0.8$ (good quality) and (*c*) and (*d*) $R_0^f=1.3$, $\alpha=0.44$ (poor quality); $\beta=0.33$ throughout. In (*a*) and (*c*), results are shown for when the fixed site is selected (dashed line) and when the varying site is selected (solid line).

The probability of one scout ceasing to dance and becoming a potential scout again in time-interval Δt is

$$\Pr\{D_j(t+\Delta t)=d_j-1|D_j(t)=d_j\}=d_j\beta_j\Delta t. \qquad (2.2)$$

The constant β_j reflects the rate that scouts cease dancing for site j and can be regarded as an indicator of the site quality; the higher β_j, the lower the quality of the site. If a site neither gains nor loses a scout in a particular time-step, then D_j remains unchanged.

The basic reproductive number for each site, $R_0=\alpha_j/\beta_j$, is the number of new scouts recruited on average by a single scout over all her dance episodes when the number of potential scouts is very close to N. Sites with $R_0>1$ are able to recruit at least one new dancer for every scout. When $R_0<1$, less than one new scout is recruited by each existing scout and the dance is very likely to go extinct. As R_0 increases, a site has a greater chance of reaching quorum. We chose the quorum to be 30 scouts (a realistic choice; see Seeley & Buhrman 1999) and the total number of potential scouts N to be 100.

We simulated these Markov processes numerically. We used a reflecting boundary condition at $D_j=0$ setting $\Pr\{D_j(t+\Delta t)=1|D_j(t)=0\}=1$. This prevented information about a site being lost to the swarm. We chose $\Delta t=0.01$ as this is small enough to ensure that two events are unlikely to occur in the same time-interval. The units of time are arbitrary and only for comparative purposes.

3. RESULTS

Figure 1 shows the effect of quality in determining nest-site choice where two sites are discovered simultaneously for two sets of two sites each. One site in each set, the *fixed site* has fixed quality, given by R_0^f. The value of α for the other site, the *varying site*, changes while β remains fixed. The quality of the varying site R_0^v is shown on the horizontal axis. Both sites in each set always have $R_0>1$, so that the dances are unlikely to become extinct. For each α value, the simulation was run 100 times and the time to quorum in each simulation was recorded for the site that was selected. From this the mean time to quorum (MTQ) was calculated. The percentage of times that each site was selected was also recorded. The sites were chosen so that the fixed site in figure 1*a*,*b* is of good quality ($R_0^f=2.3$). In the second set, the fixed site is of poor but acceptable quality ($R_0^f=1.3$).

When $R_0^f=2.3$, the selection rate of the varying site rose in an apparently linear way as R_0^v increased

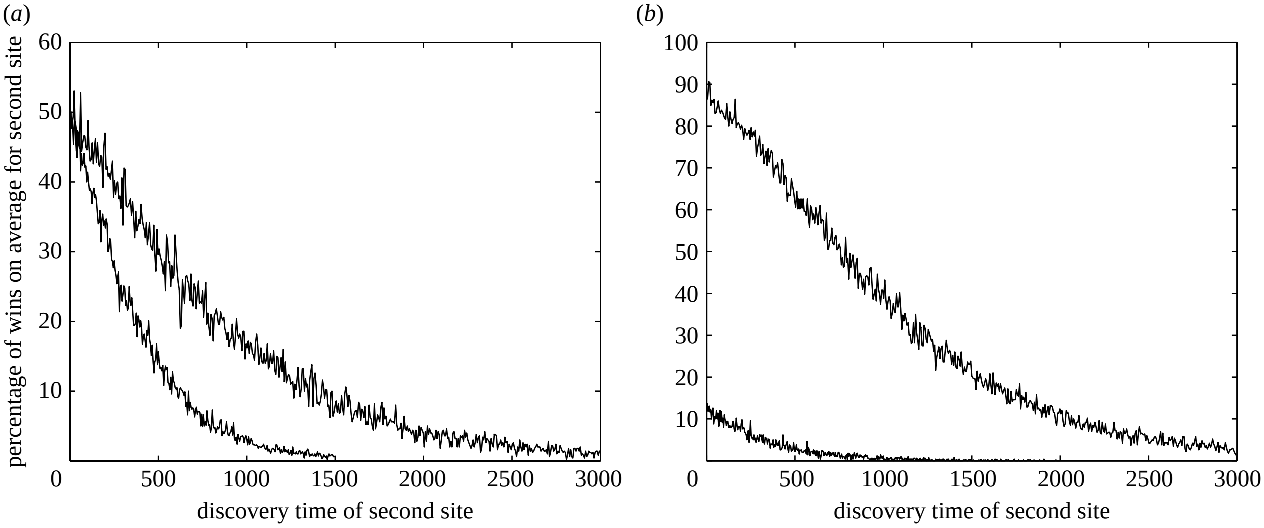

Figure 2. Percentage of time that a site discovered second will be selected, against delay in discovery of the second site. (*a*) Upper line, both sites mediocre; lower line, both sites good. (*b*) One mediocre site and one good site: upper line, good site discovered second; lower line, mediocre site discovered second.

(figure 1*b*). Even when $R_0^{\mathrm{v}} = 2.8$ (which is $R_0^{\mathrm{f}} + 0.5$), the varying site's selection rate was only 80%. When $R_0^{\mathrm{f}} = 1.3$, the selection rate of the varying site rose rapidly for R_0^{v} close to R_0^{f}. The varying site was successful close to 100% of the time when $R_0^{\mathrm{v}} = 1.8 = R_0^{\mathrm{f}} + 0.5$ (figure 1*d*).

When $R_0^{\mathrm{v}} < R_0^{\mathrm{f}}$, the MTQ for the fixed site decreased as R_0^{v} increased in all cases. This was more extreme for $R_0^{\mathrm{f}} = 1.3$. Figure 1 suggests that if the poorer of two sites is selected, this will occur comparatively quickly and will be the result of random events.

When $R_0^{\mathrm{f}} = 1.3$, the MTQ of the varying site was greatest when R_0^{v} was a little greater than R_0^{f}. This suggests that if the difference in site quality is small, particularly if both sites are comparatively poor, then site selection takes longer.

As R_0^{v} increased, the MTQ for the varying site decreases for $R_0^{\mathrm{f}} = 1.3$ (figure 1*c*). Again, if the poorer quality site was selected, it reached quorum quickly. The MTQ for the varying site did not decrease when it was competing with a high-quality fixed site (figure 1*a*).

The simulation was started with one site only and after a fixed delay a second site was introduced. Figure 2*a*,*b* shows the percentage of time that the second site is selected, against the delay in its discovery after the first site. When the competing sites are of equal quality, as the delay increased, the selection rate of the second site decreased more rapidly with delay when the competing sites are both of high quality than when they are both of mediocre quality.

In experiments of Seeley & Buhrmann (2001) where the swarm chose between four mediocre nests and one high-quality nest, in four of the five replicates, the swarm selected the high-quality nest. Selection of a mediocre nest occurred when the good nest was discovered late, and scouts failed to recruit strongly to it. We simulated nest-site selection where three mediocre nests are found at the start and a good nest site is found after a delay. Even with no delay, the model predicted that a mediocre site will be chosen between 5 and 15% of the time. The selection rate of the good site declined as the delay in its discovery increases.

4. DISCUSSION

This model predicts that random events in assessment of nest-site quality, transfer and retention of information and time of discovery of a site can result in a swarm selecting a site that is not the best available one. The model also predicts that effects of these random events increase with increasing site quality. Differences in site quality will be most significant to the survival and well-being of the colony when both sites are poor. This model suggests that then a colony will select the better site more reliably than when choosing between two good sites, which will both provide a good home. Therefore, stochasticity is most evident when selecting the higher-quality site is not crucial to the colony's survival. There is no evidence that randomness is helpful in nest-site selection.

The later that any site is discovered, the less chance it has of being selected. Quick decisions generally tend to favour poorer sites, due to random events. In choices between two sites when both sites are of high quality, this inaccuracy will be less important than when both are of poor quality. This modelling suggests that the lower the quality of two sites, the longer the swarm's decision will take but the more likely it is that it will choose the better site. An accurate choice between two good sites is less critical than between two poor sites and hence a speedy decision is desirable. When accuracy is important, it is more advantageous to spend more time for a better decision.

We have chosen to investigate stochasticity in nest-site selection using a very simple model which allows us to focus on questions of interest without modelling every aspect in detail. With some changes in interpretation, it would also be applicable to nest-site selection in ants (Pratt *et al.* 2002).

Stochastic effects and individual variation are inherent in nest-site choice by honeybees. Bees can make reliable decisions with different levels of variability in their dances (Tanner & Visscher 2006) and the model suggests that the process is most accurate when choosing between poorer sites. Since a fully deterministic process can, in principle, produce acceptable results (Myerscough 2003), the question becomes: does randomness confer any advantage in decision making or is this merely the best that bees can do? While it is clear that individual phenotypic variations within a colony can confer an advantage in other behaviour (Jones *et al.* 2004), it is not clear that this is the case in nest-site selection.

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