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Decision-making in honeybee swarms based on quality and distance information of candidate nest sites

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HIGHLIGHTS

- We model the nest-site selection process in honeybee *Apis mellifera* swarms.
- Site distance preference is moderate > near > far if the sites have low qualities.
- Site distance preference is near > moderate > far if the sites have high qualities.
- Adaptive decisions are made based on a trade-off between quality and distance.
- Large size swarms are adaptive at making decisions based on available information.

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ABSTRACT

In the nest-site selection process of honeybee swarms, an individual bee performs a waggle dance to communicate information about direction, quality, and distance of a discovered site to other bees at the swarm. Initially, different groups of bees dance to represent different potential sites, but eventually the swarm usually reaches an agreement for only one site. Here, we model the nest-site selection process in honeybee swarms of *Apis mellifera* and show how the swarms make adaptive decisions based on a trade-off between the quality and distance to candidate nest sites. We use bifurcation analysis and stochastic simulations to reveal that the swarm's site distance preference is moderate > near > far when the swarms choose between low quality sites. However, the distance preference becomes near > moderate > far when the swarms choose between high quality sites. Our simulations also indicate that swarms with large population size prefer nearer sites and, in addition, are more adaptive at making decisions based on available information compared to swarms with smaller population size.

1. Introduction

Making a choice between two or more existing alternatives by animal groups is usually crucial to the fitness of the group as a whole as well as to the fitness of individual group members (Conradt and Roper, 2005). During the decision-making process, individual group members must coordinate and share information in order to enable the whole group to choose the best available option (Conradt and Roper, 2005; Sumpter, 2006; Sumpter and Pratt, 2009). Nest-site selection by the honeybee *Apis mellifera* has attracted much attention from the scientific community for their effectiveness in making "democratic" decisions to choose the best candidate nest site for a new home (Seeley and Buhrman, 2001; Seeley, 2010). In the nest-site selection process, an individual bee performs a waggle dance to communicate information about direction, quality, and distance of a discovered site to other bees. Without the need for global control, the communication among individual bees can direct the whole swarm to make a smart collective decision. Learning from this process is fundamental and would enable us to more effectively structure decision-making

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groups in our own society (see, for example, five lessons we can learn from the honeybee swarm's decision-making process (Seeley, 2010)).

Swarming is an essential component of reproduction by *A. mellifera* swarms. In the swarming process, a large number of worker bees leave their old colony with the queen to form a cluster of a swarm typically on a tree not far away from the original hive. Then the nest-site selection process begins. Scout bees leave the swarm to explore the area around. Each scout searches for a potential nest site and when a candidate nest site is found, the scout evaluates the quality of the site. The scout then flies back to the swarm and advertises her discovery to other bees by the waggle dance, encoded with quality, distance, and direction of the discovered site (Seeley et al., 2006). The waggle dance is composed of multiple dance circuits, each of which includes the waggle and the return phases. Higher qualities of the candidate sites are encoded in the dance by higher numbers of dance circuits and more vivid movement during the return phase (Seeley et al., 2000; Seeley and Buhrman, 2001). The distance to the candidate site from the swarm is expressed by the duration of the waggle phase (Dyer, 2002). The direction of the candidate site relative to the current azimuthal position of the sun is indicated by the orientation of the dance relative to the vertical (von Frisch, 1967; Dyer, 2002). Following the clues from the dance pattern, other bees can be recruited by the dance to search for the site. The recruited bees begin their own trip to visit and evaluate the advertised site. If the recruited bees prefer the site, they return to the swarm and advertise the site, repeating the recruitment process. As information about the site is spread out, and more and more bees make visits to the site, the whole swarm reaches a decision agreement and flies off together to its new home.

The process is more complicated when there is more than one candidate site. In fact, >4–5 candidate sites can be advertised simultaneously at the swarm (Seeley and Buhrman, 1999; Seeley and Visscher, 2004a). In this situation, the dancing bees compete with one another to recruit more bees to their discovered site. Owing to the positive feedback behaviour of the recruitment process, the site with the highest quality usually wins (Seeley and Buhrman, 2001). This is because bees visiting the best site dance with the longest duration (having highest number of dance circuits) and, therefore, can recruit bees to propagate information about the site faster than bees visiting any other sites. However, this might not be the case when two or more candidate sites have similar qualities, leading to the problem of deadlock in which individual decisions split over the candidate sites with equal votes. In a recent publication, Seeley et al. (2012) observed that bees supporting one site butt their heads against bees supporting different sites to stop their dancing. Mathematical analysis shows that the cross-inhibition stop signals enable the swarms to avoid the problem of deadlock when the swarms decide between two equal quality sites (Seeley et al., 2012; Pais et al., 2013).

The swarm's decision-making process has been studied extensively using mathematical modelling. These models focused on different aspects such as speed-accuracy trade-off (Passino and Seeley, 2006; Schaerf et al., 2013; Pais et al., 2013), delay in site discovery (Perdriau and Myerscough, 2007; Nevai et al., 2010), independence and interdependence among bees (List et al., 2009; Galla, 2010), and site distance (Janson et al., 2007).

In the present work, we study the swarm decision-making behaviour of *A. mellifera* when information about the quality and the distance of the candidate sites is integrated into the dance. We use bifurcation analysis and stochastic Monte Carlo simulations to reveal how the swarms make adaptive decisions based on a trade-off between the quality and distance to candidate nest sites. We show that the swarms prefer sites with moderate distances rather than sites with near or far distances when the quality of the candidate sites is low. However, the swarms prefer sites with near distances rather than sites with moderate or far distances as the quality of the candidate sites increases. We also found that swarms with larger size prefer nearer sites and, in addition, are more adaptive at making decisions based on available information compared to swarms with smaller size.

2. Modelling the swarm's decision-making process

In this section, we construct a model of the swarm's decision-making process choosing between two candidate sites. In our model, the total number of bees participating in the nest-site selection process is N_T. These bees can be in one of the following nine states:

(1) neutral bees (N),
(2) bees searching for site 1 (S_1),
(3) bees searching for site 2 (S_2),
(4) bees evaluating at site 1 (E_1),
(5) bees evaluating at site 2 (E_2),
(6) bees returning from site 1 (R_1),
(7) bees returning from site 2 (R_2),
(8) bees dancing to support site 1 (D_1), and
(9) bees dancing to support site 2 (D_2).

The transitions between the states are described by eight ordinary different equations (ODEs) and an algebraic equation listed in Table 1. The parameters of the model are given in Table 2.

In the model, neutral bees can become searching bees either by scouting independently (with the rate k_0) or by recruitment (with the rate k_r). In principle, the scout bees would wander around for some time before randomly discovering a site whereas the recruited bees would fly directly to the site as guided by the dancers. For the sake of simplicity, we assume that the scout bees also travel directly to a site (e.g., by using information from their past experiences). Therefore, the rate of becoming a scout is the same for all sites (k_0), regardless of the site distances. In addition, the scout bees and the guided bees can be lumped into just one state, the searching state, for each site (S_1 or S_2). Searching bees that leave the swarm spend time in the searching state proportional to the duration of the flight, which depends on the site distance (dis_1 or dis_2) and the bee flying speed (v_F; assumed to be a constant). Bees that arrive the candidate site begin to evaluate the site. The average time spent for evaluating a site is T_E (assumed to be a constant for all candidate sites regardless of the qualities and

Table 1
Model equations.

$$\frac{dS_1}{dt} = k_0 \times N + k_r \times D_1 \times N + \left(1 - \frac{c}{q_1}\right)\frac{D_1}{q_1 \times (T_W \times dis_1 + T_R)} - \frac{S_1}{dis_1/v_F} \quad (1)$$

$$\frac{dS_2}{dt} = k_0 \times N + k_r \times D_2 \times N + \left(1 - \frac{c}{q_2}\right)\frac{D_2}{q_2 \times (T_W \times dis_2 + T_R)} - \frac{S_2}{dis_2/v_F} \quad (2)$$

$$\frac{dE_1}{dt} = \frac{S_1}{dis_1/v_F} - \frac{E_1}{T_E} \quad (3)$$

$$\frac{dE_2}{dt} = \frac{S_2}{dis_2/v_F} - \frac{E_2}{T_E} \quad (4)$$

$$\frac{dR_1}{dt} = \frac{E_1}{T_E} - \frac{R_1}{dis_1/v_F} \quad (5)$$

$$\frac{dR_2}{dt} = \frac{E_2}{T_E} - \frac{R_2}{dis_2/v_F} \quad (6)$$

$$\frac{dD_1}{dt} = \frac{R_1}{dis_1/v_F} - \frac{D_1}{q_1 \times (T_W \times dis_1 + T_R)} - k_i \times D_1 \times D_2 \quad (7)$$

$$\frac{dD_2}{dt} = \frac{R_2}{dis_2/v_F} - \frac{D_2}{q_2 \times (T_W \times dis_2 + T_R)} - k_i \times D_1 \times D_2 \quad (8)$$

$$N = N_T - S_1 - S_2 - E_1 - E_2 - R_1 - R_2 - D_1 - D_2 \quad (9)$$

(Initial condition: $N = N_T$ and all other variables $= 0$ at $t = 0$).