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Stability of choice in the honey bee nest-site selection process

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ABSTRACT

We introduce a pair of compartment models for the honey bee nest-site selection process that lend themselves to analytic methods. The first model represents a swarm of bees deciding whether a site is viable, and the second characterizes its ability to select between two viable sites. We find that the one-site *assessment process* has two equilibrium states: a *disinterested equilibrium* (DE) in which the bees show no interest in the site and an *interested equilibrium* (IE) in which bees show interest. In analogy with epidemic models, we define *basic* and *absolute recruitment numbers* ($\mathcal{R}_0$ and $\mathcal{B}_0$) as measures of the swarm's sensitivity to dancing by a single bee. If $\mathcal{R}_0$ is less than one then the DE is locally stable, and if $\mathcal{B}_0$ is less than one then it is globally stable. If $\mathcal{R}_0$ is greater than one then the DE is unstable and the IE is stable under realistic conditions. In addition, there exists a critical site quality threshold Q^* above which the site can attract some interest (at equilibrium) and below which it cannot. We also find the existence of a second critical site quality threshold Q^{**} above which the site can attract a quorum (at equilibrium) and below which it cannot. The two-site *discrimination process*, in which we examine a swarm's ability to simultaneously consider two sites differing in both site quality and discovery time, has a stable DE if and only if both sites' individual basic recruitment numbers are less than one. Numerical experiments are performed to study the influences of site quality on quorum time and the outcome of competition between a lower quality site discovered first and a higher quality site discovered second.

1. Introduction

1.1. Description of the honey bee nest-site selection process

In honey bee (*Apis mellifera*) nest-site selection (reviewed in Seeley and Visscher, 2004; Seeley et al., 2006; Passino et al., 2008), a cluster is formed by the colony splitting itself when the queen and about half the old colony depart and assemble nearby, typically on a tree branch. To find a new home, "scout" bees from the swarm cluster begin to search a large area for a suitable new nest-site, typically the hollow of a tree. Scouts assess the quality of sites based on cavity volume, entrance height, entrance area, and other attributes that are likely correlated with colony success. Bees that find good sites return to the cluster and their initial "dance strength" (number of waggle runs, with each run communicating the angle and radial distance to the nest-site) is in proportion to the quality of the nest-site. Such bees will revisit the site many times, but each time they return to the cluster their dance strength decreases till they no longer dance. The number of recruits to each nest-site is in proportion to the number of dances for each site on the cluster. "Unemployed" scouts either rest or seek to observe dances. If they easily find a dancer they get recruited to a relatively high quality site. If they must wait too long to find a dancer, there are not many good nest-sites currently being assessed so they explore the environment for more sites. There is a quorum-sensing process at each nest-site, where once there is a certain number of bees at the site, the bees from that site "choose it" by returning to the cluster to prompt lift-off and then they guide the swarm to its new home (Beekman et al., 2006; Schultz et al., 2008). There is significant time–pressure to complete the nest-site selection process as fast as possible since weather and energy losses pose significant threats to an exposed colony. However, enough time must be dedicated to ensure that many bees can conduct independent evaluations of the site and establish a quorum at one that is likely to be the best site that the swarm has found. Hence, during nest-site selection the swarm strikes a balance between time minimization and site quality choice maximization.

1.2. Modeling approaches

The key experimental work in the area of honey bee nest-site selection is in Seeley and Buhrman (1999), Camazine et al. (1999),

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Seeley and Buhrman (2001), Seeley (2003), Seeley and Visscher (2003), and Seeley and Visscher (2004). There have also been a number of models published. First, the differential equation models introduced in Britton et al. (2002) examine whether bees need to make direct comparisons between the qualities of more than one site in order to make a decision (they need not). A discrete-time population matrix model introduced in Myerscough (2003) studies the ability of a swarm to produce a unanimous decision when dances reproduce and propagate according to a Leslie matrix. A simulation model that was validated for a range of experiments (those in Seeley and Buhrman, 1999; Camazine et al., 1999; Seeley and Buhrman, 2001; Seeley, 2003; Seeley and Visscher, 2003, 2004), and may be one of the most biologically realistic of all existing models, is used in Passino and Seeley (2006) to study the speed-accuracy trade-off in the choice process. In Perdriau and Myerscough (2007) the authors introduce a density-dependent Markov process model of honey bee nest-site selection and study the effects of site quality, competition between sites, and delays in site discovery. Next, the work in Janson et al. (2007) introduces an individual-based model and studies the swarm's scouting behavior and the impact of distance on choice. More recently, Marshall et al. (2009) compares models of nest-site selection to models of decision-making in vertebrate brains. Finally, we note that ant colonies performing nest-site selection have some broad similarities to the bees' nest-site selection (e.g., a speed-accuracy trade-off), and corresponding models and simulations have been developed (Mallon et al., 2001; Pratt et al., 2002; Franks et al., 2003; Pratt, 2005; Pratt et al., 2005).

The purpose of this paper is to develop a modeling approach for the honey bee nest-site selection process which lends itself to analytical methods. Our ordinary differential equation model still captures the essential dynamics of the nest-site selection process appearing in Britton et al. (2002) and the biologically realistic model in Passino and Seeley (2006), but in a way that still renders the model analytically tractable. Our model does not represent additional features of the nest-site selection process not considered, for instance, in Passino and Seeley (2006) (e.g., the impact of swarm size or distance of candidate nest-sites from the cluster). Yet, our model permits us to connect equilibrium analysis to the ability of a swarm to achieve quorum at a site in finite time. This provides significant insights into the dynamics of nest-site selection, the impact of site quality on quorum achievement, and influences on the outcome of competition between a lower quality site discovered first and a higher quality site discovered second. As these issues have not been examined in the modeling studies outlined above, we believe that our modeling approach can provide new clues into the mystery surrounding the honey bee nest-site selection process.

First, we introduce a pair of continuous-time compartment models in Section 2. The main theoretical results are stated in Section 3 and numerical results are presented in Sections 4 and 5. In the concluding Discussion section we point out some ways in which the models can be made more inclusive (biologically realistic) and mention some open problems. Proofs for the theoretical results appear in the Appendix.

2. Description of models

Here we outline the basic structure of two models that we later use to study the honey bee nest-site selection process. The first model represents a swarm of bees deciding *whether* a site is viable (when no other sites are under consideration), and the second model characterizes a swarm selecting *between* two viable sites. Since bees that are not scouts play no discernable role in selecting a new home, we will make no distinction between *bees* and *scouts* unless stated otherwise.

2.1. Assessment process for one site

The *assessment process* (see Fig. 1 and Table 1) models nest-site selection dynamics after the one-time discovery of a single site by one bee and comprises movement between five compartments: resting (R), observation (O), exploration (E), assessment (A), and dancing (D). We define bees in the first two compartments to be *unemployed* and all others to be *employed*. Let the continuous state variable $X(t)$ represent the *fraction* of bees in compartment $X \in \{R, O, E, A, D\}$ at time $t \geq 0$. We remark that if bees exit a compartment at rate α then $1/\alpha$ represents the mean time spent in that compartment.

Assumptions: We assume that resters become observers $(R \to O)$ at positive constant rate a, observers become employed $(O \to E, A)$ at positive constant rate b, explorers become observers $(E \to O)$ at positive constant rate c, site assessors become dancers $(A \to D)$ at positive constant rate m and dancers cease to dance $(D \to R, A)$ at positive constant rate n. Let $p(D) = D/(D+e)$ be the fraction of newly employed bees which are successfully recruited to assess the site $(O \to A)$ when there are D bees dancing for it, and let $q(D) = 1 - p(D)$ represent the remaining fraction $(O \to E)$. Here, the half-saturation constant e is assumed to be positive. Also, a constant fraction $0 < v \leq 1$ of bees that cease to dance immediately *retire* $(D \to R)$, while the remaining fraction $w = 1 - v$ return to the site to reassess it $(D \to A)$. All bees are initially resters, observers, and explorers except for a single assessor bee that has independently made a one-time discovery of

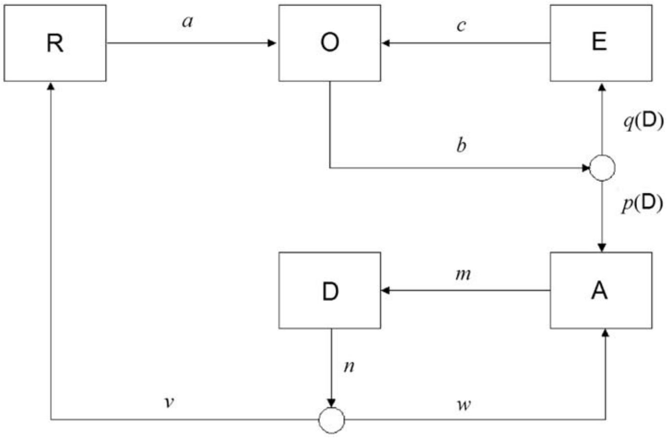

Fig. 1. Illustration of the assessment process for consideration of a single site.

Table 1
Quantities associated with the assessment process.

Notation	Meaning
R, O, E, A, D	fraction of bees resting, observing, exploring, assessing, and dancing
a, b, c, m, n	rates at which bees cease resting, observing, exploring, assessing, and dancing
$p(D), q(D)$	fraction of newly employed bees which become assessors and explorers
v, w	fraction of bees that retire and return to site after dancing