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# Honey bee social foraging algorithms for resource allocation: Theory and application

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## ABSTRACT

A model of honey bee social foraging is introduced to create an algorithm that solves a class of dynamic resource allocation problems. We prove that if several such algorithms (“hives”) compete in the same problem domain, the strategy they use is a Nash equilibrium and an evolutionarily stable strategy. Moreover, for a single or multiple hives we prove that the allocation strategy is globally optimal. To illustrate the practical utility of the theoretical results and algorithm we show how it can solve a dynamic voltage allocation problem to achieve a maximum uniformly elevated temperature in an interconnected grid of temperature zones.

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## 1. Introduction

In the last two decades there has been an increasing interest in understanding how some organisms generate different patterns, and how some of them use collective behaviors to solve problems (Bonabeau et al., 1999). In engineering, this “bioinspired” design approach (Passino, 2005) has been used to exploit the evolved “tricks” of nature to construct robust high performance technological solutions. One of the most popular bioinspired design approaches is what is called “Swarm Intelligence” (SI) (Bonabeau et al., 1999; Kennedy and Eberhart, 2001). SI groups those techniques inspired by the collective behavior of social insect colonies, as well as other animal societies that are able to solve large-scale distributed problems. Some of the algorithms that have been developed are inspired on the collective foraging behavior of ants (Dorigo and Maniezzo, 1996), bees (Nakrani and Tovey, 2003; Teodorovic and Dell’orco, 2005; Walker, 2004), or the general social interaction of different animal societies (e.g., school of fishes) (Kennedy and Eberhart, 1995). For instance, the ant colony optimization (ACO) algorithms introduced by Dorigo and colleagues (e.g., see Dorigo and Blum, 2005; Bonabeau et al., 1999; Dorigo and Stützle, 2004; Dorigo et al., 2002) mimic ant foraging behavior and have been used in the solution to classical optimization problems (e.g., discrete combinatorial optimization problems, Dorigo et al., 1996) and in engineering applications (e.g., Schoonderwoerd et al., 1996; Reimann et al., 2004). Another approach that mimics the behavior of social

organisms is the particle swarm optimization (PSO) technique, where the behavior of different types of social interactions (e.g., flock of birds) is mimicked in order to create an optimization method that is able to solve continuous optimization problems (Poli et al., 2007). Many applications have applied this type of optimization method (see Poli, 2007 for an extensive literature review on the field). For instance, in Han et al. (2005) the authors use the PSO technique in order to optimally select the parameters of a PID controller, while in Juang and Hsu (2005) the PSO is used in order to design a recurrent fuzzy controller used to perform temperature control using a field-programmable gate array (FPGA). The primary goal of this paper is to show that another SI technique (i.e., honey bee social foraging) can be exploited in a bioinspired design approach to (i) solve a dynamic resource allocation problem (Ibaraki and Katoh, 1988) by viewing it from an evolutionary game-theoretic perspective, and (ii) provide novel strategies for multizone temperature control, an important industrial engineering application. It should be pointed out that the ACO is designed and successful for primarily static discrete optimization problems, like for shortest paths and hence is not directly applicable to dynamic continuous resource allocation problems. In the other hand, PSO has been used for continuous optimization problems. Even though we might be able to formulate our problem using an objective function and solve it with PSO, the main objective of this paper is not to compare with optimization methods as it has usually been in this area (Poli, 2007). In this paper, we aim to study the game-theoretic development of the honey bee social foraging (rather than optimization), and the implementation of those game-theoretic methods.

Our model of honey bee social foraging relies on experimental studies (Seeley, 1995) and some ideas from other mathematical models of the process. A differential equation model of functional

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aspects of dynamic labor force allocation of honey bees is developed and validated for one set of experimental conditions in Seeley et al. (1991) and Camazine and Sneyd (1991). The work in Cox and Myerscough (2003) extends this model (e.g., by adding details on energetics and currency) and Sumpter and Pratt (2003) introduced a generic nonlinear differential equation model that can represent social foraging processes in both bees and ants. Like in Sumpter and Pratt (2003) and Cox and Myerscough (2003), our model of recruitment uses the idea from Seeley et al. (1991) and Camazine and Sneyd (1991) that dance strength proportioning on the dance floor shares some characteristics with the evolutionary process (e.g., with fitness corresponding to forage site profitability and reproduction to recruitment as discussed in Seeley, 1995). Here we make such connections more concrete by modeling the bee recruitment process in an analogous manner to how survival of the fittest and natural selection are modeled in genetic algorithms using a stochastic process of fitness proportionate selection (Mitchell, 1996). The authors in de Vries and Biesmeijer (1998) introduce an “individual-oriented” model of social foraging and validate it against one set of experimental conditions as was done in Seeley et al. (1991) and Camazine and Sneyd (1991). More recently, in de Vries and Biesmeijer (2002) the authors expanded and improved the model in de Vries and Biesmeijer (1998) (e.g., taking into account the findings in Seeley and Tovey (1994) and by studying an equal harvest rate forager allocation distribution). The work in Bartholdi et al. (1993) studies the pattern of forager allocation and the optimality of it. The authors in Dukas and Edelman-Keshet (1998) study the spatial distribution of solitary and social food provisioners under different currency assumptions. The work in Bartholdi et al. (1993), Dukas and Edelman-Keshet (1998), and de Vries and Biesmeijer (2002) identifies connections to the concept of the “ideal free distribution” (IFD) (Fretwell and Lucas, 1970). Here, we do not use a detailed characterization of bee and nectar energetics and currency since there is not enough experimental evidence to justify whether or when a gathering rate or efficiency-based currency is used (Seeley, 1995); instead, we develop a *generic* measure of forage site profitability. This general profitability measure approach is the same one used in Passino and Seeley (2006) to represent the nest-site quality landscape for the honey bee nest-site selection process. Our general measure has the advantage of allowing us to easily represent a wide range of density-dependent foraging currencies via the classical “suitability function” approach to IFD studies (Fretwell and Lucas, 1970). Also, it eases the transition to the multizone temperature control problem since the temperature control objective can be easily characterized with our general profitability measure.

The IFD concept has been used to analyze how animals distribute themselves across different habitats or patches of food (Fretwell and Lucas, 1970). These habitats have different characteristics (e.g., one habitat might have a higher nutrient input rate than another), but animals tend to reach an equilibrium point where each has the same correlate of fitness (e.g., consumption rate). The term “ideal” means that the animals can perfectly sense the quality of all habitats and seek to maximize the suitability of the habitat they are in (by choosing which habitat to reside in), and the term “free” means that the animals can go to any habitat. In this paper, the IFD is a central unifying concept. The IFD will emerge for one hive as the foragers are *cooperatively* allocated across sites. Moreover, if  $n$  hives *compete* in the same environment for a resource the IFD will also emerge. Here, we create a mathematical representation of the  $n$ -hive game where each hive’s strategy choice entails picking the distribution of its foragers across the environment. Our analytical study starts by showing that the IFD is a strict Nash equilibrium (Başar and Olsder, 1999) in terms of the payoffs to each hive and a special

type of evolutionarily stable strategy (ESS). The original definition of an ESS is based on one important assumption: the population size has to be infinite. In Schaffer (1988) and Maynard Smith (1988) the authors define the conditions that must be satisfied in order to prove that a strategy is evolutionarily stable for a finite-population size. Using the ideas in Schaffer (1988) we state the conditions for what we call a *one-stable* ESS, and show that the IFD satisfies those conditions. This means that in an  $n$ -hive game, if a single hive’s strategy (forager allocation) mutates from the IFD it cannot survive when competing against a field of  $n-1$  hives that use the IFD strategy. While this means that the IFD is locally optimal in a game-theoretic sense (i.e., unilateral forager allocation deviations by a hive are not profitable), here we show that the achieved IFD is a global optimum point for both single hive and  $n$ -hive allocations. For the  $n$ -hive case, this means that if the forager allocation of all hives but one is at the IFD, then the remaining hive has to distribute its effort according to the IFD if it is to maximize its return.

Finally, it is important to highlight that other algorithms have been developed using honey bee social foraging. For instance, in Teodorovic and Dell’orco (2008) the authors introduce a bee colony optimization (BCO) algorithm, which is a generalization of the bee system (BS) tested in another combinatorial optimization problems, to solve a common problem in traffic congestion. Others have used different approaches to solve different optimization problems such as energy efficient mobile ad hoc networks (Wedde and Farooq, 2005), job shop scheduling (Chong et al., 2006), or Internet servers (Nakrani and Tovey, 2003; Walker, 2004). In general, all the articles that present a honey bee social foraging algorithm do not focus on trying to mimic the whole behavior of the foraging process. They tend to concentrate on the most important part of the foraging process, i.e., the waggle dance. Also, the problems that these algorithms are trying to solve can be grouped into continuous optimization problems. As it was pointed out before, our approach seeks to illustrate concepts from a game-theoretic perspective rather than the optimization one used in most of these algorithms (Pankiw, 2005; Pham et al., 2006; Teodorovic and Dell’orco, 2005; Chong et al., 2006; Karaboga, 2005). On the other hand, the utility of the theoretical concepts introduced in this paper, and the honey bee social foraging algorithm are illustrated by means of an engineering application. In general, most of the applications that use honey bee social foraging approaches use their algorithms in simulations, or in applications where the algorithm is not directly applied to solve a real engineering application. However, in our case, the technological challenge we confront is experimental multizone temperature control. Achievement of high performance multizone temperature control is very important in a range of commercial and industrial applications. For instance, recent work in this area includes distributed control of thermal processes (Jones et al., 2003; Zaheer-uddin et al., 1993; Emami-Naeini et al., 2003; Demetriou et al., 2003; Ross, 2004), and semiconductor processing (Alaeddine and Doumanidis, 2004a,b; Schaper et al., 1999b). Particularly relevant to our work is the study in Emami-Naeini et al. (2003), where the authors use multivariable distributed control in order to maintain a uniform temperature across a wafer during ramp-up (similar to the control objective we study here). In Schaper et al. (1999a) the authors describe a lithographical system that is heated by 49 independently controlled zones. Here, we use a multizone experimental setup that is similar to the one in Quijano et al. (2005) where dynamic resource allocation methods are studied. In Quijano and Passino (2007) a multizone temperature control experiment is also used, but the dynamics are based on a replicator dynamics model. Our experiments demonstrate how one hive can achieve an IFD that corresponds to maximum uniform temperatures on the

temperature grid using a honey bee social foraging algorithm. We illustrate the dynamics of the foraging algorithm by showing how it can successfully eliminate the effects of ambient temperature disturbances. Moreover, we show that even if two hives have *imperfect information* they can be used as a feedback control that will still achieve an IFD.

The paper is organized as follows. First, in Section 2 we introduce the honey bee social foraging algorithm. In Section 3 we perform a theoretical analysis of the hives' achieved IFD equilibrium. In Section 4 we apply the honey bee social foraging algorithm to a multizone temperature control experiment and show how the IFD emerges under a variety of conditions.

## 2. Honey bee social foraging algorithm

Modeling social foraging for nectar involves representing the environment, activities during bee expeditions (exploration and foraging), unloading nectar, dance strength decisions, explorer allocation, recruitment on the dance floor, and accounting for interactions with other hive functions. The experimental studies we rely on are summarized in Seeley (1995). Our primary sources for constructing components of our model are as follows: dance strength determination, dance threshold, and unloading area (Seeley and Towne, 1992; Seeley, 1994; Seeley and Tovey, 1994); dance floor and recruitment rates (Seeley et al., 1991); and explorer allocation and its relation to recruitment (Seeley, 1983; Seeley and Visscher, 1988). Table 1 summarizes all notation used for the model that is explained next.

### 2.1. Foraging profitability landscape

We assume that there are a fixed number of  $B$  bees involved in foraging. For  $i=1,2,\dots,B$  bee  $i$  is represented by  $\theta^i \in \mathbb{R}^2$  which is its

**Table 1**  
Notation.

Variable	Description
$B$	Number of bees
$\theta^i$	Position in two dimensional space of the $i$ th bee
$J_f(\theta)$	Foraging profitability landscape
$x_j^i(k)$	Number of bees at site $j$ at step $k$
$B_f$	Employed foragers
$B_u$	Unemployed foragers
$B_o$	Bees that seek to observe the dances
$B_r$	Bees that rest
$B_e$	Forage explorers
$F^i(k)$	Foraging profitability assessment by employed forager $i$
$w_f^i$	Profitability assessment noise
$\varepsilon_n$	Lower threshold on site profitability
$L_j^i$	Number of waggle runs of bee $i$ at step $k$
$\beta$	Parameter that affects the number of dances produced for an above-threshold profitability
$F_t(k)$	Total nectar profitability assessment at step $k$
$F_d^i(k)$	Quantity of nectar gathered for $F^i(k)$
$F_{td}(k)$	Total quantity nectar influx to the hive at step $k$
$W^i(k)$	Wait time that the bee $i$ experiences
$\psi, w_w^i(k)$	Scale factor, and random variable that represents variations in the wait time
$\hat{F}_{td}^i(k)$	Estimate of the total nectar influx
$\delta$	Proportionality constant related to the site abandonment rate
$p_r(l,k)$	Probability that bee $i$ will dance for the site
$B_{fd}$	Number of employed foragers with above-threshold profitability that dance
$p_o$	Probability that an unemployed forager will become an observer
$L_d^i(k)$	Total number of waggle runs on the dance floor at step $k$
$p_e(k)$	Probability of an observer becomes an explorer
$p_d^i(k)$	Probability of an observer will follow the dance of bee $i$

position in two-dimensional space. During foraging, bees sample a “foraging profitability landscape” which we think of as a spatial distribution of forage sites with encoded information on foraging profitability that quantifies distance from hive, nectar sugar content, nectar abundance, and any other relevant site variables. The foraging profitability landscape is denoted by  $J_f(\theta)$ . It has a value  $J_f(\theta) \in [0,1]$  that is proportional to the profitability of nectar at a location specified by  $\theta \in \mathbb{R}^2$ . Hence,  $J_f(\theta) = 1$  represents a location with the highest possible profitability,  $J_f(\theta) = 0$  represents a location with no profitability, and  $0 < J_f(\theta) < 1$  represents locations of intermediate profitability. For  $\theta = [\theta_1, \theta_2]^T$ , the  $\theta_1$  and  $\theta_2$  directions for our example foraging area are for convenience scaled to  $[-1,1]$  since the distance from the hive is assumed to be represented in the landscape. We assume the hive is at  $[0,0]^T$ .

As an example of the type of foraging profitability landscape we could have four forage sites centered at various positions that are initially unknown to the bees (e.g., site 1 could be at  $[1.5, 2.0]^T$ ). The “spread” of each site characterizes the size of the forage site, and the height is proportional to the nectar profitability. For example, we could use cylinders with heights  $N_j^i \in [0,1]$  that are proportional to nectar profitability, and the spread of each site can be defined by the radius of the cylinders  $\varepsilon_j$ . Below, we will say that bee  $i$ ,  $\theta^i = [\theta_1^i, \theta_2^i]^T$ , is “at forage site 1” if  $\sqrt{(\theta^i - [1.5, 2]^T)^T (\theta^i - [1.5, 2]^T)} < \varepsilon_j$ . We use a similar approach for other sites.

### 2.2. Bee roles and expeditions

Let  $k$  be the index of the foraging expedition and assume that bees go out at one time and return with their foraging profitability assessments at one time (an asynchronous model with randomly spaced arrivals and departures will behave in a qualitatively similar manner). Our convention is that at time  $k=0$  no expeditions have occurred (e.g., start of a foraging day), at time  $k=1$  one has occurred, and so on. All bees,  $i=1,2,\dots,B$ , have  $\theta^i(0) = [0,0]^T$  so that initially they are at the hive.

Let  $x_j^i(k)$  be the number of bees at site  $j$  at  $k$ . We assume that the profitability of being at site  $j$ , which we denote by  $s_j$  for a bee at a location in site  $j$ , decreases as the number of bees visiting that site increases. A typical choice (Fretwell and Lucas, 1970; Giraldeau and Caraco, 2000) is to represent this by letting, for each  $j$ ,

$$s_j(k) = \frac{a_j}{x_j(k)}$$

In this case, we could assume that  $a_j$  is the number of nutrients per second at the  $j$ th site. With this representation we think of a site as a choice for the hive, with the site degrading in profitability via the visit of each additional bee, a common assumption in theoretical ecology. In IFD theory  $s_j$  is called the “suitability function” (Fretwell and Lucas, 1970).

Of the  $B$  bees involved in the foraging process, we assume that there are  $B_f(k)$  “employed foragers” (ones actively bringing nectar back from some site and that will not follow dances). Initially,  $B_f(0)=0$  since no foraging sites have been found. We assume that there are  $B_u(k)=B_o(k)+B_r(k)$  “unemployed foragers” with  $B_o(k)$  that seek to observe the dances of employed foragers on the dance floor and  $B_r(k)$  that rest (or are involved in some other activity). Initially,  $B_u(0)=B$ , which with the rules for resting and observing given below will set the number of resters and observers. We assume that there are  $B_e(k)$  “forage explorers” that go to random positions in the environment, bring their nectar back if they find any, and dance accordingly, but were not dedicated to the site (of course they may become dedicated if they find a relatively good site).



We ignore the specific path used by the foragers on expeditions and what specific activities they perform. We assume that a bee simply samples the foraging profitability landscape once on its expedition and hence this sample represents its combined overall assessment of foraging profitability for location  $\theta^i(k)$ . It is this value that it holds when it returns to the hive. It also brings back knowledge of the forage location which is represented with  $\theta^i(k)$  for the  $k$ th foraging expedition. Let the foraging profitability assessment by employed forager (or forage explorer)  $i$  be

$$F^i(k) = \begin{cases} 1 & \text{if } J_f(\theta^i(k)) + w_f^i(k) \geq 1 \\ J_f(\theta^i(k)) + w_f^i(k) & \text{if } 1 > J_f(\theta^i(k)) + w_f^i(k) > \varepsilon_n \\ 0 & \text{if } J_f(\theta^i(k)) + w_f^i(k) \leq \varepsilon_n \end{cases}$$

where  $w_f^i(k)$  is the profitability assessment noise. Here, we let  $w_f^i(k)$  be uniformly distributed on  $(-w_f, w_f)$  with  $w_f = 0.1$  (to represent up to a  $\pm 10\%$  error in profitability assessment). The value  $\varepsilon_n > 0$  sets a lower threshold on site profitability. Here,  $\varepsilon_n = 0.1$ . For mid-range above-threshold profitabilities the bees will on average have an accurate profitability assessment since the expected value with respect to  $k$  of  $w_f^i(k)$ ,  $E[w_f^i(k)] = 0$ . Let  $F^i(k) = 0$  for all unemployed foragers.

### 2.3. Dance strength determination

Let  $L_f^i(k)$  be the number of waggle runs of bee  $i$  at step  $k$ , what is called “dance strength.” The  $B_u(k)$  unemployed foragers have  $L_f^i(k) = 0$ . All employed foragers and forage explorers that have  $F^i(k) = 0$  will have  $L_f^i(k) = 0$  since they did not find a location above the profitability threshold  $\varepsilon_n$  so they will not seek to be unloaded and will not dance; these bees will become unemployed foragers.

#### 2.3.1. Unload wait time

Next, we will explain dance strength decisions for the employed foragers and forage explorers with  $F^i(k) > \varepsilon_n$ . To do this, we first model wait times to get unloaded and how they influence the “dance threshold.” Define  $F_t(k) = \sum_{i=1}^B F^i(k)$  as the total nectar profitability assessment at step  $k$  for the hive. Foragers at profitable sites tend to gather a greater quantity of nectar than at low profitability sites. Let  $F_q^i(k)$  be the quantity of nectar (load size) gathered for a profitability assessment  $F^i(k)$ . We assume that  $F_q^i(k) = \alpha F^i(k)$  where  $\alpha > 0$  is a proportionality constant. We choose  $\alpha = 1$  so that  $F_q^i(k) \in [0, 1]$ , with  $F_q^i(k) = 1$  representing the largest nectar load size. Notice that if we let  $F_{tq}(k)$  be the total quantity of nectar influx to the hive at step  $k$ ,

$$F_{tq}(k) = \sum_{i=1}^B F_q^i(k) = \alpha \sum_{i=1}^B F^i(k) = \alpha F_t(k)$$

so the total hive nectar influx is proportional to the total nectar profitability assessment. Also,  $F_{tq}(k) \in [0, \alpha B]$  since each successful forager contributes to the total nectar influx.

The average wait time to be unloaded for each bee with  $F^i(k) > \varepsilon_n$  is proportional to the total nectar influx. Suppose that the number of food-storer bees is sufficiently large so the wait time  $W^i(k)$  that bee  $i$  experiences is given by

$$W^i(k) = \psi \max\{F_{tq}(k) + w_w^i(k), 0\} = \psi \max\{\alpha F_t(k) + w_w^i(k), 0\} \quad (1)$$

where  $\psi > 0$  is a scale factor and  $w_w^i(k)$  is a random variable that represents variations in the wait time a bee experiences. We assume that  $w_w^i(k)$  is uniformly distributed on  $(-w_w, w_w)$ . Since  $F_{tq}(k) \in [0, \alpha B]$ ,  $\psi(\alpha B + w_w)$  is the maximum value of the wait time which is achieved when total nectar influx is maximum. For the experiments in Seeley and Tovey (1994) (July 12 and 14 data) the maximum wait time is about 30 s (and we know that it must be under this value or bees will tend to perform a tremble dance

rather than a waggle dance to recruit unloaders, Seeley, 1995); hence, we choose  $\psi(\alpha B + w_w) = 30$ . Note that  $\pm \psi w_w$  seconds is the variation in the number of seconds in wait time due to the noise and  $w_w$  should be set accordingly. We let  $\psi w_w = 5$  to get a variation of  $\pm 5$  s. If  $B = 200$  is known, we have two equations and two unknowns, so combining these we have  $\psi B + \psi w_w = 30$ , which gives  $\psi = 25/200$  and  $w_w = 40$ .

That there is a linear relationship between wait times and total nectar influx for sufficiently high nectar influxes is justified via experiments described in Seeley and Tovey (1994) and Seeley (1995, p. 112). Deviations from linearity come from two sources, the  $w_w^i(k)$  noise and the “max” in Eq. (1). Each successful forager has a different and inaccurate individual assessment of the total nectar influx since each individual bee experiences different wait times in the unloading area. The noise  $w_w^i(k)$  in Eq. (1) represents this. Some foragers can get lucky and get unloaded quickly and this will give them the impression that nectar influx is low. Other foragers may be unlucky and slow to get unloaded and this will result in an impression that there is a very high nectar influx.

#### 2.3.2. The dance decision function

Next, we assume that the  $i$ th successful forager converts the wait time it experienced into a scaled version of an estimate of the total nectar influx that we define as

$$\hat{F}_{tq}^i(k) = \delta W^i(k) \quad (2)$$

So, we are assuming that each bee has an internal mechanism for relating the wait time it experiences to its guess at how well all the other foragers are doing (Seeley, 1995). The proportionality constant for this is  $\delta > 0$  and since  $W^i(k) \in [0, \psi(\alpha B + w_w)] = [0, 30]$  s we have  $\hat{F}_{tq}^i(k) \in [0, 30\delta]$ .

So, how does total nectar influx influence the dance strength decision, and in particular the dance threshold? In order to decide how long to dance, the bee takes into account a set of forage site variables that determine the energetic profitability (e.g., distance from hive, sugar content of nectar, nectar abundance), together with a set of general foraging conditions that determine the threshold of dance response (e.g., colony's nectar influx, weather, time of day) (Seeley, 1995). Here, we build on this by defining a “decision function” for each bee that shows how the dance threshold for each individual bee shifts based on the  $i$ th bee's estimate of total nectar influx. The decision function is

$$L_f^i(k) = \max\{\beta(F^i(k) - \hat{F}_{tq}^i(k)), 0\} \quad (3)$$

which is shown in Fig. 1. The parameter  $\beta > 0$  affects the number of dances produced for an above-threshold profitability.

In Fig. 1,  $-\beta \hat{F}_{tq}^i(k)$  is the intercept on the dance strength axis. The diagonal bold line in Fig. 1 shifts based on the bee's estimation of total nectar influx since this is proportional to  $\hat{F}_{tq}^i(k)$ . Notice that since the line's slope is  $\beta$ , and since we take the maximum with zero in Eq. (3), the lowest value of nectar profitability  $F^i(k)$  that the  $i$ th bee will decide to still dance for is the “dance threshold”  $\hat{F}_{tq}^i(k)$  and from Eq. (2), the bee's scaled estimate of the total nectar influx. Note that changing  $\beta$  does not shift the dance threshold. The parameter  $\beta$  will, however, have the effect of a gain on the rate of recruitment for sites above the dance threshold. In the case where  $F_{tq}(k) = \hat{F}_{tq}^i(k) = 0$  there is no nectar influx to the hive and it has been found experimentally (Seeley, 1995) that in such cases, if a bee finds a highly profitable site, she can dance with 100 or more waggle runs. Hence, we choose  $\beta = 100$  so  $L_f^i(k) = 100$  waggle runs in this case. Then,  $L_f^i(k) \in [0, \beta] = [0, 100]$  waggle runs for all  $i$  and  $k$ .

The dance threshold in Eq. (2) is defined using the parameter  $\delta$ . What value would we expect a bee to hold for  $\delta$ ? Since the nectar profitability  $F^i(k) \in [0, 1]$ ,  $\delta$  needs to be defined so that  $\hat{F}_{tq}^i(k) \in [0, 1]$

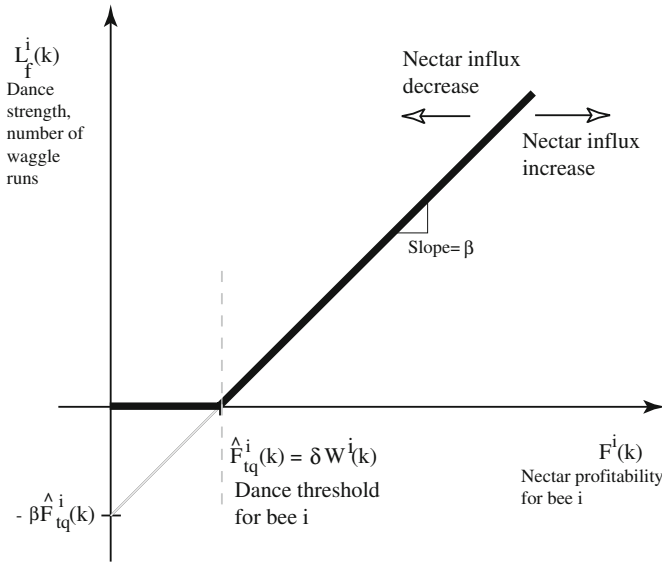


Fig. 1. Dance strength function.

so that the dance threshold is within the range of possible nectar profitabilities. This means that we need

$$0 < \delta \leq \frac{1}{30} \quad (4)$$

To gain insight into how to pick  $\delta$  in this range notice that  $\delta$  is proportional to the site abandonment rate: (i) if  $\delta \approx 0$ , then the dance threshold  $\hat{F}_{tq}^i(k) \approx 0$  independent of wait times and so sites of significantly inferior relative profitability will never be abandoned, something that does not occur in nature; and (ii) if  $\delta \approx \frac{1}{30} = 0.0333$ , then almost all sites are not danced for since the dance threshold is so high and the foraging process fails completely, something that does not occur in nature. Hence,  $\delta$  must be somewhere in the middle of the range in Eq. (4); in simulations we tuned the value of  $\delta$  to match experiments and found  $\delta = 0.02$ .

### 2.3.3. Dance/no-dance choice

The set of bees that, after dance strength determination as outlined in the previous section, have  $L_f^i(k) > 0$  are ones that consider dancing for their forage site. Here, we let  $p_r(i, k) \in [0, 1]$  denote the probability that bee  $i$  with  $L_f^i(k) > 0$  will dance for the site it is dedicated to. We assume that

$$p_r(i, k) = \frac{\phi}{\beta} L_f^i(k)$$

where  $\phi \in [0, 1]$  (which ensures that  $p_r(i, k) \in [0, 1]$ ). We choose  $\phi = 1$  since it resulted in matching the qualitative behavior of what is found in experiments. For low nectar influx, (waggle-dancing) bees will tend to dance and (waggle-dancing and non-waggle-dancing) bees stay at discovered forage sites. As nectar influx increases, waggle-dancing bees will only dance for the most profitable sites, and inferior sites will be abandoned by all bees. Hence, a bee with an above-threshold profitability is more likely to dance the further its profitability is above the threshold as seen in experiments (Seeley, 1995). In this way, relatively high quality new discoveries will typically be danced for, but as more bees are recruited for that site and hive nectar influx increases, it will become less likely that bees (e.g., the recruits) will dance for it and this will limit the number of dancers for all sites. Relatively low quality sites are not as likely to be danced for; however, bees that decide not to dance will still go

back to the site and remain an employed forager for it. If bee  $i$  dances, then it uses a dance strength of  $L_f^i(k)$ . If it does not dance, we force  $L_f^i(k) = 0$  and the bee simply remains an employed forager for its last site. We let  $B_{fd}(k)$  denote the number of employed foragers with above-threshold profitability that dance.

## 2.4. Explorer allocation and forager recruitment

### 2.4.1. Resters and observers

The bees that either were not successful on an expedition, or were successful enough to get unloaded but judged that the profitability of their site was below the dance threshold, become unemployed foragers. Some of these bees will start to rest and other dance “observers” will actively pursue getting involved in the foraging process by seeking a dancing bee to get recruited. Here, at each  $k$  we let  $p_o \in [0, 1]$  denote the probability that an unemployed forager or currently resting bee will become an observer bee; hence  $1 - p_o$  is the probability that an unemployed forager will rest or a currently resting bee will continue to rest. It has been seen experimentally (Seeley, 1983) that in times where there are no forage sites being harvested there can be about 35% of the bees performing as forage explorers, but when there are many sites being harvested there can be as few as 5%. Hence, we choose  $p_o = 0.35$  so that when all bees are unemployed, 35% will explore. In Anderson (2001) the author shows how the optimal proportion of explorers and resters depends on the profitability of available forage, and the ability to find it.

### 2.4.2. Explorers and recruits

Here, we assume that an observer bee on the dance floor searches for dances to follow and if it does not find one after some length of time, it gives up and goes exploring. To model explorer allocation based on wait-time cues, we assume that wait-time is assumed to be proportional to the total number of waggle runs on the dance floor. Let

$$L_t(k) = \sum_{i=1}^{B_f(k)} L_f^i(k)$$

be the total number of waggle runs on the dance floor at step  $k$ . We take the  $B_o(k)$  observer bees and for each one, with probability  $p_e(k)$  we make it an explorer. We choose

$$p_e(k) = \exp\left(-\frac{1}{2} \frac{L_t^2(k)}{\sigma^2}\right) \quad (5)$$

Notice that if  $L_t(k) = 0$ , there is no dancing on the cluster so that  $p_e(k) = 1$  and all the observer bees will explore (e.g.,  $L_t(0) = 0$  so initially all observer bees will choose to explore). If  $L_t(k)$  is low, the observer bees are less likely to find a dancer and hence will not get recruited to a forage site. They will, in a sense, be “recruited to explore” by the lack of the presence of any dance. As  $L_t(k)$  increases, they become less likely to explore and, as discussed below, will be more likely to find a dancer and get recruited to a forage site. Here, we choose  $\sigma = 1000$  since it produces patterns of foraging behavior in simulations that correspond to experiments.

The explorer allocation process is concurrent with the recruitment of observer bees to forage sites. Observer bees are recruited to forage sites with probability  $1 - p_e(k)$  by taking any observer bee that did not go explore and have it be recruited. To model the actual forager recruitment process we view  $L_f^i(k)$  as the “fitness” of the forage site that the  $i$ th bee visited during expedition  $k$ . Then, the probability that an observer bee will

follow the dance of bee  $i$  is defined to be

$$p_i(k) = \frac{L_f^i(k)}{\sum_{i=1}^{B_f(k)} L_f^i(k)} \quad (6)$$

In this manner, bees that dance stronger will tend to recruit more foragers to their site.

To summarize, Algorithm 1 shows the pseudo-code of the honey bee social foraging algorithm described above.

**Algorithm 1.** Honey bee social foraging algorithm

```

1: Set the parameter values.
2: for Fixed number of expeditions do
3:   Determine number of bees at each forage site, and
   compute the suitability of each forage site.
4:   for Each employed forager and explorer do
5:     Define a noisy assessment according to the location.
6:     if Bee is successful in getting an above profitability
   site then
7:       if Bee is an employed forager then
8:         Stays that way.
9:       else if Bee is an explorer then
10:        Bee becomes an employed forager.
11:       end if
12:     else
13:       Bee becomes an observer or restler.
14:     end if
15:   end for
16:   Compute the total nectar profitability, and the total
   nectar influx.
17:   for All employed foragers do
18:     Compute wait time  $W^i$ , and the noise for unload wait
   time  $w_w$ .
19:   Compute estimate of scaled total nectar influx  $\hat{F}_{tq}$ .
20:   Compute dance decision function  $L_f^i$ .
21:   if  $L_f^i = 0$  then
22:     Bee  $i$  becomes unemployed.
23:   else if Employed forager should not recruit then
24:      $L_f^i = 0$ . Bee  $i$  is removed from those that dance.
25:   end if
26:   end for
27:   Determine  $L_r$ . Employed foragers and successful forager
   explorers may dance based on sampling of profitability.
28:   Send all employed foragers back to their previous site
   (after recruiter go to the dance floor) for the next
   expedition.
29:   for Unemployed foragers do
30:     Since the unemployed foragers do not dance, we set
      $W^i = L_f^i = \hat{F}_{tq} = 0$ .
31:     We split the unemployed foragers in restlers and
     observers.
32:   end for
33:   Set  $p_e$ .
34:   for Unemployed foragers do
35:     if  $\text{rand} < p_e$  then
36:       Bee becomes an explorer. Set location for explorer
       to go to on the next expedition.
37:     end if
38:   end for
39:   for Unemployed observers do
40:     Recruit the unemployed forager by some employed
     one, in a proportional manner to how strong the
     dancing of that employed forager is relative to how much
     overall strength of dancing is occurring on the dance
     floor.
```

```

41:   Recruit the unemployed to a noisy position of the
   employed forager.
42: end for
43: end for
```

## 2.5. Discussion

We have conducted extensive simulations to validate the qualitative characteristics of our model of social foraging by honey bees. In particular, we have shown that the model represents achievement of the IFD of foragers per relative site profitabilities (Seeley, 1995) for a range of suitability functions, “cross-inhibition” seen in Seeley et al. (1991) and Camazine and Sneyd (1991) (the main experiments used in model validation for all other bee foraging models discussed earlier), reallocation when new forage sites suddenly appear or disappear, or when site qualities change (Seeley, 1995; Seeley et al., 1991; Camazine and Sneyd, 1991). In the interest of brevity we do not include these simulations here since: (i) our focus is *not* on model validation (i.e., accurate representation of numerical data from experiments on honey bee social foraging) but on bioinspired design based on the main algorithm features; and (ii) the key qualitative features of the allocation dynamics are all illustrated in our implementation of the bee algorithm for multizone temperature control in the next section.

## 3. Equilibrium analysis of hive allocations

In Section 2 we explained how the honey bee social foraging algorithm achieves the ideal free distribution (IFD). In this section we prove that the hives’ IFD is a global optimum point. For that, some assumptions have to be made. In the previous section we saw how bees in different roles were allocated to different forage sites by their behavior in the hive. In the following analysis we assume that there exists a fixed number of hives  $n$  in an environment, that each hive contains a fixed amount of employed forager bees  $B_f^i$ ,  $i=1,2,\dots,n$ , and that *all* bees are allocated to  $N$  different sites (i.e., we ignore the components of the process associated with searching for forage sites).

### 3.1. The $n$ -hive game

#### 3.1.1. Nash equilibrium

Let  $x_j^i > 0$  denote the number of bees that the  $i$ th hive allocates to the  $j$ th (forage) site choice, where  $i=1,2,\dots,n$  and  $j=1,2,\dots,N$ . We assume for simplicity that  $\sum_{j=1}^N x_j^i = B_f^i$ , for all  $i$ , is the total amount of bees the  $i$ th hive can allocate. Also, assume that  $a_j > 0$  is the constant quality of site  $j$  (e.g., in the classical IFD it is the input rate of nutrients to the  $j$ th site, in applications, this constant could be proportional to site profitability). Hence, in an  $n$ -hive game each hive has  $N$  pure strategies corresponding to choosing the sites  $j=1,2,\dots,N$ . But the strategy is the number of bees it allocates to each site, or for hive  $i$ , the strategy is

$$x^i = [x_1^i, x_2^i, \dots, x_N^i]^T$$

where  $\sum_{j=1}^N x_j^i = B_f^i$ , for each  $i=1,2,\dots,n$ . Notice that  $x^i$  is an element of the simplex

$$\Delta_x = \left\{ x = [x_1, \dots, x_N] : \sum_{j=1}^N x_j = B_f, x_j \geq 0, j = 1, 2, \dots, N \right\}$$

The strategy  $x = [x^1, x^2, \dots, x^n]^T$  is a Nash equilibrium if the following is valid for all  $y^i \neq x^i$ ,  $i=1,2,\dots,n$ :

$$f(y^i | x^{-i}) \leq f(x^i | x^{-i}) \quad (7)$$

where  $x^i$  denotes the vector of all other strategies except strategy  $x^i$ , and  $f(\cdot, \cdot)$  is the fitness payoff. Eq. (7) means that the hive must allocate the bees using the optimum strategy  $x$  so that its gain is maximum in terms of fitness payoff. Notice that if the inequality in Eq. (7) is strict, we have what is called a strict Nash equilibrium.

### 3.1.2. Evolutionarily stable strategies (ESS) for a finite population of hives

The original formulation of an evolutionarily stable strategy (ESS) introduced in Maynard Smith and Price (1973) and Maynard Smith (1982) assumes that the population size (number of hives) is infinite and hence does not apply here. There have been a number of studies that treat the ESS concept for a large and finite population sizes (e.g., Riley, 1979; Neill, 2004; Crawford, 1990). However, the seminal work is contained in Maynard Smith (1988) and Schaffer (1988) where the authors state the equilibrium and stability conditions similar to the ones defined in Hofbauer and Sigmund (1998). The  $n$ -hive game that we set up in this case can be seen as a game “against the field” (Maynard Smith, 1982), i.e., the population size is equal to the contest size. We can define the ESS for finite populations as follows.

**Definition 3.1.** Let  $y$  be a mutant strategy, and  $P_{x,y}$  a population set made up of  $n-2$   $x$ -strategists and only one  $y$ -strategist. Let  $f(y, P_x)$  be the fitness of a single  $y$ -strategist in a population set  $P_x$  of  $n-1$   $x$ -strategists. The mixed incumbent strategy  $x = [x^1, x^2, \dots, x^n]^T$  is one-stable ESS if the following condition holds:

$$f(y, P_x) < f(x, P_{x,y}) \quad (8)$$

for all  $y \neq x$ .

This is what is known as the equilibrium condition for the game against the field for a finite population size (Schaffer, 1988). It is clear that this condition only tests if the population of hives cannot be invaded by *only* one mutant. If we have more than one mutant, we have to check another condition. This condition is usually known as the stability condition, and it says that a strategy is  $Y$ -stable if the incumbent strategy cannot be invaded by a total of up to  $Y$  identical mutant strategists (Schaffer, 1988). It is said that the ESS is globally stable whenever  $Y=n-1$ . Here, we assume that there is *only* one mutant since mutants are rare; hence, we do not need to check the stability condition.

### 3.1.3. Hive/bee fitness definitions

Before we show that the IFD is a strict Nash equilibrium, we need to define the payoff of hive  $i$ . First, let us define the contribution to the fitness of hive  $i$  at site  $j$  as

$$f^i(j) = a_j \frac{x_j^i}{\sum_{k=1}^n x_j^k} = a_j \frac{x_j^i}{x_j^i + \sum_{k=1, k \neq i}^n x_j^k} \quad (9)$$

Eq. (9) can be divided into two parts. First, we have the proportion of bees allocated by the  $i$ th hive to site  $j$ , with respect to the total number of bees allocated to that site by all hives. Then, there is the  $a_j$  term that can be seen as a constant that is proportional to the profitability of the site. If  $a_j$  is in nutrients per second, then this quantity is the amount of nutrients per second hive  $i$  gets for investing  $x_j^i$  bees at site  $j$ , while the other  $n-1$  hives invest  $\sum_{k=1, k \neq i}^n x_j^k$  bees at the same site. Hence, the fitness (payoff) of hive  $i$ ,  $i=1, 2, \dots, n$ , is

$$f^i = \sum_{j=1}^N f^i(j) = \sum_{j=1}^N x_j^i \frac{a_j}{\sum_{k=1}^n x_j^k} \quad (10)$$

The IFD is achieved when the fitness of hives  $i$  and  $i'$  are equal, for all  $i \neq i'$ , as in

$$f^i = \sum_{j=1}^N f^i(j) = \sum_{j=1}^N f^{i'}(j) = f^{i'} \quad (11)$$

Using Eq. (10), Eq. (11) can be satisfied if the hive allocate bees equally in every site so that

$$x_j^i = x_j^{i'} \quad (12)$$

for all  $i, i' = 1, 2, \dots, n$ . If each hive chooses the IFD, then for each  $i=1, 2, \dots, n$ , for  $j=1, 2, \dots, N$ ,

$$\frac{x_j^i}{\sum_{k=1}^n x_j^k} = \frac{a_j}{\sum_{k=1}^n a_k} \quad (13)$$

Notice that since  $\sum_{k=1}^n x_j^k = B_f$  for all  $i=1, 2, \dots, n$ , Eq. (12) holds. Eq. (13) is a generalization of the input matching rule (Parker and Sutherland, 1986; Parker, 1978) to the  $n$ -hive game. In Quijano and Passino (2007) the authors have shown the equivalence between the input and the habitat matching rule for a general case of suitability functions. We can use the same ideas as in Quijano and Passino (2007) to prove that Eq. (13) can also be written as

$$x_k^i a_j = x_j^i a_k$$

for all  $k, j=1, 2, \dots, N$ , and  $i=1, 2, \dots, n$ .

Eq. (9) defines the fitness for multiple hives. However, when there is only a single hive, the definition for the payoff changes. For that, we can assume that each bee is identical and represented by a small  $\varepsilon_x > 0$  so that there is an arbitrarily large (integer) number  $n > 0$  of bees in the hive, where

$$n\varepsilon_x = B_f$$

Given the concept of an individual bee  $\varepsilon_x > 0$  at site  $j$ ,  $j=1, 2, \dots, N$ , we define this bee's fitness as  $f(j) = a_j/n_j$ . If  $a_j$  is nutrients per second,  $f(j)$  is the number of nutrients per second that a bee gets at site  $j$ . Notice that

$$f(j) = \frac{a_j}{n_j} = \varepsilon_x \frac{a_j}{\varepsilon_x n_j} = \varepsilon_x \frac{a_j}{x_j} \quad (14)$$

These ideas will be helpful in Section 3.3.

### 3.2. The multiple hive IFD is a strict Nash equilibrium and ESS

In the next theorem<sup>1</sup> we show that the IFD in Eq. (13) is a strict Nash equilibrium. This implies by Eq. (8) that the IFD is a *one-stable* ESS, because the IFD is the best strategy whenever one mutant hive plays against  $n-1$  incumbents in an  $n$ -hive game.

**Theorem 3.1.** For the  $n$ -hive game if the  $x_j^i, j=1, 2, \dots, N, i=1, 2, \dots, n$ , are all given by the IFD in Eq. (13), then hives are using a strict Nash equilibrium strategy to allocate the bees. Hence, the IFD in Eq. (13) is a finite population one-stable ESS.

This result shows that if the IFD is used by all hives, no hive can unilaterally deviate and improve its fitness. While the IFD is often discussed as if it were with respect to a number of animals (e.g., bees) being allocated (e.g., see Giraldeau and Caraco, 2000), this seems to be the first proof that in an  $n$ -hive game the IFD is a strict Nash equilibrium (hence, a *one-stable* ESS). It is interesting to note that if we think of achievement of Eq. (13) by each hive as “individual-level” IFD achievement, then for all  $j=1, 2, \dots, N$ ,

<sup>1</sup> Proofs of all theorems are in the Appendix.



and  $i = 1, 2, \dots, n$ ,

$$x_j^i \sum_{k=1}^N a_k = a_j \sum_{k=1}^N x_k^i$$

and if we sum over  $i$ ,

$$\left( \sum_{i=1}^n x_j^i \right) \left( \sum_{k=1}^N a_k \right) = a_j \left( \sum_{i=1}^n \sum_{k=1}^N x_k^i \right)$$

or for all  $j = 1, 2, \dots, N$ ,

$$\frac{\sum_{i=1}^n x_j^i}{\sum_{i=1}^n \sum_{k=1}^N x_k^i} = \frac{a_j}{\sum_{k=1}^N a_k} \quad (15)$$

Eq. (15) can be interpreted as a “hive population-level” or “environment-wide” IFD. Clearly, however, Eq. (13) is only one way to achieve this population-level IFD (as the next example will show). Finally, note that there may be strategies, not all the same and different from the IFD in Eq. (13), but that the hives could use and (i) still get the same fitness as each other and as the fitness achieved at the IFD in Eq. (13), and (ii) achieve the population-level IFD in Eq. (15). For example, if  $N=n=2$ ,  $B_f=1$ ,  $a_1=a_2=1$ ,  $x_1^1=x_2^2=\frac{1}{4}$ , and  $x_2^1=x_1^2=\frac{3}{4}$ ,  $f^1=f^2=1$  and this is the same fitness that results if the  $x_j^i=\frac{1}{2}$ ,  $j=1,2$ ,  $i=1,2$ , IFD strategy from Eq. (13) is used. Also, Eq. (15) holds for the alternative strategy choice.

### 3.3. Optimality of the single and multiple hive IFD

The results in Section 3.2 show that the IFD is a local optimum point in a game-theoretic sense. Here, we show that the IFD is a global optimum point for both a single hive and multiple hives.

#### 3.3.1. Single-hive allocation

First, we take the perspective that a single hive wants to allocate some number of bees  $B_f$  to  $N$  choices (sites) in order to optimize its payoff (fitness). We drop the superscript and use  $x_j$ . The percentage of the total number of bees to site  $j$  is  $x_j/B_f$ ,  $j=1,2,\dots,N$ . Using Eq. (14), the total payoff can be written as

$$J = \sum_{j=1}^N \left( \frac{x_j}{B_f} \right) \left( \frac{a_j}{x_j} \right) = \frac{\sum_{j=1}^N a_j}{B_f} \quad (16)$$

Due to the cancellation of the  $x_j$  in Eq. (16),  $J$  is a constant. Hence, any allocation involving all  $x_j$  nonzero gives the same total return to the hive. This is a consequence of the “continuous input” assumption for the IFD formulation that says that all nutrients arrive at a constant rate and are immediately consumed (Fretwell and Lucas, 1970). Eq. (16) also shows that a hive cannot use the strategy of maximizing  $J$  in order to determine how to allocate the number of bees. Does there exist a payoff function that the hive can try to optimize that does guide it to maximize its payoff? Next, we show two approaches to answer this question.

First, assume that  $a_j > 0$ ,  $x_j > 0$ , and note that  $a_j/x_j$  is the return per investment of  $x_j$ . Suppose that the hive wants to maximize its return from each investment, under the constraint that  $\sum_{j=1}^N x_j = B_f$  and  $x_j > 0$ . One approach is to try to maximize the minimum fitness as defined by Eq. (14), i.e., solve the optimization problem

$$\begin{aligned} \max \min \quad & \left\{ \frac{a_1}{x_1}, \frac{a_2}{x_2}, \dots, \frac{a_N}{x_N} \right\} \\ \text{subject to} \quad & \sum_{j=1}^N x_j = B_f \end{aligned}$$

$$x_j > 0, \quad j = 1, 2, \dots, N \quad (17)$$

The terms  $a_j/x_j$  are the fitnesses for any bee that chooses site  $j$ ,  $j=1,2,\dots,N$ . Consider a single individual  $\varepsilon_x > 0$ . If this bee is at site  $j$  and  $\varepsilon_x a_j/x_j < \varepsilon_x a_k/x_k$ ,  $j \neq k$ , then it can move to site  $k$  (i.e., change strategies). The “max min” represents that multiple bees simultaneously shift strategies to improve their fitness since at least some bees with lowest fitness shift sites (and if  $\varepsilon_x a_j/x_j = \varepsilon_x a_k/x_k$  for some  $j$  and  $k$  the min can be achieved at multiple sites). It has been shown in Quijano and Passino (2007) that the hive should invest its effort according to an IFD as it is the global maximum for that optimization problem and hence will maximize the hive’s payoff.

Second, viewing the hive’s effort allocation strategy as being adaptive (i.e., shaped by natural selection) it makes sense that it would be appropriately modeled as the optimization of some payoff (fitness) (Stephens and Krebs, 1986). However, could other payoff functions be used besides the one in Eq. (17)? Generally, the answer to this question should be yes. Eq. (17) relates decision variables  $x_j$  to payoff  $J$  and other equally valid relationships between these two could lead to optimal effort distributions, possibly even the IFD. To illustrate this point in a concrete way we introduce another candidate payoff function  $J$ .

To develop this  $J$  suppose that  $a_j > 0$  and  $x_j > 0$  for  $j=1,2,\dots,N$ , and note that  $x_j/a_j$  is the amount of bees allocated to site  $j$  per the return from site  $j$ . For instance, if  $a_j$  is in units of nutrients per second, and a hive allocated  $x_j$  in units of “bees per second” it takes of the nutrients, then  $x_j/a_j$  is in units of bees per nutrients. A hive wants to invest as few as possible bees, yet get as much return as possible. Hence, it wants to allocate bees so that it gets as many nutrients per bee as possible. If  $x_j/B_f$  is the percentage of the total number of bees allocated to site  $j$ , and if the hive tries to minimize

$$J = \sum_{j=1}^N \left( \frac{x_j}{B_f} \right) \left( \frac{x_j}{a_j} \right) = \frac{1}{B_f} \sum_{j=1}^N \frac{x_j^2}{a_j} \quad (18)$$

then it will maximize its return on investment by minimizing its losses. Or, from another perspective, it minimizes the average number of bees per nutrient across all sites. The next result shows that if a hive seeks to minimize  $J$  in Eq. (18), then it will achieve an IFD.

#### Theorem 3.2. The point

$$x_j = \frac{a_j B_f}{\sum_{k=1}^N a_k}$$

is the global minimizer for the constrained optimization problem defined as

$$\begin{aligned} \text{minimize} \quad & J = \frac{1}{B_f} \sum_{j=1}^N \frac{x_j^2}{a_j} \\ \text{subject to} \quad & \sum_{j=1}^N x_j = B_f \\ & x_j > 0, \quad j = 1, 2, \dots, N \end{aligned}$$

#### 3.3.2. Multiple hive allocations

Theorem 3.2 shows that the IFD is achieved for a single-hive allocation. Now, we want to prove that the IFD is also reached for the case when we have multiple hives that want to allocate bees across different sites. From the proof of Theorem 3.1 it should be clear that there are an infinite number of points  $x_j^i$ ,  $j=1,2,\dots,N$ ,



$i=1,2,\dots,n$ , that result in

$$\frac{\sum_{i=1}^n x_j^i}{\sum_{k=1}^N \sum_{i=1}^n x_k^i} = \frac{a_j}{\sum_{k=1}^N a_k} \quad (19)$$

which is the achievement of an IFD by the aggregate of the number of bees' allocation. In the next theorem, we show that the optimum payoff value is given by what we call the population-level IFD in Eq. (19).

**Theorem 3.3.** *If the population IFD is achieved by the distribution of the bees that achieve Eq. (19) then, if one of the  $n$  hives deviates and the others stay the same, the one that deviates cannot improve its payoff.*

The optimization problem can be interpreted as one hive allocating some number of bees at the site where  $n-1$  hives have allocated the bees in such a way that they are at the IFD. For each hive, the total number of bees across the  $N$  sites is equal to  $\sum_{j=1}^N x_j^i = B_i$ , for all  $i=1,2,\dots,n$ . Since the  $n-1$  are at the IFD, it is clear that if we add an  $n$ th hive, it can allocate all its bees across the  $N$  sites using a strategy that leads to the population-level IFD. In other words, this last hive that disrupts everybody else's return gets the same payoff that all the other hives get if it plays a strategy such that the population-level IFD is achieved.

### 3.4. Discussion

The previous analysis is based on the hypothesis that we have full static information. This means that we did not analyze the cases where there is noise, lack of information when strategies are chosen, or when the fitness functions in (9) or (14) have dynamics. Analysis for these cases remains a (challenging) research direction. In the next section, we motivate the importance of addressing these theoretical questions by showing that multiple poorly informed socially foraging honey bee hives can achieve an IFD in an application where there is significant noise.

## 4. Engineering application: dynamic resource allocation for multizone temperature control

In this section we introduce an engineering application that illustrates the basic features of the dynamical operation of the honey bee social foraging algorithm. First, we describe the hardware used and some implementation issues. Next, we provide data from three experiments that demonstrate the achievement of the ideal free distribution and the effects of cross-inhibition and imperfect information flow.

### 4.1. Experiment and honey bee social foraging algorithm design

We implemented the multizone temperature control grid shown in Fig. 2. A zone contains a lamp and a National

Semiconductors LM35CAZ temperature sensor. The temperature is acquired using four analog inputs with 16 bits resolution each on a dSPACE DS1104 card. Although we cannot guarantee that the four sensors have the same characteristics, they have  $\pm 0.2^\circ\text{C}$  typical accuracy, and  $\pm 0.5^\circ\text{C}$  guaranteed. The lamps are turned on or off by the controller using four analog outputs of the DS1104 card and a DS2003 Darlington device that drives the amount of current necessary to turn on a lamp. The lamps change their intensities drastically when we apply more than 1.6 V. We added by software a DC value of 1.25 V, which implies that there is a range where the lamps are off even if we allocate a small amount of energy in a zone.

We assume that there is a fixed total amount of voltage  $V_{tot}$  (the resource) that can be split up and applied to the zones. The goal is to allocate this fixed amount of voltage in a way that (i) makes the temperatures in all zones the same, and (ii) maximally elevates the temperature across the grid. In other words, we want a maximum uniform temperature. Achievement of this goal is complicated by interzone effects (e.g., lamps affecting the temperature in neighboring zones), ambient temperature and wind current challenges (from overhead vents), zone component differences, and sensor noise. These effects demand that voltage be dynamically allocated. For example, if there is an ambient temperature increase in zone 4 in Fig. 2 the voltage applied to the lamp in zone 4 should decrease and that voltage should be allocated across the other three zones.

Given the hardware description and the model, we choose a honey bee social foraging algorithm as follows:

1. We assume that there are a fixed number of bees involved in the foraging process,  $B$ . Each bee corresponds to a quanta of energy, which in this case corresponds to a certain amount of volts, of the  $V_{tot}$  available volts, that will be specified below.
2. We assume that the foraging landscape is composed of four forage sites, which correspond to the zones  $j, j=1,2,3,4$ .
3. Let  $T_d$  be a temperature value that *cannot* be achieved in the experiment (here we use  $T_d = 29^\circ\text{C}$ ). Let  $T_j$  be the temperature in zone  $j$ , and let

$$e_j = T_d - T_j$$

be the temperature error for zone  $j$ . We assume that the "best" (most profitable) forage site corresponds to the zone that has the highest error. Bees (quanta of voltage) that are allocated to better sites will raise the temperature there. Repetitive allocation will result in persistently raising the minimum temperature.

4. We assume that the profitability assessment of each site  $F^j(k)$  is proportional to  $e_j$  and given by

$$F^j(k) = \begin{cases} 1 & \text{if } e_j(k) \geq 1 \\ \gamma e_j(k) & \text{if } \varepsilon_n < \gamma e_j(k) < 1 \\ 0 & \text{otherwise} \end{cases} \quad (20)$$

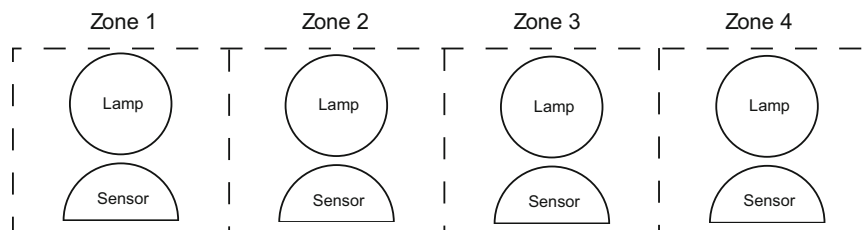


Fig. 2. Layout for the multizone temperature control grid experiment.

We let  $\gamma = \frac{1}{8}$  since given  $T_d$  the temperature error  $e_j < 8^\circ\text{C}$  so  $\gamma e_j < 1$  with  $\gamma = \frac{1}{8}$ . Then we know that  $F^j(k) \in [0, 1]$ . We let  $\varepsilon_n = 0.1$  since this means that sensor inaccuracies are not interpreted as profitability differences and, so that with  $T_d = 29^\circ\text{C}$  any temperature error is profitable for allocation.

5. The waiting time defined in Eq. (1) has two tunable parameters,  $\psi$  and  $w_w$ . In this case, we have tuned these values and we chose  $\psi = 0.25$  and  $w_w = 20$ .
6. We also chose  $\alpha = 1$ ,  $\phi = 1$ ,  $p_o = 0.35$ ,  $\sigma = 1000$ ,  $\delta = 0.02$ , and  $\beta = 100$  to ensure that bees are persistently recruited to achieve the bee (voltage) allocation and persistently explore sites for more temperature error. The particular values chosen were explained in Section 2, and these values did not need to be retuned for the application.

The experimental results shown below were obtained on different days with different ambient room temperatures.

#### 4.2. Experiment 1: one hive IFD achievement

In this experiment we seek the maximum uniform temperature when we have  $V_{tot} = 2.5\text{ V}$  of resource available. We assume that there is one hive that has 200 bees, which are equivalent to  $V_{tot}$ . In other words, we assume that each bee is equivalent to  $0.0125\text{ V}$ . Fig. 3 shows the experimental results for the temperatures (top plots), and the numbers of bees allocated in each zone (bottom plots), when the room temperature is  $T_a = 22^\circ\text{C}$ .

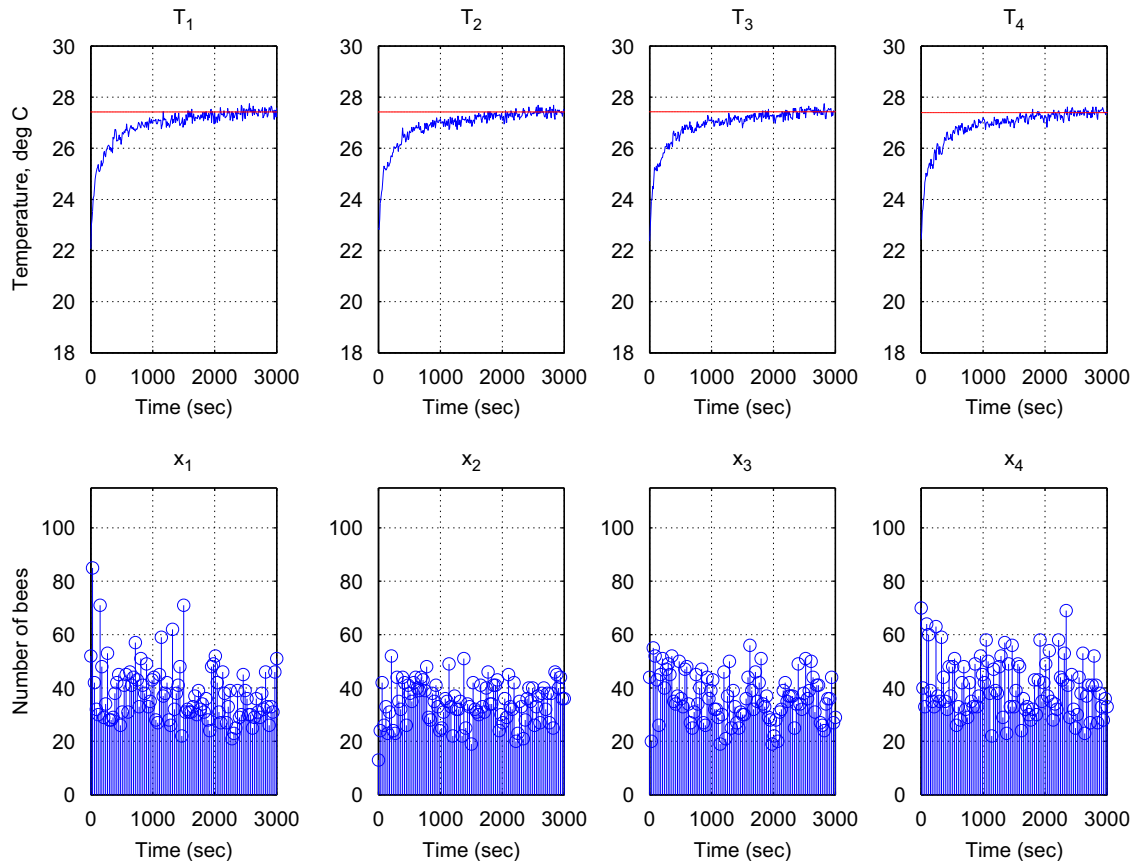
Fig. 4 illustrates how the bees are allocated to various roles. The top plot shows how the number of employed foragers  $B_f$  increases drastically at the beginning, but then it drops until it

arrives to a steady-state. The bottom plot shows the number of explorers  $B_e$ , and we can see how it stays high to ensure persistent search for temperature error. From the data obtained, it can also be seen that many bees get recruited. This implies that these bees find a site and they do not abandon it, which provides good temperature regulation.

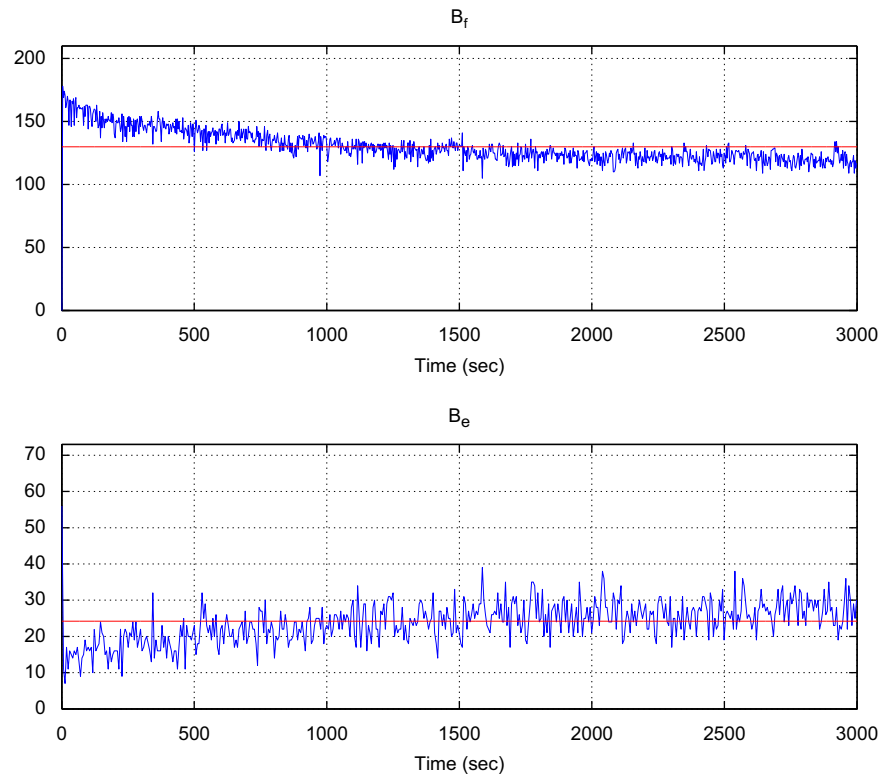
Fig. 7, which will be used to compare the results of all the experiments, shows the average temperature (top plot) and the average number of bees (bottom plot) for the last 100 s. The data for experiment 1 show how an ideal free distribution is achieved. As we can see, the final temperature reached by all zones is around  $27^\circ\text{C}$ . In terms of the average number of bees for the last 100 s, we can see that the voltage allocated is around  $1.7\text{ V}$  (DC offset included), which is equivalent to 35 bees per zone. However, due to the differences between sensors and lamps, more bees are allocated in the fourth zone (i.e., zone 4 is more difficult to heat). This result is consistent with the experimental results shown below.

#### 4.3. Experiment 2: one hive with disturbances, IFD, cross-inhibition, and site truncation

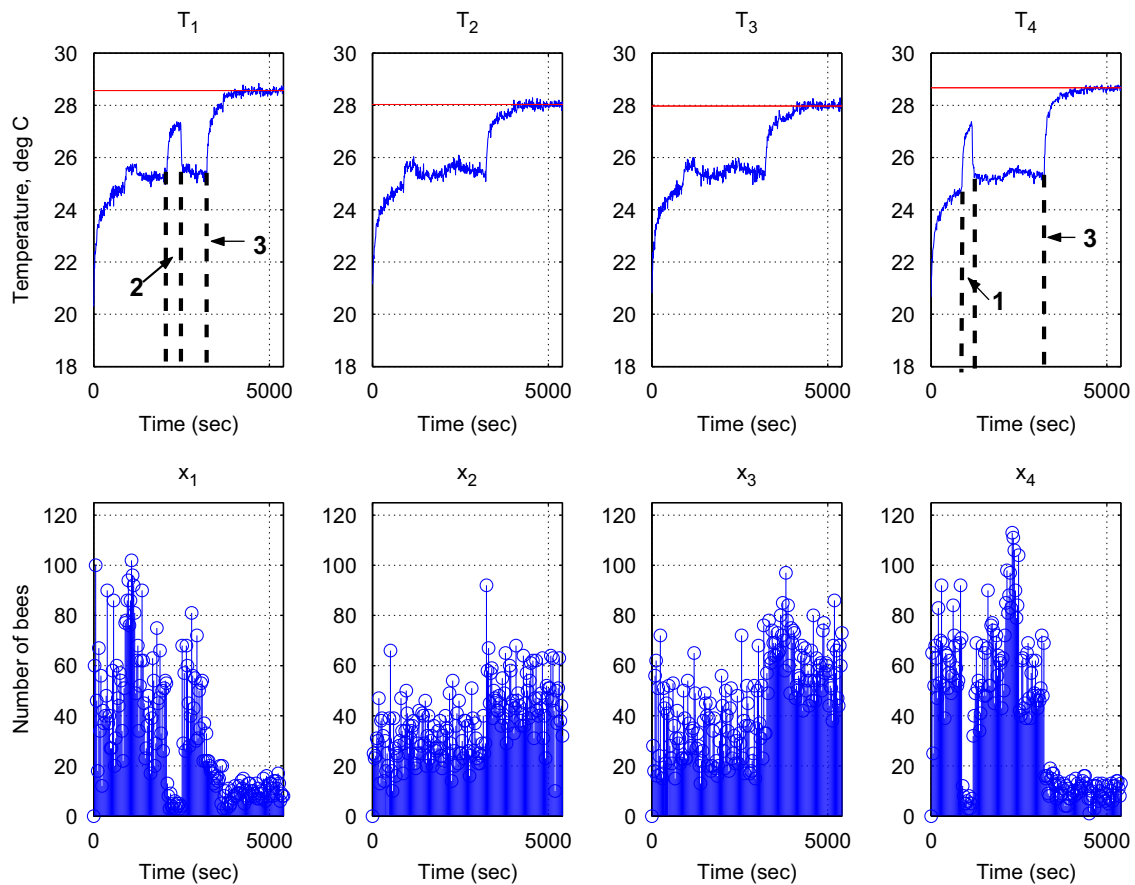
The second experiment is similar to the first one, but we add two disturbances to the system. These disturbances are created by two extra lamps, one placed next to zone 1 and another placed next to zone 4. We start the experiment at a room temperature of  $T_a = 20.6^\circ\text{C}$ . Fig. 5 shows the results. The numbers in the top left and top right plots represent the *disturbance types* applied to the



**Fig. 3.** Temperature and number of bees per zone when there is one hive and no disturbances. The top plots show the temperature in each zone, and the average of the last 100 s (solid constant line). The stems in the bottom plots represent the number of bees that were allocated to each zone.



**Fig. 4.** Number of employed foragers  $B_f$  and the average of the last 100 s (top plot). The bottom plot shows the number of explorers  $B_e$  and the average of the last 100 s.



**Fig. 5.** Temperature and number of bees per zone for the second experiment. In the top plot the solid constant line represents the average of the last 100 s in each zone. The numbers 1–3 correspond to the disturbances. The stems in the bottom plot represent the number of bees that were allocated to each zone.

system:

1. We turn on the disturbance lamp next to zone 4 at  $t=850$  s, and we turn it off at 1170 s.
2. We turn on the disturbance lamp next to zone 1 at  $t=2160$  s, and we turn it off at 2500 s.
3. We turn on the disturbance lamps next to zones 1 and 4 at  $t=3200$  s, and we turn them off at 5400 s.

When we apply disturbance 1, the temperature in zone 4 starts to increase, and the number of bees allocated in that zone decreases drastically. At the same time, the number of bees in the other three zones increases. This is because site number 4 is the least profitable of all sites, and hence the hive reallocates the bees to the other three zones; this is why the temperatures in zones 1–3 increase until the disturbance is turned off. At that moment, the temperature in zone 4 drops drastically, and the hive realizes that it must allocate more bees to that site. It does that until all four zones are practically at the same temperature. During the 5 min of disturbance, the temperatures in zones 2 and 3 remain close to 25.5 °C, while the temperature in zone 1 is around 25.4 °C. Therefore, zone 1 becomes the most profitable one, and hence more bees are allocated to that site (around 76 bees were allocated on average to zone 1, while 37, 41, and 10 bees were allocated on average to zones 2, 3, and 4, respectively). The same basic behavior occurs when disturbance 2 is applied to the system. In this case, the temperature at the first site increases to 27 °C, while the other temperatures were close to 25.6 °C. As in the previous case, the temperature in zone 4 was close to 25.5 °C, which implied that more bees were allocated to this site (5, 33, 33, and 93 bees were allocated on average to zones 1 through 4, respectively). We highlight the fact that zone 4 has more bees than the middle zones. As we mentioned in Section 4.2 this is due to the differences between sensors and lamps. After disturbance 2 is turned off and the temperatures in all zones was practically the same (i.e., around 25.4 °C), we apply disturbance 3 and for it the temperatures equilibrate but with a bee allocation where there are far fewer bees in zones 1 and 4 and more in zones 2 and 3. To see why this is the case, see the experiment 2 data in Fig. 7. As we can see in the bottom plot, the average number of bees for the last 100 s is practically the same for the middle zones (34.8 bees), and there are practically the same number of bees allocated to zones 1 and 4 where there is a disturbance (10 bees). This leads to a final temperature that is practically the same for zones 1 and 4 (i.e., around 28.6 °C) and for the middle zones (i.e., around 28 °C). However, as we mentioned before, the fact that there are 10 bees in a zone does not necessarily imply that the lamp is on. In this case, 10 bees corresponds to 0.125 V, which implies that the lamp is off (recall that the DC value was 1.25 V). Therefore, the bees allocated to zones 1 and 4 do not have any influence on the temperature. Only the disturbances affect these temperatures. Hence the residual number of 10 or so bees simply represents that the hive is continually sampling these sites in case they become profitable.

#### 4.4. Experiment 3: two hives and imperfect information

In this final experiment, we change the conditions and instead of using only one hive, we assume that we have two hives each with limited information. The first hive is assumed to only have access to the temperatures in zones 1–3, while the second hive has access to the temperatures of zones 2–4. This may happen in nature if a hive has not discovered a site. In temperature control applications such sensing restrictions commonly arise due to sensor or other hardware costs.

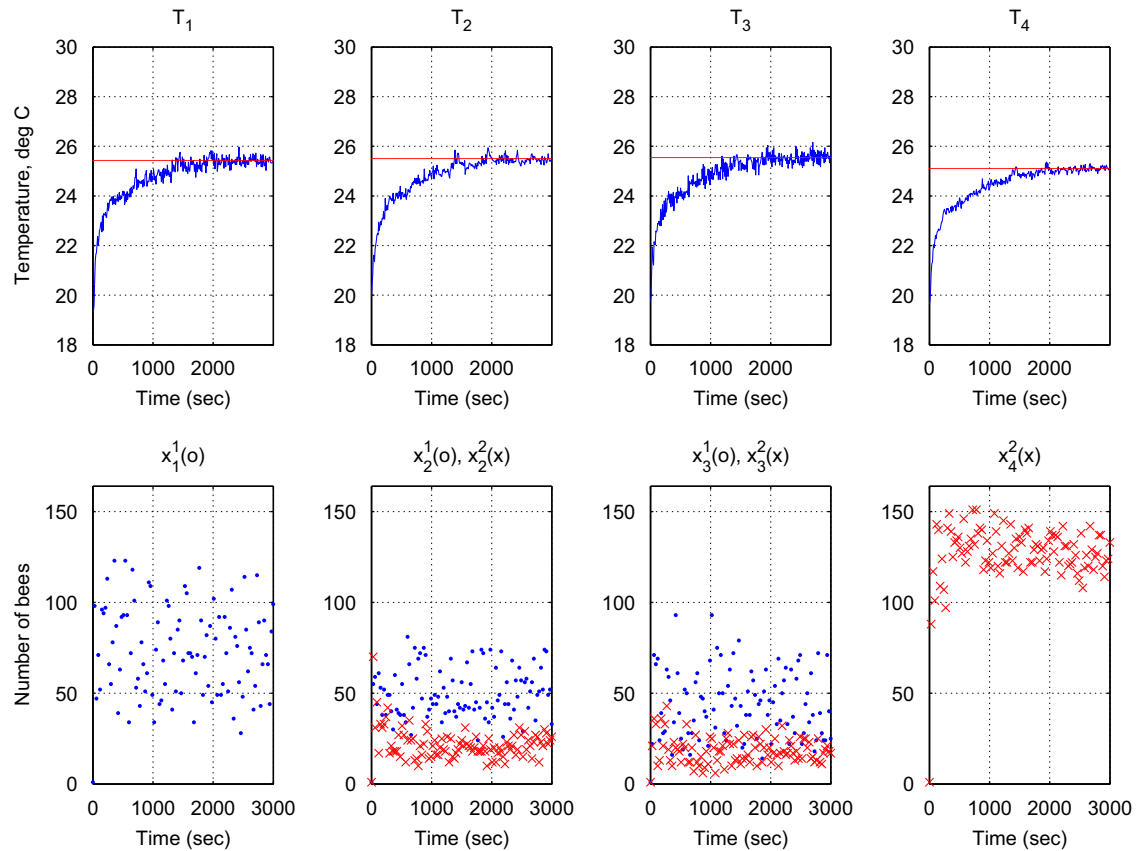
Each hive is composed of 200 bees, which implies that the 5 V that we allocate corresponds to 400 bees (i.e., each bee corresponds again to 0.0125 V). Fig. 6 shows the results for this case when the initial temperature in the room  $T_a = 19.6$  °C. The final temperature is practically the same, around 25.4 °C. The main difference in this case is that the number of bees in zones 2 and 3 depend on both hives (see the bottom plot of Fig. 6). Hive 1 allocates on average around 50 bees to zones 2 and 3, while the second hive allocates on average around 20 bees to zones 2 and 3. However, as we can see in the experiment 3 data in the bottom plot of Fig. 7, the same *total* amount of bees are allocated by the two hives except for zone 4. It is important to notice that the difference between the initial temperature and the final temperature in the first experiment is around 5 °C, while in this case is around 6 °C. Therefore, as we expect, the maximum temperature reached by the grid is higher than the first one if we compare the temperatures relative to room temperature. This is mainly due to the fact that at the end we are allocating more bees per zone, i.e., more voltage  $V_{tot} = 5$  V rather than in experiments 1 and 2 where we had  $V_{tot} = 2.5$  V. Finally, another important issue that arises in this case is the number of bees that are allocated to zone 4. Besides the fact that there is a difference between sensors and lamps in zone 4 with respect to the other zones (as it was seen in the previous experiments), there is imperfect information. As we can see, hive 1 allocates more bees to zones 2 and 3 compared to the number allocated by hive 2. This implies that the temperature errors in these zones decrease, while the temperature in zone 4 seems to be lower than the middle zones due to sensor differences. Then, the second hive allocates more bees to the most profitable site (zone 4), and less to zones 2 and 3 (these zones receive more bees from hive 1, and its total value is similar to the number of bees allocated in zone 1). The bottom plot in Fig. 6 illustrates this point.

#### 4.5. Discussion

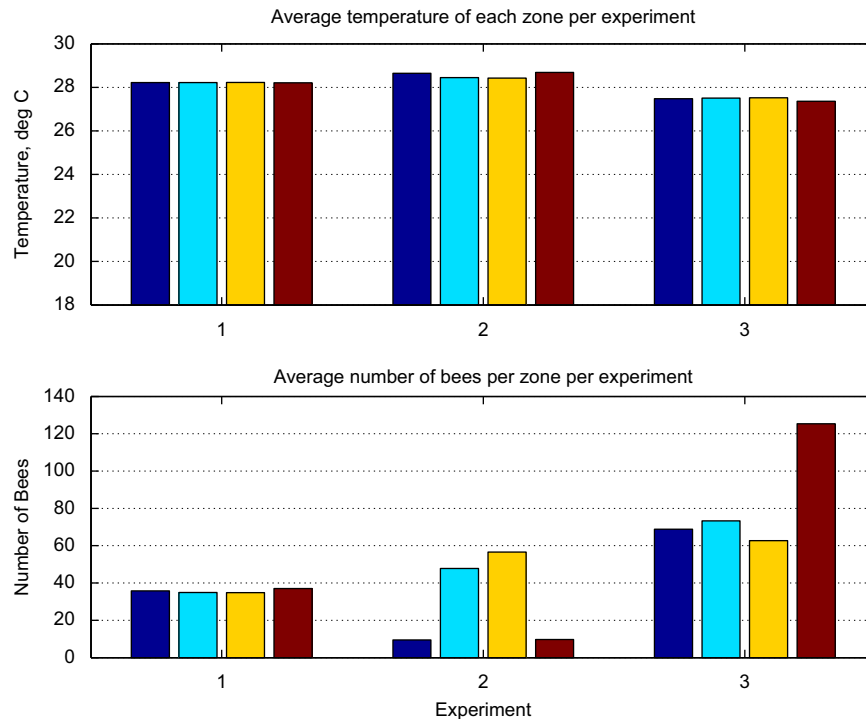
Some of the main concepts described in social foraging modeling section (Section 2) can be seen in these experiments. In Section 4.2 we have seen how an IFD is reached by all zones, and good regulation is obtained even though the search space is limited (Section 4.4). As shown in Section 4.3, an IFD is also reached when disturbances are applied to the system. The IFD obtained is in terms of the number of bees allocated to each of the zones, depending on whether the disturbance is on or not. In other words, the middle zones that are not significantly affected by any type of disturbance increase their temperature to their maximum possible value. This maximum depends on the amount of energy available. This energy is practically the same in each zone, which leads to uniformity in these zones. The other two zones have a disturbance associated with each of them, which implies that the number of bees allocated to each of these zones must be lower than for the middle ones. As we expect, the final temperature in this case is higher than in the first experiment because of the disturbances, and the numbers of bees allocated to the middle zones are higher than in the previous case (see Fig. 7). If we had reduced the magnitude of the disturbances in zones 1 and 4 then we would have gotten results analogous to those for disturbances 1 and 2. We chose the particular disturbance magnitudes in order to illustrate the *elimination* of zones 1 and 4 as possible sites (site “truncation”, Fretwell and Lucas, 1970) and how the hive can then focus most of its attention on only the best sites.

Another important idea that is illustrated in these experiments is the cross-inhibition concept (Seeley, 1995), and this can be seen in Fig. 5. First, all zones were under the same conditions, and





**Fig. 6.** Temperature and number of bees per zone for the last experiment. In the top plot the solid constant line represents the average of the last 100 s in each zone. In the bottom plot, “o” corresponds to the bees that were allocated by the first hive, while “x” corresponds to the bees that were allocated by the second hive.



**Fig. 7.** The top plot shows the final temperature, while the bottom plot shows the final value for the number of bees in each zone for each experiment. This final value corresponds to the average for the last 100 s of data. In each experiment, zone 1 corresponds to the left bar, and zone 4 to the right bar for each of the 3 groups of four bars.

practically the same number of bees visited sites 1, 2, and 3 (45, 31, 34 visited on average zones 1 through 3, respectively, while 60 bees were allocated to zone 4 due to sensor differences). When disturbance 1 is applied, more bees start visiting sites 1, 2, and 3, while the number of bees in zone 4 reduces drastically. The same thing happens when disturbances 2 and 3 are applied. It is clear that in any of these cases one or two zones becomes less profitable (the temperature increases due to the disturbance, and hence the error decreases), which implies that the hive has to reduce the number of bees recruited to these poorer sites. This is given in the algorithm by a reduction of the number of dances for those zones where the error is smaller, which leads to a reduction in the number of bees that are recruited to these sites.

Experiment 3 shows how another IFD is achieved over all zones, even though there is not perfect information (see Fig. 7). As we can see in Fig. 6, the final temperature in all zones is practically the same (taking into account the sensor differences accuracy). However, as we mentioned before, hive 2 must use more of its bees to raise the temperature in zone 4, and that is why the number of bees allocated by this hive to zones 2 and 3 is small. This problem can be seen also as having a zone with a disturbance. In this case, zone 4 needs more energy, which implies that more bees are allocated by the second hive to it. Thus, the middle zones are not visited as much by the bees since they are less profitable. They are also not as profitable as zone 1, and that is why a smaller amount of bees are allocated to zones 2 and 3 by hive 1 (compared to those that are allocated in zone 1 as it can be seen in the bottom plot in Fig. 6). However, the total number of bees (those allocated by hives 1 and 2) leads to practically the same numbers of bees in zones 2 and 3, and the grid reaches a maximum uniform temperature.

In all these cases, the temperature grid reached an equilibrium. If we compare the experimental results with the theoretical results (Section 3), we can see that the equilibrium point for the first experiment is similar to what is shown in Theorem 3.2. In this case, the  $a_j$  can be seen as the temperature error, because it is clear that the hive will allocate more bees where the error is higher. For the last experiment a population level type IFD as in (19) is achieved, again with  $a_j$  proportional to the temperature error. We have proven in Theorem 3.3 that the IFD was the optimum point, and the experiments illustrate that this equilibrium was reached for  $n=2$  hives.

## 5. Conclusions

In this paper we provided a novel bio-inspired resource allocation method, developed theory to explain key properties of the algorithm, and studied an application that illustrates the validity of the theoretical properties. The application that we have used is a multizone temperature control grid, where the control objective is to seek the maximum uniform temperature. In Quijano and Passino (2007) the authors use the same testbed to show how the replicator dynamics model leads to an ideal free distribution (IFD). Here, the honey bee social foraging algorithm gives us similar results, and also helped us to illustrate dynamic re-allocation, cross-inhibition, and the IFD. We leave as an important future direction the comparative analysis with the performance of other methods for the experimental testbed. Clearly, there are other applications for the social foraging method for allocation, for instance, in the area of formation control and task allocation of multiple agents.

The game and optimization theoretic theory that characterizes properties of the social foraging algorithm is a key contribution of this paper. One of the most important concepts in this paper is the IFD concept from theoretical ecology. We have shown that the IFD

is a strict Nash equilibrium for an  $n$ -hive game and a one-stable ESS. In other words, in an  $n$ -hive game the IFD is reached whenever  $n-1$  hives are using it as a strategy and only one hive is not using it. This hive has to choose the IFD strategy to obtain as much as the other hives. Since this is only a local concept, we extend our results to show that the IFD is a global optimum point for both a single hive and multiple hives. In this case we have limited our analysis to an optimality perspective. It is our intent to develop in the future a dynamical model of IFD achievement (e.g., adaptive dynamics such as a replicator dynamics model, Hofbauer and Sigmund, 1998).

Finally, it is clear that in the implementation we have limited our system and drawn some analogies that might not seem real from a biological perspective. For instance, consider the information structure of the algorithm (i.e., what characteristics are present to provide information to the algorithm and between components of the algorithm). In a honey bee hive, the forage allocation process does not need a centralized entity that makes the decisions and allocates bees to each site, i.e., the hive is a decentralized system (Seeley, 1995). However, if we analyze the honey bee social foraging algorithm, and more precisely Eqs. (1), (5) and (6), it is clear that the algorithm is not totally “individual-based” (e.g., Eq. (5) has to know a noisy version of the total number of waggle runs in order to decide how many observer bees will become an explorer). It is our intent to consider in the future a more fully distributed version that faithfully respects what is known by individuals. Also, other large-scale optimization problems will be considered to show the applicability of our algorithm. Finally, it is our hope to in the future conduct a more complete mathematical and experimental evaluation of the robustness of our distributed dynamical control system.

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## Appendix A. Proofs of theorems

### A.1. Proof of Theorem 3.1

We will show that if  $\bar{x}^{i*} = [x_1^{i*}, x_2^{i*}, \dots, x_N^{i*}]^T$ , where  $x_j^{i*} = B_f a_j / \sum_{j=1}^N a_j$  for all  $j=1,2,\dots,N$ , and  $i=1,2,\dots,n$ , then a single hive mutant  $\bar{y}^i \neq \bar{x}^{i*}$  will have a lower fitness for the moment, when  $\bar{y}^i \in \Delta_x - \partial \Delta_x$  (i.e., strictly inside the simplex). This is equivalent to show that Eq. (7) is satisfied for all  $i=1,2,\dots,n$ . But, it can also be seen as a constrained optimization problem of the form

$$\begin{aligned} & \text{maximize} \quad f^i = \sum_{j=1}^N x_j^i \frac{a_j}{\sum_{k=1}^N x_k^i} \\ & \text{subject to} \quad \sum_{j=1}^N x_j^i = B_f, \quad i = 1, 2, \dots, n \\ & \quad \quad \quad x_j^i > 0, \quad j = 1, 2, \dots, N \end{aligned}$$

$$x_j^k = \frac{B_f a_j}{\sum_{m=1}^N a_m}, \quad k \neq i, \quad k = 1, 2, \dots, n \quad (21)$$

This is a nonlinear optimization problem that we will solve using Lagrange multiplier theory (e.g., Bertsekas, 1995).

First, since  $x_j^i > 0$  the constraint is inactive, so it can be ignored. Second, replace in Eq. (10) the constraint  $x_j^k = B_f a_j / \sum_{m=1}^N a_m$ , for all  $k \neq i$  to get

$$f^i = \sum_{j=1}^N x_j^i \frac{a_j}{x_j^i + \phi_j} \quad (22)$$

where

$$\phi_j = \sum_{k=1, k \neq i}^n \frac{B_f a_j}{\sum_{m=1}^N a_m} = (n-1) \frac{B_f a_j}{\sum_{m=1}^N a_m}$$

The problem in Eq. (21) becomes

$$\begin{aligned} &\text{maximize } f^i \\ &\text{subject to } \sum_{j=1}^N x_j^i = B_f, \quad i = 1, 2, \dots, n \end{aligned}$$

Now, we define the vector  $x = [x_1^i, x_2^i, \dots, x_N^i]^\top$  which constitutes the points for which we want to find an extremizer point. Let  $h(x) = \sum_{j=1}^N x_j^i - B_f$ . The gradient of  $f^i$  with respect to  $x$  is equal to

$$\nabla f^i(x) = \left[ \frac{\partial f^i}{\partial x_1^i}, \frac{\partial f^i}{\partial x_2^i}, \dots, \frac{\partial f^i}{\partial x_N^i} \right]^\top$$

$$\nabla f^i(x) = \left[ \frac{a_1 \phi_1}{(x_1^i + \phi_1)^2}, \frac{a_2 \phi_2}{(x_2^i + \phi_2)^2}, \dots, \frac{a_N \phi_N}{(x_N^i + \phi_N)^2} \right]^\top$$

Also,  $\partial h / \partial x_j^i = 1$  for all  $j = 1, 2, \dots, N$ . Let  $\lambda^*$  be the Lagrange multiplier for this constrained optimization problem. Then, we have to solve the following set of equations for  $x_j^i > 0$ :

$$\frac{a_1 \phi_1}{(x_1^i + \phi_1)^2} + \lambda^* = 0$$

⋮

$$\frac{a_N \phi_N}{(x_N^i + \phi_N)^2} + \lambda^* = 0$$

$$x_1^i + x_2^i + \dots + x_N^i = B_f$$

For any  $\bar{i}, \bar{j} = 1, 2, \dots, N$  we have from the previous equations that

$$\frac{a_{\bar{i}} \phi_{\bar{i}}}{(x_{\bar{i}}^{i*} + \phi_{\bar{i}})^2} = \frac{a_{\bar{j}} \phi_{\bar{j}}}{(x_{\bar{j}}^{i*} + \phi_{\bar{j}})^2}$$

Using Eq. (22),

$$\frac{a_{\bar{i}}^2}{(x_{\bar{i}}^{i*} \sum_{m=1}^N a_m + B_f a_{\bar{i}} (n-1))^2} = \frac{a_{\bar{j}}^2}{(x_{\bar{j}}^{i*} \sum_{m=1}^N a_m + B_f a_{\bar{j}} (n-1))^2}$$

Since  $a_j > 0$  and  $x_j^i > 0$ ,  $j = 1, 2, \dots, N$ ,  $i = 1, 2, \dots, n$ , and  $n > 1$ ,

$$a_{\bar{i}} \left( x_{\bar{j}}^{i*} \sum_{m=1}^N a_m + B_f a_{\bar{j}} (n-1) \right) = a_{\bar{j}} \left( x_{\bar{i}}^{i*} \sum_{m=1}^N a_m + B_f a_{\bar{i}} (n-1) \right)$$

Simplifying, we get that for all  $\bar{i}, \bar{j} = 1, 2, \dots, N$ ,

$$a_{\bar{i}} x_{\bar{j}}^{i*} = a_{\bar{j}} x_{\bar{i}}^{i*}$$

After some algebraic manipulations, this implies that for all  $\bar{i} = 1, 2, \dots, N$ ,

$$x_{\bar{i}}^{i*} = \frac{B_f a_{\bar{i}}}{\sum_{m=1}^N a_m} \quad (23)$$

In order to see that  $x_{\bar{i}}^{i*}$  defined in Eq. (23) is a local maximum we need to prove the second order sufficiency condition. For that, we need to analyze the Hessian of  $f^i$  (because the Hessian of  $h(x)$  is 0). In this case,

$$\nabla^2 f^i(x) = \begin{bmatrix} \frac{-2a_1 \phi_1}{(x_1^i + \phi_1)^3} & 0 & \dots & 0 \\ 0 & \frac{-2a_2 \phi_2}{(x_2^i + \phi_2)^3} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \frac{-2a_N \phi_N}{(x_N^i + \phi_N)^3} \end{bmatrix}$$

It is clear that the Hessian of  $f^i(x)$  for  $x_j^i, j = 1, 2, \dots, N$ ,  $i = 1, 2, \dots, n$ , in Eq. (23) is negative definite since  $a_j > 0$ ,  $x_j > 0$ ,  $n > 1$  and  $\phi_j > 0$ ,  $j = 1, 2, \dots, N$ . Therefore we can conclude that the extremizer points defined in Eq. (23) are global maximizers (because it is clear that the cost function is convex on the simplex  $\Delta_x$ ). Hence,  $x_j^{i*}$  defined by Eq. (23) (which is equivalent to Eq. (13)) is a strict Nash equilibrium. Also, since it is a strict Nash equilibrium, Eq. (8) holds. Therefore, the IFD is a *one-stable* ESS for the finite population in a game against the field.

## A.2. Proof of Theorem 3.2

As in the case for the proof of Theorem 3.1,  $x_j > 0$  is an inactive constraint so it can be ignored. Let  $h(x) = \sum_{j=1}^N x_j - B_f$ . For this case, we will have that the gradient of  $h(x)$  is equal to

$$\nabla h(x) = [1, 1, \dots, 1]^\top$$

and the gradient for  $J(x)$  is given by

$$\nabla J(x) = \left[ \frac{2x_1}{B_f a_1}, \frac{2x_2}{B_f a_2}, \dots, \frac{2x_N}{B_f a_N} \right]^\top$$

Let  $\lambda^*$  be the Lagrange multiplier for this constrained optimization problem. Then, we have to solve the following set of equations for  $x_j > 0$ :

$$\frac{2x_1^*}{B_f a_1} + \lambda^* = 0$$

⋮

$$\frac{2x_N^*}{B_f a_N} + \lambda^* = 0$$

$$x_1^* + x_2^* + \dots + x_N^* = B_f$$

As in the proof of Theorem 3.1 this implies that

$$a_k x_j^* = a_j x_k^*$$

for all  $j, k = 1, 2, \dots, N$ , which implies that

$$x_j^* = \frac{B_f a_j}{\sum_{j=1}^N a_j} \quad (24)$$

In order to see that  $x_j^*$  defined in Eq. (24) is a local minimum we need to prove the second order sufficiency condition. For that, we need to analyze the Hessian of  $J$  (because the Hessian of  $h(x)$  is 0).

In this case,

$$\nabla^2 J(x^*) = \begin{bmatrix} \frac{2}{B_f a_1} & 0 & \dots & 0 \\ 0 & \frac{2}{B_f a_2} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \frac{2}{B_f a_N} \end{bmatrix}$$

Since,  $B_f > 0$  and  $a_j > 0$ ,  $j=1,2,\dots,N$ ,  $\nabla^2 J(x^*)$  is positive definite, which implies by the second-order sufficient condition that  $x_j^*$  in Eq. (24) is a local minimizer. However, we know that the cost function  $J$  is defined over a simplex  $\Delta_x$ , which is nonempty, convex, and a closed subset of  $\mathbb{R}^N$ . Using this fact, and since the Hessian of  $J(x^*)$  is positive definite, we can conclude that the local minimum in Eq. (24) is also global (Bertsekas, 1995).

### A.3. Proof of Theorem 3.3

From an optimization point of view, the problem that we want to solve is the same as

$$\begin{aligned} & \text{maximize } f^i \\ & \text{subject to } \sum_{j=1}^N x_j^i = B_f, \quad i = 1, 2, \dots, n \\ & \quad x_j^i > 0, \quad j = 1, 2, \dots, N \\ & \quad x_j^i = \frac{n B_f a_j}{\sum_{j=1}^N a_j} - \sum_{k=1, k \neq i}^n x_j^k, \quad \bar{i} \neq i \end{aligned} \quad (25)$$

Let  $h(x) = \sum_{j=1}^N x_j^i - B_f$ , and since  $x_j^i > 0$  that constraint is inactive, so it can be ignored. Using Lagrange multipliers, we need to find first the gradient of the cost function and the gradient of the constraint. In this case, we have

$$\nabla f^i = \left[ \frac{\partial f^i}{\partial x_1^i}, \frac{\partial f^i}{\partial x_2^i}, \dots, \frac{\partial f^i}{\partial x_N^i} \right]^T$$

where

$$\frac{\partial f^i}{\partial x_j^i} = \frac{a_j \sum_{k=1, k \neq i}^n x_j^k}{(x_j^i + \sum_{k=1, k \neq i}^n x_j^k)^2}$$

The gradient of  $h(x)$  is  $\nabla h(x) = [1, 1, \dots, 1]^T$ . Therefore, we have to solve the following set of equations for  $x_j^{i*} > 0$ :

$$\frac{a_1 \sum_{k=1, k \neq i}^n x_1^k}{(x_1^{i*} + \sum_{k=1, k \neq i}^n x_1^k)^2} + \lambda^* = 0$$

$\vdots$

$$\frac{a_N \sum_{k=1, k \neq i}^n x_N^k}{(x_N^{i*} + \sum_{k=1, k \neq i}^n x_N^k)^2} + \lambda^* = 0$$

$$x_1^{i*} + x_2^{i*} + \dots + x_N^{i*} = B_f$$

Then, for any  $\bar{i}, j = 1, 2, \dots, N$ ,

$$\frac{a_{\bar{i}} \sum_{k=1, k \neq \bar{i}}^n x_{\bar{i}}^k}{(x_{\bar{i}}^{i*} + \sum_{k=1, k \neq \bar{i}}^n x_{\bar{i}}^k)^2} = \frac{a_j \sum_{k=1, k \neq i}^n x_j^k}{(x_j^{i*} + \sum_{k=1, k \neq i}^n x_j^k)^2}$$

Replacing the constraint in Eq. (25),

$$a_{\bar{i}} \left( \frac{n P a_{\bar{i}}}{\sum_{j=1}^N a_j} - x_{\bar{i}}^{i*} \right) \frac{n^2 B_f^2 a_{\bar{i}}^2}{(\sum_{j=1}^N a_j)^2} = a_j \left( \frac{n P a_j}{\sum_{j=1}^N a_j} - x_j^{i*} \right) \frac{n^2 B_f^2 a_j^2}{(\sum_{j=1}^N a_j)^2}$$

which implies that

$$a_j x_j^{i*} = a_{\bar{i}} x_{\bar{i}}^{i*}$$

$$x_j^{i*} = \frac{a_j B_f}{\sum_{j=1}^N a_j} \quad (26)$$

The point in Eq. (26) is an extremizer for the optimization problem defined in (25). Now, let us prove that (26) is indeed a global maximizer for this problem. For that, we need to analyze only the Hessian of our cost function because  $\nabla^2 h(x) = 0$ . That is,

$$\nabla^2 f^i(x^*) = \begin{bmatrix} \frac{-2a_1 \sum_{k=1, k \neq i}^n x_1^k}{(x_1^{i*} + \sum_{k=1, k \neq i}^n x_1^k)^3} & & 0 \\ & \ddots & \\ 0 & & \frac{-2a_N \sum_{k=1, k \neq i}^n x_N^k}{(x_N^{i*} + \sum_{k=1, k \neq i}^n x_N^k)^3} \end{bmatrix}$$

Clearly, since  $a_j > 0$ ,  $B_f > 0$ ,  $x_j^{i*} > 0$ ,  $\sum_{k=1, k \neq i}^n x_k^{i*} > 0$ , and  $n > 1$ , the Hessian is negative definite. Therefore we can conclude that the extremizer points defined in Eq. (26) are global maximizers (because it is clear that the cost function is convex on the simplex  $\Delta_x$ ).

Replacing the optimum point, we can notice that the constraint becomes  $x_j^i = n B_f a_j / \sum_{j=1}^N a_j - \sum_{k=1, k \neq i}^n x_j^k$  that is equivalent to Eq. (19).

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