

The adaptive value of inactive foragers and the scout-recruit system in honey bee (*Apis mellifera*) colonies

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In honey bee (*Apis mellifera*) colonies, scouts search for productive forage sites and then recruit other workers to those locations using a waggle dance. A simple and tractable mathematical model of the honey bee scout-recruit system was developed to study the relationship between nectar availability, the efficiency of the honey bee's recruitment system, and the optimal proportion of scouts that maximizes net gain (benefit – cost), or, energetic efficiency (benefit/cost – 1). The models consider both the energetic costs and benefits of active scouts and recruits as well as the cost of an inactive forager reserve. They predict conditions when individual foraging is favored over the honey bee's recruitment system, when the colony should abandon foraging altogether, and the optimal proportion of scouts (when the scout-recruit system is favored). The models' predictions qualitatively match empirical data. Surprisingly, previous empirical data from the honey bee suggest that recruits' costs are greater than scouts'—recruits spend significantly longer searching for a forage patch than do scouts—thereby causing researchers to rethink how the scout-recruit system might be adaptive. Using average returns, the models demonstrate how the scout-recruit system is adaptive despite these apparent higher recruit costs relative to the scouts'. A sensitivity analysis demonstrates that the results are robust to a broad range of relative costs of active workers, inactive workers, and the energetic benefits of the forage. Consequently, the model is demonstrated to be relevant to many insect societies that employ a scout-recruit system. *Key words:* foraging, honey bee, inactives, recruits, reserve foragers, scouts. [*Behav Ecol* 12:111–119 (2001)]

Charles Elton once remarked that “All cold-blooded animals spend an unexpectedly large proportion of their time doing nothing at all, or at any rate, nothing in particular.” This is confirmed by comparative studies of vertebrates (Herbers, 1981) and, surprisingly, also appears true of social insects (Schmid-Hempel, 1990), individuals that are commonly associated with a high rate of activity. Contrary to popular belief, the simile “as busy as a bee” is misleading; Lindauer (1961) and colleagues followed a single honey bee throughout its life and showed that the bee “loafed” 40% of the time (70/177 h). More detailed studies (Seeley, 1995) confirm an unexpectedly high rate of inactivity in honey bees, especially for the younger non-foraging bees, with about 30% of all bees resting at any given moment (Seeley TD, personal communication; Winston, 1987).

Honey bees will forage as far as 11 km from their nest (Seeley, 1995; Visscher and Seeley, 1982) and so these resources are clearly very valuable to the colony. Why then aren't any workers who are not involved in intranidal tasks contributing to the foraging process? Some evidence (reviewed in Schmid-Hempel, 1991; but see Visscher and Dukas, 1997) suggests that honey bees have a limited lifetime energy budget, equivalent to around 800 km of flying (Gould and Gould, 1988). Because flying is so energetic (Schmid-Hempel et al., 1985; Wolf and Schmid-Hempel, 1990; Wolf et al., 1989), by conserving their efforts and only flying to known productive patches—the good sites found by scouts—recruits can lead longer and more productive lives maximizing their lifetime work contribution to the colony (Jeanne's [1986] “demo-

graphic advantage”). This idea is supported by Sekiguchi and Sakagami's (1966) findings that a considerable number of bees do not forage, or only rarely so, and that their stimulation threshold for dances and food odors is high. Thus, these bees may serve as a backup foraging force in times of “great field mortality or opportunity” (Michener, 1974).

Honey bee foragers face an additional problem to the high energetic expense of collecting nectar: the volatile nature of nectar availability and dispersion. For instance, in the space of a few days, conditions may change from nectar dearth to nectar flow (e.g., Seeley, 1995: Figure 2.15). Seasonal changes, climate, and competition can all play their part to make nectar collection, and importantly, any planning on the part of the colony, difficult. Clearly, a colony shouldn't have its foragers sitting idle in the nest when forage is available. However, because flying is so energetic there is also little point in having a large active forager force expending lots of energy flying to different potential forage sites when there is little or no forage at hand. A colony requires sufficient scouts to monitor nectar availability and ensure that quality sites are found but that scouting force should not be so large that collectors are limiting when good sites have been found. The question considered in this study is what proportion of the foraging force should scout for food, and thus how many should remain in the nest both conserving energy and acting as a recruitment pool?

In this study I present a simple and tractable model of active (scouts) and inactive (reserve) foragers in an insect society. The model is used to study the relationships between nectar availability, the efficiency of the recruitment system, and the optimal proportion of scouts. The model considers maximization of two currencies that honey bees may use: net gain and energetic efficiency (Schmid-Hempel et al., 1993; Seeley, 1994, 1995). For clarity the model refers to a population of honey bee foragers but it should be stressed this is used solely as an illustrative example; the model's assumptions and con-

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clusions should apply equally well to many other insect societies that employ a scout-recruit system. Finally, empirical data show, contrary to expectations, that time spent searching for a forage patch is higher for recruits than scouts (138 versus 85 min respectively, Seeley, 1983; 121 versus 82 min, Seeley and Visscher, 1988). These counter-intuitive results have caused researchers to reconsider how the bees' scout-recruit system is adaptive. Seeley (1983) suggested that consideration of average returns may clarify these perplexing findings. This is the approach adopted in this study and one of its main objectives.

THE MODELS

Introduction

The model considers the energetics of honey bee scouts, recruits, and unemployed foragers during a single foraging bout. Initially, a "bout" is taken to be sufficiently long so that a scout can find a site, recruit others to it, and that those recruits locate the patch. Later, longer timescales are considered. Notation is summarized in Appendix A.

I consider a population of N honey bee nectar foragers. Some proportion of these, $s \in (0,1]$, are scouts that leave the nest at the start of the bout while the remainder are unemployed foragers that remain in the nest and serve as potential recruits. Each scout searches independently for forage, and it is assumed that each can check one "forage site," such as an area of clover or heather, which may contain sufficient nectar for several foragers to exploit simultaneously. That is, each forage site may contain several "forage patches" where each patch contains sufficient forage for only a single forager to exploit. There is some probability, p , that the site contains forage, and if so, then its quality (the number of patches) is $\langle q \rangle$, the mean of some distribution $q(\cdot)$.

It is assumed that a "successful" scout, that is, one that finds a productive site, makes some heuristic judgement of the site quality and returns to the nest to recruit the appropriate number of foragers ($\langle q \rangle - 1$). This is akin to assuming that the scout's dance duration is proportional to site quality (with appropriate limits) which is roughly true of honey bees (Seeley, 1995). Unsuccessful scouts continue to search their site in vain for the rest of the foraging bout. Unemployed foragers respond to recruiting scouts and attempt to locate the advertised site. However, recruitment is not perfect. I assume that, on average, a recruit returns with a reduced load of nectar defined by a parameter $\alpha \in (0,1]$. The justification is that honey bee recruits take several trips to find the advertised forage patches (Seeley, 1983, 1995; Seeley and Visscher, 1988; see parameterization section). That is, each recruit makes several unsuccessful trips, each time returning to the nest unladen, before she finds the advertised site and returns with a single full nectar load.

At the end of the bout, four categories of workers are recognized:

1. *Successful scout*—a scout that found a productive site and returned with a load (1 unit) of nectar;
2. *Unsuccessful scout*—a scout that failed to find a productive site and returned without nectar;
3. *Recruited worker*—a worker that was recruited to a productive site and returned with some (α units of) nectar;
4. *Inactive worker*—an unemployed forager that remained in the nest throughout the foraging bout.

(Unsuccessful recruits that failed to find the advertised patch are taken into account through the parameter α .) The proportions of these four worker types are denoted f_s , f_u , f_r , and f_i respectively and sum to 1.

Energetic payoff

Model I: maximization of net gain

At the end of the bout the colony's energetic gains and losses (in Watts) are calculated for the four worker groups. Because I use an average-return approach and only consider the average nest-forage site distance it is convenient to work in Watts rather than absolute return (Joules). Model I assumes that the colony's maximand is net gain (benefit - cost). I assume that inactive workers cost the colony E_i Watts through metabolic costs. Foraging is a more costly activity because of the high energetic costs of flying, and so an unsuccessful scout costs the colony E_a Watts, where $E_a > E_i$. A successful scout however, returns with a full load of nectar worth F Watts (where $F > E_a$ and F takes into account the duration of the foraging trip) but also incurs the metabolic costs of flying (E_a) and so its net gain is $F - E_a$ Watts. A recruited worker incurs the costs of flying but requires several unsuccessful trips (on average; see parameterization section) each costing E_a Watts, before she finds the advertised site and gains F Watts from a nectar load. Thus, at the end of an average trip, she returns with a smaller reward, αF , and so her net gain is $\alpha F - E_a$ Watts.

The colony's net gain (payoff) per second per capita ($r(s)$) for some proportion of scouts is:

$$r(s) = f_s(F - E_a) + f_u(-E_a) + f_r(\alpha F - E_a) + f_i(-E_i) \\ = F(f_s + \alpha f_r) - E_a(1 - f_i) - E_i f_i. \quad (1)$$

The parameter p and the distribution $q(\cdot)$, which has mean $\langle q \rangle$, define the environment. Thus, for a given environment $\{p, q(\cdot)\}$ we can determine the following average proportions of each of the four workers:

$$f_s = ps, \\ f_u = (1 - p)s, \\ f_r = \min\{ps(\langle q \rangle - 1), 1 - s\}, \\ f_i = 1 - s - \min\{ps(\langle q \rangle - 1), 1 - s\}, \quad (2)$$

which can be substituted into Equation 1 above to obtain the colony's per capita payoff (Appendix B).

Model II: maximization of energetic efficiency

There is some evidence (Seeley, 1994, 1995) that honey bees may not always maximize net gain but a different currency, net energetic efficiency, the maximand in model II. Energetic efficiency is the marginal benefit (benefit - cost) divided by the cost, or, alternatively (benefit/cost) - 1. In both models I and II, the average benefit is $F(f_s + \alpha f_r)$ and the cost is $E_a(1 - f_i) + E_i f_i$. Thus, with this new currency the colony's payoff, now denoted $r'(s)$, is:

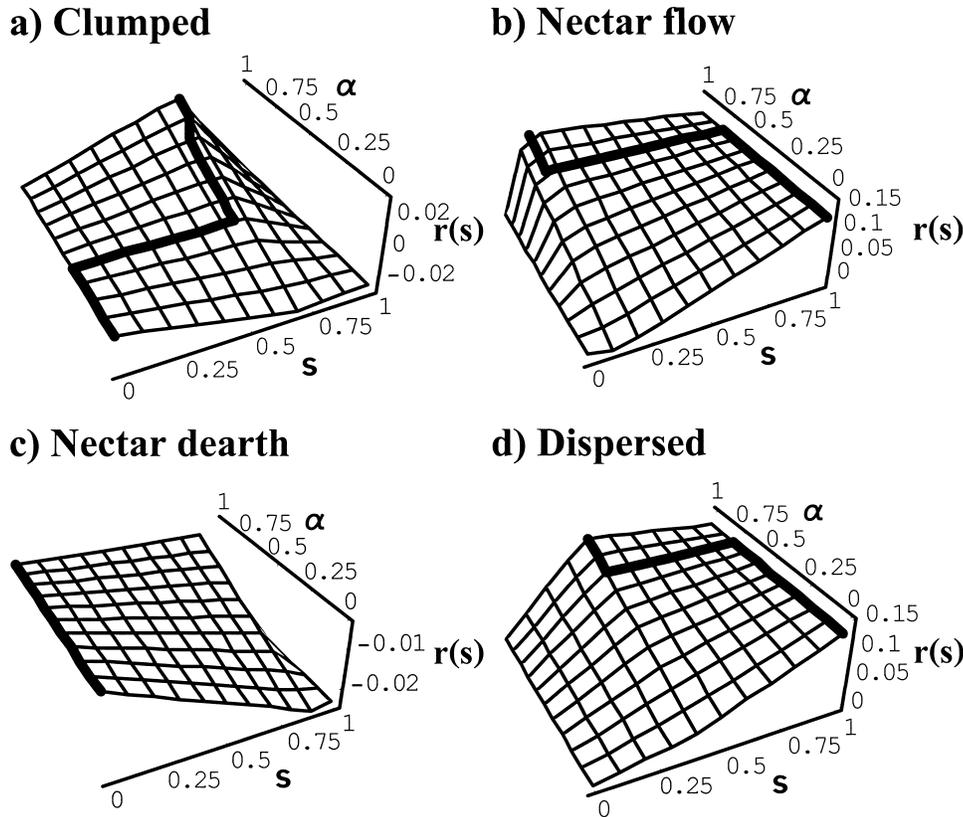
$$r'(s) = F(f_s + \alpha f_r) / (E_a(1 - f_i) + E_i f_i) - 1. \quad (3)$$

The average proportions f_s , f_u , f_r , and f_i are unchanged from Equation 2 and so can be substituted into Equation 3 to obtain the final payoff (Appendix B).

Parameterization

The model was parameterized as follows:

- a. $E_i = 0.42 \times 10^{-2}$ Watts and $E_a = 3.36 \times 10^{-2}$ Watts (Schmid-Hempel et al., 1985:63).
- b. $F = 0.196$ Watts, resulting from a crude assumption that a load of nectar, upon arrival at the nest, has an energetic value of 552 J (55 flowers \times 10.05 J / flower; Schmid-Hempel et al., 1985), and that an average foraging trip takes 47

**Figure 1**

Per capita payoffs—in the form of net gain ($r(s)$): benefit – cost—against recruitment efficiency (α) and proportion of scouts (s) for various combinations of probabilities of finding a patch of food (p) and the quality of productive patches ($\langle q \rangle$). The thick black line in each figure indicates the optimal proportion of scouts that maximizes payoff against recruitment efficiency. (a) Clumped dispersion of food ($p = .05$; $\langle q \rangle = 10$); (b) nectar flow ($p = .8$; $\langle q \rangle = 10$); (c) nectar dearth ($p = .05$; $\langle q \rangle = 3$); and (d) many small flower-patches ($p = .8$; $\langle q \rangle = 3$).

min (Anderson, 1998). This gives an energetic return of 0.196 J for each second of the foraging trip.

- c. $\alpha = 0.25$. Seeley (1995:126) reports that “on average, a bee will need to make approximately four tries, that is, conduct some four dance-guided searches, to locate a flower patch advertised by a dancer.” Earlier studies reported 4.8 ± 3.2 trips (range 1–12, $n = 20$; Seeley, 1983) and 4.1 ± 2.8 trips (range 1–12, $n = 44$; Seeley and Visscher, 1988). In the results section, α is varied from 0.1 to 1.

No values for p and $\langle q \rangle$ were estimated but they are both explored over a broad range. Because analysis of these models is in the form of a per capita payoff, the payoffs are independent of the size of the foraging population size, N .

Limitations of the models

I assume an unchanging resource distribution (constant p) and make no attempt to model daily or seasonal variations in the forage distribution, any renewal processes, or competition from other colonies. Although honey bees do face these factors, they are not relevant on the timescale of these models, a single foraging bout, because the probability of encountering a profitable site is unlikely to change.

In these models the probability of locating a patch, p , is independent of the mean quality of the patch, $\langle q \rangle$, which is not always the case in nature. However, as Jaffe and Deneubourg (1992) highlight in a similar model, it does stress the fact that the size of the forage sites is much smaller than the total forage area. For instance, Visscher and Seeley (1982) calculated that the circle encompassing 95% of their bees’ foraging sites had a radius of 6 km (Area 113 km²), and so each patch of flowers represents a tiny proportion of this range.

I assume that all bees are equal in terms of weight, crop size, searching ability, and so on, and that each patch is equi-

distant from the nest. As this model is analyzed only in terms of average payoffs, these results are not affected by these assumptions. These assumptions do, however, prevent analysis of a third possible currency that bees may use: rate of food collection (net gain/time).

Last, the models consider the optimal way to employ N foragers as scouts or potential recruits to maximize one of two currencies. Under natural conditions, N is expected to vary in response to colony needs and conditions, such as the amount of stored nectar (Schmid-Hempel et al., 1993; Seeley, 1995), and colonies may switch between different maximizing currencies during the year (Seeley, 1994, 1995). These other factors were not incorporated into the model.

RESULTS

Model I: maximization of net gain

Figure 1 shows per capita payoff (r), in the form of net gain, against proportion of recruits (s) and recruitment efficiency (α) for four environments. The thick black line in each figure represents the optimal strategy—the proportion of scouts, s^* , that maximizes payoff—against recruitment efficiency.

Clumped food dispersion

When food is clumped ($p = .05$, $\langle q \rangle = 10$; Figure 1a) two distinct optimal regimes are observed. First, the sparseness of patches (low p) combined with low recruitment efficiency mean that net gain is negative, for all s , and the colony’s best strategy is to minimize its losses and remain in the colony (i.e., $s^* = 0$). However, there appears to be a threshold at $\alpha = 0.4$ above which the scout-recruit system is favored—the few good sites found by scouts can be exploited well by recruits—and s^* remains fairly constant at around 0.7.

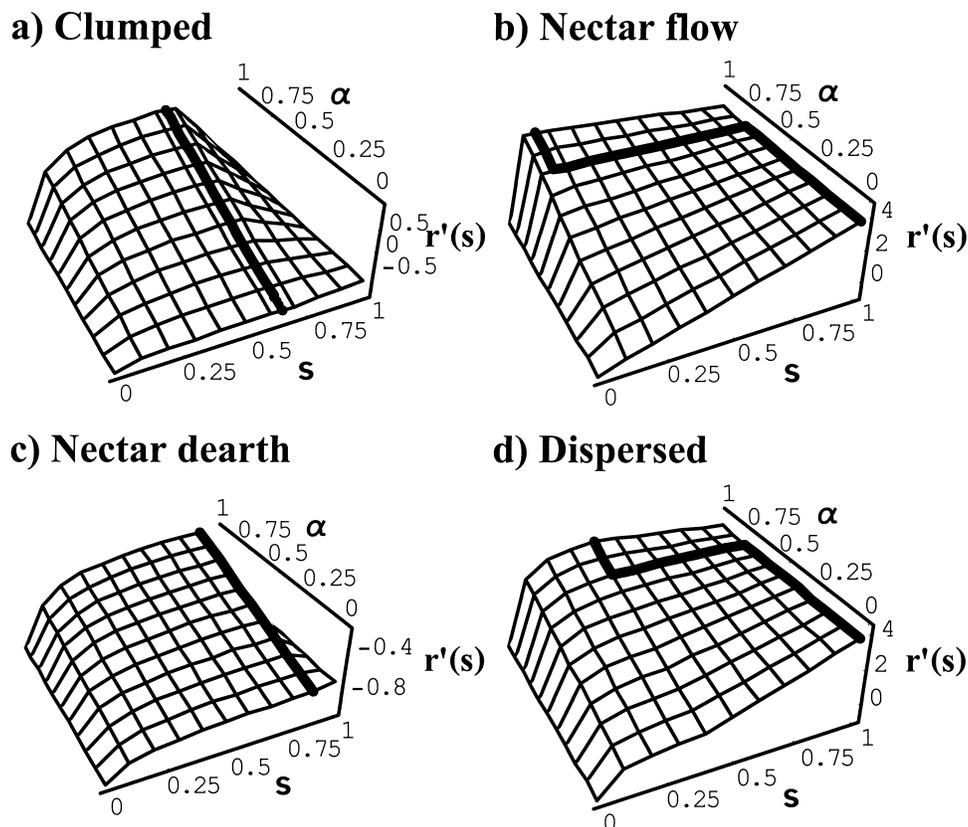


Figure 2
As in Figure 1 but with payoff in the form of energetic efficiency ($r'(s)$): net gain/cost.

Nectar flow

During nectar flow (high p , large $\langle q \rangle$; Figure 1b) two optimal regimes are also observed. When recruitment efficiency is low, *all* foragers should scout: most scouts will find productive sites, a return of $F - E_a$, which will cover the costs ($-E_a$) of the few unsuccessful scouts. However, with high recruitment efficiency only about 15% of the colony should scout because the recruits will exploit these large and profitable sites well.

Nectar dearth

During nectar dearth (low p ; small $\langle q \rangle$; Figure 1c) sites are both scarce and poor. The colony can at best minimize its costs by remaining in the nest—thus, $s^* = 0$ for all α —and drawing off its honey reserves as would occur during overwintering.

Many small flower-patches

Figure 1d shows net gain when productive sites are abundant ($p = .8$) but small ($\langle q \rangle = 3$). As in nectar flow when recruitment efficiency is low (Figure 1b), the colony should send out many scouts, but as recruitment efficiency increases the colony should keep some workers as inactive workers ready for recruitment. In general, the quality of the environment can be roughly summarized by the product $p\langle q \rangle$, the total amount of food in all the patches, and different environments with similar values of $p\langle q \rangle$ tend to exhibit similar payoff surfaces.

Model II: Maximization of energetic efficiency

Figure 2 repeats the results from Figure 1 using the new currency, energetic efficiency. The results are surprisingly similar, particularly when a broad variety of environments are considered (Figure 3). For many environments the predictions of the two models, the proportion of scouts that maximizes payoff, for either currency, are virtually identical (Figure 3). Fig-

ure 2 highlights two environments in which this is not the case. With a clumped food dispersion and low recruitment efficiency (Figure 1a versus Figure 2a) energetic efficiency favors some scouting while this is not so when net gain is considered—the cause of this difference is not clear. During nectar dearth (Figure 1c versus Figure 2c) there is a large difference in the models' predictions—net gain favors abandonment of foraging while energetic efficiency favors scouting (Figure 3). The cause of this difference is discussed later.

Multiple trips to a patch

So far, the models consider payoff for single foraging bouts. But, once a recruit has located a profitable patch it will most likely make multiple trips to that patch (e.g., Seeley and Visscher, 1988; Figure 1). A honey bee recruit takes four dance-guided trips, on average, to initially find the advertised patch ($\alpha = 1/4$) and so its average net gain for those four trips is $\alpha F - E_a = F/4 - E_a$. However, once she has located the patch, on subsequent trips she will fly directly to that patch, collect a full load of nectar, and so receive a net gain of $F - E_a$ for the trip. Therefore, subsequent successful trips increase a recruit's effective recruitment efficiency, denoted α' . Effective recruitment efficiency reflects the average nectar gain for *all* the trips that a recruit makes to a particular patch. It is a weighted average of recruitment efficiency α (for the first $1/\alpha$ trips), and a recruitment efficiency of one for the full nectar loads for all (m) subsequent trips:

$$\alpha' = \frac{\frac{1}{\alpha} \times \alpha}{m + \frac{1}{\alpha}} + \frac{m \times 1}{m + \frac{1}{\alpha}} = \frac{\alpha(m+1)}{\alpha m + 1}. \quad (4)$$

Provided $\alpha < 1$, multiple trips to a profitable patch will always

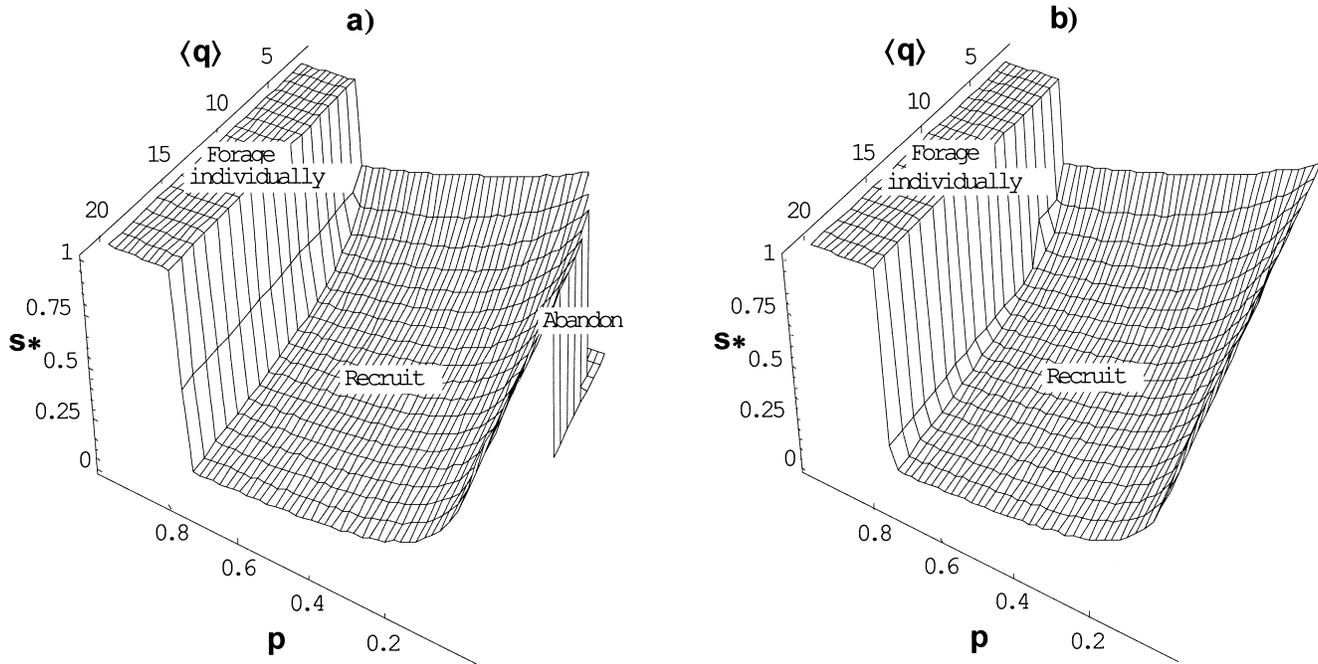


Figure 3
 Effect of nectar abundance (probability a site contains nectar, p , and quality of site, $[q]$) on optimal proportion of scouts (s^*) that maximizes (a) net gain, and (b) energetic efficiency. In (a), the surface is partitioned into three sections. When conditions are very poor (low p and $[q]$), the colony should abandon foraging (the low rightmost section). With better conditions (the central section), the colony should use its recruitment system. s^* decreases with increasing environmental quality, either in terms of p or $[q]$. When the probability a scout will find a productive patch is higher than the recruitment efficiency ($p > \alpha$) then the colony's foragers should forage individually (the highest sections). To maximize energetic efficiency (b) the colony should continue to forage even in very poor conditions.

increase a forager's effective recruitment efficiency and thus her average payoff. But by how much? Rearranging Equation 4 gives the number of subsequent trips which gives rise to a particular value of α' :

$$m = (\alpha' - \alpha) / \alpha(1 - \alpha'). \quad (5)$$

Table 1 shows values of m for $\alpha' \in \{0.5, 0.75, 0.9, 0.95\}$. The third column illustrates the number of subsequent trips needed to produce the effective recruitment efficiencies in column 1 with $\alpha = 1/4$. Only two subsequent trips doubles effective recruitment efficiency from $1/4$ to $1/2$. Only eight subsequent trips increase the payoff from $F/4 - E_a$ to $3F/4 - E_p$, that is, from 0.013 W to 0.111 W, more than an eight-fold increase. In good conditions, foraging trips can be short, so it is not unreasonable for a single bee to make many trips to the same foraging site during a day. For instance, Park (1928) reports a mean of 13.5 (maximum of 24) trips per day during heavy

nectar flow. Thus, under the right conditions, honey bees can readily achieve an effective recruitment efficiency of 0.9, or higher.

In themselves these results are not particularly surprising: recruits that miss the advertised patch on their first few attempts will increase their average return by making multiple trips to the patch. The significance of the results can be appreciated if we return to the payoff surfaces in Figure 1. Except where the colony's payoff is negative (Figure 1c), the proportion of scouts at which the maximum payoff is reaped is generally lower with higher recruitment efficiency, at least for the conditions pertinent to the honey bee, that is, $\alpha = 0.25$ vs. $\alpha' \geq 0.9$. (These results have been explored over a wider range of conditions than shown in Figure 1.) In short, multiple return trips to a forage site favor a smaller proportion of scouts and so greater forager inactivity. Not only will this increase net gain or energetic efficiency but there are additional adaptive benefits which are discussed later.

Table 1
 The relationship between recruitment efficiency, α , and effective recruitment efficiency, α' when a recruit makes m repeat trips to a profitable food patch (Equation 5)

| α' | Number of repeat trips, m | |
|-----------|-----------------------------|----------------|
| | α unspecified | $\alpha = 1/4$ |
| 0.5 | $1/\alpha - 2$ | 2 |
| 0.75 | $3/\alpha - 4$ | 8 |
| 0.9 | $9/\alpha - 10$ | 26 |
| 0.95 | $19/\alpha - 20$ | 56 |

Column three shows the number of trips to reach various levels of α' when $\alpha = 1/4$. For instance, only eight return trips to a patch will raise the recruitment efficiency from $1/4$ to $3/4$.

Environment-dependent optimal strategies

Figure 3a shows the optimal proportion of scouts (s^*) that maximizes net gain against p and $[q]$. (Effective recruitment efficiency is fixed at 0.8, a value reflecting the honey bee's low recruitment efficiency ($\alpha = 1/4$) but with multiple return trips.) The surface is partitioned into three sections. The smallest and lowest (rightmost) section in Figure 3a shows that during nectar dearth, (p and $[q]$ both low), the colony can only lose energy and so at best minimize its losses by abandoning foraging. With more productive environments, the central section, colonies should use their recruitment system and send out scouts. Importantly, the curvature of this central subsurface indicates that as forage quality increases, whether in terms of site quality (y-axis) or proportion of productive

Table 2

The optimal proportion of scouts, s^* , that maximizes (1) net gain, or, (2) energetic efficiency, when the relative values of F , E_a , and E_i are varied

| (1) Net gain | | | | (2) Energetic efficiency | | | |
|-------------------------|-------|------------------------|-------|--------------------------|-------|------------------------|-------|
| $E_a = cE_i, F = 47E_i$ | | $F = cE_i, E_a = 8E_i$ | | $E_a = cE_i, F = 47E_i$ | | $F = cE_i, E_a = 8E_i$ | |
| Range of c | s^* | Range of c | s^* | Range of c | s^* | Range of c | s^* |
| High quality | | | | | | | |
| 1–24 | 0.19 | ≤9 | 0 | 1–3 | 0.19 | All | 0.18 |
| 25–35 | 0.18 | 10–13 | 0.18 | ≥4 | 0.18 | | |
| ≥36 | 0 | ≥14 | 0.19 | | | | |
| Low quality | | | | | | | |
| 1–13 | 0.69 | 1–24 | 0 | 1–15 | 0.69 | All | 0.69 |
| 14 | 0.68 | 25–26 | 0.68 | ≥16 | 0.68 | | |
| ≥15 | 0 | ≥27 | 0.69 | | | | |

These results demonstrate the robustness of the models' predictions, and are shown for two environments: a high quality environment ($p = .05, \langle q \rangle = 10$), and a lower quality environment ($p = .05, \langle q \rangle = 10$). First, E_a is varied as some integer multiple, c , of E_i with F fixed (i.e., $E_a = cE_i, F = 47E_i$). Second, F is varied with E_a fixed (i.e. $F = cE_i, E_a = 8E_i$).

sites (x-axis), then the colony should send out a smaller proportion of scouts. Finally, when the probability of finding a productive forage site is greater than recruitment efficiency ($p > \alpha'$; highest and leftmost section of Figure 3a) then the colony should abandon its recruitment system and forage individually.

Figure 3b is as for Figure 3a but with energetic efficiency. Results are similar to those for net gain except that the decision to abandon foraging is absent. Here the colony should always forage if a chance exists of finding food (at least for these particular values of F, E_a, E_i , and α'). The difference between these currencies can be explained by considering payoffs under high costs. With net gain (benefit – cost), the payoff decreases with increasing cost. However, with energetic efficiency (benefit / cost – 1), as costs increase, the first term tends to zero and so payoff tends to a constant, –1.

Sensitivity analysis

It was anticipated that the results of the previous sections would depend strongly on the fact that flying is so much more energetic than inactivity, that is, $E_a \gg E_i$. However, a sensitivity analysis demonstrates that this is not so. The above results are robust for a broad range of values of F and E_a relative to E_i . As an example I show results for two different environments: (1) center of the recruitment section of Figure 3 ($p = 0.5, \langle q \rangle = 10$), and (2) rightmost section of Figure 3 ($p = .05, \langle q \rangle = 10$). Table 2 shows, for both currencies, how the optimal proportion of scouts changes when either E_a or F is varied as some integer multiple, c , of E_i .

When E_a is varied (with fixed F) there is some threshold value above which flying is so costly that the colony should abandon foraging (e.g., when $E_a \geq 36E_i$ for net gain, Table 2). Importantly, there is a very broad range, $c = 1$ –35, at which s^* is unaltered. Similarly, when F is varied there is some threshold value below which the benefit of the nectar load is so low, relative to the costs of collecting it, that the colony should also abandon foraging. However, any value of c above this means that the colony should collect the nectar, and s^* does not vary at all, especially for energetic efficiency in which results are particularly robust.

This robustness is due to the fact that s^* occurs when the number of productive patches found by scouts (minus the number of scouts) matches the number of inactive workers (i.e., $ps[\langle q \rangle - 1] = 1 - s$), and, crucially, this is essentially independent of F, E_a , and E_i . An important implication is that

many of the models' results hold when the costs of collecting the material are not that much greater than inactives. Thus, this model should apply equally well to the scout-recruit system in other groups, such as ants, that do not fly and in which E_a is likely only marginally greater than E_i .

Inactive foragers

Thus far, apart from when there is so little food that the colony should abandoning foraging (Figure 3), inactive workers are always recruited ($f_i = 0$) as part of the optimal strategy. However, there are two situations in nature where this is unlikely to be the case: (1) where the productivity of the environment fluctuates, and (2) where the amount of nectar in the environment is limited.

Fluctuating environment

Suppose that the environment is productive (some positive p and $\langle q \rangle$, as before) with probability β , and unproductive ($p = 0$), with probability $1 - \beta$. In this fluctuating environment, for some fixed strategy $\{s\}$ a colony expects a net gain payoff as in equation 1 with probability β and payoff $-E_a s - E_i(1 - s)$ (Appendix B with $p = 0$) with probability $1 - \beta$. Thus,

$$r(s) = (1 - \beta)[-E_a - E_i(1 - s)] + \beta[F(ps + \alpha \min\{ps(\langle q \rangle - 1), 1 - s\}) - E_a + (E_a - E_i)(1 - s - \min\{ps(\langle q \rangle - 1), 1 - s\})] \tag{6}$$

Some s, s^* , maximizes colony payoff and will be associated with some optimal fraction of inactives (f_i^* , from Equation 2):

$$f_i^* = (1 - \beta)(1 - s^*) + \beta(1 - s^* - \min\{ps^*(\langle q \rangle - 1), 1 - s^*\}). \tag{7}$$

But, at s^* the number of patches the scouts need to recruit for ($ps[\langle q \rangle - 1]$) equals the number of recruits ($1 - s$) and so

$$f_i^* = (1 - \beta)(1 - s^*). \tag{8}$$

With the following parameters values: $F = 0.196; E_a = 0.0336; E_i = 0.0042; \alpha = 0.8; p = .01; \langle q \rangle = 10$, and $\beta = 0.5$, it was found that $s^* = 0.52$ (with a per capita net gain of 0.015). Substituting these latter values into Equation 8 gives $f_i^* = 0.24$. Importantly, this demonstrates that an inactive forager force is adaptive when the environment fluctuates. The reasoning is as follows: for constant environments, when there is

no food the optimal strategy is inactivity, that is, when $p = 0$ then $s^* = 0$. When the environment is productive then there is some positive s^* ; in short, if $p > 0$ then $s^* > 0$. Thus, in a fluctuating environment the colony must come to some compromise, an intermediate and positive value of s^* and so there will be inactive foragers. Interestingly, in very rich environments (high $\langle q \rangle$), s^* will be low in any case (see earlier) and so there is less conflict between s^* in unproductive vs. rich environments.

Limited resources

If resources are limited with less productive patches than foragers (N), the forager excess should remain inactive. They are essentially a burden during poor forage: a set of workers consuming resources but who do not make a foraging contribution. Optimal behavior might be to reassign these inactive workers to other tasks, that is, adjust the size of the forager population. However, these reserve foragers come into their own when there is a sudden burst of nectar productivity (e.g., Seeley, 1995: Figure 2.15) and the nectar they can bring in during these times outweighs their energetic costs during leaner times. That is, these workers are adaptive as part of an optimal strategy for the whole set of foragers on a longer time-scale.

Based on the estimates of F , E_w , and E_r , the net gain of a successful foraging trip is roughly 40 times that of the costs of an inactive worker. Even allowing for a recruitment efficiency of 0.8, a worker only needs to bring in nectar for about 3% of her time to “pay her way.” However, because the foragers in a colony are not just bringing nectar in for themselves but for the rest of the colony and they need to produce a stockpile for the winter, the actual “break even” work proportion will be higher than 3%.

DISCUSSION

I have presented a model of a scout-recruit system that predicts the optimal proportion of foragers that should act as scouts thus leaving the remainder as energy-saving inactives, but who are available as potential recruits. To the best of my knowledge this model is unique in that it considers the energetic return for an insect society from the whole group of foragers, both active and inactive. Results show that the optimal proportion of scouts, based on maximizing either net gain or energetic efficiency, depends strongly on the quality of the environment (p/q) and the ability of recruits to locate a patch advertised through a recruitment dance (α)—the “waggle dance” in the case of honey bees (von Frisch, 1967). In an empirical study, Seeley (1983) found that the proportion of honey bee foragers which found their next forage site through scouting, as opposed to recruitment, was low (5%) in times of rich forage and high (36%) during poor forage. Also, Waddington et al. (1994) found a reduced role of recruitment as part of the overall colony foraging strategy in habitats with abundant small patches of flowers. Both these data qualitatively match the predictions of the current models (Figure 3).

Seeley (1983) and Seeley and Visscher (1988) measured the time that scouts and recruits took to find a forage site. Surprisingly, recruits took significantly longer (60% longer, Seeley, 1983; 47% longer, Seeley and Visscher, 1988) than scouts. This has caused researchers to consider other ways in which the scout-recruit system may be adaptive. Seeley (1983) suggested that an analysis based on average return per forager might clarify this perplexing result. This study adopts such an approach and sheds some light on the matter. On the basis of a single foraging trip, a scout's energetic costs may well be lower than a recruit's costs. Crucially, this is because a recruit that acts upon a waggle dance rarely finds the advertised patch

on its first attempt. On average, they require four (but up to 12) energetically expensive trips before they find the patch and receive a payoff, a nectar load. Thus, these fruitless and expensive trips can cause the search time for a recruit to exceed that of a scout. However, what must be taken into consideration is that once the recruit has located the site she may make many profitable return trips to that site. Considering average returns, multiple trips to a forage patch can then increase a recruit's profitability above that of a scout. Also, waggle dancers can recruit not just one but many recruits to the same site. This will further increase the recruit's return relative to the scout's. Last, scouts are selective in the sites they dance for and they tend to advertise quality sites. These benefits are then passed onto recruits: scouts may encounter both poor and quality sites but recruits are directed to quality forage. All these factors will increase the adaptive value of recruits.

The model predicts that for a variety of environmental conditions an inactive reserve forager force is favored. By increasing demand for comb-building, Kolmes (1985a,b) demonstrated that honey bee colonies do have reserve forces that can be called on without detrimentally affecting performance of other tasks. Thus, honey bee colonies do not fit Oster and Wilson's (1978) idealized “ergonomically efficient” colony organization in which all members are actively tackling tasks. The presence of a reserve forager force in the nest is adaptive at the colony-level (Seeley, 1997) for a variety of reasons. A reserve force acts as a buffer for the fluctuating and unpredictable demand for work because inactive workers in the nest can be recruited to other tasks while scouts out in the field cannot. Inactivity for non-foragers may be important as the workers may spend their energy producing brood food or wax (Lindauer, 1952). Last, a forager uses her own information and experience to decide to abandon a patch when the patch's profitability declines (Anderson and Ratnieks, 1999). Paradoxically, active workers only have knowledge about their current patch whereas inactive workers in the nest are exposed to many workers dancing for their respective patches. Inactive workers therefore have access to better information about forage conditions than the active workers (Seeley, 1995) and so the dance area and inactive workers may serve as information center.

As I, and others (Jaffe and Deneubourg, 1992; Johnson et al., 1987), have shown, there is a unique proportion of scouts that maximizes net gain—and also in this study, energetic efficiency—to the colony. However, there are other issues involved. There is some evidence that honey bee colonies use different currencies at different times of the year (Schmid-Hempel et al., 1993; Seeley, 1994). Small colonies or those with few nectar reserves to draw on may be better to maximize rate of nectar delivery to the nest whereas larger colonies may do better able to maximize energetic efficiency, especially when the demographic advantage is taken into account (Seeley, 1994). When forage conditions are poor the colony should sit tight in the nest and await better conditions. Unfortunately though, the colony can only monitor when forage is available by sending out scouts to check, thus incurring some energetic and unprofitable trips (Visscher and Seeley, 1982). In this sense, the colony will always be acting suboptimally. This “error” can be regarded in the same adaptive sense as ant foragers who lose a foraging trail (Deneubourg et al., 1983, 1987) or honey bee recruits that miss the advertised flower patch (Weidenmüller and Seeley, 1999) but who then explore new areas and find other new high quality sites.

The model presented here predicts an optimal proportion of scouts that maximizes some energetic currency, but how such a colony-level response is mediated is unknown. There is some evidence that honey bee scouts have a higher tempo

and exhibit more consistent foraging rates than recruits, and that a bee's scouting rate correlates with her previous foraging rate (Seeley, 1983). If this is so, then it is highly likely that there is some regulatory mechanism that adjusts the relative proportions of scouts and recruits in the forager population. However, a concerted research effort will be needed to elucidate this mechanism.

APPENDIX A

Notation

| Parameter | Description |
|---------------------|------------------------------------------------------------------------------------------------------------------------------------------------|
| N | Size of forager population = #scouts + #recruits + #inactives |
| s | Proportion of scouts in the forager population |
| s^* | Proportion of scouts in the forager population that maximizes payoff |
| f_s | Number of successful scouts at the end of a bout (as a proportion of N) |
| f_u | Number of unsuccessful scouts at the end of a bout (as a proportion of N) |
| f_r | Proportion of the forager population who were recruited to forage during the forage bout |
| f_i | Proportion of the forager population that remained inactive during the forage bout |
| f_i^* | The fraction of inactive workers when net grain is maximized (i.e., when $s = s^*$) |
| p | Probability that a forage site contains forage |
| $q(\cdot)$ | Distribution of number of productive patches at a productive forage site |
| $\langle q \rangle$ | Mean number of productive patches at a productive forage site |
| E_i | A bee's energetic costs in Watts while resting |
| E_a | A bee's energetic costs in Watts while flying |
| F | Energetic value of a load of nectar per second of foraging trip |
| α | Recruitment efficiency: the average return of a recruit's trip compared to a scout's |
| m | Number of return trips made to a particular forage site |
| α' | Effective recruitment efficiency: the average return of a recruit's trip compared to a scout's when m repeat trips to a patch are considered |
| β | The probability that $p = 0$ in a fluctuating environment |
| $r(s)$ | Energetic payoff (in Watts, per capita, per second) based on net gain (benefit - cost) |
| $r'(s)$ | Energetic payoff (in Watts, per capita, per second) based on energy efficiency (benefit/cost - 1) |
| J | 1 Joule |
| W | 1 Watt = 1 J/sec. |

APPENDIX B

Payoffs

From Equations 1 and 2, model I is defined by:

$$r(s) = \begin{cases} F(ps + \alpha(1 - s)) - E_a & \text{if } ps\langle q \rangle - 1 \geq 1 - s \\ Fps(1 + \alpha(\langle q \rangle - 1)) & \\ + (E_a - E_i)(1 - s - ps\langle q \rangle - 1) - E_a & \\ \text{otherwise,} & \end{cases}$$

where $p \in [0,1]$, $\alpha \in (0,1]$, $E_a > E_i \in (0,\infty]$, and $\langle q \rangle \in \{1,2, \dots, \infty\}$ are constants and $s \in [0,1]$ is the variable under colony control.

From Equations 2 and 3, model II is defined by:

$$r'(s) = \begin{cases} s \frac{p}{E_a} (p - \alpha) + \alpha \frac{F}{E_a} - 1 & \text{if } ps\langle q \rangle - 1 \geq 1 - s \\ \frac{Fps(1 + \alpha(\langle q \rangle - 1))}{E_a + (E_i - E_a)(1 - s(1 + p(\langle q \rangle - 1)))} - 1 & \text{otherwise,} \end{cases}$$

with parameters and variables as above.

(Note that in model II when $ps\langle q \rangle - 1 \geq 1 - s$, the payoff function is a linear function in which the sign of the gradient simply depends on the sign of $p - \alpha$. That is, reserves are favored when $\alpha > p$ implying a good recruitment system, and/or, few productive sites.)

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