Adv. Complex Systems (1998) **1**, 267–282

Simulation of the Feedbacks and Regulation of Recruitment Dancing in Honey Bees

Carl Anderson[†]
School of Mathematics and Statistics
University of Sheffield
Sheffield, S3 7RH, UK.

ABSTRACT. Honey bee nectar foragers returning to the hive experience a delay as they search for a receiver bee to whom they transfer their material. In this paper I describe the simulation of the "threshold rule" (Seeley, 1995) which relates the magnitude of this search delay to the probability of performing a recruitment dance — waggle dance, tremble dance, or no dance. Results show that this rule leads to self-organised near-optimal worker allocation in a fluctuating environment, is extremely robust, and operates over a wide range of parameter values. The reason for the robustness appears to be the particular system of feedbacks that operate within the system.
KEYWORDS: honey bees, feedback, simulation, recruitment dances, tremble dance, waggle dance.

1. Introduction

Insect societies (colonies of ants, bees, wasps, and termites) are complex adaptive systems (Bonabeau, in press) and exhibit fascinating emergent behaviour. One of the major thrusts of social insect research is to understand colony organisation and its regulation, in particular how relatively simple individual behaviours lead to the more complex colony-level behaviours.

Nectar foraging in honey bees is a partitioned task (Jeanne, 1986a; reviewed in Ratnieks and Anderson, 1999) in which the task is split into two stages each performed by a separate group of workers. The first group, foragers, collect the nectar and return to the nest. However, instead of storing the material in the

[†] Department of Genetics and Ecology, University of Århus, Århus, Denmark. email: stp95ca@sheffield.ac.uk

comb themselves, they search for a member of the second group, storer or receiver bees, to whom they transfer the material (Seeley, 1995). It is these receiver bees who then store the material in the comb. The problem that a colony faces is that nectar availability and thus ease of collection can fluctuate both enormously (over a hundredfold variation) and rapidly (on a timescale of days). During times of nectar dearth a colony's nectar influx may be only be a few grammes per day (and the colony has to draw on its reserves) but this can rise to several kilogrammes during nectar flow (Seeley, 1995). These fluctuations will affect the relative work capacities of the two groups of workers leading to a decrease in the colony's nectar processing rate (Anderson and Ratnieks, in press a, b). This necessitates some mechanism to regulate the relative numbers of workers in the two groups and rebalance the work capacities. In honey bees this is achieved through recruitment dances, the waggle dance (von Frisch 1967) and the tremble dance (Seeley 1992, 1995) in which the probability of performing a dance is related to the time it takes a forager to locate a receiver bee, *i.e.* its "queueing delay".

The aim of this study is to understand how individuals with only limited knowledge, *i.e.* their own queueing delay and no knowledge of the overall allocation of workers between the two groups, can correctly recruit workers to the group in shortage to balance the two work capacities and maximise the colony's nectar processing capacity. This is studied using stochastic "artificial life" simulation (Levy, 1993).

As insect societies are prime examples of the group-level adaptive properties that can arise from distributed control they provide a very powerful metaphor for similarly "hard" resource-allocation problems in other areas such as manufacturing, scheduling, transportation, and telecommunications (in which this paradigm has already been adopted, *e.g.* Geake 1994; Ward 1998; Appleby and Steward 1994). Thus, a greater understanding of the underlying feedback mechanisms and colony organisation and regulation in insect societies could provide significant "real-world" benefits in areas in which a more traditional centralised-control approach may not be the best way to proceed.

1.1. Recruitment dancing in the honey bee

In this study, I implement an approximation of the actual mechanism honey bees use to regulate worker allocation in nectar foraging and receiving to match the work capacity of the two groups. This is achieved by foragers performing one of two recruitment dances, either:

Waggle dance (von Frisch 1967) — in which returning foragers run through a figure-of-eight pattern on the comb and "waggle", *i.e.* vigorously vibrate their bodies back and forth laterally, during the central straight section (von Frisch 1967; Winston 1987). The direction of the "waggle run" tells the dance followers — mostly unemployed foragers — the direction of the food source in relation to the sun, and the duration of the dance conveys the distance (von Frisch 1967). Its message is "I have a found a good food source worthy of greater exploitation. It is located in direction X and distance Y" whilst its meaning is "I should help her exploit her patch" and thus has a positive feedback on the number of active foragers.

or

Tremble dance (Seeley, 1992) — in which a forager "shakes her body back and forth, at the same time rotating her body axis by about 50^{O} every second or so, all the while walking slowly across the comb" (Seeley, 1992). Its message is apparently "I have visited a rich nectar source worthy of greater exploitation, but already we have more nectar coming in than we can handle" (Seeley, 1992) and has multiple meanings. For the workers in the nest, its meaning is "I should switch to the task of nectar processing" (Seeley, 1992) and thus has a positive feedback effect on the number of receivers. However, its message to the foragers is "I should refrain from recruiting additional foragers to my nectar source" (Nieh, 1993) and thus has a negative feedback effect.

Honey bee nectar foragers use the delay experienced in locating a receiver bee to modulate recruitment dances (Lindauer, 1961; Kirchner and Lindauer, 1994; Seeley, 1995, 1997). Nectar foragers that experience a short delay are more likely to perform the waggle dance, thereby recruiting unemployed foragers to the flower patch advertised, while those experiencing a long delay are more likely to perform the tremble dance, thereby recruiting additional receivers (Seeley, 1992, 1995, 1997). Intermediate delays typically result in neither dance being performed (fig. 1a; Seeley 1992, 1995, 1997). This has been termed a "threshold rule" by Seeley (1995) as there are two thresholds which define a range outside of which a dance is more likely to be performed than not. Delays are also used by *Polybia occidentalis* wasps in harmonising the work effort of the wood pulp and water foragers collecting nest-building materials and the builders who use these materials (Jeanne, 1986b).

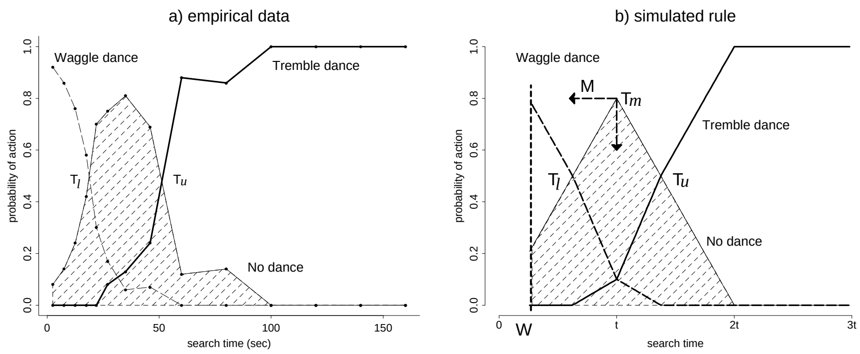

Figure 1: Threshold rules for recruitment. *a)* empirical data redrawn from Seeley (1992). *b)* approximation as used in the simulations. The "thresholds" refer to the two values T_l and T_u, *i.e.* 20 and 50 for the empirical data, above (T_u) or below (T_l) which a recruitment dance is performed with a greater probability than no dance. M is the maximum probability of not dancing and W is a search delay. (See text.)

2. Model description

Continuous-time stochastic simulation was used to model the partitioning of nectar collection and storage in the honey bee. Full details of the basic model on which the current model is based are given in Anderson and Ratnieks (in press b, and C. Anderson, Ph.D. thesis, University of Sheffield). Briefly, I solely model nectar collection and storage in the honey bee and consider only two groups of workers: foragers and receivers. No other workers in the colony are considered. There is a constant number of foragers plus receivers (1000 in this study) but workers may switch between the two tasks based on the rule detailed in the next section. Figure 2 shows the basic schema for the model. Foragers leave the nest on a foraging trip, which is always successful, and the duration of which comes from some distribution $f(\cdot)$ with mean μ_f. When a forager arrives back at the nest, it enters the "transfer area", simply an area of the comb in which transfer and recruitment dancing takes place. If there is a receiver waiting then the two workers pair up and transfer takes place. Transfer duration has mean μ_t and comes from some distribution $t(\cdot)$. However, if there are no receivers waiting then the forager forms a queue and waits, or joins an existing queue if other foragers are already waiting (and *vice versa* for receivers waiting for the arrival of foragers). The queueing discipline used when picking a partner from those waiting is "serve in random order", *i.e.* randomly choose a worker from those waiting. The length of time a returning worker has waited before it paired up with a partner is termed its "queueing delay" and may be zero. After transfer, the foragers leave on their next foraging trip and receivers leave the transfer area to store the material in another part of the comb which takes μ_r time units on average and comes from some distribution $r(\cdot)$. Simulations were run with foraging and receiving trip durations drawn from a gamma distribution with

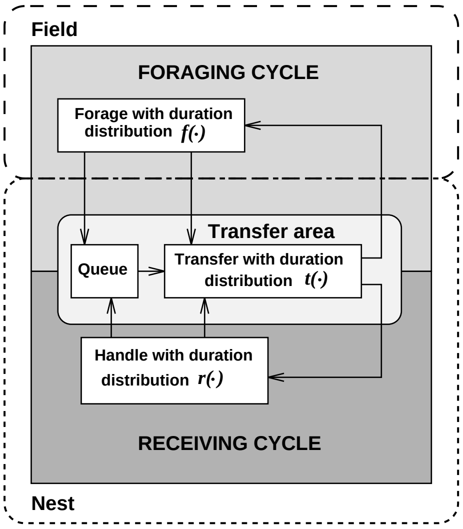

Figure 2: The foraging / receiving cycle used in the simulation model.

mean 2500, variance 3125000, and shape parameter 2. This distribution gives a positively-skewed "normal-like" distribution similar to Park's (1928) empirical data for foraging trip durations and an appropriate coefficient of variation (*e.g.* data in Table 3 in Seeley (1989) and C. Anderson, unpublished data).

Previously I have shown analytically (in Anderson and Ratnieks, in press b, and C. Anderson, Ph.D. thesis, University of Sheffield) that in this particular system when the work capacities of the two groups are equal then the mean queueing delay for all individuals, *i.e.* foragers and receivers, is minimised. Furthermore, this corresponds to a maximal nectar processing rate for the colony, a measure that is of probable selective importance in social insects (Oster and Wilson, 1978). This matching of work capacities can only occur when the proportion of workers that are foragers (p) is a certain unique value, p^*. As p increases, and the competition between foragers for the receivers intensifies, the mean queueing delay experienced by foragers increases and mean receiver queueing delay decreases. p^* is when the ratio of the numbers of foragers to receivers is the same as the ratio of the mean foraging cycle duration (mean duration of a foraging trip + mean forager queueing delay) to mean receiving cycle duration. In the deterministic case or when $\mu_f = \mu_r$, p^* is given by $(\mu_f + \mu_t)/(\mu_f + \mu_r + 2\mu_t)$.

2.1. Definition of threshold rule

Seeley (1992) demonstrated the empirical relationship between the duration of honey bee foragers' search delays and the probability of performing either a waggle dance, a tremble dance, or no dance and is shown in figure 1*a)*. My approximation of this is shown in figure 1*b)* and is defined by three parameters, M, T_m and W and is symmetric about delay T_m. Notation is summarised in Table 1. In brief, if a forager experiences a short delay then it has a high probability of performing a waggle dance and if the forager experiences a long delay then the forager is very likely to perform a tremble dance. Results from the basic simulation model (Anderson and Ratnieks, in press b) showed that at optimal

Table 1: Notation

Variable	Definition
μ_f	mean duration of foraging trips
μ_r	mean duration of receiving trips
μ_t	mean transfer duration
p	proportion of foragers
p^*	optimal proportion of foragers which minimises queueing delays and maximises the colony's nectar processing rate. $p^* \approx (\mu_f + \mu_t)/(\mu_f + \mu_r + 2\mu_t)$
$\mu_{q,f}$	mean queueing delays for foragers
$\mu_{q,r}$	mean queueing delays for receivers
M	maximum probability of not dancing
T_l	the lower threshold, *i.e.* the delay when the probability of waggle dancing is 0.5
T_m	the delay when the probability of not dancing is maximised
T_u	the upper threshold, *i.e.* the delay when the probability of tremble dancing is 0.5
T^*	the value of T_m which maximises nectar processing rate
W	a constant search delay

conditions (p^*) workers will have to wait for a partner on half of their arrivals at the transfer area and experience no delay on the other half. In reality, honey bee foragers always experience some search delay, and the total delay — search delay + queueing delay — is never zero. To account for this in the current model, a constant search delay W is added to the queueing delay and the rule applied using this delay. Without this search delay foragers would be over-zealous to waggle dance, dancing at the end of half their trips even at optimal conditions when recruitment is not required. The addition of W has a negligible effect on p^* when $W \ll \mu_f + \mu_t$, *i.e.* foraging cycle durations are much longer than any search delay, which is true for honey bees. In the most extreme situations considered in this paper in which the effect of W on p^* is expected to be greatest p^* was only shifted by 0.005. When $\mu_f = \mu_r$ there is no effect at all on p^*.

The rule is defined as follows:

Let $M \in [0.5, 1]$ be the maximum probability of not dancing.

Let $T_m \in (0, \infty)$ be the delay when the probability of not dancing is maximised.

Let $W \in [0, \infty)$ be a constant search delay.

Let d be the forager's total delay, *i.e.* search delay (W) + queueing delay.

Let D be the random variable of d.

The probability of not dancing is determined by an isosceles triangle of width $2T_m$ and height M but truncated at W (fig. 1*b*). That is,

$$\phi_n = \Pr(\text{does not dance} \mid D = d) = \begin{cases} \frac{dM}{T_m} & \text{if } W \le d \le T_m\,; \\ 2M - \frac{dM}{T_m} & \text{if } T_m < d \le 2T_m\,; \\ 0 & \text{otherwise}\,. \end{cases} \tag{1}$$

It is assumed that below the threshold T_l, where $\phi_n = \frac{1}{2}$, a worker either performs a waggle dance with probability ϕ_w, or no dance with probability $\phi_n = 1 - \phi_w$. Similarly, above the threshold T_u, where $\phi_n = \frac{1}{2}$, a worker either performs a tremble dance with probability ϕ_t, or no dance with probability $\phi_n = 1 - \phi_t$. Thus,

$$T_l = \frac{T_m}{2M} \tag{2}$$

and

$$T_u = 2T_m - \frac{T_m}{2M}\,. \tag{3}$$

At T_m, both waggle and tremble dances are performed with equal probability, *i.e.* $\frac{1-M}{2}$, and, in the ranges $T_l - T_m$ and $T_m - T_u$, a linear relationship is assumed between D and the probabilities. Thus,

$$\begin{aligned} \phi_w &= \Pr(\text{waggles dances} \mid D = d) \\ &= \begin{cases} 1 - \frac{dM}{T_m} & \text{if } W \le d \le \frac{T_m}{2M}; \\ \frac{1-M}{2} + \frac{M^2}{2M-1}\left(1 - \frac{d}{T_m}\right) & \text{if } \frac{T_m}{2M} < d \le T_m; \\ (1-M)\left(\frac{1}{2} + \frac{M}{2M-1}\left(1 - \frac{d}{T_m}\right)\right) & \text{if } T_m < d \le 2T_m - \frac{T_m}{2M}; \\ 0 & \text{otherwise}\,. \end{cases} \end{aligned} \tag{4}$$

As there are only three possible actions — waggle dancing, tremble dancing or no dancing — by definition, $\phi_n + \phi_w + \phi_t = 1$ and thus,

$$\phi_t = \Pr(\text{tremble dances} \mid D = d\,) = 1 - \phi_n - \phi_w\,. \tag{5}$$

A forager arrives at the transfer area, experiences a queueing delay, which may be zero, and adds W as a search delay. During nectar transfer, this total delay d is passed into the probabilistic equations above which decide its next action.

That is, the "threshold rule" is:

(i) perform a waggle dance with probability ϕ_w as defined in equation 4, or
(ii) perform a tremble dance with probability ϕ_t as defined in equation 5, or
(iii) perform no dance with probability ϕ_n as defined in equation 1.

This rules is only applied by foragers. If she does not perform a dance, she leaves the nest on her next foraging trip. If she decides to perform a waggle dance she recruits her receiver-partner to switch to foraging. The receiver either leaves the nest immediately or stores her nectar first before leaving the nest as a forager. The former situation was included so that the effects of time-lags — the time between a recruitment decision being made and the time when a recruited worker is available for its new task — could be studied. In effect this is a best-case scenario and will demonstrate the colony's maximal adaptiveness. Also, it is conceivable that a newly recruited receiver is more motivated than a non-recruited receiver and so will be quicker to store her nectar (but obviously there will always some delay even if small) and so the actual situation could lie between the two extremes. If the forager decides to tremble dance, she recruits a forager to switch to receiving. This has been implemented by the tremble-dancer herself switching from foraging and being available immediately or with some small delay ϵ. So, in this model task-switching has been implemented rather than the more realistic assumption of a combination of recruitment and cessation of activity. Firstly, this keeps colony size constant and so makes the model more tractable and also when there is no "performance efficiency" (Jeanne 1986), *i.e.* workers do not improve their ability to perform a task through learning and repetition, then task-switching is effectively equivalent to recruitment plus cessation (Anderson and Ratniek, unpublished manuscript). That is, all that is of importance here is that a waggle dance increases the relative proportion of foragers and that a tremble causes a decrease.

2.2. Role of parameters M, T_m and W

The way the threshold rule has been defined in the previous section leads to some very useful properties of the three parameters M, T_m and W.

(i) T_m is simply a scaling parameter. A change in T_m effectively scales the x-axis values leaving the relative probabilities of the three activities — the "shape" of the rule — unaltered.
(ii) M is a parameter that alters the *absolute* strength of the push/pull effects in this feedback mechanism and so changes $T_u - T_l$. That is, let us say waggle dancing is a mechanism which "pulls" the system to a greater

proportion of foragers and tremble dancing is "pushing" the system to a greater proportion of receivers. If T_l is low and T_u is high, *i.e.* $T_u - T_l$ is high, most delays will fall between the two thresholds (no dancing) and the push/pull effects are weak. This occurs when M is high. Conversely, low M leads to small $T_u - T_l$ and the push/pull effects are stronger. M is thus a parameter to control colony responsiveness to conditions.

(iii) W is a parameter that alters the *relative* strengths of the push/pull effects. Larger values of W lead to larger total delays. As W does not affect the shape of the rule, these increased delays result in a reduction in the probability that the forager waggle dances and an increase in the probability the forager does not dance or tremble dances. Thus increased W results in a relatively stronger "push" than "pull" through increased probability of tremble dancing for the same queueing delay.

The objective is thus to: *1)* demonstrate how this rule works, and *2)* to study the effects of altering the relative and absolute strengths of the push/pull feedback effects of the recruitment dances through the three parameters M, T_m and W.

3. Results

The main result is that the mechanism works. That is, a set of values for M, T_m and W can be found such that a colony initially in a suboptimal allocation of workers readjusts itself to maintain p^*, despite environmental perturbations. This is shown in figure 3. In figure 3*a)*, the colony was started with $\mu_f = \mu_r \Rightarrow p^* = 0.5$, *i.e.* worker allocation is optimal when there are 500 foragers and 500 receivers, but actually contained 700 foragers and 300 receivers, *i.e.* $p = 0.7$. When allowed to implement the threshold rule, the colony initially overshoots p^*, by more in fact that the initial deviation from p^*. This is an important drawback of the rule. With such a large shortage of receivers, there is a very

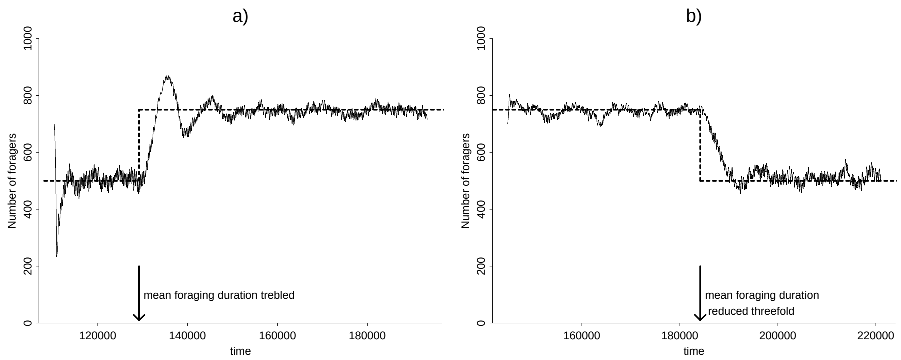

Figure 3: Colony maintaining near-optimal worker allocation — using threshold rule with $T_m = 20$, $M = 0.8$ and $W = 0.5$ — despite fluctuating environment. *a)* μ_f trebled from 2500 to 7500 at time 129000. *b)* μ_f reduced from 7500 to 2500 at time 184000. In both cases $r(\cdot)$ is a gamma distribution with mean 2500, variance 3125000, and shape parameter 2, and is unaltered. $f(\cdot)$ is either equivalent to $r(\cdot)$ or $5000 + r(\cdot)$. The dashed line shows the optimal allocation of workers.

large queue of around four hundred foragers. As each forager eventually finds a partner it naturally has a large queueing delay — in the order of hundreds of time units in this case — and so decides to tremble dance. This means that many foragers switch to receiving. This includes most of those in the queue[1] and those currently foraging who arrive whilst the queue is being cleared. Thus, the overshoot will be *at least* as big as the initial deviation from p^*.

Now, there is an excess of receivers but the number of them actually queueing is much reduced, only 80–90, as the workers are more evenly spread around the different parts of the system. Near-optimal worker allocation is achieved by foragers waggle-dancing which recruits receivers to foraging. As receivers switch, the proportion of foragers approaches the optimum and the difference between the mean queueing delays for foragers ($\mu_{q,f}$) and receivers ($\mu_{q,r}$), $\mid \mu_{q,f} - \mu_{q,r} \mid$, decreases. (At p^*, $\mu_{q,f} = \mu_{q,r}$ (Anderson and Ratnieks, in press b).) There is however still some dancing and variation about the optimum due to stochastic variation in the arrivals of workers.

At around time 129,000, I trebled the mean foraging duration (μ_f) to 7500 without altering μ_r. Thus, p^* is now ≈ 0.75. Once again there is an excess of receivers, but this time as the new foraging durations are longer, it takes longer before the new recruited foragers arrive back at the nest. There is a damped oscillation of the colony as it equilibrates to the new settings.

In figure 3*b)* the colony once again started with $p = 0.7$ but in this simulation μ_f was initially 7500 and was reduced to 2500 halfway through the simulation. There is an initial overshoot as in figure 3*a)* and the system equilibrates. However, when the mean foraging duration is reduced, there is no overshoot and the colony quickly drops to the new optimal number of foragers. The difference between the responses shown in figures 3*a)* and 3*b)* can be explained by the fact that in the latter, the reduction of the mean foraging duration means that workers return to the colony more quickly and prevent large queues building up.

3.1. Robustness of results

It was found that this "threshold rule" mechanism is very robust. If M is fixed, say as 0.8, then there are many pairs of T_m and W which result in the sort of self-organised worker allocation behaviour shown in figure 3.

Figures 4*a)* and 5*a)* shows the rate of nectar processed — the number of nectar loads transferred per unit time — for a number of combinations of $W \in \{0.5, 5, 10, 25\}$ and $T \in \{1, 2, \ldots, 30, 40, \ldots, 100\}$. Each datum comes from a single simulation as in fig. 3*b)*, *i.e.* where μ_f is reduced from 7500 to 2500 part-way through the simulation.

Apart from where $T_m < W$ and the colony skews to all receivers — shown as the hatched areas in figures 4*a)* and 5*a)* — all of the T_m and W combinations result in self-organised tracking of optimal worker allocation by the colony but to a lesser or greater degree of success. The success of the strategy is shown by the nectar processing rate (figs. 4*a* and 5*a*) and the mean deviation from p^* [2] (figs. 4*c* and 5*c*).

For each value of W, there is an optimal value of T_m, a "best response" denoted T^*, in which nectar processing rate is maximised. The results in figure 4 show that for *this particular parameter set* (compare with fig. 5), at the relevant T^*s,

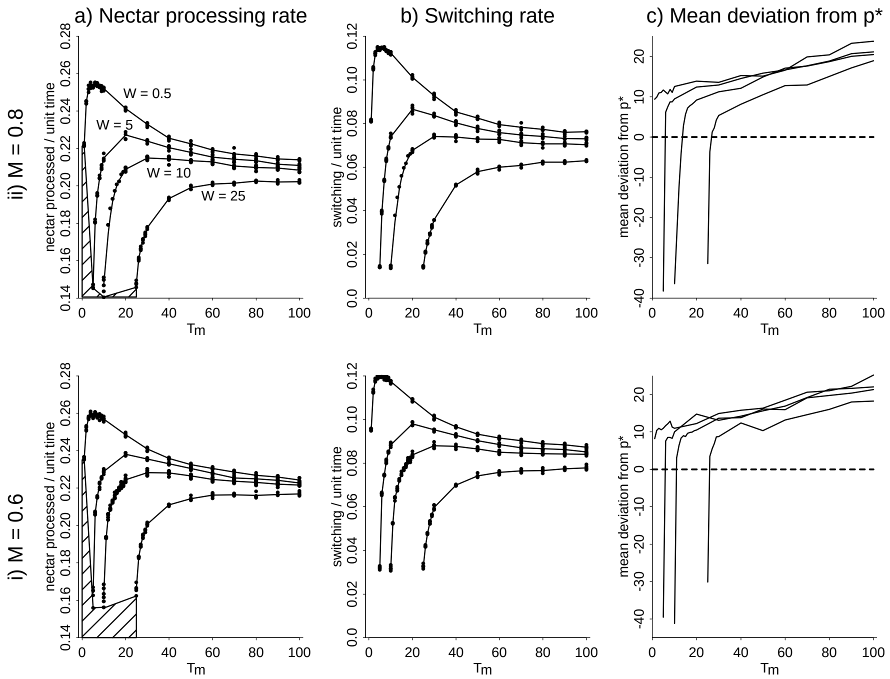

Figure 4: Combined effects of search costs (W) and thresholds (T_m) on *a)* colony's nectar processing rate; *b)* rate of switching between tasks, and *c)* mean deviation from optimal worker allocation, for two values of M; *i)* $M = 0.6$ and *ii)* $M = 0.8$. The hatched area in *a)* represents parameter combinations in which the colony skewed to all receivers. Each datum represents the results of a single simulation with the same conditions as fig. 3*b)*. 5 replicates per T_m value. In these simulations, receivers switched to foraging almost immediately upon recruitment *i.e.* only after a small delay ϵ.

smaller search costs (small W) result in a higher nectar processing rate. This is not because mean foraging cycles — $\mu_f + W + \mu_{q,f} + \mu_t$ — are shorter, as workers did not actually experience a delay of W time units but only added W to their delay when applying the rule. This was done in this way to specifically factor out this effect.

For figure 4, *i.e.* immediate availability by recruited receivers, higher nectar processing appears to be correlated with a higher rate of switching between tasks (fig. 4*b*). One important feature to note is that the nectar processing rate peaks "sharpen" with smaller W. As W increases, the response flattens out and although the nectar processing rate is lower for higher W, this difference decreases with increasing T_m. Also, if $T_m < T^*$, the colony experiences a much higher decrease in nectar processing rate than the equivalent amount of deviation of $T_m > T^*$. So, it appears that a colony with thresholds greater than the optimal value, experiences smaller decreases in nectar processing if T^* changes due to demographic or environmental perturbations. Importantly, this effect is much stronger, *i.e.* very flat curves for most values of T_m and W, in the more realistic situation in which there is a time-lag between a receiver being recruited and becoming available as a receiver (fig. 5).

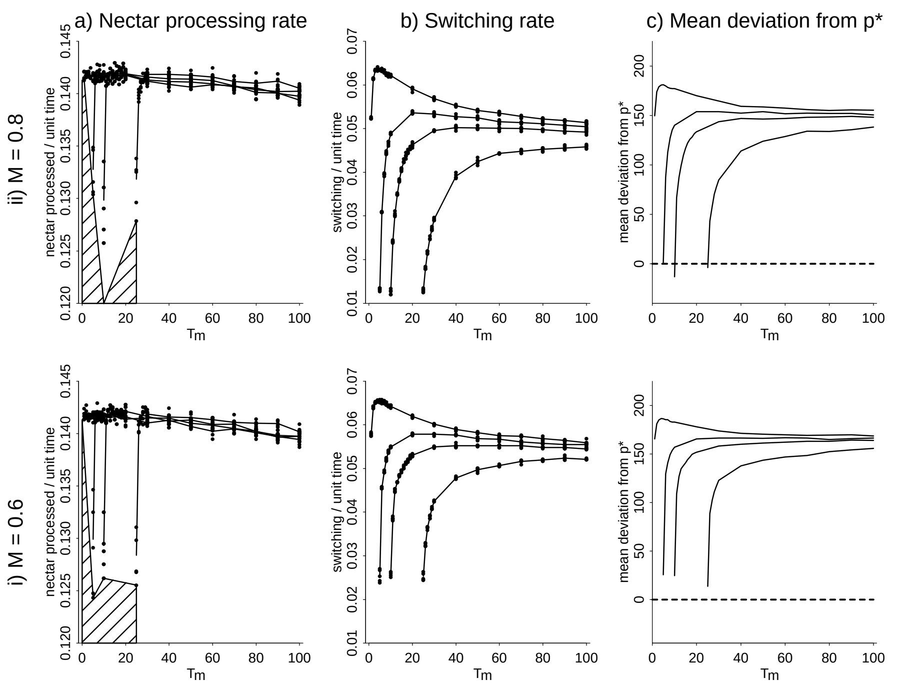

Figure 5: Results from simulations run under the same conditions as figure 4*ii)* except that in this case receivers took a "normal" receiver trip duration, $\mu_r = 500$, to store their nectar before leaving the nest as a forager.

It can be seen that nectar processing (fig. 4*a*) is maximised when the magnitude of mean deviation from p^* is minimised (fig. 4*c*). Thus, as would be expected, the colony processes nectar at the fastest rate when the colony tracks the changing optimal worker allocation as closely as possible. This is the reason for the poorer performance in figure 5 in which a lag exists between recruitment and an effective change in worker allocation: in this situation the colony cannot track changes in the environment as quickly as the colonies in figure 4 and so experiences a lower nectar processing rate and higher deviation from p^*. In figure 4 maximal nectar processing does not quite coincide with zero mean deviation as might be expected. There are two contributory factors. The most influential is that the simulations were asymmetric in the fact that p^* was reduced from 0.75 to 0.5 partway through the simulation and the number of foragers drops down to the new lower level, without overshoot, which adds positive deviation (see fig. 3*b*). A second but minor effect is that if the duration of foraging and receiving trips are variable then p^* does not always correspond to the form given on page 271 as foraging and receiving cycles include queueing delays. However, this only accounts for a maximal shift in p^* of only 0.003, *i.e.* a difference of only 3 bees in 1000.

The relationship between T_m and the mean deviation from p^* or nectar processing rate is not symmetric about T^*. If $T_m < T^*$ then there is relatively too much tremble dancing and p is less than p^*, on average. This has a large reduction on colony nectar processing rate. When $T_m > T^*$ there is relatively too much waggle dancing as the mean deviation from p^* is positive, but has a relatively smaller effect (smaller gradient in fig. 4*c*). However, it is important to note that in both these cases, the colony is still in equilibrium and does not skew to all foragers or all receivers. The asymmetry in response comes about as it is just foragers who are applying the rule and delays and responses are bounded at zero (or W) but unbounded above T_u.

From the above results, it appears that a higher rate of switching between tasks is correlated with both a higher nectar processing rate and mean deviation from optimal worker allocation. One factor that would increase the amount of switching without altering the relative strengths of the push/pull effects is to reduce the probability of not dancing and decrease $T_u - T_l$. This is achieved by reducing M. The result of decreasing M from 0.8 to 0.6 are shown in figure 4*i)*. These are on the same y-axis scales as figure 4*ii)* and although T^*s are unaltered, nectar processing rates and switching rates are higher — by up to 7.3% with the largest search costs — although the effect decreases with decreasing W. This colony-level behaviour is true for both cases considered, immediate response of recruited receivers (fig. 4) and a delay before receivers switch (fig. 5).

4. Discussion

The results in this chapter present the "threshold rule" as a very robust mechanism. For instance, with $W = 0.5$, the mechanism "works" for a very wide range of T_m *i.e.* $1 \leq T_m \leq 4200$. This is not to say that the colony is equally successful throughout this range of T_m, or that the colony always does better than if it did not employ the mechanism but simply that within this range it is able to react to environmental fluctuations by altering worker allocation and does not skew to a single worker type. The success of a particular strategy can only be evaluated in relation to the characteristics of the environment in which the colony lives. For instance, a colony which lives in a fairly constant environment and only experiences rare or short-lived "blips" in nectar availability would probably do better to have a fixed number of foragers and receivers set up for the "normal" nectar availability and suffer reduced nectar processing for short periods than a colony which tries to track the changes in the environment especially if there are time-lags in colony response. This time-lag, recruited receivers having to store their load of nectar before foraging, produced poorer colony nectar processing rates than the best-case scenario when these time-lags were not present. Could this explain why recruitment and cessation of activity — in which there are little or no time-lags — rather than task-switching — in which there are time-lags — is employed in the honey bee? That is, recruited workers from a pool of unemployed foragers could start work immediately. Clearly, this deserves further investigation.

It appears that the reason for this robustness is the system of feedbacks in operation which equilibrate the colony at a particular proportion of foragers in the colony so as to balance the push/pull effects. The feedbacks that exist between recruitment dancing, proportion of foragers and forager queueing delays are shown in figure 6.

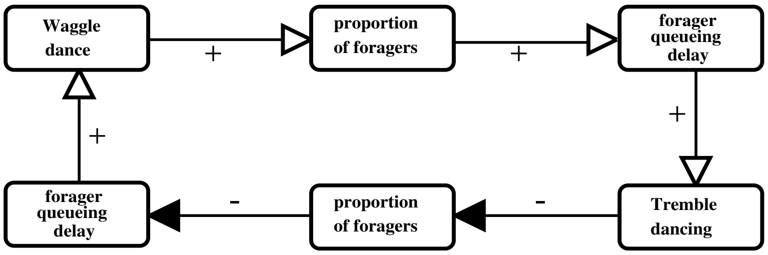

Figure 6: The cyclical nature of the feedbacks between recruitment dancing, proportion of foragers and forager queueing delays. White arrows represent positive feedbacks and black arrows negative feedback.

If T_m is large, most forager queueing delays fall below T_l and there is a high probability of foragers performing waggle dances. This increases the proportion of foragers which in turn increases the mean forager queueing delay due to increased competition for receivers. Now that the mean forager queueing delay is increased, the probability of waggle dancing is decreased. The result is that p is adjusted so the total delays fall between the two thresholds and the amount of dancing is reduced. In support of this, a near perfect linear relationship exists between T_m and mean forager queueing delay. For instance, with $M = 0.8$, $W = 0.5$ and T_m in the range 1–4200, from a least squares regression, `mean forager queueing delay` $= 1.29 \times T_m + 19.43$ ($F = 41357$, $R^2 = 0.9981$, $pval = 0$, $N = 81$). In connection with this, switching is not the proximate cause of the the increase in nectar processing rate but simply reflects the increased queueing delay which limits the number of trips, and thus the number of recruitment decisions per unit time.

The mechanism does have its limits and breaks down if $T_m < W$. This is because even adjusting the proportion of foragers to minimise forager queueing delay to zero still gives a total delay, W, which gives a high probability of tremble dancing or no dancing but negligible probability — a maximum of $\frac{1-M}{2}$ — of waggle dancing. Thus, it is not possible to balance the push/pull effects and the colony skews to all receivers. At the other extreme, large T_m, the average proportion of foragers required to balance the push/pull effects is high enough that the stochastic fluctuations experienced about this value results in a fully skewed colony, *i.e.* all foragers.

One interesting result is the asymmetric drop in nectar processing rate about T^*. Below T^*, the nectar processing rate drops sharply but above which it levels off relatively rapidly. T^* will change as the colony is subject to demographic and environmental perturbations such as forager mortality (Visscher and Dukas 1997), fluctuations in mean foraging and receiving durations, nectar quality (Seeley 1989) and queueing and search delays which depend on these. It seems unlikely that both the worker allocation and the rule that governs it will change in a self-organised manner — although in principle this could happen — and thus the thresholds are likely to be innate. If this is the case, then my results suggest that they should err on the side of caution and use a supraoptimal value, *i.e.* $T_m > T^*$ to avoid a precipitous drop in nectar processing rate.

This model is essentially a queueing theory simulation in which the foragers are "customers" and the receivers are "servers". Previously Seeley (1989) and Seeley and Tovey (1994) have investigated the relationship between the queueing delay and the relative work capacities of foragers and receivers using classical queueing theory and probability modelling. They concluded that the search time was "an accurate indicator of the relative rates of the two processes [*i.e.* nectar collecting and processing]" (Seeley and Tovey, 1994) and there was close agreement between model predictions and empirical data. By using global-level descriptions such as mean arrival rate of bees (Seeley, 1989) or the expected number of antennations until a forager meets a receiver (Seeley and Tovey, 1994) both models give a good higher-level description of the mechanisms and feedbacks in operation but I think miss the inefficiencies that arise at the individual level, and which can be best studied using stochastic models. With a "serve in random order" queueing discipline, which is the most reasonable for returning honey bee nectar foragers, a worker may, completely by chance, experience a long queueing delay and tremble dance even if the global worker allocation is near-optimal and no recruitment is required. Similarly, also by chance, a returning forager may meet a receiver bee immediately (a short queueing delay) upon arrival at the transfer area and so waggle dance unnecessarily. As an illustration, figure 3 shows switching behaviour even when the colony has reached p^*. Because of these stochastic effects at the individual-level, search times may not be as reliable an indicator as previously thought and is the focus of a paper by Ratnieks and Anderson (in press b).

This simulation is only an approximation and does not mirror the exact situation found in honey bees — unemployed foragers, recruitment and cessation of activities — although does give some valuable insights to the honey bee situation as the same feedback mechanisms generally hold. There are a host of additional factors which have to be taken into consideration in order to fully appreciate the complex and intricate regulation that occurs. For instance, workers vary in their sensitivity to search delays and differ in both the duration and intensity of their dances which will affect the rate of recruitment (Seeley 1994). This will give the colony a "broad dynamic range in responding to nectar sources, *i.e.* an ability to respond in a graded fashion to a broad range of stimuli" (Seeley 1995). In addition, it has been shown that workers are able to shift their thresholds (Lindauer 1948; von Frisch 1967; Seeley 1994). The total number of foragers and receivers also varies which affects the mean queueing delay even if at optimal worker allocation (Anderson and Ratnieks, in press a,b) and the size of the transfer area also changes with forager arrival rate affecting receiver-partner density (Seeley 1995). Also, there is an additional signal — the stop signal — mainly produced by tremble dancers and directed at waggle dancers and which retards forager recruitment effectively switching workers from foraging to receiving (Nieh 1993). (With the threshold rule in place we would expect only one type of dancing at any time but because of interindividual differences and heterogeneities in the local forager:receiver ratio within the transfer area both dances sometimes occur simultaneously.) Thus, there is still much to be learned about the interplay between this suite of regulation mechanisms.

Notes

[1] There may be some "lucky" workers who pair up quickly because of the "serve in random order" queue discipline.

[2] N observations of the number of foragers, x_i, at times, t_i, are made. Mean deviation is defined as $\frac{1}{N} \times \sum_{i=1}^{N} (x_i - Cp^*)$ where C is the colony size.

Acknowledgments

I wish to thank Prof. Chris Cannings, Drs. Paul Blackwell and Francis Ratnieks, and to Mark Pilling and an anonymous reviewer for valuable comments on earlier versions of this manuscript. This work was supported by a B.B.S.R.C. special studentship.

References

Anderson, C., and Ratnieks, F.L.W. In press a. Task partitioning in foraging: general principles, efficiency and information reliability of queueing delays. In: (Detrain, C., Deneubourg, J.L., and Pasteels, J.M., Eds) *Information Processing in Social Insects*. Berlin: Birkhäuser.

Anderson, C., and Ratnieks, F.L.W. In press b. Task partitioning in insect societies (I): effect of group size on queueing delay and colony ergonomic efficiency. *Am. Nat.*

Appleby, S., and Steward, S. (1994). Mobile software agents for control in telecommunications networks. *BT technol. J.* **12**, 104–113.

Bonabeau, E. In press. Social insect colonies as complex adaptive systems. *Ecosystems.*

Frisch, K. von. (1967). *The Dance Language and Orientation of Bees.* Cambridge, MA: Harvard University Press.

Geake, E. (1994). How simple ants can sort out BT's complex nets. *New Scientist* **141**, 20–20.

Jeanne, R.L. (1986a). The evolution of the organization of work in social insects. *Monit. zool. ital.* **20**, 119–133.

Jeanne, R.L. (1986b). Regulation of nest construction behaviour in *Polybia occidentalis. Anim. Behav.* **52**, 473–488.

Kirchner, W.F. and Lindauer, M. (1994). The causes of the tremble dance of the honeybee, *Apis mellifera. Behav. Ecol. Sociobiol.* **35**, 303–308.

Levy, S. (1993). *Artificial Life. A Quest for a New Creation.* London: Penguin Books Ltd.

Lindauer, M. (1948). Über der Einwirkung von Duft- und Geschmacksstofen sowie anderer Faktoren auf die Bienen. *Zeitsch. vergl. Physiol.* **31**, 348–412.

Lindauer, M. (1961). *Communication Among Social Bees.* Cambridge, MA: Harvard University Press.

Nieh, J.C. (1993). The stop signal of honey bees: reconsidering its message. *Behav. Ecol. Sociobiol.* **33**, 51–56.

Oster, G.F., and Wilson, E.O. (1978). *Caste and Ecology in the Social Insects.* Princeton, NJ: Princeton University Press.

Park, O.W. (1928). Time factors in relation to the acquisition of food by the honeybee. *Res. Bull. Iowa Agric. Exp. Res. Station* **108**, 183–225.

Ratnieks, F.L.W., and Anderson, C. (1999). Task partitioning in social insects. *Insectes soc.* **46**(2), to appear.

Ratnieks, F.L.W., and Anderson, C. In press a. Task partitioning in social insects (II): use of queueing delay information in recruitment. *Am. Nat.*

Seeley, T.D. (1989). Social foraging in honey bees: how nectar foragers assess their colony's nutritional status. *Behav. Ecol. Sociobiol.* **24**, 181–199.

Seeley, T.D. (1992). The tremble dance of the honey bee: message and meanings. *Behav. Ecol. Sociobiol.* **31**, 375–383.

Seeley, T.D. (1994). Honey bee foragers as sensory units of their colonies. *Behav. Ecol. Sociobiol.* **31**, 51–62.

Seeley, T.D. (1995). *The Wisdom of the Hive.* Cambridge, MA: Harvard University Press.

Seeley, T.D. (1997). Honey bee colonies are group-level adaptive units. *Am. Nat.* **150**, S22–S41.

Seeley, T.D., and Tovey, C.A. (1994). Why search time to find a food-storer bee accurately indicates the relative rates of nectar collecting and nectar processing in honey bee colonies. *Anim. Behav.* **47**, 311-316.

Visscher, P.K., and Dukas, R. (1997). Survivorship of foraging honey bees. *Insectes soc.* **44**, 1–5.

Ward, M. (1998). There's an ant in my phone. *New Scientist* **157**(2118), 32–35.

Winston, M.L. (1987). *The Biology of the Honey Bee.* Cambridge, MA: Harvard University Press.