

REVIEW

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Worker allocation in insect societies: coordination of nectar foragers and nectar receivers in honey bee (*Apis mellifera*) colonies

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Abstract Nectar collection in the honey-bee is partitioned. Foragers collect nectar and take it to the nest, where they transfer it to receiver bees who then store it in cells. Because nectar is a fluctuating and unpredictable resource, changes in worker allocation are required to balance the work capacities of foragers and receivers so that the resource is exploited efficiently. Honey bee colonies use a complex system of signals and other feedback mechanisms to coordinate the relative and total work capacities of the two groups of workers involved. We present a functional evaluation of each of the component mechanisms used by honey bees – waggle dance, tremble dance, stop signal, shaking signal and abandonment – and analyse how their interplay leads to group-level regulation. We contrast the actual regulatory system of the honey bee with theory. The tremble dance conforms to predicted best use of information, where the group in excess applies negative feedback to itself and positive feedback to the group in shortage, but this is not true of the waggle dance. Reasons for this and other discrepancies are discussed. We also suggest reasons why honey bees use a combination of recruitment plus abandonment and not switching between subtasks, which is another mechanism for balancing the work capacities of foragers and receivers. We propose that the waggle and tremble dances are the primary regulation mechanisms, and that the stop and shaking signals are secondary mechanisms, which fine-tune the system.

Fine-tuning is needed because of the inherent unreliability of the cues, queueing delays, which foragers use to make recruitment decisions.

Key words Honey bee · Signals · Nectar foragers · Receiver bees · Worker allocation · Waggle dance · Tremble dance · Shaking signal · Stop signal

Introduction

Insect societies are complex adaptive systems (Seeley 1985, 1995, 1997; Bonabeau, in press) in which the individuals form a highly coordinated and integrated unit. With little or no centralised control, many workers are able to work together and collectively tackle tasks far beyond the abilities of any one individual (Bonabeau et al. 1997). The honey-bee, *Apis mellifera*, is the best-studied social insect and is an excellent model system for understanding the emergence of adaptive group-level behaviour. Much is known about honey bee group-level coordinated activities and the proximate mechanisms used by workers to achieve this. The key factor that binds individuals together as an adaptive unit is information transfer between individuals in the form of cues and signals. A signal is taken to be a deliberate act of communication that has been shaped by natural selection (Lloyd 1983). An example of a signal is the honey bee waggle dance (von Frisch 1967). A cue is a structure or behaviour which conveys information, but only incidentally, and which has not been shaped by natural selection. For instance, the time spent searching for a nectar receiver or the carbon dioxide level in the nest (Seeley 1995, 1998) are both cues.

At least 17 signals and twice as many cues have been identified in the honey-bee (Seeley 1998). Most honey bee signals are involved in either colony reproduction or foraging which are also two areas of colony life vital to colony survival and likely to be subject to strong selection. Four, possibly five, signals, as well as numerous

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cues, regulate the number of workers involved in the nectar-harvesting process which involves both collection from flowers and storage in cells. In the honey bee, nectar foraging is a task partitioned into two subtasks in which one group of workers, the foragers, collect the material and take it to the nest. However, instead of storing the nectar themselves, they transfer it to receiver bees who then store it in cells. [Task partitioning is reviewed in Jeanne (1986a) and Ratnieks and Anderson (1999).] Nectar availability and ease of collection can fluctuate rapidly and unpredictably, creating a need to alter the total foraging effort and balance the relative work capacities of the forager and receiver groups. When these work capacities are not matched, the workers are sub-optimally allocated and the nectar processing rate is less than it could be given the total number of workers involved (Anderson and Ratnieks, in press a, in press b; Ratnieks and Anderson, in press b). Honey bees have sophisticated mechanisms to regulate the number of workers in these two groups, both to recruit additional workers to exploit the fluctuating and ephemeral nectar resources (Seeley 1995) and to balance the relative work capacities of foragers and receivers. These changes in worker allocation are mediated through four or five signals: “waggle dance”, “tremble dance”, “stop signal”, “shaking signal” and, possibly, “worker piping”.

The main focus of this paper is the interaction of these signals, together with other non-signalling feedback mechanisms such as patch abandonment, in the regulation of foraging. The following specific questions are addressed. How exactly do these signals act and cause feedback on each other in order to integrate the foraging population into a “group-level adaptive unit” (Seeley 1997)? What is the interplay between waggle dancing and tremble dancing? Why do honey bees need stop and shaking signals? Additional questions focus on why the honey bee is organised the way it is rather than in another manner. For example, why do honey-bees not need a patch abandonment signal? How best should individuals use signalling information? When signals are produced, who should produce them: the group in excess or the group in shortage? Why do honey bees use recruitment and abandonment to balance work capacities rather than switching between subtasks?

Regulation mechanisms in nectar foraging

This section provides background information on the five signals plus one other feedback mechanism, abandonment, used in regulating foraging. The emitter of the signal is referred to as the “sender” and the intended audience or target of the signal as the “recipient”. Because full details of each signal are published elsewhere, we focus on the signal “message”, i.e. the intended information transmitted by the sender, its “meaning”, i.e. the interpretation by the recipient, and its effects on worker allocation and activity.

Waggle dance

Probably the most well-known honey bee signal, and what is primarily referred to by the term “dance language”, the waggle dance was deciphered by the pioneering work of von Frisch (1967). It is a signal sent by nectar foragers and is directed at unemployed foragers (Seeley 1995), and possibly workers involved in other tasks [Fig. 1a(i)]. Waggle dances are also used to convey information about the location of water, pollen and potential nest sites (Seeley 1995). Waggle dances are normally performed by a returning nectar forager who has experienced a relatively short delay, typically less than 20 s (Seeley 1992, 1995, 1997), while searching for a receiver bee to whom she can transfer her nectar. One component of the dance, the direction of the waggle run, tells the dance followers the direction of the food source in relation to the azimuth of the sun. A second component, the duration of the waggle run, conveys the distance (von Frisch 1967). Its message is: “I have found a good food source worthy of greater exploitation. It is located in direction X and distance Y ”, while its meaning is: “I should help exploit this patch”. The waggle dance, therefore, exerts positive feedback on the number of active foragers [Fig. 1a(ii); Seeley 1995].

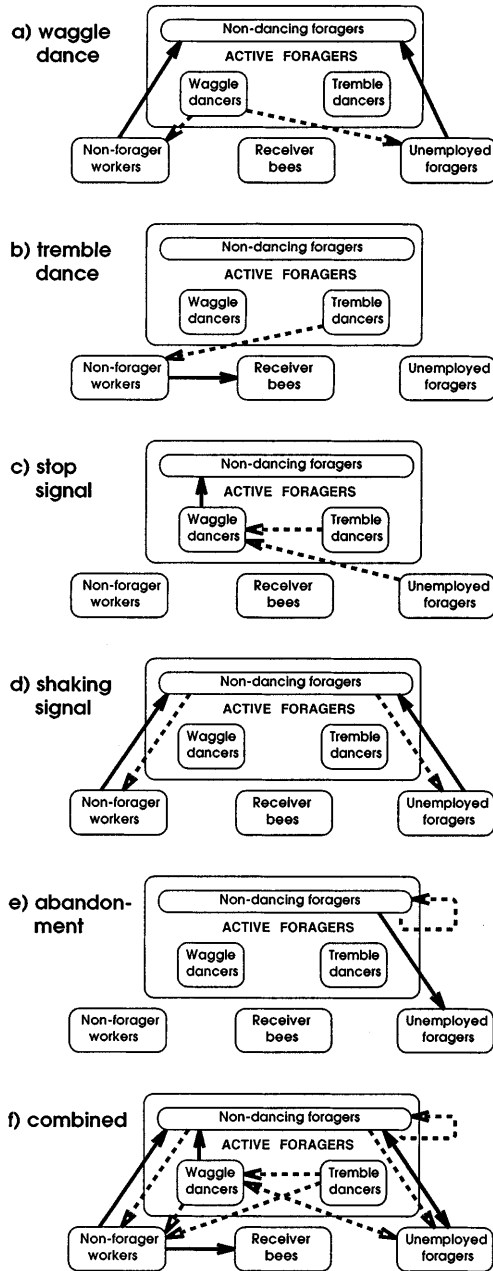
Tremble dance

Returning foragers may also perform the tremble dance [Fig. 1b(i)]. In contrast to the waggle dance, this signal is sent when a returning bee experiences a relatively *long* search delay, typically more than 50 s (Seeley 1992, 1995, 1997). 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), which has a positive feedback effect on the number of receivers. However, its meaning for other foragers is: “I should refrain from recruiting additional foragers to my nectar source” (Seeley 1992). Kirchner (1993) demonstrated that playback of artificial tremble dance sounds reduced waggle dance duration, or in some cases caused waggle dancers to stop dancing immediately, and reduced the recruitment success of the dances. Thus, the tremble dance can have a negative, or at least non-positive, effect on foragers in that it reduces forager recruitment (Seeley 1992; Kirchner 1993 and references therein). But it has a positive effect on the number of receivers, recruiting more workers to receiving (Seeley et al. 1996).

Stop signal

Originally termed a begging signal (Esch 1964), the stop signal (Nieh 1993) comprises the sender emitting an audible piping sound while head-butting the recipient,

i) Signals and workers



ii) Feedbacks

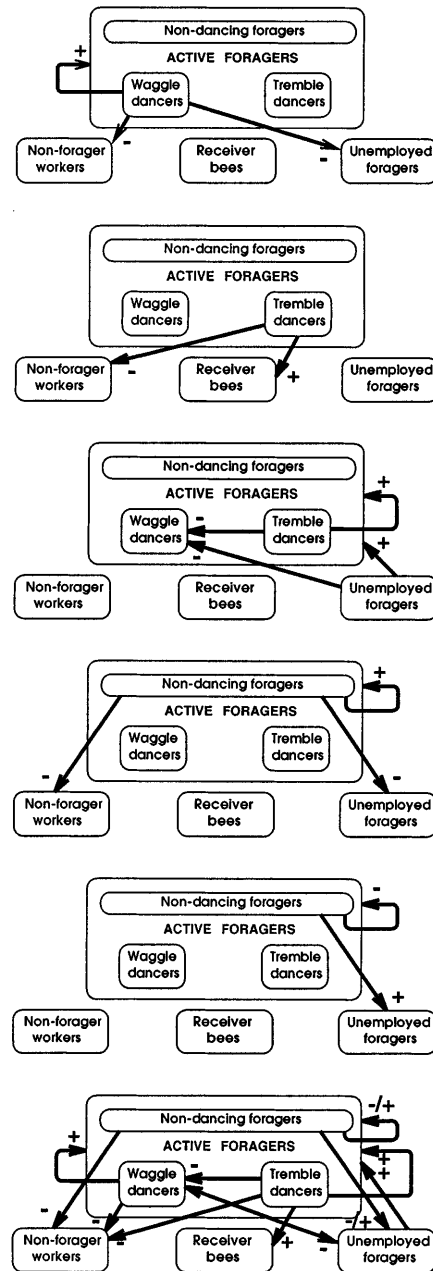


Fig. 1 Information flow and feedbacks for various regulatory signals and mechanisms used in the nectar-foraging process in the honey-bee: waggle dance (a), tremble dance (b), stop signal (c), shaking signal (d), abandonment (e), a–e combined (f). (i) Information flow from senders to recipients (*dashed arrows*) and the flow of workers that respond to the signals (*solid arrows*). (ii) Feedbacks in task allocation that result from the signals (+ excitatory, – inhibitory). c Dance followers are taken to be in the group of unemployed foragers. d Waggle dancers sometimes make shaking signals as well (Seeley et al. 1998)

who then stops moving or stops dancing. Although produced by tremble dancers, dance followers and waggle dancers, most stop signals (85%) are produced by tremble dancers – with almost all of the remaining 15% of stop signals sent by dance followers – and are

mainly directed at waggle dancers, who are 44% of all recipients [Fig. 1c(i); Nieh 1993]. Recipient waggle dancers tend to stop waggle dancing and leave the dance floor. Thus, the stop signal is mainly sent by tremble dancers, directed at waggle dancers, and inhibits additional forager recruitment [Fig. 1c(ii)].

Shaking signal

The shaking signal, also known as the dorso-ventral abdominal vibration (Milum 1955), is sent by foragers to a diverse set of recipients, i.e. workers involved in various tasks throughout the nest [Fig. 1d(i)]. Like the

stop-signal this is a “one-to-one” signal in which the sender physically shakes a single recipient (Allen 1959). Recipients tend to crawl onto the dance area (Schneider et al. 1986) or towards the entrance (Nieh 1998) where they are more likely to come into contact with other signals, typically waggle dances, and may therefore be recruited as additional foragers. Evidence (Seeley 1995; Nieh 1998; Seeley et al. 1998) suggests that shaking signals are used in conjunction with waggle dances to increase the number of active foragers [Fig. 1d(ii)] when nectar availability starts to increase after a nectar dearth and thus additional foragers are required. The message of the shaking signal appears to be “prepare for greater activity” (Seeley et al. 1998).

Abandonment

Although not a signal, abandonment of a flower patch by foragers is an important feedback mechanism in foraging regulation. In the honey bee, foragers work a small patch or flowers (Ribbands 1953) and although the profitabilities of one forager’s patch may decline or become unrewarding, this does not necessarily mean that other patches are also unrewarding. As foragers are effectively independent while outside the hive, a local mechanism enabling them to make their own decisions to abandon a patch is required. In doing so they are available for recruitment to better patches (Fig. 1e).

Worker piping

The above four signals plus abandonment may not be the only mechanisms used by honey bees. The possibility that there are more to discover can be appreciated by realising that 5 of the 17 known signals have only been elucidated within the last decade (Seeley 1998). One candidate signal is worker piping (Armbruster 1922). Little is known about this signal. It is almost certainly an aerial and substrate-mediated broadcast signal and appears to be sent by workers involved in foraging, collection and use of water, and collection of pollen and perhaps nectar, but whose recipients, messages, and meanings are unknown (Pratt et al. 1996). Pratt et al. (1996) report that in three cases in which the sender’s previous activity was known, one was a pollen collector, one was a water collector and one was a water receiver. However, the possibility that it is also a signal sent by nectar foragers cannot be discounted, especially as the only case in which more than one piper was observed was during a day of high nectar intake (Pratt et al. 1996).

A complex system of feedbacks

Figure 1f(ii) combines the feedbacks from the signals and mechanisms described in the previous section.

Clearly, regulation of nectar foraging is complex. However, various feedback systems, some of which are much simpler than that used by the honey bee, could be formulated which produce the same global regulatory properties (e.g. Fig. 2). Why then do honey bees utilise their particular and complex system?

The interplay between waggle dancing and tremble dancing

The relationship between waggle and tremble dancing is revealing. In a two-stage partitioned task (i.e. with two subtasks) with direct transfer, such as nectar collection and storage in the honey bee, queueing delays occur (Anderson and Ratnieks, in press a, in press b; Ratnieks and Anderson, in press b). These delays can increase tremendously when the work capacities of the two groups are unmatched. Ratnieks and Anderson (in press a) have shown that if queueing delays are used as an indicator of the relative work capacities of the two groups, then the group in excess (that is those that experience longer mean queueing delays) possess better-quality information than the group in shortage (who experience shorter delays). From this we would expect the group in excess to apply negative feedback to themselves and positive feedback to the group in shortage. This is true in the case of the tremble dance in which foragers indirectly apply negative feedback to the recruitment of foragers by inhibiting waggle dancing (Seeley 1992, 1995; Kirchner 1993 and references therein; Nieh 1993) and positive feedback on the number of receivers. However, foragers also perform the waggle dance (Seeley 1995) which recruits unemployed foragers. This is positive feedback from the group in shortage, and is not as expected from best use of the information available from queueing delays (Ratnieks and Anderson 1999).

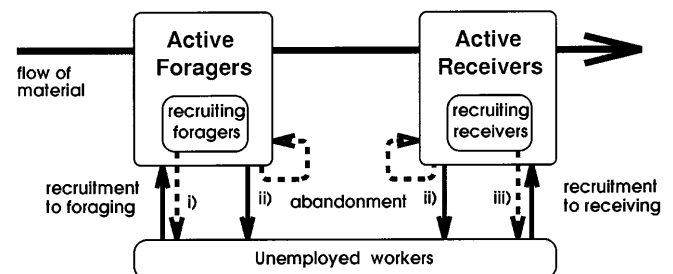


Fig. 2 One of the simplest sets of feedbacks that would produce the same global properties as the system used in the honey bee [Fig. 1f(ii)]. In this example, the foragers perform a forager recruitment signal (i) and receivers perform a receiver recruitment signal (iii), and both groups may abandon their subtask (ii), in contrast to the situation found in honey bees in which both forager and receiver recruitment is mediated solely through foragers. As in figure 1, *dashed arrows* indicate the flow of information from senders to recipients, and *solid arrows*, the flow of workers that respond to the signals

When foragers are in shortage they recruit additional foragers through the waggle dance. A priori, this is an obvious feedback solution: when in need recruit others yourself. On this basis we might expect *receivers* to recruit additional *receivers*. However, this is not the case. It is *foragers*, and not receivers, who recruit the additional receivers. Why do foragers have a greater regulatory role than receivers, and in particular, why do foragers recruit new receivers? We suggest the reason is that foragers have essential additional information not available to receivers such as the location of flowers and the rate at which nectar can be collected. The only information about the forage patch available to receivers is the nectar concentration, but even this information may be less than accurate because foragers may evaporate nectar by regurgitation whilst foraging (Heinrich 1979). Honey bee colonies would find it almost impossible to track the constantly changing locations of rewarding patches of flowers using shared information if recruitment of foragers was via receivers and the limited information at their disposal.

Why do honey bees need a stop signal?

Due to fluctuations in nectar availability, the work capacity of one of the two groups, foragers or receivers, will often exceed that of the other. To redress this imbalance, one would expect that only one type of worker should be recruited at one time. That is, the bees in a colony should either perform waggle dances or tremble dances (or neither) but not both. However, these two dances can occur together (Nieh 1993; Seeley 1995). One probable reason for this are the time lags that occur between information acquisition and dancing so that information becomes out of date. A second reason is the unreliability inherent in the cues, search delays, which foragers use to make their recruitment decisions (Ratnieks and Anderson 1999, in press a). Unsurprisingly, therefore, there is a regulatory mechanism, the “stop signal” (Nieh 1993), which directly inhibits forager recruitment. Most stop signals (85%; Nieh 1993) are sent by tremble dancers and directed at waggle dancers with the effect that 16% of the waggle dancers immediately stop dancing and leave the nest, presumably to continue foraging but without recruiting more foragers. The stop signal is a negative feedback signal on forager recruitment, conveying the message “receivers are currently overloaded: stop recruiting more foragers”. Dance followers give most of the remaining signals. Given that followers move around the dance area, on which both dances occur (Seeley 1995), they are in a good position to determine whether waggle and tremble dances are being made concurrently. Interestingly, Nieh (1993) found that tremble dancers, who were the largest group to send stop signals, directed 34% of their signals to waggle dancers and 29% to tremble dancers. However, dance followers, the only other significant group to send stop signals, directed *all* of their signals to waggle

dancers. Is there some information available to tremble dancers (active foragers) but not to dance followers (inactive workers) that can explain this difference in the target(s) of the signal sent by these two groups of stop signal emitters?

Why do honey bees need the shaking signal?

The shaking signal appears to be emitted when nectar availability increases after a period of low nectar forager activity. In such a situation, most foragers will be unemployed and inactive. Clearly, it is in the interest of the colony to recruit additional foragers rapidly to exploit this new resource before conditions deteriorate. However, there will not be many foragers to do the recruiting, because there is little forager activity. Also there will not be many unemployed foragers in the dance area to be recruited. Therefore, recruitment through waggle dances alone is likely to be slow, leading to the need for an additional signal to complement forager recruitment: the shaking signal. After having been shaken, over half of the recipients moved to the dance area where they could be recruited to foraging (Schneider et al. 1986). There appears to be a strong link between the shaking signal and the waggle dance. Seeley et al. (1998) found that bees that send shaking signals appear to follow a particular pattern of behaviour. These workers, which are generally the first workers to leave the nest and inspect potential forage patches, emit shaking signals at the end of their early trips. On the next few trips they emit a mix of both shaking signals and waggle dances and then on subsequent trips tend to send only waggle dances (see Fig. 3–6 of Seeley et al. 1998). Thus, the shaking signal, which conveys a general message that foragers are required, appears to be linked to the waggle dance which provides specific information as to where foragers should work.

Why do honey bees not use a patch abandonment signal?

Why is there no known signal indicating poor patches in honey bee foraging regulation? That is, why is abandonment an individual decision made without any information from others rather than the result of a specific patch abandonment signal? Although the absence of evidence for a patch abandonment signal does not mean that no such signal exists (5 of the 17 known honey bee signals have only been elucidated within the last 10 years), there are logical reasons why a patch abandonment signal is not expected. Honey bee foraging is a highly energetic activity (e.g. Wolf et al. 1989) and at first sight it would make sense to warn nest-mates that an area is unprofitable. In fact, bumblebees use repellent scent marks for this purpose (Stout et al. 1998). In the context of a negative signal for a particular forage patch, consider three categories of foraging honey bees –

unemployed foragers, foragers working other patches, and foragers working the same patch – and whether the patch abandonment signal would be useful to them. The absence of a negative recruitment signal will not reduce the number of unemployed foragers that are directed to a poor patch. This is because no unemployed foragers will be directed to this patch anyway because recruitment of additional foragers is via positive recruitment to good patches. For foragers working other patches, the information is not relevant. And for foragers working the same patch, the information is redundant because they already have this information. In addition, if there were a patch abandonment signal, the foragers would have to spend time receiving and transmitting this signal in the nest.

Why do honey bees not switch between subtasks?

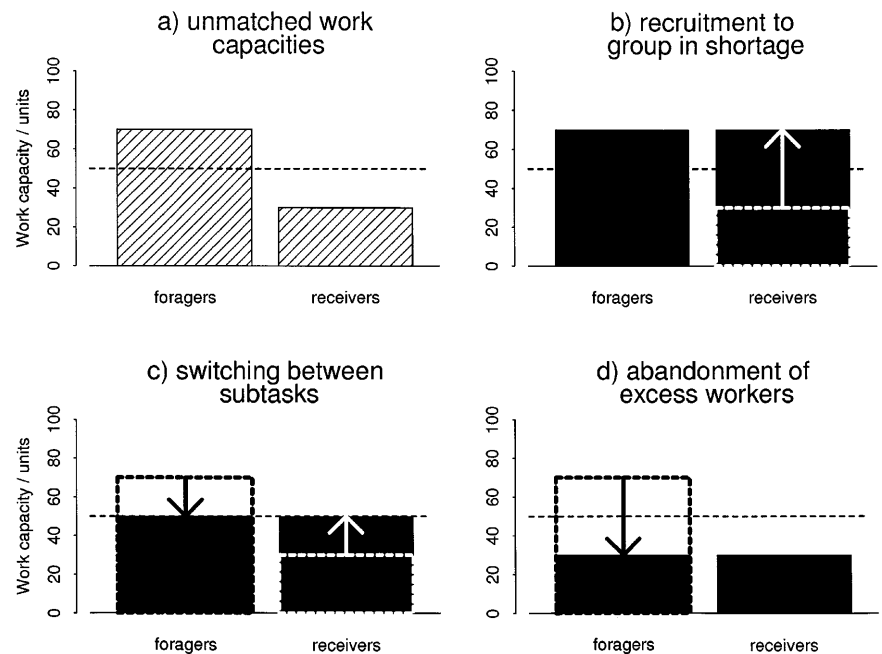
It appears that all signals and feedbacks used by honey bees in organising nectar collection are recruitment based. The only mechanism, apart from forager mortality, to reduce the number of workers involved in a subtask is abandonment. Why is this, given that there is an obvious alternative mechanism that could be used to alter worker allocation: switching between subtasks.

When the work capacities of the foragers and receivers are not matched, one solution is for some of the workers from the group in excess to switch to the overworked group, thereby balancing the work capacities, minimising mean queueing delay and maximising the nectar processing rate (Anderson 1998a, 1998b). Switching between subtasks is an important worker allocation mechanism during nest construction in small colonies of the social wasp *Polybia occidentalis*. Jeanne

(1986b) reported that in small colonies, the probability that a worker switches between the three nest-building subtasks – pulp foraging, water foraging and building – averaged 0.38. As honey-bees could use all three main mechanisms of worker allocation, i.e. recruitment, abandonment and switching (Fig. 3), why do they only use the first two? (Another mechanism which insect societies could use to balance work capacities is a change in the work rate of individuals performing a subtask. However, as this study focuses on worker allocation, the movement of workers between the different subtasks and unemployed status, this concept is not covered but could be considered as “partial abandonment”.)

Although all three mechanisms can balance work capacities, they differ in the final number of workers involved in the foraging process (Fig. 3). Switching between subtasks simply reallocates the workers currently involved whereas recruitment increases the total number of workers, and abandonment leads to a decrease. When exploiting fluctuating resources such as nectar, it may be critical to recruit unemployed foragers and workers involved in other tasks to exploit the resource before it becomes unavailable. That is, it is probably more important to recruit additional workers to collect the nectar than it is to match the work capacities of the workers currently collecting and storing nectar. When nectar availability decreases, individuals can abandon nectar collecting and receiving subtasks. Although they become unemployed foragers they remain available for rerecruitment if conditions change. Switching between subtasks, on the other hand, makes best use of a fixed number of workers but cannot respond in the same way to a change in the total amount of available nectar. Concerning the utility of switching between subtasks, a contrast can be made between honey bee nectar foraging

Fig. 3 Three possible mechanisms of worker allocation to balance work capacities in order to minimise queueing delays in a two-stage partitioned task. **a** The initial suboptimal situation that needs to be corrected. **b** Recruitment of workers to the group in shortage. **c** Switching of some workers from the group in excess to the group in shortage. **d** Abandonment by some of the workers in the excess group



and nest construction in *Polybia* wasps. In *Polybia*, the materials collected are wood and water which are not expected to fluctuate as they are superabundant – that is, freely available for the taking. In addition, *Polybia* has far fewer workers than the honey-bee and may not have excess workers to allocate to these tasks. In this way, nest construction in *Polybia* is far more suited to subtask switching than is nectar collection in the honey bee.

There are at least four additional reasons why recruitment plus abandonment might be favoured over subtask switching in the honey-bee. First, subtask switching causes workers to switch between roles. If there is any “performance efficiency” effect (Jeanne 1986a) and workers improve their ability to perform a task through repetition and learning, this increased ability will be lost when workers switch between the two subtasks. This is probably not the case with abandonment to unemployed status: skilled workers can wait in reserve until required and so the colony suffers a smaller loss of skills. However, with simple tasks or where performance efficiency is not a factor, recruitment plus abandonment is effectively equivalent to switching between subtasks when recruitment rates and abandonment rates are comparable. That is, excess workers who abandon their subtask and are then recruited to the other group, the group in shortage, are effectively switching between subtasks and the total number of active workers is unchanged. Second, switching between subtasks will reduce what is termed the “demographic advantage” (Jeanne 1986a). Foraging is generally the most risky subtask performed by a worker during her lifetime. If she performs this as the last task, she maximises her lifetime work output. Switching between subtasks would cause some young bees to switch to foraging and die early. Although there would be no cost if a living forager switched back to receiving, the costs arise from workers that have already died. [Visscher and Dukas (1997) showed that honey-bee foragers are subject to a constant probability of death per trip.] In addition, if switching between foraging and receiving is used to balance relative work capacities of the two groups, foragers are unlikely to be able to switch from foraging to receiving and prolong their life-span and thus their work contribution to the colony. This is because the necessary rate of switching from receiving to foraging required to counteract the depletion of foragers would be much higher than from foraging to receiving (Anderson 1998a, 1998b). Third, switching between subtasks in the honey-bee would introduce some time lags between being recruited and becoming available for the new subtask. A recruited receiver may first have to store any nectar in her crop before leaving as a forager, or a forager may have to store her load of nectar before she can start receiving depending on when recruitment takes place. In both cases, the ability of a colony to track a changing environment rapidly will be reduced (Anderson 1998a, 1998b). Fourth, switching between subtasks would cause some foragers, who work outside the nest and are more prone to encounter parasites, to switch to an internal

subtask thus possibly facilitating the spread of disease [see Schmid-Hempel’s (1998) “conveyor belt model”]. Moreover, task partitioning in itself increases the amount of interaction between workers (Ratnieks and Anderson 1999). Perhaps, and more importantly, the interactions will be increased between older and potentially diseased and contagious foragers with low life expectancy and in-nest workers with higher life expectancy. However, the importance of this effect is currently unknown.

Discussion

This paper has presented a functional evaluation of the proximate regulatory mechanisms employed by the honey bee in the nectar collection and storage process. Regulation involves at least four signals – the waggle dance (von Frisch 1967), the tremble dance (Seeley 1992), the stop signal (Nieh 1993) and the shaking signal (Allen 1959) – and possibly a fifth, worker piping (Pratt et al. 1996), as well as one other mechanism, patch abandonment (Seeley 1995). In theory, abandonment in combination with just two signals should be sufficient: one signal to recruit additional foragers and another to recruit additional receivers (Fig. 2). These three mechanisms could deal with all worker allocation requirements, such as the recruitment of additional workers during a nectar flow, matching of work capacities to maximise efficiency of those workers currently employed, and a reduction in colony activity during a nectar dearth. Why are at least two other signals used by the honey bee? One probable reason is the shortcomings and uncertainty in the information workers use to make recruitment decisions. This is suggested by Ratnieks and Anderson (in press a) who show that queueing delays, which are the cues honey bees use to modulate waggle and tremble dances, are inherently unreliable indicators of the relative work capacities of foragers and receivers. The mere fact that waggle dances and tremble dances occur together, necessitating a mechanism such as the stop signal, demonstrates some of the problems of decentralised control.

We have proposed various reasons why honey-bees might use a combination of recruitment and abandonment rather than switching between subtasks. During nest construction in small colonies of *P. occidentalis*, workers readily switch between the three building groups (Jeanne 1986b). However, in this situation, all three subtasks, pulp and water collection, and building, are external subtasks and thus transmission of disease into the colony is unlikely to be affected by subtask switching. Furthermore, switching between water and pulp foraging is unlikely to involve any loss of performance efficiency as both subtasks involve collecting a material that is likely to be readily available and in excess. Similarly, there is no loss in the demographic advantage as both are foraging subtasks. Interestingly, switching between subtasks in *Polybia*, and probably in

all species in which it occurs, does conform to the predicted best use of information. Workers experiencing long delays (which are more reliable sources of information than the short delays experienced by the group in shortage; Ratnieks and Anderson 1999) when trying to offload their material are the ones who switch. They apply negative feedback to themselves and positive feedback to the group in shortage, which is the best use of information.

We suggest that the two primary signals in the regulation of nectar foraging are the waggle and tremble dances and that these are complemented by two additional secondary signals, the stop signal and the shaking signal. Waggle and tremble dances are both broadcast (“one-to-many”) signals, although they only operate on quite a local scale, whereas both the stop signal and the shaking signal are clearly “one-to-one” signals. We suggest that the two broadcast signals, the waggle dance and the tremble dance, have evolved to recruit additional workers quickly. Although quick acting, they are inherently imprecise because of the unreliability in the cue used, the queuing delay experienced by the dancer (Anderson 1998b; Ratnieks and Anderson, in press a), in making the decision whether or not to dance. Thus these two signals produce a rapid coarse-tuning of the system. The stop signal and the shaking signal may be more reliable, in that they are based on a greater amount of information and therefore less likely to be made under the wrong colony conditions. For example, the shaking signal is made by foragers during changing colony conditions, something they can detect from their own experience and other cues from within the nest. Similarly, the cue that workers use when deciding to send the stop signal – the co-occurrence of waggle and tremble dancing – is also reliable. Moreover, both of the major groups of stop signal senders, the tremble dancers and dance followers, are likely to encounter the two dances if these are occurring simultaneously. Whereas an individual waggle dancer performs her dance on a small portion of comb and is unlikely to gain information on what other dancers are doing, a tremble dancer’s signal takes her over a much larger portion of comb (Seeley 1992, 1995), and dance followers are free to move across the whole dance area. It seems logical that the role of the stop and shaking signals in fine-tuning the system has evolved after coarse tuning. Whereas the stop signal operates on waggle dances and its present function has clearly evolved at a later stage, it is not clear when the shaking signal evolved. It was possibly the first signal that honey-bees used to regulate foraging (as a way of increasing total foraging effort) but could also have evolved later as fine-tuning.

Honey-bees still hold tantalising secrets concerning their colony organisation. Nectar foragers have a greater role than would be expected in that they recruit both additional foragers and receivers. What is it about foragers’ “contextual information”, that is, their own experience in addition to the information from other cues and signals from that particular trip [stretching Seeley’s

(1998) definition to include signal senders as well as recipients], which makes them more reliable recruiters than are the nectar receivers? Certainly they know the locations and qualities of various flower patches, but do they possess other valuable information? Are there any additional signals used in regulating foraging such as piping? Our analysis does not discount this possibility but the honey-bee already has more signals than the theoretical minimum needed. We predict that if more are discovered, than they will be used to fine-tune the system due to limitations in information quality which prevent the system from otherwise being precisely optimised. It is clear that the honey bee has a complex system of regulating nectar collection. But, as we have demonstrated in this review, it is also subtle and sophisticated.

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