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A self-organising network model of decision making by the honey bee swarm

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Abstract

Purpose – The purpose of this paper is to carry out a detailed investigation of the mechanisms operating during decision making by the honey bee swarm, which is now considered to be one of the best examples of collective decision making outside the human domain.

Design/methodology/approach – This investigation is based on a review of the last 60 years' published literature about swarm behaviour. It introduces a different perspective to the work by utilising a cybernetic model of a self-organising information network to analyse the findings of this body of research.

Findings – Scout bees evaluating potential nest sites accumulated support for their site by differential net recruitment, so the total scout numbers present at each site was a good measure of the total evidence in favour of the site and hence the relative probability of choosing it as the swarm's new home. The accumulation of evidence continued at a number of alternative nest site locations until a critical quorum threshold was sensed at one of them. The first alternative to reach the threshold was chosen as the preferred nest site. Quorum scouts then prepared the swarm for departure and steered it to its new home.

Originality/value – Swarm decision making has not been modelled as a self-organising information network before. This novel approach reveals how a combination of network modifications, self-amplification, self-attenuation, cross-inhibition, integration and quorum mechanisms together contribute towards accurate group decision making.

Keywords Decision making, Honey bee, Information network, Self-organization, Collective intelligence

Paper type Conceptual paper

Introduction

Strong honey bee colonies reproduce by dividing in the spring. The mother queen and about two-thirds of her workers leave the nest, fly to a nearby support such as a branch or a hedge, and form a swarm cluster. Scouts then fly out from the cluster to search the surrounding countryside for potential new nest sites (Winston, 1987). Sites judged to be of adequate quality are reported to the swarm cluster by the scouts' waggle dances, which provide information about site location and quality (Lindauer, 1955; von Frisch, 1967; Seeley and Buhrman, 1999; Seeley, 2010). The self-organising network model developed by Stafford Beer (1979) has previously been found useful for understanding this initial information gathering phase (Foss, 2015). This paper uses the model to investigate the decision-making phase in which the swarm decides which one of the 10-30 potential nest sites found is the best quality alternative. It then describes how the decision is implemented.

Decision making by the honey bee swarm is now considered to be one of the best examples of collective decision making outside the human domain (Seeley, 2010). It seems likely that a very high-selection pressure for successful nest site choice has acted on honey bee colonies during their evolution. Some swarms starve in the cluster

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stage because they fail to agree on an adequate nest site within the 3-4 day time window before they run out of food. A few die because they make a split decision between two candidate sites and the resulting swarm fractions are either too small to be viable or one lacks a queen (Lindauer, 1957). Even if they move into their new home successfully, unless it is completely survival worthy they will probably perish over the winter; in fact some 75 per cent of such swarms normally die even in good habitat (Seeley, 2010). It can be concluded that the swarm's life or death decision making has been so severely tested over the past 60 million years of evolution that it may be unusually robust and worthy of detailed investigation.

Honey bee colonies have probably evolved to deal with many of the more predictable characteristics of their environment, but the swarm is still faced by many uncertainties that affect its decision-making process. There is considerable variation in the numbers, quality and location of alternative nest sites. Also the order in which sites are discovered cannot be known in advance (Lindauer, 1955; Camazine *et al.*, 1999; Seeley and Buhrman, 1999). An effective decision-making strategy therefore needs to cope with all the variations encountered. For instance, the swarm must be able to deal with an excellent site found late on during decision-making period. Can it still be included in deliberations and even become the preferred site when the swarm is already poised to decide on a poorer but earlier found site? If many sites are found, can the swarm make an accurate decision quickly enough before it runs out of food?

Some decision-making parameters are easier to deal with. The quality of nest site cavities does not change greatly during the 3-4 day time window available, unlike forage patches which can become unprofitable within a few hours. The swarm can therefore select the best site from a number of alternatives that are being evaluated simultaneously. Also the marginal cost of discovering each additional alternative is relatively low (Lipman and McCall, 1976). It has therefore been suggested that a "best-of-N" decision-making strategy should be effective given these characteristics of its problematic environment (Seeley, 1977; Seeley and Buhrman, 2001).

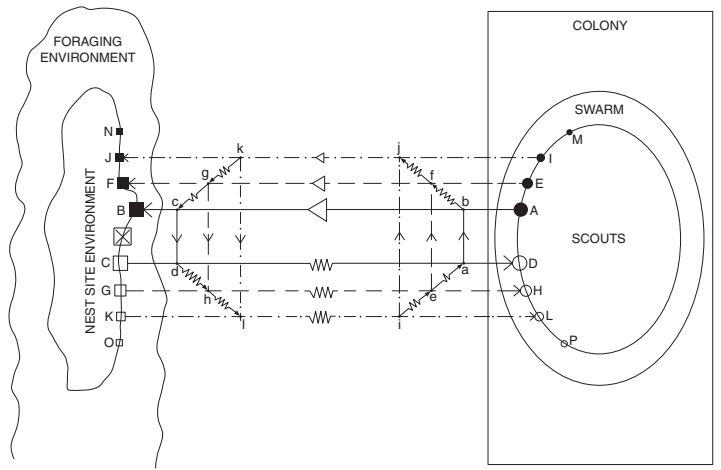
The information gathering phase was characterised by increasing rates of exploration and new site discovery, coupled with expanding recruitment to these sites from a large pool of uncommitted scouts. An increasing number of sites was being found but relatively few scouts had so far accumulated at each site (Seeley, 2010; Foss, 2015). In contrast, the decision-making phase is characterised by decreasing rates of exploration and new site discovery, coupled with slowing recruitment from a diminishing pool of uncommitted scouts. The number of sites under consideration declines but the number of scouts accumulated at the better sites is increasing. The information gathering phase overlaps the decision-making phase, but the dynamics are different (Seeley, 2010).

Results of the literature review

This investigation of decision making by the honey bee swarm is based on an extensive review of the last 60 years' published literature concerning swarm behaviour. It adopts a new approach by using a cybernetic model of self-organising information network (Beer, 1979) to analyse the decision-making process and to determine the mechanisms involved. It then goes on to show how the swarm implements its decision.

Decision making

The initial information gathering phase gradually gives way to the decision-making phase, though there is normally a certain amount of overlap because of later discovered sites (Foss, 2015). Figure 1 depicts the early stages of decision making and it shows that the scouts on



Nest site supporter loops: \longleftrightarrow ABCD; \longleftrightarrow EFGH; \longleftrightarrow IJKL

Loop MNOP abandoned following strong attenuation within the loop

Intra loop feedbacks: ab, cd; ef, gh; ij, kl (modify network processes)

Sensory cross inhibition channels: dh, ea, hl, ie (beeping stop signals)

Perceptual cross inhibition channels: bf, gc, fj, kg (competition for recruits)

Channel processes:

\triangleleft , amplification (recruitment);

WW , site non-specific attenuation (dance decay and retirement);

ZZ , cross inhibition

Transducers for: ●, navigation; ■, location; □, evaluation; ○, reporting (waggle dancing)

Ideal nest site: \boxtimes , loops nearer to it are for better quality sites

Notes: Nest site supporters on horizontal loop ABCD fly out on channel AB to evaluate potential nest site at C, then return on channel CD to report site location and quality by waggle dancing at D. The ABCD loop has vertical intra loop feedbacks ab and cd that modify amplification, attenuation and transduction processes *within* the loop. Similar mechanisms operate on loops EFGH and IJKL. There are also competitive interactions *between* the loops involving two types of mutual cross inhibition, namely sensory cross inhibition and perceptual cross inhibition (see above). These are described in more detail in the text

Figure 1.
A self-organising
network model of
decision making
by the swarm

loop MNOP have already abandoned their potential nest site because it was judged by them to be of mediocre quality. The elimination of poorer sites has therefore just started.

The scouts supporting the better quality sites fly more trips and their waggle dance reports contain more dance circuits, thereby advertising and consequently recruiting

more strongly (Seeley, 2010). This is shown by the larger transduction circles at points D and H than at L and the larger amplification symbols on channels AB and EF than on IJ. Recruits then recruit more supporters when they dance, so support for a better quality site will grow exponentially and will soon start to dominate the debate. Domination of the debate can be driven entirely by the per capita strength of advertising. This is because neutral, uncommitted scouts follow dances at random, rather than selectively, so support builds strictly in proportion to the amount of dancing for each site (Visscher and Camazine, 1999). The debate about two possible sites, for instance, can start with a 1:1 ratio of supporters, become a 3:1 ratio after three hours and after three more hours it can reach 9:1. Complete domination can therefore happen relatively quickly (Lindauer, 1955; Seeley and Buhrman, 2001).

But domination of the debate does not by itself result in complete agreement on nest site choice. Complete agreement requires that support for a poorer site eventually fades to nothing, so that deadlock does not occur between a few obstinate supporters of the poorer site and the numerous supporters of a good site. The swarm uses an ingenious attenuation process known as dance decay to prevent deadlocks from occurring.

The way this works is best described by an example from some experiments carried out by Seeley in 2003 in which he compared the patterns of waggle dancing by typical scouts advertising an excellent site or a mediocre site. He found that both dancers reduced their dance strength at the same rate (about 15 fewer dance circuits per trip back to the swarm) but the scout from an excellent site started with a stronger motivation to dance and so danced longer (six trips vs two trips) and louder ($90 + 75 + 60 + 45 + 30 + 15 = 315$ dance circuits vs $30 + 15 = 45$ dance circuits). Both dancers then retired and rested on the swarm surface before following other dances (Seeley, 2003).

The apparently constant rate of dance decay across all sites, whether excellent or mediocre, means that this attenuation process can be called site non-specific attenuation. It is shown in Figure 1 by the same-sized attenuation symbols on all three loops. It seems to be employed only by swarm scouts, in addition to the site-specific attenuation process that rejects poor sites at source without reporting them. Site non-specific attenuation is an example of modification to the original information network that was used by the foragers (Foss, 2015).

Site non-specific attenuation results in the cessation of disagreement because dance decay eventually tapers to zero and any obstinate scouts then retire from further dancing. They do not compare their old site with a new one and they do not convert to dancing for a new and better site as researchers once thought (Lindauer, 1957). Instead they lose the motivation to dance for their site and then quietly rest on the surface of the swarm cluster. Seeley (2003) found that 96 per cent of scouts stop dancing for their losing sites before they followed dances for other sites. In other words, losers first abstain, they do not compare and convert. Unlike human decision makers, scouts seem to stop supporting a position automatically, rather than only doing so after learning of a better one.

The effects of site non-specific attenuation are critical to the decision-making process. Early on it helps to eliminate the poorer sites from the debate, because support for these sites gradually dwindles away to nothing (see Figure 1, loop MNOP). This helps to focus the swarm's decision making on the better sites. Also the abstention of scouts supporting poorer sites reduces the total amount of dancing, which then stimulates uncommitted scouts to fly out and not only visit reported sites but also to search for new sites (Passino and Seeley, 2006; Janson *et al.*, 2007). In both cases,

novel opinions are introduced into the debate by new evaluation of known sites and by the discovery of previously unknown sites. Finally, later on during the debate, the chances of deadlocked decisions are reduced because potentially obstinate supporters of poorer sites automatically retire from the decision-making process. If they do so at a faster rate than they can recruit supporters, support for their site will eventually dwindle to zero (Seeley, 2010).

Decision making is also a natural selection type process. There are competitive interactions between the loops, known as mutual cross-inhibition, and this is thought to involve two main processes (Seeley, 2010; Schlegel *et al.*, 2012). In the first case, it has recently been found that during the late decision-making phase, scouts supporting a given potential nest site can produce beeping stop signals to inhibit waggle dancing by scouts from other sites (Niven, 2012; Schlegel *et al.*, 2012; Seeley *et al.*, 2012). The signalling scouts emit a high pitched beeping sound while head butting dancers from sites other than their own. This seems to stop these other waggle dancers in mid dance and it therefore reduces recruitment to the sites they are advertising. This process may be called sensory cross-inhibition, because it is the production of nest site reports, or sensory reports, that is being inhibited. Sensory cross-inhibition is a process of mutual inhibition, which means that the stronger the dancing for a site, the stronger will be the resulting inhibition of dancing for weaker competing sites and the weaker will be the dance inhibition that will be received from them in return. This is shown in Figure 1, where, for example, the strong dancing on loop ABCD attenuates very strongly the weaker dancing on loop EFGH via the channel dh, but the EFGH dancing only weakly attenuates the strong dancing on loop ABCD via the ea channel.

In the second type of mutual cross-inhibition, there is competition between different groups of scouts to recruit further supporters to their potential nest site from the finite pool of uncommitted scouts resting on the swarm surface. This pool is relatively large early on in the decision-making process, so, for example, if scouts on the ABCD loop advertise and recruit more strongly than those on the loops EFGH and IJKL, they will draw off potential recruits to their better quality nest site at a faster rate, leaving fewer available to be recruited to the poorer sites (Seeley and Buhrman, 2001). But as decision-making progresses, the pool shrinks further in size, so that one site's gain becomes another site's loss. Eventually this means that support for the poorest site visited by scouts on the IJKL loop will wither away to nothing and their recruitment dancing will peter out. The swarm will thereby have eliminated this site from further consideration. This type of mutual cross-inhibition may be called perceptual cross-inhibition because it attenuates the number of uncommitted scouts that are available to transduce the meaning of the waggle dancers' sensory reports into percepts that can be used by recruits to locate the sites (Goldstein, 2013). Perceptual cross-inhibition is also a process of mutual inhibition, which means that the stronger the recruitment on a loop, the stronger will be its inhibition of weaker competing loops and the weaker will be the inhibition that will be received from them in return (Passino and Seeley, 2006; Passino *et al.*, 2008). Figure 1 shows, for example, that the strongly recruiting loop ABCD attenuates very strongly along the bf channel, the recruiting efforts of the weaker EFGH loop, but that the EFGH loop only weakly attenuates the recruiting efforts of the ABCD loop along the gc channel.

Cross-inhibition between groups of scouts supporting different potential nest sites is a competitive process that provides the swarm with a powerful mechanism for selecting the better sites. It also tends to magnify any small differences in support

for the sites under consideration, providing the swarm with a mechanism for discriminating between them. Cross-inhibition therefore increases the reliability of swarm decision making by eliminating any residual problem of decision deadlock over sites of near equal value (Passino and Seeley, 2006; Passino *et al.*, 2008).

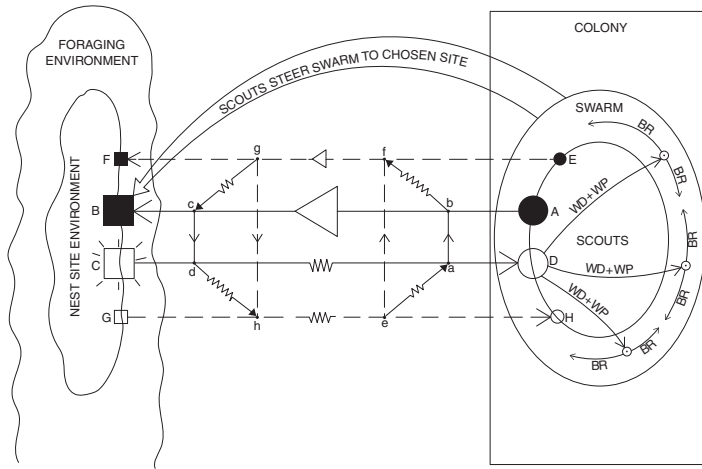
The net effect of the various amplification, attenuation and cross-inhibition processes on support for any given site can be judged by the number of scouts visiting and evaluating the site at any one point in time. This is actually a good measure of support because the number of scouts at a site is proportional to the number of dance circuits advertising it over the previous few hours (Lindauer, 1955; Seeley, 2010). There is, however, a problem of noisy individual-level reporting and the fact that reporting levels fluctuate over time. These two sources of noise are averaged out over a large number of individual scouts and over a period of time in a process of integration. Each potential nest site in fact functions as an integrator. Each site accumulates evidence of its support in terms of total scout numbers present and the evidence totals determine the relative probabilities of choosing alternative sites for the swarm's new home (Seeley, 2010).

The early experiments of Martin Lindauer suggested that swarms decided on the best potential nest site by reaching a consensus at the cluster. It was felt that each waggle dancer was in effect "voting" for a given nest site and gradually those from poorer quality sites were persuaded to dance for superior sites until their "votes" came into agreement for the best site. In order to achieve this the scouts would have to monitor progress so that they would know when agreement was reached by sensing a clear majority of dancing for one particular site. How they did this was unclear and it was suggested that it would be extremely difficult for scouts to poll fellow dancers in a jostling mêlée of bees on the surface of a swarm cluster (Lindauer, 1955; Seeley, 2010).

More recently the experiments carried out by Seeley and Visscher have shown that the swarm does not decide on the best nest site by sensing a consensus at the cluster, but by sensing a quorum at the preferred nest site (Seeley and Visscher, 2003, 2004). The number of scouts visiting the better quality nest sites increases as the number of sites under consideration falls and eventually one potential nest site may have accumulated as many as 20-30 bees simultaneously evaluating it. Because scouts spend considerable time at the cluster and flying to and from the nest site, this represents a total number of bees visiting and supporting the site in the region of 50-100 individuals. Research has shown that at this point the quorum threshold has been reached at that site and a decisive opinion poll taken. The scouts from this site now fly back to the swarm where they produce a new signal, known as worker piping, which indicates that they have decided their nest site is the best (Lindauer, 1955; Seeley and Tautz, 2001; Visscher and Seeley, 2007), (see Figure 2). Their decision is made without any knowledge of the numbers of scouts assembled at other potential nest sites.

The worker piping signal produced by the scouts from the chosen nest site is also combined with waggle dances for the site. The piping signals stimulate the swarm bees to warm up their flight muscles to at least 35°C, as they cannot fly to the chosen site otherwise. The waggle dancing by the pipers confirms their choice and probably helps to ensure a final consensus while the beeping stop signals prevent any advertising for other sites (Seeley *et al.*, 2012).

It is essential that by the time the swarm takes off it has reached a consensus among the scouts in order to fly as a single unit to one chosen site. Interestingly the rest of the swarm receives no information about the site so they have to defer to the scouts' decision. Preparations for departure take one hour or more, which is probably enough



Notes: All information as for Figure 1, but in addition note: Loop IJKL abandoned following strong cross inhibition between loops; ⊕ integration at potential nest site C accumulates critical quorum numbers of scouts; WD and WP, waggle dancing for the chosen site and worker piping signals; \odot , critical swarm temperature for flight; BR, buzz run signals

Figure 2.
Implementation of
the nest site decision
by the swarm

time for the positive feedback process of recruitment together with the negative feedback of beeeping stop signals to produce a unanimous agreement. Split decisions result in divided swarms that subsequently perish, so there has been strong selection pressure during evolution for unanimous decision making (Seeley, 2010).

Implementation of the decision

The swarm behaves like a homeothermic organism, controlling its core temperature to 34-36°C and its surface temperature above 17°C, regardless of ambient temperature (Heinrich, 1981). The scouts keep on piping until all the surface bees have also reached a thoracic temperature of at least 35°C, and it is this advance preparation that enables swarm cohesion on take-off (Seeley *et al.*, 2003). Increasing numbers of other bees also contribute to the piping signal so that the swarm starts to emit a rhythmical hum just before take-off. Many bees can be seen running about piping and gradually this changes to a new signal called the Schwirrlauf or buzz-run (Lindauer, 1955; Seeley, 2010). The buzz-run signalers push and burrow through the swarm cluster with outspread wings, whirring and buzzing noisily. This disrupts the cohesion of the cluster and eventually, when the scouts sense that all bees in the cluster are up to flight temperature, the buzz-run disruption activates a highly synchronized take off of all 10,000 bees in the swarm (see Figure 2). In conclusion, it can be seen that the scout's piping signals prime the swarm for take-off but it is the buzz-run signals that finally activate departure (Rittschof and Seeley, 2008).

Only about 400 scout bees know where the chosen nest site is and their role is to steer a small cloud of 10,000 bees several miles to one particular hole in a tree or wall (Seeley *et al.*, 1979). The scouts steer the swarm by flying very fast through the top of the slower moving swarm in the direction of their new home. These steaker bees move fast from the rear to the front of the flying swarm, then drop down below it,

rejoin the rear and repeat their rapid flight towards their home. Uninformed bees latch on to the stalker bees, accelerating after them. Soon a chain reaction develops, involving informed leader bees teaching new leader bees the direction of the nest site, so that the whole swarm gradually speeds up towards its destination (Schultz *et al.*, 2008; Latty *et al.*, 2009). The scouts slow down as they approach the nest site, then collect at the entrance, release an attractor pheromone known as Nasonov substance and move in through the hole, so that all bees are inside their new home within 10-15 minutes of arrival.

Discussion

The foregoing review of the last 60 years of research on honey bee swarming has described how the swarm integrates its information, debates its findings, reaches a consensus and implements its decision. The decision-making process is essentially a competition between groups of scouts that are visiting alternative nest sites to accumulate support for their site. The nest site chosen is the one whose accumulation of support first surpasses a critical quorum threshold. Once the quorum has been sensed, the quorum scouts prepare the swarm for departure, consolidate a consensus, initiate take off and steer the swarm to its new home (Seeley, 2010).

This paper has taken a novel approach by using the model of a self-organising information network that was developed by Stafford Beer (1979), to investigate the mechanisms operating during swarm decision making. It shows that, as decision-making progresses, the swarm makes constant modifications to its attenuation and transduction processes (see Figures 1 and 2 and Foss, 2015). Site non-specific attenuation was added to the negative feedback channels to provide the swarm with stronger site quality orientation than was found in the parent colony's former foraging operations (Gilley, 1988; Seeley, 2003). In addition, the transduction processes occurring at the potential nest sites were modified from quality evaluation to information integration and then to evidence accumulation and finally to quorum sensing. Transduction processes at the swarm also changed from site reporting by waggle dancing to departure preparations by worker piping and finally consensus consolidation by dancing and piping (Seeley, 2010; Seeley *et al.*, 2012). The results suggest that most modifications occurred on the swarm's sensory input channels, indicating that the feedback network dominates decision making. Decision making by the swarm is clearly a dynamic and ever changing process of self-organisation.

Decision making in the honey bee swarm is also a highly decentralised process. At an individual level, every scout is her own informant and chief (Free, 1977). At a group level, any nest site supporter group can decide that its site is the best once it senses that a quorum threshold has been reached (Seeley, 2010). In the human domain, people of a more dirigiste philosophy might claim that there are a number of disadvantages of decentralised decision making (Morcol, 2006; Nutt and Wilson, 2010). It can give rise to unnecessary task repetition and redundancy. But in the swarm numerous independent evaluations of the same potential nest site are needed to reduce individual and temporal noise to acceptable levels. A pool of redundant uncommitted scouts is needed to provide decision-making flexibility and a number of acceptable potential nest sites is needed in case the preferred site suddenly fails. Other critics might say that decentralised decision making can hinder a rapid global response, perhaps forgetting how slow some centralised bureaucracies are at making decisions and perhaps not knowing that the swarm saves time by starting departure preparations at the same time as it is still building a consensus (Seeley *et al.*, 1991; Seeley, 2010).

But possibly the greatest danger of decentralised decision making is that it can lead to conflicting actions (Seeley *et al.*, 1991). Studies of 19 swarms by Martin Landauer showed that just two produced split decisions because, in each case, two equally good potential nest sites elicited equally strong recruitment at about the same time. Competition between the two sites was so balanced that agreement was considerably delayed (Landauer, 1955). There is also a possibility of conflict arising because of the delay between making a local decision at a distant site and global awareness of this decision back at the swarm when the scouts arrive and announce it. Scouts from another nearer site could announce their decision first because of their shorter flight time. This is reminiscent of Libet's (1985) findings for the brain, namely, that choice is determined locally (unconsciously) before a person globally (consciously) decides to act. The delay between local decision and global awareness is probably a feature of other decentralised decision-making systems, but it is not known for certain whether the swarm can approve or veto the local decision once it has been taken.

There are, however, a number of advantages of the swarm's decentralised decision making. Any one of the 300-500 scouts in the swarm is capable of discovering a potential nest site and deciding whether it is of sufficient quality to report to the swarm. Local responses are therefore very rapid because no higher level approval is needed. Redundancy provides great flexibility and reliability for the swarm in case of scout losses or site failure and the marginal cost of finding another potential nest site is relatively low. But perhaps the greatest advantage of decentralising decision making is that it can release the full power of parallel processing, enabling the swarm to make complex decisions using relatively unsophisticated communication and computing elements (Simon, 1981). It is also likely that the natural selection type processes that operate during decision making in decentralised systems are often more effective and less biased than intentional selection by one or a small group of senior controllers (Popper, 1972; Hull, 1988).

The literature review emphasised the importance of the speed: accuracy trade-off inherent in all decision-making situations (Franks *et al.*, 2003; Chittka *et al.*, 2009). Use of the self-organising information network model indicated that there is probably an approximate balance between the two counteracting processes of recurrent amplification and gradual attenuation (Beer, 1979; Foss, 2015). This would enable the swarm to increase the accuracy of decision making because the activity of the different groups of nest site supporters would be prolonged over a greater period of time (Franks *et al.*, 2002). Increased decision time would in turn allow more comprehensive nest site surveys to be carried out, later found sites to be included in the debate, and temporal and collective integration to average out noise more effectively (Seeley, 2010). As a result, swarms do successfully implement the "best-of-N" decision rule (Seeley and Buhrman, 2001) and mathematical models of swarm decision making predict that they will be 90-95 per cent accurate at selecting the best available nest site (Passino and Seeley, 2006).

On the other hand, most authors considered that a certain amount of speed was necessary because swarm survival time is limited. Experimental research and mathematical modelling showed that, because site non-specific attenuation rapidly purged the poorest sites from the debate and cross-inhibition strongly selected out mediocre sites, the overall effects of attenuation were probably slightly stronger than amplification, which is to be expected in a decision-making system. This in theory would provide the swarm with a means of controlling the speed of its decision making by regulating various negative feedback mechanisms such as quorum size, dance

decay rate and beeping stop signals (Marshall *et al.*, 2009; Seeley, 2010). Research on ant swarms, for instance, has shown that quorum size can be reduced in harsh environmental conditions (Franks *et al.*, 2008).

Swarm decision making was found to be a non linear recursive process characterised by the expansion of information gathering and processing in multiple directions rather than in one logical linear direction (Usher and McClelland, 2001; Seeley, 2010). In systems with a central decider, it can then prove difficult to identify where to start decision making. In decentralised systems like the brain and the swarm, however, the decision is made where the requisite information first accumulates (McCulloch, 1965; Beer, 1979; Seeley, 2010). The decision-making centre is not pre-determined by rank or caste, but is determined by information flow. The actual location of the decision centre in the swarm was found to depend on a race between a number of independent accumulators of information to reach a critical decision threshold, the quorum threshold. The accumulation of information continued in a number of locations until the threshold was sensed at one of them and the first alternative to reach the threshold was chosen (Seeley and Visscher, 2004; Marshall *et al.*, 2009; Seeley, 2010). This location was where the requisite total amount of information in favour of the site had accumulated in the brains of the scouts present. Other researchers have suggested that the critical threshold may not always be determined by numbers but by density of individuals in a given space, or even their communication efficiency (Hense *et al.*, 2007). It seems more likely, however, that scouts estimate numbers of individuals present at a potential nest site not by counting them, but by encounter rate, which of course is density dependent.

It should be noted that the natural selection type processes provided by intra group attenuation and retirement and by inter group cross-inhibition, can only select the best competing alternatives, following which a quorum decision is needed to determine the best global solution. In other words a non intentional selection strategy only selects the “better-of-N”, while a final quorum decision strategy is needed to find the “best-of-N”. Hybrid algorithms combining both strategies (El Abd and Kamel, 2005) will therefore be needed to properly simulate honey bee swarm decision making. Furthermore, a distinction should be made between *bee swarm algorithms* and *bee colony algorithms*, as they describe decision making in entirely different situations.

A most interesting and unexpected discovery was that very few retired scouts switched to dancing for another site (Britton *et al.*, 2002; Seeley, 2003). Seeley, for instance, found that 96 per cent of scouts eventually retired from advertising their site and then rested quietly on the swarm surface without comparing or converting to alternative sites. It seems, therefore, that the swarm’s decision about the best potential nest site does not require direct or indirect comparisons of sites by individuals, it only needs strong unbiased recruitment to good quality sites, abandonment of poorer sites, cross-inhibition of mediocre sites and quorum sensing by the best supported sites. Decision making by the swarm is therefore a group-level process. The collective intelligence of the swarm far outstrips the cognitive capabilities of individual scouts (Franks *et al.*, 2002; Passino *et al.*, 2008).

The research made it quite clear that the scouts organise all aspects of swarming (Lindauer, 1955; Seeley, 2010). They do not just have an external nest site orientation, but attend to the needs of the swarm itself. The queen apparently contributes very little, apart from procuring the cohesion of the swarm cluster by producing the pheromone 9-oxo-trans-2-decenoic acid (Schmidt *et al.*, 1993). Nest site decision making

is widely distributed between 300-500 scouts and they almost invariably reach a dissent free decision. The rest of the swarm, however, receives no information, they just defer to the reliable, rigorously tested knowledge accumulated by the scouts. There is no global unanimity. The swarm is therefore a knowledge democracy.

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