Biological Foundations of Swarm Intelligence

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Summary. Why should a book on swarm intelligence start with a chapter on biology? Because swarm intelligence is biology. For millions of years many biological systems have solved complex problems by sharing information with group members. By carefully studying the underlying individual behaviours and combining behavioral observations with mathematical or simulation modeling we are now able to understand the underlying mechanisms of collective behavior in biological systems. We use examples from the insect world to illustrate how patterns are formed, how collective decisions are made and how groups comprised of large numbers of insects are able to move as one. We hope that this first chapter will encourage and inspire computer scientists to look more closely at biological systems.

1 Introduction

"He must be a dull man who can examine the exquisite structure of a comb so beautifully adapted to its end, without enthusiastic admiration."

Charles Darwin (1872)

When the Egyptians first started to keep honeybees 5,000 years ago, they surely must have marveled on the beauty of the bees' comb. Not only is the honeycomb beautiful to look at, but how did the bees decide to build hexagonal cells and not cells of another form? Initially it was suggested that hexagonal cells hold the most honey, but the French physicist R.A.F. de Réaumur realized that it was not the content of the cells that counts, but the amount of material, wax, that is needed to divide a given area into equal cells. Obviously at that time it was assumed that the bees were "blindly using the highest mathematics by divine guidance and command" (Ball 1999). It was not until Darwin that the need for divine guidance was removed and the hexagonal cells were thought to be the result of natural selection. In this view the bees' ancestors 'experimented' with different shaped cells, but the bees that by chance

'decided' to build hexagonal cells did better and, as a result, the building of hexagonal cells spread. In Darwin's words, *"Thus, as I believe, the most wonderful of all known instincts, that of the hive-bee, can be explained by natural selection having taken advantage of numerous, successive, slight modifications of simpler instincts; natural selection having by slow degrees, more and more perfectly, led the bees to sweep equal spheres at a given distance from each other in a double layer, and to build up and excavate the wax along the planes of intersection."* (Chapter 7, Darwin 1872).

It was exactly such 'Darwinian fables' that inspired the biologist and mathematician D'Arcy Wentworth Thompson to write his book *On Growth and Form* (Thompson 1917). The central thesis of this book is that biologists overemphasize the role of evolution and that many phenomena can be more parsimoniously explained by applying simple physical or mathematical rules. Thompson argued that the bees' hexagonal cells are a clear example of a pattern formed by physical forces that apply to all layers of bubbles that are pressed into a two-dimensional space. Bees' wax is not different, the soft wax forms bubbles that are simply pulled into a perfect hexagonal array by physical forces. Hence, the pattern forms spontaneously and no natural selection or divine interference needs to be invoked (Ball 1999).

In fact, many instances of spontaneous pattern formation can be explained by physical forces, and given the almost endless array of patterns and shapes found around us, it is perhaps not surprising that such patterns are an inspiration for many people, scientists and non-scientists alike. Upon closer examination, amazing similarities reveal themselves among patterns and shapes of very different objects, biological as well as innate objects. As we already alluded above, the characteristic hexagonal pattern found on honeycombs are not unique; the same pattern can be obtained by heating a liquid uniformly from below. Autocatalytic reaction-diffusion systems will lead to Turing patterns (think stripes on tigers) in both chemical and biological mediums (Kondo and Asai 1995; Ball 1999), and minerals form patterns that have even been mistaken for extra-terrestrial fossils (McKay et al. 1996).

The similarity of patterns found across a huge range of systems suggests that there are underlying principles that are shared by both biological and innate objects. Such similarities have been nicely illustrated by work on pattern formation in bacterial colonies. When one manipulates the amount of food available to bacteria and the viscosity of their medium, patterns emerge that are remarkably similar to those found in, for example, snowflakes (Ben-Jacob et al. 2000). In fact, the growth of bacterial colonies has proven to be an important playground for testing ideas on non-living branching systems (Ball 1999; Ben-Jacob and Levine 2001; Levine and Ben-Jacob 2004). As it turns out, many branching patterns found across nature can be explained by the same process, known as diffusion-limited aggregation, resulting from the interactions of the particles, be they molecules or individual bacteria (Ball 1999).

All patterns described above have been explained by approaching the systems from the bottom up: how do the particles interact with each other and with their immediate environment? One may not really be surprised by the fact that the same approach helps one to understand bacteria as well as molecules. After all, bacteria aren't really that different from molecules, are they? In the following we will illustrate how such a bottom-up approach can explain another remarkable feature of honeybees: the typical pattern of honey, pollen and brood found on combs.

The honeybee's comb is not only a marvel because of its almost perfect hexagonal cells, the bees also seem to fill the cells with brood (eggs that develop into larvae and then pupae and finally emerge as young workers or males), pollen (to feed the brood) and nectar (which will be converted into honey) in a characteristic pattern. This pattern consists of three distinct concentric regions: a central brood area, a surrounding rim of pollen, and a large peripheral region of honey (Fig. 1). If we envision the honeybee colony as a three-dimensional structure, this pattern is most pronounced in the central combs which intersect a large portion of the almost spherical volume of brood. How does this pattern come about? The storage of pollen close to the brood certainly makes sense as it reduces the time needed to get the pollen to the brood. But how do the bees know this? Do they use a blueprint (or template) to produce this characteristic pattern, implying that there are particular locations specified for the deposition of pollen, nectar and brood? Or is the pattern self-organized and emerges spontaneously from the dynamic interactions between the honeybee queen, her workers and the brood? Scott Camazine set out to determine which of these two hypotheses is the most parsimonious (Camazine 1991).

The beauty of working on macroscopic entities such as insects is that you can individually mark them. Honeybees are particularly suitable because we can then house them in what we call an observation hive, a glass-walled home for the bees. This means that we can study the interactions of the individually marked bees without taking them out of their natural environment (see Fig. 1).

Camazine did just that. He monitored the egg-laying behavior of the queen, of foragers that returned with pollen or nectar, and of nurse workers, those that feed the brood. The first thing that he observed was that the queen is rather sloppy in her egg-laying behavior, moving about in a zig-zag-like manner, often missing empty cells and retracing her own steps. Camazine further noticed that she has a clear preference to lay a certain distance from the periphery of the comb and never more than a few cell lengths of the nearest brood-containing cell. Interestingly, even though the queen somewhat has a preference for at least the middle of the comb and the vicinity of brood, bees returning with pollen or nectar did not seem to have a preference for specific cells at all. When an empty comb was left in the colony and the deposition of nectar and pollen observed, both could be found in any cell. Even though such absence of a preference clearly refutes the blueprint hypothesis, it does not explain how the characteristic pattern ultimately arises.

Fig. 1. Because of their relatively large size, we can easily mark individual bees in a colony. In this particular colony we marked 5,000 bees by combining numbered plates and different paint colors. This allowed us to study their behavior at an individual level. Photograph taken by M. Beekman.

As it turns out, bees do have a clear preference when they *remove* pollen or honey from cells. Both honey and pollen are preferentially removed from cells closest to the brood. By following the pattern of cell emptying during a period in which foraging activity was low (overnight or during rain), Camazine observed that all the cells that were emptied of their pollen or nectar were located within two cells or less from a cell containing brood. No cells were emptied that were further from brood cells. It is easy to see why the bees would have a preference for the removal (through use) of pollen that is found closest to the brood, as it is the brood that consumes the pollen. In addition, nurse bees are the younger bees which restrict most of their activity to the brood area (Seeley 1982).

The preferential removal of pollen and nectar from cells closest to cells containing brood and the queen's preference for laying eggs in cells close to brood made Camazine realism that this might explain the honeybee's characteristic comb pattern. But how to prove this? This is where the physicist's approach comes in. By constructing a simulation model based on his behavioral observations, Camazine was able to closely follow the emergence of the pattern. Initially, both pollen and nectar were deposited randomly throughout the frame with the queen wandering over the comb from her initial starting point. Despite the random storage of pollen and nectar, the queen's tendency to lay eggs in the vicinity of cells that already contain brood rapidly results in an area in which mostly brood is found. This is enhanced by the bees' pref-
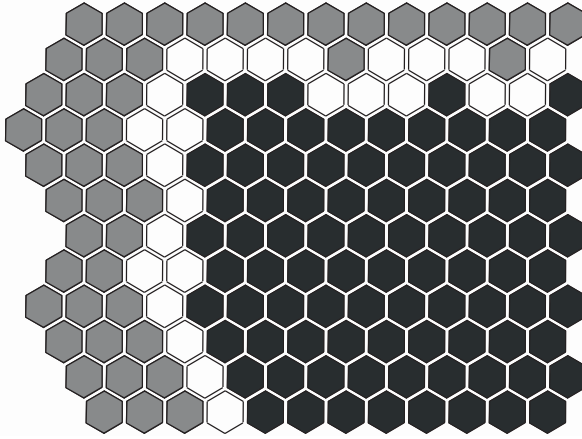
Fig. 2. The typical pattern of honey (grey cells), pollen (white cells), and brood (black cells) as seen on a honeybee's comb. Shown is the top-left corner of the comb

erence to remove honey and pollen from cells close to brood, which increases the availability to the queen of cells to lay eggs in. This further reduces the number of cells available for storage of honey or pollen. Thus, the brood area is continually freed of honey and pollen and filled with eggs resulting in a compact brood structure. But how do the pollen and nectar get separated (Fig. 2)?

Because initially both are deposited randomly, both pollen and nectar will be present in the periphery of the comb. However, most pollen that gets collected on a daily basis is consumed that same day. This means that given the normal fluctuations in pollen availability, there is often a net loss of pollen, with pollen present in the periphery being consumed at nearly the same rate as pollen being stored elsewhere. At the same time, these empty cells are most likely to be filled with nectar, as the nectar intake is much higher, and soon there is no longer space to store pollen. Where is pollen stored then?

Eventually the only place left for pollen to be stored is the band of cells adjacent to the brood. The developmental time from egg to adult is 21 days, meaning that for three weeks a brood cell cannot be used for anything else. But in the interface zone between the brood and the stores of honey at the periphery, the preferential removal of honey and pollen continuously provides a region in which cells are being emptied at a relatively high rate. And it is these cells that are available for pollen. Other cells that become available because bees emerge from them are found in the middle of the brood nest, but these will then be preferentially emptied and again filled with eggs.

Without his computer simulation Camazine would not have been able to fully understand how the behavior of the individual bees resulted in the organized pattern of brood, honey and pollen on the comb of the bees. And this

is a general principle for understanding collective animal behavior: without tools such as simulations or mathematics, it is impossible to translate individual behavior into collective behavior. And it is exactly with those tools that originally came from disciplines outside of biology, and with the view that interactions among individuals yield insights into the behavior of the collective, that we biologists have learned from physics. In fact, we began this chapter by illustrating that even biological phenomena can often more parsimoniously be understood using physical explanations, and that many systems, both innate and living, share the same physical principles. And it has exactly been these similarities and the wide applicability of the mathematical rules that govern diverse behaviors that have led to the field of Swarm Intelligence (e.g. Dorigo et al. 1996; Dorigo and Di Caro 1999).

However, it is important to realise that our biological 'particles' are more complex than molecules and atoms and that the 'simple rules of thumb' of self-organization (Nicolis and Prigogine 1977) have only limited explanatory power when it comes to biological systems (Seeley 2002). Bacterial colonies may grow in a similar pattern as minerals, Turing patterns may be found on fish, in shells and in chemical reactions, and we can understand the bees' hexagonal cells using physics, but when it comes to biological systems, an extra layer of complexity needs to be added. Besides the complexity of the individuals, we cannot ignore natural selection acting on, for example, the foraging efficiency of our ant colony, or the building behavior of our termites. If the underlying principles that govern the building behavior of termites results in colony-level behavior that is far from functional, this would be rapidly selected against. Moreover, it is of no use to assume that certain systems must behave similarly simply because they 'look' similar. It is true that if the same mathematical model or behavioral algorithm captures the behavior of different systems, then we can talk about similarities between systems that go beyond simple analogy (Sumpter 2005). However, as we will explain in the concluding section of this chapter, true biological inspiration needs to come not from the superficial similarities between systems, but from the intricate and often subtle differences between them. We shall illustrate this standpoint by drawing examples from our own study systems: decentralized decision making in social insects and the coordinated movement of animal groups.

2 Decentralized Decision Making

The evolution of sociality, the phenomenon where individuals live together within a nest such as is found in many bees and wasps, and all ants and termites, has created the need for information transfer among group members. No longer can each individual simply behave as if solitary, but actions by different group members need to be carefully tuned to achieve adaptive behavior at the level of the whole group. Insect colonies need to make many collective decisions, for example where to forage, which new nest to move to, when to

reproduce, and how to divide the necessary tasks among the available work-force. It is by now well known that such group-level decisions are the result of the individual insects acting mainly on local information obtained from interactions with their peers and their immediate environment (Bonabeau et al. 1997; Camazine et al. 2001). In other words, decision making in insect societies is decentralized. To illustrate how insect colonies achieve this, we will describe foraging and nest site selection in ants and honeybees.

2.1 Where to Forage?

In order to organize foraging, social insects need a form of recruitment. Recruitment is a collective term for any behavior that results in an increase in the number of individuals at a particular place (Deneubourg et al. 1986), and allows insect societies to forage efficiently in an environment in which food sources are patchily distributed or are too large to be exploited by single individuals (Beckers et al. 1990; Beekman and Ratnieks 2000; Detrain and Deneubourg 2002). In addition, social insects that transfer information about the location of profitable food sources can exploit an area much larger than those that lack such a sophisticated recruitment mechanism. Honeybees are a prime example. Their sophisticated dance language (von Frisch 1967) allows them to forage food sources as far as 10 km from the colony (Beekman and Ratnieks 2000).

Exact recruitment mechanisms vary greatly among the social insects but can be divided into two main classes: direct and indirect mechanisms. Mass recruitment via a chemical trail is a good example of indirect recruitment. The recruiter and recruited are not physically in contact with each other; communication is instead via modulation of the environment: the trail. The recruiter deposits a pheromone on the way back from a profitable food source and recruits simply follow that trail. In a way such a recruitment mechanism is comparable to broadcasting: simply spit out the information without controlling who receives it. The other extreme is transferring information, figuratively speaking, mouth to mouth: direct recruitment. The best-known example of such a recruitment mechanism is the honeybees' dance language. Successful foragers, the recruiters, perform a stylized 'dance' which encodes information about the direction and distance of the food source found and up to seven dance followers (Tautz and Rohrseitz 1998), potential recruits, are able to extract this information based upon which they will leave the colony and try to locate the advertised food source. Recruitment trails and the honeybee dance language can be seen as the two extremes of a whole range of different mechanisms used by social insects to convey information about profitable food sources.

Many computer scientists are familiar with the double bridge experiment as an example of the means by which foraging is organized in ant colonies. In this experiment a colony of trail-laying ants is offered two equal food sources located at the end of two paths of different lengths. After some time the

vast majority of foragers converges on the shorter path (Beckers et al. 1993). This collective choice for the nearest source is the result of a positive feedback process: Ants finding food mark the environment with pheromone trails during their return to the nest, and ants searching for food probabilistically follow these trails.

The same trail-following behavior allows an ant colony to choose the best food source out of several possibilities without the individual ants directly comparing the quality of the food sources on offer. Experiments performed on several species of ants have shown that ants modulate the amount of pheromone deposited depending on the quality of the food source, such that the better the quality, the more pheromone is left and the more likely other ants are to follow the trail to the best food source (Beckers et al. 1990; Beckers et al. 1993; Sumpter and Beekman 2003).

The success of the pheromone trail mechanism is likely to be due, at least in part, to the non-linear response of ants to pheromone trails where, for example, the distance that an ant follows a trail before leaving it is a saturating function of the concentration of the pheromone (Pasteels et al. 1986). In other words, the probability an ant will follow a trail is a function of trail strength (expressed as concentration of pheromone), but ants never have a zero probability of losing a trail, irrespective of the strength of the trail. Mathematically, non-linearity in response means an increase in the number and complexity of solutions of the model equations that may be thought of as underlying foraging (linear equations have only a single solution). Biologically, a solution to a differential equation corresponds to a distribution of ants between food sources and an increase in solutions implies more flexibility as the ants 'choose' between possible solutions. Such an allocation of workers among food sources, which assigns nearly all trail-following foragers to the best food source, is optimal provided the food source has unlimited capacity. When the food source does not have unlimited capacity, the result is that trail-following ants will be directed to a food source at which they cannot feed. In a way the colony gets 'stuck' in a suboptimal solution and can only get out of this solution by adding some layers of complexity, such as negative pheromones signalling 'don't go there', or individual memory so that the individual remembers that following that particular trail does not yield anything. A second drawback of relying on pheromone trails is that it may be difficult to compete with an existing trail, even if a better food source is found. If, due to initial conditions, a mediocre food source is discovered first, ants that have found a better quality food source after the first trail has been established will not be able to build up a trail strong enough to recruit nest mates to the newly discovered bonanza (Sumpter and Beekman 2003). Again, the ants are stuck in a sub-optimal solution.

Because of their fundamentally different recruitment mechanism, honeybees cannot get stuck in a sub-optimal solution. This direct recruitment behavior, the dance, encodes two main pieces of spatial information: the direction and the distance to the target. Both are necessary as, unlike ants, honey-

bees need to deal with a three-dimensional space. During a typical dance the dancer strides forward about 1.5 times her length vigorously shaking her body from side to side (Tautz et al. 1996). This is known as the 'waggle phase' of the dance. After the waggle phase the bee makes an abrupt turn to the left or right, circling back to start the waggle phase again. This is known as the 'return phase'. At the end of the second waggle, the bee turns in the opposite direction so that with every second circuit of the dance she will have traced the famous figure-of-eight pattern of the waggle dance (von Frisch 1967).

The most information rich phase of the dance is the waggle phase. During the waggle phase the bee aligns her body so that the angle of deflection from vertical is similar to the angle of the goal from the sun's current azimuth. Distance information is encoded in the duration of the waggle phase. Dances for nearby targets have short waggle phases, whereas dances for distant targets have protracted waggle phases.

Dance followers need to be in close contact with the dancer in order to be able to decode the directional information (Rohrseitz and Tautz 1999). Hence, directional information is transferred to a limited number of individuals. Moreover, more than one dance can take place at the same time, and these dances can be either for the same site or for different sites. This means that there is no direct competition between dances, provided the number of bees available to 'read' a dance is infinite (a likely assumption). Dances are only performed for food sources that are really worthwhile.

In order to assess the quality of the food encountered, a forager uses an internal gauge to assess the profitability of her source, based on the sugar content of the nectar and the distance of the patch from the colony, as well as the ease with which nectar (or pollen) can be collected. A bee's nervous system, even at the start of her foraging career, has a threshold calibrated into it which she uses to weigh these variables when deciding whether a patch is firstly worth foraging for at all, and secondly worth advertising to her fellow workers (Seeley 1995).

Dancing bees also adjust both the duration and the vigor of their dancing as a function of profitability of their current source (Seeley et al. 2000). The duration of the dance is measured by the number of waggle phases that the dancer performs in a particular dance, and the vigor is measured by the time interval between waggle phases (the return phase). The larger the number of waggle phases, and the smaller the return phase, the more profitable the source is and the more nest mates will be recruited to it. This means that when two dances are performed simultaneously, one for a mediocre and one for a superb site, the dance for the superb site is more likely to attract dance followers than the one for the mediocre site. At the same time, however, the dance for the mediocre site will still attract some dance followers, because potential dance followers do not compare dances before deciding which one to follow (Seeley and Towne 1992). The result is that a honeybee colony can not only focus on the best food sources to the extent that most foragers will collect food at the best sites (Seeley et al. 1991), but is also able to swiftly refocus

its foraging force in response to day-to-day, or even hour-to-hour, variation in available forage (Visscher and Seeley 1982; Schneider and McNally 1993; Waddington et al. 1994; Beekman and Ratnieks 2000; Beekman et al. 2004).

2.2 Exploration Versus Exploitation

Most, if not all, studies on the allocation of foragers over food sources have used stable environments in which the feeders or forage sites were kept constant (e.g. Beckers et al. 1990; Seeley et al. 1991; Sumpter and Beekman 2003). When conditions are stable the optimal solution from the colony's point of view is to focus solely on the best food source (provided this food source is so large that it allows an infinite number of individuals to forage it) and this is exactly what many species of ants do that collect stable food sources such as honeydew (a sugary secretion produced by aphids) (Quinet et al. 1997), or leaves (Darlington 1982; Wetterer et al. 1992). These species construct long lasting trails (trunk trails) that connect the nest to foraging locations. In some species trails are more or less permanent due to the workers actively changing the environment by removing vegetation (Rosengren and Sundström 1987; Fewell 1988). As soon as conditions are not stable, however, which is mostly the case in nature, it becomes important to have a mechanism that allows the change-over to another food source or food sources when they have become more profitable or when the initial food source has been depleted. This means that in order to do well in a dynamically changing environment, insect colonies should allow the storage of information about food patches which are currently exploited but at the same time allow the exploration for new sites.

The key to keeping track of changing conditions is the trade-off between exploitation and exploration: the use of existing information (exploitation) versus the collection of new information (exploration). How do the two extreme recruitment mechanisms, trail-based foraging and the honeybee's dance language, allow for the discovery of new food sources?

As mentioned earlier, trail-following ants never have a zero probability of losing a trail, irrespective of the trail resulting in some ants getting lost even when the trail is at its strongest. Assuming that these 'lost' ants are able to discover new food sources and thus serve as the colony's explorers or scouts, this 'strategy of errors' (Deneubourg et al. 1983; Jaffe and Deneubourg 1992) allows the colony to fine-tune the number of scouts depending on the profitability of the food source that has already been exploited. This is because the weaker the trail (indicating the presence of a mediocre food source), the more the number of ants that get 'lost' and hence become scouts. When the trail is very strong (indicating that a high-quality food source has been found) a smaller number of ants will lose the trail, resulting in a smaller number of scouts.

The regulation of scouts in honeybees similarly assures the correct balance between the number of individuals allocated to exploration and exploitation. An unemployed forager (an individual that wants to forage but does not know

where to forage) will first attempt to locate a dance to follow. If this fails because the number of dancers is low, she will leave the colony and search the surroundings, thereby becoming a scout (Beekman et al. 2007). As a result, the number of scouts is high when the colony has not discovered many profitable forage sites, as dancing will then be low, whereas the number of scouts will be low when forage is plentiful and the number of bees performing recruitment dances high (Seeley 1983; Beekman et al. 2007). This so-called 'failed follower mechanism' (Sumpter 2000; Beekman et al. 2007) provides the colony with the means to rapidly adjust its number of scouts depending on the amount of information available about profitable forage sites. Even when the colony is exploiting profitable patches, there may still be other, undiscovered, profitable sites that are not yet exploited. As soon as there is a reduction in the number of dances occurring in the colony, the probability that some unemployed foragers are unable to locate a dance increases, and the colony therefore sends out some scouts. Such fluctuations in the number of dances regularly occur in honeybee colonies, even when there is plenty of forage (Beekman et al. 2004).

2.3 Where to Live?

Amazing as an insect colony's collective food collection is, even more amazing is that the same communication mechanisms are often used to achieve a very different goal: the selection of a new nest. A colony needs to select a new home under two conditions. Either the whole colony needs to move after the old nest has been destroyed, or part of the colony requires a new nest site in the case of reproductive swarming (where the original colony has grown so much that part of it is sent off with one or more new queens to start a new colony). This means that colonies of insects need to address questions very similar to the questions we ask ourselves when changing homes (Franks et al. 2002). What alternative potential new homes are available? How do their attributes compare? Has sufficient information been collected or is more needed? House hunting by social insects is even more piquant, as it is essential for the colony that the decision be unanimous. Indecisiveness and disagreement are fatal (Lindauer 1955). House hunting has been studied in detail in two species of social insect only, in the ant and the honeybee. Both study systems have been selected for ease with which this process can be studied. The ant *Temnothorax albipennis* forms small colonies (often containing about 100 workers) and lives in thin cracks in rocks (Partridge et al. 1997) and can easily be housed in the laboratory. By simply destroying their old nest, the ants are forced to select a new one (Sendova-Franks and Franks 1995). Moreover, because of their small colony size, it is not that hard to uniquely mark all individuals (and they don't sting!), which greatly facilitates the study of their behavior.

Honeybee swarms normally have many more individuals (approximately 15,000 bees (Winston 1987)), but researchers often work with swarms that contain 4,000 to 5,000 bees (Seeley et al. 1998; Camazine et al. 1999; Seeley

and Buhrman 1999; Seeley and Buhrman 2001; Seeley 2003; Seeley and Visscher 2004; Beekman et al. 2006). The great benefit of honeybees is that we can artificially make swarms by simply taking the queen out of the colony and shaking the 5,000 or so bees needed to produce an experimental swarm. And, if necessary, we label the bees individually in the same manner as when we study foraging.

By offering our homeless insects nest sites that differ in quality, we can carefully study which attributes the ants or bees value in their new home. At the same time we can get a clear picture of the behavioral repertoire that underlies collective house hunting. These behaviors can then be used to construct individual-based models aimed at understanding precisely how the actions of the individuals result in collective choice.

House Hunting in Honeybees

Tom Seeley was the first to systematically study house hunting in social insects using the honeybee as his model organism. Seeley started out by determining what attributes the bees look for when judging the suitability of a potential new nest site. By working on a tree-less island (this species of honeybee normally inhabits tree hollows but happily lives in man-made hives when no tree hollows are available), Seeley and his colleague Buhrman could manipulate the kind of nest sites the bees could choose from. By manipulating the nest site's main attributes, such as content and size of the entrance, they could determine what constitutes a 'mediocre' and a 'superb' site from the bees' point of view. This further allowed them to study how good a bee swarm is at choosing the best nest site out of several possibilities (Seeley and Buhrman 2001). And, not surprisingly, they are pretty good at it because when offered an array of five nest boxes, four of which were mediocre because they were too small (bees like large nest sites with a small nest entrance), in four out of five trials the bees chose the superb nest site. How do they do it?

As with recruitment to forage sites, bees that have found a nest site that is considered worthwhile will perform a dance upon returning to the swarm. By filming the dances of bees returning from both mediocre and superb sites, Seeley and Buhrman (2001) could study how the dances differed between the two. What they observed was that bees tune their dance in three ways. Firstly, bees returning from a superb site dance longer than bees returning from a mediocre site. Secondly, a dance for a superb site contains more waggle phases (the part of the dance that encodes the distance to the site). Lastly, dances for superb sites are 'livelier', meaning that the period between two subsequent waggle phases is shorter. Hence, there is a clear difference in dance behavior between bees returning from mediocre and superb sites, but this is not different from bees dancing for high and mediocre quality food sources which leads to most, but not all, bees focusing on the best food source. Dances for forage will never converge; instead there will always be different sites ad-

vertised simultaneously. However, a swarm needs to select just one nest site unanimously and this suggests that dances for nest sites do converge.

Scout bees, those bees that search the environment for suitable new nest sites, fly out in every direction and return to the swarm with information about nest sites found. Initially, many dances will take place on the swarm, advertising all sites that have been judged to be good enough. Within a few hours, however, many sites are no longer danced for, and just before the swarm takes to the air to fly to its new home, most, if not all, dances will be for a single site (Seeley and Buhrman 1999). Such a unanimous decision is reached without scouts comparing multiple nest sites (Visscher and Camazine 1999) or potential dance followers selecting dances for the best nest sites. The most likely reason why the swarm is ultimately able to select one nest site that is mostly the best is dance attrition. In contrast to the dances for forage, where bees will keep dancing for a forage site provided it remains profitable, bees returning from a potential new nest site ultimately cease dancing (Seeley and Buhrman 2001; Seeley 2003) even when their discovered nest site is of superb quality.

The process goes like this. A bee that has returned from the best site possible will perform, say, 100 waggle phases during the first dance that she performs for that nest site. After she has finished her dance, she returns to the nest site to confirm that it is still superb. Upon returning to the swarm, she will advertise her site again, but will now reduce the number of waggle phases to 80. After this dance she flies off again to her site and the process repeats itself. This means that after five trips, this bee will not perform a dance upon her return (as she will have reduced the number of waggle phases after each return trip), but in the meantime she will have performed protracted and lively dances for her site. Compare this with a bee that has found a mediocre site. This bee will perform, say, only 60 waggle phases during her first dance, 40 on her second dance, etc. until she ceases dancing altogether. She not only dances for a shorter period, but the number of dances performed for her site is also less than the number of dances performed by the bee that found the superb site. Hence, the 'length of advertising' differs significantly between the mediocre and superb site and, as a result, more bees will be recruited to the superb site than to the mediocre site, and those bees, provided they also rate the site as superb, will perform lengthy dances and recruit more bees. It has been suggested, based on a mathematical model, that this dance attrition is crucial to the swarm's ability to decide on one site (Myerscough 2003), but this assumption awaits empirical testing.

Even though many behaviors of the bees involved in the swarm's decision-making process have been described in great detail (for a nice overview see Visscher 2007), without the use of a mathematical or simulation model it is not immediately obvious how individual behavior is translated into collective behavior and the swarm's ability to choose the best nest site. Understanding in more detail the swarm's decision-making process led one of us, Madeleine Beekman, together with two computer scientists, Stefan Janson and Martin

Middendorf, to construct an individual-based model of a honeybee swarm choosing a new home (Janson et al. 2007). Not only did we want to construct a model that would behave in a realistic way, we wanted also to use that model to get an idea about two aspects in particular which are hard to study using real honeybee swarms: how a swarm regulates the number of individuals that explore the surroundings for nest sites (as opposed to recruiting individuals to nest sites that have already been discovered), and how scouts search their environment. Both questions address the trade-off between using existing information (exploitation) and acquiring new information (exploration) and how this trade-off affects the quality of the decision made at the level of the swarm.

We assumed that the bees would use the same behaviors and decision rules both when foraging and when deciding on a new home. We therefore started by applying the same exploration decision rule as had been applied in the context of foraging: an individual bee that has not yet decided where to search will always start by attempting to locate a dance to follow. The longer it takes to find a dance, the more likely this bee is to fly off and search independently (explore). This simple decision rule gave the following result (see Fig. 3): when the nest site known to the swarm is only of mediocre quality, not many bees will dance for that nest site and many bees will search independently because they have a low chance of finding a dance to follow; the reverse is true when a superb nest site has been found, as now most returning bees will dance for this nest site (note that we included individual variation in our bees such that an individual has a probability of dancing that increases with increasing quality of nest site). Clearly, applying the failed follower mechanism also works very well in house hunting and ensures an elegant balance between the number of bees recruiting to a known nest site and the need to search the environment for a better nest site.

All experimental work done so far on nest site selection in honeybee swarms used nest sites which were located at equal distance from the swarm, a situation which is highly unlikely under natural conditions where nest sites are present at all distances. Imagine a situation in which the swarm has discovered a nest site nearby, but this nest site is only of very mediocre quality. We now know that under this condition the swarm allows for more bees to explore the surroundings in case a better nest site is found; but how should the swarm distribute its scouts over the environment to allow the discovery of such a further site in the first place? The great benefit of using models is that one can manipulate the experiment. Hence, in our simulation model we were able to control which nest site was discovered first by the swarm by simply sending the first scout to that particular nest site. At the same time we could give our scouts different 'search rules' to investigate how these rules affect the swarm's decision. The search rules we used were the following: scouts were sent out such that all nest sites irrespective of their distance were equally likely to be discovered (*uniform* $P_u = 1/250$); the chance of discovery decreased with increasing distance from the swarm (*distance* $P_d = 1/\text{distance}$); sites nearby had
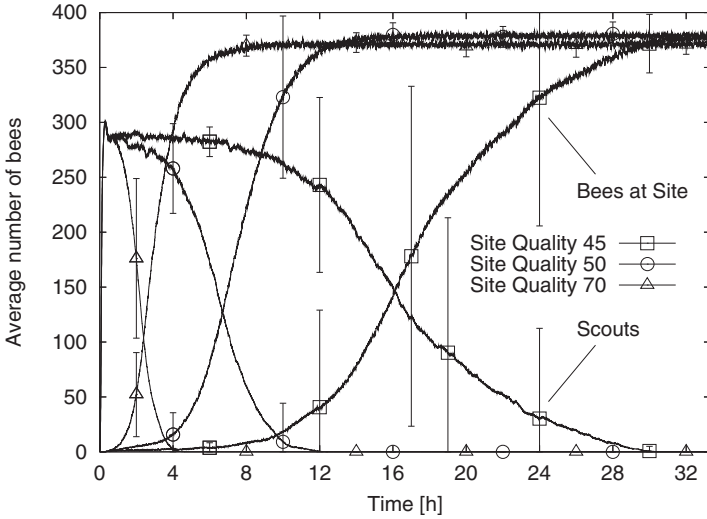
Fig. 3. Average number of bees scouting for a nest site and average number of bees assessing a nest site (e.g., the number of bees that already know about the location of a potential new nest site) when nest sites of different quality (70: good site, 50: mediocre site, 45: poor site) were offered to the swarm. The vertical bars indicate the standard variation (50 runs per experiment). (Fig. 6 in Janson et al. (2007).)

a much higher probability of being discovered than sites present further from the swarm (*distance squared* P_s =250/distance^2). Our results showed that the best search strategy from the swarm's point of view would be to focus on nearby sites without ignoring possible sites further away. Hence, most scouts are expected to search in the vicinity of the swarm, whereas some are likely to fly out further. This prediction can relatively easily be tested using real honeybee swarms.

Ants Moving House

The ant *Temnothorax albipennis* is rather different from the honeybee. Not only are its colonies much smaller, decision making seems much more dependent on individual decisions. For example, when offered a choice between two nest sites, about half of the ants directly compare the quality of those sites and can therefore make an informed choice (Mallon et al. 2001). At the same time, however, the other half does not directly compare the different options but these poorly informed ants still contribute to the colony's overall decision. How does their decision-making mechanism work?

Individual behavior of *T. albipennis* during nest site selection has been described in great detail (Mallon et al. 2001; Pratt et al. 2002). *T. albipennis* does not use pheromone trails to recruit nest mates but instead relies on

tandem running, where one individual guides a second individual by staying in close contact, and social carrying, where the recruiter simply picks up another ant and carries it across to the new nest site (the queen is always carried!). In the beginning of the process, only tandem runs are performed by scouts that have discovered a potential new nest. Similarly to the honeybee, *T. albipennis* scouts know what they want in a new home: it should be spacious and the entrance should be relatively small so that it can easily be defended. The probability that a scout will initiate tandem recruitment to the site that it has just found depends on the quality of that site. Moreover, assessment duration (the time spent inspecting the potential new nest) varies inversely with the quality of the site. Hence, the better the scout judges that site to be, the faster it will start recruiting. By leading a single individual towards the nest site discovered, the scout basically teaches the recruit how to get to the new nest site so that this recruit, if it decides that the nest site is indeed of good quality, can lead other ants to that site. The result is a build-up of ants at good quality sites, whereas sites of poor quality will not attract many ants.

When the number of ants present at a particular nest site reaches a certain level, the quorum threshold, no more tandem recruitment takes place but instead ants still present in the old nest are picked up and simply carried to the new nest site. Brood items (eggs, larvae and pupae) will also be moved in this way. Why does *T. albipennis* have two recruitment methods, one slow (tandem runs) and one fast (social carrying)?

During the period in which tandem recruitment takes place, the quality of the nest site discovered is assessed independently by each ant that either discovered that site via scouting or was led to it via tandem recruitment. This ensures that the 'opinions' of many ants about the site's quality are pooled, thereby increasing the likelihood that that site is indeed of sufficient quality. At the same time, the slow build-up of ants at the discovered site allows for a better site to be discovered, as recruitment to this site will be faster and hence the number of ants will rapidly increase. Because of the different recruitment to sites depending on their quality, the quorum will be reached faster at the better site, after which social carrying will be initiated. This last phase enables the colony to move into the chosen site rapidly (remember that these ants move when their old nest site has been destroyed).

The above is a verbal description of the ants' collective choice based on observations of their individual behaviors. But can this sequence of behaviors really account for the ants' collective choice? To answer this question Stephen Pratt and his colleagues (Pratt et al. 2005) incorporated everything they knew about individual behavior into an agent-based model of collective nest choice. They then used this model to simulate emigrations and compared the outcomes of these *in silico* emigrations with those performed by real ant colonies. When the simulated ants were presented with a single site, the time course of the emigration generally conformed to experimental data. More interesting, however, was what the simulated ants did when confronted with two potential sites that differed in quality. The model predicted that about 10% of each

colony should typically be carried to the site of lower quality by the time the old nest is completely empty, a result of many individuals basing their decision on information on one nest site only. This prediction was confirmed by using real colonies and offering them the same choice as the *in silico* ants. The agent-based model therefore provides strong support for the interpretation of the ants' individual behavior.

3 Moving in Groups

In many animal species, individuals move in groups as they perform seasonal migrations, travel to food sources and return to safe havens, often over considerable distances (Boinski and Garber 2000; Krause and Ruxton 2002; Couzin and Krause 2003). The movement of these groups is commonly self-organized, arising from local interactions between individuals rather than from a hierarchical command center. Self-organized group movement is not restricted to groups of relatively 'simple' creatures such as insect swarms or schools of fish, but may even include 'intelligent' species like us. One of the most disastrous examples of collective human group movement is crowd stampede induced by panic, often leading to fatalities as people are crushed or trampled (Helbing et al. 2000).

There are two extreme ways in which groups can 'decide' on a direction of movement. Either all individuals within the group contribute to a consensus, or else relatively few individuals (for convenience we will call these 'leaders') have information about the group's travel destination and guide the uninformed majority. Thus, in some species, all individuals within a group share a genetically determined propensity to travel in a certain direction (Berthold and Querner 1981; Berthold et al. 1992) or all are involved in choosing a particular travel direction (Neill 1979; Grünbaum 1998). In contrast, a few informed individuals within a fish school can determine the foraging movements of the group and can steer a group towards a target (Reebs 2000; Swaney et al. 2001). Similarly, very few individuals (approx. 5%) within a honeybee swarm can guide the group to a new nest site (Seeley et al. 1979).

When leaders are present, the question arises as to how these informed individuals transfer directional information to the uninformed majority. Similarly, in the absence of leaders how is a consensus reached about travel direction? Such questions are almost impossible to address without having first developed a theoretical framework that explores possible mechanisms.

Recently, two theoretical studies have addressed the issue of information transfer from informed to uninformed group members. Stefan Janson, Martin Middendorf and Madeleine Beekman (2005) modeled a situation in which the informed individuals make their presence known by moving at a higher speed than the average group member in the direction of travel. Guidance of the group is achieved by uninformed individuals aligning their direction of movement with that of their neighbors. Because the informed individuals

initially move faster, they have a larger influence on the directional movement of the uninformed individuals, thereby steering the group.

A second model by Iain Couzin and colleagues (2005) shows that the movement of a group can be guided by a few informed individuals without these individuals providing explicit guidance signals and even without any individual in the group 'knowing' which individuals possess information about travel direction. Only the informed members of the group have a preferred direction, and it is their tendency to go in this direction that steers the group. The main difference between the two models lies in the presence or absence of cues or signals from the informed individuals to the uninformed majority. Janson et al.'s (2005) leaders clearly make their presence known, whereas Couzin et al.'s (2005) model suggests that leadership can arise simply as a function of information difference between informed and uninformed individuals, without the uninformed individuals being able to tell which ones have more information. It seems likely that the exact guidance mechanism is species-dependent. When the group needs to move fast, for example a swarm of honeybees that cannot run the risk of losing its queen during flight, the presence of leaders that clearly signal their presence might be essential, as the group otherwise takes a long time to start moving into the preferred direction. However, when the speed of movement is less important than group cohesion, for example because being in a group reduces the chance of predation, leaders do not need to signal their presence.

If there are no leaders, the essential first step before a group can start to move cohesively is some level of consensus among the individuals in their alignment. How is this achieved when there are no leaders? Most likely there are a minimum number of individuals that need to be aligned in the same direction before the group can start to move in a particular direction without breaking up. If the number of equally aligned individuals is below this threshold, the group does not move cohesively. As soon as this threshold is exceeded, coordinated movement is achieved. Such a non-linear transition at a threshold is known in theoretical physics and mathematics as a phase transition. Interestingly, we have recently discovered, for the first time, similar transitions in biological systems (Beekman et al. 2001). Theoretical physicists have developed a suite of models, termed self-propelled particle (SPP) models, which attempt to capture phase transitions in collective behavior (Vicsek et al. 1995). SPP models aim to explain the intrinsic dynamics of large groups of individuals. Later we shall show how this theoretical framework can be applied to the collective movement of locusts. But first we will describe some experimental results on group movement in honeybee swarms, locusts and Mormon crickets.

3.1 Honeybees on the Move

Deciding where to live is only one part of a honeybee swarm's problem. The second problem arises once that decision has been made: how does the small

number of informed bees (about 5%) convey directional information to the majority of the uninformed bees in such a way that the swarm moves in unison? In the previous section we already described two theoretical possibilities: either leaders signal their presence to the uninformed majority, or they do not but simply move in their preferred direction. In fact, the model by Janson and colleagues was inspired by a suggestion made in the early 1950s by Martin Lindauer (1955). Lindauer observed in airborne swarms that some bees fly through the swarm cloud at high speed and in the correct travel direction, seemingly 'pointing' the direction to the new nest site. He suggested that these fast-flying bees, later named 'streakers' (Beekman et al. 2006), are the informed individuals or scouts. Lindauer got this idea while working in war-ravaged Munich where he used to run with his honeybee swarms in an attempt to find out where they were going. Like every scientist who takes himself or herself seriously, at least at that time, Lindauer used to wear a white lab coat, even when he was out in the field with the bees. One of his field sites was near a mental hospital and rumor has it that one day he was mistaken for an escaped mentally ill patient (Tom Seeley, personal communication). Luckily, Lindauer ran faster than the guards who tried to catch him, which gives one an indication of how fast a swarm of bees flies!

An alternative to Lindauer's hypothesis (which we will refer to as the 'vision' hypothesis) is the olfaction hypothesis of Avitabile et al. (1975). They proposed that the scouts provide guidance by releasing assembly pheromone from their Nasanov glands (a gland found between the last two tergites of the bee's abdomen) on one side of the swarm cloud, thereby creating an odor gradient that can guide the other bees in the swarm. Until very recently neither the vision hypothesis nor the olfaction hypothesis had been tested empirically, though other investigators have confirmed Lindauer's report that there are streakers in flying swarms (Seeley et al. 1979; Dyer 2000).

Madeleine Beekman, Rob Fathke and Tom Seeley (2006) decided that it was time to shed some light on this issue. In that study they did two things. They studied in detail the flights of normal honeybee swarms (containing approximately 15,000 bees) and smaller (4,000–5,000 bees) swarms in which the bee's Nasanov gland was sealed shut by applying paint to every single bee in the swarm. This meant that sealed-bee swarms could not emit the Nasanov pheromone (they had to apply paint to all bees in the swarm because they had no means of knowing which bees would be the scouts). By using a 'bait-nest site' that they made extremely attractive to a bee swarm, they could be almost certain that their swarms would select that nest site. This allowed them to follow the swarm (as Lindauer did through Munich, though they used an open field), measure its speed and the time it took the swarm to settle in its new home. Using this procedure and several sealed-bee swarms allowed them to show that even if every single bee in the swarm was unable to produce the Nasanov pheromone, the swarm was still able to fly more or less directly towards the new nest site. From this they concluded that scouts do not use pheromones to guide the swarm.

Proving the vision hypothesis was more difficult. They decided that a first step would be to show that there is variation in flight speed and flight direction among the individual bees within a flying swarm by taking photographs of a large swarm during its flight to the bait hive such that individual bees appear as small, dark streaks on a light background. The faster the flight speed of a bee, the longer the streak it produced using this technique (provided the bee flew in the plane of vision). Each photograph was analyzed by projecting it onto a white surface to create an enlarged image. They then measured the length (in mm) and the angle (in degrees, relative to horizontal) of each dark streak that was in focus in the enlarged image. Because a size reference was present in each photograph, and because each photograph recorded the bees' movements during a known time interval (1/30 s), they were able to calculate for each photograph the conversion factor between streak length and flight speed. Using this procedure they could quantify what they saw while running with the swarms: that a portion of the bees fly much faster in the direction of travel while the majority of the bees seem to fly much slower and with curved flight paths. Moreover, the fast-flying bees, the streakers, appeared to be most common in the upper region of a swarm. For humans, and probably also for bees, streakers are much more easily seen against the bright sky rather than the dark ground or vegetation, so by flying above most of the bees in a swarm, the streakers may be facilitating the transfer of their direction information to the other bees. Future work should focus on determining if it is indeed the streakers that are the scouts, those with information about the location of the new nest site.

3.2 Locusts

To this point we have considered examples of self-organization and swarm intelligence in highly structured social groups, in which there is a distinction between reproductive individuals and more or less sterile workers and pronounced division of labor among workers. But not all cohesively behaving animal groups are so structured. Some consist of individuals that are essentially all the same. And, as we shall see in the next section, the forces that bind and propel such groups may be very sinister indeed.

Of the approximately 13,000 described species of grasshopper that exist across the world, 20 or so are particularly notorious. For much of the time they are just like any other harmless grasshopper — but, occasionally, and catastrophically, they change and instead of living solitary lives, produce massive, migrating aggregations. As juveniles they form marching bands that may extend for kilometers. Once they become winged adults, they take to the air as migrating swarms that may be hundreds of square kilometers in area and travel hundreds of kilometers each day. More than one fifth of the earth's land surface is at risk from such plagues and the livelihood of one in ten people on the planet may be affected. These grasshoppers are called locusts.
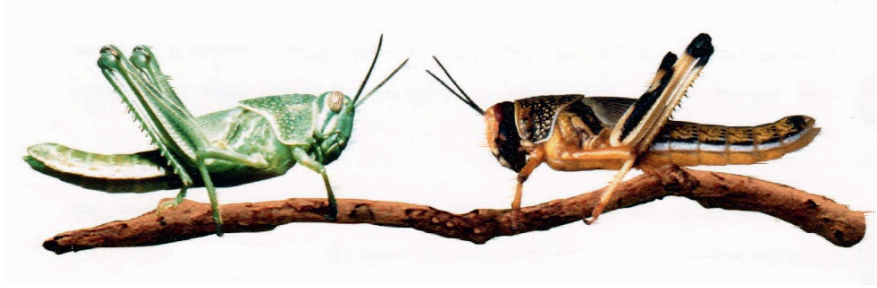
Fig. 4. The two extreme forms of juvenile desert locusts. When reared in a crowd, locusts develop into the gregarious phase, whereas the same individual if reared alone would develop into the solitarious phase (photo by S. Simpson).

Phase Polyphenism: The Defining Feature of Locust Biology

Unlike other grasshoppers, locusts express an extreme form of density dependent phenotypic plasticity, known as 'phase polyphenism'. Individuals reared under low population densities (the harmless, non-migratory 'solitarious' phase) differ markedly in behavior, physiology, color and morphology from locusts reared under crowded conditions (the swarm-forming, migratory 'gregarious' phase) (Pener and Yerushalmi 1998; Simpson et al. 1999; Simpson and Sword 2007). In some species, such as the infamous migratory locust of Africa, Asia and Australia (*Locusta migratoria*), the phenotypic differences are so extreme that the two phases were once considered to be separate species (Uvarov 1921; Fig. 4). In fact, not only are the two phases not different species, they are not even different genotypes: the same animal can develop into the solitarious or the gregarious phase depending on its experience of crowding. The genetic instructions for producing the two phases are, therefore, packaged within a single genome, with expression of one or other gene set depending on cues associated with crowding.

   At the heart of swarm formation and migration is the shift from the shy, cryptic behavior of solitarious phase locusts, which are relatively sedentary and avoid one another, to the highly active behavior and tendency to aggregate typical of gregarious phase insects. In the African desert locust, *Schistocerca gregaria*, this behavioral shift occurs after just one hour of crowding (Simpson et al. 1999). In recent years progress has been made towards understanding the physiological and neural mechanisms controlling behavioral phase change in locusts. In the desert locust the key stimulus evoking behavioral gregarization is stimulation of touch-sensitive receptors on the hind (jumping) legs. These receptors project via identified neural pathways to the central nervous system and cause release of a suite of neuro-modulators, among which serotonin initiates phase transition through its action on neural circuits controlling behavior (Simpson et al. 2001; Rogers et al. 2003, 2004; Anstey et al., unpublished).

Phase characteristics, including behavior, not only change within the life of an individual, they also accumulate epigenetically across generations (Simpson et al. 1999; Simpson and Miller 2007). Solitarious females produce hatchlings that are behaviorally gregarized to an extent that reflects the degree and recency of maternal crowding. If crowded for the first time at the time of laying her eggs, the mother will produce fully gregariously behaving offspring. In contrast, if a gregarious female finds herself alone when laying eggs, she will produce partially behaviorally solitarized young (Islam et al. 1994a,b; Bouaïchi et al. 1995). The gregarizing effect is mediated by a chemical which the mother produces in her reproductive accessory glands and adds to the egg foam in which she lays her eggs in the soil (McCaffery et al. 1998). In effect, female locusts use their own experience of being crowded to predict the population density that their young will experience upon emerging from the egg and predispose them to behave appropriately. As a result phase changes accumulate across generations.

Group Formation

Behavioral phase change within individuals sets up a positive feedback loop, which under appropriate environmental conditions promotes the rapid transition of a population from the solitarious to the gregarious phase. If they can, solitarious locusts will avoid each other. However, if the environment forces them to come together, close contact between individuals will rapidly induce the switch from avoidance to active aggregation, which will in turn promote further gregarization and lead to formation of groups. Given that gregarious phase locusts are migratory and move together, either as marching bands of juveniles or swarms of winged adults, there is the likelihood that local groups coalesce, ultimately seeding the formation of massive regional swarms. In contrast, when previously aggregated individuals become separated, they will begin to solitarize, hence reducing their tendency to aggregate and so promoting further solitarization. If the habitat tends to keep locusts apart, then this will ultimately lead to resolitarization of a gregarious population. Interestingly, the switch from solitarious to gregarious occurs more rapidly than the reverse transition (Roessingh and Simpson 1994), indicating a hysteresis effect.

Small-scale features of resource distribution determine the extent to which phase change occurs in a local population of desert locusts. Clumping of resources such as food plants, roosting sites, and areas of favorable microclimate encourages solitarious locusts to come together and as a consequence to gregarize and aggregate (Bouaïchi et al. 1996). The degree of clumping of food plants in the parental environment in turn influences the phase state of the offspring (Despland and Simpson 2000a).

The relationships between resource distribution, resource abundance, and locust population size have been explored using individual-based computer simulations, parameterized using experimental data from locusts (Collett et

al. 1998) . The extent of gregarization within a simulated population increases with rising locust population density and increasing clumping of food resources. Critical zones at which solitarious populations gregarize precipitously appear in the model across particular combinations of resource abundance, resource distribution and population size. Subsequent experimental data support the predictions from the simulation model (Despland et al. 2000).

The spatial pattern of food distribution interacts with the nutritional quality of foods to determine the spread of phase change within local populations (Despland and Simpson 2000b). Nutritional effects are mediated through differences in locust movement (Simpson and Raubenheimer 2000). Insects provided with poor quality food patches are highly active and are likely to contact one another and gregarize even when food patches are not clumped. In contrast, locusts with nutritionally optimal food patches do not move far after feeding, resulting in limited physical interactions between individuals, even when food patches are highly clumped.

It is clear that small-scale features of the habitat such as resource abundance, quality and distribution either promote or impede phase change within local populations. The same pattern seems to apply at intermediate scales of a small number of kilometers (Babah and Sword, 2004) but at higher spatial scales the relationship between vegetation distribution and desert locust outbreaks changes as different ecological processes come into play. At the scale of individual plants, a fragmented habitat with multiple dispersed patches encourages solitarization, whereas at the landscape scale the pattern is reversed: habitat fragmentation brings migrating locusts together and encourages outbreaks (Despland et al. 2004).

Understanding patterns of collective movement across local to landscape scales requires answering two questions: what causes bands of marching hoppers (the juvenile stages) and flying adults to remain as cohesive groups, and what causes them to move synchronously and collectively between patches at different scales?

Collective Movement

Locust aggregations will build into major outbreaks only if locally gregarized populations remain together and move collectively into neighboring areas of habitat, where they can recruit further locusts to the growing band. Unless such cohesive movement occurs, local aggregations will disband and individuals will return to the solitarious phase.

Within marching bands of juvenile locusts, individuals tend to synchronize and align their directions of travel with those of near neighbors (Despland and Simpson 2006). It had been shown in the laboratory that marching begins only at high locust densities (Ellis, 1951), but these experiments did not measure how and why alignment increases with density to the point that an aggregation of locusts suddenly commences collective marching.
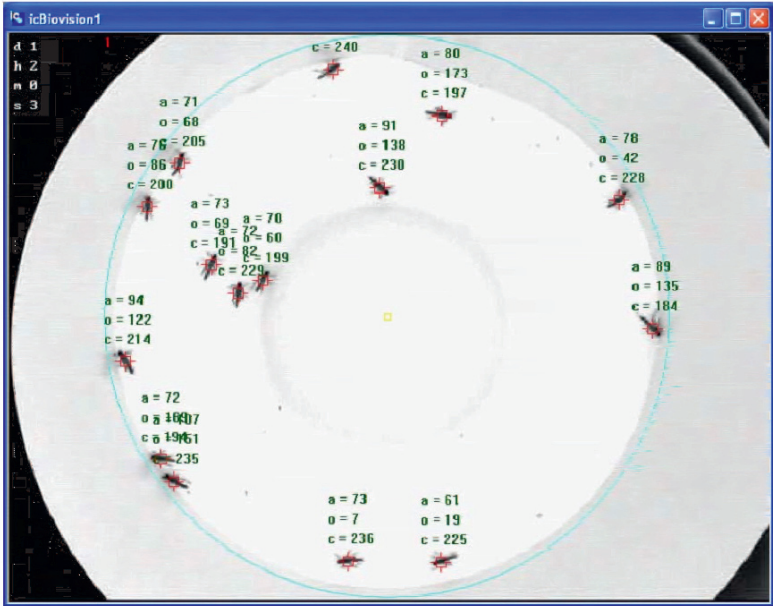
Fig. 5. An image from the Mexican hat marching arena and tracking software used in Buhl et al.'s (2006) study of collective marching in gregarious locusts. For a movie see `http://www.sciencemag.org/cgi/content/full/312/5778/1402/DC1`.

This problem has recently been studied by Jerome Buhl and colleagues (2006) by modeling locusts as self-propelled particles (SPP), each 'particle' adjusting its speed and/or direction in response to near neighbors. The model developed by Vicsek et al. (1995) was used because of its small number of underlying assumptions and the strength of the universal features it predicts. A central prediction from the model is that as the density of animals in the group increases, a rapid transition occurs from disordered movement of individuals within the group to highly aligned collective motion. Since SPP models underlie many theoretical predictions about how groups form complex patterns, avoid predators, forage, and make decisions, confirming such a transition for real animals has fundamental implications for understanding all aspects of collective motion. It is also particularly important in the case of locusts as it could explain the sudden appearance of mobile swarms.

Buhl et al.'s experiments involved studying marching in the laboratory in a ring-shaped arena, rather like a Mexican hat in shape, with a central dome to restrict optical flow in the direction opposite to that of individual motion. For data analysis, Iain Couzin developed an automated digital tracking system, allowing the simultaneous analysis of group-level and individual-level properties, which is technically extremely challenging but essential for discovering the link between these levels of organization (Fig. 5).

Juvenile locusts readily formed highly coordinated marching bands under laboratory conditions when placed in the Mexican hat arena. Individuals selected collectively either a clockwise or counter-clockwise direction of travel (the choice of which was random) and maintained this for extended periods. Experiments were conducted in which the numbers of locusts in the arena ranged from 5 to 120 insects (densities of 13 to 295 m^2). The locusts' motion was recorded for eight hours and the resulting data were processed using the tracking software to compute the position and orientation of each locust.

Coordinated marching behavior depended strongly on locust density (Figs. 6, 7). At low densities (2 to 7 locusts in the arena, equating to 5 to 17 locusts per m^2) there was a low incidence of alignment among individuals. In trials where alignment did occur it did so only sporadically and after long initial periods of disordered motion. Intermediate densities (10 to 25 locusts; 25 to 62 per m^2) were characterized by long periods of collective marching with rapid, spontaneous reversals in rotational direction. At densities higher than 74 per m^2 (30 or more locusts in the arena) spontaneous changes in direction did not occur, with the locusts quickly adopting and maintaining a common rotational direction.

Hence Buhl et al.'s experiments confirmed the theoretical prediction from the SPP model of a rapid transition from disordered to ordered movement (Figs. 6, 7) and identified a critical density for the onset of coordinated marching in juvenile locusts. In the field, small increases in density past this threshold would be predicted to result in a sudden transition to a highly unpredictable collective motion, making control measures difficult to implement. The experiments also demonstrated a dynamic instability in motion at densities typical of locusts in the field, whereby groups can switch direction without external perturbation, potentially facilitating rapid transfer of directional information. Buhl et al.'s data and model also suggest that predicting the motion of very high densities is easier than predicting that of intermediate densities.

Of course, it cannot be assumed that all of the collective behavior seen in laboratory experiments translates directly to that observed in the field. However, the wealth of mathematical and simulation-based understanding of SPP models provides tools for performing such scaling. In combination with the detailed understanding of the role of the environment in behavioral phase change, as discussed above, SPP models could now form the basis of prediction to improve control of locust outbreaks.

3.3 Mormon Crickets

As we have noted, superficial similarities in group-level characteristics of biological systems may mask subtle, but important, underlying differences among them. This scenario rings true for mass-migrating Mormon crickets (*Anabrus simplex*). Just like locusts, Mormon crickets form cohesive migratory bands during outbreak periods that march en masse across the landscape (Fig. 8a).
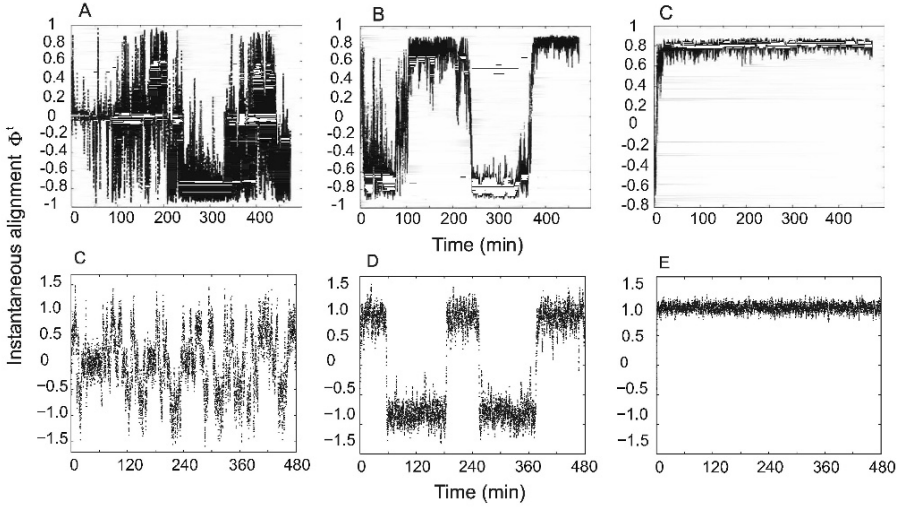
Fig. 6. Similarity between the self-propelled particles model of Vicsek et al. (1995) and experimental data as density of locusts in the arena was manipulated: (A) 7, (B) 20 and (C) 60 individuals in the arena (from Buhl et al. 2006). See text for explanation.

These bands can be huge, spanning over ten kilometers in length, several in width, containing dozens of insects per square meter, and capable of traveling up to 2.0 km per day (Cowan 1929; Lorch et al. 2005). Mormon cricket bands can cause serious damage when they enter crop systems and usually elicit prompt chemical control measures when they appear.

Although studied far less than locusts, laboratory and field analyses of Mormon cricket migratory behavior have provided important insights into the mechanisms underlying group formation and subsequent collective movement patterns. In addition, Mormon crickets have served as a key study system in the development of the nascent field of insect radiotelemetry in which the movement patterns of individual insects can be tracked across the landscape using small radiotransmitters. The use of this technology has enabled the study of landscape-scale collective movement to move beyond descriptions of observed patterns and into the realm of empirical hypothesis testing using manipulative field experiments.

Despite their name, Mormon crickets are not true crickets, but rather are classified as katydids or bush-crickets. They are flightless throughout their lives and possess small vestigial wings used by males for sound production and mate attraction (Gwynne 2001). As a result, they are incapable of forming flying swarms and travel on the ground as both juveniles and adults. Their religious name originates from a now legendary incident that occurred in the spring of 1848 involving the first Mormon settlers to arrive in the Great Salt Lake Valley in the western US. After surviving a difficult westward jour-
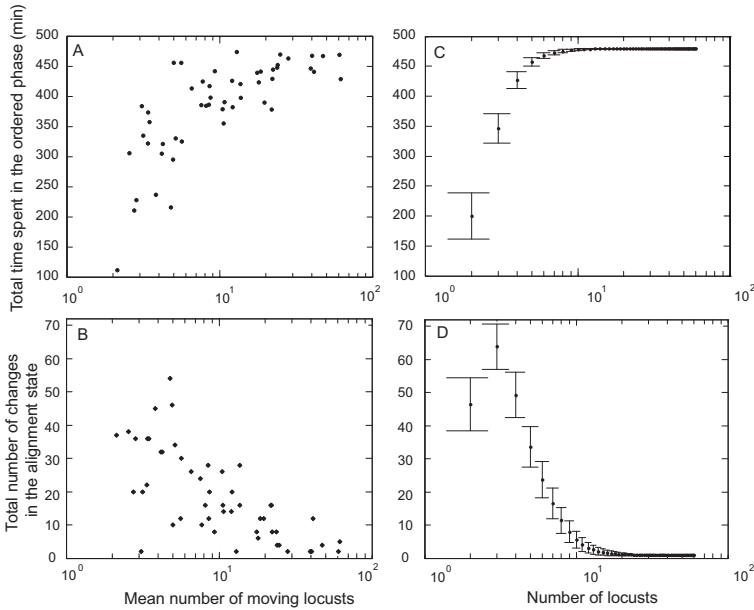
Fig. 7. The relation between the average number of moving locusts and the mean total time spent in the aligned state (A and C) and the mean number of changes in the alignment state (B and D) are displayed on a semi-log scale. Error bars, standard deviation. The 'ordered phase' refers to periods where the insects exhibited high alignment (> 0.3), and thus were moving collectively in one direction (either clockwise or anti-clockwise). From (Buhl et al. 2006).

ney and ensuing winter, the pioneers were enjoying what appeared to be a bountiful first spring in their newly established homeland. This serenity was shattered when their fields, planted with over 5,000 acres of wheat, corn and vegetables were invaded by marching hoards of large black 'crickets' that set upon their standing young crops (Hartley 1970). The devout surely interpreted this assault as an act of God analogous to the well-known Biblical plagues of Old World locusts. The settlers' attempts to battle the crickets using sticks, shovels, brooms, fire and trenches were futile, but their prayers for relief were answered by the arrival of seagulls that flew in from the Great Salt Lake and began to devour the marauding crickets. The gulls reportedly gorged themselves on crickets in the fields, often to the point of regurgitation, after which they would return to feast again (Hartley 1970). The gulls were credited with saving the remaining crops, and by extension the first settlers; a multi-trophic level interaction that resulted in the California Sea Gull being selected as the state bird of Utah. The Miracle of the Gulls was also commemorated by the erection of a monument at the headquarters of the Mormon Church in Salt Lake City, one of the few monuments, if not the only one, in the world dedicated to an insect predator (Gwynne, 2001).

Phase Polyphenism and Migratory Band Formation

Until recently, it had been widely assumed that Mormon crickets express density-dependent phase polyphenism similar to that known to occur in locusts. This assumption was due in large part to the similarities between migratory bands of locusts and those of Mormon crickets. The possibility of phase polyphenism in Mormon crickets was further supported by observed phenotypic differences in migratory behavior, coloration and body size between individuals from low-density, non-outbreak populations and their counterparts in high-density, band-forming populations (MacVean, 1987; Gwynne, 2001; Lorch and Gwynne, 2000). MacVean (1987) noted that the formation of migratory bands in the Mormon cricket "bears a striking resemblance to phase transition in the African plague locusts," and Cowan (1990) described the Mormon cricket as having gregarious and solitarious phases similar to locusts. Mormon crickets and locusts also share phase-related terminology in the scientific literature with Mormon crickets in non-outbreak populations, commonly referred to as inactive solitary forms (i.e. solitarious phase), whereas those in band-forming populations are referred to as gregarious forms (e.g. Wakeland 1959; MacVean 1987, 1990; Lorch and Gwynne 2000; Gwynne 2001; Bailey et al. 2005).

Two lines of recent evidence suggest that the expression density-dependent phase polyphenism in Mormon crickets plays little if any role in either the initial formation of migratory bands or the observed phenotypic differences between insects from high-density band-forming and low-density non-band-forming populations. Sword (2005) failed to find an endogenous effect of rearing density on Mormon cricket movement behavior in the lab, but rather demonstrated that individual movement was induced simply by the short-term presence of other nearby conspecifics. Although the lack of a behavioral phase change does not rule out the possibility of density-dependent changes in other traits, a recent phylogeographic analysis of genetic population structure suggests considerable divergence between the migratory and non-migratory forms (Bailey et al., 2005). Thus, the differences between crickets in migratory and non-migratory populations could primarily be due to genetic differences rather than the expression of phase polyphenism mediated by differences in population density.

Taken together, these studies strongly suggest, in contrast to the case with locusts, that the expression of phase polyphenism is not involved in the formation of Mormon cricket migratory bands. In other words, the expression phase polyphenism in not a prerequisite for migratory band formation.

Collective Movement

The initial formation of migratory bands in Mormon crickets and locusts appears to have convergently evolved via different underlying behavioral mechanisms. Is the same true for the mechanisms governing patterns of collective

movement once these groups have formed? Are there general rules applicable to the movement patterns of both Mormon crickets and locust bands (not to mention other organisms), or do these differ as well? The answers to these questions have important implications for the broader understanding of collective animal movement as well as considerable practical implications for the development of predictive movement models that can aid in the management of these and other migratory pests.

Given that the frequency of contact among individuals will increase with local population density, the finding that Mormon cricket movement is induced by immediate behavioral interactions among nearby individuals predicts that there should be some threshold population density above which mass movement is induced (Sword 2005). Although this remains to be demonstrated in Mormon crickets, the recent application of SPP models by Buhl et al. (2006) to explain the induction of mass movement in locusts with increasing local density stands as a promising general framework to explain the onset of mass movement in Mormon cricket bands as well. Furthermore, as we shall discuss in detail later, understanding how individual insects contend with the ecological costs and benefits of living in a group has provided considerable insight into the general mechanisms that may drive migratory band movement.

Radiotelemetry is an extremely valuable tool available to biologists for tracking the movement patterns of individual animals in the wild. The approach has traditionally been limited to larger vertebrates capable of carrying the extra weight of a radiotransmitter. However, technological advances have reduced the size of transmitters such that they can be used to track the movements of individual insects on the ground (e.g. Lorch and Gwynne 2000; Lorch et al. 2005) (Fig. 8b) as well as in flight (Wikelski et al., 2006). Lorch and Gwynne (2000) first demonstrated the utility of small radiotransmitters to track individual Mormon crickets. Their study was followed by a similar, but much more rigorous analysis by Lorch et al. (2005) who compared the individual movement patterns of insects from several different band-forming and non-band-forming populations. These studies confirmed that Mormon crickets in migratory bands cover much greater distances (up to 2 km/day) and tend to move collectively in the same direction relative to insects from low-density, non-band-forming populations (Fig. 8c, d).

In addition to consistent group directionality within as well as across days, migratory bands also exhibit group-level turns in which similar direction changes are made by individuals regardless of their position in the band (Lorch et al. 2005). Two possible explanations for these synchronous turns are that either (i) group movement direction is determined by orientation towards some landscape-scale environmental cue such as wind direction that can be detected and responded to by all group members, or (ii) they are similar to turns in bird flocks or fish schools in which individuals adjust their direction in response to the movement of near neighbors and these turns are propagated through the group like a wave (Couzin and Krause 2003). Although the Lorch et al. (2005) experiment was not designed to examine the effect of wind
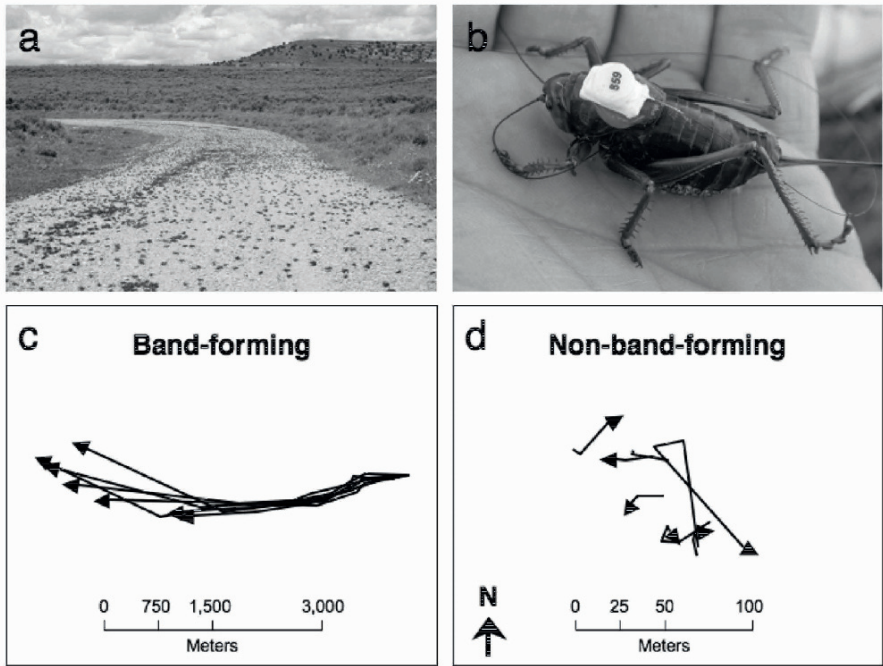
Fig. 8. Collective movement in Mormon cricket migratory bands. (a) A large migratory band crossing a dirt road in northeastern Utah, USA (photo by G. Sword). (b) A female Mormon cricket affixed with a small radiotransmitter (photo by D. Gwynne). (c) Example of individual movement patterns by radiotracked Mormon crickets in a high-density, migratory-band-forming population. Each line represents a single individual and each line segment depicts one day of movement. (d) Examples of radiotracked Mormon cricket movement patterns in a low-density, non-band-forming population. Note the differences in group directionality and scale of movement between the band-forming and non-band-forming populations. Radiotracking examples are from Lorch et al. (2005).

direction on migratory band movement, local wind direction data collected concurrently with the radiotracking data hinted that wind directions early in the day might correlate with migratory band directions. However, no effect whatsoever of wind direction on the movement of individuals within migratory bands was found in a follow-up study specifically designed to test the wind direction hypothesis. Migratory bands simultaneously tracked at three nearby sites in the same vicinity were found to travel in distinctly different directions despite experiencing very similar wind directions and other weather conditions (Sword et al., unpublished).

So what cues determine the direction in which a migratory band will move? One possible answer provided by simulation models of collective animal movement patterns is that nothing is responsible. A variety of movement models

in which individuals modify their direction and movement rate in response to others have shown that group directionality can arise from inter-individual interactions as a result of self-organization (Krause and Ruxton 2002; Couzin and Krause 2003). The hypothesis that Mormon cricket migratory band movement direction and distance are collectively determined was tested by conducting a manipulative transplant experiment in the field as originally described in Sword et al. (2005). Insects traveling in naturally occurring migratory bands were captured and radiotracked. Half of these insects were released back into the band while the other half were transported and released at a nearby site where bands had previously been, but were absent at the time. The resulting differences in movement patterns between the crickets released into the migratory band versus those that were isolated from the band were dramatic and closely resembled the previously documented differences between crickets from band-forming versus non-band-forming populations shown in Figs. 8c and d. Insects isolated from the band moved shorter distances, and were much less directional as a group relative to the insects released back into the band (Sword et al., unpublished). These findings quite clearly show that the distance and direction traveled by insects in a migratory band are group-level properties that differ considerably from the movement patterns of individuals when they are removed from the social context of the band.

A Forced March Driven by Cannibalism

Mormon crickets provide a unique model system in which understanding the costs and benefits of migratory band formation has provided a unifying framework that explains both how and why inter-individual interactions can lead to landscape-scale mass movement. The evolution and maintenance of migratory band formation in insects necessarily requires the benefits of such a strategy to outweigh its costs in terms of individual survival and reproduction. The radiotelemetry-based transplant study of Sword et al. (2005) mentioned above was originally designed to study collective movement, but it unexpectedly yielded a critical insight into the benefits and selection pressures that favor the formation of migratory bands. Individual band members were much less likely to be killed by predators than were crickets that had been separated from the group. The precise mechanisms by which individuals in bands gain protection from predators were not identified (see Krause and Ruxton 2002 for potential mechanisms), but 50–60% of the crickets removed from migratory bands were killed by predators in just two days while none within the bands were harmed during the same period. Thus, migratory bands form as part of an anti-predator strategy and there is a very strong adaptive advantage to staying in the group.

Although migratory bands confer anti-predator benefits, living in a huge group of conspecifics also has a variety of potential costs (see Krause and Ruxton 2002). It is precisely the interplay between these costs and benefits that promotes cohesive and coordinated mass movement among individual

Mormon crickets living in bands. Recent field experiments revealed that individual band members are subject to increased intraspecifc competition for nutritional resources. Individual crickets within migratory bands were shown to be deprived of specific nutrients, namely protein and salt (Simpson et al. 2006). When provided with augmented dietary protein, individual crickets spent less time walking; a response that was not found when crickets had ample carbohydrate. Thus, group movement results in part from locomotion induced by protein deprivation and should act to increase the probability that individual band members will encounter new resources and redress their nutritional imbalances.

An additional cost of group formation is that Mormon crickets are notoriously cannibalistic (MacVean 1987; Gwynne 2001). Their propensity to cannibalize is a function of the extent to which they are nutritionally deprived. Given that Mormon crickets are walking packages of protein and salt, the insects themselves are often the most abundant source of these nutrients in the habitat. As a result, individuals within the band that fail to move risk being attacked and cannibalized by other nutritionally deprived crickets approaching from the rear (Simpson et al. 2006). Thus, the mass movement of individuals in migratory bands is a forced march driven by cannibalism due to individuals responding to their endogenous nutritional state. The fact that migratory bands are maintained as cohesive groups despite these seemingly dire conditions suggests that the risk of predation upon leaving the band must outweigh the combined costs of intraspecific competition for resources and cannibalism. Importantly, ongoing experimental work strongly implicates the threat of cannibalism as a general mechanism that mediates migratory band movement in locusts as well as Mormon crickets (Couzin et al., unpublished).

4 Concluding Remarks

We have discussed in detail three cases of collective movement of large groups of animals: honeybees, locusts and Mormon crickets. A description of their movement would yield striking similarities: individuals in the group seem to keep an almost fixed distance from their neighbors; they tend to align themselves with their nearest neighbor, and show a clear tendency to stay with the group. In fact, this description can easily be extended to many other animals that move in groups, such as to schools of fish and flocks of birds (Couzin et al. 2005). However, the *reasons* for their collective movement are fundamentally different. For individual bees in a swarm it is critically important to stay with the swarm, as an individual bee cannot live. Cohesive movement in locusts is induced by the fine-scale structure of the environment they find themselves in. And if you are a Mormon cricket, moving faster than the ones behind you is essential to prevent yourself from becoming your neighbor's next meal.

We as biologists are fascinated by nature's diverse tapestry. Often, biologists tend to argue that nature is too diverse to allow its manifestations to be captured by generalist models. This is not the message that we want to convey in this chapter. As we have illustrated, many behaviors can only be understood by constructing models, which, by definition, are an abstract representation of reality. It is helpful to think about unifying theories that have the power to explain behaviors across a range of biological systems. We encourage computer scientists and mathematicians to look at biological systems and to become inspired, see patterns, and seek applications beyond biological systems. But in doing so, we hope that researchers will be awed not by the superficial similarities between natural systems but by the intricate and often subtle differences that distinguish them.

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