Chapter 9: Complicated interactions

Throughout this book I have emphasized how simple rules followed by individual animals and humans can produce surprisingly complex patterns. It is this observation, combined with the idea that we can use mathematical models to predict these patterns, upon which the idea of self-organisation is founded (Camazine et al. 2001; Nicolis & Prigogine 1977). Indeed, it is common to hear these 'complex systems' contrasted with 'complicated systems'. The former term is associated with systems in which complexity emerges from simple interactions, while the latter is associated with systems where large numbers of different components, each with its own particular role, interact to produce an output. The contrast is best illustrated by examples from physics. An example of a physicist's complex system is a sandpile. When grains of sand are dropped from above on to a particular position, a pile builds up and sand moves down the outside of the pile. The movement of sand on the outside of the pile is difficult to predict and occurs on scales ranging from small local toppling to large avalanches. Removing one or two grains of sand will not change this overall pattern. A car or an aeroplane, on the other hand, can be thought of as complicated. It consists of lots of parts that are carefully put together to drive from A to B. Removing certain components can completely change the car's capability of completing its journey.

Are animal groups sandpiles or cars? Up until now, I have emphasized the former analogy. However it is often the second analogy which is more appropriate when studying animal interactions. For example, individual honey bees are known to use at least 17 different communication signals, the most famous of which is the waggle dance, and adjust their behaviour in response to at least 34 different cues (Seeley 1998). The bees take different behavioural roles at different times during their life. Furthermore, there are certain components, such as the queen, which are essential to the smooth functioning of the colony.

In general, when building mathematical models the question of whether a system is complex or complicated is not a particularly useful one to ask. Rather, the question is whether there is a level of description at which we can formulate a mathematical model which answers our questions about a system's behaviour (Goldenfeld & Kadanoff 1999). As the preceding chapters have demonstrated there often exists such a level and mathematical models do help our understanding of collective animal behaviour. There is however no reason to believe that this level of description can be identified in all cases. For example, although in chapter 3 I showed how a model predicts how honey bees and ants balance their foraging across feeders of different quality, this does not answer the larger question of how the colony regulates its overall growth. A successful colony must balance its requirements for foraging with other tasks such as building and nursing brood (Gordon 1996). Even if we concentrate only on nectar foraging we see that honey bees exhibit at least seven different behavioural states, e.g. scout, recruit, inspector etc, (Biesmeijer & de Vries 2001) and exhibit a range of signals about the location and availability of food (Seeley 1995). We can use simple models to focus on understanding particular parts of this organization, but these do not necessarily provide a level of description that explains how the colony functions as a whole.

In this chapter I look at models that attempt to capture more fully the detailed interactions within insect societies, in particular. As hinted at in the preceding paragraphs, one of the best studied systems in this context is the foraging of honey bees. Another well studied system is the emigration of Temnothorax ants, and it is this system on which much of this chapter will focus. Here, I introduce the use of state- and agent-based models, using foraging and emigration of social insects as case studies around which the various techniques are discussed.

9.1 Social insect foraging

Behavioural state modelling

Seeley (1996) builds an understanding of honey bee organisation by identifying how individuals moved between *behavioural states* in response to signals they received from other bees and cues they received from local observations of the state of the colony. This approach lends itself naturally to some form of agent-, individual- or state-based modelling. If we can write down the behavioural states which an individual or agent can exhibit and determine the rate at which they make transitions between these states, then we can write down a model of each honey bee's behaviour. The agents interact with each other by making these transition rates change as a function of the number of individuals in other behavioural states.

One of the first examples of this approach, and one that we came across in chapter 3, is Camazine and Sneyd's model of honey bee foraging (Camazine & Sneyd 1991). The behavioural states in this model included searching for a food source, performing dances, and following dances in the hive. The transitions between behavioural states depended on the states of other individuals. For example, the transition from following dances to searching for a particular source depended on the number of individuals dancing for that source.

Box 9.A: State-based models of foraging.

Sumpter & Pratt's (2003) framework defines five different behavioural states associated with foraging. Colonies are assumed to have access to *n* food sources (e.g. patches of flowers or sugar feeders). Each state has an associated variable, indexed by source where appropriate, representing the number of individuals in that state. The states (and corresponding variables) are:

Waiting (W) Waiting at the nest and available to start foraging. Examples include honey bees waiting on the dance floor to follow recruitment dances, or ants waiting near the nest entrance to be led to a food source.

Searching (S) Searching for food sources.

Exploiting (E_i) Exploiting food source *i*. Workers in this state do not directly recruit nestmates, although they may leave signals, such as pheromone trails, that increase the likelihood of other foragers finding the source.

Recruiting (R_i) Attempting to recruit nestmates to food source *i*. Recruitment in this sense involves actively leading one or more workers, or directly communicating to nestmates the location of a food source, rather than leaving chemical signals in the environment.

Following (F_i) Attempting to follow recruiters to food source *i*. This encompasses not only literal following of recruiters, but also independent search for a source advertised by a dance or other signal.

Figure 9.1 shows how individuals change between states. For example, an individual becomes a follower from the state of waiting at the nest, and from following it can either get lost or arrive at its target.

In order to model these states in terms of differential equations we must specify the rates at which an individual changes from one state to another. For example, let's assume that λ is the probability that in a small time interval (dt) a waiting individual starts to follow dances. W is the number of waiting individuals. We then make the mean-field approximation that the rate at which a population waiting individuals is converted into dance following individuals is equal to λW, i.e.

$$\frac{dW}{dt} = -\lambda W$$

This approximation ignores any random variation or differences between individuals, and since λW is not an integer, it also ignores the fact that bees come in distinct entities. Despite these limitations such approximations work well provided the number of individuals in each behavioural state is relatively large (in practice this is more than 5 to 10 individuals). Thus, although differential equation models are ultimately written in terms of populations, the equations are initially derived from individual behaviour.

Behavioural transition rates usually depend on the number of individuals in another state. For example, the probability that dance following honey bees start looking for feeder 1 is proportional to the number of bees dancing for that feeder, i.e.

$$\frac{R_1}{R_1 + R_2 + K_0}$$

where K_0 is constant and R_1 is the number of bees dancing for feeder 1. We can thus express the number of following bees as

$$\frac{dF_1}{dt} = \lambda \frac{R_1}{R_1 + R_2 + K_0} W - \theta_1 F_1$$

where λ and θ_1 are constants determining the rate per individual bee of starting to follow dances and getting lost, respectively. Similar equations can be written down for each behavioural state giving a system of differential equations modelling how individuals change between behaviours. Based on the earlier model of Camazine & Sneyd (1991), Sumpter & Pratt proposed the following differential equation model for honey bee foraging

$$\frac{dW}{dt} = \sigma_1 E_1 + \sigma_2 E_2 + \theta_1 F_1 + \theta_2 F_2 - \lambda W + \gamma S$$
$$\frac{dF_1}{dt} = \lambda \frac{R_1}{R_1 + R_2 + K_0} W - \theta_1 F_1 - \phi_1 F_1$$
$$\frac{dF_2}{dt} = \lambda \frac{R_2}{R_1 + R_2 + K_0} W - \theta_2 F_2 - \phi_2 F_1$$
$$\frac{dS}{dt} = \lambda \frac{K_0}{R_1 + R_2 + K_0} W - (\alpha_1 + \alpha_2 + \gamma) S$$
$$\frac{dE_1}{dt} = \phi_1 F_1 + \alpha_1 S - \sigma_1 E_1 - (\rho_1 E_1 - \delta_1 R_1)$$
$$\frac{dE_2}{dt} = \phi_2 F_2 + \alpha_2 S - \sigma_2 E_2 - (\rho_2 E_2 - \delta_2 R_2)$$
$$\frac{dR_1}{dt} = \rho_1 E_1 - \delta_1 R_1$$
$$\frac{dR_2}{dt} = \rho_2 E_2 - \delta_2 R_2$$

(equations 9.A.1)

The various parameters in this model have been measured directly from experimental data and a simulation of this model for the experimental setup of Seeley et al. (1991) is given in figure 9.2.

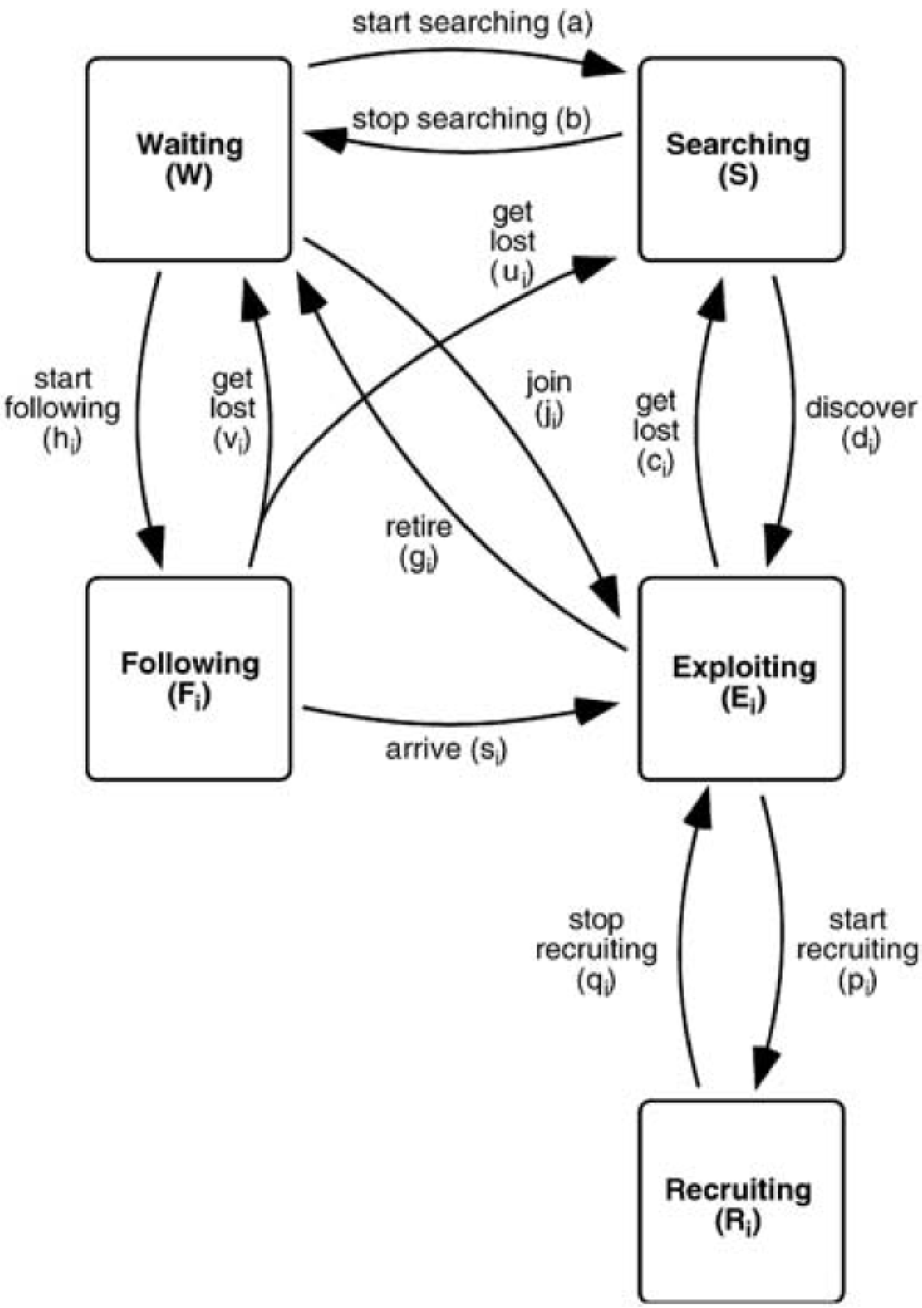

Figure 9.1: Flow diagram for behavioural state variables for Sumpter & Pratt's framework (Box 9.A). Boxes represent behavioural states, while lines connecting states indicate rate of flow of workers between states. Arrows indicate direction in which individuals change states.

Following from the Camazine and Sneyd model, Sumpter and Pratt (2003) proposed a general framework for modelling social insect foraging in terms of differential equations, based on transitions between behavioural states. This framework is described in Box 9.A.

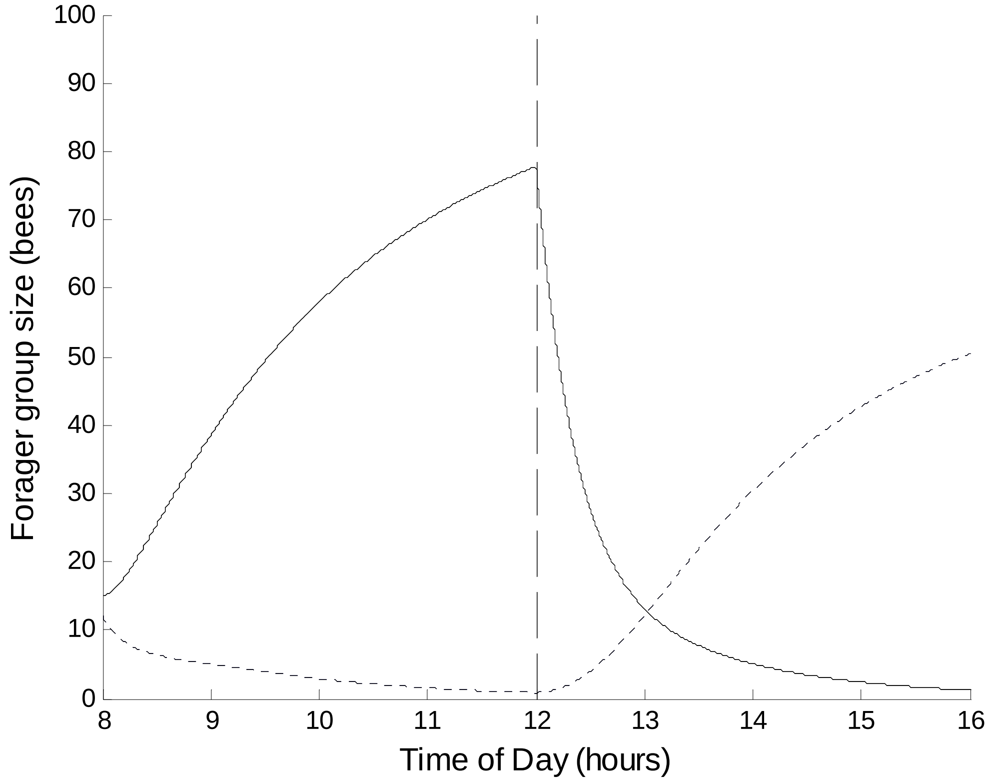

Figure 9.2: Numerical simulation of equations 9.A.1. Figure shows the total number of recruiting and dancing bees for the two sites. Solid line gives number at south feeder (E_1+ R_1) while the dotted line is the north feeder (E_2+ R_2). As in the experiments in figure 9.3, the simulation begins with $E_1(0)$=15, $E_2(0)$=12 and$W(0)$=125-15-12=98, and at time 12 the quality of the feeders is swapped. Simulation parameter values can be found in Sumpter & Pratt (2003).

The five basic behavioural states are waiting, searching, following, exploiting and recruiting (figure 9.1). For nectar foraging of honey bees: waiting corresponds to waiting on the dance floor in order to follow a dance; following corresponds to searching for nectar source advertised by a dance; searching corresponds to scouting for food without first following a dance; exploiting involves flying backwards and forwards to a known food source and recruiting involves performing recruitment dances. Similar interpretations can be made of the foraging states of ants, but with pheromone trails providing direct recruitment from waiting to exploiting instead of the indirect recruitment provided by the dance language.

In the framework in Box 9.A, the behavioural states, the transitions between the states and associated rate parameters can be determined by observations of individuals. The differential equation model is then written in terms of the number of individuals in a population with a particular state. The assumption underlying the change from individual to population description is known as the law of mass action or mean-field approximation. The basic idea of this assumption is that when considering large numbers of individuals which have the same state we do not need to consider every individual, but instead consider simply the rate at which populations of individuals switch between states (see Box 9.A).

Despite the differential equation model being an approximation of individual behaviour, it often works reasonably well in predicting colony level behaviour. Figure 9.2 shows a numerical solution of the differential equation model for honey bee foraging presented in Box 9.A for an experiment performed by Seeley et al. (1991). Figure 9.3a shows the outcome of the Seeley et al.'s experiment. The model reproduces these experimental results reasonably accurately, although it underestimates the rate at which the bees switch feeders when the quality of the feeders is switched.

Complicated individuals

Seeley describes the foraging of a honey bee colony as "an ensemble of largely independent individuals that rather infrequently exchange information with one another" (Seeley 1995). Seeley's emphasis is on conservation of communication. Rather than simple units using mass communication to form a collective solution, complicated individuals use the minimum of communication necessary to co-ordinate their work (Seeley 2002). An individual honey bee or other foraging social insect is more complicated than implied by the framework in Box 9.A. Biesmeijer & de Vries (2001) propose that the behavioural states of honey bees should include different categories for novice forager, scout, recruit, employed forager, unemployed experienced forager, inspector and reactivated forager. Their proposal is based on the studies of von Frisch (1967), Lindauer (1952), through to Seeley (1983; 1995) where honey bees are shown to use a combination of personal information of where food is located and social information gained through following dances.

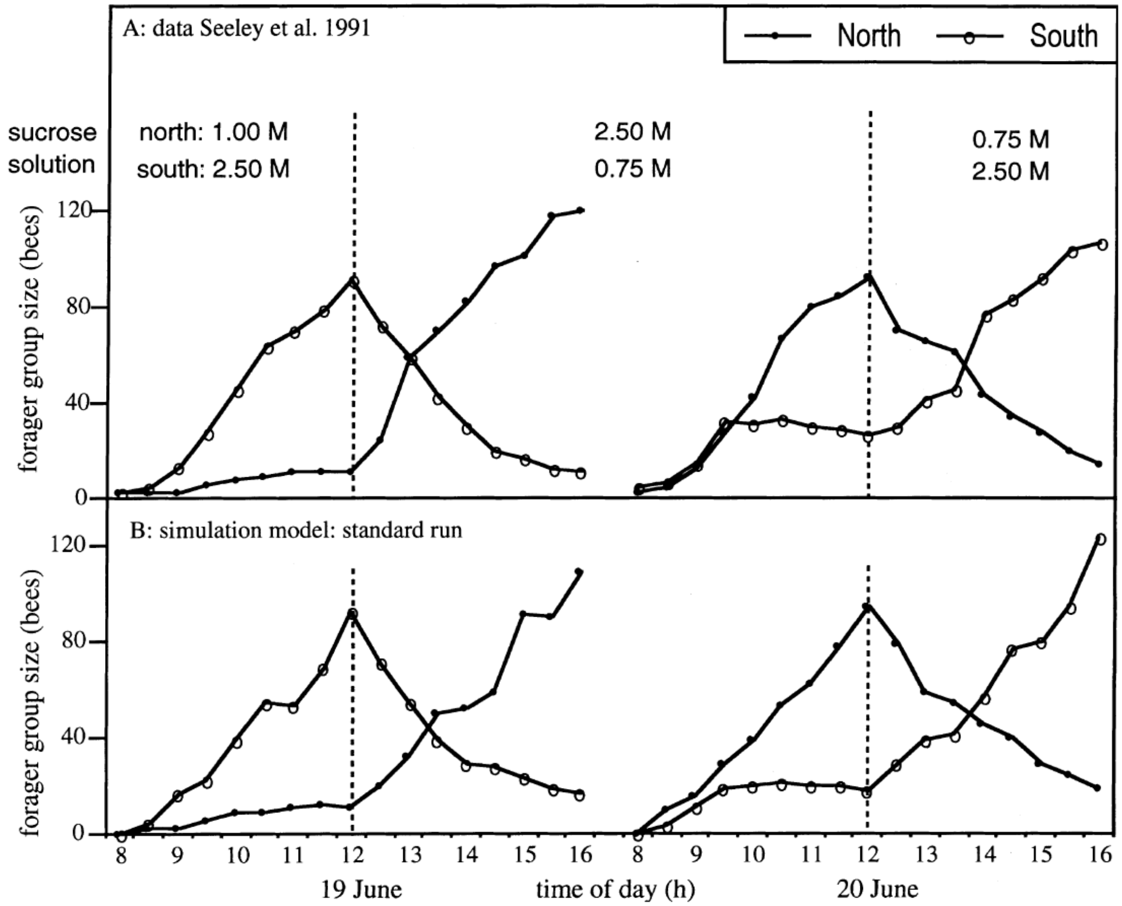

Figure 9.3: (a) Number of honey bee foragers visiting each of two feeders (north and south) recorded during 30 minute intervals in the experiment of Seeley et al. (1991). In the experiment both feeders were 400m from the hive and their quality was changed at the beginning of each day and at noon. (b) Simulation outcome of de Vries & Biesmeijer (1998) individual-based model of these experiments. Figure reproduced from de Vries & Biesmeijer (1998).

A similar individual complexity underlies ant foraging (Detrain & Deneubourg 2006; Gordon 2007). For example, harvester ants do not usually rely on pheromone trails to co-ordinate foraging, but foragers resting within the nest are activated by other foragers and by patrolling ants (Gordon 2002; Gordon et al. 2008; Greene & Gordon

2007b). Individual foragers have a memory of their own foraging patch and activation by other ants causes them to visit their own patch rather than to blindly follow the activating ants. The role of communication in this case is for ants outside the nest to indicate to ants within the nest that foraging conditions are generally good (Gordon 2007).

The advantage of state-based models is that there is no limit to the complexity that can be incorporated into them. However, increasing the number of behavioural states means decreasing the number of individuals in any particular state at any particular time. As such, the mean-field assumption underlying differential equation models can no longer hold. If only a few individuals have a particular state then we cannot assume that the transition between the states can be approximated as a transition rate of populations. Furthermore, if only one or sometimes no individuals have a particular state then our differential equation model will represent fractional individuals.

Added complications on the level of individual behaviour can be incorporated into agent-based or individual-based models which preserve individual units and the stochastic nature of interactions. de Vries & Biesmeijer (1998; 2002) developed an individual-based model of honey bee foraging where each bee was characterised by its position, speed, direction, visual perceptions, its memory of food in terms of when it was found, position and profitability, as well as internal motivation for homing, foraging and abandoning a food source. By fitting their model to Seeley et al.'s (1991) experiments they showed that previous foraging experience, and not only recently acquired dance information, were required to reproduce the experimental results (de Vries & Biesmeijer 1998). In doing so they identified a model which was sufficient to explain current experimental observations. An example simulation outcome compared to data from the experiment is given in figure 9.3b. Here the match between experiment and data is better in than the original differential equation model (figure 9.2).

de Vries & Biesmeijer's model is a useful tool for investigating hypotheses about individual honey bee behaviour. Several other authors have provided their own individual-based models of honey bee foraging (Beekman & Bin Lew 2008; Dornhaus et al. 2006) and other aspects of honey bee organisation (Schmickl & Crailsheim 2008a; Schmickl & Crailsheim 2008b). This approach is however limited in several respects. Firstly, these models have a large number of parameters, many of which could not be estimated from independent datasets. Secondly, while their model is sufficient to explain the data, it is difficult to argue that a particular model is necessary. In other words, there may exist other models that fit the data equally well. Both these limitations of individual-based models are a consequence of insufficient data and could be resolved by more experiments. I will return to this question in more detail in later sections of this chapter in relation to ant and honey bee migration.

Complicated signals

Not only do individuals have large numbers of behavioural states but their behaviour is influenced by a diversity of cues and signals. For example, foraging bees are influenced in their decision whether to dance by both their own assessment of the quality of food they carry as well as the time it takes them to unload the nectar they bring into the hive (Seeley 1992; Seeley 1995). Ant foraging is also more complicated than implied in chapter 3. Individual ants use their own information, as well as that gained through interactions with others, both to locate food and to decide whether to recruit to it. For example, *Lasius niger* ants' decision to leave a pheromone trail to a food source depends on how easily it reaches its desired volume of food (Mailleux et al. 2000; Mailleux et al. 2003b), its level of starvation (Mailleux et al. 2006) and the nutritional needs of the colony (Portha et al. 2004).

Ants use a variety of pheromones to mark the path to food discoveries (Wyatt 2003). For example, some *Myrmica* species use pheromone from different glands depending upon the type of food they locate (Cammaerts & Cammaerts 1980). Pheromone with stronger recruiting properties is laid to prey which are hard to move, thus recruiting other workers to help with transportation.

Combination of different types of pheromones with different lifetimes may allow ants to 'remember' routes to sites that were previously rewarding and may become rewarding again in the near future. Pharaoh's ants provide a good example of an ant that leaves multiple pheromone signals. Jackson et al. (2006) showed that these ants leave pheromone trail that can be detected until up to 2 days after it is laid. The ants deposit pheromone even in the absence of food (Fourcassie & Deneubourg 1994). However, Jeanson et al. (2003) established that the pheromone deposited directly after a food discovery evaporates in less than 25 minutes. Jackson and Chaline (2007) report that the intensity of trail laying, in terms of the degree of continuity of the markings made, changes only slightly between ants returning from a rewarding food source and those exploring. These experiments did not investigate the chemical composition of the trails. However, although Jackson and Chaline are cautious about concluding that different chemicals are used for marking during exploration and exploitation, the existence of distinct 'explore' and 'exploit' pheromones remains the most plausible explanation of the rapid exploitation of newly discovered food (Beekman et al., 2001; Sumpter & Beekman, 2003) and the rapid abandonment of trails which no longer lead to food (Jeanson et al. 2003). These pheromones are possibly complemented by a volatile negative pheromone that serves as a 'no entry' signal when food is not found at the extremity of a path (Robinson et al. 2005).

Much of the work on understanding foraging trails is based on behavioural analysis, and less is known about how specific chemical components within these trails act in different circumstances. Chemical communication is also seen in, for example, dance communication in honey bees (Thom et al. 2007). An interesting research challenge is to link together specific chemicals found in communication with observed behaviours.

Combining complex and complicated behaviour

By their nature, the complex, self-organised patterns seen in ant trails, nest structures and bird flocks require large numbers of individuals in order to generate them. Indeed, there is evidence that ant species which typically live in large colonies are more likely to use pheromone trails for communicating the presence of food (Beckers et al. 1989). However, there is little evidence from between species comparison that individual complexity decreases with increased colony size (Anderson & McShea 2001a). Honey bees are just one example of species with both large colony sizes and individuals that exhibit a complicated array of communication signals and behavioural states.

Some of the most interesting questions in understanding the organisation of insect societies involve the interaction of self-organising patterns with the individual behavioural state of workers (Detrain & Deneubourg 2006). For example, Beekman et al. (2001) showed that pheromone trails emerge only when the ants in a foraging arena reach a critical density (see chapter 3). For other species of ants, it has been shown that the foraging behavior of individuals changes with the number of ants in the colony (Mailleux et al. 2003a). Thus the ants may decide whether to leave pheromone or not based on whether they are sufficient in number to utilize trails.

While complicated behavioural states, multiple signals and between-individual variation are all important issues when building models of social insect foraging, these have not been the focus of a great deal of theoretical work. Indeed, the only current solution to modeling these phenomena is to incorporate all the relevant variables and parameters into a simulation model and compare the simulation model to data. It is this approach I now investigate further with regard to another aspect of social insect organization, namely emigration.

9.2 Emigration of *Temnothorax* ants

A large number of studies of social insect foraging in the 1990s were followed at the turn of the century by an increased interest in how social insects migrate to a new nest. In part, this switch of interest from foraging to emigration was due to greater experimental tractability of the latter. Emigrations have a clear beginning and an end. The start can be induced by the destruction of a colony's old nest and the end is marked by a move into their new nest. This has increased the amount of data with which to parameterize individual-based models, allowing these models to be better verified. The following sections describe *Temnothorax* emigration as a model system in the study of complicated state-based behavior. This is a system for which we have been able to clearly identify behavioural states and measure parameter values.

The ants, the emigrations of which have been studied most are the genus *Temnothorax* (Mallon et al. 2001; Möglich 1978; Pratt et al. 2002). The basic steps of this emigration are given in chapter 4, but I summarize them again here. Each ant begins in an exploration phase during which she searches for nest sites. Once she finds a site she enters an assessment phase, carrying out an independent evaluation of the site, the length of the evaluation being inversely proportional to the quality of the site (Mallon et al. 2001). Once she has accepted the site she enters a canvassing phase, whereby she leads tandem runs, in which a single follower is slowly led from the old nest to the new site. These recruited ants then in turn make their own independent assessments of the nest. Once the nest population has reached a quorum threshold the ant enters a committed phase, rapidly transporting passive adults and brood items (Pratt et al. 2002).

Tandem run recruitment has elements of the simple positive feedback seen in the pheromone trails of *Lasius* ants and the aggregation of cockroaches. Temnothorax emigration is however more than just positive feedback. The four phase decision-making process, the use of a quorum threshold to decide whether to perform a tandem run or a transport (Pratt 2005b; Pratt et al. 2002), and the fact that some ants find both nests and choose the superior one (Mallon et al. 2001), all point toward a more complex migration than seen in cockroach aggregation, for example. We could say that *Temnothorax* ants combine elements of self-organisation, whereby a global solution to the problem of finding a new nest emerges from the interactions of multiple ants, with a sophisticated behavioural algorithm, whereby individual ants continually monitor the progress of the emigration and change their behaviour accordingly.

The detailed experimental understanding of *Temnothorax* migration has made it possible to determine the ants' behavioural states and the factors influencing transitions between these states. Pratt & Sumpter have systematically refined this behavioural algorithm as new experimental data has become available (Pratt 2005a; Pratt et al. 2002; Pratt & Sumpter 2006; Pratt et al. 2005). Figure 9.4 gives a flow diagram for the behavioural states and how the ants transition between them, based on the emigration of *Temnothorax albipennis* (Pratt & Sumpter 2006; Pratt et al. 2005). This flow diagram gives a more precise description of the emigration stages described in the previous paragraphs. By individually marking all the ants in the colony and establishing how long and under what conditions they transitioned between states we were able to measure the model parameters (Pratt 2005a; Pratt et al. 2005).

A key purpose of this model is to establish whether our understanding of how the emigration proceeds is correct. If our behavioural algorithm is specified correctly then the output of simulations of the model should be similar to the outcome of experiments. There are a number of ways of making this comparison. Firstly, we can visually compare the sequence of actions performed by the real ants and those in the simulation. An example of such a comparison is given in figure 9.5. Such comparisons are qualitative since both are a single instantiation of the model and the experiment. However, we can make a series of these comparisons in order to gain insight into differences between model and reality. This approach is often very useful since it quickly reveals differences in the behaviour of the real and simulated ants.

A second way to validate the model is to compare distributions of colony level measurements in the model and in the experiment. Using such measurements, we were able to show that the data was not statistically different from the prediction of the model, i.e. the experimental outcome lay within a confidence interval generated by repeated runs of the model (Pratt et al. 2005). The final way in which we validated our model was to test it against an independent data set. The model was fitted using parameters for single nest emigrations and then tested against the outcome of emigrations to two nests. Again a confidence interval of outcomes was constructed and compared to the actual emigrations.

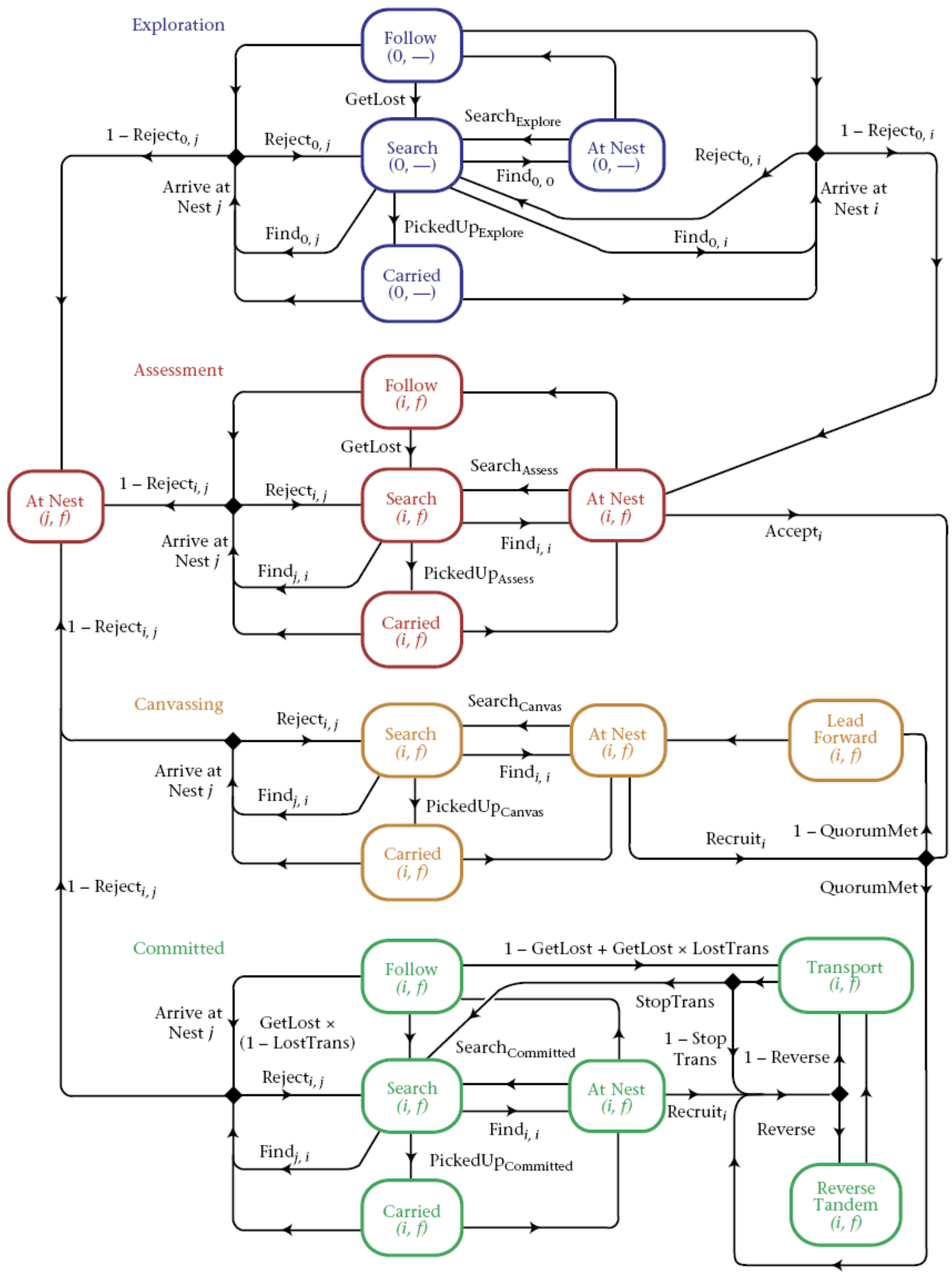

Figure 9.4: Model of the behaviour of active ants responsible for organizing emigrations of Temnothorax albipennis. Boxes represent behavioural states and arrows represent transitions between them. The four major groups of behavioural states are organized into four gropus of boxes. From top to bottom the boxes correspond to exploration, assessment, canvassing and commitment. The first subscript i in each state identifies the nest that the ant is currently assessing or recruiting to. The second subscript f identifies the nest from which the ant recruits

(either the old nest or a rejected new site to which nestmates have been brought by other ants). Figure reproduced from Prat et al. (2005).

What can be hidden in the final presentation of a detailed model are all the alternative models which could be rejected by comparison to data. For example, early versions of our model assumed that the time taken for each individual to perform a transport and tandem run was constant, but when this model failed to match the data we realised that individual ants improved their route with repeated journeys between old and new nest sites. As a result we incorporated a travel time which decreases with number of completed journeys and the model provided a better match. On the other hand, we were not required to assume different parameter values for different individuals within the colony. This was a particularly striking result since the division of labour through the emigration is suggestive of some ants being more active than others. In particular, the distribution of the number of transports and tandem runs performed by colony members is highly skewed, with some individuals much more involved in the emigration than others. Our model showed that this division of labour could arise simply as a result of some ants finding and learning the route to the new nest before the others.

The model in figure 9.4 is based on observations of an “old world” Temnothorax species collected in the UK, *Temnothorax albipennis*. Pratt (2005a) investigated how a “new world” species collected in USA, *Temnothorax curvispinosis*, performed emigrations under similar conditions. He found that the behavioural algorithm followed by these two species is very similar, with the same stages of searching, assessing, canvassing and accepting; similar division of labour between workers; and the use of a quorum threshold to mark the switch between tandem running and transport. What differed between the two species were the parameter values which determine the rates at which individuals switch between behavioural states. The most striking difference was in the quorum rule. *T. curvispinosis* required a higher threshold nest population before it switched from tandem running to transportation. Furthermore, on their first recruitment from the old nest to the new, individual *T. curvispinosis* have a larger quorum threshold than on later recruitments. As a result, more tandem runs were seen in the emigrations of *T. curvispinosis* than those of *T. albipennis*.

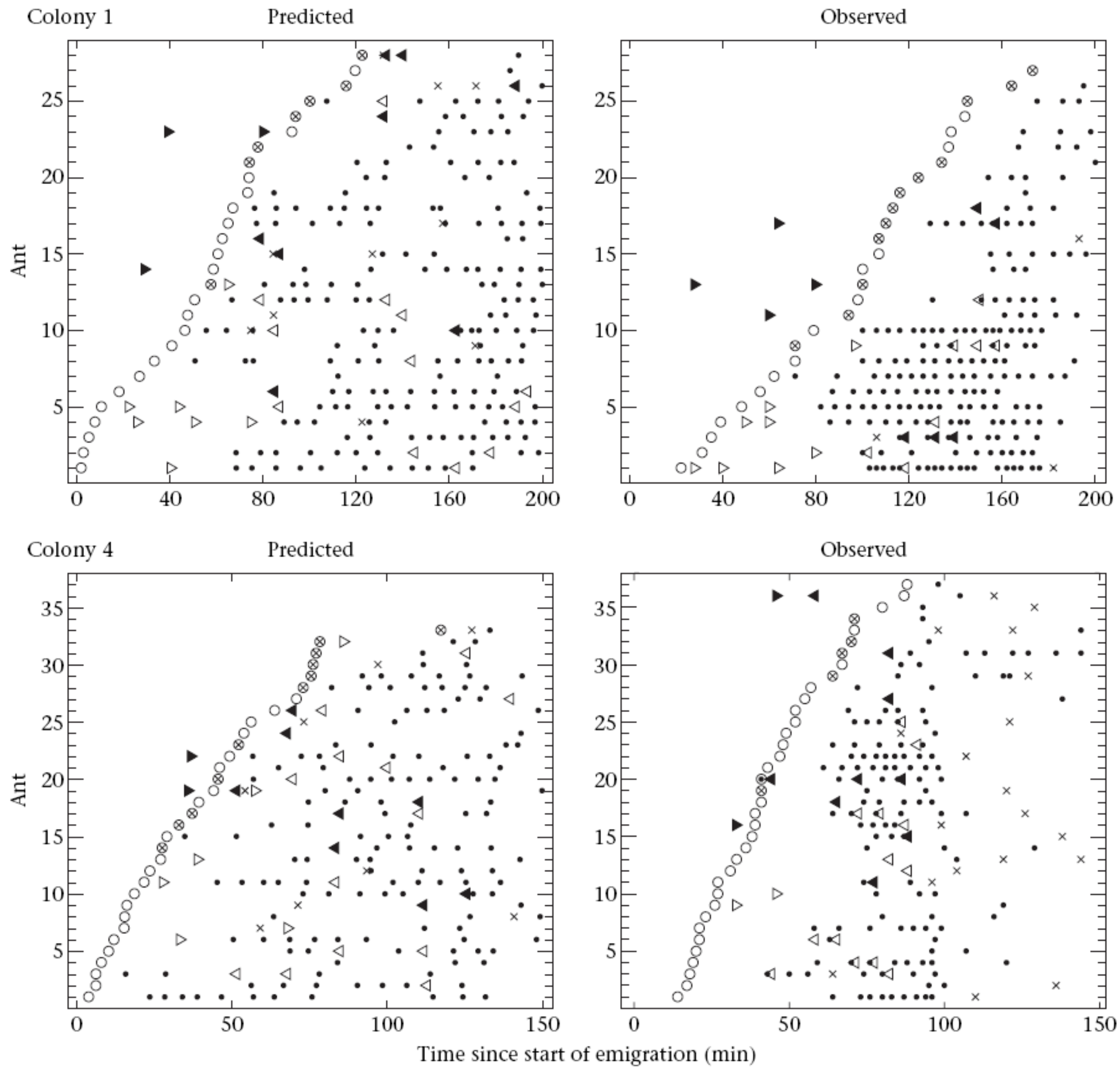

Figure 9.5: Behavioural sequences of active ants, predicted by the model and observed in single-nest emigrations by colonies 1 and 4. Within each panel, each row shows the acts of a single ant. ○: initial entry into the new nest; ▷: leading a tandem run towards the new nest; ►:

following a tandem run towards the new nest; ◁: leading a reverse tandem run; ◄: following a reverse tandem run; ●: transporting a nestmate or brood item to the new site; X: being transported into the new site. Figure reproduced from Pratt et al. (2005).

9.3 Honey bee house-hunting

Similarities in the behavioural algorithm employed during emigration are not limited to species of the same genus. As discussed in chapter 4, the movement decisions of cockroaches, fish, spiders and other animals involve quorum-like responses to others (Sumpter & Pratt 2008). Honey bees are also thought to exhibit a form of quorum response during their emigration (Seeley & Visscher 2004b). Like *Temnothorax* ants, this quorum response is just one aspect of the algorithm the bees follow in choosing a new nest.

Seeley and Visscher have together with various colleagues studied the stages of the emigration of honey bee swarms. The emigration is initiated with the decision of a swarm of bees, including the queen, to leave the hive. This departure is remarkable in that it is preceded by relative calm, as the colony continues to function as usual. Then, during a period of about 10 minutes before a swarm of thousands or tens of thousands of bees departs the nest, there is a sudden and rapid increase in ‘piping’, where an excited bee presses its thorax against a resting bee to produce a vibration in the passive bee’s flight muscles, and ‘buzz-runs’, where an excited bee runs around, pushing against other bees (Rangel & Seeley 2008). The bees lift off together and land in a nearby tree to form a bivouac shaped swarm (Cully & Seeley 2004; Seeley 1995; Winston 1987).

From this swarm the bees collectively decide where to move. The process starts with scout bees searching for potential nest sites. Only a small proportion of the swarm members, probably around 5%, act as scouts or participate in the decision-making process (Seeley & Buhrman 1999; Seeley et al. 1979). When one of these scouts finds a nest site, she assesses its quality by walking and flying around the nest’s interior (Seeley 1977). In contrast to *Temnothorax,* the time a scout takes to assess a nest is independent of the quality of the nest site and does not appear to involve the reconnaissance of other nearby sites (Seeley & Buhrman 1999; Seeley & Visscher 2008). Instead, the scout will return to the swarm and perform a waggle dance to indicate the site’s location to its nest-mates (Camazine et al. 1999; Seeley & Buhrman 1999). After the dance the scout will fly back and forth between the new nest site and the swarm, performing waggle dances at the swarm.

The swarm remains in its bivouac form for around two or three days before flying to a new nest site. During this time dances occur for a large number of potential sites, but directly before liftoff most, although usually not all, of the dances are for one of the available sites and it is to this site which the swarm flies (Camazine et al. 1999; Seeley & Buhrman 1999). Seeley & Burhman (2001) offered a colony a choice between four mediocre and one superior nest. In four out of five trials the bees moved into the superior nest. The scouts are thus usually able to reach consensus for the best available site. However, in a small number of cases substantial dancing for other sites is seen directly before swarm liftoff (Lindauer 1955; Seeley & Visscher 2003). Such swarms have been seen to take off, but then hesitate as bees try to fly in different directions before finally returning to the original resting place of the swarm bivouac. Seeley & Visscher (2003) observed that after one such failed takeoff the bees regrouped and half an hour later lifted off again and flew in unison to one of the two dance-advertised sites.

Setting these occasional failures aside, the question is how the bees manage to reach consensus. Visscher (2007) discusses four possible mechanisms which could promote consensus: individual comparison, dropout, competition and inhibition. Visscher & Camazine (1999) performed an experiment in which scout bees which visited both of two available nest boxes were captured and removed from the decision-making process. The removal had no effect on the time it took the bees to reach consensus and move to one of the available sites, suggesting that individual comparison plays a relatively minor role in consensus building.

The most important mechanisms in reaching consensus appear to be a combination of dropout and competition. Although most potential sites elicit a dance response from the scout which first locates them (Seeley & Visscher 2008), over repeated visits dance intensity is higher for better quality sites (Seeley & Buhrman 2001). Furthermore, the intensity of dances for a site fades over repeated journeys between the nest and the swarm (Seeley 2003). The less rapid dropout for higher quality sites, coupled with competition for the limited number of available scouts which can follow dances, leads to a process of competitive exclusion (Britton et al. 2002; Myerscough 2003)**.** Mathematical models of this process predict that the site at which the bees give up dancing for most slowly is eventually the focus of all dancing.

To decide whether there is sufficient support for the site for which they are dancing the scouts appear to use a quorum rule, similar to that employed by the ants (Seeley & Visscher 2003; Seeley & Visscher 2004b). Once a particular potential nest site contains around 20 or so bees then waggle dancing is replaced by the same piping behaviour seen prior to the swarm's initial departure from the old nest site. Piping is produced exclusively by scouts and acts to warm up the other bees in the swarm in preparation for lift-off (Seeley & Tautz 2001; Visscher & Seeley 2007). As in the initial lift-off from old nest to bivouac, piping is accompanied by buzz runs, which also serve to activate bees resting within the swarm (Rittschof & Seeley 2008). Once activated, the swarm takes off and the scouts lead the entire swarm to the new nest site (see section 5.6 for details of how the small number of scout bees is able to lead the swarm).

Several models have converted the above description into a behavioural algorithm. Britton et al. (2002) and Myerscough (2003) both looked specifically at the dance dropout stage, showing how this dropout contributed to consensus. Janson et al., (2007) developed an individual-based model of the process of searching, dancing and travelling back and forth between nest sites, investigating the role of scouting and how the colonies could cope with assessing nests at differing distances from the swarm bivouac. As well as dancing and dropout, Passino & Seeley (2006) include and investigate the quorum rule for the commencement of piping. As such, this is the most comprehensive individual-based model of honey bee house hunting.

9.4 Algorithm analysis and robustness

Once a behavioural algorithm is developed, the role of its various components can be tested. The algorithm can be analysed and compared across systems. Indeed, rather than simply simulating algorithms in order to reproduce experiments, the algorithms can be studied to find out the principles that underlie them (Fewell 2003; Sumpter 2006).

An important way of gaining understanding of algorithms is between species comparison. Honey bees and *Temnothorax* ants both exhibit four main stages of the decision-making process: search (look for new nest sites both independently and through following dances/tandem runs), assess (evaluate discovered sites), canvass (dance/tandem run for an accepted site) and commit (bees pipe and perform buzz runs before leading the swarm to the new site, while ants transport to the new site). In both cases the switch from canvass to commit occurs when a quorum is reached at the perspective nest site. Pratt et al. (2002) showed that in *Temnothorax* ants quorum leads to a reduction in incidence of colony splitting. Similarly, Passino & Seeley (2006) used their model to demonstrate that the quorum improved decision-making accuracy. Passino & Seeley (2008) also note strong similarities between the mechanisms through which the bees reach a decision about which nest to move to and how populations of neurons reach decisions between different options.

Honey bees and ants differ in their respective requirements for speed and accuracy in decision-making. If a honey bee swarm takes off before a high level of consensus is reached then the swarm may split, an outcome that can prove fatal to those bees that do not move into the new nest site (Lindauer 1955). Splitting during emigration occurs in ants too, but colonies are later able to re-coalesce in the best of the available nests. Thus accuracy is more important than speed in the decision-making of honey bees. These differences may be reflected in differences in the way that quality is encoded in the recruitment by the two species. For the ants the assessment period is longer for lower quality nests, but once an ant has accepted a site her rate of recruitment is independent of site quality. Commitment by different ants to different nests can result in the quorum being reached for more than one site and higher degree of colony splitting.

For the honey bees, the assessment period is independent of quality but dancing is more vigorous for better quality sites. This quality based recruitment, combined with more rapid dropout of dancers for inferior sites allows the scouts to reach near consensus before lift-off (Myerscough, 2003). Thus, while dropout might lead to slower decision times, it provides an improvement in decision accuracy.

How behavioural algorithms are employed in different situations can give further insight into the tradeoff between speed and accuracy. Franks et al. (2003a) showed that the ants reduce the size of their quorum in situations where migration speed takes priority over the avoidance of splitting. Pratt & Sumpter (2006) went on to look at how the ants tune their behavioural algorithm to different challenges. As well as moving nest when their current nest is destroyed, *Temnothorax* ants are known to move up the ‘housing ladder’ as better nest sites are made available to them (Dornhaus et al. 2004). We compared how the ants migrated under these ‘unforced’ conditions, when the ants live in a poor quality nest and one or more better quality nests becomes available, with ‘forced’ conditions, where their current nest is destroyed. When choosing between a good and a mediocre nest, colonies showed different behaviour depending on the urgency of their need to move. In the unforced situation colonies took a long time to emigrate, but they more often chose the better of the two available nests. In forced emigrations, colonies moved much faster but often made poor choices, splitting their population between the good and mediocre nests or even moving entirely into the inferior one.

We showed that while the speed and accuracy of decision-making was tuned to the circumstances of forced and unforced emigrations, the behavioural algorithm employed by the ants was the same in both cases. The four stages of searching, assessing, canvassing and finally accepting and transporting after a quorum is met were seen in both forced and unforced emigrations. The difference in speed and accuracy in the two different circumstances resulted from an increased urgency on the part of individual ants in forced emigrations. The rates of leaving the old nest to search and of accepting a newly found nest were larger and the quorum threshold was lower in forced emigrations. The ants changed the parameters of the algorithm, but the algorithm itself remained unchanged. The ants appear to have evolved a single algorithm which can be tuned to differing requirements of speed and accuracy.

The behavioural algorithm adopted by the ants appears remarkably robust to differences in the number of and distance to the available nests. Pratt (2008) compared emigrations to nearby and distant nests. He found that emigrations to distant nests involve more tandem runs, with the followers of these tandem runs responsible for more transportation, than in emigrations to nearby nests. In terms of the behavioural algorithm, the quorum is reached slower for distant nests, leading to a later switch to transportation and a greater effort in tandem runs which inform other ants where the new nest site is. The quorum rule thus tunes the amount of tandem running to the level of difficulty in finding a new nest. Model simulations confirm this interpretation of the data (Sumpter and Pratt, unpublished results).

Franks et al. (2008) examined how the ants cope when offered one nearby nest of poor quality and a distant nest of better quality. Even when the better nest was nine times further away than a poor quality nest the colony successfully moved into the better nest. Individual comparison and the assessment delay, which allowed ants that had found the nearby poor quality nest to find the far away good quality nest before they commenced transportation, played important roles in decision-making. In cases where transportation did commence to the poor qulity nest it was quickly superseded by recruitment to the better nest. Similar results have been found when a better quality nest is introduced once an emigration has already commenced to a mediocre nest. The ants are often able to swap mid-emigration to the better nest (Franks et al. 2007).

While the algorithm is robust to different environmental conditions, how robust is it to changes in parameter values? One interpretation of the similarities in the algorithm but differences in parameter values between *T. albipennis* and *T. curvispinosis* is that the algorithm offers a degree of robustness that is independent of particular parameter values (Pratt 2005a). Natural selection acts to shape the algorithm, but parameter values are not strongly constrained. A similar argument could also explain why no consistent relationship has been found between the size of the quorum and the size of emigrating colonies (Dornhaus & Franks 2006; Franks et al. 2006; Pratt 2005a). Such a robustness has also been hypothesised as a design property of the gene networks which regulate development (von Dassow et al. 2000).

9.5 Formalising individual-based models

Often the presentation of individual-based models in the scientific literature consists of a flow chart or written description without a precise mathematical specification of the model. The lack of mathematical specification can be contrasted with differential equation or simpler stochastic models where papers clearly specify the equations underlying the model, allowing other researchers to reproduce the results.

One of the ambitions of building the individual-based model of *Temnothorax* migration was to provide a reliable tool against which to predict and understand future experimental results. To fulfil this aim Pratt et al. (2005) provided an unambiguous specification of the model in terms of a specification language WSCCS. Box 9.B introduces some of the basic aspects of WSCCS. This specification language was proposed by Chris Tofts for modelling various aspects of social insect organisation (Tofts 1991; Tofts 1993; Tofts 1994).

There is a strong advantage to using a specification language if all researchers adopt the same language. Unfortunately, there are also several disadvantages to using formal specification languages in model building. Firstly, keeping a clear specification can become burdensome when attempting to develop in parallel a number of different models of the same system. For example, previous to the individual-based model we had written a differential equation model of the quorum mechanism (Pratt et al. 2002). This model proved extremely powerful in understanding why the ants employed a quorum threshold. While it was possible to see the quorum model as a simplification of the full individual-based model under a certain set of assumptions, the formal steps required to make this simplification were cumbersome and revealed nothing new.

A second disadvantage of formal specification is that particular specification languages are not always designed to address all modelling problems. WSCCS is not good for representing processes which occur on very different time scales or problems which are spatially explicit. For *Temnothorax* emigration, several researchers have developed their models in order to investigate different aspects of the emigration. These range from differential equation to various individual-based models. Thus, although the ideal would be for everyone to use a consistent language for specifying

Box 9.B: Process algebra models

Process algebras were first proposed to aid the analysis of the performance of distributed computer systems (Bruns 1997; Milner 1989). They allow formal specification of the individual components, which make up a system, and then provide means for proving properties of component interactions. Standard process algebras are designed to examine conditions under which a system will fail or attempt to prove that a system will never fail. As such they look at properties of a system which are time-independent and are unaffected by stochastic variations. In modelling insect societies it is usually the timing and probability of events which are of greatest interest to us. To this end, Tofts (1991; 1993) developed a probabilistic and time-dependent version of one of the most widely-used process algebras, Calculus of Communicating Systems (CCS). Toft's Weighted Synchronous Calculus of Communicating Systems (WSCCS) allowed him to specify models where ants were the components, and then answer questions about properties of the colony they composed.

A simple example is as follows. We can define an ant waiting at a nest as follows

ATNEST = s: $\surd$.SEARCH + (1-s): $\surd$.LOOKCALL

LOOKCALL = ω:*call*.FOLLOW+1: $\surd$.ATNEST

This definition can be interpreted as follows. An agent in state ATNEST will with probability s enter the state SEARCH and with probability (1-s) enter the state LOOKCALL. The symbol $\surd$ denotes that one time step of the simulation will pass when the state is updated. The agent LOOKCALL also has two possible actions, *call* or $\surd$. ω denotes that the action *call* is prioritized over $\surd$. These actions can only be understood in the context of the interaction of two or more agents. In particular, in order for the action call to be performed it is required that there is another agent performing the complementary action $\underline{\textit{call}}$. For example, if we define two further agents

GIVECALL = ω:$\underline{\text{call}}$.LEAD+1: $\surd$.GIVECALL

WALK = 1: $\surd$.WALK

When these three agents are defined in parallel, written as

LOOKCALL ×GIVECALL×WALK

Then on one time step these agents will become

FOLLOW×LEAD×WALK

On the other hand the parallel definition

LOOKCALL ×WALK×WALK

will become

ATNEST ×WALK×WALK

Thus if two parallel agents wish to perform the complementary actions, *call* and $\underline{\mathit{call}}$, then this takes priority.

Since the idea of WSCSS is to give a formal definition of agents, the above informal discussion does not give an unambiguous explanation of how process algebras are defined. A more complete description can be found in Tofts (1991; 1993) and Sumpter et al. (2001). WSCCS can however be used to provide formal definitions of complicated state-based models of animal interactions. It can also be used to develop Markov chain and differential equation representations of these models (Sumpter et al. 2001). In the supplementary material Pratt et al. (2005) a full description is given of the *Temnothorax* nest choice model in WSCCS.

their models, in practice this is a very difficult aim to fulfil. The burden of making every model consistent outweighs the advantage of rigorous comparison between models.

The lack of agreed-upon framework for developing individual-based models and the difficulty in measuring the large number of parameter values discussed at the end of section 9.1, are the two major reasons for a limited acceptance of this type of modelling approach (Grimm & Railsback 2005). Individual-based models are often viewed as ill-defined and unreliable by researchers versed in the use of differential equations or other mathematical approaches. This is unfortunate, because in some sense they are the only tool available in the study of truly complicated systems. Exactly how the lack of standards and reproducibility in individual-based modelling can be overcome in the future is unclear, but it remains an important problem.

In this chapter I have focused on individual- and state-based models in the context of social insect foraging and migration. These examples should serve primarily as case studies of the successes and limitations of this type of approach. However, individual-based models are by no means limited to these applications. In particular, agent-based modeling is a powerful tool for understanding the social sciences (Edmonds et al. 2008; Miller & Page 2007), ecology (Grimm & Railsback 2005) and microbiology (Ferrer et al. 2008).

9.6 Dimension reduction

If real world systems consist of large numbers of variables and parameters, and models with large number of variables and parameters are unwieldy, then how can we hope to model complicated systems? One answer to this question lies in the very art of modelling: to find a way of expressing the key elements of a system in only a few well defined variables. It is the art of modelling to try to produce a model which is as “simple as possible but no simpler”, as the quote attributed to Einstein goes.

The number of variables in a model is often referred to as the model’s dimension. With the exception of the models discussed in this chapter, most of the models in this book have a small dimension, e.g. a small number of variables describing the number of ants visiting a particular feeder or the proportion of individuals that scrounge or produce food opportunities. In cases where the model’s dimension is higher, for example when we have a pair of variables for the position and speed of each particle in the SPP models of chapter 5, we try to derive a smaller number of variables, such as the instantaneous alignment or average neighbour distance, that somehow characterise the group. The aim here is to characterise large or infinite dimensional models by a much smaller number of variables. If we can characterise a system by a model that has only a small number of dimensions then it becomes easier to make mathematical predictions about its behaviour.

Complications should never be over-estimated. When viewed at certain spatial and temporal scales very complex individuals can produce very simple group level dynamics, provided they exhibit a reasonable degree of independence. For example, though a highly complex algorithm may have brought shoppers to town in the first place, the number of people passing by a point on a quiet shopping street during a five minute interval is likely to be randomly distributed. This prediction is based on the ‘law of small numbers’, that independent low frequency events in a large population follow a Poisson distribution (Bortkiewicz 1898). While on very small time scales there are socially enforced gaps between people and on very large time scales there are patterns determined by shops opening and closing, on the time scale of an hour on a Monday morning pedestrians pass by more or less at random. Once a large number of factors begin to influence behaviour, the complex begins to seem simple again.

Another example of a single distribution characterizing large numbers of independent individuals is the central limit theorem. In Box 4.B in chapter 4 I show how the normal distribution, which is defined by its mean and variance, characterises the sum of the actions of *n* independent individuals. The 'law of small numbers' and the central limit theorem are just two examples of mathematical results which allow a system of high dimension to be simplified to one of low dimension. The mean-field approximations used to derive differential equation models in Box 9.A are another. Mathematical techniques such as moment closure (Keeling & Ross 2008), equation free methods (Kevrekidis et al. 2004) and others all act to reduce the dimension of complex models and bring clearer analytical understanding of systems (Sethna 2006; Sornette 2004).

Complications should not be underestimated either. The fact that I have written seven chapters on models with a small number of dimensions and one chapter on those with high dimension should not suggest that most problems in collective animal behaviour can be modelled using a small number of variables. The decision to study a particular scientific problem is based not only on its intrinsic importance, but also upon whether we believe we can make progress solving it. Low dimensional models are mathematically tractable. If such a model can be applied in understanding a system, it becomes more likely to be the subject of experimental research. While a large number of mathematical techniques have been discovered to reduce biological systems to lower dimensions, there is no a-priori reason that the majority of these systems should be low dimensional. Indeed, while we can accept the idea that the complex is sometimes simple, our everyday experience tells us that the biological world is truly complicated.