

## Chapter 4: Making decisions

The previous chapter looked at how information is transferred between individuals, in particular when they are looking for food. In one sense we can talk about individuals making decisions about where to collect food from. The ants decide which of two food sources to exploit. Under natural conditions, however, food is often depleted or moves. As a result the available alternatives change and it is hard to define when or if a decision has been made, or to even usefully talk about decisions between alternatives.

There are however many situations when animals have to decide between two or more options, whose qualities remain stable through time. This chapter focuses on such situations, where individuals have a number of options to choose between and where we can define an end point at which all individuals have made a choice. Most of the examples I consider concern how groups choose a new shelter or migrate to a new home. Here we can sensibly talk about decision-making: once all individuals have settled at their new home or shelter, then we can say that a collective decision has been reached. The collective decision-making investigated in this chapter is thus information transfer in a specific, albeit interesting and important, setting. A setting in which there are multiple alternative choices available to a group, and the alternatives remain stable until a point at which we can say a decision has been made.

There are a number of important benefits to an individual in using the information possessed by others in reaching decisions (Sumpter & Pratt 2008). One benefit is the maintenance of cohesion. Choosing the same destination taken by others, for example, can make an animal less likely to be picked out by a predator. In the search for a new home there are often benefits to consensus, simply because group members do not want to have to invest time and effort re-coalescing because of an initial split.

While information transfer often results in cohesion, the underlying reason individuals followed or copied each other was not necessarily to promote group cohesion. Information transfer can be a form of social parasitism, and cohesion is a disadvantage to the individual who first found the food. There are, however, other potential benefits of information transfer in decision-making. Most importantly, the speed and accuracy of decision-making can both be improved

by copying the choice of a better-informed neighbour. Decisions in which cohesion, speed and accuracy are important factors and in which all or nearly all group members come to agree on the same option are often referred to as consensus decisions (Britton et al. 2002; Conradt & Roper 2005). The key question is how individuals reach a rapid consensus for the best of a number of available options.

## **4.1 Consensus decisions**

### **Cockroaches**

Various species of cockroach benefit from increased growth rates when in aggregations (Prokopy & Roitberg 2001). The German cockroach *Blattella germanica* can reduce water loss in dry conditions by clustering together with other cockroaches (Dambach & Goehlen 1999). These cockroaches rest during daytime periods in dark shelters where they aggregate in stable populations (Ishii & Kuwahara 1968; Rivault 1989). These aggregations are at least in part due to attraction to chemical odours on the body of the cockroaches (Rivault et al. 1998). Cockroaches that are collected from different locations and kept isolated as different strains have different odours and are attracted more strongly to the odour of their own strain (Rivault & Cloarec 1998).

Ame et al. (2004) performed symmetry breaking experiments to test the extent of aggregation due to social interactions. Figure 4.1 shows the result of these experiments. Cockroaches were placed in an arena with two identical shelters both with sufficient capacity to shelter all of the cockroaches. In a majority of experiments over 80% of the cockroaches chose the same shelter. These results held even when two different cockroach strains were put in the arena, with different strains usually choosing the same shelter (Ame et al. 2004). Independent of difference in strain, the cockroaches make a consensus decision about which of the two shelters to occupy.

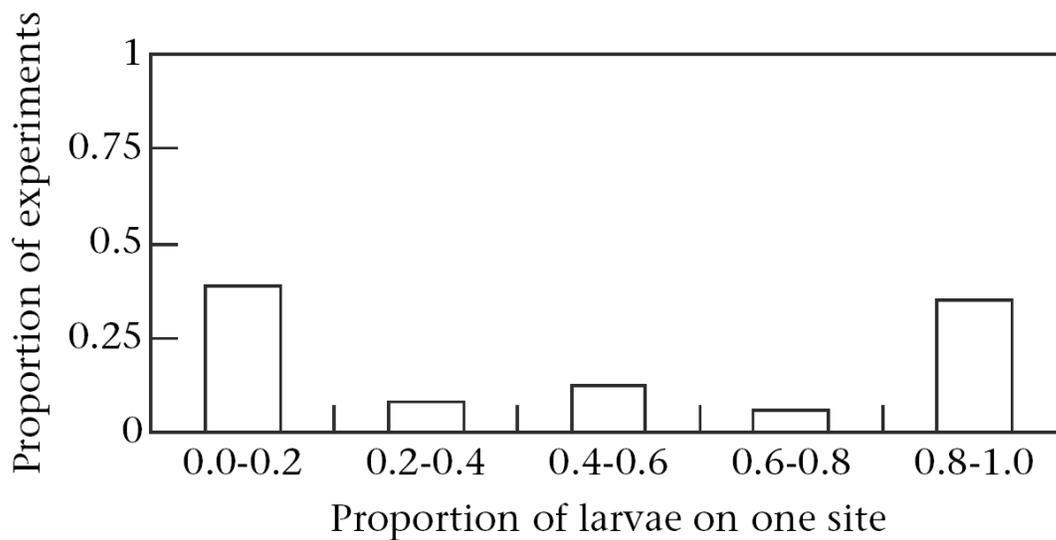
The consensus decision is reached through a very simple rule followed by individual cockroaches: the probability per unit time of an individual leaving a shelter decreases as a function of the number of cockroaches under the shelter. This probability of leaving decreases rapidly as the number of cockroaches under the shelter increases (figure 4.2a). By incorporating this quorum response into differential equation and stochastic simulation models of cockroaches finding and leaving shelters, Ame et al. (2004) showed that it could explain consensus shelter choice. The model they used has strong similarities to the

models of ant foraging described in Box 3.A. A disproportional response to the presence of other cockroaches is the key to a consensus decision. Ame fitted the function

$$\frac{\theta}{1 + \rho \left(\frac{x}{S}\right)^\alpha} \quad (3.1)$$

to the probability per second per cockroach of leaving a shelter, where  $x$  is the number of cockroaches under the shelter.

Figures



**Figure 4.1:** Results of Ame’s experiments (2004) where cockroaches were offered two identical shelters. Shows the frequency distribution of the proportion of individuals choosing one of the two shelters over 49 experiments.

The model predicts that if  $\alpha=1$ , i.e. the time spent in the shelter is directly proportional to the number of cockroaches under it, then the cockroaches would divide equally between the two shelters. If  $\alpha>1$ , i.e. the time spent in the shelter increases more than linearly with the number of cockroaches under the shelter, then symmetry breaking occurs and a consensus is reached for one of the two shelters (Millor et al. 2006). The experimentally measured value of  $\alpha\approx 2$  thus accorded with the consensus decisions seen in the earlier experiments (figure 4.1). Further investigation of the model shows that provided that  $\alpha > 1$ , only a relatively weak positive response to the presence of conspecifics is sufficient to produce symmetry breaking. This could explain why combinations of different

strains exhibit an equally strong tendency to make consensus decisions, despite the fact that each strain has only a weak attraction to the odour of the other strain (Leoncini & Rivault 2005).

### **Social insect migration**

As with many other aspects of collective behaviour, social insects provide the most detailed experimental studies of decision-making. For many social insects, the survival of the colony depends upon remaining together and making a good decision about where to live. For example, honey bees invest heavily in comb construction, brood-rearing, and food storage at their nest. A poor initial choice of nest site or a failure of all colony members to choose the same nest site can greatly reduce the colony's reproductive success.

**function fit to these data: probability of transport =  $\frac{x^k}{x^k + T^k}$ , where x is the new site population.**

**Reproduced from Pratt (2005c).**

Ants of the genus *Temnothorax* live in colonies of between 50 and 500 individuals in small rock or wood cavities. In the laboratory, a colony whose nest has been damaged moves to a new site within a few hours, reliably choosing the best site from as many as five alternatives, discriminating among sites according to cavity area and height, entrance size, and light level (Franks et al. 2003b; Pratt & Pierce 2001). Around 30% of the ants actively partake in the process of choosing a new nest site. These active ants undergo four phases of graded commitment to a particular nest site (Pratt et al. 2005). 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 scout follower is led from the old nest to the new site. These recruited ants then in turn make their own independent assessments of the nest and also recruit once the assessment period is over. The nest population thus increases through a process of recruitment and of independent discoveries of the nest. Since ants take longer to accept lower quality nests, when two alternative nests are presented to the ants recruitment is more rapid to the better quality nest (Pratt et al. 2002).

Recruitment via tandem runs is rather inefficient: ants move at one third of the usual walking speed when leading a tandem run (Pratt et al. 2005). However, rather than indefinitely continuing to recruit using tandem runs, ants recruit in this manner only when the nest population is below a threshold population, referred to as the quorum threshold. Once the population exceeds this quorum threshold a recruiting ant enters a committed phase, where she carries passive adults and brood items to the new nest site (Pratt et al. 2002). These transports are rapid, as carrying another ant does not significantly reduce an ant's walking speed. The meeting of the quorum thus marks a shift from slow to rapid movement into the new nest.

Honey bee emigration usually occurs in spring, when the queen and a swarm of roughly 10,000 worker bees leave their nest and cluster in a densely packed swarm in a nearby tree. Several hundred scout bees then fly from the swarm and search for tree cavities and other potential new homes. Successful scouts use the

waggle dance to recruit other scouts to these sites, and those recruited bees may in turn dance for a site. A positive feedback loop of recruitment to sites begins, similar to that seen when honey bee colonies forage for food (section 3.1). Dances are more frequent for, and thus recruitment is stronger to, better quality sites so the population of recruited scouts grows faster (Seeley & Buhrman 1999; Seeley & Visscher 2004a). Once the number of bees at a site reaches a quorum the bees begin an additional recruitment strategy to dancing, known as piping (Seeley & Visscher 2003; Seeley & Visscher 2004b). Piping is a signal to other non-scout bees at the swarm to warm their flight muscles in preparation for the entire swarm to lift off and fly to the new nest site (Seeley et al. 2003). Over the two or so days during which the scouts search and recruit to new nests, there is dancing for a large number of alternative sites but usually only one site reaches quorum and induces swarm liftoff. Usually at the point of liftoff only one site has reached the quorum threshold population, but in rare cases, split decisions are observed. In these case the bees lift off in different directions but are then forced to return to the tree branch to begin the process again (Lindauer 1955; Lindauer 1961).

There are strong similarities between the decision processes of *Temnothorax* ants, honey bees, and even cockroaches. All three species exhibit positive feedback and quorum responses (figure 4.2b). The ubiquity of these features and their importance in producing asymmetrical choices (see again Box 3.A) suggests that these similarities are, at least in part, an evolutionary consequence of a need by individuals to reach consensus. Non-quorum based recruitment would not give the same degree of consensus.

There are also illuminating differences between species. The ants' and bees' recruitment signals, such as tandem runs, dances and piping noises, are highly sophisticated. Communication between cockroaches is through attraction to hydrocarbons present on all parts of the cockroaches' bodies (Rivault et al. 1998). Attraction to other cockroaches is thus likely to be cue-based, although the fact that these hydrocarbons differ between strains may indicate that they are an evolved signal to individuals of the same strain (section 3.1). Whether the hydrocarbons are signals or cues, they are certainly a less complicated and probably less costly form of communication than those employed by migrating ants and bees. This greater complexity on the part of the ants and the bees is probably due to a greater requirement for consensus and colony unity. In chapter 9 I discuss how the complex migration algorithms employed by ants and

honey bees provide for improved accuracy and an ability to tune decision-making to different environmental conditions.

### **Other insects and spiders**

U-shaped distributions, such as that in figure 4.1 for cockroaches and figure 3.1d in the previous chapter for ant foraging, are a ubiquitous feature of binary choices by social and gregarious animals (Deneubourg et al. 2002). When offered a t-shaped climbing structure, spiders construct draglines between the bottom and only one side of the two ends at the top of the t-shape (Saffre et al. 2000); when confronted with the choice between ascending from one of two ends of a t-shaped structure, weaver ants build a chain down from only one side (Lioni & Deneubourg 2004); caterpillars forage on only one of two available branches (Dussutour et al. 2007); and migrating *Messor* ants leave pheromone trails to only one of the available nest sites (Jeanson et al. 2004a) all show such U-shaped choice distributions. Jeanson et al. (2004b) showed that even 'solitary' spiderlings have the same pattern of decision-making when building with draglines. By using the dragline shortcuts provided by the spiders that have already climbed up one side of a Y-shaped cotton thread these spiderlings remain cohesive.

In cases such as these, where individuals modify their environment, it is not entirely clear whether decisions arise because it is advantageous for individuals to be in a group, or because a choice made by one individual alters the environment in a way that makes it easier for other individuals to follow the same path. Thus, while U-shaped distributions are indicative of decision-making in response to the previous actions of others, they should not be necessarily interpreted as resulting from individuals acting in order to promote cohesion.

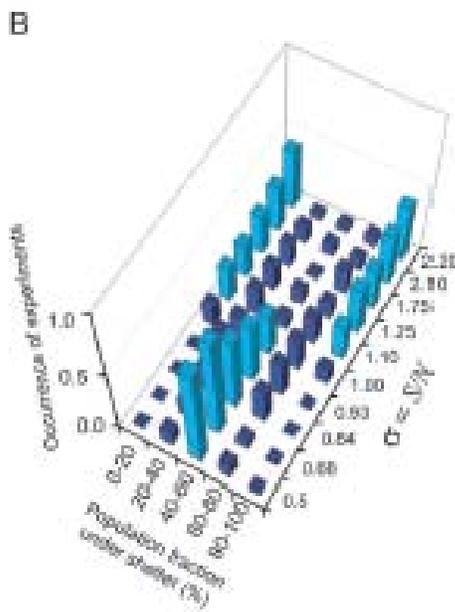
From a mechanistic viewpoint, U-shaped choice distributions imply a disproportional response to the actions of others. For many of the examples listed above individuals exhibit some form of quorum threshold, similar to those seen in the migrating *Temnothorax* ants and cockroaches. Either the probability of leaving a group decreases as a sharply non-linear function of the number of members (figure 4.2a), or the probability of joining a group increases as a sharply non-linear function of the number of members (figure 4.2b). These empirical observations demonstrate a basic property of all collective decision-making and

information transfer: positive feedback together with quorum responses lead to U-shaped choice distributions.

## 4.2 Evolutionarily stable decisions

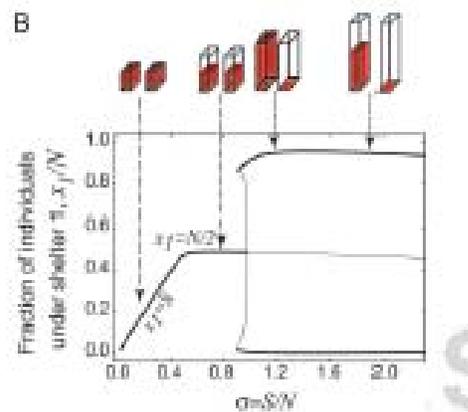
There are many situations where it is beneficial for individuals to reach consensus, but the number of individuals that can take a particular action is limited. Again looking at how cockroaches divided themselves between two shelters, Ame et al. (2006) investigated how the capacity of shelters affected the distribution of cockroaches between them. They found that when the capacity of a single shelter was insufficient to house all the cockroaches, the cockroaches split 50:50 between the two shelters, but when the capacity of both shelters was sufficient for all then the majority would choose the same shelter. The split in this case was nearer to 80:20 or 20:80. Furthermore, the switch from 50:50 to 80:20 occurred when both shelters had almost exactly the capacity to house all of the cockroaches (figure 4.3a). These results were consistent with predictions of their earlier mechanistic model of cockroach aggregation, with equation 4.1 playing a central role in determining that a majority choose the same shelter (figure 4.3b).

(a)

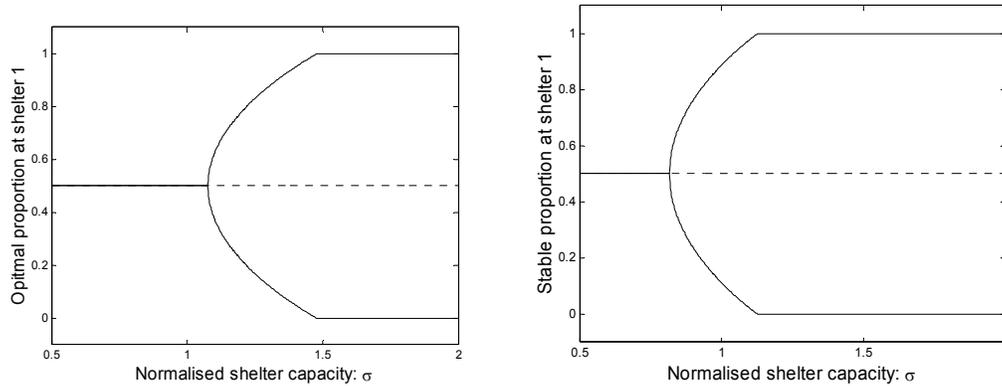


(c)

(b)



(d)



**Figure 4.3:** Distribution of cockroaches amongst shelters for different shelter size (a) experimental results (reproduced from Ame et al, 2006); (b) predictions of Ame’s mechanistic model (reproduced from Ame et al, 2006); (c) predictions of optimal group size model (see Box 4.0); (d) predictions of stable group size model (again see Box 4.0).

Based on these experimental results and earlier studies of the advantages of aggregation, Ame et al. (2006) suggested an optimality model for shelter choice. They proposed that the benefit of being in a shelter increases at first with number under the shelter, but as the capacity of the shelter is reached this benefit decreases due to overcrowding and the possibility of being exposed on the edge of the shelter. Box 4.A describes how the fitness function arising from their analysis can be used to determine both the optimal group size and the evolutionarily stable group size as a function of shelter capacity (see chapter 2 for a discussion of optimal and stable group sizes).

#### Box 4.A Optimal and stable cockroach distributions.

Ame et al (2006) proposed the following fitness function for a cockroach under a shelter where a fraction  $x$  of the other cockroaches are under the same shelter:

$$f(x) = \left(1 + p(x/\sigma)^2\right) \left(1 - x/\sigma\right)$$

where  $p$  is a constant and  $\sigma = S/n$ , where  $S$  is the size (or capacity) and  $n$  is the total number of cockroaches in the arena. In order to maximise the group fitness, i.e. the average fitness per individual, when there are two shelters is the proportion  $x$  which maximises

$$xf(x) + (1 - x)f(1 - x)$$

Differentiating this expression and solving equal to zero gives three solutions at  $x=1/2$  and

$$x = \frac{p \pm \sqrt{-3p^2 - 2p\sigma^2 + 3\sigma^2}}{2p}$$

The solutions corresponding to maxima are shown in figure 4.3c as a function of the normalised shelter capacity  $\sigma$ . At a critical value of  $\sigma$  group fitness goes from having a single maximum at  $x=1/2$  to having two maxima corresponding to an aggregation in one of the two shelters. The exact value of this critical point is determined by the value of  $p$ , but for a wide range of these values the critical point is close to  $\sigma=1$ .

As we saw in chapter 2, and is further illustrated in a number of examples in chapter 10, the strategy or behaviour that is optimal for the group is not necessarily that which is stable with respect to individuals attempting to maximise their own fitness. For example, lets assume that  $n=10$ ,  $\sigma=1$  and  $p=10$ . It is then optimal for the group to split 5:5 between the two shelters. In this case  $f(5/10)=1.75$  but  $f(5/10+1/10)=1.84$ . Thus if one of the five individuals at one shelter moves to another shelter it will increase its fitness, while simultaneously decreasing the fitness of those in the shelter it leaves as well as the average fitness of all individuals in the population. The group optimal distribution between shelters is not the stable distribution between the shelters. Individuals trying to maximise their own fitness will not choose the group optimal distribution.

The stable distribution of cockroaches amongst shelters are the values of  $x$  at which  $f(x) = f(1 - x)$ . At this proportion it is no longer beneficial for individuals to move to another shelter. Solving  $f(x) = f(1 - x)$  gives

$$x = \frac{p \pm \sqrt{-3p^2 - 4p\sigma^2 + 4\sigma p^2}}{2p}$$

Provided  $p > 2\sigma$  then there will exist carrying capacities where an equal division between the two shelters is optimal but not stable. Figure 4.3c and 4.3d show an example where an equal division between shelters becomes unstable when  $\sigma=0.815$ , but is optimal for the group up until the point that  $\sigma=1.017$ . In general, a range of carrying capacities exists where the stable and optimal proportions at the shelter differ.

Ame et al. (2006) looked only at the optimal group size (figure 4.3c) and concluded that the mechanisms employed by the cockroaches and the experimental data supported the hypothesis that the cockroaches are able to make optimal decisions. This result is surprising from the viewpoint of individuals maximising their own fitness, since the stable group size gives a quantitatively different prediction (figure 4.3d). The optimal group size model predicts that the distribution of cockroaches between shelters will bifurcate from 50:50 to being biased towards one of the two shelters at roughly  $S=N$ , i.e. when the size of each shelter equals the number of cockroaches. The stable group size model predicts that the switch to a biased distribution will occur while  $S < N$ . Even when each shelter is too small to house all cockroaches, it is often beneficial for an individual cockroach to aggregate with the majority. Thus if each cockroach tries to

maximise its own fitness, the average cockroach does worse than were they to aggregate according to the optimal group size.

Theoretical comparison of optimal and stable group size raises a number of interesting questions. Assuming that cockroaches are not highly related to each other and/or are competing locally for resources we would expect them to adopt the evolutionarily stable rather than the optimal strategy in shelter choice (see chapter 10). Despite this, at first sight it is the optimal model (figure 4.3c) that gives the best fit to the data (figure 4.3a) and best matches the mechanistic model (figure 4.3b). However, the data is a distribution of experimental outcomes and it is difficult to be sure at exactly which point the bifurcation occurs. Different parameterisations of the models give different bifurcation points and tuning the parameters, none of which have been measured for the fitness function, can give quite different quantitative predictions. The experimental setup, where cockroaches are placed in an unfamiliar arena, is different from their natural environment, where they also learn about and use navigational cues in finding shelter (Durier & Rivault 1999). More detailed studies are needed to find out exactly what individual cockroaches might be trying to optimise.

Despite these potential problems, Ame's results are powerful because of their simultaneous study of experimental, mechanistic, and functional explanations within a single system. Theoretical studies of evolutionarily stable strategies for choosing resource sites have also found bifurcations in site choice. For example, Moody et al. (1996) model individuals which can choose between two patches with the aim of maximising food intake rate while minimising predation risk. Both food intake and predation risk decrease with the number of conspecifics at the patch, but with differing functional forms. They found that as a predator dilution factor increased, i.e. there were greater benefits to cohesion, a bifurcation occurred from a relatively even distribution of individuals between patches to individuals aggregating at one of two patches. This study, based on a functional explanation of patch choice, shows that even if the exact functional form of Ame's cost/benefit function is not correct, the mechanism adopted by cockroaches in decision-making is consistent with the principle of individuals making decisions that attempt to increase their fitness.

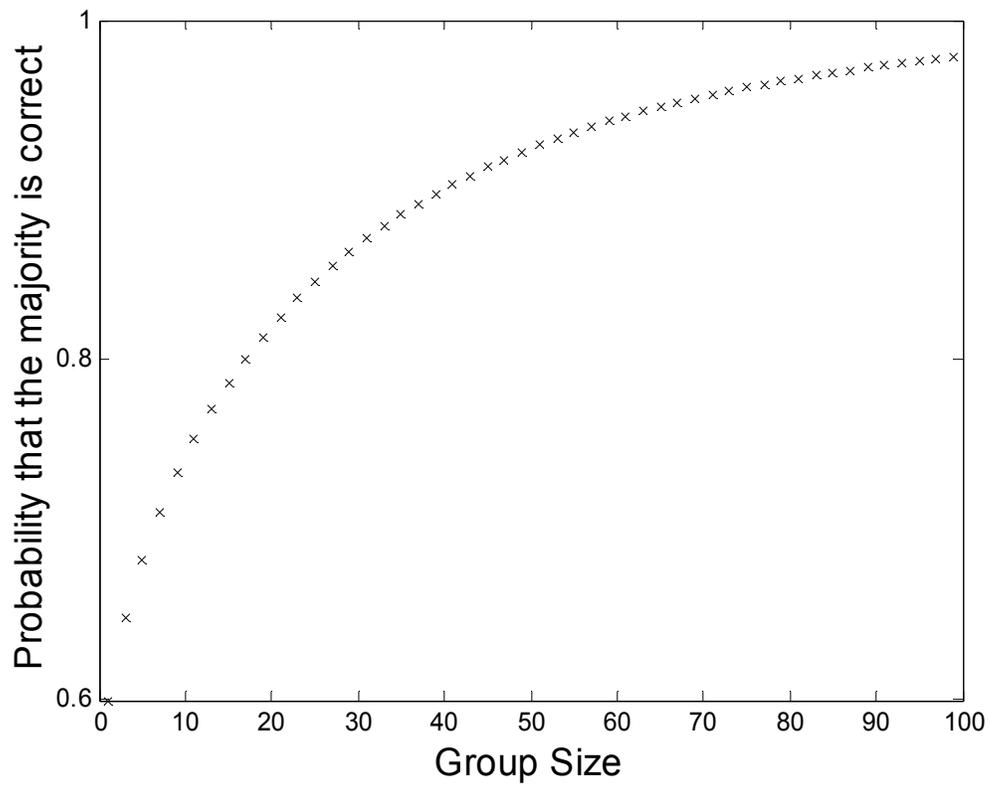
As with many aspects of information transfer in groups, an exciting challenge in this area is linking mechanistic and functional approaches. Jackson et al. (2006b) have begun to address this challenge by looking at how natural selection might

act on mechanistic rules for how individuals change their vigilance behaviour and decide to migrate between patches when confronted with a predation risk. These models again predict bifurcations and U-shaped distributions of numbers of individuals choosing different patches. Indeed, many of the predictions are highly reminiscent of the predictions first arising from purely mechanistic models (Camazine et al. 2001). This would suggest that the models of Jackson and others could benefit by incorporating the response thresholds, emphasised by Deneubourg, Ame and co-workers, into evolutionary models of decision-making.

### **4.3 Many wrongs**

In the last chapter I looked at situations where one individual has a piece of information, such as the location of some food, which is transferred to others through positive feedback. In such situations it is often clear that there is an advantage to copying the behaviour of the individual with the information. There are however many decision-making situations when a group of individuals are faced with two or more options, with none of them having more information than the rest about which of the options is best. For example, in an unfamiliar environment individuals must choose where to look for food. In such cases, each individual has some probability of making the 'correct' decision, but no individual is a-priori more likely to be correct than any other.

In binary choices, we can assume that each individual has a probability  $p$  of making a correct decision in the absence of others with which to confer. Figure 4.4 shows the probability that the majority make a correct decision, provided each individual makes its decision independently of the others (see Box 4.B for details). Although the probability that each individual is correct is only  $p=0.6$ , the probability that the majority of the group is correct increases steeply with group size. Groups of size 100 will hardly ever make a majority error. This result was first applied in the 18<sup>th</sup> century by Condorcet to designing the jury system. In general, it illustrates that majority decisions are good at pooling information and improve decision-making accuracy (King & Cowlshaw 2007; List 2004).



**Figure 4.4:** Condorcet's theory. The probability that the majority of individuals are correct (for odd numbers of individuals) when each is correct with probability  $p=0.6$ .

## Box 4.B Condorcet's theorem and the Central Limit Theorem

Condorcet's theorem is as follows. Assume that an odd number of individuals  $n$  have to make a choice between two options independently of the others and each has a probability  $p$  of being correct. The probability that the majority make the correct choice follows directly from the derivation of the binomial distribution, i.e.

$$m(n, p) = \sum_{i=\frac{n+1}{2}}^n \binom{n}{i} p^i (1-p)^{n-i}$$

Figure 4.4 plots this function for  $p=0.6$ . As the number of individuals goes to infinity,  $m(n, p) \rightarrow 1$  and the majority decision is always correct. In the case where  $n$  is an even number we have to make a choice about how we treat cases where an equal number make the same decision, but the overall shape of the curve remains the same.

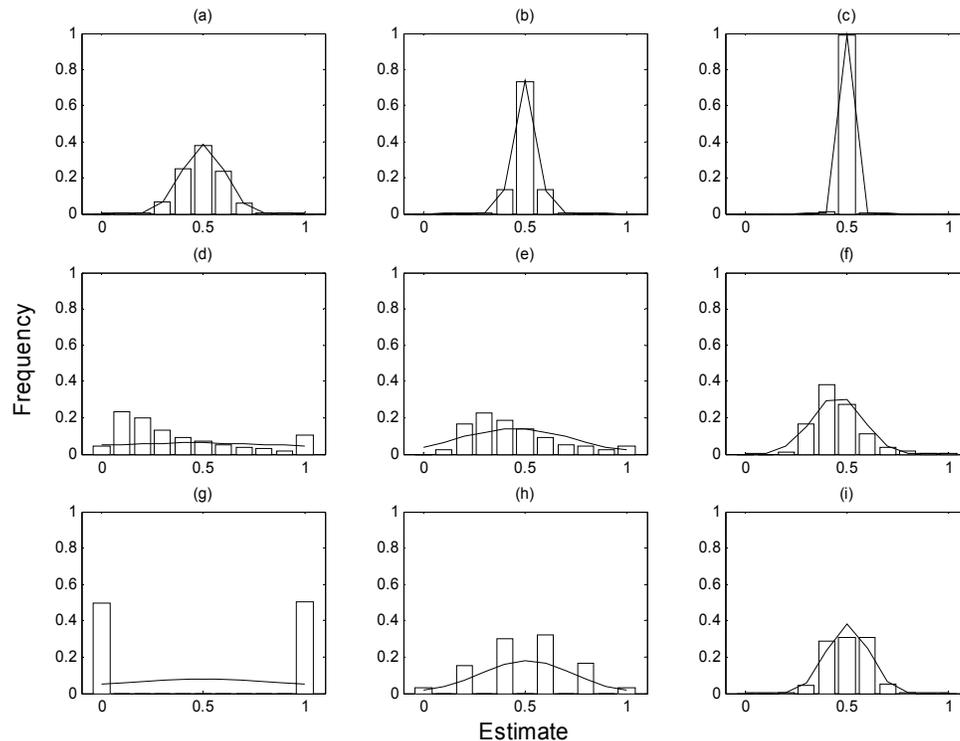
The principle of many wrongs assumes that there are  $n$  independent individuals each of which attempts to estimate some continuous variable which has a correct value  $v$ . We let  $X_i$  be the estimate of the value by individual  $i$ , such that the expectation is unbiased, i.e.  $E[X_i] = v$ , and the variance in the estimate  $Var[X_i] = \sigma^2$  is the same for all individuals. The  $X_i$  can be distributed according to any distribution with finite variance. Figure 4.4 shows the distribution of average estimates of  $n=1, 5$  and  $25$  individuals under various estimate distributions. For distributions with large variance, such as the Bernoulli and lognormal, the estimate of a single individual often lies a long way from the correct value  $v$ . Indeed, individuals making estimates according to a Bernoulli distribution never estimate correctly. However, even if the individual estimates are widely scattered the average of  $25$ , and even only  $5$ , estimates lies much closer to the true value. As in Condorcet's theorem, the more individuals that we average over the closer we come to the true value.

The central limit theorem states that for large  $n$  the mean estimate,  $\frac{1}{n} \sum_{i=1}^n X_i$ , is distributed

normally with mean  $v$  and variance  $\sigma^2/n$ . This theorem gives us three useful pieces of information: (1) that independent of the distribution of estimates by a single individual, the mean estimate becomes Normally distributed; (2) the degree of error in the average of  $n$  estimates has standard deviation  $\sigma/\sqrt{n}$ ; and (3) for very large  $n$  this error tends to zero. Figure 4.5 shows the frequency of average estimates predicted by the central limit in comparison with the actual distribution. By  $n=25$  this mean estimate is very close to the correct value.

Although the many wrongs principle seems to provide a powerful way for groups to make correct decisions it relies on two key assumptions, that individuals are independent and that they are unbiased. In the main text I discuss the various problems with the assumption of independence.

The assumption of lack of bias must also be treated with care. For example, if we set up a navigation experiment that deliberately misleads subjects then no matter how many subjects we independently examine they will each be misled and thus choose a biased and less accurate route. Determining variation due to error and that due to internal bias thus poses a difficult problem in practice.



**Figure 4.5: The many wrongs principle and the central limit theorem.** The distribution of average estimates when estimates are distributed according to: (a-c) Normal distribution with  $\nu=0.5$  and  $\sigma=0.1$ ; (d-f) Log-normal distribution with  $\nu=0.5$  and  $\sigma=0.58$ ; and (g-i) A bernoulli distribution with  $\nu=0.5$  and  $\sigma=0.5$ . The histograms give the frequency distribution for: (a, d & g) the estimate of a single  $n=1$  individual; (b, e & h) the average estimate of  $n=5$  individuals; and (c, f & i) the average estimate of  $n=25$  individuals. The solid lines overlaid on the histogram gives the prediction for the distribution of estimates by the central limit theorem, i.e. the predicted frequency for a normal distribution with mean  $\nu=0.5$  and variance  $\sigma^2 / n$ .

A related concept is that of many wrongs. For example, navigating animals possess directional information—from visual landmarks, internal compass, smell and so on—which is subject to error. Assuming this error is unbiased then the average direction of the group is more likely to be correct than that adopted by one randomly chosen individual (Simons 2004; Wallraff 1978). This argument can be formalised as an application of the central limit theorem, which predicts that the error in the average direction decreases in proportion to the square root of the group size. Experimental tests of this theory on navigating birds have had

mixed results, but do appear to show some increase in accuracy with group size (Biro et al. 2006; Simons 2004; Tamm 1980). Oldroyd et al. (2008) looked at the dances of *Apis florea* honey bees within a swarm prior to liftoff. These dances encode the direction of proposed nest sites. They found that the actual direction taken by the swarm was very close to that of the average direction indicated by the dances. This would suggest that the dancing bees can effectively integrate their directional information and lead a large group of uniformed individuals in the average of their proposed directions.

In humans, the 'many wrongs' principle is highlighted by an observation by Galton (1907). He examined 800 entries into a 'guess the weight of the ox competition', where a crowd of fairgoers each paid a small amount to guess how much a large ox would weigh after slaughter, with the most accurate guess winning a prize. Although the guesses had a wide variation the average guess was only 1 pound (450 g) less than the 1197 pounds (544.5 kg) that the ox weighed. Acting independently, the crowd 'knew' the weight of the ox. There are many such examples of collective accuracy in humans: ask the audience on 'Who wants to be a millionaire?'; the accurate prediction of American presidential elections by betting; and the Google search engine using links to a webpage to measure its popularity are just some (Surowiecki 2004).

Variability is an inherent feature of animal groups, including insect societies (Jeanne 1988; Seeley 1995). From only one week old, before they have left the hive for the first time, honey bees have different levels of response to sucrose, which later in life determines their propensity to collect water, nectar and pollen (Pankiw & Page 2000). This variability can lead to benefits for the colony. For example, genetically diverse honey bee colonies keep a more constant brood nest temperature than genetically uniform ones (Jones et al. 2004; Mattila & Seeley 2007). Stability is thought to be maintained because of individual differences in the temperatures at which individuals begin and stop fanning (Graham et al. 2006; Jones et al. 2007; Weidenmuller 2004). Individuals responding at different temperatures avoid all or nothing responses that could lead to the colony overshooting its target temperature (Sumpter & Broomhead 2000).

#### **4.4 Integrating many wrongs**

The assumption that individuals are independent leads to a paradox in the theory of many wrongs. On the one hand the theory says that the group is collectively wise, but on the other hand it requires individuals to be independent. If there is too much conferring between individuals before they reach a final decision then their decisions are no longer independent. Positive feedback can spread particular information quickly through the group, encouraging all individuals to make the same, possibly incorrect, choice. Alternatively, if there is too little conferring then each individual will act independently and fail to benefit from the input of others.

In human decision-making, in situations where all individuals are agreed on the best outcome but are individually unsure about the best course of action to secure this outcome, the many wrongs paradox lies at the basis of the phenomena of 'groupthink' (Janis 1972; Janis 1982). Groupthink is where pressures of group members on each other lead to a narrowing down of opinions. It is most likely to occur in groups where members have similar backgrounds and interests. Janis (1972) proposed that groupthink can be prevented by allowing a large number of individuals to first collect information independently before presenting their recommended course of action to a smaller number of centralised evaluators. By correctly weighting the information presented by the independent individuals, which is itself no easy task, the evaluators can then make a decision based on an average of the opinions presented.

While human groups may be able to integrate complex information from a large number of sources when making decisions, this is not always possible for animal groups. In most cases decision-making by animal groups is decentralised (Seeley 1995; Seeley 2002) and as such positive feedback plays a necessary role in their decision-making (Bonabeau et al. 1997; Deneubourg & Goss 1989). As we saw in the last chapter, although not always leading to the correct choice, positive feedback through pheromone trails usually allowed ants to choose the best of two available food sources. Similarly, not only do *Temnothorax* ants and honey bees make consensus decisions, but they are able to choose the best of a number of alternatives (Mallon et al. 2001; Seeley & Buhrman 2001).

Box 4.C investigates how positive feedback combined with quorum responses can aid accuracy in decision-making by groups without full consultation of all group members. The model assumes very limited cognitive powers on the part of individuals. In particular, they have no way of directly comparing the two available options. Instead the probability of choosing an option is simply an increasing function of the number already there. The question is what functional form of response gives the most accurate decisions? The model shows the accurate decision-making is achieved with quorum-like responses at a fixed threshold, rather than smooth linear responses (figures 4.6 and 4.7). This modelling result suggests that response thresholds not only provide cohesion, but also facilitate accuracy (Sumpter & Pratt 2008).

### Box 4.C Quorum responses and decision-making accuracy

Consider a group of  $n$  individuals initially uncommitted to either of two available options. Each of these finds one of the two options with a constant probability  $r$  per time step. This probability is independent of the actions of others. If an individual arrives at an option and no one else is there, then she commits to it with probability  $ap_x$  for option  $X$  and  $ap_y$  for option  $Y$ . If an individual arrives at an option and other individuals are present, the probability of her committing and remaining at the option is an increasing function of the number already committed. Specifically, if  $x$  is the committed number at the option then the probability that the arriving individual commits is

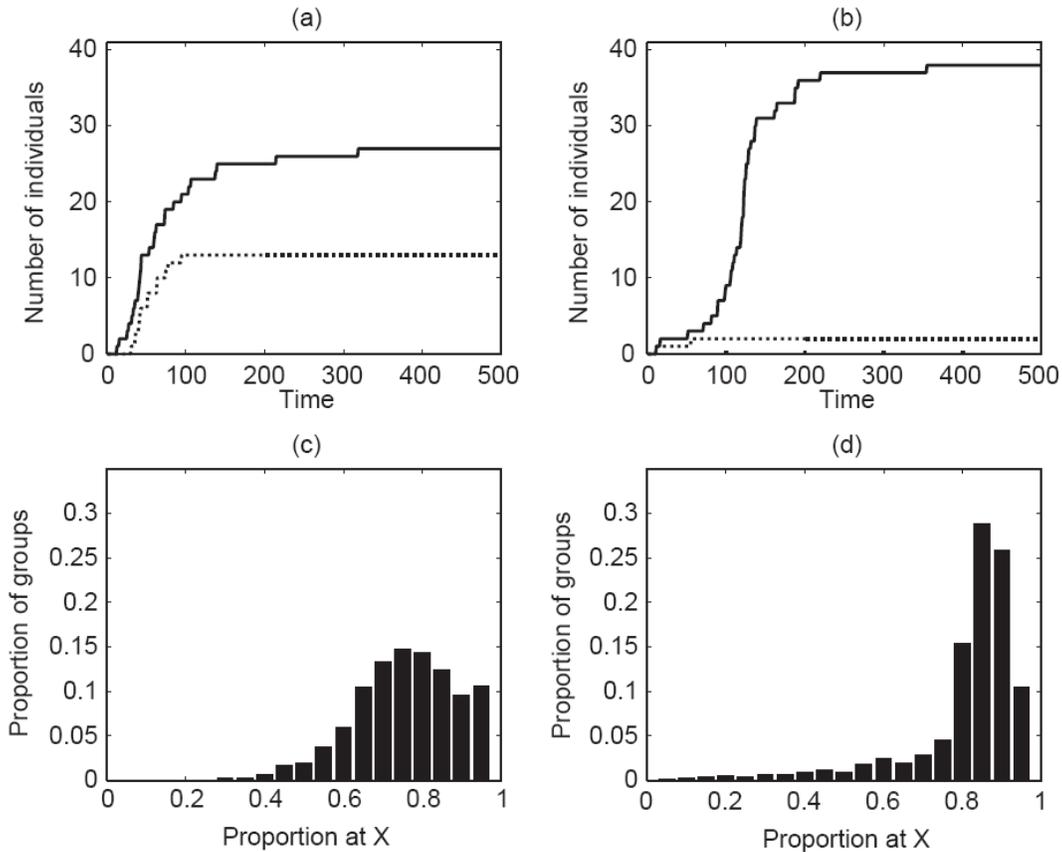
$$p_x \left( a + (m - a) \frac{x^\alpha}{T^\alpha + x^\alpha} \right) \quad (\text{equation 4.C.1})$$

where  $a$  and  $m$  are respectively the minimum and maximum probability of committing;  $T$  is the quorum threshold at which this probability is halfway between  $a$  and  $m$ ; and  $\alpha$  determines the steepness of the function. Equation 4.C.1 encodes a range of possible responses to the number that have chosen a particular option. In particular, as  $\alpha$  increases the response approaches a step-like switch, or quorum response, at the threshold  $T$ . In the model, a similar function determines the probability of selecting option  $Y$ , and by setting  $p_x > p_y$ , we assume that individuals prefer  $X$  to  $Y$ .

Figures 4.6a and 4.6b give examples of the choices over time of  $n=40$  individuals for shallow proportional responses ( $T=10$  and  $\alpha=1$ ) and steep quorum responses ( $T=10$  and  $\alpha=9$ ), respectively. For both types of responses, the proportion of committed individuals grows slowly for the two options, but slightly faster for the preferred option  $X$ . After the number of adherents to  $X$  reaches the threshold  $T$ , commitment to  $X$  significantly outpaces commitment to  $Y$ . Averaged over 1000 simulations, 75.5% of individuals choose  $X$  for a shallow response, while 83.3% do so for the steep quorum response. In both cases the proportion choosing the better option is higher than were each to make an independent decision, in which case  $p_x/(p_x+p_y)=66.7\%$  would be expected to choose  $X$ . Thus, in these simulations choices based on copying others reduce individual errors and make group decision-making more accurate than independent assessment alone. While a steep quorum response led on average to more accurate decisions, the distribution of decision-making accuracy is wider for  $\alpha=9$  than for  $\alpha=1$  (Figures 4.6c and 4.6d). This observation reflects the amplification of small initial errors for steep responses. If, through random fluctuations, the least favourable option happens to be chosen by more than a threshold number of individuals, then the quorum rule amplifies these early errors and nearly all individuals make the same incorrect choice.

Decision-makers typically face a trade-off between speed and accuracy. In the simulations, a steep quorum function,  $\alpha=9$ , yielded a more accurate decision, but the time taken for all individuals to choose was longer on average ( $307.8 \pm 71.0$  time steps, mean  $\pm$  standard deviation) than when  $\alpha=1$  ( $253.7 \pm 64.0$  time steps). In order to investigate how different values for  $\alpha$ ,  $T$  and  $a$  affect speed and accuracy, the parameters are systematically varied and their affect on the time needed for all individuals to make a choice and the proportion choosing the better option are measured (Figure 4.7). The results show that speed is maximized by setting  $a$  to its maximum

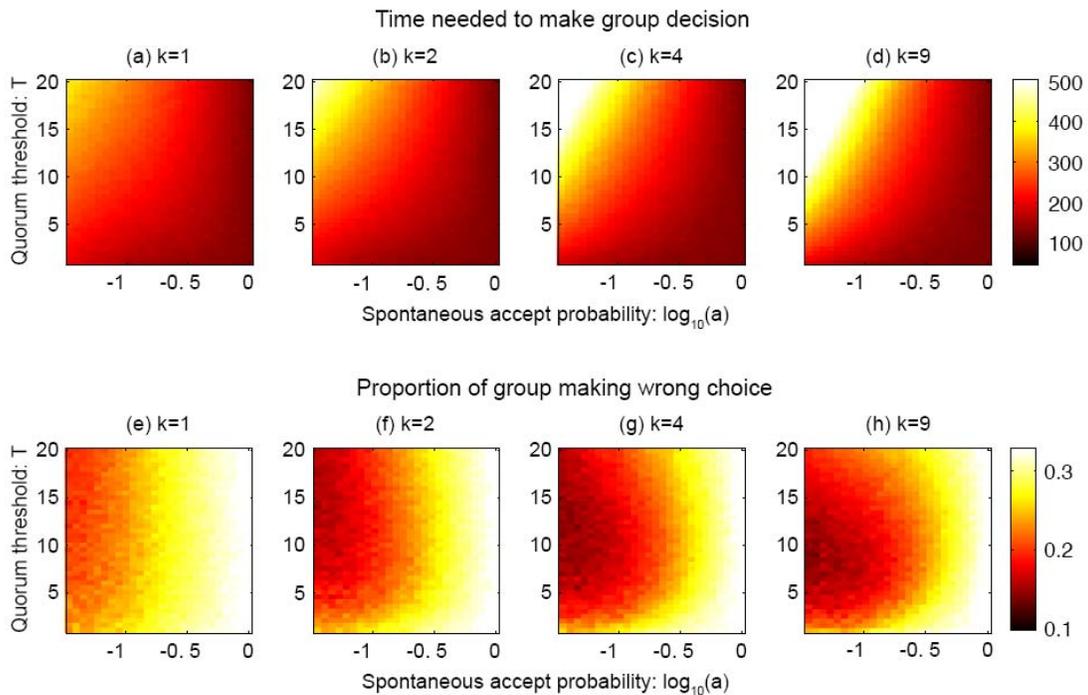
value of 1 (assuming that  $m=1$  as well). Greater speed, however, comes at the expense of more individuals choosing the worse option. Accuracy is maximized with low  $a$ , high  $\alpha$ , and  $T$  of around 10, but these values also produce relatively slow emigrations. For a more detailed analysis of this model see Sumpter & Pratt (2008).



**Figure 4.6: Simulations of a simple quorum response model**, for (a,c) shallow ( $k=1$ ) and (b,d) steep ( $k=9$ ) thresholds. (a) and (b) plot the change in the number of individuals committed to options X (solid line) and Y (dotted line) for one simulation with  $k=1$  and  $k=9$ , respectively. (c) and (d) show the distribution of the proportion of individuals choosing X after everyone has decided. Other parameters are  $r=0.02$ ,  $p_x=1$ ,  $p_y=0.5$ ,  $T=10$ ,  $a=0.1$ , and  $m=0.9$ . Reproduced from Sumpter & Pratt (2008).

While the quorum mechanism leads to some improvement in accuracy over individual decisions, it does not achieve the level predicted by Condorcet's theorem. Indeed, Condorcet's theorem provides an upper bound for the accuracy of collective decision-making. For example, given  $N=40$  individuals,

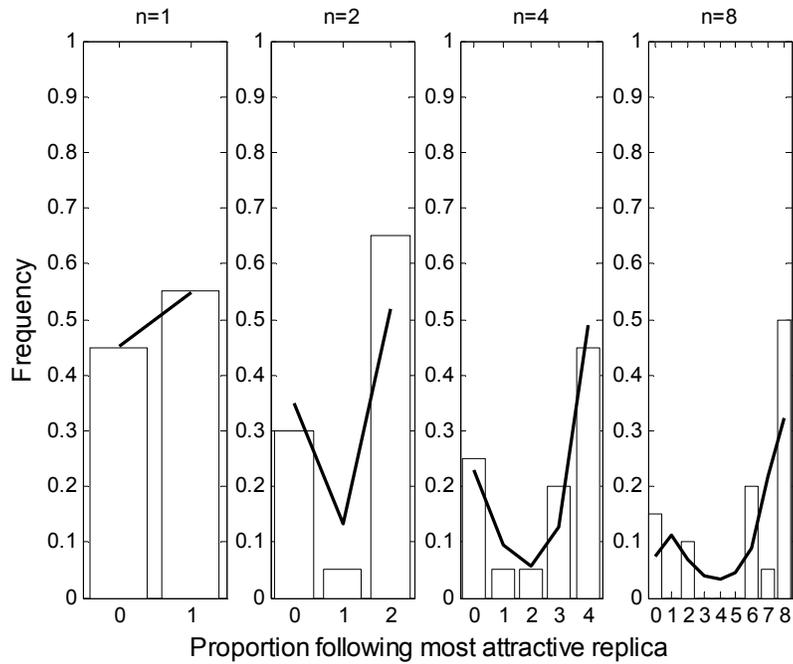
each with a 1/3 probability of making the wrong choice, then by Condorcet's theorem, the probability of a majority error is just 3.33%. This is lower than even the most accurate decisions made using quorum responses: for steep thresholds of between 5 and 15 and low spontaneous accept rates, approximately 10% of individuals take the least favourable option. Despite not reaching the upper bound for accuracy, a simple copying rule based on threshold responses substantially reduces errors compared to purely independent decision-making.



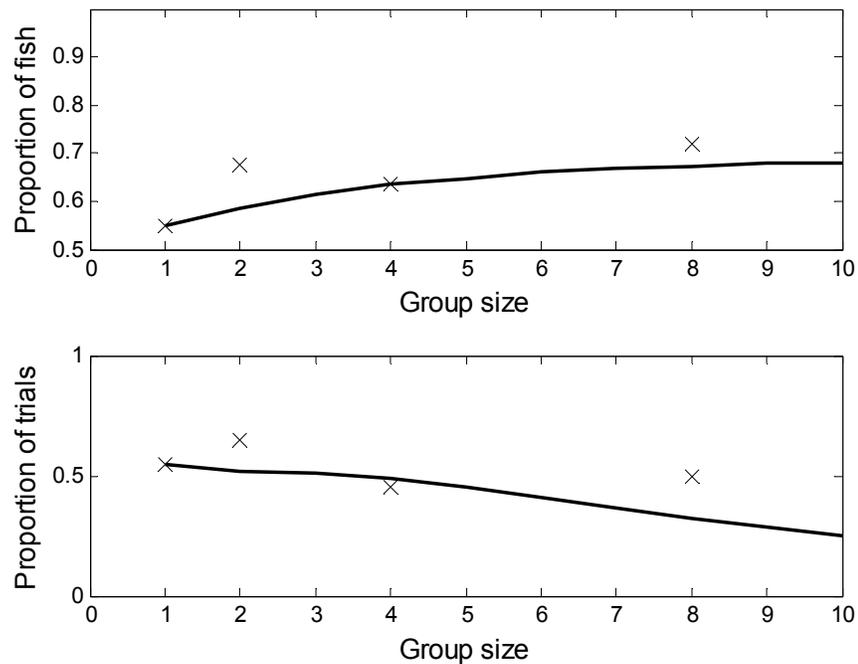
**Figure 4.7: Speed and accuracy of decision-making for the simple quorum response model.** Predicted effects of the parameters  $a$ ,  $T$  and  $k$  on (a-d) the time until all individuals have made a decision and (e-h) the accuracy of that decision. In each image,  $a$  and  $T$  are varied for different threshold steepness,  $k$ . The plots show mean duration (time steps of the model) and accuracy (proportion of individuals choosing the less attractive option  $Y$ ) over 1000 simulations for each parameter combination. Reproduced from Sumpter & Pratt (2008).

To test both decision-making mechanisms and the extent to which decision-making improves with group size, Ward et al. (2008) investigated how fish make movement decisions in response to others. We presented small groups

of three-spine sticklebacks with a Y-shaped maze. A drag line was set up down either side of the maze, along which replica conspecifics were drawn. We looked at the proportion of individuals following to either side of the maze as a function of the number of replicas travelling in each direction and the group size. Figure 4.8 shows the experimental results from these experiments. The sticklebacks tend to follow the replica, with smaller groups (1 or 2 fish) more likely to be influenced by the replicas than large groups (4 or 8 fish). If the difference between the number of replicas going to the two sides was only 1 (e.g. if left:right was 1:0 or 2:1) the larger groups were not influenced by the majority. If the majority was 2 however (e.g. if left:right was 2:0 or 3:1) then the larger groups were much more likely to follow the majority.



(a)



(b)

**Figure 4.8: Fish movement decisions in response to different replicas.** In the experiments a large (more attractive) replica fish moved in one direction and a standard sized fish moved in the other direction. (a) Comparison of data (histogram) and model (solid lines) in terms of proportion of fish following most attractive replica (b) The proportion fish making the 'more attractive' choice

(top panel) and proportion of trials in which all fish make the 'more attractive' choice (bottom panel) for the data (crosses) compared to the average of 1000 simulations of the quorum-response model (solid line).

The data was fitted by a model similar to that presented in Box 4.C. The main difference in this case is the inclusion of the number of undecided fish in an individual's decision to go left or right. In particular, we assumed that the probability of an individual going left on time step  $t+1$  is

$$a + (m - a) \frac{(L(t) - L(t - \tau))^\alpha}{U(t)^\alpha + (L(t) - L(t - \tau))^\alpha + (R(t) - R(t - \tau))^\alpha} \quad (\text{equation 4.1})$$

where  $m$  is the maximum probability of committing to a decision;  $U(t)$  is the number of uncommitted individuals at time  $t$ ; and  $L(t)$  and  $R(t)$  are, respectively, the total number of individuals that have gone left and right by time  $t$ . Three parameters— $a$  which is the spontaneous accept rate,  $\alpha$  which is the steepness of response and  $\tau$  which is the number of time steps over which fish are influenced by individuals which have already made decisions—determine the shape of this response (Ward et al. 2008). We estimated the parameters of this model from the experiments and found that a steep quorum-like response ( $\alpha \approx 3$ ) gave the best fit to the data. It appears that in deciding whether to go left or right the fish weigh the numbers going in each direction and their current group size and are disproportionately likely to take the direction of the majority.

In further experiments we looked at the likelihood of a group following a leader into a potentially dangerous situation. Groups of 4 or 8 fish swam past a predator replica only when guided by 2 or more replicas whereas single replicas were mostly ignored in this situation. On the other hand, single individuals could be fooled into following a single replica past a predator which they would almost never approach when alone. Interpreting these results in terms of our model we see that uncommitted individuals in larger groups only follow above a threshold number of leaders. This threshold dramatically reduces the probability of errors being amplified throughout a group because if the probability one individual makes an error is small, say  $a$ , then the probability that two fish independently make errors at the same time becomes very small, i.e.  $a^2$ . Interestingly, this rule of following only when two other individuals make a particular choice is consistent with experiments where humans are asked to make a decision after hearing the opinions of others (section 3.7; figure 3.9).

The quorum rule allows fish to make more accurate decisions as group size increases. Sumpter (2008b) looked at how well groups of fish could discern between two replica leader fish as a function of group size. Figure 4.8a shows the results of an experiment in which a group observed one large replica fish move in one direction and one standard sized fish move in another direction. As group size increases more of the fish follow the larger, more attractive fish. Similar results were observed in 9 other trait comparisons (e.g. fat vs thin, dark vs. light etc.). These results were reproduced by a model based on in equation 4.1. The model predicted that the frequency with which fish choose the correct option would increase with group size while the frequency with which all fish would choose the correct option would decrease with group size. This prediction was confirmed in the data (figure 4.8b). The data also confirms Condorcet's prediction that decision-making improves with group size (Sumpter et al. 2008b).

As with the cockroaches, ants, honey bees and humans (see section 3.6), we see that positive feedback and quorum responses are a key mechanism in fish decision-making. Measuring the form of these responses across species will further help determine the importance of information transfer in the evolution of group-living in these species. Interestingly, these steep threshold responses can sometimes amplify random fluctuations and lead to mass adoption of incorrect choices (Sumpter et al. 2008b). This sort of process may account for observations of mass copying (Dall et al. 2005; Laland 1998) or peer pressure in humans (Milgram 1992; Milgram et al. 1969) and may lead animals to make decisions in groups they would not have made by themselves. Although quorum responses lead to poor decisions in some notable cases, on average they allow greater accuracy than do complete independence or weak responses to the behaviour of others. Quorum responses allow effective averaging of information without the need of complex comparison between options.