

Quorum responses and consensus decision making

David J.T Sumpter and Stephen C Pratt

Phil. Trans. R. Soc. B 2009 **364**, 743-753
doi: 10.1098/rstb.2008.0204

References

[This article cites 61 articles, 8 of which can be accessed free](#)
<http://rstb.royalsocietypublishing.org/content/364/1518/743.full.html#ref-list-1>

Subject collections

Articles on similar topics can be found in the following collections

[behaviour](#) (357 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

Quorum responses and consensus decision making

David J. T. Sumpter^{1,*} and Stephen C. Pratt²

¹Department of Mathematics, Uppsala University, PO Box 480, 75106 Uppsala, Sweden
²School of Life Sciences, Arizona State University, PO Box 874501, Tempe, AZ 85287, USA

Animal groups are said to make consensus decisions when group members come to agree on the same option. Consensus decisions are taxonomically widespread and potentially offer three key benefits: maintenance of group cohesion, enhancement of decision accuracy compared with lone individuals and improvement in decision speed. In the absence of centralized control, arriving at a consensus depends on local interactions in which each individual's likelihood of choosing an option increases with the number of others already committed to that option. The resulting positive feedback can effectively direct most or all group members to the best available choice. In this paper, we examine the functional form of the individual response to others' behaviour that lies at the heart of this process. We review recent theoretical and empirical work on consensus decisions, and we develop a simple mathematical model to show the central importance to speedy and accurate decisions of *quorum responses*, in which an animal's probability of exhibiting a behaviour is a sharply nonlinear function of the number of other individuals already performing this behaviour. We argue that systems relying on such quorum rules can achieve cohesive choice of the best option while also permitting adaptive tuning of the trade-off between decision speed and accuracy.

Keywords: quorum responses; collective animal behaviour; Condorcet's theorem; social insect migration; decision making

1. INTRODUCTION

Group decision-making is characterized by individuals making choices that rely on the decisions of others. One benefit of this interdependency 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. Other potential benefits are in the *speed* and *accuracy* of an individual's decisions, both of which can be improved by copying the choice of a better-informed neighbour. This paper concerns group decisions in which cohesion, speed and accuracy are important factors. We will refer to these as consensus decisions, defined as cases when all members of a group come to agree on the same option (Britton *et al.* 2002; Conradt & Roper 2005).

Consensus decisions are well illustrated by the choice of a shelter or nest site, and many experimental studies have addressed this phenomenon (Visscher & Camazine 1999; Pratt *et al.* 2002; Jeanson *et al.* 2004a; Seeley & Visscher 2004a; Ame *et al.* 2006; Seeley *et al.* 2006; Visscher 2007). Experimenters typically offer a group of animals a choice between two or more alternative shelters and observe the process by which they make their choice. A decision is assumed to have been made once all individuals have settled at a shelter. The degree to which individuals are aggregated at a single choice gives a measure of their cohesion; the time taken for

everyone to choose an option measures decision speed; and the proportion of individuals choosing the 'best' option gives the decision accuracy.

How does consensus arise from interactions among group members, and how does individual behaviour influence the cohesion, speed and accuracy of decision making? In recent years, these questions have been addressed by the theoretical and experimental study of self-organization (Deneubourg & Goss 1989; Bonabeau *et al.* 1997; Camazine *et al.* 2001; Deneubourg *et al.* 2002; Sumpter 2006). In general, self-organization explains how positive feedback created by imitative behaviour can generate heterogeneous social patterns in uniform environments. In the context of decision making, this implies that a group faced with a choice between two or more identical options can spontaneously and cohesively choose only one of them. Self-organization can also address decision making when options clearly differ in quality. For example, positive feedback provided by pheromone trail recruitment allows ants to choose the shorter of two routes to a food source (Goss *et al.* 1989). Colonies of ants and honeybees (*Apis mellifera*) can also direct their foragers to the better of two or more food sources, because recruitment effectiveness is graded according to source quality (Seeley *et al.* 1991; Sumpter & Beekman 2003). Quality-dependent recruitment differences similarly underlie nest site selection in social insects (Mallon *et al.* 2001; Franks *et al.* 2003b; Seeley 2003). These studies show that positive feedback mediated by relatively simple interactions can allow social groups to make accurate consensus decisions.

* Author for correspondence (david@math.uu.se).

One contribution of 11 to a Theme Issue 'Group decision making in humans and animals'.

In this paper, we examine in detail a key feature of consensus decisions, namely the functional form of an individual's response to others' behaviour. We argue for the central importance of *quorum responses*, in which an animal's probability of exhibiting a behaviour is a sharply nonlinear function of the number of other individuals already performing this behaviour. We first review the theory for why and how consensus can yield more accurate decisions than those of lone individuals. We then describe a taxonomically diverse array of cases in which quorum-like responses have been found to underlie group decision-making. Next, we present a simple mathematical model to investigate how the functional form of the response to the behaviour of others affects cohesion, accuracy and speed of decision making. We show that the sharply nonlinear nature of a quorum response allows cohesive choice of the best option while also permitting adaptive tuning of the inevitable trade-off between decision speed and accuracy. Finally, we investigate these ideas and compare them with data using a more detailed model of nest choice by *Temnothorax* ants.

2. THE WISDOM OF CROWDS

In his popular science book *The wisdom of crowds*, James Surowiecki gives a number of powerful examples of how a large group of poorly informed individuals can make better decisions than a small number of informed 'experts'. A telling example is provided by Galton (1907), who examined 800 entries in a 'guess the weight of the ox competition', where a crowd of fairgoers competed to guess how much a large ox would weigh after slaughter. Although, the estimates varied widely, their average value was only 1 pound (450 g) less than the true weight of 1197 pounds (544.5 kg). Acting independently, the crowd 'knew' the weight of the ox. There are many such examples of heightened collective accuracy in humans, including the reliability of audience opinions on 'Who wants to be a millionaire'; the accurate prediction of American presidential elections by betting; and Google's successful ranking of World Wide Web search results by the number of links to each website (Surowiecki 2004).

The collective wisdom argument was first formalized by a French intellectual of the 18th century, the Marquis de Condorcet (Borland 1989; List 2004; Austen-Smith & Feddersen 2009). He considered binary choices between two options, in which each individual has a probability p of making a correct decision in the absence of others with which to confer. In this situation, one can apply the binomial theorem to find the probability that the majority of the individuals are correct. Assuming that an odd number of individuals n must each make a decision independently of one another, then the probability that the majority make the correct choice is

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

Figure 1 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. If n is even a rule

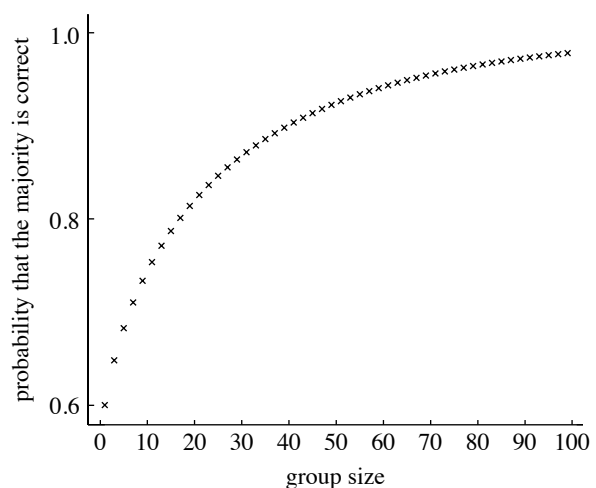


Figure 1. Condorcet's theory. The probability that the majority of individuals are correct (for odd numbers of individuals) when each is correct with probability $p=0.6$.

must be made to settle ties, but the overall shape of the curve is unchanged. For groups of size 100, the majority is almost never wrong, showing that majority decisions are good way to pool information and improve decision accuracy (List 2004; King & Cowlshaw 2007).

Although, Condorcet's theorem seems to provide a powerful method for groups to make correct decisions, it relies on two key assumptions—that individuals are unbiased, and that they are independent. Both these assumptions must be treated with care. For example, if a group of navigating birds each follow an internal compass with a consistent clockwise bias, then no matter how many individual headings are averaged, each will be similarly misled and the group decision will be inaccurate. Distinguishing variation due to random error from that due to consistent bias can therefore pose a difficult problem.

The second assumption of independent individual choices presents a larger challenge. Indeed, this assumption contradicts the very definition of group decision-making given in the first sentence of this paper—that individuals condition their own choices on those of others. How can collective decisions preserve independence but still come to a final consensus? In human decision-making, this paradox lies at the basis of 'groupthink' (Janis 1972, 1982). Groupthink occurs when the pressures of group members on one another narrow down the range of opinions. It is most likely when group 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 centralized evaluators. By correctly weighting these independent recommendations, itself no easy task, the evaluators can arrive at an average of the opinions presented. While effective for humans, this solution demands complex information-processing mechanisms that may not be available to animal societies. We now turn our attention to how these groups can solve the problem of groupthink.

3. POSITIVE FEEDBACK AND QUORUM RESPONSES

The collective behaviour of animal groups is often decentralized, with no leader integrating different sources of information or telling the others what to do (Seeley 1995, 2002). Instead, a pattern emerges from a large number of strictly local interactions that carry information throughout the group. A key feature of these interactions is positive feedback, in which an animal's probability of exhibiting a particular behaviour is an increasing function of the number of conspecifics already performing this behaviour (Deneubourg & Goss 1989; Bonabeau *et al.* 1997). In the context of collective decision-making, positive feedback allows the selection of a particular option to cascade through the group, as the growing number of adherents to an option increases its attractiveness to undecided animals. Moreover, this imitative behaviour often takes a step-like form, with an individual's probability of selecting an option changing sharply when the number of like-minded conspecifics crosses a threshold. Here we refer to this functional form as a quorum response, following well-studied cases in which threshold group sizes trigger key changes in behaviour (Pratt *et al.* 2002; Seeley & Visscher 2004b).

(a) *Cockroach aggregation*

Various species of cockroach benefit from increased growth rates when in aggregations (Prokopy & Roitberg 2001). German cockroaches (*Blattella germanica*) can reduce water loss in dry conditions by clustering together (Dambach & Goehlen 1999) and typically gather in dark shelters during the daytime (Ishii & Kuwahara 1968; Rivault 1989). Ame *et al.* (2004) tested the contribution of social interaction to these aggregations. They presented a group of cockroaches with two identical shelters, each with sufficient capacity to shelter all the insects. In the majority of trials over 80 per cent of the insects chose the same shelter. Thus even in the absence of a difference between the two options a consensus is reached for only one of them.

Consensus is reached through a very simple rule: an individual's probability of leaving a shelter decreases as the shelter's population increases. The probability drops quite sharply with population, giving rise to a step like quorum response (figure 2a). By incorporating this quorum rule into models of cockroach behaviour, Ame *et al.* (2004) showed that it could explain consensus shelter choice. A disproportional response to the presence of other cockroaches was the key element. Ame *et al.* (2006) fitted the function

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

to the probability per second per cockroach of leaving a shelter, where x is the number of cockroaches under the shelter (figure 2a). The parameters determine the shape of the response: θ is the rate at which cockroaches leave an unoccupied shelter; ρ and S determine the density at which cockroaches respond to conspecifics and α determines the steepness of this response. The model predicted that a consensus will be reached for one of the shelters as long as $\alpha > 1$, that is, the time spent in the

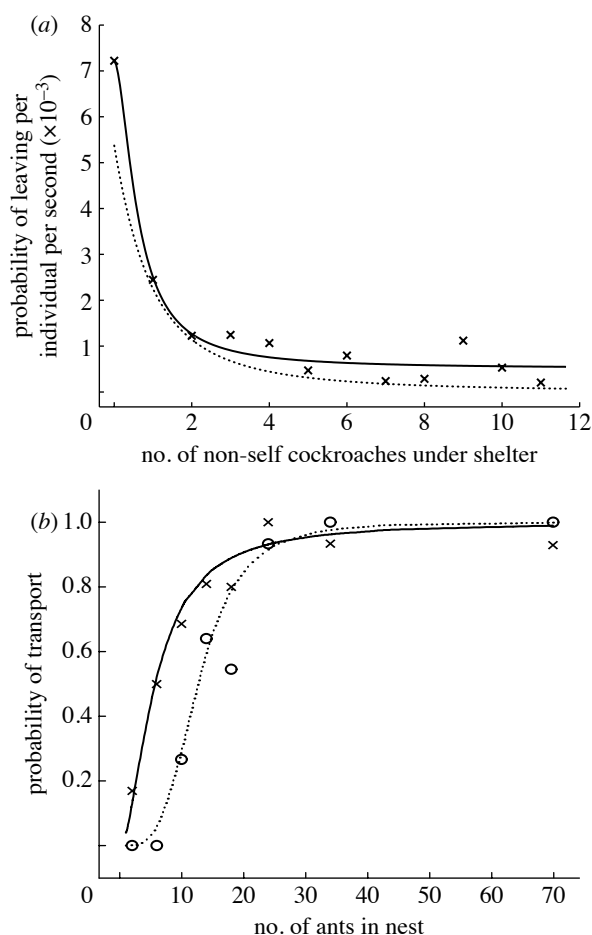


Figure 2. Examples of empirical quorum responses in the decisions of migrating insects. (a) Cockroaches. Crosses indicate measured leaving times, dashed line is fit given by Ame *et al.* (2006) of

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

with parameter values $S=40$, $\theta=0.01$, $\rho=1667$ and $\alpha=2$ and solid line is the best fit of the equation

$$\phi + \frac{\theta}{1 + \rho\left(\frac{x-1}{S}\right)^\alpha},$$

with parameter values $S=40$, $\phi=0.00051$, $\theta=0.0067$, $\rho=1667$ and $\alpha=1.73$. This second fitted line allows for the fact that the probability of leaving does not go to zero with the number under the shelter. (b) A quorum rule governs the probability of a *Temnothorax* scout switching from tandem run recruitment of fellow scouts to faster transport of the bulk of the colony. Crosses show proportions of scouts choosing transport over tandem runs at different populations under high urgency. Open circles show corresponding data under low urgency. Solid and dashed lines, respectively, show a Hill function fit to these data: probability of transport = $x^k/(x^k + T^k)$, where x is the new site population.

shelter increases more than linearly with the number of cockroaches under the shelter. This prediction accorded with the value of $\alpha \approx 2$ measured from the experiments. Further investigation of the model shows that provided that $\alpha > 1$, even a relatively weak positive response to the presence of conspecifics is sufficient to generate a consensus (Millor *et al.* 2006). It was thus the sharply nonlinear reaction to others—the quorum response—that generated a collective decision.

(b) Nest site selection by social insects

For many social insects, the survival of the colony depends crucially upon remaining together and making a good decision about where to live. This is especially true when colonies live in preformed cavities, such as honeybees nesting in tree cavities and *Temnothorax* ants in rock crevices or hollow nuts. These colonies have limited opportunities to repair a poor initial choice, but must instead live with the consequences or emigrate to a new home. Emigration is especially costly for honeybees, because they have to abandon their investment in comb construction, brood-rearing and food storage. A poor initial choice can therefore greatly reduce a colony's reproductive success.

Honeybee emigration usually occurs in spring, when the queen and a swarm of roughly 10 000 worker bees leave their old nest and temporarily settle in a densely-packed swarm. Several hundred scout bees then fly out to search for a new home. Successful scouts use the waggle dance to recruit fellow scouts to the sites they have found. Recruited bees may in turn dance for a site, creating a positive feedback loop that drives up the population of scouts visiting a site. Bees tune their dancing to the quality of the site they are advertising, hence better sites enjoy more effective recruitment and faster population growth (Seeley & Buhrman 1999; Seeley & Visscher 2004a). Scouts periodically return to the site they are advertising and somehow assess its population. Once this exceeds a threshold value, or quorum, they return to the swarm to perform a behaviour called piping (Seeley & Visscher 2003, 2004b). Piping induces the thousands of non-scout bees to warm their flight muscles in preparation for the swarm to fly to the new nest site, guided by the minority of knowledgeable scouts (Seeley *et al.* 2003). This process unfolds over one to several days, during which a large number of sites are found and advertised by at least a few bees. Usually, only one site reaches quorum and induces swarm lift off, but rare split decisions have been observed, in which the bees engage in an aerial tug-of-war as rival groups of scouts attempt to lead the swarm in different directions. In these cases, the bees are forced to re-settle and begin the process again (Lindauer 1955, 1961).

Ants of the genus *Temnothorax* form much smaller colonies than honeybees, typically with no more than 100–200 individuals. Colonies can be easily kept in artificial nests and induced to emigrate in the laboratory. They typically move within a few hours, reliably choosing the best site from as many as five alternatives that they discriminate according to cavity area, ceiling height, entrance size, light level and other features (Pratt & Pierce 2001; Franks *et al.* 2003b). Approximately 30 per cent of a colony's workers actively partake in the selection process. These active ants go through four phases of graded commitment to any potential new home (Pratt *et al.* 2005). Each ant begins in an exploration phase during which she searches for nest sites. After finding one, she enters an assessment phase in which she evaluates its quality. The length of this phase is inversely related to the quality of the site (Mallon *et al.* 2001), and is followed by a canvassing phase during which the ant leads fellow scouts to the site, using a slow recruitment method

called tandem running. These recruited ants in turn make their own independent assessments and may also begin to recruit, a process that gradually increases the population of ants visiting the site. Once the scouts perceive their site's population to have reached a threshold, they enter the final phase of full commitment (Pratt *et al.* 2002) (figure 2b). They abandon tandem runs from the old nest in favour of speedier transports, by which the passive majority of the colony's workers, as well as the queens and brood, are brought to the new site (Pratt *et al.* 2005).

Despite the many differences between honeybee and ant emigration, their nest site selection relies on a fundamentally similar strategy. There is no requirement for direct comparison of multiple sites by well-informed insects. Instead, scouts aware of only a single candidate site recruit to it with a strength that depends on their independent assessment of its quality. Because the recruited scouts themselves recruit, this generates positive feedback on site populations that is stronger for better sites. This advantage is then amplified by a quorum rule that accelerates movement to the site with the fastest early population growth. Owing to the quality-dependent recruitment advantage, this will usually be a superior site.

(c) Other insects and spiders

Together with various colleagues, Jean-Louis Deneubourg has shown that a variety of gregarious arthropods respond to a choice between two identical options by randomly selecting one of them (Deneubourg *et al.* 2002). Repeated over many experimental trials, this leads to a U-shaped distribution of outcomes, with roughly half of the groups unanimously choosing each option, and very few splitting between them. Examples include selection between feeders by foraging ants (Goss *et al.* 1989; Beckers *et al.* 1993; Jeanson *et al.* 2004a), between settlement locations by social spiders (Saffre *et al.* 2000; Jeanson *et al.* 2004b) and between escape routes for ants fleeing a disturbance (Altshuler *et al.* 2005). Positive feedback is seen in each of these cases: ants grow more likely to join a foraging trail as its concentration of recruitment pheromone increases; spiders are more likely to follow a route to a settlement location as it is reinforced with the silk strands of other spiders; and escaping ants are more likely to take an exit chosen by many nest-mates. All of these cues increase in strength with the number of other individuals that have already selected that option. Moreover, the function relating joining probability to cue strength is sharply nonlinear, or quorum-like. These empirical observations demonstrate a basic property of all collective decision-making: positive feedback together with nonlinear quorum responses lead to U-shaped choice distributions and consensus decisions.

(d) Birds, fish and primates

For vertebrate groups migrating over long distances, consensus building may improve navigational accuracy. The analogue to Condorcet's theorem in this case is the theory of many wrongs (Wallraff 1978; Simons 2004). This theory assumes that each animal has imprecise information about the route to its target, and shows that averaging these estimates allows the group to reach

consensus on a more accurate path. Biro *et al.* (2006) showed that interactions between a pair of homing pigeons (*Columba livia*) were important in determining their navigational route. When conflict between routes was small the birds followed an average of the two, but when conflict was large one bird led and the other followed. Pairs of pigeons flew more direct routes home than did solo birds. This result is consistent with the many wrong hypothesis, but it could also be explained by birds flying more 'confidently' when in pairs. Experiments on larger groups would be needed to say whether quorums play a role, but in other contexts birds do make choices based on threshold responses to conspecific numbers (Collins & Sumpter 2007).

Ward *et al.* (2008) showed clear use of quorum-like rules by fish making binary movement decisions in the presence of replica 'leader' fish. They found that fish chose a movement direction as a function of group size and the number of fish (or replicas) going left and right. The probability of following in a particular direction was a steeply increasing function of the number already moving in that direction. Ward *et al.* (2008) further showed that if two or three replica fish swam past a replica predator then the group of fish could be induced to follow, despite the fact that lone fish would seldom pass the same replica predator.

Despite their relatively high cognitive abilities, the movement decisions of capuchin monkeys (*Cebus capucinus*) have also proven consistent with simple copying of the decisions of others (Meunier *et al.* 2007). Their response is not quorum-like: the probability of following increased in proportion to the number taking a particular direction. In general, the movement decisions of primate groups may depend on dominance hierarchies, past experience and complex social structure (Boinski & Garber 2000). However, the interactions of these monkeys provide evidence that simple copying should not be ruled out as an explanation of complex movement decisions.

4. ACCURACY THROUGH QUORUM RESPONSES

Why are quorum responses such a ubiquitous feature of group decision-making? In particular, why do individual response probabilities change sharply when a threshold is exceeded rather than varying in proportion to the stimulus? A first answer to these questions is given by several theoretical models that show how quorum responses generate cohesion (Nicolis & Deneubourg 1999; Millor *et al.* 2006). This effect is seen empirically in the U-shaped distributions of groups choosing between two identical options. However, cohesion is just one of the three desirable properties of consensus decision-making. The others we quoted in the introduction are accuracy and speed, to which we can add the ability to adjust the trade-off between these two properties. Here we investigate all these aspects within the framework of a simple quorum response model.

(a) Quorum response model

We developed a simple model of how a population of partially informed individuals chooses between two options. This model is designed to look at how

individuals can observe the choices of others in order to improve their decision-making accuracy.

We begin with a group of n individuals not committed to either option. 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 the 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

$$p_x \left(a + (m - a) \frac{x^k}{T^k + x^k} \right), \quad (4.1)$$

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 k determines the steepness of the function. 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 .

Equation (4.1) includes a range of possible responses to conspecifics. If $k = 1$ then the probability of an individual choosing an option is proportional to the number that have already made that choice. If $k > 1$ then equation (4.1) has a point of inflection and the function is sigmoidal. As k increases the response approaches a step-like switch at the threshold T .

In order to define a quorum response, we first consider a purely linear response function

$$p_x \left(a + (m - a) \frac{x}{2T} \right), \quad (4.2)$$

which shares with equation (4.1) the property that when $x = T$ the probability of committing is half way between m and a . We define a quorum response to be one in which the probability of committing is always less than the linear response whenever the number of conspecifics is less than T and is greater or equal to that of the linear response for some number of conspecifics greater or equal to T . This definition captures the concept of a less than linear response to numbers below the threshold and a greater than linear response above the threshold. By identifying conditions under which our linear equation is equal to equation (4.1), we find that a quorum response occurs if only if $k \geq 2$ (figure 3). We note, however, that it may be equally valid to argue that the existence of a point of inflection defines a quorum response, so that quorum responses occur for $k > 1$. The important biological point is that quorum responses involve a sharply increasing nonlinear response to the conspecifics.

The above model demands very limited cognitive powers on the part of individuals. In particular, they have no way of directly comparing the two options. We assume that rejecting one option does not increase an individual's probability of accepting the other. The population already committed gives individuals an indirect method to gather information about available options.

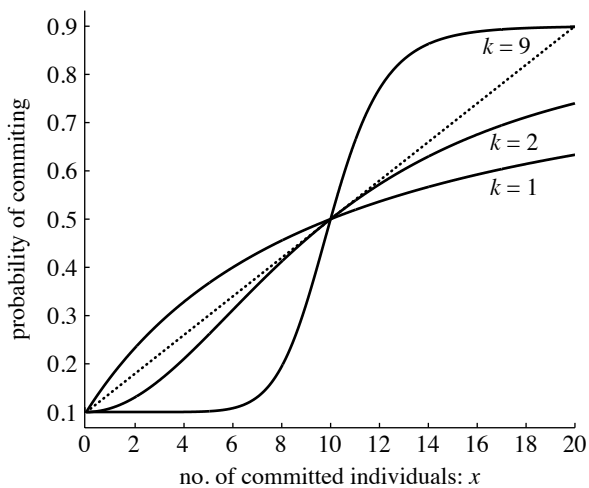


Figure 3. Commitment to an option as a function of the number of conspecifics that have already chosen it (x). The dashed line shows the purely linear response given by equation (4.2). The solid lines show nonlinear responses given by equation (4.1), for different values of k . For $k > 2$ equation (4.1) gives a quorum response: that is, the probability of committing is less than the linear response for $x < T$ and greater than or equal to the linear response for $x \geq T$. Other parameters are $p_x = 1$, $T = 10$, $a = 0.1$ and $m = 0.9$.

(b) Model simulation

Figure 4*a,b* give examples of the choices over time of $n = 40$ individuals for shallow proportional responses ($T = 10$ and $k = 1$) and steep quorum responses ($T = 10$ and $k = 9$), 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 per cent of individuals choose X for a shallow response, while 83.3 per cent do so for the steep quorum response. In both cases the proportion choosing the better option is higher than that were each to make an independent decision, in which case $p_x/(p_x + p_y) = 66.7$ per cent 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 $k = 9$ than for $k = 1$ (figure 4*c,d*). 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.

(c) Speed-accuracy trade-off

Decision makers typically face a trade-off between speed and accuracy. In the simulations, a steep quorum function ($k = 9$) yielded a more accurate decision, but the time taken for all individuals to choose was longer on average (307.8 ± 71.0 time steps, mean \pm s.d.) than when $k = 1$ (253.7 ± 64.0 time steps). In order to

investigate how different values for k , T and a affect speed and accuracy, we systematically varied these parameters and measured their affect on the time needed for all individuals to make a choice and the proportion choosing the better option (figure 5). 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 k and T of approximately 10, but these values also produce relatively slow decisions. Thus, for a given quorum threshold, the trade-off between speed and accuracy can be tuned by altering the base acceptance probability, a .

The quorum threshold, T , has more complex effects than does a . For large k , T can be also be used to tune speed and accuracy. For example, when $k = 4$ or 9, decision speed is maximized for $T = 0$, but accuracy is maximized when $T \approx 10$. However, for a wide range of threshold values (T between approximately 5 and 15), relatively small differences in choice quality produce high levels of commitment to the better option.

There is also an important difference between a and T in how speed and accuracy change when one parameter is fixed and the other varied. If T is chosen to maximize accuracy (e.g. $T \approx 10$ when $k = 9$) a can be tuned to achieve either the maximum possible accuracy (over all tested combinations of T and a values) or the maximum possible speed (i.e. by choosing $a = 1$). The same is not the case for fixed a and varying T . If a is large then tuning T can do little to improve the resulting low accuracy; if a is small then setting $T = 0$ improves speed but not as much as would setting a to a value of 1. Thus by choosing appropriate values of T and k , and adjusting a as needed, individuals can tune the speed and accuracy of their decisions to particular circumstances.

The simulations also showed that tuning speed and accuracy with a works best with an intermediate threshold value and a steep quorum response (high k). For fixed k , we determined the parameter values of a and T that give the fastest possible average time until a decision is made given a minimum requirement for accuracy (figure 6). When the requirement for accuracy is low, a similarly high speed can be achieved for any value of k , by choosing appropriate values for T and a . For higher accuracy requirements, however, a k value of 1 leads to distinctly slower attainable speeds. Thus steep thresholds not only give more accurate decisions, they also allow them to be made more rapidly.

(d) Comparison to Condorcet's theorem

Given 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 per cent. This is notably lower than even the most accurate decisions made using quorum responses: for steep thresholds between 5 and 15 and low spontaneous accept rates, approximately 10 per cent of individuals take the least favourable option. This result is not particularly surprising. Condorcet's theorem provides an upper bound for the accuracy of collective decision-making. What is striking is that a simple copying rule based on threshold responses can

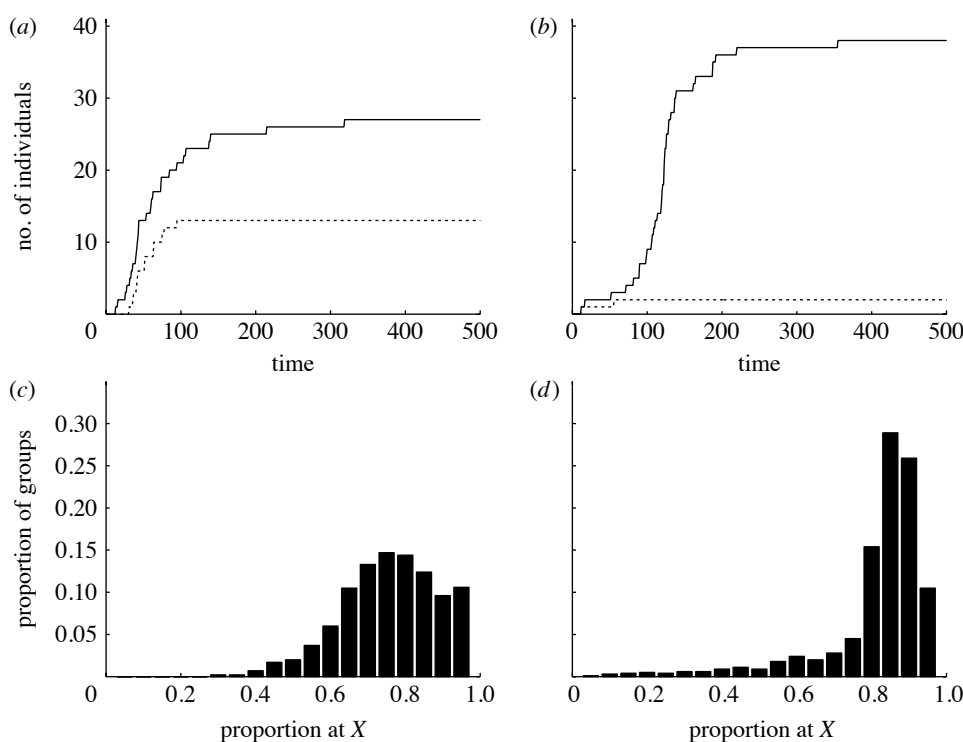


Figure 4. Simulations of a simple quorum response model, for (a,c) shallow ($k=1$) and (b,d) steep ($k=9$) thresholds. (a,b) plot the change in the number of individuals committed to options X, solid line; and Y, dotted line for one simulation with $k=1$ and $k=9$, respectively. (c,d) show the distribution taken over 1000 simulation runs 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 $m=0.9$.

substantially reduce errors compared with purely independent decision-making.

5. SPEED VERSUS ACCURACY TRADE-OFFS IN ANT MIGRATION

The decision making of animal groups can be considerably more complicated than a simple threshold response to the decisions of others. We described earlier the complex, multistage algorithm used by *Temnothorax* ants to evaluate candidate nest sites during colony emigration. Progress through four stages of increasing commitment to a site is governed both by each scout's independent assessment of site quality and by the indirect influence of her nest-mates, via a quorum rule (figure 2b). Complicating this basic structure are a host of behavioural nuances, including 'reverse' recruitment of scouts from the new to the old nest, direct comparison of multiple sites by individual ants, changes in the efficiency of recruitment with time and many others (Pratt *et al.* 2005; Pratt & Sumpter 2006).

Experiments have shown that this complex algorithm allows colonies to tune the trade-off between decision speed and accuracy (Pratt & Sumpter 2006). When choosing between a good and a mediocre nest, colonies showed dramatically different behaviour depending on the urgency of their need to move. In the low-urgency situation colonies in an intact but poor-quality nest had an opportunity to improve their housing. They took a long time to emigrate, but they generally made very accurate decisions, moving their entire population directly to the better candidate nest. Greater urgency was created by destroying the colony's old nest, leaving them completely exposed. Under

these circumstances, colonies moved much faster but often made poor choices, splitting their population between the two candidate nests or even moving entirely into the inferior one.

We have previously developed a detailed agent-based model of *Temnothorax* emigration (Pratt *et al.* 2005). This agent-based model is more complex than the general quorum model described earlier, but both include the same fundamental mechanisms: an intrinsic rate of accepting an option that depends on that option's quality, and a quorum function described by parameters for threshold value (T) and steepness (k). Furthermore, both models make similar predictions for the effects of T and the acceptance rate on speed and accuracy: for a wide range of T values, the acceptance rate provides a sensitive mechanism for adjusting speed and accuracy. The model predicted that ants achieve a speed/accuracy trade-off by quantitative tuning the acceptance rate and, to a lesser degree, the quorum threshold (Pratt & Sumpter 2006). The small effect of the quorum threshold is at first surprising, because one might suppose that the reaching of a threshold marks the point at which transportation can commence and the emigration can be completed. However, as Franks *et al.* (2009) rightly point out in another paper in this issue, reaching the threshold too soon can result in an insufficient number of committed ants to complete the transportation of ants from the old nest.

Our agent-based model was not previously examined for effects of k , so we systematically varied this parameter and monitored its effect on emigration speed and accuracy. The results match those for the simpler model, with greater accuracy as quorum steepness increases, and little cost in speed (figure 7).

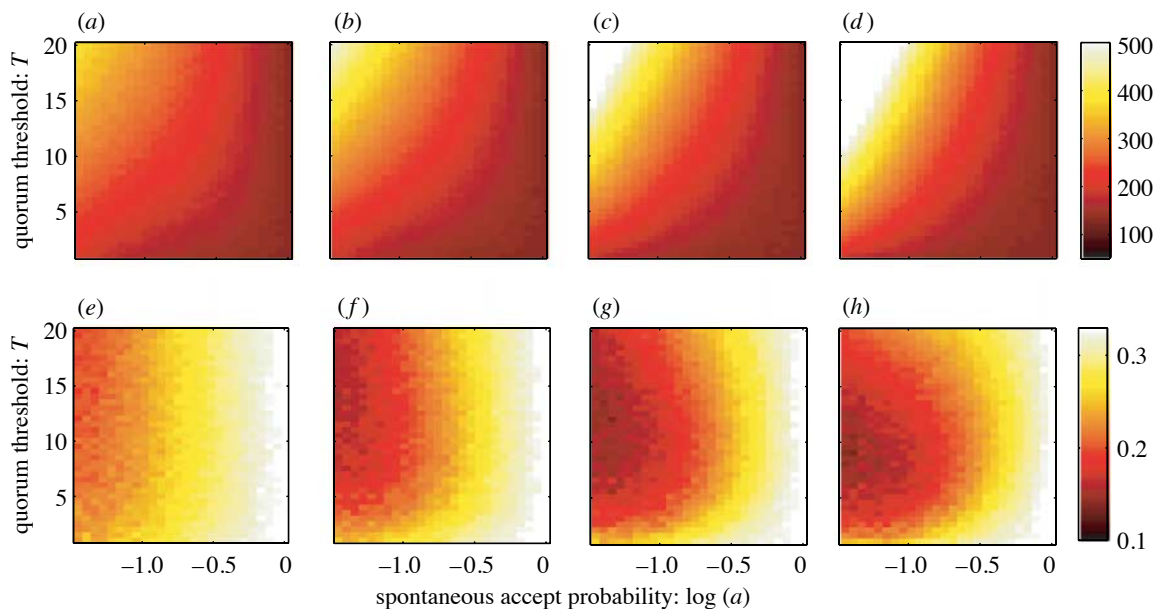


Figure 5. Speed and accuracy of decision making for the simple quorum response model. Predicted effects of the parameters a , T and k on (a–d) the time until all individuals have made a decision and (e–h) the accuracy of that decision. In each image, a and T are varied for different threshold steepness, 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. (a) $k=1$; (b) $k=2$; (c) $k=4$; (d) $k=9$; (e) $k=1$; (f) $k=2$; (g) $k=4$; (h) $k=9$.

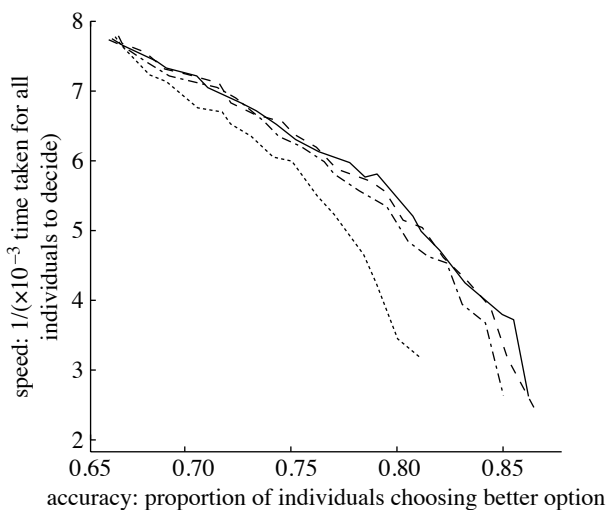


Figure 6. Speed–accuracy trade-off for the simple quorum response model. For fixed k and for a fixed minimum requirement for decision accuracy, we searched over all parameter values of a and T which give the fastest possible average time until all individuals have made a decision. This was done repeatedly for different minimum accuracy requirements to give a speed versus accuracy trade-off. Solid line, $k=9$; dashed line, $k=4$; dashed-dotted line, $k=2$; dotted line, $k=1$.

In accordance with these predictions, our experiments showed that ants made dramatic increases in acceptance rate, and smaller decreases in T , in response to increased urgency of emigration (Pratt & Sumpter 2006). Re-analysis of this data further shows that ants also used a significantly steeper quorum function when accuracy was emphasized under low urgency (ANOVA: $k_{\text{lowUrgency}}=3.7$, $k_{\text{highUrgency}}=1.7$, $F_{415}^1=10$, $p<0.01$). These experiments provide strong evidence of the ants tune their responses to their speed versus accuracy requirements without changing their underlying behavioural algorithm.

6. DISCUSSION

Quorum responses are a ubiquitous feature of consensus decision-making. While previous work has emphasized the importance of these responses in generating aggregation and cohesion, here we have emphasized that they also improve decision accuracy. The shape of the response curve is particularly important in this context. Individuals can make more accurate decisions if they sharply increase their probability of committing to an option at a threshold number of individuals already committed. Interestingly, these steep threshold responses can sometimes amplify random fluctuations and lead to mass adoption of incorrect choices. This sort of process may account for observations of mass copying (Laland & Williams 1998; Dall *et al.* 2005) or peer pressure in humans (Milgram *et al.* 1969; Milgram 1992) 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.

Another important property of quorum responses is that they can be used to tune speed and accuracy. By fixing a steep threshold and then tuning the baseline rate at which an option is accepted, decisions can be made either more accurately or more quickly. The same is not true in the absence of a threshold, where reducing baseline acceptance slows decision making but does little to increase accuracy. *Temnothorax* ants take advantage of this property to tune their decision making for speed or accuracy (Pratt & Sumpter 2006). Our simple model suggests that many other animals exhibiting quorum responses may also be able to tune their decisions in this way.

Other studies have emphasized the precise tuning of quorum size itself for the balancing of decision speed and accuracy, either over evolutionary time

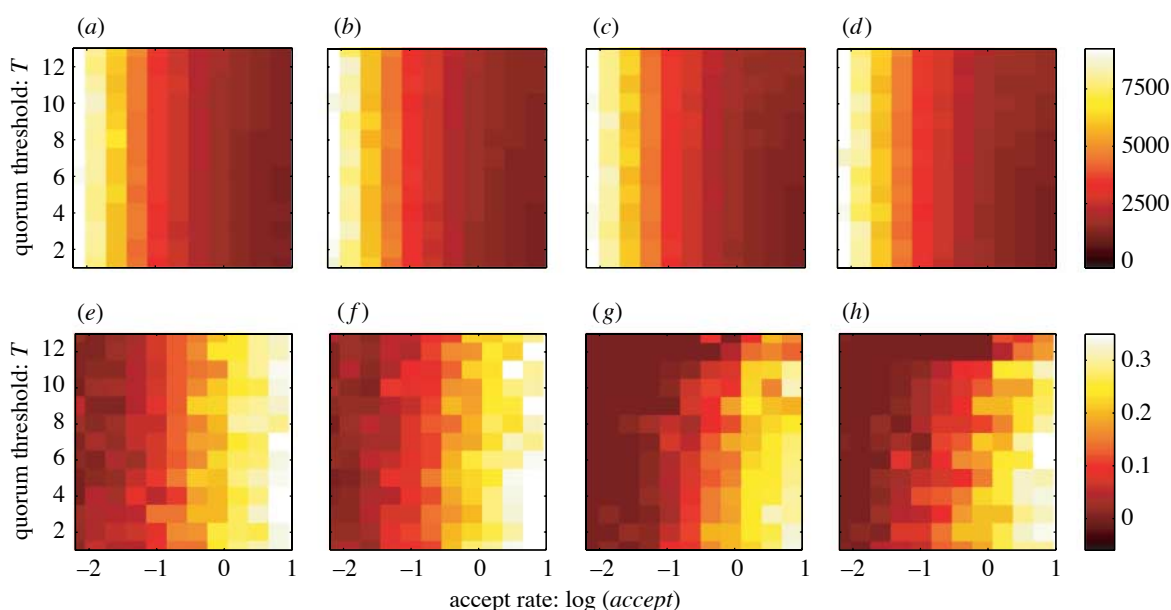


Figure 7. Trade-off of decision speed and accuracy for an agent-based model of *Temnothorax* emigrations. Predicted effects of the parameters *accept*, *quorum threshold* and *k* on the (a–d) duration and (e–h) accuracy of emigrations. In each image, the intrinsic accept rate and quorum threshold are varied for different threshold steepness, *k*. The plots show mean duration and accuracy over 32 simulations for each parameter combination. All other parameters are set to values estimated as described in Pratt (2005). *Accept* gives the recruitment initiation rate at good nests; the rate for mediocre nests was obtained by multiplying by the factor 0.52 (the ratio of observed values of *accept* for mediocre and good nests). (a) *k* = 1; (b) *k* = 2; (c) *k* = 4; (d) *k* = 8; (e) *k* = 1; (f) *k* = 2; (g) *k* = 4; (h) *k* = 8.

(Passino & Seeley 2006), or dynamically in response to the changing conditions experienced by a society (Franks *et al.* 2003a). Our results suggest instead that the quorum size may not require tight regulation or have a particularly large direct influence on speed and accuracy. As long as individuals employ a quorum rule, the threshold can vary quite widely with little effect, and the group can achieve both accuracy and tunability, by adjusting the more sensitive acceptance parameter. Nonetheless, as discussed above for *Temnothorax*, there is empirical evidence that individuals change their quorum size and steepness according to circumstances (Franks *et al.* 2003a; Dornhaus *et al.* 2004; Pratt & Sumpter 2006). Thus a functional role for tuning the quorum cannot be ruled out.

An important question that we have not addressed in this paper is conflict in consensus decision-making (Conradt & Roper 2005, 2009; Wood & Acland 2007; Sumpter *et al.* 2008). The models presented here assume no conflict of interest between group members and that the inherent tendency to lead or follow others does not vary between individuals. These are reasonable assumptions for many insect societies, but are less likely to hold for the movements of more loosely associated vertebrate groups. A first step to incorporating conflict would be to test the evolutionary stability of quorum responses; that is, to determine whether selfish individuals could exploit the quorum parameter values that optimize group accuracy to improve their own accuracy. For example, by waiting until everyone else has made a decision, an individual might be able to maximize its own probability of making an accurate choice. This strategy that should evolve when each individual aims to increase its own performance without regard to the outcome for others might produce group decisions that are neither fast nor

accurate. Because quorum responses are clearly used by animals with conflicting interests, the effect of this conflict on quorum parameter values remains as an exciting theoretical and experimental challenge.

REFERENCES

- Altshuler, E., Ramos, O., Nunez, Y., Fernandez, J., Batista-Leyva, A. J. & Noda, C. 2005 Symmetry breaking in escaping ants. *Am. Nat.* **166**, 643–649. (doi:10.1086/498139)
- Ame, J. M., Rivault, C. & Deneubourg, J. L. 2004 Cockroach aggregation based on strain odour recognition. *Anim. Behav.* **68**, 793–801. (doi:10.1016/j.anbehav.2004.01.009)
- Ame, J. M., Halloy, J., Rivault, C., Detrain, C. & Deneubourg, J. L. 2006 Collegial decision making based on social amplification leads to optimal group formation. *Proc. Natl Acad. Sci. USA* **103**, 5835–5840. (doi:10.1073/pnas.0507877103)
- Austen-Smith, D. & Feddersen, T. J. 2009 Information aggregation and communication in committees. *Phil. Trans. R. Soc. B* **364**, 763–769. (doi:10.1098/rstb.2008.0256)
- Beckers, R., Deneubourg, J. L. & Goss, S. 1993 Modulation of trail laying in the ant *Lasius niger* (Hymenoptera, Formicidae) and its role in the collective selection of a food source. *J. Insect Behav.* **6**, 751–759. (doi:10.1007/BF01201674)
- Biro, D., Sumpter, D. J. T., Meade, J. & Guilford, T. 2006 From compromise to leadership in pigeon homing. *Curr. Biol.* **16**, 2123–2128. (doi:10.1016/j.cub.2006.08.087)
- Boinski, S. & Garber, P. A. 2000 *On the move: how and why animals travel in groups*. Chicago, IL: University of Chicago Press.
- Bonabeau, E., Theraulaz, G., Deneubourg, J. L., Aron, S. & Camazine, S. 1997 Self-organization in social insects. *Trends Ecol. Evol.* **12**, 188–193. (doi:10.1016/S0169-5347(97)01048-3)

- Borland, P. J. 1989 Majority systems and the Condorcet jury theorem. *Statistician* **38**, 181–189. (doi:10.2307/2348873)
- Britton, N. F., Franks, N. R., Pratt, S. C. & Seeley, T. D. 2002 Deciding on a new home: how do honeybees agree? *Proc. R. Soc. B* **269**, 1383–1388. (doi:10.1098/rspb.2002.2001)
- Camazine, S., Deneubourg, J. L., Franks, N. R., Sneyd, J., Theraulaz, G. & Bonabeau, E. 2001 *Self-organization in biological systems*. Princeton studies in complexity. Princeton, NJ: Princeton University Press.
- Collins, L. M. & Sumpter, D. J. T. 2007 The feeding dynamics of broiler chickens. *J. R. Soc. Interface* **4**, 65–72. (doi:10.1098/rsif.2006.0157)
- Conradt, L. & Roper, T. J. 2005 Consensus decision making in animals. *Trends Ecol. Evol.* **20**, 449–456. (doi:10.1016/j.tree.2005.05.008)
- Conradt, L. & Roper, T. J. 2009 Conflicts of interest and the evolution of decision sharing. *Phil. Trans. R. Soc. B* **364**, 807–819. (doi:10.1098/rstb.2008.0257)
- Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M. & Stephens, D. W. 2005 Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193. (doi:10.1016/j.tree.2005.01.010)
- Dambach, M. & Goehlen, B. 1999 Aggregation density and longevity correlate with humidity in first-instar nymphs of the cockroach *Blattella germanica*. *J. Insect Physiol.* **45**, 423–429. (doi:10.1016/S0022-1910(98)00141-3)
- Deneubourg, J. L. & Goss, S. 1989 Collective patterns and decision-making. *Ethol. Ecol. Evol.* **1**, 295–311.
- Deneubourg, J. L., Lioni, A. & Detrain, C. 2002 Dynamics of aggregation and emergence of cooperation. *Biol. Bull.* **202**, 262–267. (doi:10.2307/1543477)
- Dornhaus, A., Franks, N. R., Hawkins, R. M. & Shere, H. N. S. 2004 Ants move to improve: colonies of *Leptothorax albipennis* emigrate whenever they find a superior nest site. *Anim. Behav.* **67**, 959–963. (doi:10.1016/j.anbehav.2003.09.004)
- Franks, N. R., Dornhaus, A., Fitzsimmons, J. P. & Stevens, M. 2003a Speed versus accuracy in collective decision making. *Proc. R. Soc. B* **270**, 2457–2463. (doi:10.1098/rspb.2003.2527)
- Franks, N. R., Mallon, E. B., Bray, H. E., Hamilton, M. J. & Mischler, T. C. 2003b Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. *Anim. Behav.* **65**, 215–223. (doi:10.1006/anbe.2002.2032)
- Franks, N. R., Dechaume-Moncharmont, F.-X., Hanmore, E. & Reynolds, J. K. 2009 Speed versus accuracy in decision-making ants: expediting politics and policy implementation. *Phil. Trans. R. Soc. B* **364**, 845–852. (doi:10.1098/rstb.2008.0224)
- Galton, F. 1907 Vox populi. *Nature* **75**, 450–451. (doi:10.1038/075450a0)
- Goss, S., Aron, S., Deneubourg, J. L. & Pasteels, J. M. 1989 Self-organized shortcuts in the Argentine ant. *Naturwissenschaften* **76**, 579–581. (doi:10.1007/BF00462870)
- Ishii, S. & Kuwahara, Y. 1968 Aggregation of German cockroach *Blattella germanica* nymphs. *Experientia* **24**, 88–89. (doi:10.1007/BF02136814)
- Janis, I. L. 1972 *Victims of groupthink*. New York, NY: Houghton Mifflin.
- Janis, I. L. 1982 *Groupthink: psychological studies of policy decisions and fiascoes*, 2nd edn. New York, NY: Houghton Mifflin.
- Jeanson, R., Deneubourg, J. L., Grimal, A. & Theraulaz, G. 2004a Modulation of individual behavior and collective decision-making during aggregation site selection by the ant *Messor barbarus*. *Behav. Ecol. Sociobiol.* **55**, 388–394. (doi:10.1007/s00265-003-0716-y)
- Jeanson, R., Deneubourg, J. L. & Theraulaz, G. 2004b Discrete dragline attachment induces aggregation in spiderlings of a solitary species. *Anim. Behav.* **67**, 531–537. (doi:10.1016/j.anbehav.2003.06.013)
- King, A. J. & Cowlshaw, G. 2007 When to use social information: the advantage of large group size in individual decision making. *Biol. Lett.* **3**, 137–139. (doi:10.1098/rsbl.2007.0017)
- Laland, K. N. & Williams, K. 1998 Social transmission of maladaptive information in the guppy. *Behav. Ecol.* **9**, 493–499. (doi:10.1093/beheco/9.5.493)
- Lindauer, M. 1955 Schwarmbienen auf Wohnungssuche. *Z. Vgl. Physiol.* **37**, 263–324. (doi:10.1007/BF00303153)
- Lindauer, M. 1961 *Communication among social bees*. New York, NY: Atheneum.
- List, C. 2004 Democracy in animal groups: a political science perspective. *Trends Ecol. Evol.* **19**, 168–169. (doi:10.1016/j.tree.2004.02.004)
- Mallon, E. B., Pratt, S. C. & Franks, N. R. 2001 Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* **50**, 352–359. (doi:10.1007/s002650100377)
- Meunier, H., Leca, J. B., Deneubourg, J. L. & Petit, O. 2007 Group movement decisions in capuchin monkeys: the utility of an experimental study and a mathematical model to explore the relationship between individual and collective behaviours. *Behaviour* **143**, 1511–1527. (doi:10.1163/156853906779366982)
- Milgram, S. 1992 *The individual in the social world*. New York, NY: McGraw-Hill.
- Milgram, S., Bickman, L. & Berkowitz, L. 1969 Note on the drawing power of crowds of different size. *J. Pers. Soc. Psychol.* **13**, 79–82. (doi:10.1037/h0028070)
- Millor, J., Ame, J. M., Halloy, J. & Deneubourg, J. L. 2006 Individual discrimination capability and collective decision-making. *J. Theor. Biol.* **239**, 313–323. (doi:10.1016/j.jtbi.2005.07.020)
- Nicolis, S. C. & Deneubourg, J. L. 1999 Emerging patterns and food recruitment in ants: an analytical study. *J. Theor. Biol.* **198**, 575–592. (doi:10.1006/jtbi.1999.0934)
- Passino, K. M. & Seeley, T. D. 2006 Modeling and analysis of nest-site selection by honeybee swarms: the speed and accuracy trade-off. *Behav. Ecol. Sociobiol.* **59**, 427–442. (doi:10.1007/s00265-005-0067-y)
- Pratt, S. C. 2005 Behavioral mechanisms of collective nest-site choice by the ant *Temnothorax curvispinosus*. *Insect. Soc.* **52**, 383–392. (doi:10.1007/s00040-005-0823-z)
- Pratt, S. C. & Pierce, N. E. 2001 The cavity-dwelling ant *Leptothorax curvispinosus* uses nest geometry to discriminate between potential homes. *Anim. Behav.* **62**, 281–287. (doi:10.1006/anbe.2001.1777)
- Pratt, S. C. & Sumpter, D. J. T. 2006 A tunable algorithm for collective decision-making. *Proc. Natl Acad. Sci. USA* **103**, 15 906–15 910. (doi:10.1073/pnas.0604801103)
- Pratt, S. C., Mallon, E. B., Sumpter, D. J. T. & Franks, N. R. 2002 Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* **52**, 117–127. (doi:10.1007/s00265-002-0487-x)
- Pratt, S. C., Sumpter, D. J. T., Mallon, E. B. & Franks, N. R. 2005 An agent-based model of collective nest choice by the ant *Temnothorax albipennis*. *Anim. Behav.* **70**, 1023–1036. (doi:10.1016/j.anbehav.2005.01.022)
- Prokopy, R. J. & Roitberg, B. D. 2001 Joining and avoidance behaviour in nonsocial insects. *Annu. Rev. Entomol.* **46**, 631–665. (doi:10.1146/annurev.ento.46.1.631)
- Rivault, C. 1989 Spatial distribution of the cockroach, *Blattella germanica*, in a swimming-bath facility. *Entomol. Exp. Appl.* **53**, 247–255. (doi:10.1007/BF00162856)

- Saffre, F., Mailleux, A. C. & Deneubourg, J. L. 2000 Exploratory recruitment plasticity in a social spider (*Anelosimus eximius*). *J. Theor. Biol.* **205**, 37–46. (doi:10.1006/jtbi.2000.2042)
- Seeley, T. D. 1995 *The wisdom of the hive*. Cambridge, MA: Belknap Press of Harvard University Press.
- Seeley, T. D. 2002 When is self-organization used in biological systems? *Biol. Bull.* **202**, 314–318. (doi:10.2307/1543484)
- Seeley, T. D. 2003 Consensus building during nest-site selection in honey bee swarms: the expiration of dissent. *Behav. Ecol. Sociobiol.* **53**, 417–424.
- Seeley, T. D. & Buhrman, S. C. 1999 Group decision making in swarms of honey bees. *Behav. Ecol. Sociobiol.* **45**, 19–31. (doi:10.1007/s002650050536)
- Seeley, T. D. & Visscher, P. K. 2003 Choosing a home: how the scouts in a honey bee swarm perceive the completion of their group decision making. *Behav. Ecol. Sociobiol.* **54**, 511–520. (doi:10.1007/s00265-003-0664-6)
- Seeley, T. D. & Visscher, P. K. 2004a Group decision making in nest-site selection by honey bees. *Apidologie* **35**, 101–116. (doi:10.1051/apido:2004004)
- Seeley, T. D. & Visscher, P. K. 2004b Quorum sensing during nest-site selection by honeybee swarms. *Behav. Ecol. Sociobiol.* **56**, 594–601. (doi:10.1007/s00265-004-0814-5)
- Seeley, T. D., Camazine, S. & Sneyd, J. 1991 Collective decision-making in honey bees: how colonies choose among nectar sources. *Behav. Ecol. Sociobiol.* **28**, 277–290. (doi:10.1007/BF00175101)
- Seeley, T. D., Kleinhenz, M., Bujok, B. & Tautz, J. 2003 Thorough warm-up before take-off in honey bee swarms. *Naturwissenschaften* **90**, 256–260. (doi:10.1007/s00114-003-0425-4)
- Seeley, T. D., Visscher, P. K. & Passino, K. M. 2006 Group decision making in honey bee swarms. *Am. Sci.* **94**, 220–229.
- Simons, A. M. 2004 Many wrongs: the advantage of group navigation. *Trends Ecol. Evol.* **19**, 453–455. (doi:10.1016/j.tree.2004.07.001)
- Sumpter, D. J. T. 2006 The principles of collective animal behaviour. *Phil. Trans. R. Soc. B* **361**, 5–22. (doi:10.1098/rstb.2005.1733)
- Sumpter, D. J. T. & Beekman, M. 2003 From nonlinearity to optimality: pheromone trail foraging by ants. *Anim. Behav.* **66**, 273–280. (doi:10.1006/anbe.2003.2224)
- Sumpter, D. J. T., Buhl, J., Biro, D. & Couzin, I. D. 2008 Information transfer in moving animal groups. *Theory Biosci.* **127**, 177–186. (doi:10.1007/s12064-008-0040-1)
- Surowiecki, J. 2004 *The wisdom of crowds*. London, UK: Little, Brown.
- Visscher, P. K. 2007 Group decision making in nest-site selection among social insects. *Annu. Rev. Entomol.* **52**, 255–275. (doi:10.1146/annurev.ento.51.110104.151025)
- Visscher, P. K. & Camazine, S. 1999 Collective decisions and cognition in bees. *Nature* **397**, 400. (doi:10.1038/17047)
- Wallraff, H. G. 1978 Social interrelations involved in migratory orientation of birds—possible contribution of field studies. *Oikos* **30**, 401–404. (doi:10.2307/3543490)
- Ward, A., Sumpter, D. J. T., Couzin, I. D., Hart, P. J. B. & Krause, J. 2008 Quorum decision-making facilitates information transfer in fish shoals. *Proc. Natl Acad. Sci. USA* **105**, 6948–6953. (doi:10.1073/pnas.0710344105)
- Wood, A. J. & Acland, G. J. 2007 Evolving the selfish herd: emergence of distinct aggregating strategies in an individual-based model. *Proc. R. Soc. B* **274**, 1637–1642. (doi:10.1098/rspb.2007.0306)