

# Six Predictions about the Decision Making of Animal and Human Groups

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**We review and extend theoretical and empirical studies of how groups make decisions using combinations of private information and preference copying. We give six tested or testable predictions arising from models: (i) group decisions involve both true and false cascades; (ii) a small number of leaders can heavily influence a decision; (iii) individuals in groups make accurate and fast decisions; (iv) irrelevant alternatives change preferences; (v) optimal group size depends on the number of options; and (vi) pairs of higher quality options are more difficult to distinguish than lower quality options. We discuss our approach in the context of human organisations. Copyright © 2012 John Wiley & Sons, Ltd.**

## 1. INTRODUCTION

There are many ways to model decision making within groups. Physicists see opinion as a magnetic spin that points to or away from different options depending on the spin of your colleagues (Weidlich, 2003; Suchecki *et al.*, 2005; Weidlich, 2005; Castellano *et al.*, 2009). Economists and political scientists identify the rational thing to do, subject to the constraints imposed by lack of information. Psychologists identify the heuristics we employ for balancing private and personal information (Gigerenzer and Todd, 1999; Katsikopoulos *et al.*, 2010). For animals, behavioural ecologists look both at how natural selection has shaped their decisions, along with describing how they interact with each other (Conradt and Roper, 2005; Couzin, 2009). Even microbiologists are in on the act: describing the decisions made by amoeba and bacteria by showing that these organisms can choose between different quality foods (Dussutour *et al.*, 2010; Latty and

Beekman, 2011). We start by reviewing some of the key features of these approaches.

At the core of neoclassical economics is the idea of the individual as a maximising agent. Individuals make decisions that maximise some utility function, which may be economic but can also relate to aspects such as happiness (Bruni and Porta, 2005). Despite our everyday experience to the contrary—few people would claim that they or the people around them are perfectly rational—there are several good reasons for viewing rational agents as the standard model for economic decision making (Binmore, 1999, 2005). One argument is that although in watching any given individual we might have the impression of an illogical sequence of decisions, we see a collective rationality in which bad decisions are averaged away when the decisions of many individuals are observed. Furthermore, through time bad decisions will become less common as individuals learn the optimal thing to do. Another convincing argument is that there is no viable alternative to the rationality model. We want to create a general model of reality, and this model needs a baseline assumption. If we say that people are irrational, we might as well say that they could be doing anything at all. Without

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an assumption about what people do, we cannot build models and cannot do economics.

The aforementioned arguments alone do not imply that rationality is the only ingredient in economic models. Indeed, most economists recognise the limitations of basing models on an all-seeing rationality (Kahneman, 2003). This recognition has led to the idea of bounded rationality, where agents are constrained by the costs of obtaining and processing information. Incorporating information and opportunity costs allows the economics approach to be applied to a much wider range of situations. For example, organisation economics look at ways in which public and private organisations can become constrained by their culture: how they can find themselves with rapidly inflating pay for their chief executives and exhibit herding towards mediocre practices (Posner, 2010). Similar questions arise in political economics, where the focus is on designing institutions that can avoid the type of agenda sending that inhibits independence and new ideas (Vermeule and List, 2010).

The concept of bounded rationality turns away from the idea of *homo economicus*, the perfectly rational utility maximiser, and instead looked at how people respond in different economic situations (Thaler and Sunstein, 2008). Despite these adjustments, researchers working both inside and outside the field still regularly attack economics research. Physicists in particular have provided some of the most scathing comments and criticism (Farmer, 1999; Sornette, 2003). To a physicist, models should be motivated first by observation. The physicists look at what individuals do, in for example buying and selling shares (finance is physicists' favourite example of economic behaviour), and then build models on that basis. Several behavioural psychologists share this skepticism of the idea that rationality should be a central principle in decision making (Gigerenzer and Todd, 1999). Gigerenzer (2006) argues that we should not see rationality as the starting point and then produce a list of exceptions where it fails to apply. Instead, one should start by identifying heuristics that describe how individuals act in particular situations. Once the heuristics are identified can one ask questions like 'In what environments will a given heuristic work? Where will it fail?'

A similar distinction as that between rational and heuristic approaches comes up in study of the behavioural ecology of animals (Krebs and Davies, 1993). Here, the two approaches are often called functional and mechanistic (Sumpter, 2010). The functional approach is to watch animals and identify how

behavioural strategies produce increases and decreases in fitness. Natural selection has acted over many generations to ensure that individuals that do not increase their fitness relative to their peers will die out. Animal behaviour is then understood through studies of what animals are trying to maximise in different scenarios. This approach, like that of rationality, is based on the idea of the individual as the maximising agent (Grafen, 1999; Houston and McNamara, 2005). Another approach is to concentrate on mechanisms or 'rules of thumb'. Let us forget about whether what animals are doing maximises their fitness or allows them to optimise some variable or not. Instead, we just look at what they do, how do they respond to their environment, how do they interact with each other and what are the consequences of these interactions.

Unlike in the heated exchanges between rationalists and heurists/physicists (Sornette, 2003; Binmore, 2005; Gigerenzer, 2006; Binmore, 2010; Eckel and Gintis, 2010), the functional and mechanistic approaches to behavioural ecology are mainly seen as complementary (Krebs and Davies, 1993; Rankin, 2011). This linking of approaches is particularly well developed in the study of collective decision making by animal groups (Sumpter, 2010). Animals make decisions together in a wide range of contexts. Birds navigate together and choose a shared route home (Biro *et al.*, 2006; Nagy *et al.*, 2010). Fish moving through open water collectively decide which of many sheltered areas is least likely to contain a predator (Ward *et al.*, 2008, 2011). Ants decide which of many food sources to feed from (Nicolis and Deneubourg, 1999; Dussutour *et al.*, 2009). Even cockroaches collectively decide in which dark corner of the kitchen they will aggregate (Ame *et al.*, 2004). These decisions have been studied both in terms of their mechanisms and how they provide fitness benefits to group members.

In this paper, we show how, in the context of group decision making, mathematical models allow one to achieve a unifying view of the concepts of choice and rationality. We show how problems regarding rationality and optimality can be side stepped. We discuss first the Condorcet model, which represents the optimal strategy for a group or the optimal usage of information possessed by all group members. We then turn to the BHW model, which is a model based on bounded rationality for single selfish individuals. Both of these are interesting in their own right but do not provide a 'rule of thumb' or a heuristic that is consistent with how real animals behave when making decisions in groups.

Remarkably, there are a small number of 'rules of thumb' that underlie many situations in which

individual animals make decisions within groups. It is these rules of thumb in the context of group decision making that are the focus of our review. The most important of these is positive feedback between group members (Deneubourg and Goss, 1989). Positive feedback occurs when commitment to a particular option increases as a function of the number of individuals already committed to it (Deneubourg *et al.*, 1990; Nicolis and Deneubourg, 1999; Camazine *et al.*, 2001; Sumpter, 2006). In many animals and humans, this takes the form of copying behaviour, where the choices of others are copied by the decision maker (Petit *et al.*, 2009).

Another key heuristic in group decision making is the use of quorums (Sumpter and Pratt, 2009). A quorum response is one in which an animals' probability of exhibiting a behaviour increases sharply at a threshold number of other individuals already performing this behaviour. For example, Temnothorax ants decide to move to a new nest site when the number of other ants at that site is exceeded (Pratt *et al.*, 2002); small groups of sticklebacks follow two or more leader fish but will ignore a single leader (Sumpter *et al.*, 2008); and meerkats will only leave a foraging site when at least two of them have elicited moving calls (Bousquet *et al.*, 2011).

The study of animal decision making provides a tight link between theory and experiment. Models of animal decision making have been developed from empirical observations and then used to make predictions in further experiments. This research has also linked the identification of heuristics with questions of how they produce decision making that benefits individuals within groups. We present an overview of this research, focusing on the interplay between experiment and models. We build around the presentation of two key models, look at how they have been applied in the study of animal groups and give a number of clear cut predictions made by these models.

## 2. MODELS

In this section, we present three dynamic models of collective decision making—the BHW model (Bikhchandani *et al.*, 1992, 1998), the Deneubourg model (Deneubourg *et al.*, 1990; Nicolis and Deneubourg, 1999) and the Quorum model (Sumpter and Pratt, 2009)—along with a static model of optimal group decision making proposed by Condorcet (Condorcet, 1785).

The dynamic models describe how commitment to each of two or more options evolves in time. When

two options are available, there are a fixed number of individuals  $n$ , each of whom has one of three states of mind: 'uncommitted', 'committed to option 1' or 'committed to option 2'. The variable  $x_1$  denotes number of individuals committed to 1, and  $x_2$  denotes number committed to 2; therefore,  $n - x_1 - x_2$  are the number of uncommitted individuals. Decision making proceeds as follows. For the uncommitted individuals, we assume that their rate of deciding to commit depends on (i) a parameter measuring the attractiveness or 'quality' of the two options, denoted as  $q_1$  and  $q_2$ , respectively, and (ii) the number of individuals already committed to each of the options. In other words, the rate of commitment depends on both a private evaluation of the options and social information. We refer to  $q_1$  and  $q_2$  as the intrinsic quality of the two options.

A basic assumption adopted throughout this work is that of 'homogeneous' populations, in the sense that all individuals share common characteristics and, in particular, perceive 'quality' in an identical fashion. Still, even within this framework, a particular individual is unable to decide in a fully reliable fashion which option is best and which variation can occur in decision outcome. Indeed, when  $x_1 = x_2 = 0$ , then the probability that an individual will choose option 1 under all models is  $p_1 = q_1/(q_1 + q_2)$ . This limited reliability of private information is the key reason for the important role played by social information.

### 2.1. Condorcet's Model

Before we describe the three dynamic models, it is worth pausing to consider what would be the optimal utilisation of individual information when the aim is to maximise the group's probability of choosing correctly. If each individual has a probability  $p_1$  of choosing the best option (we assume option 1 is best), then the probability that a majority of an odd number of  $N$  individuals has correct private information is

$$C(N, p_1) = \sum_{i=(N+1)/2}^N \binom{N}{i} p_1^i (1 - p_1)^{N-i} \quad (1)$$

This is the famous Condorcet jury theorem for decision making (List, 2004; Ame *et al.*, 2006; Sumpter and Pratt, 2009).  $C(N, p_1)$  rapidly nears 1 as  $N$  increases, implying that larger groups make better decisions.

The Condorcet theorem implies that if each individual can independently assess the evidence and a majority vote is taken, then large groups will almost always make correct decisions. Given this interpretation, why

do we need to discuss other dynamic models of decision making? For animal groups, one answer is clear. Most animals lack the cognitive power to recognise that they are in such a decision-making situation, create a suitable voting mechanism and elect a centralised authority to count up the votes. For humans, another answer to the need for dynamic models is that in many cases, decisions are made sequentially and through, for example, discussion. Often, we cannot wait until everyone has formed an opinion before we start to integrate opinions (Sumpter, 2010). Although our cognitive power is greater than animals, there are many situations in which human groups fail to allow all group members to independently assess information in the manner suggested by Condorcet.

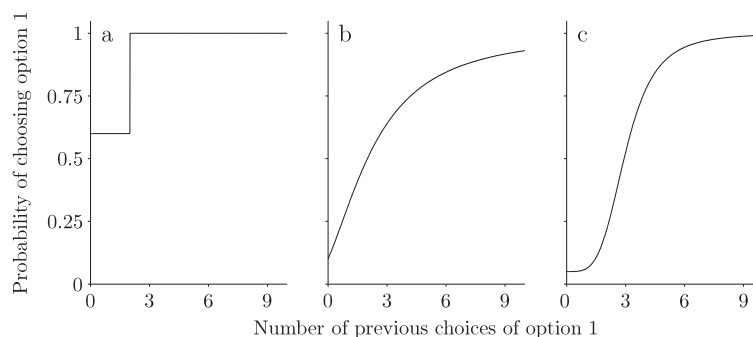
## 2.2. The BHW Model

The BHW model describes the rational strategy for a sequence of decision makers, each attempting to optimise her own probability of making the correct decision (Bikhchandani *et al.*, 1992, 1998). Under the model, the first individual chooses on the basis on private information and thus chooses option 1 with probability  $p_1$ . The second individual in the sequence now has access to the information of the first individual, along with his own information. If his private information agrees with that of the first individual, then he will choose the same option. If the private information is inconsistent with the first individual, then he will choose the option at random. The probability of choosing option 1 for the second individual is thus  $p_1^2 + (1 - p_1)p_1 = p_1$ . For all individuals from the third onwards, the rational action is to look at the previous two choices. If both are for the same option, then the individual should always choose that option; if the choices differ, he or she should choose according to her own preference.

Figure 1(a) shows how the probability of choosing option 1 changes as a function of the number of preceding individuals that have chosen that option.

The BHW model predicts a rational information cascade, whereby after only a small number of decisions, all individuals will choose the same option. The accuracy of this cascade is however rather low. For example, for  $p_1 = 0.6$ , the probability of a correct cascade is 0.63. Furthermore, the probability of a correct decision does not increase with group sizes greater than two individuals. This result can be contrasted with equation (1), where larger groups become more and more accurate. As such, the BHW model provides an example of how what is best for the individual is not best for the group (Vermeule and List, 2010). The third person in the sequence has no incentive to reveal its information for the benefit of the fourth person and instead acts on the information available to it at the point of making a decision. This property makes BHW a good conceptual model of, for example, stock market investor behaviour (Conlisk, 1996), where ‘incorrect’ cascades are commonly observed (Sornette, 2003).

Does the BHW model agree with data on human decision making in an experimental context? Anderson and Holt performed the first experiment testing the BHW model, using balls drawn from urns (Anderson and Holt, 1997). When the private information of the third individual in a sequence was inconsistent with that of the two preceding individuals, he or she disregarded his or her own information in 70% of cases, whereas in 26% of cases, experimental subjects behaved ‘irrationally’ in trusting their own information. These results have not been particularly well supported in further tests and other experimental setups. For example, in a similar setup, experimental subjects were willing to pay for their own information even when they could see that two individuals had already chosen one particular



**Figure 1.** How probability of choosing an option changes with number already committed in (a) the BHW model with  $p_1 = 0.6$ ; (b) the Deneubourg model with  $k = 1, x_2 = 2$  and  $m = 2$  (equation (4)); and the Quorum model with  $a = 0.05, T = 3$  and  $m = 4$  (equation (3)).

option (Kubler and Weizsacker, 2004). Similarly, in experiments where economics students are presented with a paper and pencil exercise of calculating the best strategy, they err on the side of personal information use even when this is not a mathematically correct choice (Huck and Oechssler, 2000; Spiwoks *et al.*, 2008). Overall, these experiments support the existence of information cascades, but in contrast to the prediction of the BHW model, the probability of a cascade starting increases with group size and does not necessarily start after two individuals have made their choices (Kubler and Weizsacker, 2005).

### 2.3. The Deneubourg Model

One of the first models highlighting the role of positive feedback in the context of group decision making is due to Deneubourg and co-workers (Deneubourg *et al.*, 1990; Nicolis and Deneubourg, 1999). They chose the following functional form for the rate of commitment to option 1:

$$q_1 \frac{(k + x_1)^m}{(k + x_1)^m + (k + x_2)^m} \quad (2)$$

This equation implies that the more individuals that have already chosen option 1 ( $x_1$ ), the greater the rate of commitment to that option. Figure 1(b) gives an example of how rate of commitment to option 1 changes as a function of  $x_1$ , for fixed  $x_2$ . The parameters  $m$  and  $k$  determine the form of the response. Larger values of  $k$  mean less attention is paid to the decisions of others. The parameter  $m$  measures the sensitivity of the particular choice. The larger the  $m$ , the sharper the choice, and for  $m > 1$ , positive feedback for the more popular option is disproportionately stronger than for the less popular option. For a detailed discussion of the assumptions and role of the parameters in this model, see Sumpter (2010).

Deneubourg's model was initially proposed in the context of foraging by ants, but it was soon noted by Kirman that this model could be equally relevant to human decision making (Kirman, 1993). Granovetter (1978) and Shelling (1978) had earlier proposed similar models for tipping points or thresholds at which a decision to adopt a particular action is taken. The underlying assumptions of such models appear to be consistent with experiments on both information cascades and human conformity. In information cascades, individuals only adopt a particular choice when others have also adopted that choice (Kubler and Weizsacker, 2005). For example, Milgram *et al.*

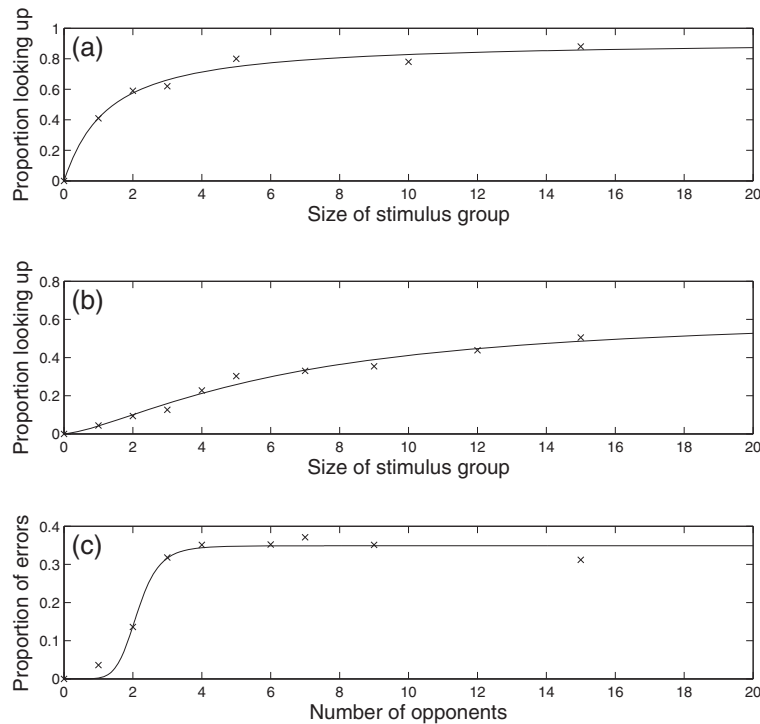
(1969) placed a small stimulus crowd of individuals, each of which looked up at a window of a nearby building, on a New York Street. They then observed passersby as they walked past the crowd. They found that the larger the crowd, the larger the proportion of passersby who would stop and/or look up. Gallup *et al.* (2012) repeated these experiments in Oxford and found similar results, although with a weaker response by passersby. Figure 2(a) and (b) shows how proportion of passersby looking up increases with crowd size in both cases.

Similar responses have been identified in conformity experiments (Asch, 1955; Latane and Wolf, 1981). In these experiments, experimental subjects are asked to answer a simple question after hearing a group of confederates give an incorrect answer, subjects have a probability of answering incorrectly which increases with group size (Figure 2(c)). Here, the probability of answering incorrectly increases sharply when the size of the incorrect group exceeds two or three individuals (Asch, 1955). The social contexts of the Milgram and Asch experiments are very different. In the Milgram setup, copying is probably the outcome of information transfer about the location of interesting features of the environment, whereas in the Asch setup, it is related to social conformity. In both cases, the form of the response is similar and can be modelled in a similar manner.

We would note that the aforementioned experimental evidence is limited and not collected for the purpose of testing the Deneubourg model. We present it here to provide some background for why the Deneubourg model and the Quorum model, which we will discuss in the next section, are relevant in the context of group decision making by humans. We would however go as far as to claim that experimental work up to now on humans is more consistent with models in which commitment increases smoothly at a particular threshold (i.e. as in Figure 1(b)) than with BHW type models, where there is an all or nothing response to the behaviour of others (i.e. as in Figure 1(a)). The Deneubourg model is also more in keeping with the idea that heuristics, rather than some pure form of rationality, should underlie an individual's reaction to private and social information.

### 2.4. The Quorum Model

Sumpter and Pratt (2009) proposed a model based on the idea that individuals observe the choices of others with respect to only one option at a time. The idea is



**Figure 2.** Responses of humans to the behaviour of others. The relationship between the probability that passersby will copy the gaze of the stimulus group as a function of stimulus group size in (a) New York (Milgram, 1969) and (b) Oxford (Gallup *et al.*, 2012). (c) The probability that an individual will concur with a group of opponents as a function of the number of opponents (Asch, 1955). The fitted line is the function,  $P(N) = bN^m / (T^m + N^m)$  is the observed frequency of looking up and  $N$  is the group size (opponents or crowd). The fitted parameters,  $T$ ,  $m$  and  $b$  characterise the type of response:  $b$  is the maximum proportion of individuals that will look up,  $T$  is the threshold group size at which  $b/2$  individuals will look up and  $m$  determines the shape of the response. The parameters are (a)  $b = 0.91$ ,  $T = 1.2$  and  $m = 1.05$ ; (b)  $b = 0.63$ ,  $T = 6.4$  and  $m = 1.42$  and (c)  $b = 0.35$ ,  $T = 2.13$  and  $m = 6.66$ .

that the individual finds an option at some rate and then assesses it using both an intrinsic probability of accepting and a probability of accepting that increases with the number of individuals that have already accepted it. As such, the rate of commitment to option 1 takes here the form

$$q_1 \left( a + (1 - a) \frac{x_1^m}{T^m + x_1^m} \right) \quad (3)$$

Here,  $a$  is the minimal probability to choose an option,  $T$  is the quorum threshold at which the rate of commitment suddenly increases and  $m$ , like in Deneubourg's model, is the steepness of this response. This is illustrated in Figure 1(c).

Although sharing common mechanisms, the Quorum and Deneubourg models differ in one important point. The choice functions in Deneubourg's model (2) depend on both the number choosing option 1 and the number choosing option 2 and are thus strongly coupled. In the Quorum model, the choice functions are independent

to each other. Accordingly, the coupling in the choice between two options is weak and rests entirely on the competition between the pool  $N - x_1 - x_2$  of uncommitted individuals. The Quorum model demands very limited cognitive powers on the part of individuals. In particular, they have no way of directly comparing the two options. It is assumed 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.

### 3. MODEL PREDICTIONS

In the previous section, we presented three dynamic models of decision making and provided background on their relevance to human and animal decision making. In this section, we investigate what the latter two models imply about the outcome of decision-making processes.

We organise this section under a number of subheadings, each of which describes a particular set of predictions obtained from the Deneubourg and Quorum models. Here, we refer only to model predictions and to cases where these predictions have been supported by experiments on animal groups, and we return to a discussion of human decision making in the discussion.

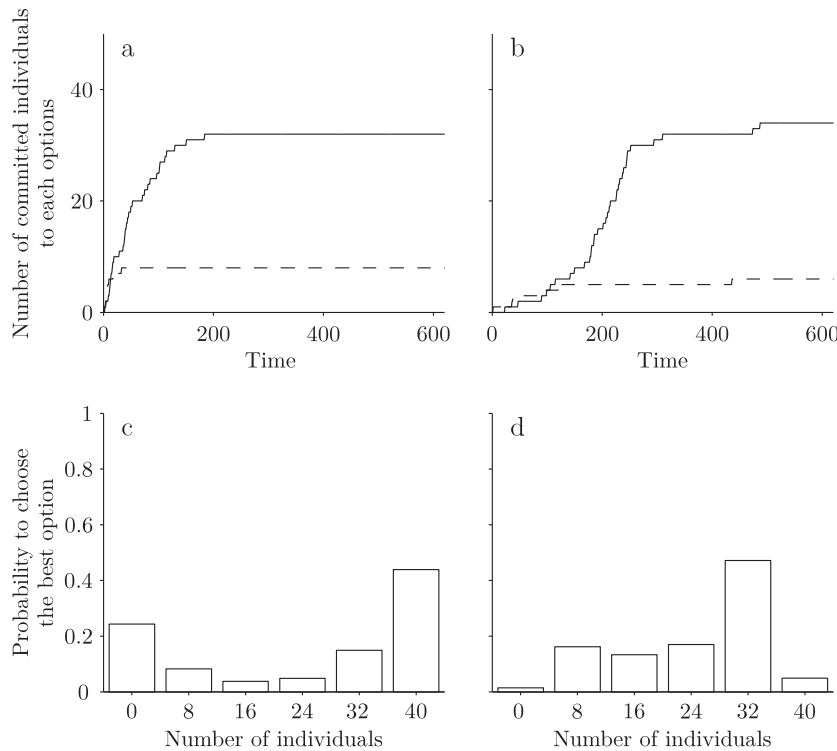
### 3.1. Group Decisions Involve Both True and False Cascades

Figure 3(a) shows the outcome of a single Monte Carlo simulation of the Deneubourg model (Nicolis *et al.*, 2003; Nicolis and Dussutour, 2008). In the simulation, we start with  $N$  uncommitted individuals. The stochastic rate of committing to an option is then determined by equation (2), and individuals commit one after another to one of the options. In this simulation, there is a cascade for superior option 1. A small initial preference for option 1 becomes strongly exaggerated, and by the end of the simulation, nearly all individuals have chosen option 1. Whereas this simulation shows a true positive cascade, where nearly all individuals choose the

superior option, these parameters also allow for false positive cascades, where nearly all individuals choose the inferior option.

Similar results are shown in Figure 3(b) for the Quorum model. The main difference between the Deneubourg model and the Quorum model is that in the latter, there is an initial build up period where commitment to both options is slow. Option 1 then reaches a threshold commitment level, and further commitment to it then rapidly accelerates. Both models predict a J-shaped distribution of final decision outcome (Figure 3(c) and (d)). The peaks of these distributions show that the most common outcomes are for nearly all or nearly none of the individuals to choose option 1.

U-shaped (rather than J-shaped) final decision distributions occur when options 1 and 2 have the same quality. Such distributions have been shown experimentally in a whole range of animal species. The standard experimental set-up is to offer a group a choice between two identical options. The most well-studied example are pheromone-laying ants, which lay stronger to one of two equal options (Beckers *et al.*, 1992a, 1992b; Sumpter and Beekman, 2003; Jeanson



**Figure 3.** (a)–(b) A Monte Carlo realisation of the time evolution of  $x_1$  and  $x_2$  and (c)–(d) probability distribution of the selection of the best option. (a)–(c) Deneubourg's model for parameter values  $k=5$ ,  $q_1=1$ ,  $q_2=0.5$ ,  $m=2$  and  $N=40$ . (b)–(d) Sumpter and Pratt model for parameter values  $T=10$ ,  $m=9$ ,  $q_1=1$ ,  $q_2=0.5$ ,  $a=0.1$  and  $N=40$ . Number of realisations equal to 5000.

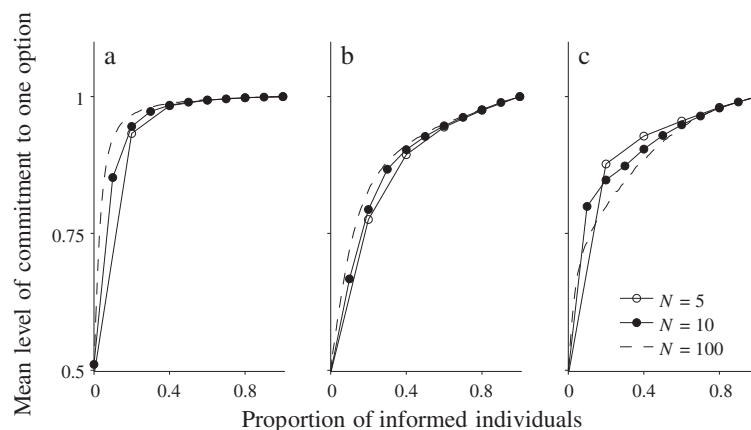
*et al.*, 2004; Dussutour *et al.*, 2009). Similarly, spiders construct draglines between the bottom and only one side of the two ends at the top of the t-shaped structure (Saffre *et al.*, 2000); when confronted with the choice between ascending from one of two ends of a t-shaped structure, weaver ants build a chain down from only one side (Lioni and Deneubourg, 2004); caterpillars forage on only one of two available branches (Dussutour *et al.*, 2008; Nicolis *et al.*, 2008); cockroaches aggregate under only one of two available shelters (Ame *et al.*, 2004, 2006). J-shaped distributions are often observed when groups are offered two different options. For example, when groups of sticklebacks show two slightly different replica fish going in different directions, they nearly all follow the same ‘leader’ (Sumpter *et al.*, 2008; Ward *et al.*, 2008). Some leaders are however more popular than others, and this leads to one peak of the distribution of number of followers being larger for one of the leader types (i.e. as in Figure 3(d))

### 3.2. A Small Number of Leaders can Induce a Decision

All three models share the idea that there exists a threshold beyond which the response becomes effective. In Deneubourg’s model, the threshold is determined by parameter  $k$ , whereas in the quorum model, it is characterised by  $T$  and in some respects by parameter  $a$ , which accounts for a minimal probability to commit to an option. Like in the BHW model, the decision outcome depends strongly on the choices of the first individuals to decide, although in the case of the Deneubourg and Quorum models, the choice is not as extreme.

Figure 4(a) shows the mean level of commitment to one option achieved eventually (i.e. in the steady state) by the population as a function of the proportion of leaders for the Deneubourg model for four different group sizes. An increase of fraction of initially informed individuals leads to a highly nonlinear response of the fraction of population settling eventually to the particular option favoured by the initial bias. The sharpness of this response increases significantly with the size  $N$  of the group. In other words, given the same initial proportion of leaders, a large group of individuals will be led more strongly than a small one. As a result, only a small number of leaders are required to lead a large group. This result goes some way to explaining why large animal flocks and swarms can be led by just a small number of informed individuals (Couzin *et al.*, 2005; Beekman *et al.*, 2006; Oldroyd *et al.*, 2008; Schultz *et al.*, 2008; Ward *et al.*, 2008).

The situation becomes more involved for the Quorum model (Figure 4(b) and (c)). When the threshold  $T$  is large (Figure 4(b)), the results partially resemble those described by Deneubourg’s model, although the sharpness of the response for different  $N$  in the quorum model is less pronounced. The situation is reversed when  $T$  is smaller (Figure 4(c)). Small populations now follow leaders more strongly than large populations. This result can be explained by the fact that information is shared only locally in the Quorum model. If the group size is large, then because each individual sees only one of the options at a time, the threshold is exceeded at both options. The options then become more or less indistinguishable, and the probabilities to choose either option 1 or option 2 become equal. On the contrary, the Deneubourg model, where information



**Figure 4.** Mean level of commitment to one option versus the proportion of initially informed individuals for  $N=5, 10$  and  $100$ . (a) Deneubourg’s model for parameter values are  $k=0.1$ ,  $q_1=q_2=1$  and  $m=2$ . (b)–(c) Sumpter and Pratt model for parameter values  $a=0.1$ ,  $q_1=q_2=1$ ,  $m=2$  and  $T=0.5$  (b),  $T=0.1$  (c).



about all options is simultaneously available, becomes deterministic beyond some threshold, and all individuals choose the most popular option. In many biological situations, individuals cannot compare all options, and we see the outcome predicted by the Quorum model (Pratt *et al.*, 2002). For example, colonies of *Temnothorax* ants, which use a quorum threshold to decide whether to commit to a new nest site, often initially split when offered two nests that many ants discover (Pratt and Sumpter, 2006). Similarly, larger numbers of cockroaches split between two shelters, whereas smaller numbers aggregate under the same shelter (Ame *et al.*, 2006).

### 3.3. Individuals in Groups Make More Accurate and Faster Decisions

Up to now, we have considered models in which once an individual commits to an option, then it cannot ‘uncommit’. There are many situations in which individuals can retire from the decision-making process. For example, those participating earlier in the process can disappear out of the sight of those currently making a decision. With the use of the assumption of an exponentially fading effect of earlier decision makers, the rate of commitment for two options can be expressed as two coupled differential equations

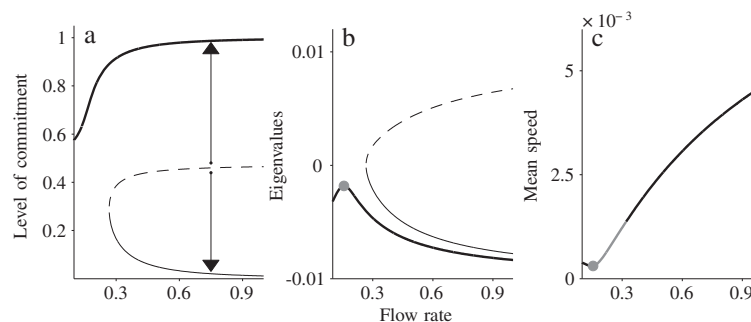
$$\begin{aligned}\frac{dx_1}{dt} &= \phi q_1 \frac{(k+x_1)^m}{(k+x_1)^m + (k+x_2)^m} - vx_1 \\ \frac{dx_2}{dt} &= \phi q_2 \frac{(k+x_2)^m}{(k+x_1)^m + (k+x_2)^m} - vx_2\end{aligned}\quad (4)$$

Here, we have assumed that there is a constant flow  $\phi$  of decision makers who make a decision one after another. We have also assumed that these remain

committed to an option for a time proportional to  $1/v$  before becoming uncommitted. This model differs from that of the previous sections in that the number of individuals is not conserved, but rather, the flow is constant. The best way to interpret this model in biological terms is to think of a constant flow of ants leaving their nest or fish swimming up a channel. Each of these animals approaches a branching bridge where it makes a decision to go left or right as a function of the intensity of a signal left by the number of individuals that have already gone left or right (i.e. as in equation (4)). This flow is inexhaustible, but over time, the effect of the decision of previous choices fades with rate  $v$ .

Figure 5(a) gives the equilibrium solution of equation (4), that is the values of  $x_1$  that satisfy  $dx_1/dt=0$  and  $dx_2/dt=0$ . As the flow rate increases, the system switches from having one stable state with a small majority committed to the option 1 (again,  $q_1 > q_2$ ) to having two steady states with stronger commitment to one of the two options. In this latter situation, there is one steady state corresponding to a high level of commitment to the highest quality option and another stable state corresponding to commitment to option 2. Like in the J-shaped distributions of Figure 3c, the chosen option depends on initial conditions. For example, in Figure 5a, the arrows show how different initial commitment levels will evolve. If commitment is initially strong for the lower quality option, then the system moves towards choosing this option.

Figure 5(b) and (c) gives two measurements of the speed of decision making. The first measurement (Figure 5(b)) is the value of the eigenvalues associated with each of the steady states of equation (4). Eigenvalues here measure the rate of convergence to the steady state,



**Figure 5.** (a) Steady-state solutions of equation (4), (b) the corresponding eigenvalues of the linearised equations around these solutions (each of the solutions has two eigenvalues of which one is always negative – equal to  $v$  – and not plotted here (see Nicolis and Deneubourg (1999) for details)) and (c) the time needed to reach the steady state corresponding to the better option as a function of the flow rate  $\phi$  (obtained by numerical integration and where the condition for steady state is given by the simultaneous conditions  $x_{1,s}(1 - 10^{-4}) \leq x_1(t) \leq x_{1,s}(1 + 10^{-4})$ ,  $x_{2,s}(1 - 10^{-4}) \leq x_2(t) \leq x_{2,s}(1 + 10^{-4})$ ). Parameter values are  $k=1$ ,  $v=0.01$ ,  $q_1=0.11$ ,  $q_2=0.1$  and  $m=2$ . Initial conditions for (c) are  $x_{1,0}=2 \times 10^{-4}$ ,  $x_{2,0}=1 \times 10^{-4}$ .

and a larger magnitude implies a faster approach to that steady state. The eigenvalue associated with a choice of  $x_1$  is always negative (solid line in Figure 5(b)) because this state is always stable. Furthermore, its magnitude depends upon  $\phi$ , reaching a minimum when  $\phi = 0.156$  (gray dot in Figure 5(b)). For  $\phi > 0.156$ , increasing  $\phi$  leads to an increasing magnitude of the eigenvalue and thus faster decisions. The second measure of decision-making speed is taken directly from numerical solution of equation (4). This confirms our eigenvalue analysis. There is a minimum value of  $\phi$  at which decisions are slowest, after which speed of decision making increases.

We now turn to accuracy of decision making. Decision accuracy depends on whether or not the best option is chosen, as well as the level of commitment to that option. In Figure 5(a), when  $\phi = 0.1$ , only 58% chooses the best option at equilibrium. This is to be compared with  $\phi = 0.6$  where 99% chooses the best option. On the other hand, when  $\phi = 0.1$ , this small majority always chooses the better option, whereas when  $\phi = 0.6$ , there is an alternative false cascade steady state where nearly all individuals choose option 2. We thus define accuracy to be a combination of (i) the proportion of individuals committed to the better option and (ii) the proportion of cases where this option is selected over the less favourable one. This latter quantity depends on initial conditions and/or random factors and cannot be calculated from equation (4) alone. We therefore use a Monte Carlo simulation to calculate (ii) (Nicolis *et al.*, 2003; Nicolis and Dussutour, 2008).

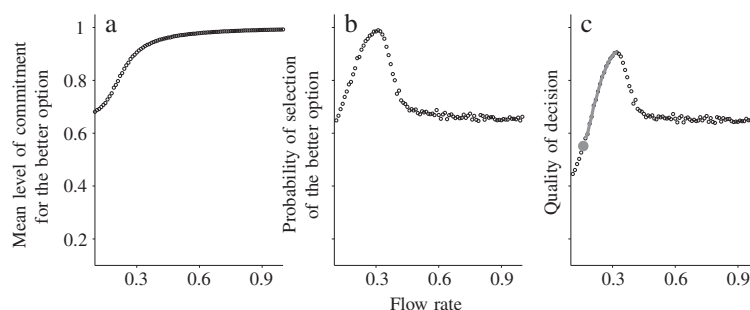
Figure 6 illustrates how the accuracy of decision making depends on flow rate  $\phi$ . Figure 6(a) presents the proportion of individuals selecting the higher quality option in the case of a true cascade. This plot corresponds to the upper branch of Figure 5(a). Figure 6(b) provides the number of cases in which the higher quality option is preferred over the total

number of Monte Carlo realisations (i.e. cases in which  $x_1 > x_2$  at steady state). Figure 6(c) multiplies these curves pointwise to provide an overall measure of how quality of decision depends on flow rate  $\phi$  for different numbers of options. In all cases, the strongest bias to the highest quality option occurs near to the bifurcation point,  $\phi_*$ , where the system goes from one to more than one steady states.

Taken together, Figures 5 and 6 describe how different flow rates produce different levels of speed and accuracy. It is interesting to note the changing relationship between speed and accuracy as we increase  $\phi$ . When  $\phi$  is very small, increases in flow rate lead to an increase in accuracy but a decrease in the speed. Here, increased accuracy is produced by the information provided by the decisions of others, but the time taken to reach the equilibrium increases because the equilibrium is moving further away from a 50/50 split between option 1 and option 2.

When  $\phi > 0.156$ , speed now increases with flow rate. Accuracy also continues to increase. Because both speed and accuracy increase with flow rate, it is beneficial for the group to increase its flow rate until at least  $\phi_* = 0.320$ . For flow rates indicated with a light grey line in Figures 5(c) and 6(c), we see that both speed and accuracy increase with flow rate up until  $\phi_* = 0.320$ . The simultaneous increase can be explained by the fact that speed by which information is communicated increases with flow. Provided this flow is not too fast, then good decisions are quickly communicated through all group members (Conradt, 2011). This prediction has been shown to hold for fish (Ward *et al.*, 2011). When the number of fish swimming up a channel was increased, the fish were able to detect a predator faster and more accurately than when alone.

Past  $\phi_*$  decision accuracy starts to fall, whereas speed continues to increase. Here, there is a trade-off between speed and accuracy: increasing the flow leads



**Figure 6.** Mean level of commitment for the better option  $\epsilon_1$  (a), probability of selection of the better option (b) and quality of decision (c) as a function of the flow rate  $\phi$  as obtained by Monte Carlo simulations in the case of  $n = 2$ . Parameter values as in Figure 3.

to increased speed but decreased accuracy (Franks *et al.*, 2003; Marshall *et al.*, 2006; Sumpter and Pratt, 2009; Conradt, 2011). However, given that for a wide range of parameters accuracy is not traded off against speed, the relevance of this trade-off is of limited relevance with respect to group size.

### 3.4. Irrelevant Alternatives Change Group Preferences

Several recent studies have begun to investigate the collective rationality of distributed biological systems (Edwards and Pratt, 2009; Latty and Beekman, 2011; Sasaki and Pratt, 2011). A striking experimental result is that a cellular slime mould *Physarum polycephalum* violates independence from irrelevant alternatives (IIA) because a new option of lesser value apparently alters the value of two superior options (Latty and Beekman, 2011). Such preference changes can be classified as ‘irrational’ (Luce, 1959).

Positive feedback is implicated in the formation of tube networks in slime moulds (Tero *et al.*, 2007; Ito *et al.*, 2010), making the Deneubourg model a good model of how slime moulds make decisions. Nicolis *et al.* (2011) investigated the Deneubourg model in the case of more than two options. The introduction of a third option whose attractiveness is equal to the second, poorer option changed the relationship between flow and probability of choosing option 1. These results are shown in Figure 7(a). The results in Figure 7(a) thus go some way to explaining the outcome of the Latty and Beekman (2011) experiments. Changing the number of options, while keeping the mass of the slime mould constant, means changing the proportion of

instances in which particular options will be chosen (Nicolis *et al.*, 2011).

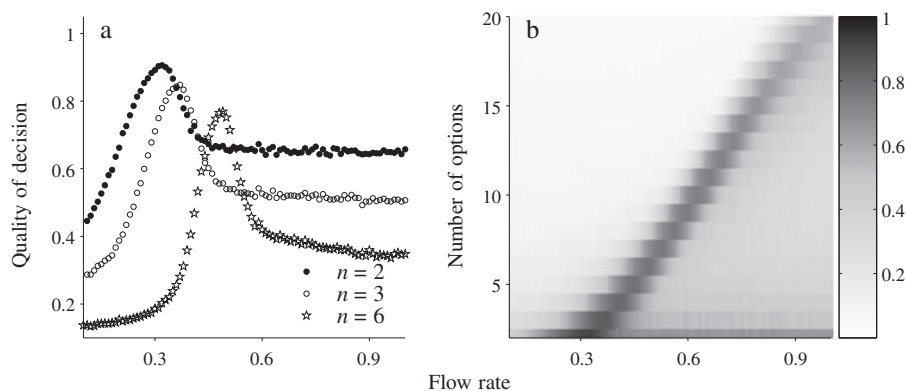
### 3.5. Optimal Group Size Depends on the Number of Options

Nicolis *et al.* (2011) extended the aforementioned results to any number of options. Figure 7(b) gives the quality measure for an exhaustive scan of the two principal parameters of the model for multiple options, namely number of options and flow rate  $\phi$ . Again, the maximal decision quality occurs near the bifurcation point,  $\phi_*$ . The position of the bifurcation point increases linearly with the number of options, as witnessed by the rightward drift of the maxima of the response curves in Figure 7(a).

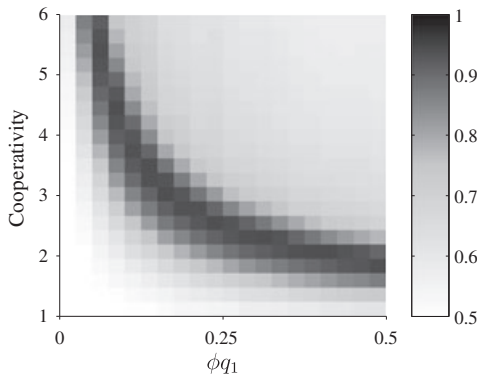
For any given number of options, the decision-making outcome is different. In particular, the flow level at which the highest quality option is chosen most often depends on this particular value. We can see that the flow level  $\phi_*$  that is optimal for choosing between, for example, two options is not optimised for choosing between three or more options. Likewise, a flow level that might make good decisions between six options can perform poorly when faced with a decision between two. This result is counterintuitive because we would not expect a system capable of coping successfully with a complex medium offering a large number of options to make a worse decision when confronted with a more restricted environment involving a smaller number of options.

### 3.6. The Influence of Intrinsic Quality of the Pair

How do the intrinsic values of the qualities of the options influence the decision-making process? Figure 8 shows the decision quality as a function of parameters



**Figure 7.** Decision quality as a function of the flow rate for  $n=2$ ,  $n=3$  and  $n=6$  (a) and (b) quality of decision as a function of number of options  $n$  and of the flow rate as obtained by Monte Carlo simulations for  $m=2$ . The colour code in (b) represents the level of the quality of decision, the maximum one corresponding to black. Parameter values as in Figure 3.



**Figure 8.** Decision quality as a function of the flow rate of individuals and of the cooperativity parameter  $m$  for  $n=2$ . The ratio  $p_1 = q_1/(q_1 + q_2) = 0.56$  is kept constant, whereas the absolute values of  $q_1$  and  $q_2$  are increased. Parameter values as in Figure 3 and colour code as in Figure 7(b).

$m$  and  $q_1$  measuring the steepness of response and the quality of the better option (cf. equation (4)). For each value of  $q_1$ ,  $q_2$  is set such that  $p_1 = q_1/(q_1 + q_2)$  is kept constant (and equal to 0.56). These results reflect the idea that the options become more and more valuable whereas their relative importance remains the same.

The optimal values for the decision quality changes as a function of both  $m$  and  $q_1$ . When  $m=2$ , the group is unable to make good decisions when confronted with two poor options. If the steepness of the response is larger, for example  $m > 3$ , the group becomes unable to choose between two good options. On the other hand, the group is more able to detect the better option among options that are both poor. These results mean that the capacity to perform optimal decisions is due to not only the relative quality of options but also the steepness of response to the behaviour of others.

#### 4. DISCUSSION

That decision making of animals and humans involve cascades of commitment to particular options is widely accepted as an empirical fact. For animals, the evidence for this comes from studies of cockroaches (Ame *et al.*, 2004, 2006), social spiders, various species of ants (Beckers *et al.*, 1992b; Sumpter and Beekman, 2003; Dussutour *et al.*, 2009), fish (Sumpter *et al.*, 2008; Ward *et al.*, 2008, 2011), chickens (Collins and Sumpter, 2007), meerkats (Bousquet *et al.*, 2011) and monkeys (Petit *et al.*, 2009). Humans are prone to peer pressure (Asch, 1955; Latane and Wolf, 1981) and copying. Individuals' choices depend on the choices of others when deciding what trends to follow (Salganik *et al.*, 2006),

whether to find a job (Hedstrom, 2005) and what shares to buy (Sornette, 2003).

We have shown that the Deneubourg model makes a large number of testable predictions about group decision making involving copying or positive feedback. Many of these predictions have been tested empirically for animal groups and presented here. J-shaped distributions of true and false cascades, improved decision making with group size and changing preferences with increased numbers of alternatives have all been tested empirically for particular species. Other predictions, such as how the optimal flow rate depends on the number of options, remain to be tested.

The Deneubourg and Quorum models, as well as similar models by Granovetter (1978), Shelling (1978) and Hedstrom (2005), are in fact generic models for the type of positive feedback and quorum/threshold-like heuristic employed by animals when making decisions. The same generality cannot be claimed for the BHW model, which is derived from a 'bounded rationality' argument. For making quantitative predictions about animal groups, we have argued that the BHW model overestimates the importance individuals place in social as opposed to private information. It also fails to account for a softer functional response that individuals use when deciding which group to follow (Figure 1). These properties lead the BHW model to predict copying cascades more frequently than is observed in practice. It also fails to predict an increase in decision-making accuracy with group size.

The recent prediction and experimental confirmation of fast and accurate decision making by systems based on positive feedback and quorums is a key development in animal studies (Pratt and Sumpter, 2006; Sumpter, 2010; Ward *et al.*, 2011). Copying behaviour is often described in the context of human decision making as a problem for the individual within the group. It is suggested that it leads to reinforcement of unpopular norms (Willer *et al.*, 2009), market crashes (Bikhchandani *et al.*, 1998; Sornette, 2003), the prevalence of 'yes men' in intelligence organisations (Posner, 2010) and social problems (Granovetter, 1978; Hedstrom, 2005; Hedstrom *et al.*, 2008). Although the existence of false cascades justifies the problem status attributed to positive feedback in some cases, it is important not to forget the possibility that false cascades may also arise as a side effect of systems in which decisions are on the whole accurate and efficient (Sumpter and Pratt, 2009).

It is in this sense that we see work on animal decision making as a case study in what is now known as the

heuristic approach (Gigerenzer, 2006). Over 20 years ago, Deneubourg and co-workers captured the basic properties of positive feedback and quorum response heuristics in a simple model. The assumptions of the model were then empirically validated on ants and other species. More recently, the empirical questions have turned to how ants, fish and other species can use these heuristics to discern quickly and accurately between two options of varying quality. In taking the heuristic approach, this last step is of central importance because it lays the ground for explaining why these heuristics evolved through natural selection (an argument that we do not pursue here, but see Sumpter, 2010). Through this approach, the link between heuristics and optimality becomes clear. First, we find out what individuals do, and then we look at the consequences of their actions. We hope that the work presented here will encourage a similar approach in the study of decision making within human organisations.

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