

Introduction

Group decisions in humans and animals: a survey

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Humans routinely make many decisions collectively, whether they choose a restaurant with friends, elect political leaders or decide actions to tackle international problems, such as climate change, that affect the future of the whole planet. We might be less aware of it, but group decisions are just as important to social animals as they are for us. Animal groups have to collectively decide about communal movements, activities, nesting sites and enterprises, such as cooperative breeding or hunting, that crucially affect their survival and reproduction. While human group decisions have been studied for millennia, the study of animal group decisions is relatively young, but is now expanding rapidly. It emerges that group decisions in animals pose many similar questions to those in humans. The purpose of the present issue is to integrate and combine approaches in the social and natural sciences in an area in which theoretical challenges and research questions are often similar, and to introduce each discipline to the other's key ideas, findings and successful methods. In order to make such an introduction as effective as possible, here, we briefly review conceptual similarities and differences between the sciences, and provide a guide to the present issue.

Keywords: collective decisions; communal decisions; conflict resolution; cooperation; information sharing; social behaviour

1. GENERAL BACKGROUND

Humans usually live in highly sophisticated societies. This implies that many important decisions are made not by individuals acting alone, but by groups of individuals acting collectively. Group decisions in humans range from small-scale decisions, such as those taken by groups of relatives, friends or colleagues, to large-scale decisions, such as nation-wide democratic elections and international agreements. Clearly, human societies cannot function without group decisions, and some of the most pressing problems facing humanity result from failures to reach a group consensus (e.g. the signing of the Kyoto treaty on controlling greenhouse gas emissions). Group decision making has been a central topic in all of the social sciences for millennia (e.g. Plato: *The Republic* 360 BC). Nevertheless, many questions remain open, particularly how conflicting interests and the sharing of dispersed information are actually, and should be, in principle, reconciled so as to facilitate cooperation and to reach outcomes that meet various optimality criteria. These are some of the fundamental questions of social choice theory (e.g. Arrow 1951/1963; Austen-Smith & Banks 1999, 2005; Sen 1999; Dryzek & List 2003).

A large number of animal species also live in groups (Krause & Ruxton 2002), some of which can be very complex (e.g. eusocial bees, wasps, ants, termites and

mole rats). Group decision making is just as important for social animals as it is for us (see Conradt & Roper 2005 for a review). Dispersing swarms of bees and ants collectively choose new nest sites on which their survival depends (Seeley & Buhrman 1999; Visscher 2007; Visscher & Seeley 2007; Franks *et al.* 2009). Homing and migrating birds collectively decide on communal routes that determine their chances of survival and successful arrival (Wallraff 1978; Simons 2004; Biro *et al.* 2006). Bats collectively select roosting sites that are crucial for survival (Kerth *et al.* 2006). Swarms of insects (Buhl *et al.* 2006), shoals of fishes (Reebs 2000; Hemelrijk & Hildenbrandt 2008; Ward *et al.* 2008), flocks of birds (Selous 1931; Ballerini *et al.* 2008), groups of carnivores (Gompper 1996), herds of ungulates (Gueron *et al.* 1996; Prins 1996; Conradt 1998; Ruckstuhl 1998; Fischhoff *et al.* 2007; Gautrais *et al.* 2007) and troops of primates (Stewart & Harcourt 1994; Trillmich *et al.* 2004; Meunier *et al.* 2006; Sellers *et al.* 2007; Sueur & Petit 2008) collectively decide group movements and group activities with important fitness consequences to all individuals (Conradt & Roper 2003; Rands *et al.* 2003; Dostalkova & Spinka 2007). Cooperative species, such as eusocial insects and communal breeders, collectively decide job allocation in crucial communal enterprises, such as supplying forage to the hive (Beshers & Fewell 2001), rearing young (Clutton-Brock 1998) and hunting prey (Courchamp *et al.* 2002). In contrast to the human case, the study of group decisions in social animals is relatively young, but is now rapidly expanding in the natural sciences (see Conradt & Roper 2005 for the

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most recent review). It emerges that group decisions in animals pose many similar questions to those in humans, as discussed below.

2. PURPOSE OF THE PRESENT ISSUE

The purpose of the present issue is to integrate and combine approaches in the social and natural sciences in an area in which theoretical challenges and research questions are often similar. Each discipline can benefit from being introduced to the other's key ideas, findings and successful methods. Over the centuries, the social sciences have developed a large body of theory on human group decisions, including many sophisticated modelling tools, which can be modified to study animal group decisions. List *et al.* (2009) give an example for this in the present issue, drawing on social-scientific methods and ideas to develop a model of nest-site choice by honeybee (*Apis mellifera*) swarms. On the other hand, by focusing on relatively less complex group decisions, the natural sciences can concentrate on fundamental features that might also be applicable to humans but are much harder to detect in the sophisticated and complex contexts of human group decisions. A good example is Dyer *et al.*'s (2009) work in the present issue. In addition, natural scientists, by looking at group decisions from an evolutionary point of view, can add a different approach to human group decisions from the one which most social scientists adopt. For example, group decision outcomes that, in evolutionary terms, are 'good' for the individual are often 'not good' for the group, and vice versa (Conradt & Roper 2003, 2007, 2009). Game theorists recognize such tensions, but usually cast them in terms of conflicts between individual rationality and group optimality rather than in evolutionary terms. A natural-scientific perspective suggests that social-scientific analyses of group decisions might be enriched by taking our natural and social evolutionary past into account too (e.g. Helbing *et al.* 2000).

Although cross-referencing of natural science publications by social scientists (e.g. List 2004; Hastie & Kameda 2005), and vice versa (e.g. Conradt & Roper 2005), has already begun, indicating the mutual interest in interdisciplinary exchange, the language and thinking in the social and natural sciences are disparate enough to hamper communication. This introduction is an attempt to bridge that gap, render the present issue as useful as possible to both social and natural scientists and set a common ground for future exchanges.

First, we suggest a categorization of group decisions into aggregate/consensus decisions, on the one hand, and interactive/combined decisions, on the other and introduce some key concepts for the analysis of group decisions in each category. Second, we discuss some common factors influencing group decisions in both humans and animals. Third, we review the contributions in the present issue against this background. Finally, we make some remarks on the differences between human and non-human group decisions and suggest some possible directions for future research. We have also compiled a brief and informal glossary of common social and natural science terms (appendix A), which is intended to help social

and natural scientists when reading cross-disciplinary literature in the present issue and beyond.

3. KEY CONCEPTS FOR THE ANALYSIS OF GROUP DECISIONS

(a) *Aggregate/consensus versus interactive/combined decisions*

Group decisions can be roughly divided into two categories: (i) those in which the group makes a single collective decision, e.g. between multiple options, that is 'binding' in some way for all members, and (ii) those in which there need not be a single collectively binding decision, but in which individuals decide interdependently with one another. In the social sciences, the former are often described as 'aggregate' or 'collective' decisions and are the subject of social choice theory; the latter are described as 'interactive' decisions and are the subject of game theory. In the natural sciences, the two categories have become known as 'consensus' and 'combined' decisions, respectively (Conradt & Roper 2005; see table 1 for social- and natural-scientific examples and a categorization of the group decisions discussed in this issue). Examples of aggregate/consensus decisions are national elections, parliamentary decisions on whether to pass a new law, choices of joint movement directions in cohesive groups (e.g. Couzin *et al.* 2005) and nest-site choices in eusocial insects (e.g. Seeley & Buhrman 1999). Examples of interactive/combined decisions are the processes by which many individual consumer choices lead to market prices, sharing of reproductive roles in cooperative breeders (e.g. Clutton-Brock 1998) and job allocations in honeybee workers (e.g. Beshers & Fewell 2001).

Within each of these two categories, decision problems come in many different shapes and sizes. The objects of choice in aggregate/consensus decisions can be just two options (as in a choice between the acceptance and rejection of some proposal or policy, or between leaving or staying in a foraging patch), more than two, but finitely many, options (as in a choice between several electoral candidates, nest sites or food sources), or even infinitely—specifically, continuously—many options (as in the choice of a rate of taxation, which can theoretically take any value between 0 and 100%, or of a movement orientation, which can theoretically be any angle between 0° and 360°, or of a movement speed, which may also take a continuum of values). As we illustrate below, the number and structure of options matters.

Similarly, in interactive/combined decisions, the choices that individuals face can be of many different kinds. Sometimes they are binary, as in the choice between cooperation and defection in a Prisoner's Dilemma or similar situation. At other times, individuals have a choice between more than two possible actions or strategies, perhaps even a continuum of possibilities, as in the choice between different movement directions. Furthermore, the mechanisms by which individual choices lead to certain consequences can vary greatly across different interactive/combined decision problems. Recognizing the large variety of different possible decision problems is important in so far as different concepts and modelling tools are needed for their analysis.

Table 1. Examples of different categories of group decisions.

	social sciences	natural sciences
<i>groups with global overview</i>		
decision category: interactive/ combined decisions		
group decision perspective references	<i>democratic/parliamentary votes</i> voting strategies Austen-Smith & Feddersen (2009), Hix <i>et al.</i> (2009) and many more	<i>group activity synchronization</i> who decides and why? Conrard & Roper (2003, 2007, 2009), Rands <i>et al.</i> (2003) and Dostalkova & Spinka (2007)
group decision perspective references	<i>common goods</i> individual strategies Gächter & Herrmann (2009) and many more	<i>movements in small groups</i> who decides and how? Stewart & Harcourt (1994), Gompper (1996), Conrard & Roper (2005), Amé <i>et al.</i> (2006), Biro <i>et al.</i> (2006), Meunier <i>et al.</i> (2006), Fischhoff <i>et al.</i> (2007) and Sueur & Petit (2008)
group decision perspective references	<i>international agreements</i> strategies a large body of literature	<i>cooperative breeding</i> individual strategies Clutton-Brock (1998)
decision category: aggregate/ consensus decisions		
group decision perspective references	<i>international agreements</i> patterns a large body of literature	<i>group activity synchronization</i> segregation Conrard (1998), Ruckstuhl (1998, 1999), Conrard & Roper (2000), Ruckstuhl & Neuhaus (2000, 2002) and List (2004)
group decision perspective references	<i>democratic/parliamentary votes</i> systems a large body of literature	<i>movements in small groups</i> outcomes, speed, accuracy List (2004), Trillmich <i>et al.</i> (2004), Kerth <i>et al.</i> (2006), Gautrais <i>et al.</i> (2007), Sumpter <i>et al.</i> (2008) and Ward <i>et al.</i> (2008)
group decision perspective references	<i>military orders or hierarchical decisions</i> any	<i>cooperative hunting</i> patterns Courchamp <i>et al.</i> (2002)
<i>self-organizing systems</i>		
decision category: interactive/ combined decisions		
group decision perspective references	<i>consumer choice</i> how do consumers make choices? a large body of literature	<i>movements in large groups</i> mechanisms, individual strategies Selous (1931), Gueron <i>et al.</i> (1996), Prins (1996), Couzin & Krause (2003), Couzin <i>et al.</i> (2005), Ballerini <i>et al.</i> (2008), Hemelrijk & Hildenbrandt (2008), Conrard & Roper (2009) and Conrard <i>et al.</i> (in press)
group decision perspective references	<i>traffic movements</i> individual behaviours Couzin & Krause (2003) and Ishaque & Noland (2008)	<i>job allocation in eusocial insects</i> individual decisions Beshers & Fewell (2001)
group decision perspective references	<i>panic behaviour in crowds</i> individual strategies Aube & Shield (2004)	<i>nest choice in eusocial insects</i> behaviour of individual scouts Seeley & Buhrman (1999), Franks <i>et al.</i> (2009), List <i>et al.</i> (2009) and Sumpter & Pratt (2009)
decision category: aggregate/ consensus decisions		
group decision perspective references	<i>consumer choice</i> market prices a large body of literature	<i>movements in large groups</i> speed, accuracy, patterns Wallraff (1978), Krause <i>et al.</i> (1992), Reeb (2000), Couzin & Krause (2003), Simons (2004), Couzin <i>et al.</i> (2005), Buhl <i>et al.</i> (2006) and Dyer <i>et al.</i> (2009)
group decision perspective references	<i>panic behaviour in crowds</i> evacuation time Helbing <i>et al.</i> (2000)	<i>nest choice in eusocial insects</i> decision speed and accuracy List <i>et al.</i> (2009) and Sumpter & Pratt (2009)

The central concept for the analysis of aggregate/
consensus decisions is that of an ‘aggregation rule’, as

discussed in §3*b*. Formally, an aggregation rule is defined
as a function which assigns to each combination of

Box 1. Aggregation rules in choices between two options.

1. Basic definitions

Suppose a group of n individuals has to choose between two options, A and B. Each individual, i , can cast a ‘vote’, v_i , which can take one of the following three values:

$$v_i = \begin{cases} +1 & : \text{ a vote for option A,} \\ 0 & : \text{ an abstention,} \\ -1 & : \text{ a vote for option B.} \end{cases}$$

An ‘aggregation rule’ is a function, f , which assigns to each vector of votes across individuals, (v_1, \dots, v_n) , a corresponding ‘decision’, $v = f(v_1, \dots, v_n)$, which can also take one of the following three values:

$$v = \begin{cases} +1 & : \text{ a decision for option A,} \\ 0 & : \text{ a tie,} \\ -1 & : \text{ a decision for option B.} \end{cases}$$

Majority voting, for instance, assigns to each vector (v_1, \dots, v_n) the value $+1$ if there are more $+1$ s than -1 s in (v_1, \dots, v_n) , the value -1 if there are more -1 s than $+1$ s and the value 0 if the numbers of $+1$ s and -1 s are equal. Thus, ‘majority voting’ is defined as the function f with the property that, for each (v_1, \dots, v_n) ,

$$f(v_1, \dots, v_n) = \text{sign}(v_1 + \dots + v_n),$$

where, for any x ,

$$\text{sign}(x) = \begin{cases} +1, & \text{if } x > 0, \\ 0, & \text{if } x = 0, \\ -1, & \text{if } x < 0. \end{cases}$$

2. Generalized weighted majority rules

A ‘generalized weighted majority rule’ is a function f with the property that, for each (v_1, \dots, v_n) ,

$$f(v_1, \dots, v_n) = \text{sign}(w_1 v_1 + \dots + w_n v_n + m),$$

where (w_1, \dots, w_n) is a vector of ‘weights’ across individuals and m is a ‘decision margin’. In the special case of equal positive weights $w_1 = \dots = w_n$ and a decision margin of 0 , a generalized majority rule reduces to (simple) majority voting again. If $m > 0$, the rule becomes super-majoritarian for B (meaning that a super-majority of votes is required for a decision in favour of B), and if $m < 0$, it becomes sub-majoritarian for B (meaning that a sub-majority of votes is sufficient for a decision in favour of B). In the limiting case in which only one individual has a positive weight and all other individuals have zero weight, the rule becomes dictatorial.

individual inputs (e.g. votes) a resulting collective output (e.g. a decision outcome). The classic example is majority voting between two options, under which the group selects the option that receives more votes than the other. However, a dictatorial decision rule, under which the group always adopts the choice of a fixed single individual, the ‘dictator’, is also an aggregation rule.

The central concept for the analysis of interactive/combined decisions is that of an ‘equilibrium’, also discussed in §3c. Formally, an equilibrium is defined as a combination of strategies across individuals, which satisfies certain ‘best-response’ or ‘stability’ criteria. Two classic examples of equilibrium concepts are ‘Nash equilibrium’ in the social sciences and ‘evolutionarily stable strategies’ in the natural sciences (Maynard Smith & Price 1973). However, many other equilibrium concepts have been proposed in the game-theoretic literature using a range of different best-response or stability criteria for different contexts.

Whether a particular group decision falls into the aggregate/consensus category or into the

interactive/combined category is often in the eye of the beholder. Scientists will characterize a group decision as an aggregate/consensus decision if they are interested in the aggregation rule that leads to the decision outcome. On the other hand, they will characterize a group decision as an interactive/combined decision if they are interested in the individual behaviours and strategies underlying the collective phenomenon (table 1). For example, social scientists comparing the outcomes of different electoral systems for the same configurations of votes may view elections primarily as aggregate/consensus decisions, but if they are interested in strategic voting behaviour of individuals, they may view elections as interactive/combined decisions. Natural scientists studying the accuracy of navigational decisions in animal groups may view these as aggregate/consensus decisions, but if they are interested in the underlying individual behaviours, they may view such decisions as interactive/combined.

As these examples illustrate, aggregate/consensus decisions can often be seen as resulting from interactive/combined decisions. The relationship between

Table 2. Some empirical examples for unshared, partially shared and equally shared decision making in social animals.

decision making	object of group decision
unshared	forage patch choice in primates (King <i>et al.</i> 2008) travelling start in dolphins (Lusseau & Conradt in press)
at least partially shared	cohesive group movements in small groups of birds (Black 1988; Biro <i>et al.</i> 2006), carnivores (Gompper 1996), ungulates (Conradt & Roper 2003) and primates (Stewart & Harcourt 1994; Boinski & Campbell 1995; Byrne 2000; Milton 2000) cohesive group movements in large swarms of insects (Buhl <i>et al.</i> 2006), shoals of fishes (Ward <i>et al.</i> 2008), flocks of birds (Wallraff 1978; Simons 2004) or herds of ungulates (Prins 1996) group activity synchronization (Conradt 1998; Ruckstuhl 1998, 1999) nest-site choice in eusocial insects (Seeley & Buhrman 1999; Franks <i>et al.</i> 2009) and bats (Kerth <i>et al.</i> 2006) coordination of cooperative hunts (Courchamp <i>et al.</i> 2002) coordination of reproduction (Clutton-Brock 1998)
equally shared	group flight from potential predators

the two is a key theme in the theory of mechanism design in economics, which investigates what mechanisms or systems of incentives would induce rational individuals to behave so as to bring about an outcome that could also result from some aggregation rule. Mechanism design has become an important area of research, as the three Economics Nobel Prizes in 2007 illustrate (see the survey article by the Royal Swedish Academy of Sciences 2007). In the natural sciences, some recent developments focus on behavioural mechanisms resulting in the implementation of particular aggregation rules. A key mechanism is that of ‘quorum response’ whereby an individual’s probability of commitment to a particular decision option increases sharply once a critical number of other individuals (the ‘quorum threshold’) have committed to that option (e.g. Sumpter *et al.* 2008; Ward *et al.* 2008; Sumpter & Pratt 2009). Through this positive feedback mechanism, interactive/combined decisions among multiple individuals can effectively bring about an aggregate/consensus decision in the group.

(b) Aggregation rules

In aggregate/consensus decisions, a group’s aggregation rule is important as it greatly influences the costs and benefits of the group’s decisions to individual members and to the group as a whole (e.g. Seeley & Buhrman 1999; Conradt & Roper 2003; Rands *et al.* 2003; Couzin *et al.* 2005; Hastie & Kameda 2005; Austen-Smith & Feddersen 2009). We discuss such costs and benefits in detail when we address different factors influencing group decisions. In this section, we briefly review possible aggregation rules.

The set of logically possible aggregation rules for a given group decision is enormous. For example, in a group of 10 individuals making a decision between just two options, there are already $2^{10} = 1024$ possible combinations of individual votes. Since the aggregation rule has to assign one of two possible outcomes to each such combination, there are, in principle, 2^{1024} possible aggregation rules for this decision. This is more than the estimated number of elementary particles in the Universe. In more complex decision problems, the combinatorial explosion is even more dramatic. Of course, most of these rules are of no

practical relevance. One of the aims of social choice theory is to identify those aggregation rules that could be practically relevant.

In order to do so, social choice theorists investigate which aggregation rules, if any, satisfy certain properties of potential interest. An example of such a property is ‘universal domain’, which requires the aggregation rule to assign a decision outcome to every possible combination of individual inputs. Universal domain can be a desirable property because it guarantees a clear decision outcome in all situations. Another example is ‘anonymity’, which requires that all individual group members have equal weight in determining the outcome. Anonymity is an important democratic principle. A third example is ‘neutrality’, which requires that the different decision options be treated symmetrically. Neutrality guarantees that no bias towards one option is built into the aggregation rule itself. A fourth example is ‘positive responsiveness’, which requires, roughly speaking, that the decision outcome be a positively monotonic function of individual inputs. Positive responsiveness rules out the perverse possibility that a winning option becomes losing by gaining additional individual support. If we restrict our attention to aggregation rules satisfying such properties, the set of possibilities shrinks dramatically. In particular, it has been proved that, in group decisions between two options, majority voting is the only aggregation rule simultaneously satisfying the four properties just introduced (May 1952; for an extension and further discussion, see Goodin & List 2006a).

One particularly important class of aggregation rules for the case of decisions between two options is that of ‘generalized weighted majority rules’ (box 1). The simplest example of an aggregation rule in that class is majority voting itself. This is the special case in which each individual has one vote, all votes have equal weight, and the option that gets more votes than the other wins. This could be modified by giving different weights to different individuals. In this case, the option whose sum total of weighted votes exceeds that of the other wins. For example, in the European Council of Ministers, larger countries have greater voting weight than smaller countries. In animal groups, hungrier group members can gain more influence on group movement directions than well-fed members (Krause *et al.* 1992;

Box 2. Equilibria in interactive/combined decisions.

1. A Prisoner's Dilemma

Suppose two individuals interact. Each of them has a choice between two strategies, cooperation and defection, and the individual's pay-off depends on his or her own choice and that of the other individual. In a Prisoner's Dilemma, the pay-off structure is as shown in the following table. In each cell, the bottom left entry is individual 1's pay-off and the top right entry is individual 2's pay-off.

		individual 2	
		cooperate	defect
individual 1	cooperate	3	4
	defect	0	1

If both individuals cooperate, each receives a pay-off of 3. If both defect, each receives a pay-off of 1. If one cooperates and the other defects, the defector receives 4 (sometimes called the pay-off from 'free-riding') and the cooperator receives nothing (sometimes called the 'sucker's pay-off'). It is easy to see that the situation in which both individuals defect is the unique Nash as well as dominant strategy equilibrium: regardless of what the other individual does, each individual receives a higher pay-off from defecting than from cooperating. It is also easy to see that defection is the unique evolutionarily stable strategy in this game.

2. Coordination games

Again, two individuals interact, and each of them has a choice between two strategies, A and B, with a pay-off structure as shown in the following table.

		individual 2	
		A	B
individual 1	A	3	0
	B	0	1

What matters in this game is that they both choose the same strategy (a biological example would be reproductive synchronization). If they fail to coordinate, they both receive nothing. However, they receive a higher pay-off if they coordinate on strategy A (namely 3, e.g. the optimal time for reproduction) than if they coordinate on strategy B (namely 1, e.g. a less optimal time). Here, there exists no dominant strategy equilibrium. For each individual, the best response depends entirely on the strategy of the other individual. However, both the situation in which the two individuals coordinate on A and the one in which they coordinate on B constitute Nash equilibria. Assuming the other individual chooses A, it is best to respond by choosing A too, and similarly for B. Furthermore, both the strategies are evolutionarily stable in this game, since each gets a higher pay-off from playing against itself than the other strategy gets from playing against it, and so clause (i) of the definition of evolutionary stability is met. Nonetheless, it is interesting to note that a population that coordinates on strategy A will receive higher pay-offs than the one that coordinates on strategy B.

To illustrate the differences between the concept of a Nash equilibrium and that of an evolutionarily stable strategy, consider the following modification of the coordination game, as given by the pay-off structure in the following table.

		individual 2	
		A	B
individual 1	A	0	3
	B	1	0

(Continued.)

Box 2. (*Continued.*)

Here again, it matters that both individuals coordinate their strategy. However, this time, they have to coordinate on opposite strategies: one individual must play strategy A and the other individual strategy B; otherwise, neither individual receives any pay-off. Moreover, if they coordinate correctly, the individual who plays strategy B receives a higher pay-off (namely 3) than the individual who plays strategy A (namely 1). A biological example would be the allocation of roles in a cooperative hunting expedition: the hunt is only likely to be successful if different roles are adequately allocated, but different roles will incur different costs in terms of energy and risks. As in the earlier coordination game, there exists no dominant strategy equilibrium, but two Nash equilibria: (i) individual 1 plays A and individual 2 plays B, and (ii) individual 1 plays B and individual 2 plays A. However, this time, neither strategy A nor B is evolutionarily stable, since each gets a lower pay-off from playing against itself than the other strategy gets from playing against it. In an evolutionary situation, a population of individuals could, instead, reach an evolutionarily stable state, in which the proportions of individuals playing strategy A or B, respectively, reach a dynamic equilibrium (here, 25% playing A and 75% playing B). Note that a mixed strategy (play A 25% of the time and B 75% of the time) would be an evolutionarily stable strategy.

Conrard *et al.* in press). A limiting case is a dictatorial aggregation rule, in which only one individual has a positive weight while all others have zero weight. For instance, in many animal groups, decisions are probably made by a dominant individual (e.g. King *et al.* 2008).

Generally, the assignment of weights can lie anywhere between an equal weight for all group members ('egalitarian', 'equally shared' or 'dispersed' decision making) and a concentration on one individual ('dictatorial', 'unshared' or 'concentrated' decision making). Intermediate cases, in which some group members (e.g. the highest ranking ones), but not all, contribute to the group decision, are particularly common in practice. Examples in the social sciences are oligarchic or meritocratic decisions. However, even in democracies, at least some group members are typically excluded from group decisions (e.g. children, adolescents and non-citizens). While truly equally shared decisions are very rare in animals, decisions ranging from nearly equally shared to completely unshared ones have been reported in animals from insects to primates (table 2; for a review, see also Conrard & Roper 2005).

Another way to modify majority voting is to adjust the decision threshold, so as to make the aggregation rule 'super-majoritarian' (e.g. Goodin & List 2006b) or 'sub-majoritarian' (e.g. Vermeule 2005). The 'decision threshold' for a given option specifies the vote share required for that option to win. For example, one of the options might win only if the sum total of weighted votes for it is at least twice as large as the sum total of weighted votes for the other ('super-majority'), while the other option would win otherwise ('sub-majority'). An example is a legislature that agrees to change its constitution if a super-majority of at least two-thirds of its members supports the proposed change (e.g. Grundgesetz der Bundesrepublik Deutschland 1949). Another example is a group of foraging animals that leaves a patch when a sub-majority of at least one-third of group members are in favour of leaving. By permitting the combination of different individual weight assignments with different decision thresholds, the class of generalized weighted majority rules is very flexible.

If there are more than two options, some additional complications arise. If each individual gets to cast a vote

just for one option, then 'plurality rule', which selects the option with the largest number of votes, has many of the properties of majority voting (List & Goodin 2001; Goodin & List 2006a). However, if decisions between multiple options are decomposed into pairwise choices, majority voting and its various generalizations may run into problems. It can then happen that there are majorities for option A against option B, for option B against option C and also for option C against option A. An illustrative situation in which such 'cyclical' majority preferences occur is the one in which one-third of the group prefers A to B to C, a second third prefers B to C to A and the remaining third prefers C to A to B. When majority preferences are cyclical, majority voting yields no stable winner—a phenomenon known as 'Condorcet's paradox' (e.g. Gehrlein 1983). Moreover, this problem is not restricted to majority voting. A classic theorem, proved by Nobel laureate Kenneth Arrow (1951/1963), shows that, among aggregation rules that preserve the pairwise character of majority voting and meet a few other minimal conditions, only dictatorial rules generally avoid the occurrence of cyclical collective preferences ('Arrow's impossibility theorem'). Important questions in social-choice-theoretic research are therefore (i) how much of a difficulty Arrow's impossibility theorem poses for successful aggregate/consensus decision making over more than two options, and (ii) how the problem can be circumvented by either giving up the pairwise format of choices between multiple options—as, for instance, plurality rule does—or relaxing some of the other conditions of Arrow's theorem (e.g. Sen 1999; Dryzek & List 2003).

(c) *Equilibrium concepts*

When we analyse interactive/combined decisions, the aim is to identify combinations of strategies that are 'equilibria' (for a good introduction to game theory, see Osborne & Rubinstein 1994). To explain this idea in more detail, consider some interactive situation in which each individual has to choose a certain action or strategy such that the combination of actions or strategies across individuals leads to a resulting outcome. For example, each individual may have to choose between cooperating and defecting, or between different movement directions, or between different

investment options. A resulting social outcome or pattern—e.g. a collective action, the location of the group or a set of market prices—is then determined by those choices. In game theory, such an interactive situation is called a ‘game form’ and is formally defined as a specification of a set of possible strategies for each individual, together with a mapping from combinations of strategies across individuals to resulting outcomes.

To determine when a combination of strategies is an equilibrium, we need to know what the individuals’ pay-offs or preferences are. A game form together with a specification of the individuals’ pay-offs or preferences over outcomes is called a ‘game’. A combination of strategies now constitutes an equilibrium if every individual’s strategy satisfies a certain best-response or stability criterion in relation to the other individuals’ strategies. Different equilibrium concepts result from different ways of spelling out the notion of best response or stability. The best-known equilibrium concept in the social sciences is that of Nash equilibrium. Here, an individual’s strategy counts as a best response to the other individuals’ strategies if the individual prefers (or is at least indifferent to) the outcome of choosing that strategy, compared with the outcome of deviating from it, *assuming that the others do not deviate*. A stronger notion of best response is that of a ‘dominant strategy’. An individual’s strategy is ‘dominant’ if the individual prefers (or is at least indifferent to) the outcome of choosing that strategy, compared with the outcome of deviating from it, *regardless of what the other individuals do*. In coordination games (box 2), for example, there are typically multiple Nash equilibria, but there is no dominant strategy equilibrium. In a Prisoner’s Dilemma, by contrast, there is a unique Nash equilibrium, which is also a dominant strategy equilibrium (box 2). There is a huge game-theoretic literature on various more refined equilibrium concepts.

In the natural sciences, the best-response or stability criteria used for defining equilibria are usually evolutionary ones. Here, we illustratively explain the approach pioneered by Maynard Smith & Price (1973). Consider an interactive situation in which interactions take place between pairs of individuals. A strategy, call it S, is called evolutionarily stable if it satisfies the following condition: for any alternative (‘mutant’) strategy T, either (i) S receives a greater pay-off from playing against S than T receives from playing against S, or (ii) S receives the same pay-off from playing against S as T receives from playing against S, and S receives a greater pay-off from playing against T than T receives from playing against T. Formally, S is evolutionarily stable if, for any T, either $E(S, S) > E(T, S)$ or $[E(S, S) = E(T, S) \text{ and } E(S, T) > E(T, T)]$, where $E(A, B)$ is the pay-off of playing a strategy A against a strategy B. The central consequence of this definition is that, if sufficiently many individuals in a population play an evolutionarily stable strategy and pay-offs represent evolutionary fitness, no mutant strategy can successfully invade the population.

Just as the concept of Nash equilibrium is only one of many equilibrium concepts proposed in the social sciences, there are a number of different approaches to defining evolutionary stability, some of which explicitly

model the dynamics of evolutionary replications (for a survey of evolutionary game theory, see Alexander 2003). Particularly relevant to group decision making is the extension of the concept of evolutionarily stable strategies to multi-player games (Blackwell 1997; Van Doorn *et al.* 2003; Bukowski & Miekisz 2004; Kaminski *et al.* 2005; Platkowski & Stachowska-Pietka 2005; Bach *et al.* 2006; Conradt & Roper 2007, 2009; Skyrms 2009).

(d) *Global overview versus self-organization*

In many groups, at least some members can gain a global overview of the decision-relevant actions of all other group members (see table 1 for examples in the social and natural sciences). When there is a global overview, group decisions could, at least in principle, be reached by general negotiations among all members and explicit voting (e.g. Austen-Smith & Feddersen 2009; Hix *et al.* 2009; for a brief review in animals, see also Conradt & Roper 2003), or by central orders or coercion (Gavre 1977; Clutton-Brock *et al.* 1982; King *et al.* 2008; Lusseau & Conradt *in press*). In modern human societies, owing to the sophisticated means of mass communication, many group decisions fall into the category in which a global overview is at least in principle possible (table 1). In animals, only relatively small groups can normally make group decisions based on a global overview. For such groups, voting has been reported in several mammal and bird species (e.g. Prins 1996; for a review, see also Conradt & Roper 2005), and dictatorial or coerced decisions in others (Clutton-Brock *et al.* 1982; King *et al.* 2008). Animals employ special postures, vocalizations and/or movements to cast their votes (for a brief review, see Conradt & Roper 2003).

Sometimes groups are so large that no group members can have a global overview of the entire group. In such cases, individual group members can only react to local information and communication, and group decisions are made in a self-organizing manner. That is, all group members follow their own local behavioural rules, which rely on local information (which can be continuously updated), local communication and local reaction to neighbouring group members’ actions. The overall result is a global group behaviour that is not centrally orchestrated, but ‘self-organized’ (Camazine *et al.* 2003; Couzin & Krause 2003; Amé *et al.* 2006; Sumpter 2006; Couzin 2007; Hemelrijk & Hildenbrandt 2008; Sumpter & Pratt 2009). A good example is given by the movements of large flocks of starlings (*Sturnus vulgaris*; Ballerini *et al.* 2008). In flying starling flocks, first of all, each individual starling avoids collision with direct (local) neighbours by keeping a minimum distance to them. At the same time, because group cohesion is advantageous for social animals (Krause & Ruxton 2002), each starling does not want to get too far away from the rest of the group. Thus, when the distance to its direct neighbours gets too large, it moves towards those neighbours and aligns its direction of movement with them. Finally, each starling avoids any physical obstacles it encounters, and especially predators. The overall result is the fascinatingly synchronized and well-coordinated movement of starling flocks that we observe

in nature, and which does not require anybody ‘in command’ (Selous 1931). Self-organization also occurs in humans (e.g. in the movements of pedestrians, traffic or panicking/escaping crowds, or even markets; table 1). However, we do not usually think of such cases as ‘group decisions’, mainly because social cohesion (and, thus, the need for consensus) is not generally their aim.

At first sight, self-organization seems to prohibit decisions by general negotiation or voting (but see Prins 1996; Seeley & Buhrman 1999), or by central orders or coercion. Therefore, most natural scientists studying self-organized group decisions do not ask questions such as ‘which group members make the decision?’. It is tempting to assume that all group members contribute equally (via similar local behavioural rules) to the overall outcome, rendering a question such as ‘who makes the decision?’ irrelevant. However, as game theorists know, asymmetric equilibria are entirely possible, and recent theoretical work has suggested that non-equal contributions of group members to self-organized group decisions (via dissimilar local behavioural rules) are not only possible, but also likely to evolve under natural conditions. Some group members could use tactics to influence group decision outcomes disproportionately in their own interest, even within relatively large groups (Conradt *et al.* in press). Some participants’ disproportionate influence on self-organized decisions has also been observed in the social sciences. For example, the evacuation pattern of a crowd in an emergency situation could be more influenced by individuals in certain spatial positions within the crowd than by others (Aube & Shield 2004; Dyer *et al.* 2009). Notoriously, some participants in markets, e.g. monopolists, have disproportionate influence when compared with others.

4. FACTORS INFLUENCING GROUP DECISIONS

At least three central factors influence group decisions: (a) information, (b) interests, and (c) side constraints (e.g. time, decision costs, fairness constraints). We address them in turn.

(a) Information

When groups make decisions, the pay-offs (costs and benefits) of the decision outcomes (both for the individuals and for the group as a whole) often depend on some state of the environment; for example, how the weather will develop, which location yields the most food, whether there is a predator, which travel route is optimal. Decisions typically take place under uncertainty, i.e. group members have only incomplete and noisy information about the state of the environment. An individual’s decision-relevant information constitutes the individual’s ‘belief’, and the probability that a belief is correct (i.e. it correctly represents the relevant state of the environment) is its ‘accuracy’ or ‘reliability’. If there exists an unambiguously ‘best’ decision outcome for the group, e.g. an objectively best foraging patch, nest site or economic policy, we further define the accuracy or reliability of the group decision as the probability that the best outcome is selected.

In decisions under uncertainty, the way in which information is aggregated across group members can greatly influence the decision pay-offs or accuracy (Seeley & Buhrman 1999; Conradt & Roper 2003; List 2004; Simons 2004; Couzin *et al.* 2005; Amé *et al.* 2006; Biro *et al.* 2006; Passino & Seeley 2006; Codling *et al.* 2007; Lusseau 2007; Ward *et al.* 2008; Dyer *et al.* 2009; Franks *et al.* 2009; List *et al.* 2009; Skyrms 2009; Sumpter & Pratt 2009). To illustrate this, let us focus on cases in which the group makes an aggregate/consensus decision and there exists an unambiguously best outcome, i.e. any ‘disagreements’ between group members are informational: they may have different beliefs, but no conflicts of interest (we discuss such conflicts in §4b). The most classic result on the effects of the aggregation rule on decision accuracy is ‘Condorcet’s jury theorem’ (e.g. Grofman *et al.* 1983; List & Goodin 2001; List 2004), which can be summarized as follows. Suppose a group has to make a choice between two options. Each individual has some independent information about which option is better (the ‘independence’ condition), and each individual’s information is correct with an equal probability greater than 1/2 but below 1 (the ‘competence’ condition). Assuming that such independent and equally competent individuals vote according to their own information, Condorcet’s jury theorem states that the probability that majority voting yields the correct outcome (i) is greater than the probability that each group member is individually correct, and (ii) converges to 1 (certainty) as the group size increases (see box 3 for a numerical example). This result is a consequence of the law of large numbers.

Condorcet’s jury theorem suggests that shared decisions are better than unshared ones. The more the group members participate in a group decision, the more accurate the outcome is likely to be. However, it is not invariably the case that giving all individuals equal weight in the decision always leads to the most accurate outcome. In particular, if the quality of information—the individual accuracy or reliability—differs between group members, an unequal distribution of voting weights can lead to more accurate decisions, where the weights are assigned as a function of individual accuracy (see box 3 for an example and a general result; Ben-Yashar & Nitzan 1997). This could explain why in many animal groups adults or more experienced group members are the main decision makers (Poole *et al.* 1988; Stewart & Harcourt 1994; Prins 1996; Conradt & Roper 2003).

An unequal distribution of weights is not the only deviation from majority voting which can improve the group’s overall decision accuracy. The size of the decision threshold also matters. If one option has a greater prior probability of being best than any other option, then, other things being equal, a suitable sub-majority threshold for the high-probability option results in the most accurate decision outcome (box 3).

Moreover, the costs and benefits that result from a decision depend not only on the decision accuracy, which was defined as the probability that the best option is selected, but also on the costs of different types of error. The costs of not choosing one particular

Box 3. Informational differences between group members.

1. Unshared decisions versus equally shared decisions

Assume that a group of five animals has to decide between two foraging patches A and B. Each group member has a probability of 0.75 of choosing the better foraging patch individually. If the group employs a dictatorial (unshared) aggregation rule, with the dominant member making the decision, the group has a chance of 0.75 of correctly choosing the better foraging patch (which is the probability that the dominant individual makes a correct decision). On the other hand, if members share the decision equally and use majority voting as their aggregation rule, the group will choose the better patch correctly as long as at least three group members 'vote correctly'. That is, the group chooses the better patch with a probability of

$$\sum_{i=3}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} \approx 0.90,$$

which is a 15 per cent increase in accuracy.

2. Difference in information between group members

Assume that the dominant individual is most experienced and can determine the better foraging patch correctly with a probability of 0.75, while the other four members can do so only with a probability of 0.6. A majority decision would lead to the better patch if at least three group members voted for the better patch. That is, with a probability of

$$0.75 \cdot \sum_{i=2}^4 \binom{4}{i} 0.6^i \cdot 0.4^{4-i} + 0.25 \cdot \sum_{i=3}^4 \binom{4}{i} 0.6^i \cdot 0.4^{4-i} \approx 0.73,$$

the group chooses the better patch. This is a lower accuracy than that of 0.75 for the unshared decision by the dominant individual alone. In such a case, instead of sharing the decision equally, it would be beneficial for the animals to give the more knowledgeable individual more weight in the decision. Assume, for example, the dominant individual is given three times the voting weight of the others. The group would then choose the better foraging patch correctly if either the dominant individual and at least one other individual voted correctly (resulting in at least 4 : 3 weighted votes for the correct patch) or if the dominant individual voted incorrectly but all others voted correctly. The unequally shared decision outcome would have an accuracy of

$$0.75 \cdot \sum_{i=1}^4 \binom{4}{i} 0.6^i \cdot 0.4^{4-i} + 0.25 \cdot \sum_{i=4}^4 \binom{4}{i} 0.6^i \cdot 0.4^{4-i} \approx 0.76,$$

which is better than that of an unshared or an equally shared decision. More generally, assuming differentially reliable group members but an equal prior probability and equal benefits of each foraging patch being best, the optimal aggregation rule is a weighted majority rule where each individual's weight is proportional to $\log(p/(1-p))$, with p being the individual's reliability (e.g. [Grofman et al. 1983](#)). The fully general result ([Ben-Yashar & Nitzan 1997](#)) is discussed below.

3. Influence of the decision threshold on decision accuracy

(a) Skewed likelihood of a particular option to be the 'best'

Assume that foraging patch A has a probability of 0.9 of being better than patch B, and that all five group members have a probability of 0.75 of detecting the better patch correctly. The accuracy of an equally shared decision depends on the size of the decision threshold. Suppose that at least two members are required to vote in favour of patch A in order for the group to choose patch A (i.e. the threshold is a sub-majority of two in favour of A). Then, the group will choose the better patch correctly if either patch A is the better patch and at least two members vote correctly, or if patch B is the better patch and at least four members vote correctly. That is, the expected accuracy of an equally shared group decision with a sub-majority threshold of two for patch A is

$$0.9 \cdot \sum_{i=2}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} + 0.1 \cdot \sum_{i=4}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} \approx 0.95.$$

The respective accuracy for a (simple) majority threshold is 0.90 (as above in subsection 1). Finally, if there is a super-majority threshold for A (e.g. at least four members are required to vote in favour of patch A for the group to choose patch A), the expected accuracy of the group decision outcome will be

$$0.9 \cdot \sum_{i=4}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} + 0.1 \cdot \sum_{i=2}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} \approx 0.67.$$

(Continued.)

Box 3. (Continued.)

Thus, the most accurate decision here is a shared group decision with a sub-majority threshold in favour of the foraging patch that is more likely to be the better patch.

(b) Benefits are also skewed

Assume that we still have the same situation as under (a), but now patch A and patch B yield different benefits when they are the ‘best’ yielding patch, respectively. Assume that when patch B is best, it yields 50 times as much as patch A yields when it is best. The expected benefits of an equally shared group decision with a sub-majority threshold of two for patch A are

$$0.9 \cdot 1 \cdot \sum_{i=2}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} + 0.1 \cdot 50 \cdot \sum_{i=4}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} \approx 4.1.$$

The expected benefits with a majority threshold are

$$0.9 \cdot 1 \cdot \sum_{i=3}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} + 0.1 \cdot 50 \cdot \sum_{i=3}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} \approx 5.3.$$

The expected benefits with a super-majority threshold of four for patch A are:

$$0.9 \cdot 1 \cdot \sum_{i=4}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} + 0.1 \cdot 50 \cdot \sum_{i=2}^5 \binom{5}{i} 0.75^i \cdot 0.25^{5-i} \approx 5.5.$$

Here, the threshold that yields the most benefits is a super-majority threshold for patch A (i.e. a sub-majority threshold for patch B).

(c) The fully general result

Consider a choice between two options, A and B, without any conflict of interests. Suppose that r is the prior probability of option A being better and each individual i in an n -member group has an individual accuracy p_i of identifying the better option. There are four possible scenarios: (i) option A is better and is chosen, (ii) option A is better and is not chosen, (iii) option B is better and is chosen, and (iv) option B is better and is not chosen. Let us write u_+ for the pay-off difference between (i) and (ii), and u_- for the pay-off difference between (iii) and (iv). The general result (Ben-Yashar & Nitzan 1997) states that the expected pay-off is maximized by a weighted generalized majority rule of the form

$$f(v_1, \dots, v_n) = \text{sign}(w_1 v_1 + \dots + w_n v_n + m),$$

where

- for each i , individual i 's weight w_i is proportional to $\log(p_i/(1-p_i))$ and
- the decision margin m is the sum of two parameters:
 - the base-rate bias, $\log(r/(1-r))$, and
 - the pay-off-asymmetry bias, $\log(u_+/u_-)$.

It is easy to see that this rule becomes super-majoritarian for B (i.e. a super-majority is required for a decision in favour of B) if option A has a higher prior probability than option B or the cost of erroneously deciding against A is higher than the cost of erroneously deciding against B. In the opposite case, it becomes super-majoritarian for

option when it is best need not be the same as the costs of not choosing another when that option is the best. Asymmetries in the costs of different errors can even make a decision threshold optimal that fails to maximize overall decision accuracy. For example, one decision option might rarely be the best option, but when it is the best, it might yield much higher benefits than alternative options. In such a case, a sub-majority threshold for the low-probability option could result in the highest expected benefits, despite the fact that a super-majority threshold would maximize overall decision accuracy (box 3). A good animal example is given by group decisions about fleeing or not fleeing

from a potential predator. Fleeing is only the best option if there really is a predator, which might be less likely than there being none. However, if there is a predator and fleeing is best, then the potential costs of not fleeing are extremely high (e.g. losing one's life). On the other hand, if not fleeing is the best option (because there is no predator), the potential costs of fleeing nonetheless (e.g. to miss the opportunity of some additional foraging) are relatively modest in comparison. In such cases, theory predicts that a shared group decision with a sub-majority threshold for fleeing is optimal (box 3; Ben-Yashar & Nitzan 1997; List 2004). Indeed, this is what we usually observe in nature: a relatively small number of group

members (i.e. a sub-majority) can trigger the flight of a whole group (e.g. Krause & Ruxton 2002; Lingle & Pellis 2002; Boland 2003; Stankowich & Blumstein 2005; Carter *et al.* 2008). A social science example is given by decisions about constitutional changes. Owing to the central importance of a state's constitution, changing it involves great risks and thus much higher potential costs (i.e. negative benefits) than keeping the *status quo*. In recognition of this, as we have already noted, constitutional changes often require a super-majority of two-thirds or more of legislators, rather than just a simple majority (e.g. Grundgesetz der Bundesrepublik Deutschland 1949). Similarly, in criminal trials, juries are usually required to make decisions by super-majority rules, which implement a presumption of innocence, because it is considered to be far more costly in moral terms to convict the innocent than to acquit the guilty. The idea is captured by the famous principle, in the words of the English legal scholar Blackstone (1765–1769), that it is ‘better that ten guilty persons escape than that one innocent suffer’.

The standard results building on Condorcet's jury theorem are based on the assumption that the votes or information of different decision makers are independent. Crucially, the filtering of errors that is ensured by the pooling of a large number of signals requires that errors are uncorrelated. In the limiting case in which different individuals' votes, and thereby their errors, are perfectly correlated with each other, aggregation yields no gains in accuracy. The benefits of information pooling in the presence of less extreme interdependencies depend on the nature of these interdependencies (Boland 1989; Ladha 1992; Dietrich & List 2004; Berend & Sapir 2007). Among the kinds of interdependencies that can significantly compromise decision accuracy are ‘informational cascades’, in which a plurality or majority that accidentally emerges in support of some option is mistakenly interpreted by others as evidence for the optimality of that option and thereby attracts further support, although few or any individuals originally had any information in support of that option (e.g. Bikhchandani *et al.* 1992). Market bubbles or instances of groupthink in committees are phenomena of this kind in human contexts (e.g. Sunstein 2006), and they could, in principle, also occur in animals (Giraldeau *et al.* 2002; Dugatkin 2005; List *et al.* 2009; Sumpter & Pratt 2009), and sometimes do so in practice (Seeley & Buhrman 2001; Dyer 2008; Ward *et al.* 2008).

In summary, it is obvious that the problem of pooling dispersed information across a group of individuals is a complex one, and so far we have even ignored an important additional complicating factor, namely the influence of conflicts of interests between group members. We now turn to this issue.

(b) *Interests*

The pay-offs of a decision outcome for a group of individuals obviously depend on whether the outcome promotes, or is at least consistent with, the members' interests. In §4a, we have made the simplifying assumption that all group members share the same interests. In many cases, this assumption is warranted: all group members want to prevent decision-induced

disasters, find good foraging sites or avoid predators, for instance. However, there are also frequent cases in which the members' interests come apart. What is good for one individual may be bad for another. Consider, for example, different configurations of market prices: some favour consumers and others producers; or different tax laws or redistributive policies: some are better for big companies and others for low-income individuals. In social animals, group members of different size, sex, age or physiological state are likely to have different requirements, which often lead to different interests. For example, larger individuals may favour longer activity durations than smaller individuals (e.g. Clutton-Brock *et al.* 1982; Conrard 1998; Ruckstuhl 1998, 1999), females with vulnerable dependent offspring may favour safer sites than males (Ruckstuhl & Neuhaus 2000, 2002), older or larger individuals may favour sites with different forage than younger or smaller individuals (Clutton-Brock *et al.* 1982; Gompper 1996; Prins 1996), non-starving individuals may favour less exposed sites than starving individuals (e.g. Krause *et al.* 1992; Rands *et al.* 2003), and so on (for the most recent review, see Conrard & Roper 2005). When pay-offs are not only different across individuals but lead to different relative rankings of decision options, we speak of ‘conflicting interests’. Social scientists also describe the ranking of decision options from an individual's perspective as this individual's ‘preference’ over options.

Assuming a conflict of interests within a group, it is obvious that the way in which different individuals' interests or preferences are aggregated can make a great difference to the group's overall pay-offs, and also to the individual pay-offs received by each group member. Social choice theory has studied the aggregation of conflicting interests or preferences in great depth, beginning with Arrow's (1951/1963) seminal work. While Arrow's classic theorem, as we have already mentioned, uncovers some of the difficulties of aggregation in decisions between more than two options, we can say something positive about majority voting in two-option choices. Just as majority voting is good at pooling dispersed information in such choices, so it also has some appealing properties with regard to the aggregation of conflicting interests or preferences (see box 4 for more details). Suppose that some group members prefer option A to option B, while others have the reverse preference. It is easy to see that majority voting, uniquely among aggregation rules, maximizes the number of group members whose preference is respected. Indeed, this property can be seen as a defining characteristic of majority voting. Furthermore, if we assume that each individual receives a pay-off of 1 from having his or her preference respected and a pay-off of -1 otherwise, then majority voting maximizes the sum total of pay-offs across the group (this is the key insight underlying a theorem by Rae 1969 and Taylor 1969).

However, in many real-world cases, different group members have different ‘stakes’ in a decision. Formally, an individual's ‘stake’ in a decision between two options is defined as the pay-off difference between the better option from the individual's perspective and the worse one (in the natural sciences, this is also called the

Box 4. Interest differences between group members.

Suppose, as before, that a group of n individuals has to choose between two options, A and B. Suppose that each individual i receives pay-offs of $u_i(\text{A})$ and $u_i(\text{B})$ from options A and B, respectively. Assume that when a vote is taken between A and B, each individual votes for the option with the higher pay-off, i.e. each individual i 's vote is

$$v_i = \begin{cases} +1 \text{ (a vote for A),} & \text{if } u_i(\text{A}) > u_i(\text{B}), \\ 0 \text{ (an abstention),} & \text{if } u_i(\text{A}) = u_i(\text{B}), \\ -1 \text{ (a vote for B),} & \text{if } u_i(\text{A}) < u_i(\text{B}). \end{cases}$$

Recall that if each individual i gets a voting weight of w_i , the outcome of a weighted (simple) majority vote is

$$f(v_1, \dots, v_n) = \text{sign}(w_1 v_1 + \dots + w_n v_n).$$

Note that option A yields a higher sum total pay-off than option B if and only if

$$u_1(\text{A}) + u_2(\text{A}) + \dots + u_n(\text{A}) > u_1(\text{B}) + u_2(\text{B}) + \dots + u_n(\text{B}),$$

i.e. if and only if

$$(u_1(\text{A}) - u_1(\text{B})) + (u_2(\text{A}) - u_2(\text{B})) + \dots + (u_n(\text{A}) - u_n(\text{B})) > 0,$$

which, in turn, is equivalent to

$$s_1 \times v_1 + s_2 \times v_2 + \dots + s_n \times v_n > 0,$$

where, for each i , s_i is individual i 's 'stake' $s_i = |u_i(\text{A}) - u_i(\text{B})|$, with $|x|$ defined as the absolute value of x . Similarly, option B yields a higher sum total pay-off than option A if and only if the reverse inequalities hold. Rewriting this observation in slightly more general terms, we obtain

$$\text{sign}(s_1 \times v_1 + s_2 \times v_2 + \dots + s_n \times v_n) = \begin{cases} +1, & \text{if } u_1(\text{A}) + u_2(\text{A}) + \dots + u_n(\text{A}) > u_1(\text{B}) + u_2(\text{B}) + \dots + u_n(\text{B}), \\ 0, & \text{if } u_1(\text{A}) + u_2(\text{A}) + \dots + u_n(\text{A}) = u_1(\text{B}) + u_2(\text{B}) + \dots + u_n(\text{B}), \\ -1, & \text{if } u_1(\text{A}) + u_2(\text{A}) + \dots + u_n(\text{A}) < u_1(\text{B}) + u_2(\text{B}) + \dots + u_n(\text{B}). \end{cases}$$

From this, we can immediately infer that weighted majority rule produces as its winner the option that maximizes the sum total pay-off, provided that each individual i 's voting weight w_i is proportional to his or her stake s_i (Fleurbaey 2008).

individual's 'potential consensus cost'). For example, a civil servant with a high level of job security has a lower stake in a decision about unemployment benefits than someone on a short-term contract; a resident of Central London has a higher stake in a decision about inner-city congestion charging than an infrequent visitor to the city. In animals, for example, starving or hungrier individuals might have higher stakes in foraging decisions than do well-fed ones (e.g. Prins 1996; Rands *et al.* 2003; Conrads *et al.* in press); small, vulnerable individuals have higher stakes in decisions about predator avoidance than do large, less vulnerable ones (e.g. Ruckstuhl & Neuhaus 2000, 2002; Lingle & Pellis 2002).

Generalizing the earlier result about majority voting, one can show that when different individuals have different stakes in a decision, and the decision is between two options, a weighted majority rule with weights assigned to the individuals in proportion to their stakes maximizes the sum total of pay-offs across the group (Fleurbaey 2008). In decisions between more than two options, the picture is more complicated, but it is widely agreed among social choice theorists that successful preference or interest aggregation with respect to certain social optimality criteria in such cases requires taking into account the individuals'

decision stakes or something equivalent. We briefly return to these issues towards the end of the paper.

However, while maximizing the sum total of pay-offs across the group is sometimes an explicitly intended outcome in a human context, it is of less direct relevance to the natural sciences (e.g. Conrads & Roper 2007; see also §6c). Animals do not ordinarily have an incentive to try to maximize the pay-offs for the group as a whole (Smith 1964, 1976, 1998). Rather, each individual is likely to try to maximize its own pay-offs, possibly at the expense of other group members. Nevertheless, it is not unlikely that constraints on each individual group member often act in such a manner that the decision outcome takes individual stakes into account, and might even approach the outcome that gives the maximal group pay-offs (Conrads & Roper 2003; Rands *et al.* 2003; Conrads *et al.* in press). The reason is that in many aggregate/consensus decisions by social animals, one aspect that is likely to be important to all group members is to maintain group cohesion (Krause & Ruxton 2002). As a consequence, individuals have to trade-off, on the one hand, influencing a decision outcome assertively in their own interest and thereby risking group fragmentation against, on the other hand, maintaining group cohesion by being less assertive (e.g. Conrads 1998; Couzin *et al.* 2005).

The likely result is that those individuals whose stakes are higher will be more assertive than those whose stakes are lower, so that the former have more influence on the decision outcome than the latter (Conradt *et al. in press*). There is empirical evidence which supports this argument (e.g. Krause *et al. 1992*). However, the rationale also implies that those individuals within a group for which group cohesion is least important (as opposed to those for which the stakes are highest) might gain the most weight in a group decision (Conradt *et al. in press*). Again, there is empirical evidence that this can occur (Prins 1996).

So far, we have discussed information aggregation in the case of no conflict of interests, and interest aggregation without considering the possibility of unreliability of information. Under natural conditions, of course, there may be both, unreliability of information and conflicts of interest, at the same time. Thus, the most difficult question remains: what happens when group members differ in their quality of information and have differing interests? While this is a frequently discussed scenario in the social sciences (e.g. Austen-Smith & Feddersen 2009), there has been very little natural-scientific work done in this direction. Couzin *et al. (2005)* suggest that if the numbers of individuals within a group which prefer either of two options are fairly balanced, the differences in information reliability can topple the decision in favour of the better informed individuals. Intuitively, when stakes are relatively low and information unreliable, information should be the dominant factor influencing group decisions. For example, it might be better to follow others reliably to a slightly less optimal foraging patch than to seek, but not to find, a more optimal patch. Similarly, if stakes are high and information relatively reliable, interests might be expected to be the dominant factor. However, it is less clear what will happen in situations in which either (i) stakes are high and information is unreliable, or (ii) stakes are low and information is relatively reliable. There is much scope for further research into these questions.

(c) *Side constraints*

Group decisions are often subject to important side constraints such as time constraints (e.g. Passino & Seeley 2006; Franks *et al. 2009*; Sumpter & Pratt 2009), decision costs, computational limitations (e.g. Gigerenzer & Selten 2002) and fairness constraints (e.g. Brosnan & de Waal 2003; Brosnan *et al. 2005*; Dawes *et al. 2007*; Fehr *et al. 2008*). Although a fully optimal solution to a given decision problem may exist in theory, it can often be difficult or costly in practice to find it. First, owing to search costs or time constraints, not all theoretically possible decision options can be considered by the decision makers. Instead, the decision makers may be restricted to the consideration of some practically salient or easily identifiable ones (e.g. Seeley & Buhrman 2001; Franks *et al. 2009*). Second, owing to time constraints or other computational limitations, the full calculation to solve a particular optimization problem may often be infeasible, and certain shortcuts, which may lead to less optimal decisions, may have to be taken in practice (e.g. Gigerenzer & Selten 2002; consider also quorum

responses in animals; for the most recent review, see Sumpter & Pratt 2009). Third, considerations of fairness, legitimacy or preservation of future good relations (Brosnan & de Waal 2003; Brosnan *et al. 2005*) may rule out certain decision-making arrangements that might be optimal from the perspective of accuracy or benefit maximization alone. For instance, in many democratic settings, weighted majority rules—even if they might occasionally be accuracy maximizing—are considered democratically unacceptable as well as potentially open to abuse due to the inbuilt power asymmetries. Similarly, considerations such as respect for certain rights may trump the maximization of accuracy or benefits alone.

5. PRESENT ISSUE

(a) *Sharing information*

The first contribution to this issue, by Sumpter & Pratt (2009), gives a concise and comprehensive review of the empirical and theoretical literature on quorum responses in animal group decision making. In many social animals, quorum responses are a likely and plausible mechanism of reaching aggregate/consensus decisions, which can ultimately be interpreted in terms of social science's aggregation rules, but do not require complex cognitive abilities. In addition to the review, the authors present an elegant and effective model of how animals could optimize decision accuracy (in the form of information sharing) or decision speed, or solve the trade-off between speed and accuracy, by adjusting simple parameters in their quorum response.

As we have noted, Condorcet's jury theorem requires the independence of individual judgements. On the other hand, without any interdependencies between individuals, real-world groups may often find it difficult to reach a consensus. This raises some important questions about how independence and interdependence interact in determining aggregate/consensus decision outcomes and their accuracy. In response to these questions, the contribution by List *et al. (2009)* brings together social- and natural-scientific insights by applying a social-choice-theoretic model to an animal system: swarming honeybees choosing a new nest site. The authors show that both a sufficient degree of independence and a sufficient degree of interdependence between individual bees are needed to predict the high accuracy of nest-site choice observed empirically. Specifically, bees have to be relatively independent in assessing the quality of prospective nest sites once they visit them, while they also have to be relatively interdependent in signalling to each other which sites are worth inspecting. The interplay between independence and interdependence allows the bees to reach a consensus with high accuracy within a realistic time frame. List *et al.'s (2009)* model can be seen as complementary to the quorum response model by Sumpter & Pratt (2009), the crucial parameters of which could also be interpreted in terms of 'independence' and 'interdependence'.

Austen-Smith & Feddersen (2009) examine individual deliberation and voting strategies underlying aggregate/consensus decisions in small groups of

humans. The authors illustrate that, surprisingly, informative voting—truthfully revealing private information—need not be individually rational even when all group members share the same interests (the case of ‘common values’). On the other hand, strategic voting can lead to suboptimal decision outcomes. When there are no conflicts of interests, such problems can be overcome by communicating private information prior to voting. Moreover, the incentives for informativeness depend on the voting rule used. However, when individuals can differ not only in their information but also in their interests, these positive results break down. The authors point out that, even when there is only a small degree of uncertainty about whether or not group members share common values, there may not exist a voting rule that leads all individuals to vote informatively, and individuals may also have incentives not to reveal their private information truthfully in deliberation prior to voting. The authors give some illuminating insights into the complexity that human strategic considerations add to the more straightforward processes of information sharing described by List *et al.* (2009) and Sumpter & Pratt (2009). They also show how group decision making is greatly complicated when there are informational and interest differences between group members.

As illustrated by the first three contributions to this issue, coordinated action requires the transmission and processing of information among group members. Information transmission in groups usually involves signalling between multiple senders and receivers. As discussed in Skyrms’ (2009) contribution, this can be modelled in terms of ‘sender–receiver games’, in which senders observe certain states of the world, transmit particular signals—which may or may not accurately convey their information—and elicit resulting acts in the receivers. Sender–receiver games can have multiple Nash equilibria, but the only evolutionarily stable ones are so-called ‘signalling systems’, in which information transmission is accurate. Despite their evolutionary stability, Skyrms reports that, surprisingly, signalling systems need not generally evolve. Other equilibria, which are not evolutionarily stable as defined by Maynard Smith & Price (1973), can still be ‘dynamically stable’ in a sense defined in the paper, and Skyrms discusses the properties of such equilibria. With respect to group decision making, this implies that suboptimal information transmission in animal groups can, in principle, persist over evolutionary time scales, even when the aim of information sharing is not hampered by conflicts of interest between senders and receivers.

Although signalling systems might not be guaranteed to evolve, Dyer *et al.* (2009) show that decision-relevant information can nevertheless be shared efficiently within groups and without having to employ any intentional signalling at all. The authors review theoretical and empirical studies on leadership in social animals and humans. They report that, in self-organizing groups, a relatively small minority of informed group members can already lead a large majority of uninformed members in a preferred direction with high accuracy. This can happen without any intentional signalling by the informed members, and when the informed members are not even identifiable to uninformed

members. As in the models by List *et al.* (2009) and Sumpter & Pratt (2009), the balance between independence and interdependence plays a significant role here. Individual group members are attracted towards, and align with, neighbouring group members within a local interaction range in order to maintain social cohesion (interdependence). Additionally, informed members balance this interdependence of social attraction against moving in the direction of a known resource (independence). If interdependence is too low, the group splits. If independence is too low, the group does not move efficiently towards the resource.

(b) *Resolving conflicts*

Often groups have to make decisions in situations with considerable conflicts of interests between members with respect to the optimal decision outcome. Resolving such conflicts requires cooperation. Gächter & Herrmann (2009) investigate the basis of cooperative behaviour in humans in ‘common goods’ experiments, in which the best interest of the individual is different from the best interest of other group members. Direct and indirect reciprocity, and peer punishment, are the most important determinants of successful cooperation in such situations. However, a large number of individuals cooperate (or punish free riders) altruistically even when there is no opportunity for either direct or indirect reciprocity. Culture has a strong influence on such behaviour. Surprisingly, the authors also find that antisocial punishment, where cooperators rather than free riders are punished, is much more widespread than previously assumed. Understanding antisocial punishment is an important task for future research, because antisocial punishment is a strong inhibitor of cooperation.

Conflicts can be resolved, for example, by sharing decisions equally between members. Conradt & Roper (2009) explore which conditions favour the evolution of equally shared decisions. Interestingly, these conditions depend crucially on whether the modality about which the group decides is ‘continuous’ or ‘disjunct’. A continuous modality is, for example, *timing of communal activities* if the mean of all the timings preferred by individual group members could constitute a sensible compromise. On the other hand, an example for a disjunct modality is *communal spatial destination* if the mean of all preferred destinations (e.g. the space in the middle between two foraging patches) is not a sensible compromise. In decisions on continuous modalities, the higher the potential consensus costs are, the more likely it is that an equally shared decision evolves. By contrast, in decisions on disjunct modalities, the higher the potential consensus costs are, the more likely it is that an unshared decision evolves, or a decision that is only shared between certain like-minded group members.

In humans, important decisions are often about disjunct modalities, and potential consensus costs can be high. As Conradt & Roper’s (2009) work suggests, in such cases, it could be important for like-minded individuals to try to form an alliance to influence decision outcomes in their joint interest. Hix *et al.* (2009) investigate alliance formation in the European Parliament. Although cohesion is neither enforced, nor

directly rewarded or punished, group association to cross-national ‘political groups’ with similar political views can explain 90 per cent of an MEP’s voting behaviour (by contrast, nationality only explains 10%). Reasons for forming such voluntary alliances are division of labour (e.g. with respect to information gathering), reciprocal altruism and voting cooperation within political groups. Cohesive voting within alliances is also maintained by the possibility of punishment of individuals through the prospect of withholding future influential positions within the alliance. These observations are in good agreement with Gächter & Herrmann’s (2009) results about the basis of cooperation in humans. However, Hix *et al.* (2009) also report that political group association can break down when there is a chance that a vote is pivotal and there are strong national interests at stake. The authors further illustrate the power that is conveyed by setting the agenda: which issues are put up for a vote, and how this is done, can significantly influence decision outcomes and policies. Again, cooperation within alliances with respect to agenda setting can offer great advantages to individual MEPs.

In parliamentary and electoral decisions, there are often more than two alternatives. While many countries and other political units use plurality rule as their electoral method—under which each voter casts a vote for only one option—many legislatures decompose many-option choices into multiple pairwise choices. For instance, a parliament that ultimately seeks to decide between the *status quo*, a particular policy proposal and an amended version of that proposal may first take a pairwise vote between the original proposal and its amended version, and next between the winner of that first vote and the *status quo*. As noted earlier, Condorcet’s classic paradox highlights the possibility that majority voting over multiple pairs of options may produce cyclical majority preferences, meaning, for instance, that an amended proposal may be majority preferred to the original proposal, the original proposal to the *status quo* and the *status quo*, in turn, to the amended proposal. In such cases, there exists no stable majority winner, and the decision outcome may arbitrarily depend on the order in which pairwise votes are taken. Although a large body of work in social choice theory suggests that this phenomenon should be ubiquitous (e.g. Gehrlein 1983), there is strikingly little empirical evidence for it. Regenwetter *et al.* (2009) survey some recent developments in behavioural social choice theory that seek to account for the discrepancy between the standard theoretical predictions and the lack of empirical support for them. In particular, they show that the predicted ubiquity of majority cycles is based on some statistical assumptions about the distribution of voter preferences (so-called ‘cultures of indifference’) that are not empirically supported. Once the theory is revised by taking into account the kinds of preference distributions that we find in many real-world political settings, its new prediction is that majority cycles should be much less frequent than commonly assumed. The authors discuss a number of implications of this finding and consider the application of their insights about aggregation paradoxes to other, non-voting settings in which

researchers construct summary statistics of individual preferences (e.g. psychologists aggregating the responses given by several experimental participants to preference questions).

(c) *Respecting side constraints*

While the pooling of information and the resolution of conflicts play important roles in group decision making, we have also pointed out that group decisions are often subject to important side constraints, such as time, costs, computational and fairness constraints. Several of the issue’s contributions either implicitly or explicitly discuss such constraints. As already noted, Sumpter & Pratt (2009) address some of the trade-offs between speed and accuracy in group decisions, and List *et al.* (2009) suggest that the interplay between independence and interdependence is one of the factors contributing to solving such a trade-off. Fairness constraints feature in Gächter & Herrmann’s (2009) analysis of human cooperative behaviour in common goods experiments, and at least implicitly in Hix *et al.*’s (2009) discussion of some of the properties of political alliances.

The paper by Franks *et al.* (2009) puts its central focus on temporal side constraints on decisions. In the case of emergencies, urgency constrains the time available for group decision making: groups may have to make quick decisions, often at the expense of decision accuracy. Franks *et al.* describe an empirical example of the speed–accuracy trade-off in nest-site choices by emigrating ants. The authors highlight the different stages at which such group decisions can be sped up and traded against accuracy, and the role played by the ants’ quorum response mechanism. An important side constraint in the ants’ decision making is the number of active scouts available at each stage of the process, not only during the decision making itself, but also during the implementation of its outcome. Since high scout numbers at one stage can lead to a low availability of scouts at another stage, recruiting scouts optimally to different stages is crucial in order to avoid decisions that are neither accurate nor fast.

6. DIFFERENCES BETWEEN HUMAN AND NON-HUMAN GROUP DECISIONS

So far, we have emphasized concepts for the analysis of group decisions and factors influencing such decisions, which are common to humans and non-humans. In conclusion, it is also worth looking at some of the differences between human and non-human group decisions. We focus on three central areas in which such differences arise: first, the kind of ‘rationality’ at work; second, the role of language, which affects both the sort of communication that can take place prior to a group decision and the possible content of the decision itself; and third, the kinds of optimality concepts that are relevant for the assessment of group decisions.

(a) *Rationality*

An important difference between the social-scientific and natural-scientific analysis of group decisions lies in the kind of rationality that is attributed to the agents under investigation (humans versus non-humans).

In the social sciences, human individuals are usually modelled as being ‘rational’ in some appropriate sense. On standard game- and decision-theoretic approaches, this means, roughly, that individuals act in such a way as to maximize the utility or pay-offs they expect to attain, in the light of their beliefs about the environment. This makes them very flexible. If they are presented with a new situation and a new pay-off structure, they will adjust their strategies or actions so as to maximize their individual expected utility or pay-offs in the new situation, so long as they have enough information to update their beliefs accordingly. In the recent, more psychologically informed approaches in the areas of behavioural game and decision theory, this picture is somewhat refined. It is acknowledged, in particular, that humans exhibit a number of cognitive constraints, some of which may be traced back to our evolutionary history. Instead of explicitly maximizing expected utility, for example, individuals often use simple rules of thumb (‘heuristics’), which may lead to systematic errors (‘biases’) (e.g. Gigerenzer & Selten 2002). Nonetheless, behavioural game and decision theory retain at least the assumption that humans choose their strategies or actions relatively flexibly—albeit under some psychological constraints—in response to their beliefs and preferences about the environment.

In the natural sciences, by contrast, the way in which rationality comes into play is quite different. While some variant of the standard game- and decision-theoretic understanding of rationality may still be applicable, with further constraints, to animals with relatively sophisticated cognitive systems (e.g. primates, mammals or birds; Dennett 1987), it seems clear that many insects or fishes, for example, cannot be usefully understood in this way. Instead, the notion of rationality is thought to apply at an evolutionary level. Thus, it is no longer the case that individuals themselves make rational choices between different possible strategies, but the selection of strategies takes place through an evolutionary process. In this picture, seemingly rational strategies can be found in individual animals not because these individuals explicitly chose them, but because their ancestors who happened to play these strategies received sufficient fitness benefits.

At the risk of oversimplification, the difference between a social-scientific, non-evolutionary understanding of rationality and a natural-scientific, evolutionary one lies in the place at which the rational choice or selection of strategies is located. In the non-evolutionary picture, it is the individual itself that makes rational choices. In the evolutionary picture, the seemingly rational selection of strategies takes place as a by-product of an evolutionary process. More optimal strategies lead to greater reproductive fitness. Individuals themselves, however, cannot be described as rational choosers.

(b) Language

One of the most significant differences between human and non-human group decisions lies in the role that language can, or cannot, play in such decisions. While humans and non-humans share the capacity both to communicate prior to making a decision and to decide, by ‘voting’ or acting, to bring about a particular outcome, the nature of the communication and

decision in the two cases is very different. In the non-human case, communication takes the form of the exchange of relatively simple signals and the subsequent decision consists in the support for one particular option or in the choice of a concrete behavioural strategy. In the human case, by contrast, the expressive resources of language can make both stages—the ‘communication stage’ and the ‘decision stage’—much more complex.

At the communication stage, language allows humans to exchange not only simple informational signals, but also complex arguments, hypothetical considerations, analogies and anecdotes and entire beliefs systems or theories. The theory of deliberative democracy addresses the ways in which linguistic communication can affect—sometimes positively and at other times adversely—successful group decision making (e.g. Cohen 1989; Gutman & Thompson 1996; Elster 1998; Dryzek & List 2003; Sunstein 2006). In so-called ‘deliberative polling’ experiments, for example, it has been shown that a period of group deliberation among randomly chosen participants, before and after which they are individually interviewed, can significantly change their opinions on political issues. In the best-case scenario, group deliberation not only increases the participants’ factual information, but also makes them more other-regarding and leads them to develop a shared understanding of their decision problem (Luskin *et al.* 2002; Fishkin & Luskin 2005; List *et al.* 2000/2006). Under less benign circumstances, for instance when groups are too homogeneous and share an initial bias towards certain opinions (e.g. pro-war), group deliberation can further reinforce this bias, a phenomenon sometimes described as ‘group polarization’ and related to the phenomenon of informational cascades mentioned earlier (Bikhchandani *et al.* 1992; Sunstein 2002, 2006).

Similarly, at the decision stage, human language allows the expression of much more complex decision ‘contents’ than we find among animals. The goal of a human group decision need not merely be to select one option from a given set of options, but, instead, it can be to generate an explicit ranking of all the options in an order of collective preference (Arrow 1951/1963). In such cases, the decision makers often do not merely cast a ‘vote’ for one option each, but express an entire ranking over options.

The options under consideration can also be extremely complex. Committees, expert panels, multi-member courts and boards of organizations frequently make choices between entire belief systems or theories, with a complex internal structure. The Intergovernmental Panel on Climate Change or the United Nations Development Programme, for example, regularly produce extensive reports on some complex natural or socio-economic phenomena and arrive at these reports through the interaction of a large number of experts. The theory of judgement aggregation seeks to develop a general theoretical framework for modelling how groups of individuals can make consistent collective judgements on several, often logically connected propositions on the basis of the group members’ individual judgements on these propositions (e.g. List & Pettit 2002; for an

introductory survey, see [List in press](#)). Familiar aggregation rules such as majority voting are not generally satisfactory in such cases. For example, assume that a group of city councillors has to decide about three propositions:

p : 'we will have £10 000 left over at the end of the year',

$p \rightarrow q$: 'if we have £10 000 left over at the end of the year, then we should renovate the hospital'

and

q : 'we should renovate the hospital.'

If a third of the councillors believes p , $p \rightarrow q$ and q , a second third believes $p \rightarrow q$, but also *not* p and *not* q , and a final third believes p , but *not* $p \rightarrow q$, and *not* q , then there are majorities for p , for $p \rightarrow q$ and yet also for *not* q , a logically inconsistent set of propositions. An important theoretical challenge is to provide good models of how real-world groups and committees avoid such collective inconsistencies. In conclusion, it should be apparent that the availability of language both enriches and complicates group decision making.

(c) *Optimality concepts*

In the natural sciences, the principle of natural selection automatically introduces optimality concepts (in a metaphor: 'the survival of the fittest') to group decision making (see also §6a). Natural selection is the process by which certain heritable units become relatively more common in successive generations of a population of reproducing organisms due to differential reproduction. However, the kinds of optimality constraints these processes adhere to are very different from those that play a role in human contexts. In the social sciences, moral criteria (e.g. fairness, justice or the achievement of the greatest 'social welfare') play an important part in defining what the 'optimum' is. These moral criteria are, as such, irrelevant to evolutionary concepts.

While natural selection can, in principle, occur on different levels (e.g. genes, individuals, groups), genuine group-level selection (i.e. selection which cannot be explained equally well, or better, on a lower level) is likely to be rare (Smith 1964, 1976, 1998). Maximization of group-level pay-offs is therefore unlikely to be a driving factor in the biological evolution of group decision making. In many human contexts, by contrast, the maximization of group-level pay-offs—or, less crudely, group-level or social 'welfare'—is a desired outcome. One way of achieving this outcome in decisions between two options, as we have seen, is to use weighted majority voting with weights proportional to stakes (at least when group-level welfare is defined as the sum total of individual pay-offs). More generally, a substantial literature in welfare economics and political philosophy addresses the question of how social welfare can be defined and measured (e.g. Arrow 1951/1963; Rawls 1971; Sen 1999).

There are examples of both weighted majority rule and explicit social-welfare-oriented decision-making arrangements in human societies. As already mentioned, weighted majority rule is used in the European Union Council of Ministers, where larger countries, which may have a higher stake in many decisions, have a greater voting weight than smaller countries. Implicit applications of weighted majority rule can also take the form of the inclusion (a weight of 1) or exclusion (a weight of 0) of certain individuals within or from the franchise (Fleurbaey 2008). For example, in most democratic countries, citizens are allowed to vote while visitors and temporary residents are not. Although many criticisms of this arrangement could be raised, one rationale behind it might be that citizens have a higher stake in national decisions than visitors or temporary residents.

An explicit social-welfare-oriented decision-making arrangement might involve a 'social planner'—e.g. a government official or organization—who is instructed to assess the welfare consequence of different policy options for the affected individuals and to make a recommendation as to which policy maximizes overall welfare, according to the appropriate welfare standard (Sen 1999). Often, the implementation of such a recommendation is further expected to be 'incentive compatible', meaning that whenever the policy implementation involves situations of interactive/combined decisions, the intended outcomes should constitute equilibria (see, again, the survey article by the Royal Swedish Academy of Sciences 2007). Finding good solutions to the kinds of decision problems such a social planner is faced with is a significant challenge and an important topic within welfare economics and the theory of mechanism design. However, such a topic is unlikely to find room for exploration in the natural sciences as such. As we have seen, here, there is no human planner consciously seeking to realize a previously defined goal. Instead, the pursuit of some optimum is a by-product of the process of natural selection.

7. CONCLUDING REMARKS

Perhaps the most striking observation that both the social and the natural scientist have made while preparing the present introduction is that, in current work on group decision making, the natural sciences are to some extent 'reinventing the wheel'. Many concepts and mathematical tools that have been available in an advanced and sophisticated form in the social sciences for some time are being rediscovered, sometimes in a slightly different form, by natural scientists. This suggests that communication between the two fields could save natural scientists a considerable amount of time. However, the social-scientific literature on group decisions is so vast that it is difficult for a natural scientist to digest this literature and to see the forest for all the trees. We hope that the present issue will help to open the door.

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REFERENCES

- Alexander, J. M. 2003 Evolutionary game theory. *Stanford encyclopedia of philosophy*. See <http://plato.stanford.edu/entries/game-evolutionary/>.
- Amé, 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)
- Arrow, A. K. 1951/1963 *Social choice and individual values*. New York, NY: Wiley.
- Aube, F. & Shield, R. 2004 Modeling the effect of leadership on crowd flow dynamics. *Cell. Automat. Proc.* **3305**, 601–611.
- Austen-Smith, D. & Banks, J. S. 1999 *Positive political theory I: collective preference*. Ann Arbor, MI: University of Michigan Press.
- Austen-Smith, D. & Banks, J. S. 2005 *Positive political theory II: strategy and structure*. Ann Arbor, MI: University of Michigan Press.
- 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)
- Bach, L. A., Helvik, T. & Christiansen, F. B. 2006 The evolution of n -player cooperation—threshold games and ESS bifurcations. *J. Theor. Biol.* **238**, 426–434.
- Ballerini, M. *et al.* 2008 Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. *Anim. Behav.* **76**, 201–215. (doi:10.1016/j.anbehav.2008.02.004)
- Ben-Yashar, R. & Nitzan, S. 1997 The optimal decision rule for fixed-size committees in dichotomous choice situations: the general result. *Int. Econ. Rev.* **38**, 175–186. (doi:10.2307/2527413)
- Berend, D. & Sapir, L. 2007 Monotonicity in Condorcet's jury theorem with dependent voters. *Soc. Choice Welfare* **28**, 507–528. (doi:10.1007/s00355-006-0179-y)
- Beshers, S. N. & Fewell, J. H. 2001 Models of division of labor in social insects. *Annu. Rev. Entomol.* **46**, 413–440. (doi:10.1146/annurev.ento.46.1.413)
- Bikhchandani, S., Hirshleifer, D. & Welch, I. 1992 A theory of fads, fashions, custom, and cultural change as informational cascades. *J. Polit. Econ.* **100**, 992–1026. (doi:10.1086/261849)
- 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)
- Black, J. M. 1988 Preflight signaling in swans—a mechanism for group cohesion and flock formation. *Ethology* **79**, 143–157.
- Blackstone, W. 1765–1769 *Commentaries on the laws of England*. Oxford, UK: Clarendon Press.
- Blackwell, P. G. 1997 The n -player war of attrition and territorial groups. *J. Theor. Biol.* **189**, 175–181. (doi:10.1006/jtbi.1997.0504)
- Boinski, S. & Campbell, A. F. 1995 Use of trill vocalizations to coordinate troop movement among white-faced capuchins—a 2nd field-test. *Behaviour* **132**, 875–901. (doi:10.1163/156853995X00054)
- Boland, P. J. 1989 Majority systems and the Condorcet jury theorem. *Statistician* **38**, 181–189. (doi:10.2307/2348873)
- Boland, C. R. J. 2003 An experimental test of predator detection rates using groups of free-living emus. *Ethology* **109**, 209–222. (doi:10.1046/j.1439-0310.2003.00860.x)
- Brosnan, S. F. & de Waal, F. B. M. 2003 Monkeys reject unequal pay. *Nature* **425**, 297–299. (doi:10.1038/nature01963)
- Brosnan, S. F., Schiff, H. C. & de Waal, F. B. M. 2005 Tolerance for inequity may increase with social closeness in chimpanzees. *Proc. R. Soc. B* **272**, 253–258. (doi:10.1098/rspb.2004.2947)
- Buhl, J., Sumpter, D. J. T., Couzin, I. D., Hale, J. J., Despland, E., Miller, E. R. & Simpson, S. J. 2006 From disorder to order in marching locusts. *Science* **312**, 1402–1406. (doi:10.1126/science.1125142)
- Bukowski, M. & Miekisz, J. 2004 Evolutionary and asymptotic stability in symmetric multi-player games. *Int. J. Game Theory* **33**, 41–54. (doi:10.1007/s001820400183)
- Byrne, R. W. 2000 How monkeys find their way: leadership, coordination and cognitive maps of African baboons. In *On the move: how and why animals travel in groups* (eds S. Boinski & P. A. Garber), pp. 491–518. Chicago, IL: University of Chicago Press.
- Camazine, S., Deneubourg, J. L., Franks, N. R., Sneyd, J., Theraulaz, G. & Bonabeau, E. 2003 *Self-organization in biological systems*. Princeton, NJ: Princeton University Press.
- Carter, J., Lyons, N. J., Cole, H. L. & Goldsmith, A. R. 2008 Subtle cues of predation risk: starlings respond to a predator's direction of eye-gaze. *Proc. R. Soc. B* **275**, 1709–1715. (doi:10.1098/rspb.2008.0095)
- Clutton-Brock, T. H. 1998 Reproductive skew, concessions and limited control. *Trends Ecol. Evol.* **13**, 288–292. (doi:10.1016/S0169-5347(98)01402-5)
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982 *Red deer: behaviour and ecology of two sexes*. Chicago, IL: University of Chicago Press.
- Codling, E. A., Pitchford, J. W. & Simpson, S. D. 2007 Group navigation and the “many-wrongs principle” in models of animal movement. *Ecology* **88**, 1864–1870. (doi:10.1890/06-0854.1)
- Cohen, J. 1989 Deliberation and democratic legitimacy. In *The good polity: normative analysis of the state* (eds A. Hamlin & P. Pettit), pp. 17–34. Oxford, UK: Blackwell.
- Conradt, L. 1998 Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proc. R. Soc. B* **265**, 1359–1363. (doi:10.1098/rspb.1998.0442)
- Conradt, L. & Roper, T. J. 2000 Activity synchrony and social cohesion: a fission–fusion model. *Proc. R. Soc. B* **267**, 2213–2218. (doi:10.1098/rspb.2000.1171)
- Conradt, L. & Roper, T. J. 2003 Group decision-making in animals. *Nature* **421**, 155–158. (doi:10.1038/nature01294)
- 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. 2007 Democracy in animals: the evolution of shared group decisions. *Proc. R. Soc. B* **274**, 2317–2326. (doi:10.1098/rspb.2007.0186)
- 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)
- Conradt, L., Krause, J., Couzin I. D. & Roper, T. J. In press. Leading according to need in animal groups. *Am. Nat.* **173**.
- Courchamp, F., Rasmussen, G. S. A. & Macdonald, D. W. 2002 Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behav. Ecol.* **13**, 20–27. (doi:10.1093/beheco/13.1.20)

- Couzin, I. D. 2007 Collective minds. *Nature* **445**, 715. (doi:10.1038/445715a)
- Couzin, I. D. & Krause, J. 2003 Self-organization and collective behavior in vertebrates. *Adv. Study Behav.* **32**, 1–75. (doi:10.1016/S0065-3454(03)01001-5)
- Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. 2005 Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516. (doi:10.1038/nature03236)
- Dawes, C. T., Fowler, J. H., Johnson, T., McElreath, R. & Smirnov, O. 2007 Egalitarian motives in humans. *Nature* **446**, 794–796. (doi:10.1038/nature05651)
- Dennett, D. 1987 *The intentional stance*. Cambridge, MA: MIT Press.
- Dietrich, F. & List, C. 2004 A model of jury decisions where all jurors have the same evidence. *Synthese* **142**, 175–202. (doi:10.1007/s11229-004-1276-z)
- Dostalkova, I. & Spinka, M. 2007 Synchronisation of behaviour in pairs: the role of communication and consequences in timing. *Anim. Behav.* **74**, 1735–1742. (doi:10.1016/j.anbehav.2007.04.014)
- Dryzek, J. S. & List, C. 2003 Social choice theory and deliberative democracy: a reconciliation. *Br. J. Polit. Sci.* **33**, 1–28. (doi:10.1017/S0007123403000012)
- Dugatkin, L. A. 2005 Mistakes and the evolution of copying. *Ethol. Ecol. Evol.* **17**, 327–333.
- Dyer, J. R. G. 2008 Leadership, decision making and collective behaviour in animal groups. PhD thesis, University of Leeds, UK.
- Dyer, J. R. G., Johansson, A., Helbing, D., Couzin, I. D. & Krause, J. 2009 Leadership, consensus decision making and collective behaviour in humans. *Phil. Trans. R. Soc. B* **364**, 781–789. (doi:10.1098/rstb.2008.0233)
- Elster, J. (ed.) 1998 *Deliberative democracy*, Cambridge, UK: Cambridge University Press.
- Fehr, E., Bernhard, H. & Rockenbach, B. 2008 Egalitarianism in young children. *Nature* **454**, 1079–1084. (doi:10.1038/nature07155)
- Fischhoff, I. R., Sundaresan, S. R., Cordingley, J., Larkin, H. M., Sellier, M. J. & Rubenstein, D. I. 2007 Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Anim. Behav.* **73**, 825–831. (doi:10.1016/j.anbehav.2006.10.012)
- Fishkin, J. S. & Luskin, R. C. 2005 Experimenting with a democratic ideal: deliberative polling and public opinion. *Acta Polit.* **40**, 284–298. (doi:10.1057/palgrave.ap.5500121)
- Fleurbaey, M. 2008 Weighted majority and democratic theory. Working paper, CNRS-CERSES, University Paris-Descartes, LSE and IDEP.
- 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)
- Gächter, S. & Herrmann, B. 2009 Reciprocity, culture and human cooperation: previous insights and a new cross-cultural experiment. *Phil. Trans. R. Soc. B* **364**, 791–806. (doi:10.1098/rstb.2008.0275)
- Gautrais, J., Michelena, P., Sibbald, A., Bon, R. & Deneubourg, J. L. 2007 Allelomimetic synchronization in merino sheep. *Anim. Behav.* **74**, 1443–1454. (doi:10.1016/j.anbehav.2007.02.020)
- Gavre, M. 1977 Essay on theory of enlightened despotism—Krieger, L. *Am. Polit. Sci. Rev.* **71**, 1141–1142. (doi:10.2307/1960129)
- Gehrlein, W. 1983 Condorcet's paradox. *Theory Decis.* **15**, 161–197. (doi:10.1007/BF00143070)
- Gigerenzer, G. & Selten, R. (eds) 2002 *Bounded rationality: the adaptive toolbox*. Cambridge, MA: MIT Press.
- Giraldeau, L. A., Valone, T. J. & Templeton, J. J. 2002 Potential disadvantages of using socially acquired information. *Phil. Trans. R. Soc. B* **357**, 1559–1566. (doi:10.1098/rstb.2002.1065)
- Gompper, M. E. 1996 Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. *Behav. Ecol.* **7**, 254–263. (doi:10.1093/beheco/7.3.254)
- Goodin, R. E. & List, C. 2006a A conditional defense of plurality rule: generalizing May's theorem in a restricted informational environment. *Am. J. Polit. Sci.* **50**, 940–949. (doi:10.1111/j.1540-5907.2006.00225.x)
- Goodin, R. E. & List, C. 2006b Special majorities rationalized. *Br. J. Polit. Sci.* **36**, 213–241. (doi:10.1017/S0007123406000135)
- Grofman, B., Owen, G. & Feld, S. L. 1983 Thirteen theorems in search of the truth. *Theory Decis.* **15**, 261–278. (doi:10.1007/BF00125672)
- Gueron, S., Levin, S. A. & Rubenstein, D. I. 1996 The dynamics of herds: from individuals to aggregations. *J. Theor. Biol.* **182**, 85–98. (doi:10.1006/jtbi.1996.0144)
- Gutman, A. & Thompson, D. 1996 *Democracy and disagreement*. Cambridge, MA: Harvard University Press.
- Hastie, R. & Kameda, T. 2005 The robust beauty of majority rules in group decisions. *Psychol. Rev.* **112**, 494–508. (doi:10.1037/0033-295X.112.2.494)
- Helbing, D., Farkas, I. & Vicsek, T. 2000 Simulating dynamical features of escape panic. *Nature* **407**, 487–490. (doi:10.1038/35035023)
- Hemelrijk, C. K. & Hildenbrandt, H. 2008 Self-organized shape and frontal density of fish schools. *Ethology* **114**, 245–254. (doi:10.1111/j.1439-0310.2007.01459.x)
- Hix, S., Noury, A. & Roland, G. 2009 Voting patterns and alliance formation in the European Parliament. *Phil. Trans. R. Soc. B* **364**, 821–831. (doi:10.1098/rstb.2008.0263)
- Ishaque, M. M. & Noland, R. B. 2008 Behavioural issues in pedestrian speed choice and street crossing behaviour: a review. *Trans. Rev.* **28**, 61–85. (doi:10.1080/01441640701365239)
- Kaminski, D., Miekisz, J. & Zaborowski, M. 2005 Stochastic stability in three-player games. *Bull. Math. Biol.* **67**, 1195–1205. (doi:10.1016/j.bulm.2005.01.004)
- Kerth, G., Ebert, C. & Schmidtko, C. 2006 Group decision making in fission–fusion societies: evidence from two-field experiments in Bechstein's bats. *Proc. R. Soc. B* **273**, 2785–2790. (doi:10.1098/rspb.2006.3647)
- King, A. J., Douglas, C. M. S., Huchard, E., Isaac, N. J. B. & Cowlshaw, G. 2008 Dominance and affiliation mediate despotism in a social primate. *Curr. Biol.* **18**, 1833–1838. (doi:10.1016/j.cub.2008.10.048)
- Krause, J. & Ruxton, G. D. 2002 *Living in groups*. Oxford, UK: Oxford University Press.
- Krause, J., Bumann, D. & Todt, D. 1992 Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (*Rutilus rutilus*). *Behav. Ecol. Sociobiol.* **30**, 177–180. (doi:10.1007/BF00166700)
- Ladha, K. 1992 The Condorcet jury theorem, free speech and correlated votes. *Am. J. Polit. Sci.* **36**, 617–634. (doi:10.2307/2111584)
- Lingle, S. & Pellis, S. M. 2002 Fight or flight? Antipredator behavior and the escalation of coyote encounters with deer. *Oecologia* **131**, 154–164. (doi:10.1007/s00442-001-0858-4)
- 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)

- List, C. In press. Judgment aggregation: a short introduction. In *Handbook of the philosophy of economics* (ed. U. Maki). Amsterdam, The Netherlands: Elsevier. (<http://personal.lse.ac.uk/list/pdf-files/ja-intro.pdf>)
- List, C. & Goodin, R. E. 2001 Epistemic democracy: generalizing the Condorcet jury theorem. *J. Polit. Philos.* **9**, 277–306. (doi:10.1111/1467-9760.00128)
- List, C. & Pettit, P. 2002 Aggregating sets of judgments: an impossibility result. *Econ. Philos.* **18**, 89–110.
- List, C., Luskin, R. C., Fishkin, J. & McLean, I. 2000/2006 Deliberation, single-peakedness, and the possibility of meaningful democracy: evidence from deliberative polls. Working paper, London School of Economics. See <http://personal.lse.ac.uk/list/PDF-files/DeliberationPaper.pdf>.
- List, C., Elsholtz, C. & Seeley, T. D. 2009 Independence and interdependence in collective decision making: an agent-based model of nest-site choice by honeybee swarms. *Phil. Trans. R. Soc. B* **364**, 755–762. (doi:10.1098/rstb.2008.0277)
- Luskin, R. C., Fishkin, J. S. & Jowell, R. 2002 Considered opinions: deliberative polling in Britain. *Br. J. Polit. Sci.* **32**, 455–487. (doi:10.1017/S0007123402000194)
- Lusseau, D. 2007 Evidence for social role in a dolphin social network. *Evol. Ecol.* **21**, 357–366. (doi:10.1007/s10682-006-9105-0)
- Lusseau, D. & Conradt, L. In press. The emergence of unshared consensus decisions in bottlenose dolphins. *Behav. Ecol. Sociobiol.*
- May, K. O. 1952 A set of independent, necessary and sufficient conditions for simple majority decision. *Econometrica* **20**, 680–684. (doi:10.2307/1907651)
- Maynard Smith, J. & Price, G. 1973 The logic of animal conflict. *Nature* **246**, 15–18. (doi:10.1038/246015a0)
- Meunier, H., Leca, J. B., Deneubourg, J. L. & Petit, O. 2006 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)
- Milton, K. 2000 Tactics of food search and group movements in primates and other animals. In *On the move: how and why animals travel in groups* (eds S. Boinski & P. A. Garber), pp. 375–418. Chicago, IL: University of Chicago Press.
- Osborne, M. J. & Rubinstein, A. 1994 *A course in game theory*. Cambridge, MA: MIT Press.
- 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)
- Platkowski, T. & Stachowska-Pietka, J. 2005 ESSs in *n*-player mixed games. *Appl. Math. Comput.* **167**, 592–606. (doi:10.1016/j.amc.2003.10.063)
- Poole, J. H., Payne, K., Langbauer, W. R. & Moss, C. J. 1988 The social contexts of some very low-frequency calls of African elephants. *Behav. Ecol. Sociobiol.* **22**, 385–392. (doi:10.1007/BF00294975)
- Prins, H. H. T. 1996 *Ecology and behaviour of the African buffalo*. London, UK: Chapman and Hall.
- Rae, D. W. 1969 Decision-rules and individual values in constitutional choice. *Am. Polit. Sci. Rev.* **63**, 40–56. (doi:10.2307/1954283)
- Rands, S. A., Cowlshaw, G., Pettifor, R. A., Rowcliffe, J. M. & Johnstone, R. A. 2003 Spontaneous emergence of leaders and followers in foraging pairs. *Nature* **423**, 432–434. (doi:10.1038/nature01630)
- Rawls, J. 1971 *A theory of justice*. Cambridge, MA: Harvard University Press.
- Reebs, S. G. 2000 Can a minority of informed leaders determine the foraging movements of a fish shoal? *Anim. Behav.* **59**, 403–409. (doi:10.1006/anbe.1999.1314)
- Regenwetter, M., Grofman, B., Popova, A., Messner, W., Davis-Stober, C. P. & Cavagnaro, D. R. 2009 Behavioural social choice: a status report. *Phil. Trans. R. Soc. B* **364**, 833–843. (doi:10.1098/rstb.2008.0259)
- Royal Swedish Academy of Sciences 2007 Mechanism design theory: scientific background on the Sveriges Riksbank prize in economic sciences in memory of Alfred Nobel 2007, Stockholm. See http://nobelprize.org/nobel_prizes/economics/laureates/2007/eoadv07.pdf.
- Ruckstuhl, K. E. 1998 Foraging behaviour and sexual segregation in bighorn sheep. *Anim. Behav.* **56**, 99–106. (doi:10.1006/anbe.1998.0745)
- Ruckstuhl, K. E. 1999 To synchronise or not to synchronise: a dilemma for young bighorn males? *Behaviour* **136**, 805–818. (doi:10.1163/156853999501577)
- Ruckstuhl, K. E. & Neuhaus, P. 2000 Sexual segregation in ungulates: a new approach. *Behaviour* **137**, 361–377. (doi:10.1163/156853900502123)
- Ruckstuhl, K. E. & Neuhaus, P. 2002 Sexual segregation in ungulates: a comparative test of three hypotheses. *Biol. Rev.* **77**, 77–96.
- 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. & Buhrman, S. C. 2001 Nest-site selection in honey bees: how well do swarms implement the “best-of-N” decision rule? *Behav. Ecol. Sociobiol.* **49**, 416–427. (doi:10.1007/s002650000299)
- Sellers, W. I., Hill, R. A. & Logan, B. S. 2007 An agent-based model of group decision making in baboons. *Phil. Trans. R. Soc. B* **362**, 1699–1710. (doi:10.1098/rstb.2007.2064)
- Selous, E. 1931 *Thought-transference (or what?) in birds*. London, UK: Constable & Co.
- Sen, A. K. 1999 The possibility of social choice. *Am. Econ. Rev.* **89**, 349–378.
- 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)
- Skyrms, B. 2009 Evolution of signalling systems with multiple senders and receivers. *Phil. Trans. R. Soc. B* **364**, 771–779. (doi:10.1098/rstb.2008.0258)
- Smith, J. M. 1964 Group selection and kin selection. *Nature* **201**, 1145–1147. (doi:10.1038/2011145a0)
- Smith, J. M. 1976 Commentary—group selection. *Q. Rev. Biol.* **51**, 277–283. (doi:10.1086/409311)
- Smith, J. M. 1998 Unto others: the evolution and psychology of unselfish behavior. *Nature* **393**, 639–640. (doi:10.1038/31383)
- Stankowich, T. & Blumstein, D. T. 2005 Fear in animals: a meta-analysis and review of risk assessment. *Proc. R. Soc. B* **272**, 2627–2634. (doi:10.1098/rspb.2005.3251)
- Stewart, K. J. & Harcourt, A. H. 1994 Gorillas vocalizations during rest periods—signals of impending departure. *Behaviour* **130**, 29–40. (doi:10.1163/156853994X00127)
- Sueur, C. & Petit, O. 2008 Shared or unshared consensus decision in macaques? *Behav. Process.* **78**, 84–92. (doi:10.1016/j.beproc.2008.01.004)
- 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. & Pratt, S. C. 2009 Quorum responses and consensus decision making. *Phil. Trans. R. Soc. B* **364**, 743–753. (doi:10.1098/rstb.2008.0204)
- Sumpter, D., Buhl, J., Biro, D. & Couzin, I. 2008 Information transfer in moving animal groups. *Theory Biosci.* **127**, 177–186. (doi:10.1007/s12064-008-0040-1)
- Sunstein, C. R. 2002 The law of group polarization. *J. Polit. Philos.* **10**, 175–195. (doi:10.1111/1467-9760.00148)
- Sunstein, C. R. 2006 *Infotopia: how many minds produce knowledge*. New York, NY: Oxford University Press.

- Taylor, M. 1969 Proof of a theorem on majority rule. *Behav. Sci.* **14**, 228–231. (doi:10.1002/bs.3830140307)
- Trillmich, J., Fichtel, C. & Kappeler, P. M. 2004 Coordination of group movements in wild Verreaux's sifakas (*Propithecus verreauxi*). *Behaviour* **141**, 1103–1120. (doi:10.1163/1568539042664579)
- Van Doorn, G. S., Hengeveld, G. M. & Weissing, F. J. 2003 The evolution of social dominance—II: multi-player models. *Behaviour* **140**, 1333–1358. (doi:10.1163/156853903771980611)
- Vermeule, A. 2005 Submajority rules: forcing accountability upon majorities. *J. Polit. Philos.* **13**, 74–98. (doi:10.1111/j.1467-9760.2005.00214.x)
- 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. & Seeley, T. D. 2007 Coordinating a group departure: who produces the piping signals on honeybee swarms? *Behav. Ecol. Sociobiol.* **61**, 1615–1621. (doi:10.1007/s00265-007-0393-3)
- 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. J. W., Sumpter, D. J. T., Couzin, J. D., Hart, P. J. B. & Krause, J. 2008 Quorum decision making facilitates information transfer in fish schools. *Proc. Natl Acad. Sci. USA* **105**, 6948–6953. (doi:10.1073/pnas.0710344105)

APPENDIX A. GLOSSARY

- Accuracy/reliability*: The probability that a belief is correct; in the context of a decision in which there exists an independently best outcome, the probability that this outcome is reached.
- Acyclic binary relation*: A binary relation, R , with the property that it is never the case that $x_1Rx_2, x_2Rx_3, \dots, x_kRx_1$; for example, ' $<$ ' is an acyclic binary relation, while ' $=$ ' is not; preference relations are typically required to be acyclic; Condorcet's paradox, however, shows that majority preferences may violate this requirement.
- Aggregate/consensus decision*: A single collective decision, e.g. between multiple options, that is 'binding' in some way for all group members.
- Aggregation rule (sometimes also called voting rule)*: A function which assigns to each combination of individual inputs (e.g. votes) a resulting collective output (e.g. a decision outcome); different aggregation rules differ in what the admissible inputs and outputs are; see, for example, social welfare functions.
- Anonymity*: A requirement that all individual group members should be given equal weight in determining the outcome of an aggregate/consensus decision; anonymity is frequently imposed as a condition on democratic aggregation rules, e.g. in May's theorem.
- Antisymmetric binary relation*: A binary relation, R , with the property that if x_1Rx_2 and x_2Rx_1 , then $x_1=x_2$; for example, ' \leq ' is an antisymmetric binary relation.
- Arrow's impossibility theorem*: A classic result in social choice theory showing that, in decisions between more than two alternatives, the only aggregation rules satisfying some minimal conditions (among which is the decomposition of decisions into pairwise choices) and guaranteeing complete and transitive collective preferences are dictatorial ones.
- Behavioural decision theory*: An area of decision theory that seeks to construct empirically informed models of human decision making. See also behavioural economics.

- Behavioural economics*: An area of economics that seeks to explain economic phenomena by taking into account empirical findings on the psychology of human decision making; one of its key questions is whether, and to what extent, economic agents satisfy, or violate, various classical conditions of rationality.
- Behavioural finance*: An area of behavioural economics that studies how financial market behaviour is affected by the psychology of human decision making.
- Behavioural game theory*: An area of game theory that models strategic behaviour on the basis of empirically informed assumptions about human rationality; see also behavioural economics.
- Behavioural social choice theory*: An area of social choice theory that empirically tests social-choice-theoretic results and their underlying assumptions.
- Borda efficiency*: The probability that the winning outcome (top-ranked option) of a given aggregation rule coincides with the winner under the Borda rule, assuming that all possible combinations of individual preferences are equally probable.
- Borda rule/Borda count*: An aggregation rule whose input is a combination of individual preference orderings over some options and whose output is either a collective preference ordering over these options or a top-ranked option, defined as follows; each option gets a score from each voter: if the option is ranked top among k options, it gets a score of k ; if it is ranked second from top, it gets a score of $k-1$, and so on; collectively, the option with the highest sum total score comes top, the option with the second highest comes second, and so on; for example, if 10 individuals have the preferences $A > B > C$ and 25 individuals have the preferences $B > C > A$, then A gets a score of $10 \times 3 + 25 \times 1 = 55$, B gets a score of $10 \times 2 + 25 \times 3 = 95$ and C gets a score of $10 \times 1 + 25 \times 2 = 60$; consequently, the social preference is $B > C > A$.
- Complete/connected binary relation*: A binary relation, R , with the property that, for any x_1 and x_2 , either x_1Rx_2 or x_2Rx_1 (or both).
- Common values*: The case in which different group members have identical interests and their differences are at most informational.
- Condorcet's jury theorem*: If all members of a group have an independent and equal accuracy/reliability better than random but less than perfect of making a correct judgement on some binary issue, then the majority judgement is more likely to be correct than any individual judgement and the probability of a correct majority judgement converges to 1 as the group size increases.
- Condorcet's paradox*: The phenomenon that majority preferences may be cyclic even when all individual preferences are acyclic; for example, if one-third of a group prefers A to B to C, a second third prefers B to C to A and the remaining third prefers C to A to B, there are majorities for A against B, for B against C and for C against A.
- Condorcet winner*: An option which beats, or at least ties with, all other options in pairwise majority voting.
- Consensus cost*: A difference between the fitness benefits which a particular group member would have gained if the group decision outcome had been the option that is optimal for that member and the benefits gained in the realized aggregated/consensus decision outcome.
- Coordination game*: See box 2 for an example.
- Culture of indifference*: A generic term for probability distributions of individual preferences within a population

- with particular symmetry properties; examples are the impartial culture and the impartial anonymous culture.
- Cyclic binary relation*: A binary relation, R , with the property that, for some set of options x_1, \dots, x_k , we have x_1Rx_2 , x_2Rx_3, \dots, x_kRx_1 .
- Cyclic majority preference*: See Condorcet's paradox.
- Decision theory*: A mathematical theory of individual decision making; focuses on various, often idealized, properties of individual rationality.
- Dictatorial rule/dictatorship*: An aggregation rule whose output is always the input of a fixed individual.
- Direct reciprocity*: An act of altruism towards an individual in the expectation of later repayment through a reciprocal act of altruism by this individual; see also reciprocal altruism.
- Dominant strategy equilibrium*: A combination of strategies across individuals in a game such that every individual prefers (or is at least indifferent to) the outcome of choosing his or her strategy, compared with the outcome of deviating from it, regardless of what the other individuals do; the situation in which all individuals defect in a Prisoner's Dilemma is a dominant strategy equilibrium.
- Equally shared decision*: A natural science term for a decision with an aggregation rule in which all group members have equal weights (anonymity).
- Equilibrium*: A combination of strategies across individuals that satisfies certain 'best-response' or 'stability' criteria; different best-response or stability criteria lead to different equilibrium concepts.
- Eusociality/eusocial*: Reproduction is confined to one or few members of a colony and workers are functionally sterile; mainly found in bees, wasps, ants and termites.
- Evolutionarily stable strategy (ESS)*: A strategy S such that, for any other strategy T , either $E(S, S) > E(T, S)$ or $[E(S, S) = E(T, S) \text{ and } E(S, T) > E(T, T)]$, where $E(A, B)$ is the pay-off of playing a strategy A against a strategy B ; the central consequence of this definition is that, if sufficiently many individuals in a population play an evolutionarily stable strategy and pay-offs represent evolutionary fitness, no mutant strategy can successfully invade the population.
- Evolutionarily stable state*: A dynamic evolutionary equilibrium of a population; every population in which all individuals use an evolutionarily stable strategy is in an evolutionarily stable state, but populations can also be in an evolutionarily stable state if nobody uses an evolutionarily stable strategy; for example, a population with a proportion x of 'hawks' and $1 - x$ of 'doves' is in an evolutionarily stable state if the expected pay-offs for doves and hawks in random pairings within the population are equal and increase for hawks (decrease for doves) if $x' < x$, and vice versa if $x' > x$ (and if no further alternative strategies to hawks and doves are biologically possible); here, neither hawks nor doves play evolutionarily stable strategies; see also box 2 for a further example.
- Expected utility theory*: An area of decision theory in which individual decision making is modelled as the maximization of the expected value of some utility function.
- Experimental economics*: An area of economics in which experiments (with real human subjects, e.g. volunteers or college students) are used to test various hypotheses about human economic behaviour; to create realistic incentives, subjects usually receive monetary pay-offs depending on their performance in the relevant strategic tasks.
- Fads, stock market bubbles*: Examples of informational cascades.
- Game theory*: A mathematical theory of interactive decision making; focuses on various kinds of strategic situations (games) and models how rational players would behave in them; investigates the existence and properties of different kinds of equilibria in games.
- Generalized weighted majority rule*: See box 1.
- Global overview*: All members of a group can directly communicate with and/or observe all other members of the group.
- Groupthink*: The adoption of a particular viewpoint by a group as a result of conformism or the minimization of conflict, without sufficient critical testing; related to informational cascades.
- Heuristics and biases*: Rules of thumb in decision making (heuristics), which may lead to systematic errors (biases); a central topic in behavioural decision theory.
- Impartial anonymous culture*: A probability distribution of individual preferences according to which all possible frequencies across different preference orderings are equally likely to occur; statistically, this is subtly different from an impartial culture.
- Impartial culture*: A probability distribution of individual preferences according to which all possible preference orderings are equally likely to occur.
- Indirect reciprocity*: An act of altruism towards an individual in the expectation of gaining a positive 'reputation' resulting in later repayment through altruistic acts by other individuals.
- Informational cascade*: A phenomenon in markets or other information pooling settings where a plurality or majority that accidentally emerges in support of some proposition is mistakenly interpreted by others as evidence for the truth of that proposition and thereby attracts further support, although few or any individuals originally judged the proposition to be true; examples of informational cascades include fads or stock market bubbles.
- Informative voting*: Casting a vote (e.g. in a jury decision) that reveals one's private information (e.g. about the guilt or innocence of the defendant).
- Interactive/combined decision*: A set of interdependent decisions by group members affecting each other.
- Linear order*: A transitive, antisymmetric and complete/connected binary relation; for example, ' \leq ' is a linear order.
- May's theorem*: In a two-option choice, majority voting is the only aggregation rule that simultaneously satisfies universal domain, anonymity, neutrality and positive responsiveness.
- Mechanism design theory*: Investigates what mechanisms or systems of incentives induce rational individuals to behave so as to bring about a particular intended outcome (e.g. sincere voting, truthful bidding in auctions).
- Mixed strategy*: A strategy which can be seen as a lottery/randomization over pure strategies; an individual has a mixed strategy if he or she has fixed probabilities p_1, \dots, p_k (with $k \geq 1$, $p_i \geq 0$ for each i , and $p_1 + \dots + p_k = 1$) of playing pure strategies S_1, \dots, S_n , respectively.
- Nash equilibrium*: A combination of strategies across individuals in a game with the property that no individual would prefer the outcome if it unilaterally deviated from its strategy.
- Neutrality*: Requires that all options should be treated equally in an aggregate/consensus decision; neutrality is frequently imposed as a condition on democratic aggregation rules,

- e.g. in May's theorem; super- or sub-majority rules, for example, violate neutrality.
- Oligarchic rule*: An aggregation rule whose output is determined by the inputs of a subset of the group members; the limiting case of an oligarchic rule is a dictatorial rule (here, the subset of decisive group members is a singleton).
- Plurality rule*: An aggregation rule in which each individual casts one vote and the option with the largest number of votes is selected.
- Positional voting rule*: A class of aggregation rules based on the assignment of scores to options as a function of their position within individual preference orderings; the most prominent example is the Borda rule.
- Positive responsiveness*: A requirement that the output of an aggregate/consensus decision should be a positively monotonic function of the individual inputs (e.g. votes); formally, if some option A wins or is tied with another option B in pairwise voting, then any change of votes in favour of A should preserve A as the winner or break the tie in favour of A; positive responsiveness is frequently placed as a desideratum on democratic aggregation rules, e.g. in May's theorem.
- Potential consensus costs (also called decision stake)*: A difference between the (fitness) benefits which a particular group member would gain if the group decision outcome were the optimal option for that member and the benefits which this member would gain otherwise.
- Prisoner's Dilemma*: See box 2 for an example.
- Prospect theory/cumulative prospect theory*: Prominent psychologically informed theories of human decision making under risk.
- Pure strategy*: A strategy which involves no lottery/randomization.
- Quorum response*: A feedback mechanism in group decisions whereby an individual's probability of commitment to a particular decision option increases sharply once a critical number of other individuals (the 'quorum threshold') have committed to that option.
- Quorum threshold*: See quorum response.
- Reciprocal altruism*: (i) An altruistic behaviour of one individual towards another in the expectation of later repayment through acts of altruism by the same, or other, individuals ('if you scratch my back, I scratch yours'; see also direct and indirect reciprocity), and (ii) a theory about how altruism could evolve in unrelated individuals.
- Self-organization in groups of animals or humans*: Emerging group behaviour when individual group members behave according to individual rules that are based on local information and/or local communication and have some interdependence with the behaviour of neighbouring group members, but there is no individual that has a global overview and directs the behaviour of the group as a whole; a good example is a moving flock of starlings.
- Social choice theory*: A mathematical theory of collective decision making; focuses on various kinds of aggregation problems and studies the properties of different aggregation rules, often using an axiomatic approach.
- Social welfare function*: Arrow's (1951/1963) term for an aggregation rule whose input is a combination of individual preference orderings over some given options and whose output is a single collective preference ordering over these options; the term 'social welfare' comes from the fact that Arrow introduced this concept in the context of welfare economics.
- Stake*: See potential consensus costs.
- Stake holders*: All individuals affected by a particular decision.
- Sub- or super-majority rule*: A special case of a generalized weighted majority rule in which the decision threshold is tilted in favour of one and against the other option (and group members typically have equal weight).
- Transitive binary relation*: A binary relation, R , with the property that if $x_1 R x_2$ and $x_2 R x_3$, then $x_1 R x_3$. For example, ' $<$ ' is a transitive binary relation.
- Universal domain*: A requirement that any possible combinations of individual inputs (e.g. votes) should be admissible in an aggregate/consensus decision; universal domain is frequently imposed as a desideratum on democratic aggregation rules, e.g. in May's theorem and Arrow's theorem.
- Unshared decision*: A natural science term for a decision with a dictatorial aggregation rule.
- Utility function*: A function which assigns to each option a real number, interpreted as the utility, a measure of desirability, of that option; while a probability function represents beliefs or information, a utility function represents desires or interests.