

Consensus decision making in animals

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Individual animals routinely face decisions that are crucial to their fitness. In social species, however, many of these decisions need to be made jointly with other group members because the group will split apart unless a consensus is reached. Here, we review empirical and theoretical studies of consensus decision making, and place them in a coherent framework. In particular, we classify consensus decisions according to the degree to which they involve conflict of interest between group members, and whether they involve either local or global communication; we ask, for different categories of consensus decision, who makes the decision, what are the underlying mechanisms, and what are the functional consequences. We conclude that consensus decision making is common in non-human animals, and that cooperation between group members in the decision-making process is likely to be the norm, even when the decision involves significant conflict of interest.

Introduction

A ‘consensus decision’ (see Glossary) is when the members of a group choose between two or more mutually exclusive actions with the aim of reaching a consensus. Humans make consensus decisions all the time, from large-scale international agreements and democratic elections, to small-scale agreements reached by a few people. Human societies are unable to function without consensus decisions, and some of the most pressing problems facing humanity result from large-scale failures to reach a consensus (e.g. the signing of the Kyoto Agreement relating to climate change). Therefore, understanding how consensus decision making works, and why humans sometimes fail at it, is fundamental.

Non-human social animals also frequently make consensus decisions. Consider, for example, a group of primates deciding where to travel after a rest period [1], a small flock of birds deciding when to leave a foraging patch [2], or a swarm of bees choosing a new nest site [3]. In each of these cases, unless all members decide on the same action, the group will split and its members will forfeit many of the advantages of group living [4]. Everyday examples such as these, together with an increasing body of empirical evidence [1–3,5–10], suggest that consensus decisions have an important role in the lives of social animals.

The existence of consensus decision making in animals that do not communicate verbally raises intriguing questions. For example, which group members contribute

to consensus decisions (Box 1)? How do they communicate and reach a consensus? What are the fitness consequences for individual group members? Here, we address these questions while reviewing the relevant literature and placing it into a systematic framework (Figure 1).

Empirical examples of consensus decisions that differ in the extent to which they involve conflict of interest

Glossary

Combined decision: members of a group choose individually (but not necessarily independently) between two or more actions. They do not aim for consensus but the combined results of their decisions usually affect the group as a whole.

Consensus costs: if there is a conflict of interest involved in a consensus decision, individual members can incur ‘consensus costs’ (in terms of reduced fitness) of forgoing their own optimal action to comply with the decision outcome.

Consensus decision: members of a group choose between two or more mutually exclusive actions with the specific aim of reaching a consensus.

Consistent leadership: the same member (e.g. dominant) always leads group actions.

Equally shared consensus decision: all members contribute equally (and independently of individual identity) to the decision outcome. The consensus is usually determined by a quorum or by averaging over all votes.

Fission–fusion society: a society consisting of casual groups of variable size and composition, which form, break up and reform at frequent intervals.

Global communication: all group members can communicate directly with all other group members.

Group decision: a decision made by the animals within a group. Group decisions can be ‘consensus decisions’ or ‘combined decisions’.

Information pooling: integration of information that is available to all individual decision makers during a consensus decision-making process.

Large group: groups in which members can only communicate locally (i.e. with neighbouring group members).

Local communication: group members can only communicate with neighbouring members.

Partially shared consensus decision: a proportion of members (often a demographic subset, such as all adult males) contribute to the decision outcome. Partially shared decisions are ‘little shared’ if few members contribute and ‘widely shared’ if many contribute. There is a logical continuum from unshared, via partially shared, to equally shared decisions.

Public information sampling: members of a group observe the behaviour of other members and glean information (e.g. about foraging rates or breeding success) to make individual decisions (e.g. about leaving or staying).

Quorum: minimum number of group members that need to take or favour a particular action for the whole group to adopt this action. In principle, the quorum could be a majority, sub-majority (less than a majority) or super-majority (more than a majority) of members. In practice, animals are likely to determine whether a quorum has been reached by estimating the relative numerosness of members contributing to the quorum, often by relying on indirect cues.

Self-organizing system: individual group members follow local behavioural rules, resulting in organized behaviour by the whole group without the need for global control.

Small group: a group in which members can communicate globally (i.e. with all other group members).

Unshared consensus decision: one particular group member (e.g. the dominant) makes the decision on behalf of all group members. All other members abide by this decision.

Variable leadership: different group members lead group actions on different occasions.

Voting: an animal communicates its individual preference with regard to the decision outcome.

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Box 1. Who should make the decision?

Which group members should contribute to consensus decisions? If conflicts of interest are involved, consensus costs to groups are, in theory, considerably higher for unshared than for equally shared decisions [8]. Equally shared decisions should be more beneficial primarily because they tend to produce less extreme decisions, rather than because each individual has an influence on the decision *per se* [8]. Depending on the symmetry in consensus costs between different decision outcomes, equally shared decisions with sub-majoritarian, majoritarian or super-majoritarian quorums, respectively, should generate the lowest costs [8,33]. For example, in groups of two, the animal with the lowest energy reserves (i.e. potentially the highest consensus costs) should always initiate activity changes from resting to foraging, irrespective of dominance relationships, leading to an equally shared decision with a quorum of one for initiating foraging [29]. Simple rules of thumb (e.g. 'always forage when your resources drop below a threshold or when the other animal forages') can result in such decisions [29].

However, it is not immediately obvious whether simple rules could also lead to equally shared decisions in larger groups. Using self-organizing rules, Couzin *et al.* [15] modelled large groups containing individuals that preferred one of two different travel destinations but had a propensity to stay within a cohesive group. On a local scale, each individual adjusted its movement direction so as to compromise between the direction of its personally preferred goal and being attracted to its local neighbours. If the differences in direction between the preferred goals were not too large, the whole group moved in the average preferred direction; if the differences in direction between the preferred goals were large, the whole group moved in the direction of the goal preferred by a majority of individuals.

Self-organizing models have frequently been used to predict and explain the coordination of movement of individuals in large groups (reviewed in [26]), but when and how self-organizing rules lead to shared consensus decisions, and what the underlying selective pressures are [52], has received little attention. Couzin *et al.*'s work [15] is an important first step in this direction by showing that shared decisions do not require complex mechanisms or advanced cognitive abilities, even in very large groups. Interesting in this context are empirical observations that the local rules adopted by group members can change by consensus [53].

between group members are described in Boxes 2–4. Nest site choice in eusocial insects (Box 2), and navigation in homing and migrating birds (Box 3), involve relatively little conflict of interest because the goal (to find the best nest site) is similar for all group members. By contrast, the synchronization of group activities and travel destinations in birds, fish and mammals (Box 4) can involve significant conflicts [11–14]. In each case, we ask who makes the decision, what are the mechanisms underlying the decision-making process, and what are the functional consequences.

Consensus versus combined decisions

We begin by distinguishing two conceptually different kinds of group decision. The first type consists of decisions that are made together by group members, with the aim of reaching a consensus. (In this context, 'together' means that all members abide by the decision outcome, not that all contribute to it.) We term these 'consensus decisions'. Consensus decisions are made by spatially cohesive groups [12] and usually concern movement direction [15], travel destination [1] and activity timing [8], but they also include decisions by cooperative hunters about prey targets [16].

The second type of group decision making is when animals decide individually, without requiring a consensus but in a manner that is dependent on the behaviour of other group members. The combined results of these individual decisions usually affect the group as a whole. We term these 'combined decisions'. Combined decisions include decisions about task allocation in eusocial species [17]; reproductive skew in cooperatively breeding species [18]; group joining or leaving in fission–fusion societies [19], including public information use [20]; and various consumer decisions in humans [21]. If combined decisions involve little conflict of interest, individual members decide freely. For example, eusocial insects often allocate themselves tasks, such as foraging or nest cleaning, according to local necessity and without being regimented [17]. If combined decisions involve significant conflict of interest, individuals can struggle for control [18]. For example, in many eusocial insects, queens and workers compete for producing male offspring and police each other by destroying eggs [22]. In some species, the queen gains control, in others the workers [22].

The distinction between consensus and combined decisions is important for several reasons. First, there is a conceptual difference between, for example, the decision made by a group of coatis *Nasua narica* that remains cohesive when choosing between different sites [23] ('consensus decision'), and a fission–fusion flock of starlings *Sturnus vulgaris* in which individuals frequently join or leave, leading to an aggregated pattern of spatial distribution [20] ('combined decision'). Second, there is also a conceptual difference between the complex cooperative process of information pooling during consensus decision making in honey bees *Apis mellifera* (Box 2 [24,25]), and the vicarious sampling of public information that occurs during the making of combined decisions by birds in fission–fusion flocks [20]. Third, consensus decisions aimed at agreement require different mechanisms (e.g. voting [10]) from individual-based combined decisions [18,20,22]. Finally, consensus decisions involve consensus costs for all individuals involved [11–14], whereas the costs for combined decision makers depend on the outcome of control struggles [18]. The remainder of this review is concerned only with consensus decisions.

A theoretical framework for consensus decisions

Because interest in consensus decisions has expanded only recently [3,8,15,25,26–29], the field lacks a unifying conceptual framework and a consistent terminology. Here, we suggest a conceptual framework within which to place the existing literature (Figure 1) and define the relevant terminology (see Glossary). The framework classifies examples of consensus decisions into categories according to: (i) the extent to which they involve conflict of interest between group members; and (ii) whether they involve either local or global communication between group members. The logic of this classification is as follows.

First, whether consensus decisions involve conflict of interest can influence which group members contribute to the decision outcome, and it can affect the fitness consequences of the decision [8]. For example, the fitness advantages of information pooling change if conflicts of

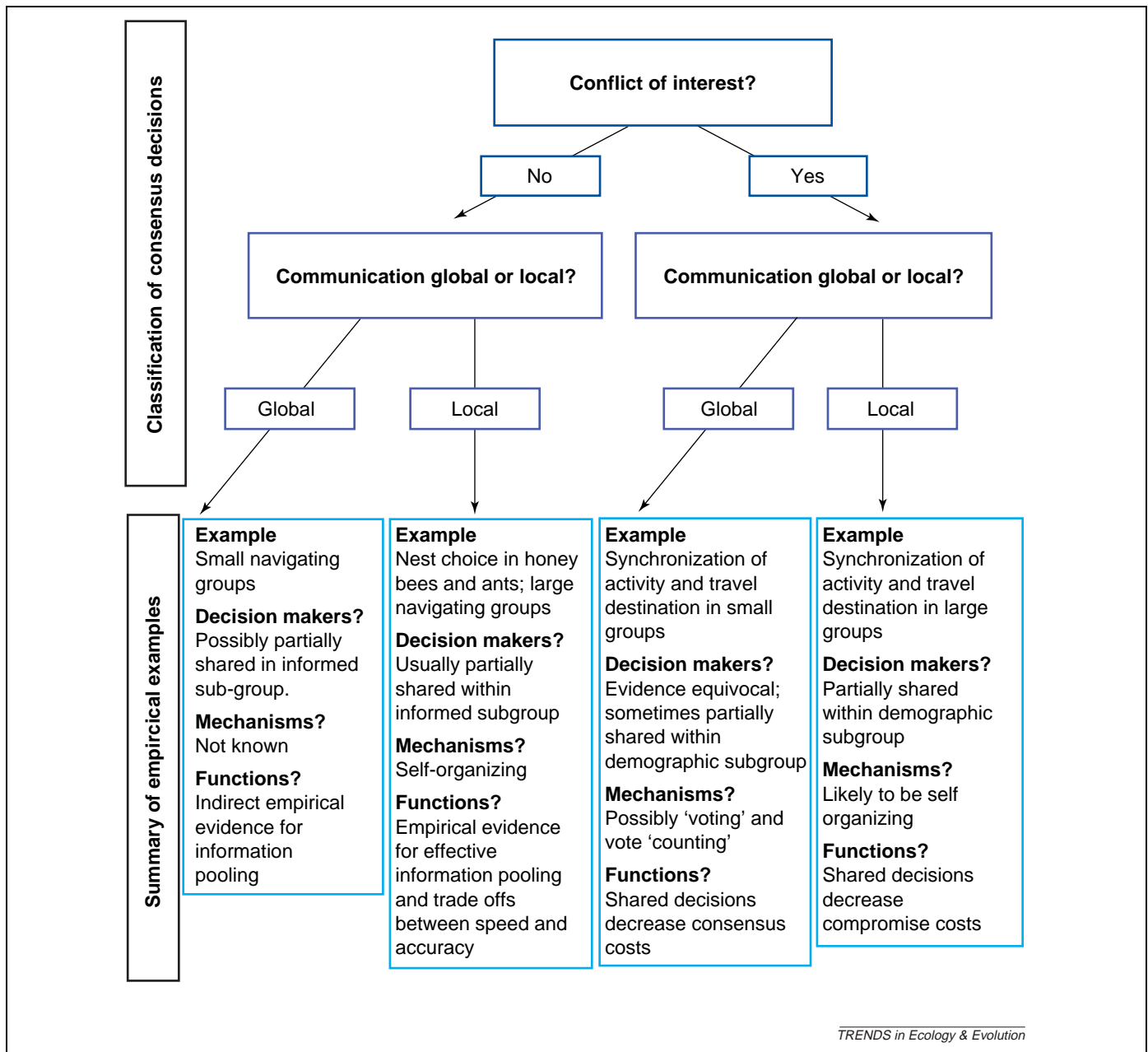


Figure 1. Schematic overview of a framework for understanding consensus decisions. The upper part of the figure classifies consensus decisions according to presence or absence of conflict of interest, and global versus local communication between group members. The lower part of the figure provides empirical examples for each category of consensus decision.

interest lead to dishonesty; consensus costs can also arise in conflict situations [12,30]. Second, whether communication between group members is local or global can also influence which group members contribute to the decision (because it is more difficult to monopolize decisions in large than in small groups: [31]), and it affects the decision-making mechanism. For example, groups with local communication usually have to rely on self-organizing rules [26], whereas more-complex negotiating behaviour can occur only in groups that are small enough to enable global communication [8].

These two features of consensus decisions (conflict of interest and communication) are so important that we discuss them in more detail below. For each consensus decision category, we ask three fundamental questions:

‘Who makes the decision?’; ‘What are the underlying mechanisms?’; and ‘What are the functions?’ (Boxes 2–4). The decision maker(s) can be the dominant animal (unshared decision), particular subsets of group members (partially shared decision) or all group members (equally shared decision) [8]. Potential mechanisms consist of self-organizing rules [15,26] and voting behaviour [8,10]. Potential functions and fitness consequences include information pooling [25], tradeoffs between speed and accuracy [32], and the distribution of consensus costs between group members [8] (Figure 1).

Decision makers in consensus decisions

There are three theoretical possibilities concerning the identity of the decision makers in consensus decisions

Box 2. Consensus decisions about nest choice in eusocial insects

Nest choice in bees and ants is a well studied example of a decision-making process involving little or no conflict of interest.

Who makes the decision?

In swarming honey bees *Apis mellifera* (Figure 1; reproduced with permission from Tom Seeley), ~5% of dispersing bees ('scouts') explore the surrounding area [3,24,25,34–39]. They return to the swarm and advertise their findings by dancing [25,34], whereupon all dancing scouts eventually reach a consensus about the new nest site [25]. The 'opinion' of each scout contributes equally to the decision and is independent of the identity of the individual scout [25]. However, the remaining 95% of bees do not contribute to the decision. Thus, this is an example of a relatively little-shared consensus decision (see Glossary) where the subgroup of scouts makes the decision. A similar situation occurs in *Leptothorax* (*Temnothorax*) *albipennis* ants [27,28,32,40–42,54].

What are the mechanisms?

Individual bee or ant scouts have to communicate their 'opinions' to each other [35], which have to be weighed and pooled [25,27,28] until a consensus is reached by all group members [34]. Communication is only possible on a local level. In bees, scouts that have found a good site dance at a higher intensity and for longer than do scouts that have found a poorer site [3,25,34]. Thus, more scouts are recruited to better sites. These recruits explore the advertised nest sites, return to the swarm and, in turn, advertise their findings, skewing the dancing progressively further in favour of better sites ('positive feedback' [34,36]), until a consensus decision is reached [25]. Initiation of swarm take-off starts before a consensus is reached, when the number of bees at the chosen nest site reaches a certain quorum [39]. In ants, scouts recruit other ants to new nest sites by leading them there, and nest-site quality is encoded in the speed at which an ant begins recruiting [28,41]. Recruited ants return to the colony and recruit other ants in turn. Thus, the positive feedback process begins sooner for better nest sites, and the number of ants increases fastest at the best new site. When the number of ants reaches a particular quorum at a potential new site, the recruiting ants carry the remainder of the colony to that site.

These two decision-making mechanisms have several important features in common: (i) individual group members only communicate locally; (ii) no direct comparison of nest sites by single individuals is necessary; (iii) all information contributes to the decision outcome but no single individual has to 'hold' or 'compare' the total available information; and (iv) the consensus decision is coordinated by a self-organizing system [26], whereby each scout follows relatively simple rules that use only local information but result in a meaningful integration of all available information [24,25,26–28,36–41].

What are the functions and fitness consequences of the decision-making process?

Consensus decision outcomes should be more accurate when more



Figure 1.

group members contribute to the decision [33]. Without information pooling by scouts, bees and ants would be unable to choose the best available nest site because individual scouts often visit only one or a few potential sites [25,27,28,38]. Effective information pooling is important because nest-site quality influences the fitness of the colony [24,27,28,42]. However, it is often also important for nest-site choice to happen quickly owing, for example, to bad weather [25]. The more scouts that are involved, and the higher the quorum threshold needed for a consensus, the longer it is likely to take to make a decision [27,28,42]. Thus, bees and ants face a tradeoff between the accuracy and the speed of a consensus decision, and should choose the number of scouts and quorum threshold accordingly. The tradeoff between speed and accuracy is illustrated by the observation that *L. albipennis* ants lower the quorum required for a consensus when environmental conditions are harsh and a quick decision is needed [32,42].

(Box 1 [8,33]). First, a decision could be made in an 'equally shared' manner, whereby all group members contribute equally to the decision, independently of their individual identities or social status. The consensus is usually reached via a quorum (i.e. a majority, sub-majority or super-majority of members: [33]) or by averaging over all the 'votes' (e.g. [3,10]). Second, the decision could be 'unshared'; that is, taken by a single dominant animal with all other members abiding by its decision. Third, the decision could be made in an intermediate manner ('partially shared', ranging from 'little' to 'widely' shared), whereby several or many group members (typically a demographic subset of members, such as all adult males [1]) contribute more to the decision outcome than do others. There is a continuum from equally shared, via

partially shared, to unshared decisions. Whether a decision is unshared, partially shared or equally shared does not necessarily imply whose interests are being served. For example, unshared decisions can be disadvantageous to the dominant if it is badly informed [33], whereas equally shared decisions rarely profit all members to the same extent [8].

Conflicts of interest and consensus costs

In many groups, conflicts of interest arise between group members about the outcome of a consensus decision [8,11–14]. The presence or absence of such conflicts determines the exchange of decision-related information between group members [26,33], the degree of cooperation during decision making [15,25] and the fitness

Box 3. Consensus decisions about travel routes in navigating birds

Agreements about travel routes in navigating birds (Figure 1) are examples of decisions involving relatively little conflict of interest.

Who makes the decision?

Evidence here is equivocal. Experienced birds sometimes contribute more to the decision than inexperienced birds [55,56], but sometimes not [57,58]. Indirect evidence from flocks of pigeons *Columba livia* and skylarks *Alauda arvensis* suggests that the number of individuals contributing to the decision increases with flock size [59,60]. If flocks of birds are large, it is likely that decisions are widely shared [31].

What are the mechanisms?

Little is known empirically. In principle, individual orientation differences could be suppressed by group cohesion [61]: one model suggests that a compromise by individuals between attraction to neighbours and their own preference for a particular direction can lead to the group travelling in the direction that is preferred by a majority of individuals [15]. Self-organization, whereby individuals follow relatively simple rules requiring only local information, is likely to be a general mechanism underlying cohesive group navigation in large groups [26,45].

What are the functions of the decision-making process?

Assuming that individuals within a group influence one another's navigation [61], information pooling [33] should enable a group to orient more precisely than the individuals comprising it could do if they navigated separately [43,61]. Consequently, directional variability between groups should be inversely related to group size [62] and empirical data on the relationship between group size and directional variability could even be used to determine how many group members contribute to a navigation decision [31]. Other predictions are that grouping should be more prevalent where environmental factors limit the efficiency of orientation tools or where target



Figure 1.

destinations are small; group size should increase until sufficiently accurate navigation is guaranteed; and smaller groups should either have better navigational tools than larger ones or should suffer greater losses during migration [43]. Few empirical data are available to test these predictions. In one study, small flocks of homing pigeons showed a reduction in both directional scatter and homing times compared with single birds [60], but another study contradicts this [63]. Data on migrating skylarks support the prediction that directional scatter between groups should be inversely correlated with group size [59]; and observed navigational accuracy in migrating flocks of birds often exceeds that expected from the navigational abilities of single individuals [43,64].

consequences of the decision outcome to individual members [8]. Typical examples of consensus decisions with no or little conflict of interest are decisions made by eusocial insects about choosing a new nest site (Box 2 [3,24,25,27,28,32,34–42]), or by navigating birds about travel routes (Box 3 [31,43]), because the goal (finding the best nest site, or taking the best route, respectively) is similar for all group members. However, most consensus decisions (e.g. about group activities or travel destinations; Box 4) are likely to involve conflicts of interest between at least some group members [14,23]. The reason for this is as follows. Groups often have to decide between mutually exclusive activities (e.g. resting at a site versus foraging and moving [12,14,23,29,30]) or between moving to different sites (e.g. one offering food versus one offering water [1,2,5–10]). Usually, however, individual group members differ in their optimal timing of activities or their preference for one travel destination over another [4,10,14,23], so that each would prefer to change its activity at a slightly different time from other group members [14,30], or move to a different site [23]. In coatis, for example, some members are better at exploiting one food source, and others at exploiting another [23].

Generally, there is a cost ('consensus cost') involved in timing activities suboptimally [12] or moving to less optimal sites [23] to compromise with other group members. Given that decisions about activity timing and travel destination have to be made regularly during each day, day after day, related consensus costs can augment. That consensus costs (and, thus, conflict) can be

substantial is illustrated by many sexually dimorphic ungulate species (e.g. red deer *Cervus elaphus* [12]), in which conflicts between the sexes about activity budgeting are so large that they lead to intersexual social segregation [8,10–13].

The question of who makes the decision is particularly interesting in relation to consensus decisions involving conflict of interest. Coercion by a dominant individual is potentially a mechanism for resolving conflicts. However, coercion is unlikely to work in practice because of the inability of a dominant animal to force a consensus decision, either because it is physically unable to do so [4,23,29,44], particularly in large groups [10,26,31,45], or because it would not gain sufficiently to outweigh the costs of coercion [8]. Thus, consensus decisions involving conflicts of interest typically have to be made through voluntary compliance to either unshared, equally shared, or other decision-making rules [8,25,27–29,33,43,46]; that is, they require a mechanism for reaching a compromise.

Local and global communication

Communication influences consensus decisions because it limits the mechanisms available for reaching a consensus. For example, in relatively small groups, such as those of many social primates [1,5–7,9], carnivores [23,47] or ungulates [8,11–14], group members can usually communicate directly (i.e. 'globally') with all other members [1,2,48]. Consequently, complex 'negotiating' behaviours and coalitions during consensus decision making are

Box 4. Consensus decisions about activity timing and travel destinations in birds, fish and mammals

These decisions are of interest because they can involve significant conflict of interest between group members [11–14].

Who makes the decision?

Researchers have often assumed *a priori* that a particular group member (usually the most dominant) leads consensus decisions about travel destinations and group activities (Figure 1, [46,65,66]). However, more recent studies have reported variable leadership and the absence of a correlation between leadership and dominance status in several bird and mammal species in captivity ([44,67,68], but see also [69]). Information about decision makers in wild birds and mammals is often based on small data sets or anecdotal reports but in general, decisions seem to be made in a partially shared manner between the adult group members of at least one sex [1,2,5–10].

What are the mechanisms?

In small groups, the opportunity exists for all members to vote [7,8]. Empirical examples of ‘voting’ include specific vocalizations [1,7,48], ritualized signals [2], or more subtle means, such as body orientation [8–10] and initiation movements [5,6,67]. The observation that a majority of ‘votes’ is often decisive suggests that group members can estimate the relative numerosness of votes and, thus, arrive at a consensus decision via a quorum. However, little is known about this process. In large groups with only local communication, no empirical evidence is available about possible mechanisms but self-organizing rules could lead to equally shared consensus decisions [15,26].

What are the functions and fitness consequences of the decision-making process?

Individual group members often have to compromise their own optimal activity budgets to synchronize group activities [14]. The resulting ‘consensus costs’ can be an important factor in shaping the social organization of populations [10–14]. Widely shared decisions decrease total group consensus costs (Box 1) and provide additional benefits via information pooling. However, where there are conflicts of interest, it might pay group members to ‘lie’ about their information in order to bias the consensus decision in favour of their own selfish interest [33]. The need to find a resolution to conflicts of interest between group members might also slow the decision-making process, because individuals might only reluctantly agree to compromise or might take time to negotiate ‘terms of acceptance’.



Figure 1.

conceivable, such as occur in humans where global communication is available [49].

However, in large groups, such as large flocks of birds [31], shoals of fish [50], herds of mammals [10,45] or colonies of social insects [25,27,28], individual group members cannot communicate directly with all other members and are, therefore, dependent on local communication with their spatial neighbours [15,26,37,51]. In such

groups, mechanisms of consensus decision making are probably restricted to self-organizing rules [15,26,37,51]. Self-organizing rules are behavioural rules that individuals can follow using only local information, and which result in an organized group behaviour without the need for global control [15,26,51].

Information pooling

Which group members contribute actively to the decision affects the transfer of information between group members [3,27,28] and the accuracy of the decision outcome. Every group member usually has some information relevant to the decision, but this information contains some error [26,31,43,49]. Depending on which members contribute to the decision outcome, the information from individuals can be more or less efficiently pooled, so that the error in the information available to the whole group will be smaller than the error of a solitary decision maker [8,31,33,41,43,49]. In theory, wider sharing of consensus decisions should increase the probability of a beneficial decision outcome [33,43]. For example, if a group of animals has to decide between two alternatives, of which one is better for the whole group, and each member has a probability of 0.75 of correctly identifying the better alternative, an unshared decision made by one dominant individual would be wrong with a probability of 0.25. However, if an equally shared consensus decision is made, with a simple majority constituting a quorum, the probability of choosing the ‘wrong’ alternative is 0.16 for a group with three members, 0.10 with five members, 0.07 with seven members, and so on. This is because the group only decides on the wrong alternative if a majority of members ‘vote’ for the wrong choice [33]. Mathematical logic implies that, even if the dominant is more experienced and better informed, its error is often larger than the combined error of several inexperienced group members [8].

The accuracy of decisions also depends on quorum size [8]. In the example above, if a consensus decision requires a super-majority of four votes in a group of five animals, the group settles on the ‘wrong’ alternative with a probability of only 0.02. However, a disadvantage of requiring a large quorum is that the group risks reaching no decision if an insufficient number of members is in favour of either alternative.

Information pooling is well known in humans. A famous example, involving the statistician Galton, is of a weight-judging competition at a cattle fair in which people in the crowd, mainly amateurs, were asked to place wagers on the weight of an ox [49]. Galton noted down all the wagers, of which there were nearly 800. Although individual wagers varied widely, the average of all wagers was only different from the real weight of the ox by 0.5 kg. Thus, the errors of all the individual wagers had cancelled each other out, and the crowd as a whole had out-performed the best single wager that was placed. This striking phenomenon of the ‘wisdom of crowds’ is also used, for example, by bookmakers in the context of betting and by the search engine Google (<http://www.google.co.uk>) [49].

In theory, the same principles apply to non-human animals. Consequently, the possibility of information

pooling, leading to a more accurate decision outcome, can result in fitness advantages to consensus decision makers (e.g. [3,27,28]). However, the speed with which a consensus decision can be made might also depend on the number of decision makers, because a larger number might take longer to reach a consensus than a smaller number [27,28,32]. If this is the case, groups might have to adjust the number of decision makers so as to optimize a tradeoff between speed and accuracy (Box 2 [27,28,32]).

Conclusions and future directions

Evidence and theory suggest that consensus decision making is common in animals, across a wide range of species and in many different behavioural contexts. There remain, however, many opportunities for further research. In theory, equally shared decision making enables disagreements about group activities to be resolved in the most profitable way for a majority of group members (Box 1). Consequently, at least moderate cooperation between group members during the decision-making process is expected, even when the decision involves significant conflict of interest. However, in such decisions, evidence is still equivocal as to whether decision making is equally shared or unshared in small groups; more evidence is also needed about the underlying mechanisms in both small and large groups. Studies of dispersing eusocial insects and of homing or migrating animals show that the pooling of information via self-organizing rules might offer fitness advantages that are not available to solitary decision makers. However, little attention has been given to how the advantages provided by information pooling influence the sociality of the species in question. In addition, little information is available about how the effectiveness of information pooling, and the cooperation of group members during the decision-making process, are modified in cases involving significant conflict of interest.

Interest in consensus decision making in non-human animals is relatively recent but is expanding rapidly and is already offering novel and interesting perspectives on various aspects of social behaviour and cognition. Investigation of the relatively simple consensus decisions that are faced by animals might also yield insights into the evolution of cooperation, communication and group decision making in humans. We hope that the present review will stimulate further empirical and theoretical work in this exciting area.

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References

- Stewart, K.J. and Harcourt, A.H. (1994) Gorillas vocalizations during rest periods – signals of impending departure. *Behaviour* 130, 29–40
- Black, J.M. (1988) Preflight signaling in swans – a mechanism for group cohesion and flock formation. *Ethology* 79, 143–157
- Seeley, T.D. and Visscher, P.K. (2004) Group decision making in nest-site selection by honey bees. *Apidologie* 35, 101–116
- Krause, J. and Ruxton, G.D. (2002) *Living in Groups*, Oxford University Press
- Milton, K. (2000) Quo vadis? Tactics of food search and group movement in primates and other animals. In *On the Move* (Boinski, S. and Garber, P.A., eds), pp. 357–418, University of Chicago Press
- Byrne, R.W. (2000) How monkeys find their way: leadership, coordination and cognitive maps of African baboons. In *On the Move* (Boinski, S. and Garber, P.A., eds), pp. 491–518, University of Chicago Press
- Boinski, S. and Campbell, A.F. (1995) Use of trill vocalizations to coordinate troop movement among white-faced capuchins – a 2nd field-test. *Behaviour* 132, 875–901
- Conradt, L. and Roper, T.J. (2003) Group decision making in animals. *Nature* 421, 155–158
- Norton, G.W. (1986) Leadership decision processes of group movement in yellow baboons. In *Primate Ecology and Conservation* (Else, J.G. and Lee, P.C., eds), pp. 145–156, Cambridge University Press
- Prins, H.H.T. (1996) *Ecology and Behaviour of the African Buffalo*, Chapman & Hall
- Ruckstuhl, K.E. and Neuhaus, P. (2002) Sexual segregation in ungulates: a comparative test of three hypotheses. *Biol. Rev.* 77, 77–96
- Conradt, L. (1998) Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proc. R. Soc. Lond. B Biol. Sci.* 265, 1359–1363
- Ruckstuhl, K.E. and Neuhaus, P. (2000) Sexual segregation in ungulates: a new approach. *Behaviour* 137, 361–377
- Ruckstuhl, K.E. (1998) Foraging behaviour and sexual segregation in bighorn sheep. *Anim. Behav.* 56, 99–106
- Couzin, I.D. et al. (2005) Effective leadership and decision-making in animal groups on the move. *Nature* 433, 513–516
- Courchamp, F. et al. (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
- Beshers, S.N. and Fewell, J.H. (2001) Models of division of labor in social insects. *Annu. Rev. Entomol.* 46, 413–440
- Clutton-Brock, T.H. (1998) Reproductive skew, concessions and limited control. *Trends Ecol. Evol.* 13, 288–292
- Deneubourg, J.L. et al. (2002) Dynamics of aggregation and emergence of cooperation. *Biol. Bull.* 202, 262–267
- Valone, T.J. and Templeton, J.J. (2002) Public information for the assessment of quality: a widespread social phenomenon. *Philos. Trans. R. Soc. Lond. B Biol. Sc.* 357, 1549–1557
- Hemelrijk, C.K. and Kunz, H. (2003) Introduction to special issue on collective effects of human behavior. *Artif. Life* 9, 339–341
- Hammond, R.L. and Keller, L. (2004) Conflict over male parentage in social insects. *PLoS Biol.* 2, 1472–1482
- Gompper, M.E. (1996) Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. *Behav. Ecol.* 7, 254–263
- Seeley, T.D. and 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
- Seeley, T.D. and Buhrman, S.C. (1999) Group decision making in swarms of honey bees. *Behav. Ecol. Sociobiol.* 45, 19–31
- List, C. (2004) Democracy in animal groups: a political science perspective. *Trends Ecol. Evol.* 19, 168–169
- Couzin, I.D. and Krause, J. (2003) Self-organization and collective behavior in vertebrates. *Adv. Stud. Behav.* 32, 1–75
- Franks, N.R. et al. (2003) Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. *Anim. Behav.* 65, 215–223
- Franks, N.R. et al. (2002) Information flow, opinion polling and collective intelligence in house-hunting social insects. *Philos. Trans. R. Soc. Lond. B Biol. Sc.* 357, 1567–1583
- Rands, S.A. et al. (2003) Spontaneous emergence of leaders and followers in foraging pairs. *Nature* 423, 432–434
- Conradt, L. and Roper, T.J. (2000) Activity synchrony and social cohesion: a fission–fusion model. *Proc. R. Soc. Lond. B Biol. Sci.* 267, 2213–2218
- Wallraff, H.G. (1978) Social interrelations involved in migratory orientation of birds – possible contribution of field studies. *Oikos* 30, 401–404
- Franks, N.R. et al. (2003) Speed versus accuracy in collective decision-making. *Proc. R. Soc. Lond. B Biol. Sci.* 270, 2457–2463

- 34 Seeley, T.D. (2003) Consensus building during nest-site selection in honey bee swarms: the expiration of dissent. *Behav. Ecol. Sociobiol.* 53, 417–424
- 35 Seeley, T.D. (1997) Honey bee colonies are group-level adaptive units. *Am. Nat.* 150, S22–S41
- 36 Camazine, S. *et al.* (1999) House-hunting by honey bee swarms: aggregated decisions and individual behaviors. *Ins. Soc.* 46, 348–360
- 37 Seeley, T.D. and Visscher, P.K. (2003) Choosing a home: how the scouts in a honey bee swarm perceive the completion of their group decision making. *Behav. Ecol. Sociobiol.* 54, 511–520
- 38 Seeley, T.D. (2002) When is self-organization used in biological systems? *Biol. Bull.* 202, 314–318
- 39 Britton, N.F. *et al.* (2002) Deciding on a new home: how do honeybees agree? *Proc. R. Soc. Lond. B Biol. Sci.* 269, 1383–1388
- 40 Pratt, S.C. *et al.* (2002) Quorum sensing, recruitment, and aggregated decision making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* 52, 117–127
- 41 Mallon, E.B. *et al.* (2001) Individual and aggregated decision making during nest site selection by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* 50, 352–359
- 42 Dornhaus, A. *et al.* (2004) Ants move to improve: colonies of *Leptothorax albipennis* emigrate whenever they find a superior nest site. *Anim. Behav.* 67, 959–963
- 43 Simons, A.M. (2004) Many wrongs: the advantage of group navigation. *Trends Ecol. Evol.* 19, 453–455
- 44 Beauchamp, G. (2000) Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour* 137, 301–314
- 45 Gueron, S. *et al.* (1996) The dynamics of herds: from individuals to aggregations. *J. Theor. Biol.* 182, 85–98
- 46 Kummer, H. (1968) *Social Organisation in Hamadryas Baboons*, University of Chicago Press
- 47 Clutton-Brock, T.H. *et al.* (2001) Effects of helpers on juvenile development and survival in meerkats. *Science* 293, 2446–2449
- 48 Poole, J.H. *et al.* (1988) The social contexts of some very low-frequency calls of African elephants. *Behav. Ecol. Sociobiol.* 22, 385–392
- 49 Surowiecki, J. (2004) *The Wisdom of Crowds*, Doubleday
- 50 Krause, J. *et al.* (2000) Fish shoal composition: mechanisms and constraints. *Proc. R. Soc. Lond. B Biol. Sci.* 267, 2011–2017
- 51 Huse, G. *et al.* (2002) Modelling changes in migration pattern of herring: collective behaviour and numerical domination. *J. Fish Biol.* 60, 571–582
- 52 Parrish, J.K. *et al.* (2002) Self-organized fish schools: an examination of emergent properties. *Biol. Bull.* 202, 296–305
- 53 Grunbaum, D. *et al.* (2005) Extracting interactive control algorithms from group dynamics of schooling fish. In *Lecture Notes in Control and Information Sciences* (Kumar, V. *et al.*, eds), pp. 103–117, University of San Francisco
- 54 Pratt, S.C. (2005) Quorum sensing by encounter rates in the ant *Temnothorax albipennis*. *Behav. Ecol.* 16, 488–496
- 55 Schueze, E. (1971) *Grundriss der Vogelzugkunde*, Parey
- 56 Wagner, G. (1975) Zur Frage des Flugfuehrens in heimkehrenden Brieftaubengruppen. *Zeit. Tierpsychol.* 39, 61–74
- 57 Guilford, T. and Chappell, J. (1996) When pigeons home alone: does flocking have a navigational function? *Proc. R. Soc. Lond. B Biol. Sci.* 263, 153–156
- 58 de Perera, T.B. and Guilford, T. (1999) The social transmission of spatial information in homing pigeons. *Anim. Behav.* 57, 715–719
- 59 Rabol, J. and Noer, H. (1973) Spring migration in the skylark (*Alauda arvensis*) in Denmark. *Vogelwarte* 27, 50–65
- 60 Tamm, S. (1980) Bird orientation: single homing pigeons compared with small flocks. *Behav. Ecol. Sociobiol.* 7, 319–322
- 61 Bergman, G. and Donner, K.O. (1964) An analysis of the spring migration of the common scoter and the longtailed duck in southern Finland. *Acta Zool. Fenn.* 105, 1–60
- 62 Hamilton, W.J. (1967) Social aspects of bird orientation mechanisms. In *Animal Orientation and Navigation* (Storm, R.M., ed.), pp. 57–59, Oregon State University Press
- 63 Keeton, W.T. (1970) Comparative orientational and homing performance of single pigeons and small flocks. *Auk* 87, 797–799
- 64 Thorup, K. and Rabol, J. (2001) The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns. *J. Avian Biol.* 32, 111–119
- 65 Dunbar, R.I.M. (1983) Structure of Gelada baboon reproductive units: 4. Integration at group level. *Zeit. Tierpsychol.* 63, 265–282
- 66 Wagenknecht, E. (1980) *Der Rothirsch*, Ziemsen
- 67 Lamprecht, J. (1992) Variable leadership in bar-headed geese (*Anser indicus*) – an analysis of pair and family departures. *Behaviour* 122, 105–120
- 68 Leca, J.B. *et al.* (2003) Distributed leadership in semifree-ranging white-faced capuchin monkeys. *Anim. Behav.* 66, 1045–1052
- 69 Radford, A.N. (2004) Vocal coordination of group movement by green woodhoopoes (*Phoeniculus purpureus*). *Ethology* 110, 11–20

Articles of Interest in *Current Opinions and Trends* Journals

- T.A. Richards and D. Bass (2005) Molecular screening of free-living microbial eukaryotes: diversity and distribution using a meta-analysis. *Current Opinion in Microbiology* 8, 240–252
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- W.J. Foley and B.D. Moore (2005) Plant secondary metabolites and vertebrate herbivores – from physiological regulation to ecosystem function. *Current Opinion in Plant Biology* doi: 10.1016/j.pbi.2005.05.009
- G.Q. Romero and W.W. Bension (2005) Biotic interactions of mites, plants and leaf domatia. *Current Opinion in Plant Biology* doi: 10.1016/j.pbi.2005.05.006
- C. Zipfel and G. Felix (2005) Plants and animals: a different taste for microbes? *Current Opinion in Plant Biology* doi: 10.1016/j.pbi.2005.05.004
- D.J. Buller (2005) Evolutionary psychology: the emperor's new paradigm. *Trends in Cognitive Sciences* 9, 277–283