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**

**Consensus 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.
between group members are described in Boxes 2–4. Nest synchronization of group activities and travel destinations (nest site) is similar for all group members. By contrast, the homing and migrating birds (Box 3), involve relatively site choice in eusocial insects (Box 2), and navigation in

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 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].

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
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.
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 I; 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 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].

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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 I) 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 [55,66], 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 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
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 I, [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?
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’.

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].

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 conception, 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
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 trade-off 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 sociability 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

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