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**Article (Accepted version)
(Refereed)**

The University of Chicago

Swarm Intelligence: When Uncertainty Meets Conflict

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abstract: Good decision making is important for the survival and fitness of stakeholders, but decisions usually involve uncertainty and conflict. We know surprisingly little about profitable decision-making strategies in conflict situations. On the one hand, sharing decisions with others can pool information and decrease uncertainty (swarm intelligence). On the other hand, sharing decisions can hand influence to individuals whose goals conflict. Thus, when should an animal share decisions with others? Using a theoretical model, we show that, contrary to intuition, decision sharing by animals with conflicting goals often increases individual gains as well as decision accuracy. Thus, conflict—far from hampering effective decision making—can improve decision outcomes for all stakeholders, as long as they share large-scale goals. In contrast, decisions shared by animals without conflict were often surprisingly poor. The underlying mechanism is that animals with conflicting goals are less correlated in individual choice errors. These results provide a strong argument in the interest of all stakeholders for not excluding other (e.g., minority) factions from collective decisions. The observed benefits of including diverse factions among the decision makers could also be relevant to human collective decision making.

Keywords: collective behavior, conflict resolution, cooperation, quorum decision, shared decision, social choice.

Introduction

From insects to mammals, animals that live in groups need to make vital decisions collectively (Conradt and Roper 2005). Group members have to decide together about communal nesting sites; communal activities; when and where to forage, shelter, or rest; communal migration routes; and communal enterprises (Seeley and Buhrman 1999; Ame et al. 2006; Biro et al. 2006; Kerth et al. 2006; Ballerini et al. 2008; Petit et al. 2009; Ramseyer et al. 2009; Kerth 2010; Nagy et al. 2010; McComb et al. 2011; Pyritz et al. 2011; Sueur et al. 2011). Often, outcomes of collective

decisions have important implications with respect to individual survival, fitness, and group cohesion and can even shape the social organization of a species (Krause and Ruxton 2002; Ruckstuhl and Neuhaus 2002). Thus, successful group living requires the ability to make good collective decisions.

Good decisions often require good information. However, decisions usually involve large uncertainties (Codling et al. 2007; List et al. 2009; Sumpter and Pratt 2009; Krause et al. 2010; Ward et al. 2011). That is, no single animal holds all the decision-relevant information, and personal information can contain errors. In such situations, by sharing the decision making (e.g., through majority vote), several decision makers can pool their personal information and eliminate individual errors, often resulting in better informed decision outcomes (List 2004; Couzin et al. 2005, 2011; Hastie and Kameda 2005; Krause et al. 2010). This wisdom of the crowd (in humans) or swarm intelligence (in other animals) is an important phenomenon that is utilized by stock markets, betting agents, and web search engines and, in animals, by house-hunting insect swarms, predator-avoiding fish shoals, and migrating bird flocks (Seeley and Buhrman 1999; Biro et al. 2006; List et al. 2009; Krause et al. 2010; Ward et al. 2011).

In addition to information uncertainty, collective decisions often involve conflicting personal goals. That is, individual stakeholders in the decision often disagree, in principle, as to what would constitute a desirable decision outcome (Conradt and Roper 2003, 2007, 2009; King et al. 2008; Conradt et al. 2009; Hix et al. 2009; Bousquet and Manser 2011). For example, hungry animals often prefer different communal activities than do well-fed group members, and small vulnerable animals have other priorities in communal enterprises than do larger animals (Clutton-Brock et al. 1982; Krause et al. 1992; Prins 1996; Ruckstuhl and Neuhaus 2002; King et al. 2008; Lingle et al. 2008). Such conflicting personal goals can have important survival and fitness implications (Conradt and Roper 2005).

Conflicting personal goals might influence the manner

with which individuals treat and use the information provided by others, so that, in situations with conflict, the sharing of decision making could have disadvantages as well as advantages to an individual. This is because decision sharing might pool information that is biased and, in particular, because it could hand influence of the decision outcome to others whose personal goals differ from the individual's own personal goals (Austen-Smith and Feddersen 2009; Schulte 2010; Conradt 2012). Thus, conflicting goals and information uncertainty are likely to interact to shape the decision-making strategies of individuals and, hence, the resulting group behavior (Austen-Smith and Feddersen 2009; Schulte 2010; see also app. B, available online). Consequently, we need to look at the influence of uncertainty and conflict on individual strategies concurrently in order to properly understand collective decision-making strategies.

While a huge body of research in a wide range of disciplines looks at collective decisions in situations with information uncertainty (e.g., Gigerenzer and Goldstein 1996; Couzin et al. 2005, 2011; Lusseau and Conradt 2009; Marshall et al. 2009; Moussaid et al. 2009; Sumpter and Pratt 2009; Katsikopoulos and King 2010; Krause et al. 2010) or in situations with conflicting goals (e.g., Conradt and Roper 2003, 2007, 2009; Rands et al. 2003; Kerth et al. 2006; Dostalkova and Spinka 2007; King et al. 2008; Conradt et al. 2009; Petit et al. 2009; Bousquet and Manser 2011), surprisingly few studies in biology have looked at both factors concurrently (Schulte 2010; Conradt 2012; for a detailed review, see "Discussion").

In this study, we ask what are, in principle, profitable (adaptive) decision-making strategies in collective decisions that involve simultaneously information uncertainty and conflicting goals. First, we develop an animal collective decision-making model that is formulated with a view to being as general and widely applicable as possible. Next, we use the model to investigate the principal consequences of different empirical decision-making strategies in animals (e.g., decision sharing, unshared decision making; Conradt and Roper 2005) with respect to (1) decision errors (i.e., decision accuracy) and (2) individual decision gains. Finally, on the basis of the model results, we make predictions about adaptive strategies of animals in collective decisions in different environments. We discuss our results including a (tentative) view to human collective decision making.

Methods: The Model

In order to make the model widely applicable, we consider animal collective decisions with a typical conflict structure for noneusocial species, namely that of large-scale goal agreement in conjunction with small-scale goal conflict (box 1).

Brief Model Summary

We consider a decision between two mutually exclusive decision options. In accordance with relevant animal decisions (box 1), we assume that all animals have the same large-scale goal to decide in favor of a productive option, but there is goal conflict between animals with respect to smaller-scale feature(s) of the options (conflicting goals). In our model, these large- and small-scale goals are reflected in the gains that different animals can achieve from a given decision outcome. Additionally, we assume that animals have only uncertain personal information about the productivity state of either option (information uncertainty).

We consider the following potential decision-making strategies (based on observed decision-making strategies in animals; for a review, see Conradt and Roper 2005). First, an animal makes an individual decision on the basis

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Box 1: Large-scale goal agreement in conjunction with small-scale goal conflict

We considered only animals that live in relatively stable groups (Krause and Ruxton 2002; Kerth 2010). These frequently make collective decisions about issues that matter for fitness and survival (Conradt and Roper 2003). Members of any such group typically share large-scale goals since they would otherwise not live socially (Krause and Ruxton 2002). For example, in migration decisions, all animals prefer to use routes that lead to a communal viable destination over routes that do not; in foraging decisions, all prefer to visit foraging patches that yield at least some food; in decisions about collective activities, all animals prefer those that lead to success of the communal enterprise over those that do not (Clutton-Brock et al. 1982; Creel and Creel 1995; Biro et al. 2006; Nagy et al. 2010; McComb et al. 2011). However, at the same time, individual animals within a group often differ in their goals with respect to smaller-scale issues, depending on their personal needs (Ruckstuhl and Neuhaus 2002; Conradt and Roper 2003, 2005, 2007). For example, when faced with a choice between different migration routes that all lead to a viable destination, vulnerable animals often prefer the safest route, while others might prefer the shortest one; if there is a choice between different foraging patches that each yield food, smaller animals often prefer a patch with a higher forage quality and larger animals one with a higher forage quantity; or in a choice of collective activities, animals in different physiological states often have different priorities and risk aversity (e.g., Clutton-Brock et al. 1982; Ruckstuhl and Neuhaus 2002; King et al. 2008; Lingle et al. 2008; Nagy et al. 2010). Thus, if there are conflicts, then most commonly they take the form of large-scale goal agreement in conjunction with small-scale goal conflict in social (but noneusocial) species (Conradt and Roper 2005). We have developed a decision model that captures this typical conflict structure of noneusocial species.

of either an uninformed or an informed personal choice. Second, a number of animals make the decision by following/being a dictator/leader. Third, a number of animals share the decision. In a shared decision, the number of decision makers can vary, and decision makers can be either homogeneous or diverse with respect to their small-scale goals. We use the model to predict for each potential decision-making strategy (1) the likelihood of a large-scale decision error (i.e., the decision accuracy) and (2) the expected decision gains to different animals.

Decision Options

We assume that a group of animals is making a decision between two mutually exclusive options A and B. These two options could be, for example, two migration routes, two foraging patches, or two communal activities. We further assume that each of the two options can be in one of two states (independent of the state of the other option): it can be either productive or unproductive with respect to the communal large-scale goal of all group members (box 1). Here, the term "productive" is to be understood in a very broad and general sense; for example, a migration route is productive if it leads to the desired communal migration destination, a foraging patch is productive if it yields food, an activity is productive if it leads to success of the communal enterprise, and so on (Clutton-Brock et al. 1982; Packer and Ruttan 1988; Boesch 1994; Creel and Creel 1995; Nagy et al. 2010; McComb et al. 2011). We define the probability that option A is productive as prod_A and the probability that option B is productive as prod_B. In order not to bias the situation, we assume for this purpose that these probabilities are equal (i.e., $\text{prod}_A = \text{prod}_B = \text{prod}$; table 1).

Conflict Structure

Large-Scale Goal Agreement. On the basis of the typical conflict structure in relevant animal decisions (box 1), we assume that there is general goal agreement with respect to the crucial large-scale state of the environment (termed "productivity"), so that all animals prefer a productive to an unproductive option. Large-scale goal agreement is typical for members of stable groups since they would otherwise not live socially (Clutton-Brock et al. 1982; Creel and Creel 1995; Krause and Ruxton 2002; Biro et al. 2006; Nagy et al. 2010; McComb et al. 2011; see also box 1). Large-scale goal agreement also occurs frequently in more open groups in fission-fusion societies (Kerth et al. 2006; Sueur et al. 2011; see also "Fission-Fusion Societies" in app. B). Here, we do not explore situations where there is no large-scale goal agreement, because these are not typical for stable groups and in such situations there is, in principal, no ad-

vantage in information sharing. These situations are, therefore, already covered by existing models that deal with conflict alone (for a review, see Conradt 2012).

Small-Scale Goal Conflict. Further, we assume that there is small-scale goal conflict between at least some individuals (box 1). That is, we assume that options A and B differ with respect to some (smaller-scale) feature(s) (e.g., route safety vs. length, food quality vs. quantity, activity risk vs. expenditure: Clutton-Brock et al. 1982; Packer and Ruttan 1988; Krause et al. 1992; Biro et al. 2006; King et al. 2008; Lingle et al. 2008; Nagy et al. 2010; note that in a two-option decision, the detailed structure of the small-scale feature[s] is not relevant). We further assume that individuals differ in their goals with respect to the small-scale feature(s), so that if both options are productive, then some animals prefer option A (A-animals) and others option B (B-animals).

Individual Gains

The described large-scale goal agreement and small-scale goal conflict are reflected in the potential gains (payoffs) to individuals resulting from different decision outcomes (table 1). If the decision outcome is in favor of an unproductive option, no animal gains benefits (large-scale error). If the decision outcome is in favor of a productive option, then all animals gain at least one unit of benefits (large-scale goal is achieved). If this decision outcome is option A, and if option A is productive, then animals with a small-scale goal preference for option A (A-animals) additionally gain g ($g > 0$) units of benefit. Vice versa, if the decision outcome is option B, and if option B is productive, then animals with a small-scale goal preference for option B (B-animals) additionally gain g units of benefit. These extra gains g reflect the degree of small-scale goal conflict between A- and B-animals: a small g implies a low small-scale conflict, and a high g implies a high small-scale conflict. Since large-scale goals are generally more important than small-scale goals (Clutton-Brock et al. 1982; Krause and Ruxton 2002), we assume that $g < 1$. We are interested in the standardized individual gains (i.e., the ratio of expected gains to maximally possible gains). These are as follows for an A-animal (for details of derivation, see "Individual Gains" in app. A):

$$\text{gains to A-animal} =$$
$$\{\text{prod}^2[1 + P_{\text{outcome}_A}(A_{\text{prod}}, B_{\text{prod}})g]$$
$$+ \text{prod}(1 - \text{prod})P_{\text{outcome}_A}(A_{\text{prod}}, B_{\text{unprod}})(1 + g) \quad (1)$$
$$+ (1 - \text{prod})\text{prod}[1 - P_{\text{outcome}_A}(A_{\text{unprod}}, B_{\text{prod}})]\}$$
$$/[\text{prod}(1 + g) + (1 - \text{prod})\text{prod}],$$

Table 1: Formal summary of basic model assumptions

True state of environment	Likelihood of state	Gains depending on decision outcome A or B				Probability that individual believes (wrongly or rightly) state to be				Probability P_A that informed personal choice is option A ($P_B = 1 - P_A$)		
		A-animal		B-animal		$A_{\text{prod}}, B_{\text{prod}}$	$A_{\text{prod}}, B_{\text{unprod}}$	$A_{\text{unprod}}, B_{\text{prod}}$	$A_{\text{unprod}}, B_{\text{unprod}}$	A-animal $P_A(A)$	B-animal $P_A(B)$	Unbiased animal $P_A(U)$
		A	B	A	B							
$A_{\text{prod}}, B_{\text{prod}}$	prod^2	$1+g$	1	1	$1+g$	q^2	$q(1-q)$	$(1-q)q$	$(1-q)^2$	$1-(1-q)q$	$q(1-q)$	.5
$A_{\text{prod}}, B_{\text{unprod}}$	$\text{prod}(1-\text{prod})$	$1+g$	0	1	0	$q(1-q)$	q^2	$(1-q)^2$	$(1-q)q$	$1-(1-q)^2$	q^2	q
$A_{\text{unprod}}, B_{\text{prod}}$	$(1-\text{prod})\text{prod}$	0	1	0	$1+g$	$(1-q)q$	$(1-q)^2$	q^2	$q(1-q)$	$1-q^2$	$(1-q)^2$	$1-q$
$A_{\text{unprod}}, B_{\text{unprod}}$	$(1-\text{prod})^2$	0	0	0	0	$(1-q)^2$	$(1-q)q$	$q(1-q)$	q^2	$1-(1-q)q$	$(1-q)q$	.5

Note: $A_{\text{prod}}/A_{\text{unprod}}$ = option A is productive/unproductive; $B_{\text{prod}}/B_{\text{unprod}}$ = option B is productive/unproductive.

whereby the P_{outcome_A}'s are the probabilities that the decision outcome is in favor of option A, depending on the true productivity states of both options ($A_{\text{prod}}/A_{\text{unprod}}$ and $B_{\text{prod}}/B_{\text{unprod}}$) and on the decision-making strategy (see below; table 2).

an animal judges the true productivity state of both options correctly with probability q^2 (table 1). The size of q also represents the uncertainty/predictability of the environment: if q is small, the environment has high uncertainty; if q is large, the environment is very predictable.

Information Uncertainty

Since decisions usually involve uncertainty (Krause et al. 2010), we assume that each animal has only imperfect personal information about the productivity state of either option, so that an individual animal privately judges the productivity state of an option correctly with probability q. We term this the animal's information reliability q. The probability that an animal judges correctly is assumed to be greater than chance (i.e., $q > 0.5$) but less than certain (i.e., $q < 1$). For the present purpose, we assumed that all individuals have the same information reliability q. Thus,

Personal Choices

Before animals can make collective decisions by aggregating choices, they first have to establish their own personal choice. In this setting, there are exactly two adaptive candidate heuristics for an animal with small-scale goals to make a personal (i.e., individual, noncollective) choice between options A and B (for detailed arguments, see "Personal Choice" in app. B), which we both consider. One candidate heuristic is to ignore all personal information about the large-scale states of the options and to always choose the option with the preferred small-scale

Table 2: List of candidate strategies and their implications for the decision outcome

Candidate strategies	Probability P_{outcome_A} that the decision outcome is in favor of option A[a] if the true states of productivity are[b]		
	$A_{\text{prod}} + B_{\text{prod}}$	$A_{\text{prod}} + B_{\text{unprod}}$	$A_{\text{unprod}} + B_{\text{prod}}$
S1: random decision	.5	.5	.5
S2: individual decision (A-animal):			
S2a: uninformed personal choice	1	1	1
S2b: informed personal choice	$1 - (1 - q)q$	$1 - (1 - q)^2$	$1 - q^2$
S2′: individual decision (B-animal):			
S2′a: uninformed personal choice	0	0	0
S2′b: informed personal choice	$q(1 - q)$	q^2	$(1 - q)^2$
S3: dictator (A-animal):			
S3a: uninformed personal choice	1	1	1
S3b: informed personal choice	$1 - (1 - q)q$	$1 - (1 - q)^2$	$1 - q^2$
S3′: dictator (B-animal):			
S3′a: uninformed personal choice	0	0	0
S3′b: informed personal choice	$q(1 - q)$	q^2	$(1 - q)^2$
S4: Shared decision making:[c]			
S4a: uninformed personal choice	1 if $n_A > n_B$, 0 if $n_A < n_B$	1 if $n_A > n_B$, 0 if $n_A < n_B$	1 if $n_A > n_B$, 0 if $n_A < n_B$
S4b: informed personal choice	$\sum\limits_{i=\max[0,(n+1)/2-n_B]}^{n_A} \sum\limits_{j=\max[0,(n+1)/2-i]}^{n_B} \left[\binom{n_A}{i} P_A(A)^i (1 - P_A(A))^{n_A - i} \binom{n_B}{j} P_B(A)^j (1 - P_B(A))^{n_B - j} \right]^{\text{d}}$		
S4c: majority makes informed personal choice/minority makes uninformed personal choice[e]	$P_A(A^{(n+1)/2})^{\text{d}}$		
5: Condorcet jury[f]	$\sum\limits_{i=(n+1)/2}^{n} \left[\binom{n}{i} P_A(U)^i (1 - P_A(U))^{n_A - i} \right]^{\text{d}}$		

[a] Probability that the decision outcome is in favor of option B is $P_{\text{outcome}_B} = 1 - P_{\text{outcome}_A}$.

[b] $A_{\text{prod}}/A_{\text{unprod}}$ = option A is productive/unproductive; $B_{\text{prod}}/B_{\text{unprod}}$ = option B is productive/unproductive.

[c] Set of decision makers: n_A, A-animals; n_B, B-animals. Number of decision makers: $n = n_A + n_B$. Diversity: div $= 4n_A n_B/n^2$.

[d] $P_A(A)$, $P_A(B)$, and $P_A(U)$ are the probabilities that the informed personal choice of an A-animal, B-animal, and unbiased animal, respectively, is option A. $P_A(A)$, $P_A(B)$, and $P_A(U)$ depend on the true productivity state of either option and on the information reliability q. Their various values are given in table 1.

[e] A majority of decision makers of +1 is assumed, and the value is given for a situation in which the majority are A-animals (i.e., $n_A = (n + 1)/2$ and $n_B = (n - 1)/2$).

[f] Set of n unbiased decision makers. This strategy is not available to animals in a conflict situation and is for comparison only.

feature(s) (uninformed personal choice; i.e., an A-animal's personal choice is always option A, a B-animal's option B). The other candidate heuristic is to choose the option with the preferred small-scale feature(s) unless the animal believes that that option is unproductive and, at the same time, that the other option is productive (in which case, the animal chooses the other option; informed personal choice; table 1; note that these are the only two candidate heuristics for making an adaptive personal choice; for details, see "Personal Choice" in app. B).

For reasons of comparison only, we also consider the choice that an animal would make that has no small-scale goal preferences (an unbiased animal). If an unbiased animal believes that either both options or none are pro-

ductive, it makes a random personal choice; otherwise, it makes (an informed) personal choice in favor of the option that it believes to be productive (table 1).

Candidate Decision-Making Strategies

We are deliberately not looking for an abstract optimal decision-making strategy, since it is highly unlikely that animals have the cognitive and rational abilities to find and implement an optimal strategy, and an optimal strategy (outside of the range of observed or basic strategies) would therefore be unrealistic (bounded rationality; Gigerenzer and Goldstein 1996). Instead, it is reasonable to assume that animals always use, from a range of feasible
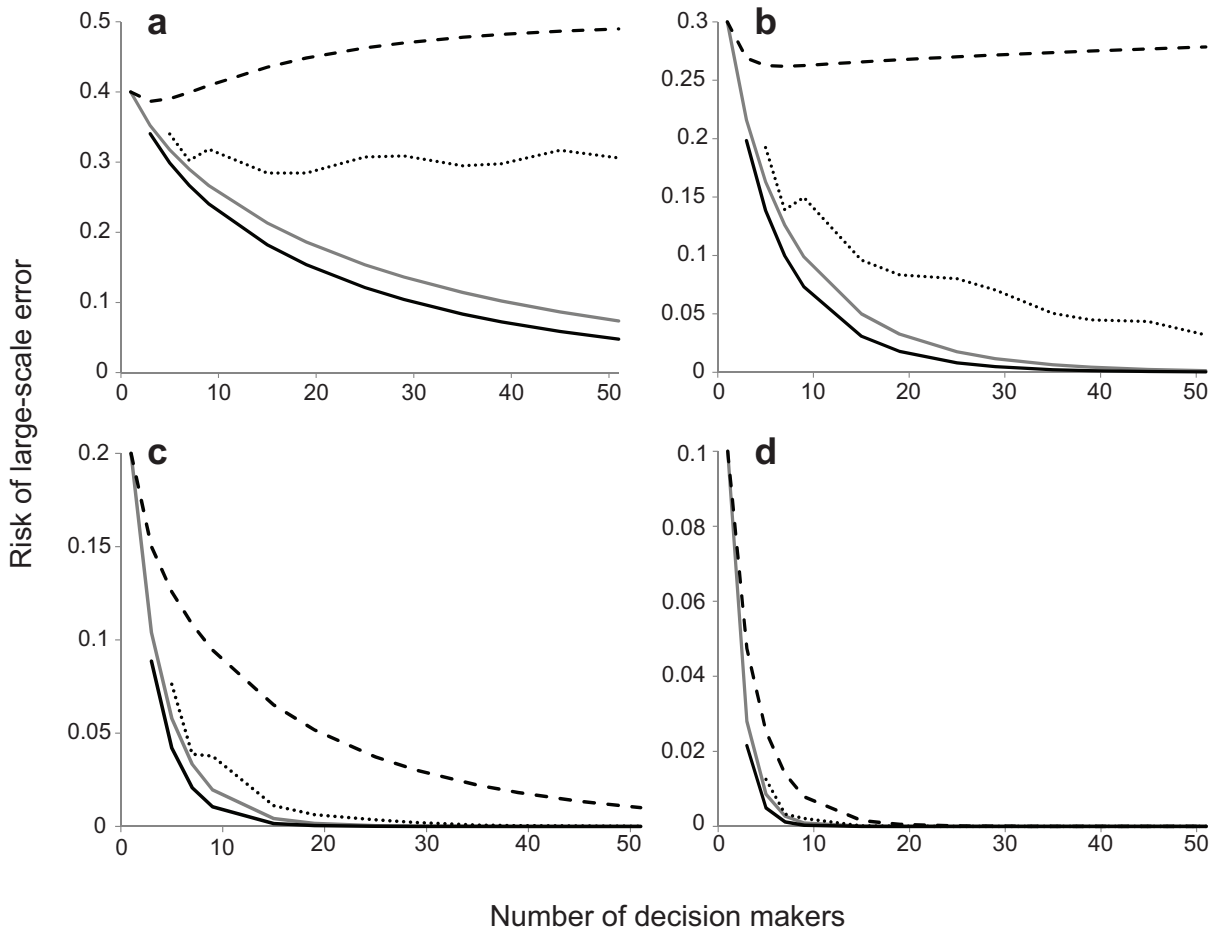

Figure 1: Risk of large-scale error as a function of the number of decision makers (for clarity, scaling of the vertical axis differs between panels). Black lines, sets of decision makers consist of A- and B-animals with a common large-scale goal but conflicting small-scale goals. The decision makers are either homogeneous with respect to small-scale goals (dashed lines, all decision makers have the same small-scale goal; div = 0), medium diverse (dotted lines, approximately three-fourths of decision makers have one small-scale goal and one-fourth the other; div = 0.75; $n_A + n_B \geq 3$), or maximally diverse (solid lines, approximately one-half of decision makers are A-individuals and one-half are B-individuals; div = 1; $n_A + n_B \geq 3$; see fig. 2). Gray solid lines, sets of unbiased decision makers without small-scale goals (Condorcet juries, given for reasons of comparison). Individual information reliability: $q = 0.6$ (*a*), $q = 0.7$ (*b*), $q = 0.8$ (*c*), $q = 0.9$ (*d*).
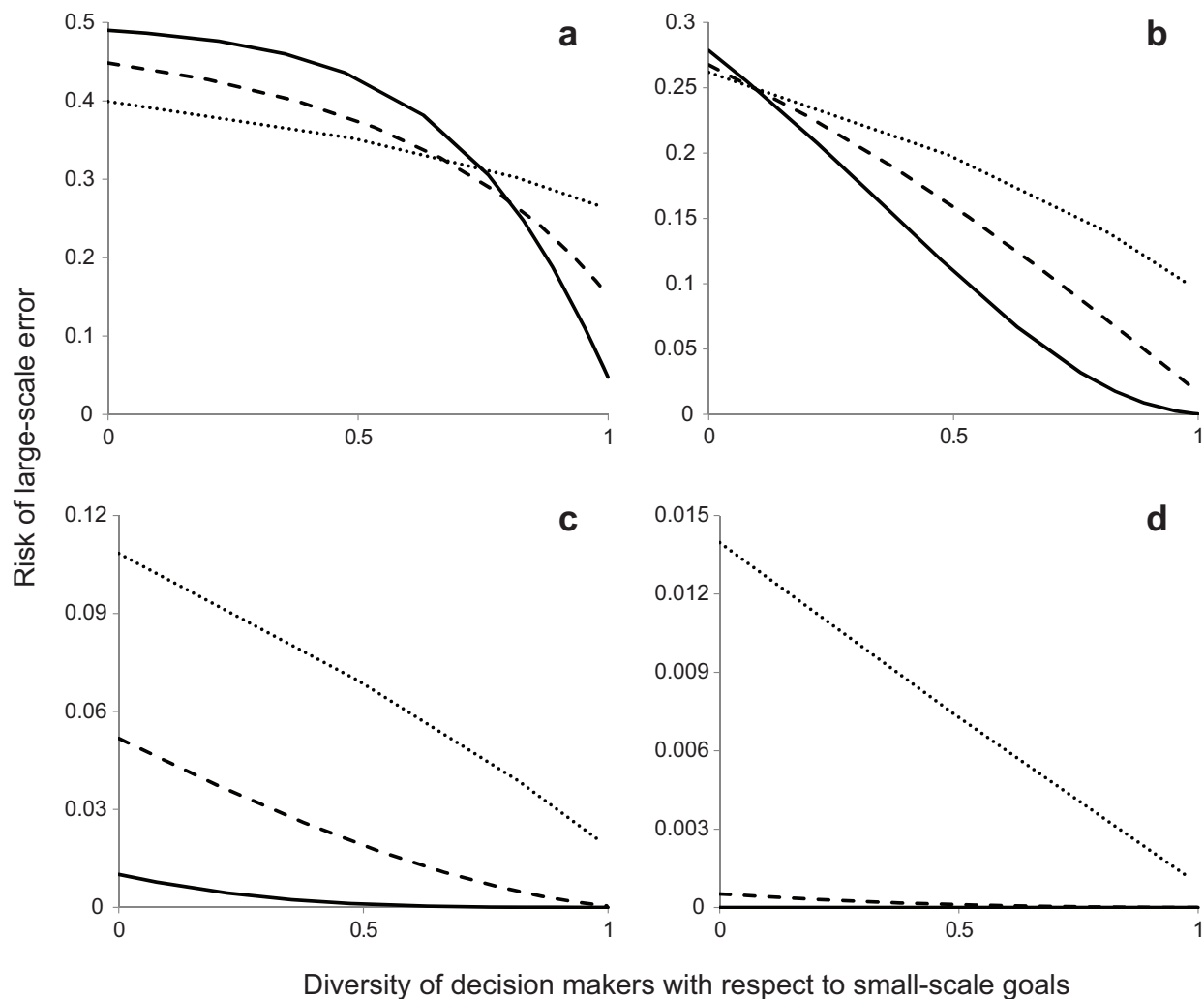
Figure 2: Risk of large-scale error as a function of diversity of decision makers (for clarity, scaling of the vertical axis differs between panels). Dotted lines, seven decision makers; dashed lines, 19 decision makers; solid lines, 51 decision makers. Individual information reliability ranges from low to high: $q = 0.6$ (*a*), $q = 0.7$ (*b*), $q = 0.8$ (*c*), $q = 0.9$ (*d*).

strategies, the strategy that is most appropriate in a given situation. Consequently, we investigate a comprehensive range of observed animal decision-making strategies as candidate strategies and then ask which of those strategies does best in a given situation (for more details, see "Shared Decisions: Aggregation of Personal Choices into a Collective Choice" in app. A). Candidate strategies to decide between options A and B are as follows:

Strategy 1 (S1): as a baseline, we consider a random decision between options.

Strategy 2 (S2): an animal makes the decision individually so that the decision is its own personal choice (individual decision; table 2; for the present purpose, we ignore restrictions imposed by the necessity for group cohesion; Kerth 2010).

Strategy 3 (S3): the animal follows (or is) a dictator/leader. The decision outcome is the dictator's personal choice (Ramseyer 2009).

Strategy 4 (S4): the group makes a shared decision whereby a subset of group members (the decision makers) make the decision by majority vote, on the basis of the decision makers' personal choices (which can be informed or uninformed; see above), and all group members accept the decision outcome (consensus decision; Conradt and Roper 2003, 2005; for details of shared decisions and decision makers, see "Shared Decisions: Aggregation of Personal Choices into a Collective Choice"). To ensure generality, we cover the possible and empirically observed range of the number and composition of decision makers, from dictatorial to equally shared decisions (Conradt and
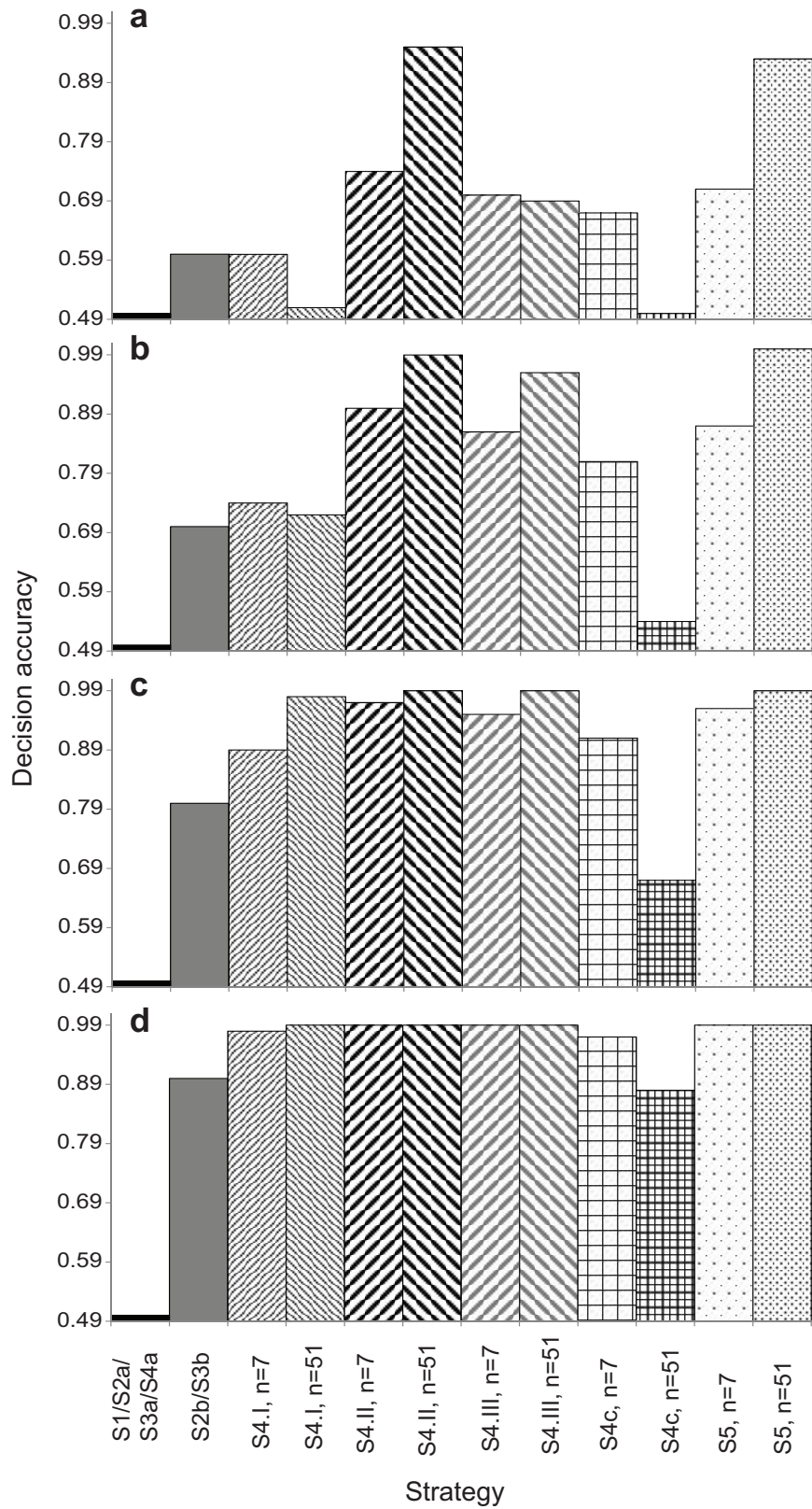
Figure 3: Decision accuracy for different decision-making strategies. Strategy coding (from left to right) as follows. Solid black bars, random decision (S1)/uninformed individual decision (S2a)/uninformed dictatorial decision (S3a)/majority makes uninformed shared decision (S4a).

Roper 2005; Kerth et al. 2006; King et al. 2008; Petit et al. 2009). Decision makers can be diverse with respect to small-scale goals. Thus, we define a variable div that measures the diversity with respect to small-scale goals between decision makers (see "Shared Decisions: Aggregation of Personal Choices into a Collective Choice") and three substrategies:

Substrategy S4.I: shared decisions by decision makers that are homogeneous with respect to small-scale goals.

Substrategy S4.II: shared decisions by decision makers that are maximally diverse with respect to small-scale goals.

Substrategy S4.III: shared decisions by decision makers that are medium diverse with respect to small-scale goals.

Strategy 5 (S5): for reasons of comparison, we also consider the shared decision that a set of hypothetical, unbiased decision makers (see above) would make, since this is equivalent to the decision by a Condorcet jury (here a set of decision makers that have no small-scale goals).

Depending on the decision-making strategy, we calculate the likelihood that the decision outcome is in favor of option A (or option B, respectively; table 2; for more details, see "Shared Decisions: Aggregation of Personal Choices into a Collective Choice").

Risk of a Large-Scale Error and Decision Accuracy

The worst error that a group of animals can make is to decide in favor of an unproductive option when a productive option is available (large-scale error; e.g., a decision in favor of a migration route that does not lead to a viable destination, a decision in favor of a foraging patch that does not contain food, a decision in favor of a communal activity that is not successful; box 1), so that the gains are zero to all animals (table 1). Such a large-scale error arises if either (1) option A is productive, option B is unproductive, and the decision outcome is in favor of option B; or (2) option A is unproductive, option B is productive, and the decision outcome is in favor of option A. Thus, when a large-scale error is possible, the condi-

tional risk of such a large-scale error, $P_{\text{large-scale error}}$, is as follows:

$$P_{\text{large-scale error}} =$$
$$\{\text{prod}(1 - \text{prod})[1 - P_{\text{outcome}_A}(A_{\text{prod}}, B_{\text{unprod}})]$$
$$+ (1 - \text{prod})\text{prod} \times P_{\text{outcome}_A}(A_{\text{unprod}}, B_{\text{prod}})\} \quad (2)$$
$$/[2\text{prod}(1 - \text{prod})]$$
$$= \frac{[1 - P_{\text{outcome}_A}(A_{\text{prod}}, B_{\text{unprod}})] + P_{\text{outcome}_A}(A_{\text{unprod}}, B_{\text{prod}})}{2},$$

whereby $P_{\text{outcome}_A}(A_{\text{prod}}, B_{\text{unprod}})$ and $P_{\text{outcome}_A}(A_{\text{unprod}}, B_{\text{prod}})$ are the probabilities that the decision outcome is in favor of option A, depending on the decision-making strategy and the true productivity states of either option. They are given in table 2. Accordingly, we define the decision accuracy as

$$\text{accuracy} = 1 - P_{\text{large-scale error}}. \quad (3)$$

Parameter Space

We have covered the parameter space extensively and investigated the influence of productivity, gains (=degree of conflict), information reliability, and diversity across the whole parameter ranges (prod, g: 0.05–0.95; q: 0.51–0.99; div: 0–1), a wide range of number of decision makers (n: 3–101; note that 101 is very large for most relevant noneusocial animal species), and the possible combinations of these parameters. For brevity and clarity, we provide results for only the combination of a restricted number of representative parameter values (e.g., low/high productivity × low/high conflict × low/high information reliability × low/high diversity × small/large number of decision makers). These parameter values capture all the qualitative results of our model.

Solid dark gray bars, informed individual decision (S2b)/informed dictatorial decision (S3b). Thin black right-striped bars, informed shared decision by a small, homogeneous set of decision makers (div = 0, n = 7; S4.I). Thin black left-striped bars, informed shared decision by a large, homogeneous set of decision makers (div = 0, n = 51; S4.I). Thick black right-striped bars, informed shared decision by a small, maximally diverse set of decision makers (div = 1, n = 7; S4.II). Thick black left-striped bars, informed shared decision by a large, maximally diverse set of decision makers (div = 1, n = 51; S4.II). Thick gray right-striped bars, informed shared decision by a small, medium-diverse set of decision makers (div = 0.75, n = 7; S4.III). Thick gray left-striped bars, informed shared decision by a large, medium-diverse set of decision makers (div = 0.75, n = 51; S4.III). Large checkered bars, shared decision whereby the majority makes informed personal choice and the minority makes uninformed personal choice (small set of decision makers, $|n_A - n_B| = 1$, n = 7; S4c). Small checkered bars, shared decision whereby the majority makes informed personal choice and the minority makes uninformed personal choice (large set of decision makers, $|n_A - n_B| = 1$, n = 51; S4c). For comparison only: sparsely dotted bars, informed shared decision by a small Condorcet jury (n = 7; S5). Dotted bars, informed shared decision by a large Condorcet jury (n = 51; S5). Individual information reliability: q = 0.6 (a), q = 0.7 (b), q = 0.8 (c), q = 0.9 (d).

Results

Decision Accuracy

In a shared decision, the risk of a large-scale error is lower than a random error (0.5) and decreases with the number of decision makers, unless information reliability and decision maker diversity is relatively low (fig. 1). Thus, shared decisions (strategy 4) usually lead to fewer large-scale errors than do random decisions (strategy 1), individual decisions based on personal choice (strategy 2), or decisions made by following a dictator/leader (strategy 3). Further, the risk of large-scale error always decreases with the diversity of decision makers div, independent of number of decision makers n, and reliability of information q (fig. 2). Thus, our model results suggest that large-scale errors are reduced (and thus decision accuracy is enhanced) if decisions are shared as widely as possible among animals that are both diverse and well balanced with respect to their small-scale goals.

Consequently, the best decision-making strategy with respect to decision accuracy—of all the considered strategies—is a shared decision by decision makers that are maximally diverse with respect to their small-scale goals and are, at the same time, as numerous as possible (fig. 3, S4.II, $n = 51$, thick black left-striped bars). Moreover, such diverse groups can achieve higher decision accuracy than comparable groups without goal conflicts (strategy 5: Condorcet juries; fig. 3, S5, $n = 51$, sparsely dotted bars). This result directly contradicts the intuition that conflicts hinder efficient information pooling.

If decision makers all have the same small-scale goal and if individual judgement reliability is at most moderate, then the risk of a large-scale error not only is relatively high but also can even increase with the number of decision makers (fig. 1a, 1b, dashed line; fig. 1a, dotted line). This is because as judgement reliability drops, personal biases become more crucial, and animals with a similar small-scale goal are likely to err in their choice in similar situations. For example, A-animals are most likely to err when option A is unproductive, while B-animals are most likely to err when option B is unproductive. Consequently, choice errors of animals with similar small-scale goals are likely to be correlated even when individual judgements per se are independent of each other. Such correlations undermine the information pooling benefits that are suggested by Condorcet's classic jury theorem. To conclude, if animals have preferences over large-scale goals as well as smaller-scale goals, then excluding particular factions from decision making (e.g., those animals whose small-scale goals are in the minority) can result in less accurate decision outcomes for all group members.

Individual Decision Gains

Decision gains to individuals are crucial for the evolution of decision-making strategies. While avoiding decision errors is in the interest of all animals, individual fitness is the ultimate driving force in the evolution of collective decision-making strategies (Conradt and Roper 2003; Rands et al. 2003), and individual fitness is likely to be related to individual gains (Maynard Smith 1979).

We found that decision gains to a focal animal depend crucially on the number and diversity of decision makers and the interaction of those two factors. If diversity of decision makers is high with respect to small-scale goals, decision gains to a focal animal increase (and then plateau) with the number of decision makers (fig. 4, solid black lines). This is due to the advantages of information pooling by diverse decision makers (fig. 1, solid black lines). In such situations, it is better for a (selfish) animal to share decisions with others (strategy 4) than to make decisions randomly (strategy 1) or individually (strategy 2) or to follow a dictator/leader (strategy 3).

However, the situation is different if decision makers are not diverse. If productivity and conflict are both high and a distinct majority of decision makers have the opposite small-scale goal of that of the focal animal, then the gains to a focal animal decrease with the number of decision makers (fig. 4d, 4h, gray lines) for the following reason. At high productivity, often both options are productive so that the advantages of informed choices and information pooling are relatively small. Moreover, when both options are productive at the same time, an increasingly large majority of decision makers with opposite small-scale goal preferences is increasingly likely to decide in favor of the focal animal's less preferred option. Therefore, the focal animal loses out on extra gains, particularly if those extra gains are large and the disadvantages of conflict are high. Consequently, conflict disadvantages outweigh information-pooling advantages. Finally, if diversity is low and information reliability is also low, gains to a focal animal usually decrease with the number of decision makers (fig. 4a–4d). This is due to the above-mentioned disadvantages of error pooling by large numbers of similarly biased decision makers (fig. 1a, dotted lines).

Thus, goal diversity is important for decision gains. So much so that decision gains to a focal individual often peak when the decision makers include a considerable proportion of animals with opposite (conflicting) small-scale goal preferences and decision makers are diverse and relatively balanced with respect to individual small-scale goals (fig. 5a–5c, 5e–5g). This is particularly so when productivity, information reliability, and conflict costs (i.e., extra gains) are low or the number of decision makers is large (fig. 5).
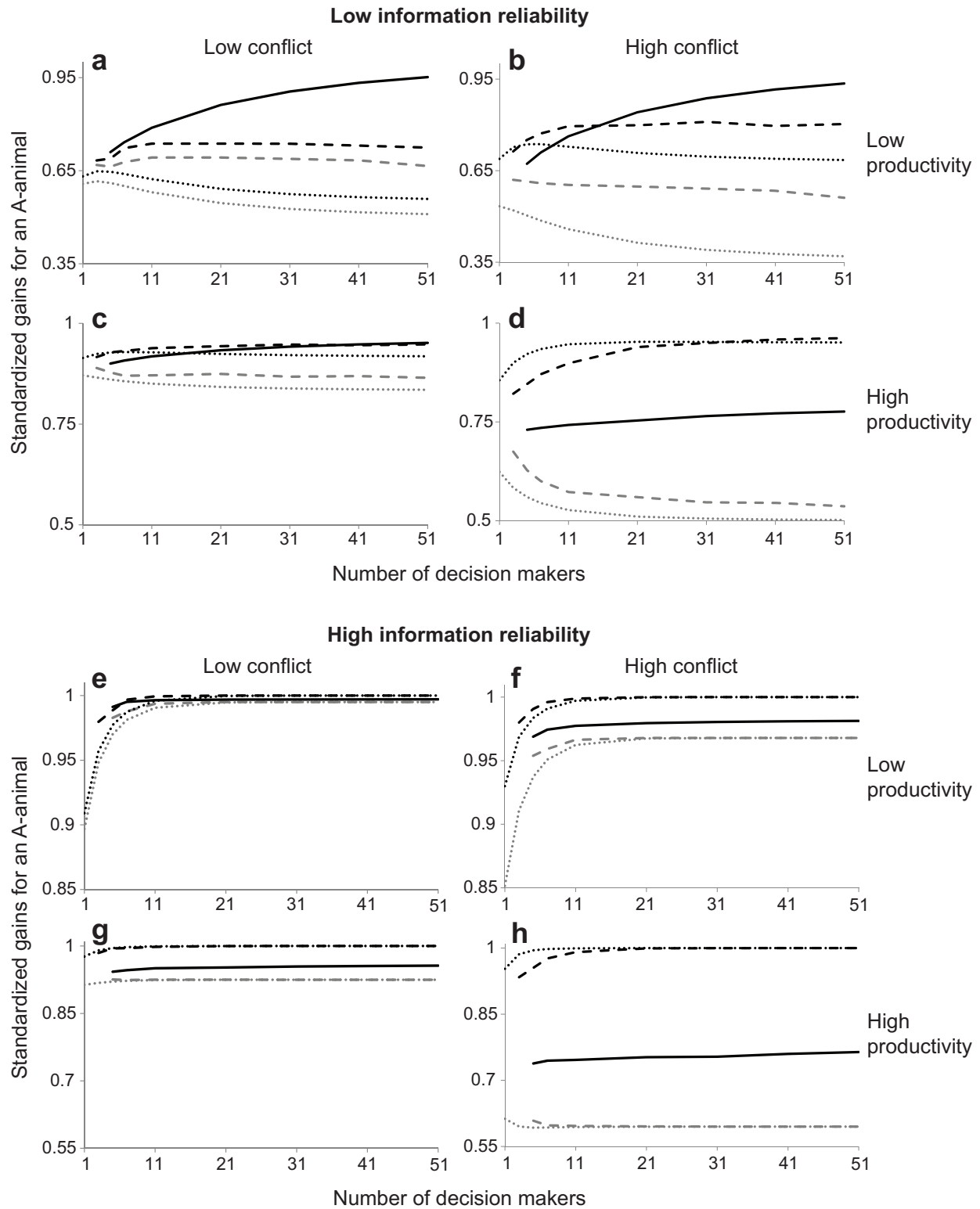
Figure 4: Standardized decision gains for an A-animal as a function of the number of decision makers (for clarity, scaling of the vertical axis differs between panels). Proportion of decision makers that are A-animals: $prop_A = 0$ (dotted gray lines; div $= 0$), $prop_A = 0.25$ (dashed gray lines; div $= 0.75$), $prop_A = 0.5$ (solid black lines; div $= 1$), $prop_A = 0.75$ (dashed black lines; div $= 0.75$), $prop_A = 1$ (dotted black lines; div $= 0$). Productivity: low, prod $= 0.1$ (a, b, e, f); high, prod $= 0.9$ (c, d, g, h). Extra gains (indicative of degree of small-scale conflict): low, $g = 0.1$ (a, c, e, g); high, $g = 0.9$ (b, d, f, h). Information reliability: low, $q = 0.6$ ($a–d$); high, $q = 0.9$ (e, f).

Small number of decision makers

Low conflict

a

High conflict

b

Low productivity

c

d

High productivity

Standardized gains for an A-animal

Proportion of A-animals amongst decision makers
Diversity peaks when proportion is 0.5

Large number of decision makers

Low conflict

e

High conflict

f

Low productivity

g

h

High productivity

Standardized gains for an A-animal

Proportion of A-animals amongst decision makers
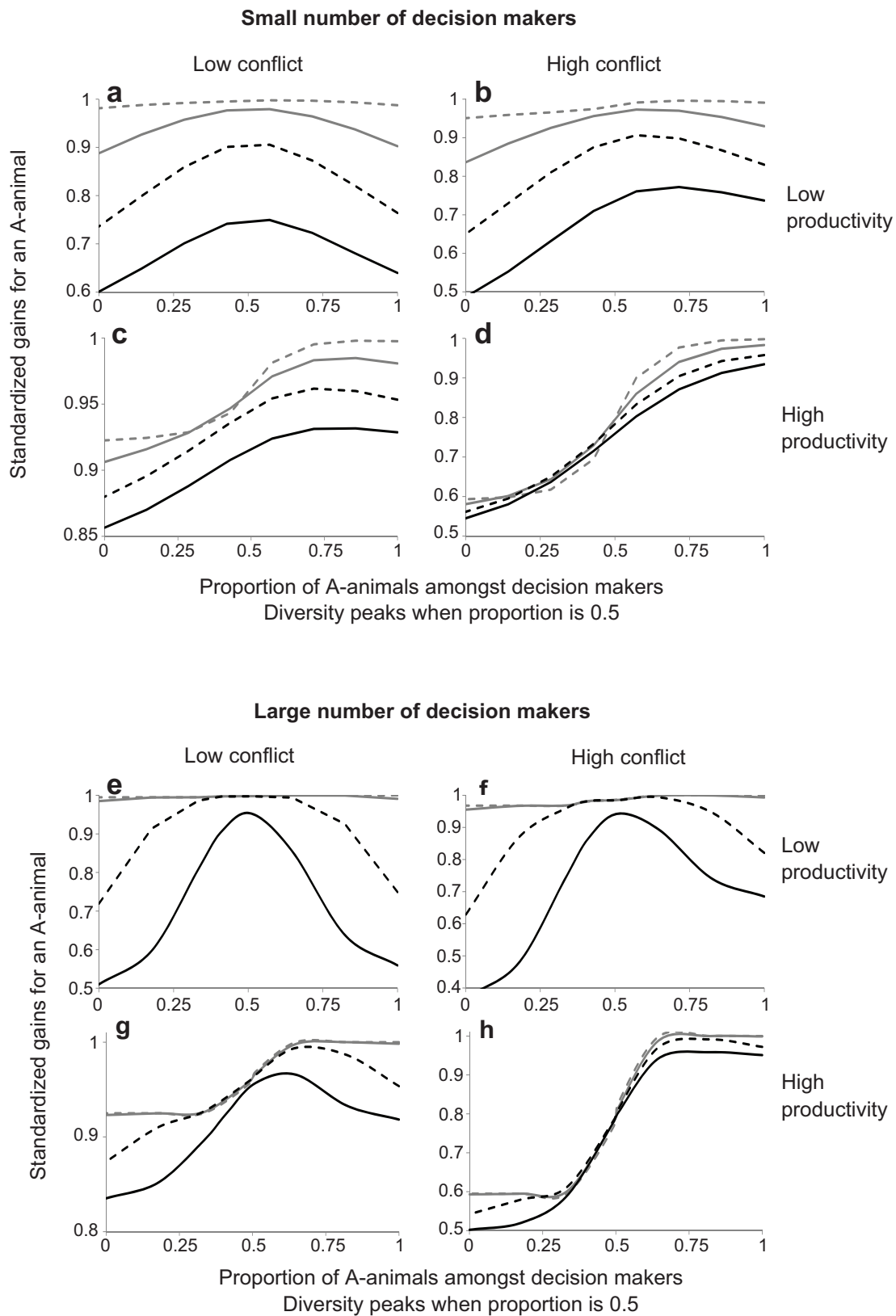Diversity peaks when proportion is 0.5

Figure 5: Standardized individual decision gains for A-animals as a function of the proportion of A-animals in the set of decision makers $(n_A/(n_A + n_B))$; for clarity, scaling of the vertical axis differs between panels). The individual panels give results for different parameter com-

Therefore, a relatively balanced and diverse mixture of decision makers with different small-scale goals is often of greater advantage to any individual than is a decision in which all decision makers have the same small-scale goals as the individual itself (i.e., there is no conflict). Consequently, the best decision-making strategy for all stakeholders (in terms of decision gains) is often a shared decision by a large number of maximally diverse decision makers, particularly in relatively unproductive and/or unpredictable environments (fig. 6*a*–6*c*, 6*e*, S4.II, *n* large). Even when this is not the best strategy, the next best strategy is usually also a widely shared decision by at least medium-diverse decision makers (fig. 6*d*, 6*f*). Only if the environment is very productive and predictable is a decision strategy by a set of homogeneous, like-minded (with respect to small-scale goals) individuals of advantage to an animal (fig. 6*g*, 6*h*). However, in this case, the best strategy for A-animals is not good for B-animals (fig. 6*g*, 6*h*; compare strategies "S4.I: Homogenous, A" and "S4.I: Homogeneous, B"). Here, which strategy ultimately evolves will depend on additional factors (such as the need for group cohesion; Conradt and Roper 2007, 2009).

In all environments, individual (unshared) decision-making strategies (S2 and S3) yielded generally lower decision gains than did at least some of the shared strategies (fig. 6). However, additional factors (such as differences in individual expertise) could change this result. Also remarkable is the fact that in all environments, Condorcet juries (i.e., decisions by unbiased decision makers; strategy S5) yielded lower decision gains than did at least one of the shared decision-making strategies by biased decision makers (i.e., A- and B-animals; fig. 6).

In conclusion, we suggest that once diverse groups arise, selection will often favor a relatively large and diverse set of decision makers (strategy 4.II). Selection for diversity will also depend on the environmental productivity and predictability.

Discussion

Intuitively, when there is conflict, one might expect that a decision made dictatorially by the animal itself—or at least by like-minded individuals with the same goal—is of advantage to an animal in terms of its ultimate decision gains. However, our results suggest otherwise: individual decision gains often peak when there are several decision makers, and these decision makers include a considerable proportion of animals with opposite (conflicting) small-scale goal preferences of that of the focal individual. This is particularly so in unproductive and uncertain environments.

The underlying mechanism is a fundamental and general one: animals with conflicting goals make decision choice errors more independently, so that those errors more frequently cancel out. Thus, a large, balanced, and diverse mixture of decision makers with different (conflicting) small-scale goals is often best, even from the point of view of a selfish animal. This suggests that conflict, far from hampering information pooling and effective decision making, can even improve the situation for all stakeholders, as long as they share large-scale goals. Thus, it provides a strong argument in the interest of all stakeholders for including other (e.g., minority) factions in collective decisions.

Benefits of diversity to collective decision making have been reported in house sparrows and humans (Sunstein 2002; Jarzabkowski and Searle 2004; Page 2007; Liker and Bukony 2009). In those cases, diversity relates to a distinctly different notion as discussed here, namely to differences in problem-solving strategies between individuals. Our results add a new dimension: they suggest that diversity in goals (even in connection with exactly the same problem-solving strategy) can have additional benefits for decision outcomes in terms of accuracy and gains. The reason is that diversity in small-scale goals leads to adaptive but biased personal choices. The consequence of these biases is that animals with different goals are principally less likely to be correlated in their decision errors than are animals with similar goals, thus enabling better compensation of individual errors (Codling et al. 2007; List et al. 2009; Krause et al. 2010; Ward et al. 2011). To our knowledge, this principle has not been suggested before.

Some social animals live in more open societies (fission-fusion societies; Kerth et al. 2006; Sueur et al. 2011), in

binations (small/large number of decision makers × low/high degree of conflict × low/high level of productivity), and the different lines indicate different levels of information reliability. In each panel, the diversity of decision makers is highest when the proportion of A-animals = proportion of B-animals = 0.5 (i.e., in the middle of each *X*-axis). When the curves of gains peak at around a proportion of A-animals = 0.5, then the gains peak at around highest diversity of decision makers. This is the case if productivity is low or the number of decision makers is large (*a*, *b*, *e*–*g*). If the curves of gains peak at a higher proportion of A-animals (here, around 0.75), then gains peak at medium diversity among decision makers with a bias toward A-animals (here, approximately three A-animals to one B-animal). This is the case if productivity is high and the number of decision makers is small (*c*, *d*) or if conflict, productivity, and number of decision makers are simultaneously high (*h*). The differences between levels of information reliability within each situation (i.e., within each panel) were largely quantitative rather than qualitative. Information reliability: low, $q = 0.6$ (solid black lines); low-medium, $q = 0.7$ (dashed black lines); medium-high, $q = 0.8$ (solid gray lines); high, $q = 0.9$ (dashed gray lines). Productivity: low, prod $= 0.1$ (*a*, *b*, *f*); high, prod $= 0.9$ (*c*, *d*, *g*, *h*). Extra gains (indicative of degree of small-scale conflict): low, $g = 0.1$ (*a*, *c*, *e*, *g*); high, $g = 0.9$ (*b*, *d*, *f*, *h*). Number of decision makers: small, $n = 7$ (*a*–*d*); large, $n = 51$ (*e*, *f*).
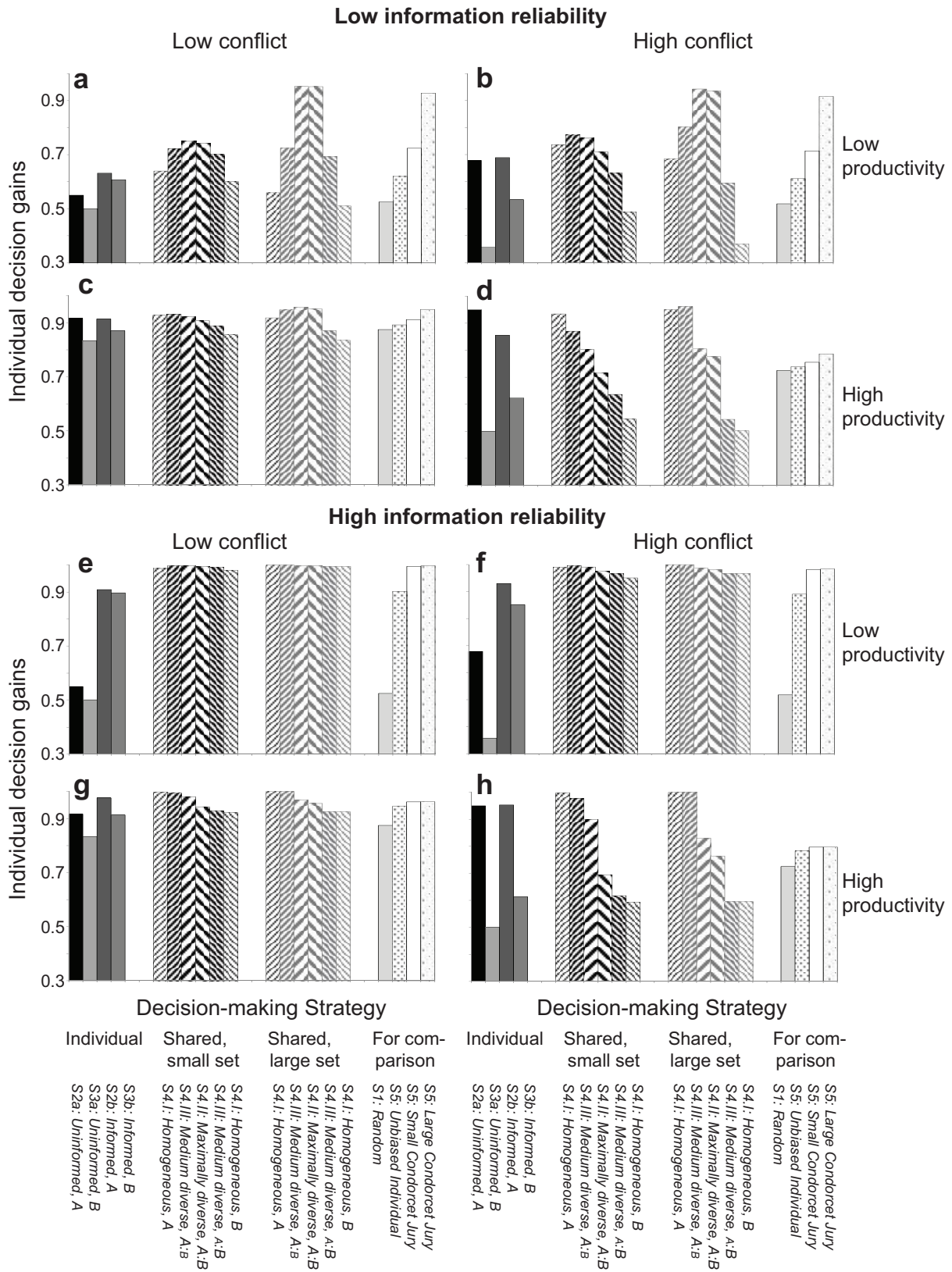
Figure 6: Standardized expected decision gains to an A-animal for different decision-making strategies (note that the decision gains to B-animals are symmetric and can be deduced by looking at the respective alternative strategies in which the number of A- and B-animals as

which our assumption that the gains from large-scale goals exceed those from small-scale goals might sometimes not hold. In environments with relatively low conflict, low productivity, high uncertainty, or high population density, the results of our model also apply to animals in such fission-fusion societies (for detailed arguments, see "Fission-Fusion Societies" in app. B). However, if conflict is high, and as the productivity of the environment and the certainty increase, it becomes increasingly more beneficial for animals in fission-fusion societies to segregate into homogeneous subgroups with similar small-scale goals.

While a huge body of research in a wide range of disciplines looks at collective decisions in situations with information uncertainty (e.g., Couzin et al. 2005, 2011) or in situations with conflicting goals (e.g., Conradt and Roper 2003, 2005), surprisingly few studies have looked at both factors concurrently (Schulte 2010). There appears to be no study in biology (i.e., behavioral ecology) that makes predictions about adaptive strategies in such situations (Conradt 2012). Of the few relevant studies in the social sciences, not many ask predictive questions. For example, studies in social psychology confirm that individuals reveal information differently in collective decisions when they have conflicting goals and that strategies can differ between individuals (De Dreu et al. 2008; Toma and Butera 2009). However, these studies do not investigate the why. Therefore, they do not allow us to make predictions about profitable (adaptive) strategies. On the other hand, relevant studies in engineering on multicriteria decision making usually treat information finding and conflict resolution as relatively independent (and, by definition, cooperative) processes (Tsiporkova and Boeva 2006), thereby limiting the generality of their findings. Finally, a number of studies in social choice theory that

make relevant predictions (Austen-Smith and Feddersen 2009; Schulte 2010) are restricted to a very specific sense of conflicting goals (i.e., the avoidance of false positives vs. false negatives).

Our results provide some first, testable predictions for decision under uncertainty and conflict. In particular, we predict the conditions under which groups of animals with diverse (conflicting) small-scale goals will make more accurate decisions and achieve larger gains than groups of animals in which all animals have the same small-scale goal. Further, we predict that decision accuracy and individual gains increase with the number of decision makers if there is diversity in small-scale goals but not if decision makers have the same small-scale goals and information reliability of individuals is at most moderate.

Our study is mainly aimed at understanding collective decision making in social animals. How far it can also be applied to human collective decision making requires further investigation. Social animals offer the possibility of applying a simple systems approach: they allow us to explore fundamental principles of collective decision making that involve uncertainties and conflict without having to address at once the full complexity of human behavior that arises through the use of language (Conradt and List 2009). Thus, our study might guide future questions and hypotheses for human studies. In particular, our results suggest that it might be profitable to examine the role of minority factions in human collective decisions from a novel point of view, as long as there are some large-scale goals that are common to all stakeholders.

To conclude, surprisingly little is known about decision-making strategies that (selfish) individuals are likely to employ in collective decisions that simultaneously involve uncertainty and conflicting goals (Conradt 2012). We hope

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decision makers is reversed). Strategy coding (from left to right) as follows. Individual decision-making strategies: solid black bars, uninformed individual/dictatorial decision by an A-animal (S2a/S3a). Solid light gray bars, uninformed dictatorial decision by a B-animal (S3a). Solid dark gray bars, informed individual/dictatorial decision by an A-animal (S2b/S3b). Solid medium gray bars, informed dictatorial decision by a B-animal (3b). Shared decision-making strategies, small set of decision makers ($n = 7$): thin black right-striped bars, homogeneous set of decision makers consisting of A-animals (div $= 0$, $\mathrm{prop_A} = 1$; S4.I). Medium-thick black right-striped bars, medium-diverse set of decision makers, majority are A-animals (div ≈ 0.75, $\mathrm{prop_A} = 5/7$; S4.III). Thick black right-striped bars, maximally diverse set of decision makers, majority are A-animals (div ≈ 1, $\mathrm{prop_A} = 4/7$; S4.II). Thick black left-striped bars, maximally diverse set of decision makers, majority are B-animals (div ≈ 1, $\mathrm{prop_A} = 3/7$; S4.II). Medium-thick black left-striped bars, medium-diverse set of decision makers, majority are B-animals (div ≈ 0.75, $\mathrm{prop_A} = 2/7$; S4.III). Thin black left-striped bars, homogeneous set of decision makers consisting of B-animals (div $= 0$, $\mathrm{prop_A} = 0$; S4.I). Shared decision-making strategies, large set of decision makers ($n = 51$): thin gray right-striped bars, homogeneous set of decision makers consisting of A-animals (div $= 0$, $\mathrm{prop_A} = 1$; S4.I). Medium-thick gray right-striped bars, medium-diverse set of decision makers, majority are A-animals (div ≈ 0.75, $\mathrm{prop_A} = 38/51$; S4.III). Thick gray right-striped bars, maximally diverse set of decision makers, majority are A-animals (div ≈ 1, $\mathrm{prop_A} = 26/51$; S4.II). Thick gray left-striped bars, maximally diverse set of decision makers, majority are B-animals (div ≈ 1, $\mathrm{prop_A} = 25/51$; S4.II). Medium-thick gray left-striped bars, medium-diverse set of decision makers, majority are B-animals (div ≈ 0.75, $\mathrm{prop_A} = 13/51$; S4.III). Thin gray left-striped bars, homogeneous set of decision makers consisting of B-animals (div $= 0$, $\mathrm{prop_A} = 0$; S4.I). For comparison: densely dotted bars, random decision (S1). Dotted bars, informed decision by an unbiased animal (S5). White bars, small Condorcet jury ($n = 7$; S5). Sparsely dotted bars, large Condorcet jury ($n = 51$; S5). Individual information reliability: low, $q = 0.6$ (*a–d*); high, $q = 0.9$ (*e–h*). Productivity: low, $p = 0.1$ (*a, b, e, f*); high, $p = 0.9$ (*c, d, g, h*). Extra gains (=degree of small-scale conflict): low, $g = 0.1$ (*a, c, e, g*); high, $g = 0.9$ (*b, d, f, h*).

that our study will encourage scientists to no longer skirt the problem by treating uncertainties and conflict in collective decision making separately and independently of each other.

APPENDIX A

Computation Details of Individual Gains, Choice Aggregation, and Decision Outcome

Individual Gains

The expected individual gains depend on the true productivity state of either option and the decision outcome. With probability $prod^2$, both options are productive, and we define the probability that the decision outcome is option A as $P_{outcome_A}(A_{prod}, B_{prod})$. The probability $P_{outcome_A}(A_{prod}, B_{prod})$ depends on the fact that both options are productive, on the consequent beliefs of animals (table 1), and on the decision-making strategies of animals (see below; table 2). Thus, with probability $prod^2 \times P_{outcome_A}(A_{prod}, B_{prod})$, both options are productive, the decision outcome is in favor of option A, and an A-animal gains $1 + g$ units of benefits; with probability $prod^2 \times [1 - P_{outcome_A}(A_{prod}, B_{prod})]$, the decision outcome is in favor of option B, and the A-animal gains 1 unit of benefits. The opposite is true for a B-animal. Similarly, with probability $prod(1 - prod) \times P_{outcome_A}(A_{prod}, B_{unprod})$, option A is productive but option B is unproductive, the decision outcome is in favor of option A, and an A-animal gains $1 + g$ units of benefits and a B-animal 1 unit of benefits. Finally, with probability $(1 - prod)prod \times [1 - P_{outcome_A}(A_{unprod}, B_{prod})]$, option A is unproductive but option B is productive, the decision outcome is in favor of option B, and an A-animal gains 1 unit of benefits and a B-animal $1 + g$ units of benefits. Thus, the expected gains to an A-animal are

$$prod^2[1 + P_{outcome_A}(A_{prod}, B_{prod})g]$$
$$+ prod(1 - prod)P_{outcome_A}(A_{prod}, B_{unprod})(1 + g)$$
$$+ (1 - prod)prod[1 - P_{outcome_A}(A_{unprod}, B_{prod})].$$

We standardize these expected gains relative to the maximally possible gains as follows. With probability prod, option A is productive, and an A-animal can maximally gain $1 + g$; with probability $(1 - prod)prod$, only option B is productive, and an A-animal can maximally gain 1 (table 1). Thus, the maximally possible gains are $prod(1 + g) + (1 - prod)prod \times 1$. The standardized expected individual gains to an A-animal (i.e., the ratio of expected gains to maximally possible gains) are thus as follows:

$$\text{gains to A-animal} =$$
$$\{prod^2[1 + P_{outcome_A}(A_{prod}, B_{prod})g]$$
$$+ prod(1 - prod)P_{outcome_A}(A_{prod}, B_{unprod})(1 + g) \quad \text{(A1a)}$$
$$+ (1 - prod)prod[1 - P_{outcome_A}(A_{unprod}, B_{prod})]\}$$
$$/[prod(1 + g) + (1 - prod)prod].$$

Accordingly, the standardized expected individual gains to a B-animal are as follows:

$$\text{gains to B-animal} =$$
$$(prod^2\{1 + [1 - P_{outcome_A}(A_{prod}, B_{prod})]g\}$$
$$+ prod(1 - prod)P_{outcome_A}(A_{prod}, B_{unprod}) \quad \text{(A1b)}$$
$$+ (1 - prod)prod[1 - P_{outcome_A}(A_{unprod}, B_{prod})](1 + g))$$
$$/[prod(1 + g) + (1 - prod)prod].$$

Shared Decisions: Aggregation of Personal Choices into a Collective Choice

Group living offers the possibility of sharing the decision with other group members by aggregating personal choices (Conradt and List 2009). We therefore consider a range of different decision-sharing strategies (table 2). The range of empirically observed choice aggregation rules in animal collective decision making ranges from dictatorial decisions—via decisions shared among a subset of group members—to decisions shared equally by all group members (Prins 1996; Seeley and Buhrman 1999; Conradt and Roper 2003, 2005; Biro et al. 2006; Kerth et al. 2006; King et al. 2008; Petit et al. 2009; Ramseyer et al. 2009; Nagy et al. 2010; McComb et al. 2011; Ward et al. 2011). Reflecting this, our model assumes majority decisions that are restricted to a certain subset of group members (i.e.,

the set of decision makers; Conradt and List 2009). That is, each animal in the set of decision makers has a vote (its personal choice), while animals outside the set have none, and the majority of personal choices determines the collective choice and, thereby, the decision outcome. The number of animals in the set of decision makers n can range from one to all group members ($1 \leq n \leq N$, where N is group size; for reasons of simplicity, n is assumed to be odd), so that the model's admissible aggregation rules cover the range of observed animal aggregation rules reported in the literature (i.e., from dictatorial to equally shared; Conradt and Roper 2005). Since the model assumes that all animals have small-scale goals (see "Methods: The Model"), the set of decision makers consists of n_A A-animals and n_B B-animals ($n_A + n_B = n$; $0 \leq n_A \leq N_A$; $0 \leq n_B \leq N_B$; N_A, N_B, number of A- and B-animals in the group, respectively). The proportion of A-animals among the set of decision makers is thus $\text{prop}_A = n_A/n$. It can range from 0 to 1. Additionally, we define the diversity div of decision makers with respect to small-scale goals as $\text{div} = 4n_A n_B/n^2$. Diversity of decision makers div can range from 0 (i.e., decision makers are homogenous with respect to small-scale goals, so that either $\text{prop}_A = 0$ or $\text{prop}_A = 1$) to approximately 1 (i.e., decision makers are maximally diverse with respect to small-scale goals, and approximately half of decision makers are A-animals and half are B-animals; $\text{prop}_A \approx \text{prop}_B \approx 0.5$; note that n is assumed to be odd). For comparison, we also consider sets of unbiased decision makers that consist of animals without small-scale goals (this is for comparison only, since a conflict-free strategy is not available to the animals in our model). The collective choice of the decision-making group is the option that is the personal choice (vote) of a majority of animals within the set of decision makers.

Probability of a Decision Outcome in Favor of Option A versus B in a Shared Decision

Here we derive the probability of a decision outcome in favor of option A for shared decisions. In a shared decision, the decision outcome is determined by the majority of personal choices by the n decision makers. Thus, the probability P_{outcome_A} that the decision outcome is in favor of option A is as follows:

$$P_{\text{outcome}_A} =$$

$$\sum_{i=\max[0,(n+1)/2-n_B]}^{n_A} \sum_{j=\max[0,(n+1)/2-i]}^{n_B} \quad \text{(A2)}$$

$$\left[\binom{n_A}{i}\binom{n_B}{j} P_A(A)^i (1 - P_A(A))^{n_A-i} P_B(A)^j (1 - P_B(A))^{n_B-j} \right],$$

whereby $P_A(A)$ and $P_A(B)$ are the probabilities that the informed personal choice of an A-animal and of a B-animal, respectively, is in favor of option A. The probabilities $P_A(A)$ and $P_A(B)$ depend on the animal's beliefs about the large-scale state of the environment (i.e., about the productivity of either option) and thus on the true large-scale states themselves (table 2). Thus, P_{outcome_A} takes the following values in different situations (using eq. [A2] and the values for $P_A(A)$ and $P_A(B)$ that are given in table 2 for different productivity states).

Case 1: both options are productive:

$$P_{\text{outcome}_A}(A_{\text{prod}}, B_{\text{prod}}) =$$

$$\sum_{i=\max[0,(n+1)/2-n_B]}^{n_A} \sum_{j=\max[0,(n+1)/2-i]}^{n_B} \quad \text{(A3)}$$

$$\left[\binom{n_A}{i}\binom{n_B}{j} [1 - (1-q)q]^{i+n_B-j} [(1-q)q]^{n_A-i+j} \right].$$

Case 2: option A is productive, option B is unproductive:

$$P_{\text{outcome}_A}(A_{\text{prod}}, B_{\text{unprod}}) =$$

$$\sum_{i=\max[0,(n+1)/2-n_B]}^{n_A} \sum_{j=\max[0,(n+1)/2-i]}^{n_B} \quad \text{(A4)}$$

$$\left[\binom{n_A}{i} [1 - (1-q)^2]^i (1-q)^{2n_A-2i} \binom{n_B}{j} q^{2j}(1-q^2)^{n_B-j} \right].$$

Case 3: option A is unproductive, option B is productive:

$$P_{\text{outcome}_A}(A_{\text{unprod}}, B_{\text{prod}}) =$$

$$\sum_{i=\max[0,(n+1)/2-n_B]}^{n_A} \sum_{j=\max[0,(n+1)/2-i]}^{n_B} \quad \text{(A5)}$$

$$\left[\binom{n_A}{i}(1-q^2)^i q^{2n_A-2i} \binom{n_B}{j}(1-q)^{2j} [1-(1-q)^2]^{n_B-j} \right].$$

Case 4: if both options are unproductive, it is irrelevant which option the group chooses.

Literature Cited

Ame, J. M., J. Halloy, C. Rivault, C. Detrain, and J. L. Deneubourg. 2006. Collegial decision making based on social amplification leads to optimal group formation. Proceedings of the National Academy of Sciences of the USA 103:5835–5840.

Austen-Smith, D., and T. J. Feddersen. 2009. Information aggregation and communication in committees. Philosophical Transactions of the Royal Society B: Biological Sciences 364:763–769.

Ballerini, M., N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I.

Giardina, A. Orlandi, et al. 2008. Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. Animal Behaviour 76:201–215.

Biro, D., D. J. T. Sumpter, J. Meade, and T. Guilford. 2006. From compromise to leadership in pigeon homing. Current Biology 16: 2123–2128.

Boesch, C. 1994. Cooperative hunting in wild chimpanzees. Animal Behaviour 48:653–667.

Bousquet, C. A. H., and M. B. Manser. 2011. Resolution of experimentally induced symmetrical conflicts of interest in meerkats. Animal Behaviour 81:1101–1107.

Clutton-Brock, T. H., F. E. Guiness, and S. D. Albon. 1982. Red deer: behaviour and ecology of two sexes. University of Chicago Press, Chicago.

Codling, E. A., J. W. Pitchford, and S. D. Simpson. 2007. Group navigation and the "many-wrongs principle" in models of animal movement. Ecology 88:1864–1870.

Conradt, L. 2012. Models in animal collective decision-making: information uncertainty and conflicting preferences. Interface Focus 2:226–240.

Conradt, L., J. Krause, I. D. Couzin, and T. J. Roper. 2009. "Leading according to need" in self-organizing groups. American Naturalist 173:304–312.

Conradt, L., and C. List. 2009. Group decisions in humans and animals: a survey. Philosophical Transactions of the Royal Society B: Biological Sciences 364:719–742.

Conradt, L., and T. J. Roper. 2003. Group decision-making in animals. Nature 421:155–158.

———. 2005. Consensus decision making in animals. Trends in Ecology and Evolution 20:449–456.

———. 2007. Democracy in animals: the evolution of shared group decisions. Proceedings of the Royal Society B: Biological Sciences 274:2317–2326.

———. 2009. Conflicts of interest and the evolution of decision sharing. Philosophical Transactions of the Royal Society B: Biological Sciences 364:807–819.

Couzin, I. D., C. C. Ioannou, G. Demirel, T. Gross, C.J. Torney, A. Hartnett, L. Conradt, et al. 2011. Uninformed individuals promote democratic consensus in animal groups. Science 334:1578–1580.

Couzin, I. D., J. Krause, N. R. Franks, and S. A. Levin. 2005. Effective leadership and decision-making in animal groups on the move. Nature 433:513–516.

Creel, S., and N. M. Creel. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Animal Behaviour 50:1325–1339.

De Dreu, C. K. W., B. A. Nijstad, and D. van Knippenberg. 2008. Motivated information processing in group judgment and decision making. Personality and Social Psychology Review 12:22–49.

Dostalkova, I., and M. Spinka. 2007. Synchronization of behaviour in pairs: the role of communication and consequences in timing. Animal Behaviour 74:1735–1742.

Gigerenzer, G., and D. G. Goldstein. 1996. Reasoning the fast and frugal way: models of bounded rationality. Psychological Review 103:650–669.

Hastie, R., and T. Kameda. 2005. The robust beauty of majority rules in group decisions. Psychological Review 112:494–508.

Hix, S., A. Noury, and G. Roland. 2009. Voting patterns and alliance formation in the European Parliament. Philosophical Transactions of the Royal Society B: Biological Sciences 364:821–831.

Jarzabkowski, P., and R. H. Searle. 2004. Harnessing diversity and collective action in the top management team. Long Range Planning 37:399–419.

Katsikopoulos, K. V., and A. J. King. 2010. Swarm intelligence in animal groups: when can a collective out-perform an expert? PLoS ONE 5:e15505.

Kerth, G. 2010. Group decision-making in animal societies. Pages 241–265 *in* P. Kappeler, ed. Animal behaviour: evolution and mechanisms. Springer, Berlin.

Kerth, G., C. Ebert, and C. Schmidtke. 2006. Group decision making in fission-fusion societies: evidence from two-field experiments in Bechstein's bats. Proceedings of the Royal Society B: Biological Sciences 273:2785–2790.

King, A. J., C. M. S. Douglas, E. Huchard, N. J. B. Isaac, and G. Cowlishaw. 2008. Dominance and affiliation mediate despotism in a social primate. Current Biology 18:1833–1838.

Krause, J., D. Bumann, and D. Todt. 1992. Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (*Rutilus rutilus*). Behavioral Ecology and Sociobiology 30:177–180.

Krause, J., and G. D. Ruxton. 2002. Living in groups. Oxford University Press, New York.

Krause, J., G. D. Ruxton, and S. Krause. 2010. Swarm intelligence in animals and humans. Trends in Ecology and Evolution 25:28–34.

Liker, A., and V. Bokony. 2009. Larger groups are more successful in innovative problem solving in house sparrows. Proceedings of the National Academy of Sciences of the USA 106:7893–7898.

Lingle, S., A. Feldman, M. S. Boyce, and W. F. Wilson. 2008. Prey behavior, age-dependent vulnerability, and predation rates. American Naturalist 172:712–725.

List, C. 2004. Democracy in animal groups: a political science perspective. Trends in Ecology and Evolution 19:168–169.

List, C., C. Elsholtz, and T. D. Seeley. 2009. Independence and interdependence in collective decision making: an agent-based model of nest-site choice by honeybee swarms. Philosophical Transactions of the Royal Society B: Biological Sciences 364:755–762.

Lusseau, D., and L. Conradt. 2009. The emergence of unshared consensus decisions in bottlenose dolphins. Behavioral Ecology and Sociobiology 63:1067–1077.

Marshall, J. A. R., R. Bogacz, A. Dornhaus, R. Planque, T. Kovacs, and N. R. Franks. 2009. On optimal decision-making in brains and social insect colonies. Journal of the Royal Society Interface 6:1065–1074.

Maynard Smith, J. 1979. Game theory and the evolution of behaviour. Proceedings of the Royal Society B: Biological Sciences 205:475–488.

McComb, K., G. Shannon, S. M. Durant, K. Sayialel, R. Slotow, J. Poole, and C. Moss. 2011. Leadership in elephants: the adaptive value of age. Proceedings of the Royal Society B: Biological Sciences 278:3270–3276.

Moussaid, M., S. Garnier, G. Theraulaz, and D. Helbing. 2009. Collective information processing and pattern formation in swarms, flocks, and crowds. Topics in Cognitive Science 1:469–497.

Nagy, M., Z. Akos, D. Biro, and T. Vicsek. 2010. Hierarchical group dynamics in pigeon flocks. Nature 464:890–893.

Packer, C., and L. Ruttan. 1988. The evolution of cooperative hunting. American Naturalist 132:159–198.

Page, S. E. 2007. Making the difference: applying a logic of diversity. Academy of Management Perspectives 21:6–20.

Petit, O., J. Gautrais, J. B. Leca, G. Theraulaz, and J. L. Deneubourg.

2009. Collective decision-making in white-faced capuchin monkeys. Proceedings of the Royal Society B: Biological Sciences 276: 3495–3503.

Prins, H. H. T. 1996. Ecology and behaviour of the African buffalo. Chapman & Hall, London.

Pyritz, L. W., P. M. Kappeler, and C. Fichtel. 2011. Coordination of group movements in wild red-fronted lemurs (*Eulemur rufifrons*): processes and influence of ecological and reproductive seasonality. International Journal of Primatology 32:1325–1347.

Ramseyer, A., O. Petit, and B. Thierry. 2009. Patterns of group movements in juvenile domestic geese. Journal of Ethology 27:369–375.

Rands, S. A., G. Cowlishaw, R. A. Pettifor, J. M. Rowcliffe, and R. A. Johnstone. 2003. Spontaneous emergence of leaders and followers in foraging pairs. Nature 423:432–434.

Ruckstuhl, K. E., and P. Neuhaus. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. Biological Reviews 77:77–96.

Schulte, E. 2010. Information aggregation and preference heterogeneity in committees. Theory and Decision 69:97–118.

Seeley, T. D., and S. C. Buhrman. 1999. Group decision making in swarms of honey bees. Behavioral Ecology and Sociobiology 45: 19–31.

Sueur, C., A. J. King, L. Conradt, G. Kerth, D. Lusseau, C. Mettke-Hofmann, C. M. Schaffner, et al. 2011. Collective decision-making and fission-fusion dynamics: a conceptual framework. Oikos 120: 1608–1617.

Sumpter, D. J. T., and S. C. Pratt. 2009. Quorum responses and consensus decision making. Philosophical Transactions of the Royal Society B: Biological Sciences 364:743–753.

Sunstein, C. R. 2002. The law of group polarization. Journal of Political Philosophy 10:175–195.

Toma, C., and F. Butera. 2009. Hidden profiles and concealed information: strategic information sharing and use in group decision making. Personality and Social Psychology Bulletin 35:793–806.

Tsiporkova, E., and V. Boeva. 2006. Multi-step ranking of alternatives in a multi-criteria and multi-expert decision making environment. Information Sciences 176:2673–2697.

Ward, A. J. W., J. E. Herbert-Read, D. J. T. Sumpter, and J. Krause. 2011. Fast and accurate decisions through collective vigilance in fish shoals. Proceedings of the National Academy of Sciences of the USA 108:2312–2315.

Associate Editor: J. Albert C. Uy
Editor: Judith L. Bronstein
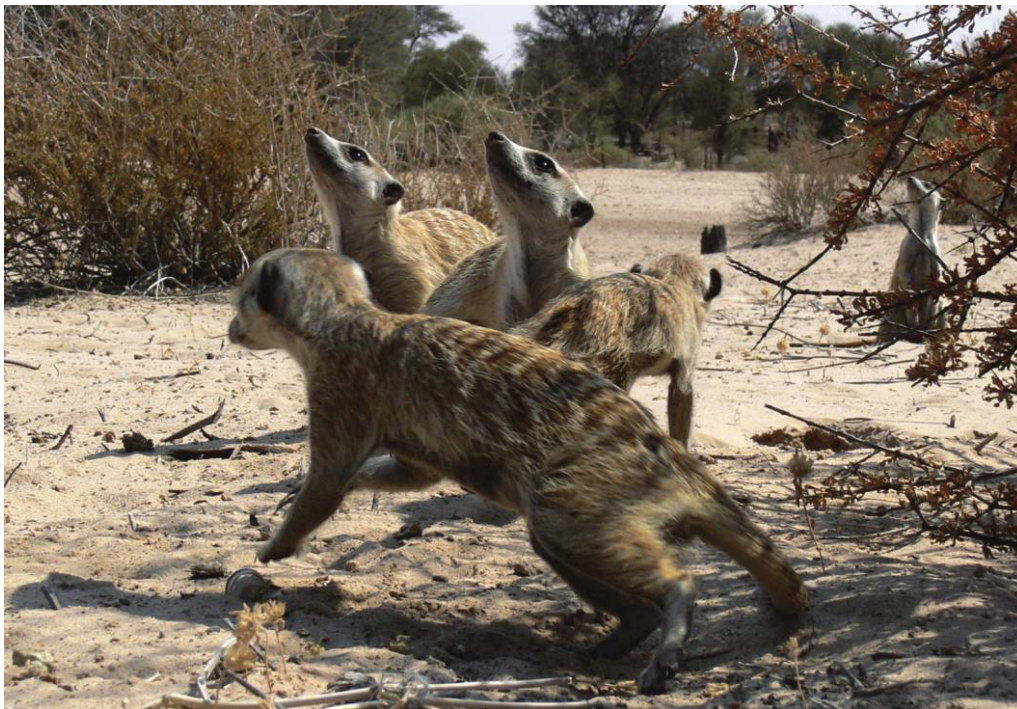
Meerkats are one of many species in which collective decisions can involve uncertainties and conflicts. Photograph credit: Kalahari Meerkat Project, http://www.kalahari-meerkats.com, ©Evelyne Zehntner.