

“Leading According to Need” in Self-Organizing Groups

L. Conradt,^{1,*} J. Krause,² I. D. Couzin,³ and T. J. Roper¹

1. Department of Biology and Environmental Science, University of Sussex, Brighton BN1 9QG, United Kingdom; 2. Ecology and Evolution Group, School of Biology, University of Leeds, Leeds LS2 9JT, United Kingdom; 3. Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544

Submitted February 11, 2008; Accepted August 25, 2008; Electronically published January 29, 2009

Online enhancements: appendixes.

ABSTRACT: Self-organizing-system approaches have shed significant light on the mechanisms underlying synchronized movements by large groups of animals, such as shoals of fish, flocks of birds, or herds of ungulates. However, these approaches rarely consider conflicts of interest between group members, although there is reason to suppose that such conflicts are commonplace. Here, we demonstrate that, where conflicts exist, individual members of self-organizing groups can, in principle, increase their influence on group movement destination by strategically changing simple behavioral parameters (namely, movement speed, assertiveness, and social attraction range). However, they do so at the expense of an increased risk of group fragmentation and a decrease in movement efficiency. We argue that the resulting trade-offs faced by each group member render it likely that group movements are led by those members for which reaching a particular destination is most crucial or group cohesion is least important. We term this phenomenon leading according to “need” or “social indifference,” respectively. Both kinds of leading can occur in the absence of knowledge of or communication about the needs of other group members and without the assumption of altruistic cooperation. We discuss our findings in the light of observations on fish and other vertebrates.

Keywords: behavioral synchrony, collective group decisions, democracy and egalitarianism in animals, public goods experiments, sexual segregation, social choice theory.

Introduction

The coordinated movements of large flocks of birds, shoals of fish, herds of ungulates, or swarms of insects have puzzled naturalists for centuries, because it is hard to explain how large numbers of individuals can achieve precise and apparently instantaneous organization (Selous 1931). In the past decade, self-organizing-system approaches have done much to elucidate the mechanisms underlying such group movements (Gueron et al. 1996; Reeb 2000; Couzin and Krause 2002; Parrish et al. 2002; Seeley 2002; Franks

et al. 2003; Simons 2004; Couzin et al. 2005; Ame et al. 2006; Sumpter 2006). However, models of self-organizing systems usually do not consider conflicts of interest between members (Gueron et al. 1996; Reeb 2000; Couzin and Krause 2002; Parrish et al. 2002; Couzin et al. 2005; Sumpter 2006) or, in the rare cases when they do, are typically “egalitarian” in the sense that they assume that all members of the group operate according to the same local behavioral rules (Couzin et al. 2005; Dyer et al. 2008). Consequently, conflicts about movement directions are assumed to be solved in a “democratic” manner (Couzin et al. 2005; Hastie and Kameda 2005), whereby the group is most likely to move either in the average preferred direction of all members (“average winner”; Hastie and Kameda 2005) or in the direction on which the largest number of members “agree” (“majority/plurality rule”; Hastie and Kameda 2005).

Empirical evidence suggests that individual members of a group may often have different optimal target destinations, resulting in significant within-group conflicts of interest (Clutton-Brock et al. 1982; Gompper 1996; Conradt 1998; Ruckstuhl and Neuhaus 2002; Rands et al. 2003). Here, we ask three closely interrelated questions. First, can, in principle, any group members in large, self-organizing groups gain meaningful influence on global group behavior (e.g., group movement direction, group movement efficiency, and group fragmentation) so as to further their own interests? In sociological terms, can members use selfish tactics to gain a disproportionately high “weight” in group movement decisions (Cremer and Palfrey 1999; Hastie and Kameda 2005; Barbera and Jackson 2006; Dietrich 2006; Diecidue et al. 2007)? Second, if they can do so, what are the mechanisms? Finally, what are the wider implications for group movement decisions? To answer these questions, we developed a simulation model (Couzin et al. 2005) by assuming that all members have a preference concerning the target destination (so that all experience potential conflict) and by allowing different group members to operate according to different behavioral parameters (specifically, to vary their own movement speed, “as-

* Corresponding author; e-mail: l.conradt@sussex.ac.uk.

sertiveness,” and social attraction range relative to those of other members of the group).

Basic Model Assumptions

Conflict of Interest

To create conflict of interest between members, we assume that each individual member prefers to move to either of two possible, mutually exclusive target destinations. We assume that these target destinations are equidistant (500 spatial units) but lie in opposite directions (see app. B in the online edition of the *American Naturalist* for the rationale of this assumption) from the group’s starting position. Thus, at the start, there is a difference in preferred direction φ_0 ($\varphi_0 = \pi$) between group members that prefer to move to target destination 1 and those that prefer to move to target destination 2. Model parameters are chosen so that group members can maximally move about half the distance toward, but not arrive at, a target destination during a simulation run (see below).

Majority Size

Since all members have a preference for one of the two target destinations, one subgroup of members (e.g., the majority) shares a preference for target destination 1 and another (e.g., the minority) a preference for target destination 2 (Conradt and Roper 2003; List 2004; Hastie and Kameda 2005). We consider two relatively extreme cases, namely, that the subgroup containing the majority of members consists of either (i) a small majority of members (i.e., one member more than the other subgroup) or (ii) a large majority (i.e., 80% of group members; List 2004; Hastie and Kameda 2005).

Simulation Model

Starting Position

Individual group members start with a random movement direction and from a random position within a cohesive group (see below for group fragmentation criteria) in a circular area A of radius ρ around point (0, 0), with a minimum distance of α between members.

Basic Movement Rules

All members move simultaneously in discrete time steps, each at its own speed s_i . Each individual member moves at each time step according to behavioral rules that depend only on local information, as follows.

Collision Avoidance. For each individual, the highest pri-

ority is to avoid collision. Thus, if there are neighbors within a collision range α ($\alpha = 2$), the individual simply tries to turn away from those neighbors. Let $N_{i\alpha}(t)$ be the number of neighbors within range α of individual i at time t . Thus, if $N_{i\alpha}(t) > 0$,

$$\mathbf{d}_i(t) = -\frac{1}{N_{i\alpha}(t)} \cdot \sum_{j=1}^{N_{i\alpha}(t)} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{|\mathbf{c}_j(t) - \mathbf{c}_i(t)|}, \quad (1)$$

where $\mathbf{d}_i(t)$ is the preliminary desired movement direction and $\mathbf{c}_i(t)$ the position vector for individual i at time t .

Balance between Social Attraction and Preferred Target Direction.

If there are no neighbors within range α (i.e., if $N_{i\alpha}(t) = 0$), the individual makes a movement step based on its desire to maintain group cohesion as well as to move toward its preferred target destination, as follows. In order to maintain group cohesion, the individual is attracted to neighbors within a range ρ_i ($\rho_i > \alpha$) so as to move toward them and align travel direction with them (“social attraction”). However, the resulting “social-attraction vector” might differ from the vector toward the individual’s preferred spatial target destination. Therefore, the individual “balances” attraction to its preferred target destination against social attraction to neighbors with a factor ω_i (“degree of assertiveness”). That is, an individual tries to move in the direction given by social attraction + $\omega_i \times$ preferred target direction (where preferred target direction is the vector between the individual’s position and the preferred target destination position, scaled to unit length). Let $N_{\rho_i}(t)$ be the number of neighbors within range ρ_i of individual i at time t . Thus, if $N_{i\alpha}(t) = 0$ and $N_{\rho_i}(t) > 0$,

$$\mathbf{d}_i(t) = \frac{1}{4N_{\rho_i}(t)} \cdot \sum_{j=1}^{N_{\rho_i}(t)} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{|\mathbf{c}_j(t) - \mathbf{c}_i(t)|} + \frac{1}{4N_{\rho_i}(t)} \cdot \sum_{j=1}^{N_{\rho_i}(t)} \mathbf{v}_j(t) + \omega_i \cdot \frac{\mathbf{g}_i - \mathbf{c}_i(t)}{2 \cdot |\mathbf{g}_i - \mathbf{c}_i(t)|}, \quad (2)$$

where $\mathbf{v}_j(t)$ is the unit vector of movement direction for individual j at time t and \mathbf{g}_i is the position vector of the preferred target destination of individual i . It follows that if ω_i is large (and the individual is very assertive), the individual tries to move at each time step predominantly in the direction of its preferred target destination; if ω_i is small (and the individual is very unassertive), it predominantly tries to move toward and align with its neighbors; and if ω_i is intermediate, the individual compromises between its own target destination preference and moving toward and aligning with its neighbors.

Absence of Neighbors. If there are no neighbors within

ranges α or ρ , the individual always tries to move in the direction of its preferred target destination. Thus, if $N_{i\alpha}(t) = 0$ and $N_{i\rho}(t) = 0$,

$$\mathbf{d}_i(t) = \frac{\mathbf{g}_i - \mathbf{c}_i(t)}{|\mathbf{g}_i - \mathbf{c}_i(t)|}. \quad (3)$$

Movement Steps and Simulation Duration

From $\mathbf{d}_i(t)$, we derived the new position and movement direction of each individual after each time step by adding an individual random directional error (Couzin et al. 2005) and considering a maximum turning angle and the individual's movement speed (see app. B for details). A simulation ran for 2,500 time steps of $\Delta t = 0.1$, and 500 simulations were run per parameter combination. We used C as programming language.

Parameter Space

Group sizes range from 3 to 99, which covers most naturally occurring groups in which there are conflicts of interest about movement direction (Krause and Ruxton 2002; Conradt and Roper 2005, 2007; Couzin et al. 2005). To investigate the potential for different members to influence movement direction in their own interest, we assigned to individual group members degrees of assertiveness of ω_{low} (0.05), ω_{medium} (0.4–0.7; see app. B for details), or ω_{high} (10.0); social attraction ranges of ρ_{small} (10), ρ_{medium} (20), or ρ_{large} (30); and movement speeds of s_{slow} (0.95), s_{medium} (1.0), or s_{fast} (1.05). To limit the possible parameter space to a manageable size, we assumed that group members that share a preference also share the same degree of assertiveness, speed, and social range size. This is a biologically sensible assumption, since individuals that share a target destination preference are usually of the same type (e.g., same sex, size, age class, or physiological state; Conradt 1998; Ruckstuhl and Neuhaus 2002). They are therefore likely to have similar behavioral parameters because they are physiologically similar, because environmental influences on them are likely to be similar, and because evolutionary pressures on them are likely to have been similar (Clutton-Brock et al. 1982; Gompper 1996; Conradt 1998; Ruckstuhl and Neuhaus 2002; Conradt and Roper 2003, 2005). All possible combinations of focal and other subgroups' behavioral parameters and majority/minority relations were investigated, so as to cover the parameter space comprehensively.

Communication

We make the conservative assumption that there is no communication among members (Couzin et al. 2005), so individuals do not know whether they are in the majority or minority subgroup or how large the majority is. Thus, individuals cannot adjust their behavior to this information (Conradt and Roper 2003). In addition, we make the conservative (and, for self-organizing groups, generally realistic; Couzin et al. 2005) assumption that members have no information about the other subgroup's assertiveness (both of these assumptions are relaxed in app. B).

Analysis of Simulation Results

Leading Rate, Group Fragmentation Risk, and Group Movement Efficiency

For the purposes of analysis, we focus on each subgroup in turn. At the end of each simulation, three results are possible: (i) the group has fragmented (i.e., group members fall into at least two clusters, and there is a distance of at least ρ_{max} between all individuals in one cluster and all remaining group members); (ii) the group has not fragmented, and the members of the focal subgroup have more influence on the movement direction (i.e., they “lead,” so that the group's end distance to the focal subgroup's preferred target destination is smaller than that to their non-preferred target destination); or (iii) the group has not fragmented and the members of the focal subgroup have less influence (i.e., they “follow,” so that the group's end distance to the focal subgroup's nonpreferred target destination is smaller than that to their preferred target destination). The “leading rate” of a subgroup is defined as the proportion of all simulations in which that subgroup led the movement (note that a low leading rate can therefore be due to a high likelihood of group fragmentation or of following). The “fragmentation risk” is the proportion of simulations in which the group fragments. If a group has not fragmented, we determine the “group movement efficiency” of the group as the maximum distance that the group has moved toward a target destination (i.e., mean starting distance of all group members from target destination minus mean end distance) divided by the maximum distance that the group could have moved (i.e., 2,500 time steps \cdot 0.1 time units \cdot min(s_i)).

Statistics

Results were analyzed using multiple linear regression (with GENSTAT software). We examined the influence of the behavior parameters of individuals from a focal subgroup on that subgroup's leading rate (logit-transformed data, binomial distribution assumed), on group fragmen-

tation risk (logit-transformed data, binomial distribution assumed), and on group movement efficiency (logit-transformed data, normal distribution assumed; residuals were tested for normality). The influence of the following behavior parameters was tested: (i) degree of assertiveness; (ii) size of social attraction range (relative to that of the individuals in the other subgroup); and (iii) speed (relative to that of the individuals in the other subgroup). To control for potentially confounding factors, a basic model was first fitted to the data that controlled for group size, majority size, minority/majority identity of focal subgroup, and the degree of assertiveness of individuals in the other subgroup. Since focal members have no information about the degree of assertiveness by members of the other subgroup, the influence of the focal subgroup's behavior is explored under the assumption that the other subgroup is equally likely to choose any degree of assertiveness.

Results

Could Members Gain Disproportionate Influence over Group Movement Patterns?

The degree of assertiveness, relative speed, and relative size of the social attraction range of focal group members had a considerable effect on the following group level patterns: group movement direction (see "Leading Rate"), group movement efficiency, and group fragmentation (fig. 1; see also tables A1–A3 in the online edition of the *American Naturalist* for more details). The group often did not always move in the direction preferred by a simple majority (see tables B1–B6 in the online edition of the *American Naturalist* for details). Thus, members could, in principle, adjust their behavior so as to gain systematic influence on group level patterns.

How Could Members Gain Disproportionate Influence over Group Movement Patterns (i.e., What Are the Mechanisms)?

Leading Rate. Changes in behavioral parameters by members of the focal subgroup led to systematic differences in the likelihood that they would lead the whole group in the direction of their own preferred target destination (fig. 1, *top*; table A1). If members of a subgroup wish to maximize their leading rate, they should use a medium degree of assertiveness, a relatively slow movement speed, and a relatively small range of social attraction. Such choice of behavioral parameters increases the estimated odds ratio that they would lead the group (relative to an individual that behaves randomly and is equally likely to have a high, medium, or low degree of assertiveness; a slow, medium, or high speed; and a small, medium, or large social range)

nearly tenfold, by a factor of 9.7 (for the source and explanation of this estimate, see app. A in the online edition of the *American Naturalist*).

Access to information about the minority/majority relationships within the group or about the degree of assertiveness used by members of the other subgroup does not lead to differences in the best strategy to optimize leading rate (tables B1, B2). Thus, such information is of surprisingly little help to members when deciding behavioral rules to maximize their leading rate.

Group Fragmentation Risk. Generally, the risk that the group would fragment increased with the degree of assertiveness of the focal subgroup and with the difference in speed and social attraction range between the two subgroups (fig. 1, *middle row*; table A2). Thus, if members of a subgroup wish to minimize group fragmentation risk, they should choose a low degree of assertiveness and a speed and social attraction range similar to those of conflicting members.

Access to information about the minority/majority relationships within the group and about the degree of assertiveness used by members of the other subgroup would allow members some finer tuning of strategies to avoid group fragmentation (tables B3, B4). While group fragmentation risk still always increases steeply with degree of assertiveness by the focal group (tables B3, B4), members could benefit additionally from information when choosing speed and social attraction range. In particular, in order to minimize group fragmentation risk, members of the minority subgroup and the less assertive subgroup should react faster and within a wider social range than members of the majority subgroup or the more assertive subgroup.

Group Movement Efficiency. Generally, the most important single factor for improving group movement efficiency was for members of the focal subgroup to have a high degree of assertiveness (fig. 1, *bottom*; table A3), while social attraction range and speed played relatively minor roles. Again, additional information has little relevance for optimizing group movement efficiency (tables B5, B6).

Wider Implications for Group Movement Decisions

Trade-Offs. Our most important result that follows from the above is that group members could not simultaneously optimize their chances of leading, group cohesion, and movement efficiency (fig. 1; cf. tables A1–A3; app. B). If they maximize their leading rate (e.g., by having a medium degree of assertiveness), they automatically increase group fragmentation risk and decrease group movement efficiency, and vice versa. It follows that group members face

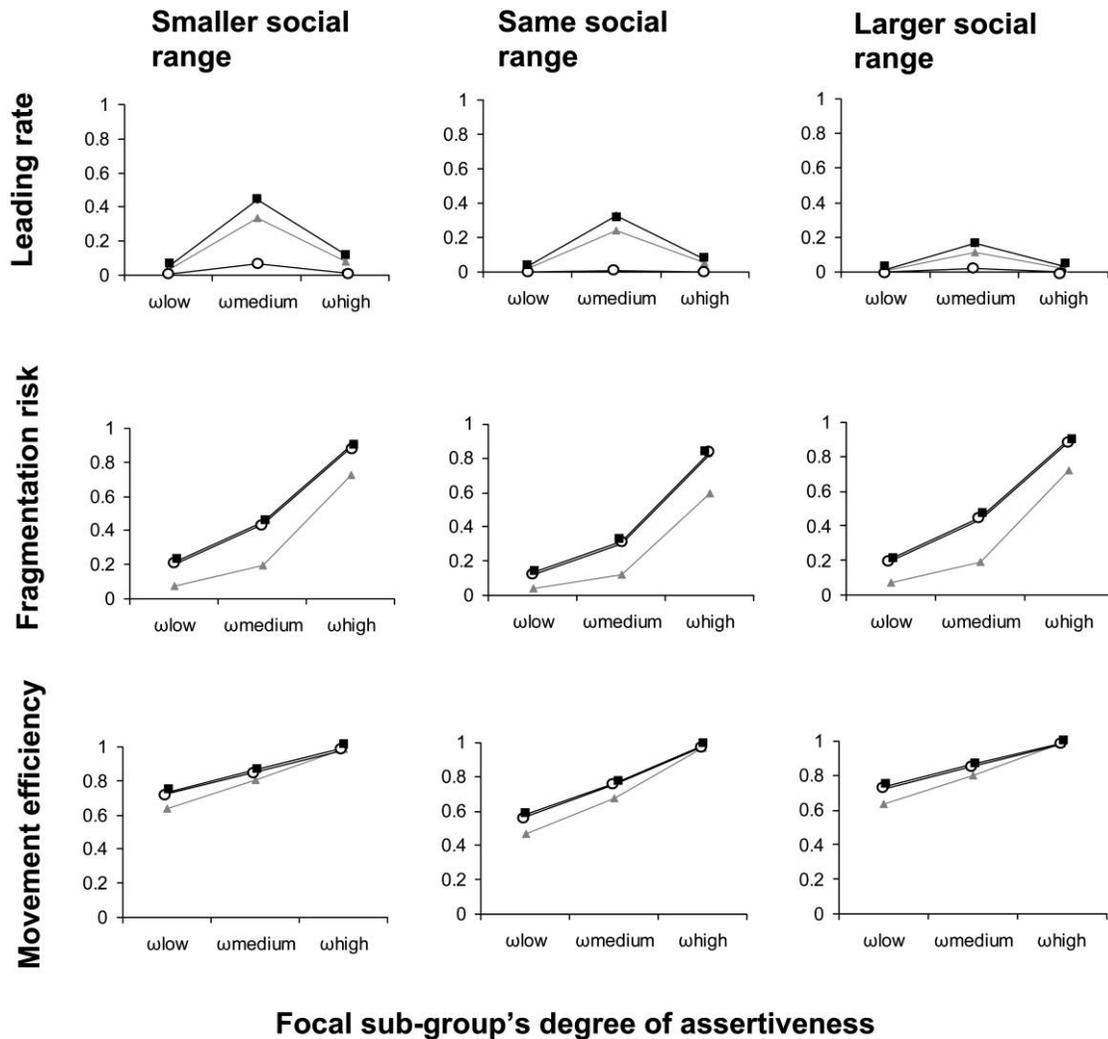


Figure 1: Results of the multiple-linear-regression models. Estimated leading rate (*top*), group fragmentation risk (*middle*), and group movement efficiency (*bottom*) as a function of (i) focal subgroup's degree of assertiveness (*X*-axes), (ii) relative social attraction range size (columns), and (iii) relative speed (slower: *black line and squares*; same speed: *gray line and triangles*; faster: *black line and circles*). For reasons of clarity, standard deviations are not shown in the graphs but are given in tables A1–A3 in the online edition of the *American Naturalist*, together with further details of results. In these models, the other subgroup was equally likely to use any degree of assertiveness, to be a large or small majority, or to be a large or small minority.

trade-offs between leading a group, not risking group fragmentation, and moving efficiently, as follows.

Generally, individuals are likely to gain a benefit from moving efficiently to their own preferred target destination, for example, the destination offering them the most suitable forage, shelter, refuge, or other conditions (Clutton-Brock et al. 1982; Gompper 1996; Conradt 1998; Ruckstuhl and Neuhaus 2002; Conradt and Roper 2003). On the other hand, individuals in social species also gain a benefit from remaining in cohesive groups (Krause and Ruxton 2002; Lusseau 2007). Thus, if group members can-

not maximize group leading rate and minimize group fragmentation risk at the same time, they might have to lose out on either the benefits of moving to their own preferred target destination or the benefits of remaining in a large, cohesive group. These benefits, and therefore the resulting optimal trade-offs, can differ for different group members. To illustrate this, assume that TB is the benefit to a particular member of moving to its preferred target destination and SB is the benefit to that member of remaining in a large, cohesive group. Our results suggest that the likelihood of the member gaining TB and/or SB depends

mainly on its degree of assertiveness ω (fig. 1). The expected net benefits EB to the member are

$$EB = TB \cdot (lr(\omega) + fr(\omega)) + SB \cdot (1 - fr(\omega)), \quad (4)$$

where $lr(\omega)$ is the leading rate and $fr(\omega)$ the fragmentation rate (we assume that members move to their own preferred target destination if the group fragments). Both $lr(\omega)$ and $fr(\omega)$ depend on the degree of assertiveness ω of the member (see fig. 1). Using the simulation results in figure 1, we have predicted the net benefits EB to a member, depending on its degree of assertiveness ω and its ratio of SB to TB (fig. 2). If the benefits to the member of moving to its preferred target destination are similar to those of maintaining group cohesion (i.e., if $SB \approx TB$), the member is predicted to maximize its net benefits if it adopts a medium degree of assertiveness. If the benefits to the member of moving to its preferred target destination are significantly lower than those of maintaining group cohesion (i.e., if $SB \gg TB$), the member is predicted to maximize its net benefits if it adopts a low degree of assertiveness. Finally, if the benefits to the member of moving to its preferred target destination significantly outweigh those of maintaining group cohesion (i.e., if $SB \ll TB$), it is predicted to maximize its net benefits if it adopts a high degree of assertiveness. The ratio between SB and TB can be different for different members within the same group (Clutton-Brock et al. 1982; Gompper 1996; Prins 1996; Conradt 1998; Ruckstuhl and Neuhaus 2002), and thus, the optimal degree of assertiveness in order to maximize expected net benefits EB can differ for different members.

Leading According to "Need" or "Social Indifference" or by Majority. If all members maximized their expected net benefits EB, the group decision outcome would depend on the ratio of SB to TB for members of the two subgroups (table 1). A group would split if the SB : TB ratios were relatively low for both subgroups. If the group remained cohesive, it would move toward the target destination preferred by the subgroup with the lower SB : TB ratio. This is because the subgroup with the lower SB : TB ratio would use a higher degree of assertiveness to optimize its net benefits than the subgroup with the higher SB : TB ratio (see fig. 2) and consequently would be more likely to lead than the other subgroup (see tables A1, A2). If both subgroups had similar SB : TB ratios (and the group did not fragment), the group would be most likely to move to the target destination preferred by the majority subgroup.

In practice, a subgroup could have a lower SB : TB ratio than the other subgroup for two reasons. First, the benefits it derives from reaching its preferred goal (TB) might be relatively greater than those of the other subgroup (i.e., one subgroup has a greater "need" to reach its preferred

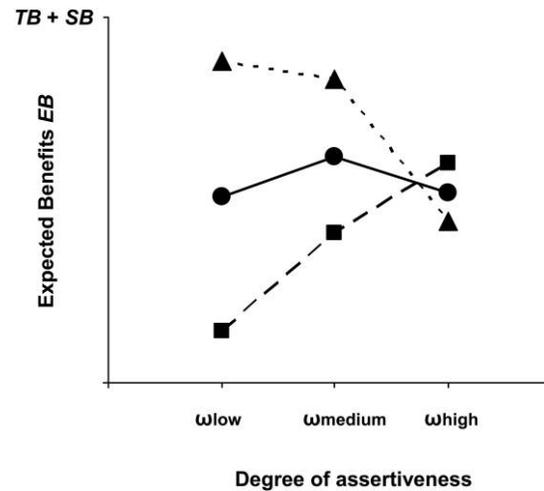


Figure 2: Expected net benefits EB to a member as a function of its degree of assertiveness ω and depending on its ratio of SB (its own benefits of group cohesion) to TB (its own benefits of reaching preferred target destination): (i) $SB = TB$ (circles, solid line); (ii) $SB = 10 \cdot TB$ (triangles, thin dashed line); and (iii) $SB = TB/10$ (squares, thick dashed line). Values of EB are based on equation (4); $fr(\omega)$ and $lr(\omega)$ were estimated using results shown in figure 1, assuming, for simplicity, equal speed and equal social range size for all members.

goal). In this case, any resulting leading by the subgroup is termed "leading according to need." Second, a subgroup could have a lower SB : TB ratio because the benefits it derives from social cohesion (SB) are relatively lower than those of the other subgroup. Any resulting leading is termed "leading according to social indifference."

To summarize, if all members maximized expected net benefits, groups would (i) fragment, (ii) be led according to need, (iii) be led according to social indifference, or (iv) be led by a majority. Which of the four would depend exclusively on the ratios of group cohesion benefits to target-reaching benefits for the two subgroups. No communication or knowledge about other members' needs and benefits would be required, nor would any true cooperation. However, whether all members indeed maximize their expected net benefits and whether evolution would favor such behavior are beyond the scope of this model.

No Arms Race. Trade-offs also mean that one should rarely observe "arms races" of local behavior parameters, whereby all members try competitively to maximize their own influence on the group movement direction (i.e., their own leading rate). This is because arms races, combined with conflicts of interest between group members, invariably lead to group fragmentation. Social animals would, therefore, probably benefit collectively by avoiding arms races. Even if we assume a Prisoner's Dilemma situation,

Table 1: Predicted degrees of assertiveness and resulting group decision outcome

Subgroup I		Subgroup II		Group cohesion and movement outcome
Benefits	Trade-off assertiveness	Benefits	Trade-off assertiveness	
SB \gg TB	Low	SB \gg TB	Low	Cohesive, moves to majority target
SB \gg TB	Low	SB \approx TB	Medium	Cohesive, moves to target of subgroup II (lower SB : TB)
SB \gg TB	Low	SB \ll TB	High	As above
SB \approx TB	Medium	SB \approx TB	Medium	Cohesive, moves to majority target
SB \approx TB	Medium	SB \ll TB	High	Usually fragments
SB \ll TB	High	SB \ll TB	High	Always fragments

Note: Predicted degrees of assertiveness for members of two subgroups with different trade-offs between SB and TB and different preferred target destinations (based on results shown in fig. 2) and the resulting group decision outcome (based on results shown in fig. 1), if all group members maximize their expected net benefits EB (see eq. [4]).

we would not expect to observe many groups with an arms race and a conflict of interest between members, simply because such groups are unstable and cannot exist for long.

Discussion

At first glance, it seems intuitively unlikely that any members of large, self-organizing groups would be able to exert deliberate and disproportionate influence over the behavior of the group as a whole, simply because of the size and nature of such groups. Consequently, previous models have tended to assume that group members contribute equally to the collective behavioral outcome (see Conradt and Roper 2009, for a review). Here, however, we show, by building on a previous self-organizing-systems model (Couzin et al. 2005), that individual group members could indeed, at least in principle, deliberately increase or decrease their influence over group movement direction. In addition, we show that this can be achieved by adjustments in a small number of simple, local behavioral parameters. Specifically, an individual can gain a greater degree of influence over group movement direction by increasing its degree of assertiveness, reducing its speed (cf. Gueron et al. 1996; Beekman et al. 2006), and reducing the range within which it is attracted to neighbors. Knowledge of or communication about the motivation of other members of the group is not required.

In view of this, and given that moving toward a preferred target destination is likely to be beneficial (Clutton-Brock et al. 1982; Gompper 1996; Conradt 1998; Ruckstuhl and Neuhaus 2002), the question arises as to why we do not see individuals engaging in behavioral-parameter arms races, whereby group members with conflicting preferences increase their assertiveness and reduce their speed and social attraction range to an ever-increasing extent. Our model suggests that this is prevented by trade-offs. For example, an increase in assertiveness increases the probability of group fragmentation as well as increasing the likelihood that the group will move toward the desired

target destination; and group fragmentation is usually disadvantageous to social animals (Krause and Ruxton 2002).

These trade-offs have some interesting implications. If a member cannot increase its chance of leading the group efficiently to its preferred target destination without, at the same time, increasing the risk of group fragmentation, the member has to decide which of the two is more important to itself. The more beneficial it is for a member to reach a particular target destination, the higher the risk of group fragmentation that member might be prepared to accept and the higher the degree of assertiveness it might adopt; and vice versa. There are potentially interesting consequences. If all group members maximized their own expected net benefits (and were accordingly assertive or unassertive), then not all members would always contribute equally to group decisions about movement targets. In particular, if, for some members, the benefits of reaching a particular target destination significantly outweighed the benefits of remaining in a large, cohesive group but this was not so for other members, the first members would exert a stronger influence over the group's movement direction (leading according to need). On the other hand, if, for some members, the benefits of remaining in a large, cohesive group significantly outweighed the benefits of reaching a particular target destination but this was not so for other members, the latter would have a stronger influence on the group's movement direction (leading according to social indifference). Only if the benefits of remaining in a large, cohesive group and the benefits of reaching a particular target destination were similar for all members would all have a similar influence; in which case the group would move to the target preferred by a majority of members ("leading by majority"). Our model cannot predict whether all individual members would indeed act so as to optimize their expected net benefits or whether evolution would favor such a behavior. Nevertheless, there is some empirical evidence that supports the notions of leading according to need and leading according to social indifference, as follows.

Possible evidence for leading according to need is provided by experiments on fish (Krause et al. 1992; Krause 1993). Food-deprived fish take the front position in shoals, where they have a stronger influence on movement direction, whereas well-fed fish, which are predicted to have a stronger interest in group cohesion, follow behind. The mechanism for this is probably that food-deprived fish maintain a larger intersocial distance (Hoare et al. 2004), implying, as our model predicts, a smaller social attraction range and/or a larger degree of assertiveness.

There are further possible examples for leading according to need. In ungulate herds, individuals with higher needs in terms of forage requirements (e.g., pregnant and lactating females) often assume the leading position (Gueron et al. 1996; Prins 1996). Flexibility between compromising and leading has also been reported in birds (Biro et al. 2006), implying interindividual differences in assertiveness. However, in this case the driving factor is probably a difference in certainty of knowledge between individuals. It is theoretically interesting that a model by Rands et al. (2003), within a different context (activity synchronization between two foragers) and starting from different assumptions, also predicts that the “more needy” forager (in this case, the one with the lower energy resources) should be leading the other. Possible examples of leading according to social indifference can be found in ungulates, where, under some conditions, females lead groups and males follow behind (Prins 1996; Conradt and Roper 2003). It has been suggested that this is because males have a larger incentive (in terms of mating advantages) to avoid group fragmentation than do females (Prins 1996). Leading according to social indifference might also explain why, in many species, juveniles, for whom social cohesion is often more crucial than for adults (Lingle 2003; Lingle et al. 2005), have much less influence on group movement decisions than do adults (see Conradt and Roper 2003 for a brief overview).

Fish shoals, which are easily filmed (Bumann and Krause 1993), would be a good system with which to test our model experimentally. Benefits to individual fish of reaching a target destination (e.g., a foraging patch) can be manipulated by differential food deprivation (Krause et al. 1992). Benefits of group cohesion can be manipulated by exposing individual fish to “predator” models before observations (Hoare et al. 2004). We predict that the more food deprived a fish is, the larger should be its intersocial distance, the slower its speed, and the more likely it should be to lead the group (leading according to need). On the other hand, fish exposed to a predator model should have lower intersocial distances and faster speeds and be less likely to lead the group than nonexposed fish (leading according to social indifference). The effects of food deprivation and predator-model exposure should combine,

making food-deprived, nonexposed fish the most likely to lead and well-fed, predator-model-exposed fish the least likely to lead. By grading and combining different food-deprivation and predator-model-exposure manipulations, quantitative predictions of our model could be tested as well as qualitative ones.

The outcome of our model bears some resemblance to the outcome of models of escape panic in human crowds (Helbing et al. 2000; Altshuler et al. 2005). These have also reported trade-offs (in this case, between finding exits efficiently and blockage of exits by overcrowding) that are decided by a single behavioral parameter (“degree of panic”). The latter is mathematically analogous to the parameter “degree of assertiveness” in our model. However, while our model examines decision outcomes from the point of view of individuals, panic models judge decision outcomes from the point of view of the group (e.g., what proportion of the group succeeds in leaving the danger zone in a given time). In addition, group cohesion is generally advantageous to social animals, whereas group fragmentation is usually advantageous in panic situations.

Acknowledgments

L.C. is supported by a Royal Society University Research Fellowship. She specifically wishes to thank the Royal Society for support with maternity leave and part-time work. I.D.C. gratefully acknowledges support by Defense Advanced Research Projects Agency grant HR0011-05-1-0057 to Princeton University.

Literature Cited

- Altshuler, E., O. Ramos, Y. Núñez, J. Fernández, A. J. Batista-Leyva, and C. Noda. 2005. Symmetry breaking in escaping ants. *American Naturalist* 166:643–649.
- 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.
- Barbera, S., and M. O. Jackson. 2006. On the weights of nations: assigning voting weights in a heterogeneous union. *Journal of Political Economy* 114:317–339.
- Beekman, M., R. L. Fathke, and T. D. Seeley. 2006. How does an informed minority of scouts guide a honeybee swarm as it flies to its new home? *Animal Behaviour* 71:161–171.
- Biro, D., D. J. T. Sumpter, J. Meade, and T. Guilford. 2006. From compromise to leadership in pigeon homing. *Current Biology* 16: 2123–2128.
- Bumann, D., and J. Krause. 1993. Front individuals lead in shoals of three-spined sticklebacks (*Gasterosteus aculeatus*) and juvenile roach (*Rutilus rutilus*). *Behaviour* 125:189–198.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behaviour and ecology of two sexes. University of Chicago Press, Chicago.
- Conradt, L. 1998. Could asynchrony in activity between the sexes

- cause intersexual social segregation in ruminants? *Proceedings of the Royal Society B: Biological Sciences* 265:1359–1363.
- 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 & 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 (forthcoming).
- Couzin, I. D., and J. Krause. 2002. Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior* 32:1–75.
- 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.
- Cremer, J., and T. R. Palfrey. 1999. Political confederation. *American Political Science Review* 93:69–83.
- Diecidue, E., P. P. Wakker, and M. Zeelenberg. 2007. Eliciting decision weights by adapting de Finetti's betting-odds method to prospect theory. *Journal of Risk and Uncertainty* 34:179–199.
- Dietrich, F. 2006. General representation of epistemically optimal procedures. *Social Choice and Welfare* 26:263–283.
- Dyer, J. R. G., C. C. Ioannou, L. J. Morrell, D. P. Croft, I. D. Couzin, D. A. Waters, and J. Krause. 2008. Consensus decision making in human crowds. *Animal Behaviour* 75:461–470.
- Franks, N. R., A. Dornhaus, J. P. Fitzsimmons, and M. Stevens. 2003. Speed versus accuracy in collective decision making. *Proceedings of the Royal Society B: Biological Sciences* 270:2457–2463.
- Gompper, M. E. 1996. Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. *Behavioral Ecology* 7: 254–263.
- Gueron, S., S. A. Levin, and D. I. Rubenstein. 1996. The dynamics of herds: from individuals to aggregations. *Journal of Theoretical Biology* 182:85–98.
- Hastie, R., and T. Kameda. 2005. The robust beauty of majority rules in group decisions. *Psychological Review* 112:494–508.
- Helbing, D., I. Farkas, and T. Vicsek. 2000. Simulating dynamical features of escape panic. *Nature* 407:487–490.
- Hoare, D. J., I. D. Couzin, J. G. J. Godin, and J. Krause. 2004. Context-dependent group size choice in fish. *Animal Behaviour* 67:155–164.
- Krause, J. 1993. The relationship between foraging and shoal position in a mixed shoal of roach (*Rutilus rutilus*) and chub (*Leuciscus cephalus*): a field-study. *Oecologia* (Berlin) 93:356–359.
- Krause, J., and G. D. Ruxton. 2002. *Living in groups*. Oxford University Press, Oxford.
- 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.
- Lingle, S. 2003. Group composition and cohesion in sympatric white-tailed deer and mule deer. *Canadian Journal of Zoology* 81:1119–1130.
- Lingle, S., S. M. Pellis, and W. F. Wilson. 2005. Interspecific variation in antipredator behaviour leads to differential vulnerability of mule deer and white-tailed deer fawns early in life. *Journal of Animal Ecology* 74:1140–1149.
- List, C. 2004. Democracy in animal groups: a political science perspective. *Trends in Ecology & Evolution* 19:168–169.
- Lusseau, D. 2007. Evidence for social role in a dolphin social network. *Evolutionary Ecology* 21:357–366.
- Parrish, J. K., S. V. Viscido, and D. Grunbaum. 2002. Self-organized fish schools: an examination of emergent properties. *Biological Bulletin* 202:296–305.
- Prins, H. H. T. 1996. *Ecology and behaviour of the African buffalo*. Chapman & Hall, London.
- Rands, S. A., G. Cowlshaw, R. A. Pettifor, J. M. Rowcliffe, and R. A. Johnstone. 2003. Spontaneous emergence of leaders and followers in foraging pairs. *Nature* 423:432–434.
- Reebs, S. G. 2000. Can a minority of informed leaders determine the foraging movements of a fish shoal? *Animal Behaviour* 59: 403–409.
- Ruckstuhl, K. E., and P. Neuhaus. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews* 77:77–96.
- Seeley, T. D. 2002. When is self-organization used in biological systems? *Biological Bulletin* 202:314–318.
- Selous, E. 1931. *Thought transference (or what?) in birds*. Constable, London.
- Simons, A. M. 2004. Many wrongs: the advantage of group navigation. *Trends in Ecology & Evolution* 19:453–455.
- Sumpter, D. J. T. 2006. The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361:5–22.

Associate Editor: Benjamin M. Bolker
 Editor: Michael C. Whitlock