Deciding group movements: Where and when to go

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ABSTRACT

A group of animals can only move cohesively, if group members “somehow” reach a consensus about the timing (e.g., start) and the spatial direction/destination of the collective movement. Timing and spatial decisions usually differ with respect to the continuity of their cost/benefit distribution in such a way that, in principle, compromises are much more feasible in timing decision (e.g., median preferred time) than they are in spatial decisions. The consequence is that consensus costs connected to collective timing decisions are usually less skewed amongst group members than are consensus costs connected to spatial decisions. This, in turn, influences the evolution of decision sharing: sharing in timing decisions is most likely to evolve when conflicts are high relative to group cohesion benefits, while sharing in spatial decisions is most likely to evolve in the opposite situation. We discuss the implications of these differences for the study of collective movement decisions.

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1. Background

For social animals, staying together (i.e., group cohesion) is often of great selective advantage (Krause and Ruxton, 2002; Trillmich et al., 2004; Kerth et al., 2006; King et al., 2008; Austen-Smith and Feddersen, 2009; List et al., 2009) and, therefore, a priority (Conradt and List, 2009; Conradt and Roper, 2009; Conradt et al., 2009). In order to maintain group cohesion, social animals frequently have to make consensus decisions, not least about group movements (Conradt and Roper, 2003, 2005; Sumpter et al., 2008; Sumpter and Pratt, 2009). A ‘consensus decision’ is when the members of a group choose, collectively, between mutually exclusive actions (Conradt and Roper, 2007). With respect to group movements, this means group members have to reach a consensus about the timing of group movements (Black, 1988; Stewart and Harcourt, 1994; Boinski and Campbell, 1995; Conradt, 1998; Ruckstuhl, 1999; Conradt and Roper, 2000; Rands et al., 2003; Trillmich et al., 2004; Dostalkova and Spinka, 2007; Sueur and Petit, 2008a) and, often simultaneously, about their direction/destination (Couzin et al., 2005; Biro et al., 2006; Ward et al., 2008; Dyer et al., 2009). If group members fail to do this, the group is likely to split and the benefits of group living are reduced (Krause and Ruxton, 2002; Trillmich et al., 2004; Conradt and Roper, 2007). However, synchronising the timing of activities or aligning movement destinations with those of other group members can also involve fitness costs (‘consensus costs’: Conradt and Roper, 2005). This is because an individual might be obliged to time its activities, or choose its movement destination, sub-optimally with respect to its own individual requirements in order to synchronise and align with others that differ in requirements (Clutton-Brock et al., 1982; Gompper, 1996; Conradt, 1998; Ruckstuhl, 1999). Because consensus costs can lead to conflicts in collective movement decisions, they can be crucial in shaping animal social behaviour (Ruckstuhl, 1999; Ruckstuhl and Neuhaus, 2000; King et al., 2008).

2. Differences between timing and spatial decisions

Since coherent collective movements of groups require consensus decisions about both, the timing and the destination of the movements (i.e., spatial decision), it is worth looking more closely at the two types of decisions. Considering first timing decisions, here the costs and benefits are often continuous (Conradt and Roper, 2003, 2009; Dostalkova and Spinka, 2007): that is, the earlier (or the later) a collective movement starts relative to an individual’s optimal start time, the less optimal is the individual’s resulting time budget (e.g., Clutton-Brock et al., 1982) and the higher are the fitness costs to the individual (Conradt, 1998; Ruckstuhl, 1999). Thus, often fitness costs increase continuously with the difference between optimal and actual start time (Clutton-Brock et al., 1982; Ruckstuhl, 1999; Conradt and Roper, 2003). For example, if an individual is hungry and would therefore optimally leave a resting place now (in order to go to a foraging patch), then the later the individu-
The evolution of decision sharing

In humans, consensus decisions are often made democratically or in an 'equally shared' manner, i.e., all group members contribute to the decision. In the past few years more and more studies have also reported shared consensus decisions in social non-human animals (Stewart and Harcourt, 1994; Seeley and Buhrman, 1999; Franks et al., 2002, 2009; Trillmich et al., 2004; Biro et al., 2006; Kerth et al., 2006; Codling et al., 2007; Lusseau, 2007; Stueckle and Zinner, 2008; Sueur and Petit, 2008a; Bourjade et al., 2009; Petit et al., 2009; Ramseyer et al., 2009a, 2009b; Sueur et al., 2009). Sharing of decisions is, in principle, more profitable for groups than accepting the 'unshared' decision of a single dominant member (Conradt and Roper, 2003; King et al., 2008). However, this is not true for all individual group members, posing a question as to how and when shared decision making evolves.

For collective decisions on activity timing, it has been argued that sharing of decisions is particularly likely to evolve when (i) groups are heterogeneous in composition; (ii) potential consensus costs are large; (iii) grouping benefits are marginal; or (iv) groups are close to, or above, optimal size (Conradt and Roper, 2007). By contrast, sharing of spatial decisions is most likely to evolve when (i) groups are homogeneous; (ii) potential consensus costs are relatively low; (iii) grouping benefits are high; or (iv) groups are above optimal group size (Conradt and Roper, 2009). Thus, the conditions favourable decision sharing are diametrically opposite for timing and spatial decisions.

The reasons for this are as follows. Assume a consensus can be reached through a shared or unshared decision. Generally, a group either reaches a consensus or it splits (Conradt, 1998; Ruckstuhl, 1999); and it is likely to split when consensus costs outweigh the benefits of group cohesion for at least some individuals. In shared timing decisions, consensus costs are spread between individuals, so that each individual pays some cost but usually none pays an excessively high cost (see above; and Conradt and Roper, 2003). On the other hand, in unshared timing decisions, some individuals pay no or very little cost, while others pay a relatively high cost. If conflicts are large or the benefits of group cohesion are low, it is likely that in unshared (but less so in shared) decisions some individuals' costs will outweigh the benefits, and the group will split. Thus, in timing decisions, if conflicts are large (e.g., if the group is heterogeneous in requirements and/or potential consensus costs are high) and/or benefits of group cohesion are low (e.g., when grouping benefits are generally low and/or group size is above optimal size), only groups with shared decision making are likely to persist (Conradt and Roper, 2007).

Consider now spatial decisions between two potential destinations A and B (see Conradt and Roper, 2009 for details of a game theory model). Here, compromises are not possible in the same way as in timing decisions. Consequently, some individuals will always pay relatively high consensus costs and other individuals none. Therefore, if the group splits, it is likely to split along the dividing lines between group members that prefer destination A ('part A') and those that prefer B ('part B'). Let us assume part A consists of a majority of group members and part B of a minority. If the group is above optimal size, it might not be greatly disadvantageous for part A to move off on its own and to risk a group split. This will be the more so, the larger the majority is (i.e., the more homogeneous the group as a whole is). The minority part B must then either follow or split from the rest of the group. If consensus costs are high relative to grouping benefits, it is better for part B to split. In this case, neither shared nor unshared decision making evolves within the original group. On the other hand, if grouping benefits are high relative to consensus costs, it pays part B to follow the majority part A. Hence, if the group is likely to be above optimal group size and relatively homogeneous, or if consensus costs are low and grouping benefits large, a shared decision (in which the majority leads) is likely to evolve.

By contrast, if the group is below optimal group size, both parts A and B might benefit from maintaining group cohesion (assuming that consensus costs are not too large relative to grouping benefits). This is especially so if the majority is relatively small (i.e., if the group is relatively heterogeneous). Now, who evolves to lead a group decision is likely to depend on the starting point of the system (e.g., once one class of individuals is more assertive, evolution favours them further as ‘leaders’): Dyer et al., 2009; King et al., 2009; Magnhagen and Bunnefeld, 2009) or on chance (Rands et al., 2003).
Thus, we would expect decisions to evolve that are unshared or partially shared, but not necessarily led by a majority.

5. Implications for the study of movement decisions

As argued above, it is likely that slightly different ways of reaching collective decisions might evolve depending on the nature of the decision (temporal or spatial). Given that a group movement often involves both types of decisions, it is necessary to investigate separately (i) who initiates the start of group movements and how; and (ii) who determines group movement directions/destinations and how. Perhaps, some of the differences in empirical observations concerning unshared (King et al., 2008; Lusseau and Conradt, 2009) or shared movement decisions (Seeley and Buhlmann, 1999; Biro et al., 2006; Lusseau, 2007; Stueckle and Zinner, 2008; Sueur and Petit, 2008a, 2008b; Bourjade et al., 2009; Faria et al., 2009; Petit et al., 2009; Ramseyer et al., 2009a, 2009b) arise from differences in how important these two aspects of the decision (timing or spatial) are to group members: consensus costs of the timing and the spatial part of a movement decision could differ and be independent of one another. That is, the issue of when to move could be more crucial for individual group members (e.g., flight movements from predators: List, 2004), or the issue of where to move could be more important (e.g., many foraging decisions).

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References