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Shared decision-making drives collective movement in wild baboons

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Abstract

Conflicts of interest about where to go and what to do are a primary challenge of group living. However, it remains unclear how consensus is achieved in stable groups with stratified social relationships. Tracking wild baboons with high-resolution GPS and analyzing their movements relative to one another reveals that a process of shared decision-making governs baboon movement. Rather than preferentially following dominant individuals, baboons are more likely to follow when multiple initiators agree. When conflicts arise over the direction of movement, baboons choose one direction over the other when the angle between them is large, but compromise if not. These results are consistent with models of collective motion, suggesting that democratic collective action emerging from simple rules is widespread, even in complex, socially-stratified societies.

Individuals living in stable social groups may often disagree about where to go, but must reconcile their differences to maintain cohesion and thus the benefits of group living. Consensus decisions could be dominated by a single despotic leader (1), determined by a hierarchy of influence (2), or emerge from a shared, democratic process (3). Because decisions are typically more accurate when information is pooled (4, 5), theory predicts that shared decision-making should be widespread in nature (6). However, in species that form

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long-term social bonds, considerable asymmetries in dominance and social power often exist, and some have proposed that these differences give high-ranking individuals increased influence over group decisions (1, 7, 8). Determining how consensus is achieved in these types of societies remains a core challenge for understanding the evolution of social complexity (6, 9, 10).

We studied the collective movement of a troop of wild olive baboons (*Papio anubis*) at Mpala Research Centre in Kenya to examine how group members reach consensus about whether and where to move. Baboons, long a model system for studying the evolutionary consequences of social bonds (11–13), live in stable multi-male, multi-female troops of up to 100 individuals (11). Despite differing needs, capabilities and preferred foraging strategies (14–16), troop-members remain highly cohesive, travelling long distances each day as a unit, while foraging for diverse but widely dispersed foods. How troops make collective movement decisions, and whether specific individuals determine decision outcomes, remains unclear. Attempts to identify influential individuals by observing which animals initiate departures from sleeping sites (17, 18) or are found at the front of group progressions (19) have yielded conflicting results (9). Studying collective decision-making events requires many potential decision-makers in a group to be monitored simultaneously–a significant logistical challenge.

To tackle this “observational task of daunting dimensions” (8), we analyzed data from 25 wild baboons (~80% of our study troop’s adult and subadult members, Table S1), each fitted with a custom-designed GPS collar that recorded its location every second (Fig. 1, Movies S1–2 (20)). We developed an automated procedure for extracting “movement initiations” based on the relative movements of pairs of individuals (20). These were defined as sequences in which one individual (the initiator) moved away from another (the potential follower), and was either followed (a “pull”, Fig. 1 inset, left), or was not and subsequently returned (an “anchor”, Fig. 1). This definition is agnostic to individual intention and motivation. While any particular movement sequence may or may not reflect a causal relationship between initiator and follower (Supplementary Online Text), analyzing aggregate patterns across many sequences nonetheless yields insight into the processes driving collective movement.

Our method is based on finding all minima and maxima in the distance between pairs of individuals, allowing it to capture pulls and anchors occurring over a range of timescales, from seconds to minutes (Fig. S8, (21)). It also detects simultaneous movement initiations. We aggregated concurrent pulls and anchors on the same potential follower into “events” (20). We then examined the behavior of potential followers during these events, including if they followed any initiators, and if so in which direction they moved.

Our data show that the probability of following depends on both the number of initiators and their level of directional agreement. To quantify directional agreement among concurrent initiators in an event, we calculated the circular variance (*cv*) of the unit vectors pointing from the potential follower to each initiator, and defined agreement as 1-*cv*. This measure approaches 0 when individuals initiate in opposing directions (low agreement), and 1 when all individuals initiate in the same direction (high agreement). Fitting a binomial Generalized

Estimating Equation (GEE) model revealed a baboon's probability of following depends on an interaction between the number of initiators and their directional agreement (Fig. 2, Table S2). Overall, baboons are most likely to follow when there are many initiators with high agreement. However, when agreement is low, having more concurrent initiators decreases the likelihood that a baboon will follow anyone. This pattern suggests that decisions are delayed when opinions are split.

If social dominance plays a role in determining the outcomes of movement decisions (1), the disproportionate influence of high-ranking animals should be easiest to observe when single individuals make movement initiations (single-initiator events). We found no evidence of this. The dominant male did not have the highest probability of being followed, dominance rank (20) did not correlate with initiation success, and no sex differences existed in initiation success (Fig. S1, binomial GLMM: coefficient (male)±SE=-0.222±0.159, z=-1.402, P=0.161, initiator and follower fit as random effects), despite males being dominant over females (11). Instead, we found that baboons are more likely to follow initiators who move in a highly directed manner (Fig. S2), consistent with the findings of a previous study (17).

When multiple members of the troop initiate movement simultaneously, followers must decide in which direction to move. Theory (22) predicts that, when preferred directions conflict, the type of consensus achieved will depend on the angle between these directions (angle of disagreement, Fig. 3A). When this angle is large, the group travels in one direction or the other ("choose"). Below a critical angle, the same individual rules result in the group moving in the average of preferred directions ("compromise"). Our data reveal that baboon followers exhibit these two predicted regimes. In events with two initiators, followers consistently choose one direction or the other when the angle between the initiators' directions is greater than approximately 90 degrees, but compromise when the angle falls below this threshold (Fig. 3B, (20)). The same pattern emerges in events with multiple initiators clustered into two subgroups (Fig. 3C).

When initiators have strongly conflicting directions, how do followers choose which direction to take? When facing a choice between two subgroups of initiators, followers are more likely to move towards the direction of the majority. This tendency grows stronger as the numeric difference between the two subgroups increases (Fig. 4), consistent with theoretical (3, 6, 22) and empirical studies (3, 5, 23). Individuals' choices also scale up to group movement. Following such conflicts, the troop's travel direction is positively correlated with the direction associated with successful (but not failed) subgroups of initiators (Fig. S4). Thus, failed initiators ultimately move in the direction of the majority (away from their original initiation directions), maintaining cohesion with others.

The failure of high-ranking individuals to dominate movement decisions highlights an important distinction between social status and leadership in wild baboons. Although field-based experiments suggest that dominant individuals, when highly motivated, can shape group movement patterns to their advantage (1), our results provide evidence that the decision-making process driving day-to-day movement patterns in baboons is fundamentally shared. Our study emphasizes the power of using high-resolution GPS tracking data to uncover the interdependencies of animal movements. In conjunction with the rich individual-level data that long-term observational studies provide, these methods open up a new window into the social dynamics of wild animal groups.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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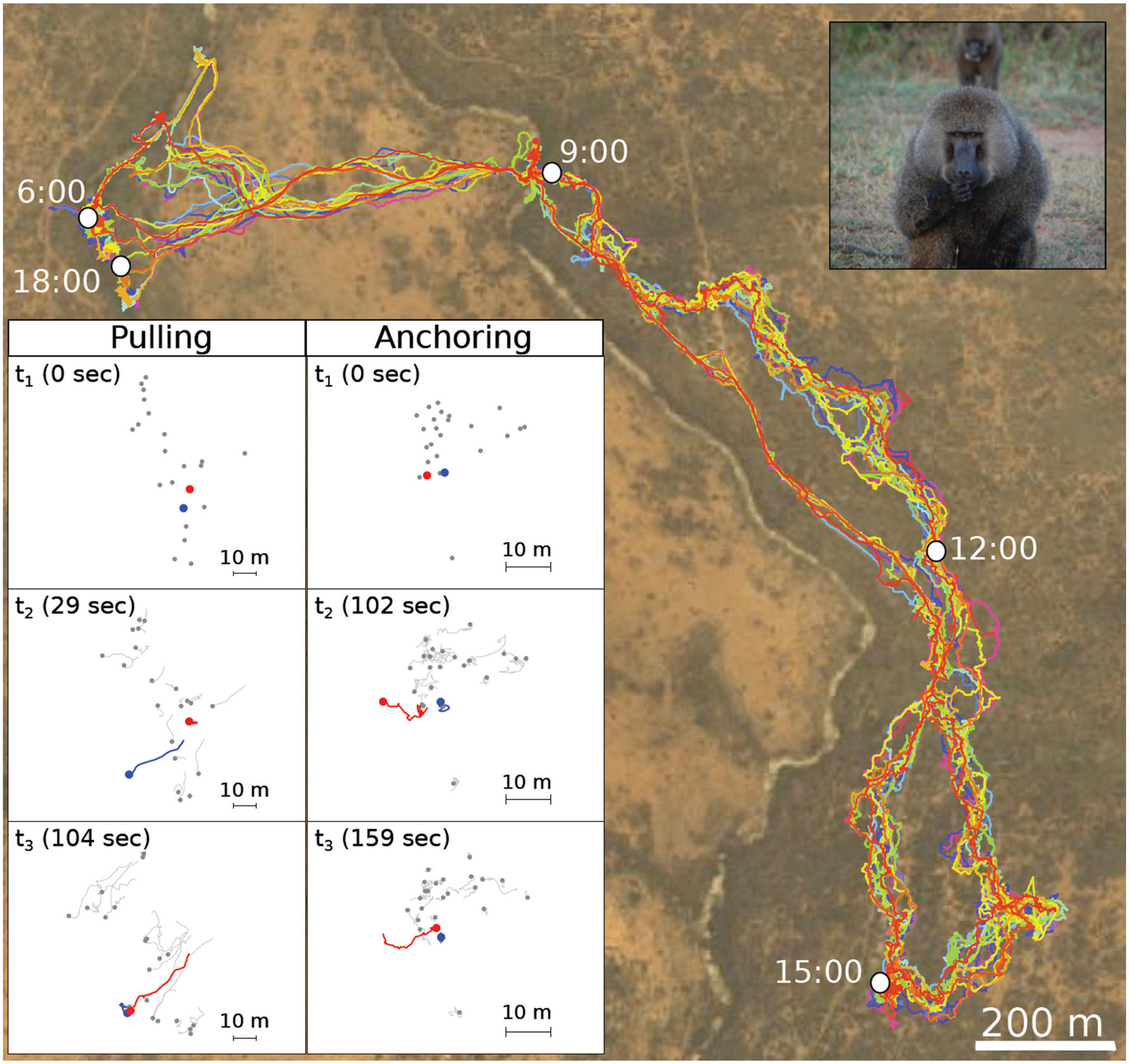

Fig. 1. Extracting pulls and anchors from movement data

Baboon trajectories (25 individuals) during the first day of tracking. (inset, left) Successful initiation (pull), where the initiator (red) recruits the follower (blue). (inset, right) Failed initiation (anchor), where the initiator (red) fails to recruit the potential follower (blue). Other individuals' trajectories are in gray.

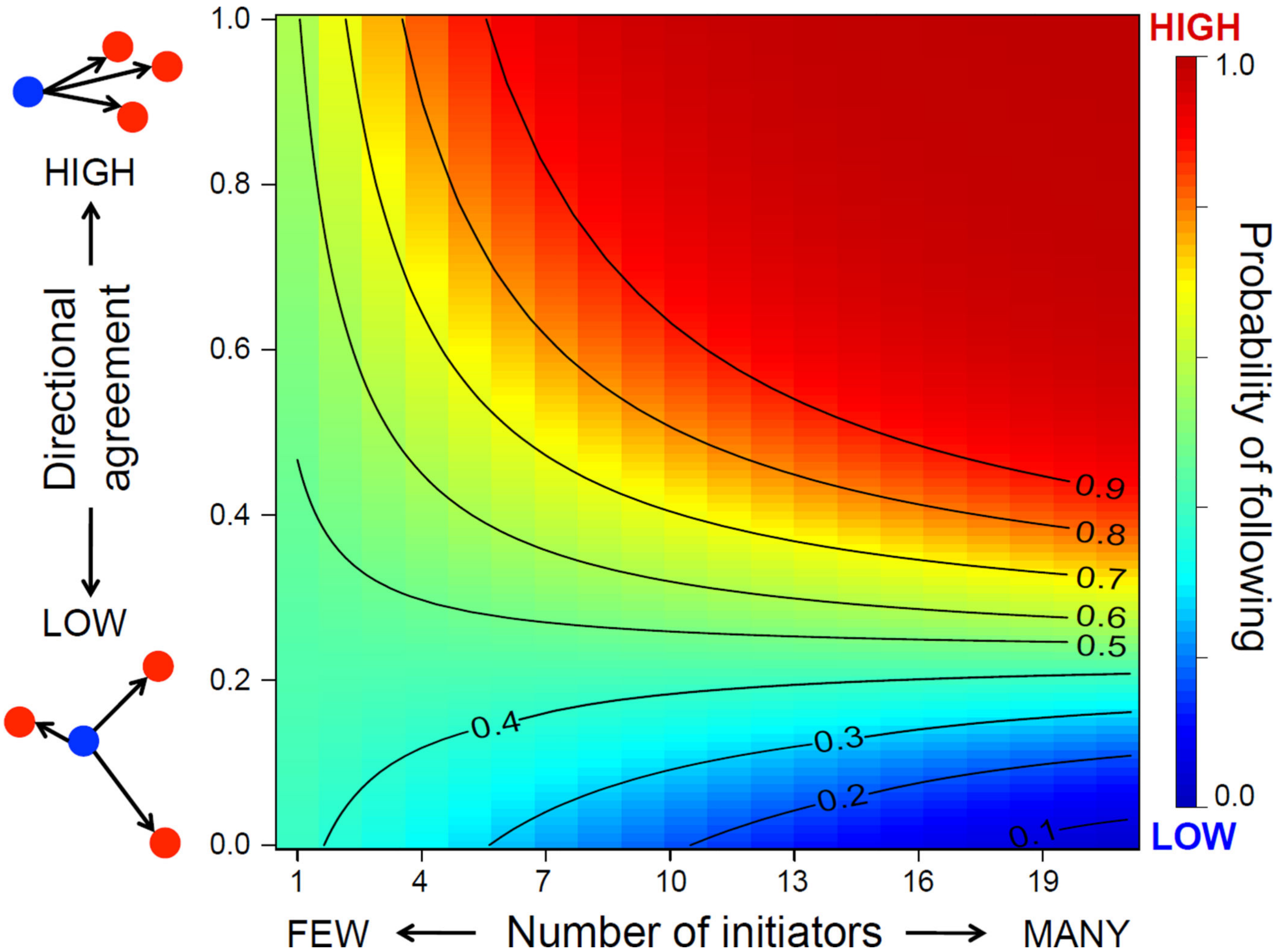

Fig. 2. Probability of following depends on the number of initiators and their directional agreement

Baboons are most likely to follow when there is high agreement among many initiators. When agreement is low, additional initiators do not improve the chances of following, and may decrease them. Surface plot shows a GEE fit to the data (Table S2).

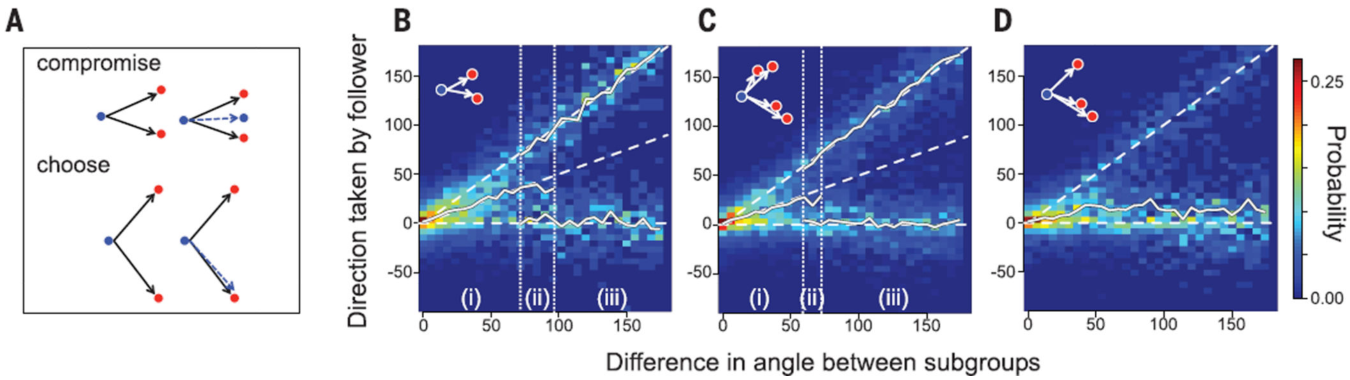

Fig. 3. As predicted by collective movement models (A), as the angle between initiation directions increases, baboon followers exhibit a transition from compromising (moving in the average of the two directions) to choosing one direction over the other

(B–D). Plots show the empirical distribution of follower movement directions as a function of the angle of disagreement between two initiators (**B**) or two clusters of initiators (**C**). Regions divided by dotted lines are statistically assigned to (i) compromise, (ii) transitional, and (iii) choose (see Fig. S9). Solid white lines show the median of the directions taken for each mode. Dashed white lines represent the expected direction when compromising (middle line) or choosing (top/bottom lines). When the number of individuals in the clusters differs by 1, followers are more likely to move towards the majority (i.e. along the horizontal line) (**D**).

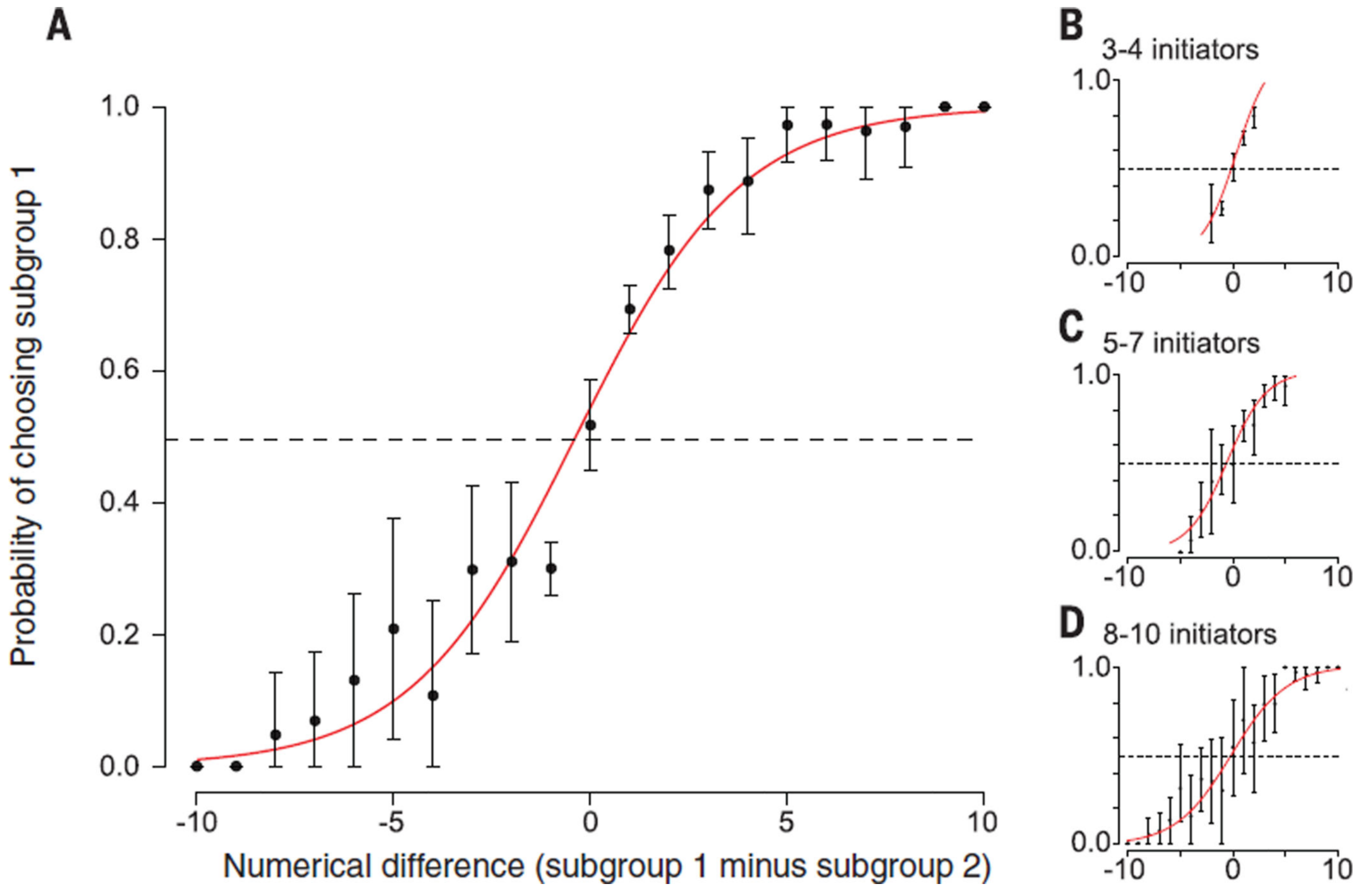

Fig. 4. When initiation directions conflict, followers choose the direction of the largest subgroup of initiators

(**A**) Empirical data are in black; error bars are 95% confidence intervals estimated by 1000 bootstrapped replications of the data. Red line shows a sigmoidal fit to the data. The tendency to follow the majority is maintained regardless of the total number of initiators (**B–D**), or whether the troop is moving or stationary (Fig. S6).