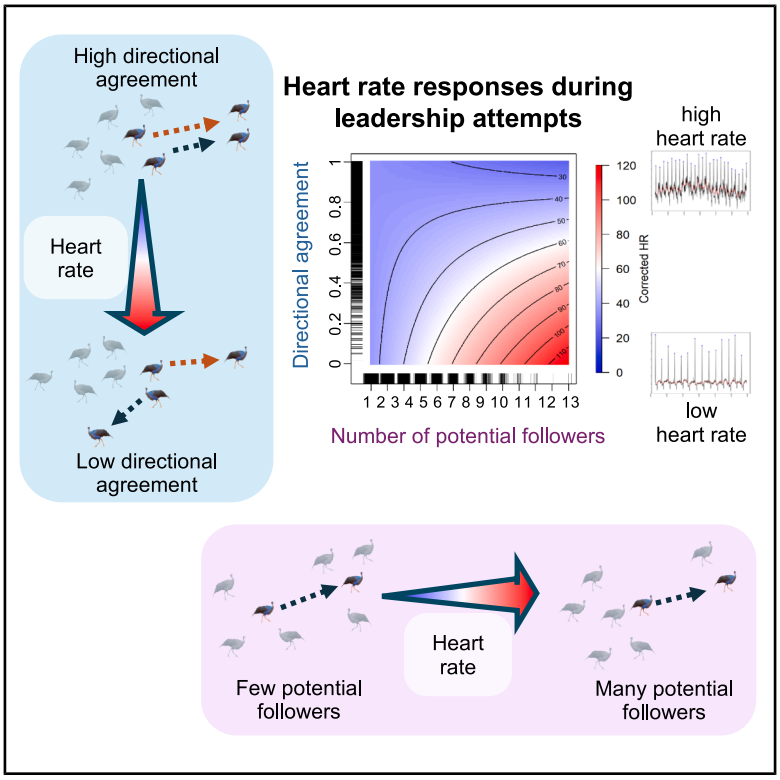
Report

Current Biology

The physiological cost of leadership in collective movements

Graphical abstract



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In brief

Using heart rate and GPS data from wild vulturine guineafowl, Brandl et al. show that initiating group movements is physiologically costly—especially when consensus is low. These findings reveal hidden energetic costs and trade-offs associated with leadership in collective decision-making.

Highlights

- Initiating collective movement increases heart rates of vulturine guineafowl
- Leadership costs can exceed those of movement speed alone
- Failed leadership attempts under low consensus are particularly costly
- Spatial position in the group has only minor effects on heart rate and stress

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Report

The physiological cost of leadership in collective movements

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SUMMARY

Individuals can gain substantial benefits from collective actions.[1–7] However, collective behaviors introduce new challenges, like coordinating actions, maintaining cohesion, and meeting the needs of different individuals. When making collective movements, leaders are typically thought to gain disproportionate benefits through the choice of more beneficial resources[3] and/or earlier access to resources.[8] However, reaping these benefits can also come with costs. Attempting to influence group movements can increase energy expenditure[4,9,10] and predation exposure.[11,12] Moreover, leadership involves a process of negotiation in many animal groups. Within-group differences in directional preferences are typically resolved by some individuals initiating directional movements, after which they are either followed (if they are successful in leading) or return to the group (if they fail).[13–30] By combining data on movement initiations (using whole-group global positioning system [GPS] tracking[31]) and individual heart rate (from implanted electrocardiogram [ECG] loggers) in wild vulturine guineafowl, we found significant increases in heart rate (and decreases in heart rate variability) during collective movements. Further, we found that attempting—and failing—to initiate directional movement was physiologically costly, especially for leadership attempts when consensus among group members was low and when potential leaders acted against the majority. The scale of these costs far outweighed those arising from increased movement speeds alone, suggesting that leadership can induce physiological stress, entailing increased energy expenditure and potential physiological damage. These results suggest that behaviors often thought beneficial to individuals (by influencing group behaviors) are also physiologically costly, representing a constraint on group-living and explaining why sometimes individuals opt out of contributing to leadership.

RESULTS AND DISCUSSION

We studied the physiological consequences of collective movements and leadership in a group of wild vulturine guineafowl (*Acryllium vulturinum*) in Kenya. Vulturine guineafowl are large, predominately terrestrial birds endemic to East Africa. They live in multi-male, multi-female groups with temporally stable membership,[32] ranging from 15 to >65 individuals.[33] Despite steep dominance hierarchies,[23,34] groups reach consensus about where to go, maintaining cohesion using shared decision-making.[23] Individuals move in their preferred direction (i.e., initiate) and are either followed (success) or not (failure) by others. All group members can lead,[24] but some engage in leadership more often. The highly dynamic nature of group movements (Video S1) means all individuals occupy every spatial position (front, middle, back, and side) within the group throughout the day.

To determine when, and for whom, costs arise from individuals' contributions to collective movements, we analyzed data collected simultaneously from global positioning system (GPS) and electrocardiogram (ECG) loggers (Figure 1; STAR Methods). GPS loggers were fitted to ~70% of the members of a vulturine guineafowl group (n = 20 of 28, collecting data at 1 Hz; see He et al.[31]) from which we quantified individual spatial position, individual and group movement speeds, and both

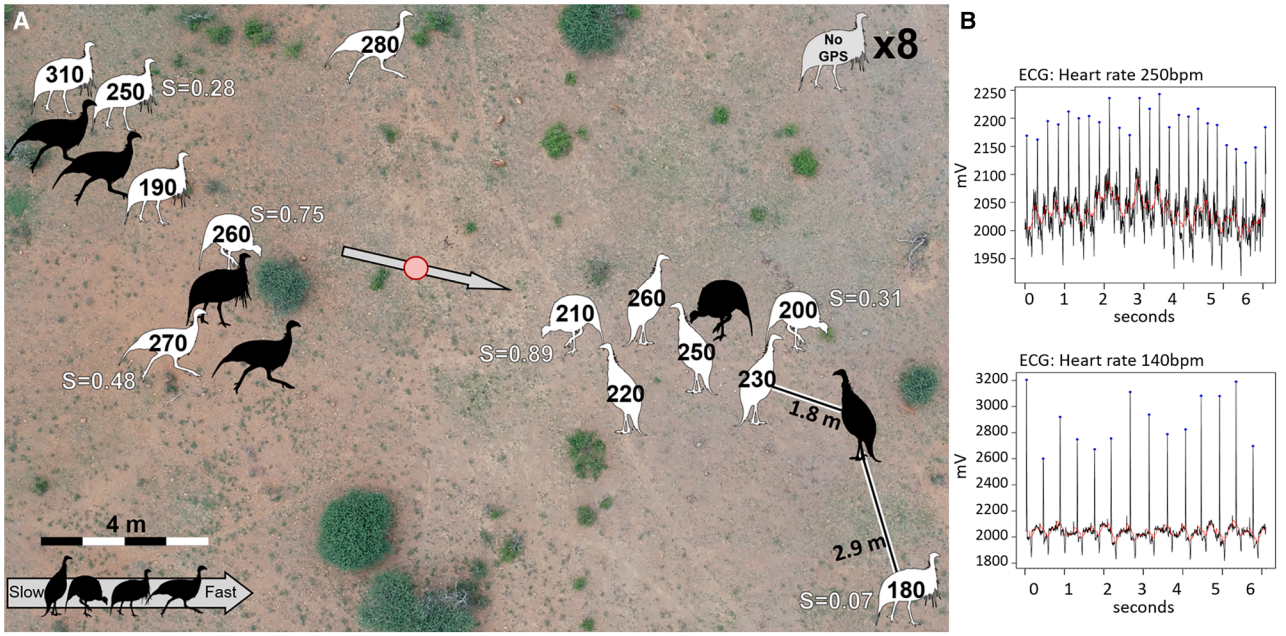

Figure 1. Snapshot of GPS and ECG data collected from a social group of vulturine guineafowl

(A) Spatial positions of individuals with GPS loggers only (black) or both ECG and GPS loggers (white) from one ECG window. Black numbers within silhouettes indicate individual HRs. Group centroid and movement direction are shown by the red dot and gray arrow, respectively. White text shows surroundedness (S) values for a subset of individuals. Nearest neighbor (NN) distances are given for the two leading individuals (black and white bars, bottom right).

(B) ECG data from a 6-s window for an individual with high (top) and low (bottom) HRs (both with low HRV). Background image courtesy of Blair Costello.

See also Figure S1.

successful and unsuccessful movement initiations (following Papageorgiou et al.[24]). Additionally, an ECG logger was fitted to 65% of the GPS birds (n = 13), from which we were able to collect high-quality data from 55% of the GPS birds (n = 11), at 180 Hz for 6 s in every 20 s window from 6 a.m. to 12 p.m., and corrected for individual daily resting heart rate (HR). Data were collected every fourth day over 4.5 months (31 days total), providing simultaneous information on group movements, individual spatial position, leadership, and HR.

Behavior and HR are tightly linked because behavioral states and actions influence physiological arousal and vice versa. HR, the frequency of heartbeats over time, is regulated by the autonomic nervous system, which responds to environmental and internal cues and is thus modulated during physical exercise, social interactions, or in response to stressors.[35,36] Positively correlated with metabolic rate, increased HR also reliably indicates higher energy expenditure.[37,38] Guineafowl absolute HRs in our group ranged from 90 to 386 bpm during daytime, averaging 181 bpm ± 31 SD, thus showing the potential for up to 4-fold increases in certain contexts. These values are comparable with graylag geese, whose HRs range from approximately 40 bpm at rest to around 400 bpm during take-off or social interactions.[39] Consistently elevated HR can cause long-term physiological damage, such as oxidative stress.[40] In addition, HR variability (HRV), calculated as the root-mean-square of successive differences (RMSSDs) between heartbeats,[41,42] serves as a physiological stress proxy. Reduced HRV (lower RMSSD) results from the balance between sympathetic and parasympathetic activity and indicates active physiological stress responses.

Moving as a collective increases the physiological costs of individual movement

To unravel how the activity of the group affects individual movement costs, we fit a linear mixed model (LMM, model 1; Data S1A) to the baseline-corrected HR of vulturine guineafowl, based on their speed and position relative to the group. This revealed that collective movement strongly modulated individual HR (Figure 2A). As expected, higher individual speeds corresponded to higher HRs (model 1: coefficient(individual speed) ± SE = 22.97 ± 0.78, t = 29.36, $p < 0.001$; Figure 2A). However, the effect of individual speed on HR was contingent on group speed (model 1: coefficient(individual speed × group speed) ± SE = 13.97 ± 0.97, t = 14.41, $p \leq 0.001$; Figure 2A). Specifically, the faster the group moved, the higher the individual's HR for a given individual speed (Figure 2A). A density plot showing the distribution of individual speeds in relation to different group speeds, with individual speeds being higher on average, is provided in Figure S1. These results suggest that collective movements impose physiological costs over and above those incurred from moving at a given speed. This aligns with previous work on aerial birds, where moving as a group can require greater mechanical effort when flying in clustered formations,[10] suggesting that the need to maintain cohesion during group movements can also introduce costs in terrestrial movements.

Spatial position has marginal physiological effects

We also analyzed the contribution of individuals' spatial position during group movements. Theory suggests individuals can gain safety from predators by positioning themselves between others

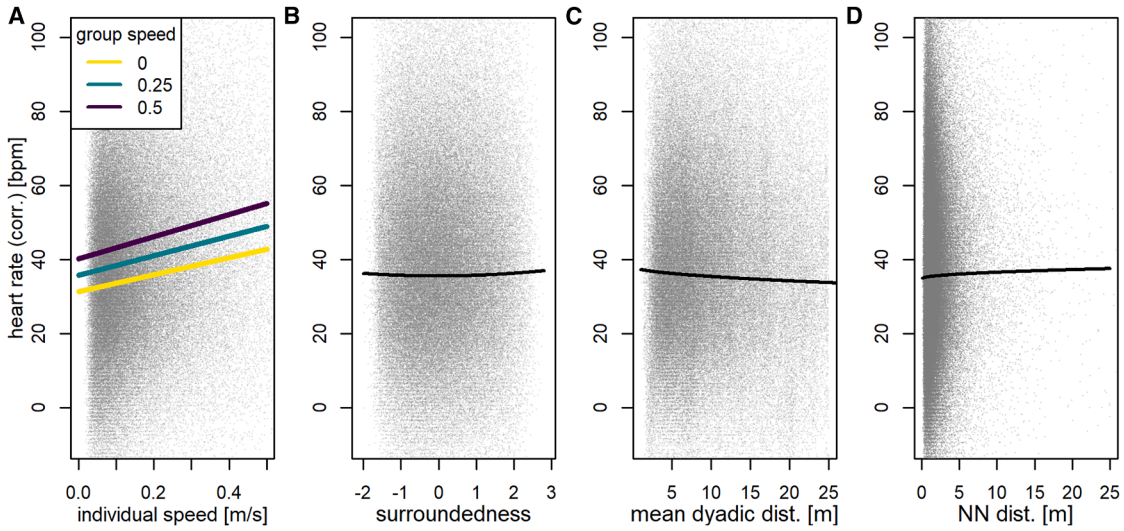

Figure 2. HR responses to group movement and different within-group positions

(A) Collective movement increases HR, whereas (B) greater surroundedness, (C) higher group density, and (D) isolation from others (NN) have only minimal effects. Lines show model predictions from 118,553 ECG data windows. Corrected HRs are the difference between individual absolute HR and their daily resting HR. All panels are from the same model (model 1, full results shown in Data S1A), and average values are used for all covariates not shown: individual speed = 0.1 m s^{-1} and group speed = 0.1 m s^{-1} (representing slow movements), scaled and cantered surroundedness = 0 (range: −2.05 to 2.77; *Z* scores), mean dyadic distance = 9.8 m (range: 1.13–25.0), and NN distance = 2.11 m (range: 0.06–117.91). Gray points show 95% of raw data (excluding upper and lower 2.5%), jittered to reduce overlap. See also Figure S1 for the raw HR data in relation to individual and group movement speeds and Figure S2 for HRV responses.

to minimize exposure (sensu Hamilton's "selfish herd"[43]), whereas peripheral positions might increase danger[44] and induce stress.[45] However, central positions—where individuals are typically more tightly packed—also require individuals to pay substantially more attention to other group members (e.g., in scramble competition[46]), potentially counteracting potential safety benefits. Our data show that individuals pay only marginally greater costs—from a physiological perspective—when they are more central or more peripheral (Figures 2B–2D). Specifically, HR was slightly higher at both extremes of surroundedness, a robust measure of spatial centrality[31,47,48] (model 1: coefficient(scaled surroundedness2) ± SE = 0.18 ± 0.07, t = 2.41, p = 0.016; Figure 2B; Data S1A). Correspondingly, HR also increased slightly when groups were more tightly packed (model 1: coefficient (sqrt(mean dyadic distance)) ± SE = −0.89 ± 0.10, t = −9.3, $p < 0.001$; Figure 2C) and when individuals were more isolated (model 1: coefficient (sqrt(nearest neighbor distance)) ± SE = 0.54 ± 0.15, t = 3.61, $p < 0.001$; Figure 2D). Increases in HR associated with spatial positioning also corresponded to decreases in HRV (model S1; Data S1B; Figure S2), consistent with stress arousal. However, although the direction of all spatial positioning effects aligned with theory,[43] changes in HR and HRV were small—at least one order of magnitude lower than movement speed effects—and thus unlikely to impose substantial costs. Further, because spatial positions are highly dynamic in moving animal groups[9,28,49] these effects are unlikely to accumulate into significant physiological burdens.

Overall, we found clear evidence for collective movements driving increases in individual physiological costs but only marginal effects of the moment-by-moment spatial position of individuals—relative to group members—on these costs. Previous studies have linked individual physiological state to spatial position. For example, unfed individuals can be found at the front of groups[9,23] (a.k.a. leadership according to need[50]). Such patterns reflect differences in preferences among group members, creating potential conflict within the group over movement decisions. A key question is, therefore, whether these conflicts—and the role of leadership in resolving them—introduces physiological costs at the individual level.

Disagreement drives a physiological cost of leadership

Central to functioning as a social group is the ability to overcome difference in preferences among group members, as failure to reach consensus can lead to group splits.[51,52] In many group-living animals, including primates,[28] other mammals,[53] fish,[54] and birds,[23] group members reach consensus about movement directions through a process akin to voting. Some group members initiate movement by moving away from others, in their desired direction of travel. Conflicts in preferences—when to move and in what direction if more than one directional preference exists—are then resolved by having multiple individuals initiate together[55] and followers select the direction of the majority of initiators.[56] Although leading has been widely shown to offer benefits, such as access to preferred resources, there has been much less focus on the costs that leadership entails, particularly when attempting to lead a group with a degree of internal conflict.

To test the prediction that directional disagreement among group members (i.e., leadership conflicts) can be costly, we summarized co-occurring initiations detected from the GPS data into events and identified the level of directional agreement among co-initiators according to the distribution of their movement vectors (using the methods from Papageorgiou et al.[24]). Initiations are inferred from dyadic changes in distance (per

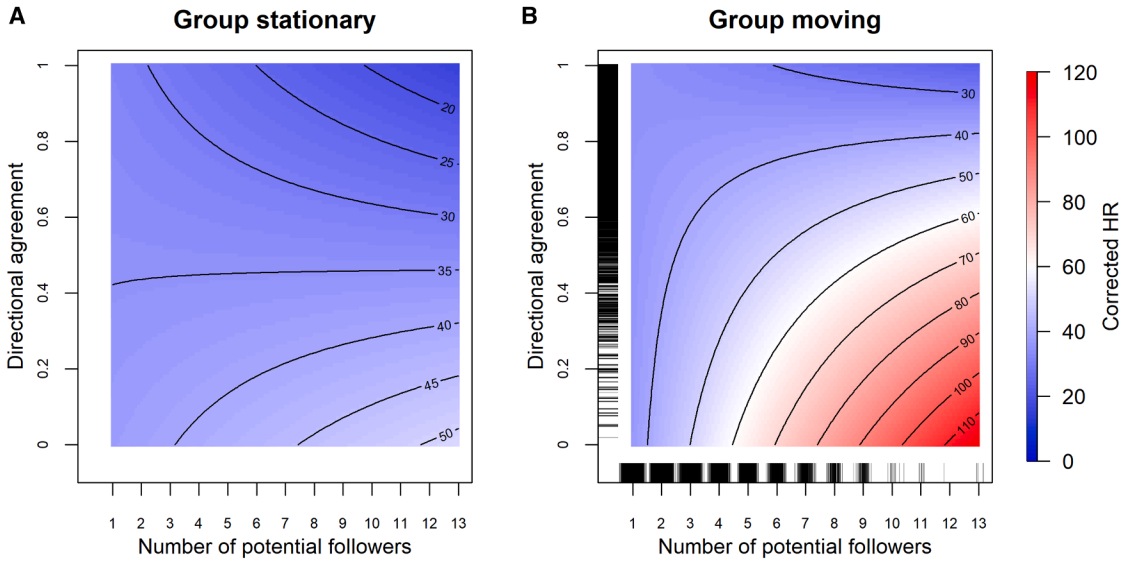

Figure 3. The cost of leadership is greatest with more potential followers and low directional agreement among initiators, especially when the group is moving

Model predictions from 64,126 ECG data windows (20 s each) in which the focal individual was initiating movement. The color-coded HR measure is corrected and thus shows the increase in HR, in beats per minute, relative to their resting HR. All panels are from the same model (model 2; Data S1C), with group speed set to either 0 m s^{-1} "not moving" (A) or 0.2 m s^{-1} "moving" (B) and all other terms set to 0 as these only had weak effects. Density distributions of raw data points are shown along the axes. See also Figures S3A and S3B for HRV responses.

Strandburg-Peshkin et al.[28]), such that an initiator is the individual responsible for a temporary increase in dyadic distance, with the other individual becoming a potential follower (i.e., it may follow, causing the initiator to be successful, or not, causing the initiator to be "anchored" by returning). This prediction was supported by an LMM (model 2; Data S1C) fit to the corrected HR, together with group speed, directional agreement among simultaneous initiators (potentially) acting on the same followers, and the number of potential followers (i.e., the number of group members that an initiator simultaneously increased its dyadic distance with) as a measure of behavioral disagreement, alongside other movement and position variables (from model 1). We first found that, when initiating movement, individuals had the highest HR when the overall directional agreement among initiators was low and when there were many potential followers (suggesting that the initiator was acting against a majority and that there was a stronger consensus among group members). The size of this effect was greatest when the group was on the move (model 2: coefficient(directional agreement × group speed × *n* potential followers) ± SE = −24.77 ± 9.87, t = −2.51, $p = 0.012$; Figures 3A and 3B; see Data S1C for individual effects and other interactions). We also found the same pattern (low agreement with high numbers of followers) being linked to higher stress levels (i.e., lower HRV; see model S2; Figures S3A and S3B; Data S1D). These results confirm that initiations are costly and that these costs are highest when disagreements arise during collective movements.

A key question is how the costs arising from conflict scale in relation to the costs arising from moving to initiate. During initiations, we found that initiators (leaders) move faster than potential followers. However, as found in previous studies,[28] this increase is small (average 0.016 ms^{-1} more; Figure S4A; Data S1G). Our data suggest that this speed difference accounts for an average marginal effect of 0.4 bpm increase in HR relative to baseline (inferred from model 1; Data S1A) during a leadership initiation. By contrast, the effect of within-group conflict when actively attempting to lead (initiate movement) can contribute to an increase in HR of, on average, 80 bpm (from 35 bpm increase when there is little conflict to over 115 bpm increase when there is a high degree of conflict among group members; Figure 3; Data S1C). These results show that the effect of conflict on HR, when initiating, can be as much as 200-fold greater than the effect of changes in movement alone.

Failed initiations are costly, especially when directional disagreement is high

Although initiating movement is costly, a final question is whether the outcome of the initiation modulates these costs. We determined the outcome of initiations (successful if the initiator was followed, unsuccessful if not) by investigating the period after the initiation, predicting that failed initiations would be more costly. An LMM (model 3; Data S1E) fitted to the post-initiation outcomes, with an interaction between the outcome (individual initiated successfully or not) and the level of directional agreement among initiators prior to the event, confirmed our prediction. Individuals had the highest HRs (controlling for spatial position and movement) when their initiation failed, especially when agreement among the initiators was low (model 3: coefficient (successful × directional agreement) ± SE = 7.23 ± 3.29, t = 2.20, $p = 0.028$; Figure 4; see Data S1E for each individual effect and Data S1F for HRV results). These results were not simply explained by movement, as individuals that were followed (i.e., successful) typically moved faster than those that were unsuccessful during the same period (Figure S4B; Data S1H). Thus,

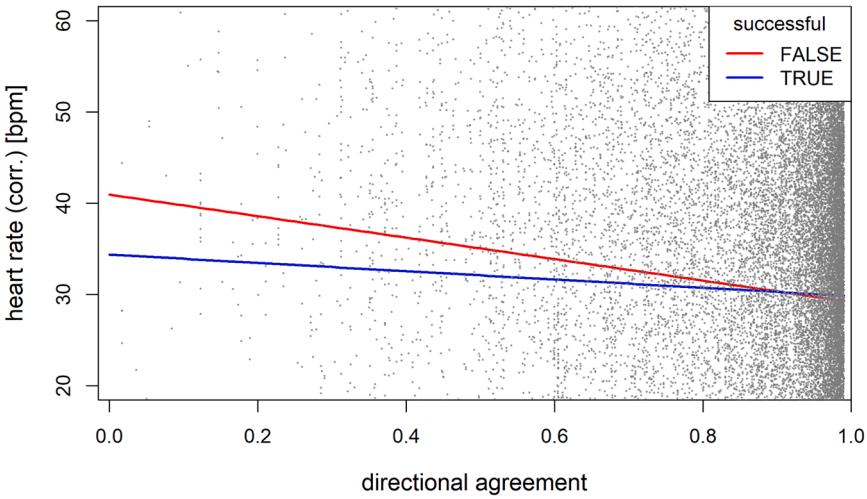

Figure 4. Unsuccessful initiators have a higher HR than successful initiators, especially in the presence of directional conflict among initiators (low agreement)

Model predictions from 22,398 ECG data windows (20 s each), where an individual was either successful (TRUE; blue line) or unsuccessful (FALSE; red line) in initiating. Corrected HR reflects increases relative to individual daily resting HR in beats per minute. Fits are from model 3 (Data S1E), with other variables set to 0 as these only scaled the results up or down along the *y* axis. Gray points show 95% of the raw data. We found little evidence that initiation outcomes impacted HRV; see also Figure S3C and Data S1F. Further, the effects for unsuccessful initiators were not explained by differences in movement speed (see Figure S4).

these results confirm that the social context in which an individual initiates movement, and the collective outcome of that initiation, can have physiological consequences.

Conclusions

Substantial emphasis has been put on highlighting the role of collective behaviors in driving benefits of group living, with much less focus on the costs borne by individuals participating in collective behaviors. Our results demonstrate a historically overlooked trade-off of group living, showing that the dynamics of collective behavior—and specifically leadership—can also have physiological consequences. Previous studies in aerial birds have shown that although flying in aerodynamic formations can reduce energetic costs,[57] less-structured flock formations can cause individuals to exert greater mechanical effort during cohesive flights.[10] However, less is known about social contributions of collective behaviors to the energetics of terrestrial movements (e.g., Harel et al.[58]) and, in particular, whether it is costly to lead.

We found significant costs associated with engaging in collective movement and with leadership dynamics in a predominantly terrestrial species. In both cases, increases in HRs were substantially greater than any effects of individual movement or spatial positioning alone. For example, the increase in HR for a stationary individual when the group is moving is similar to the increase in HR if the stationary individual began moving itself, meaning that moving cohesively is likely contributing to additional energy expenditure over the course of the day. Conversely, the physiological cost associated with peripheral positions in the group—which, in theory, increases exposure to predators—is relatively negligible.

The physiological costs of collective actions are most evident in individuals attempting to lead when there is directional conflict among group members. Initiators have the highest HRs (1) when the directional agreement among initiators is low, (2) when they are trying to influence more group members (i.e., initiating against the majority), and (3) when the group is already on the move, with the scale of increases in HR far outweighing any effects arising from increases in movement speed. Moreover, the outcome of initiations, and the consequences that these have on individuals, is also affected by conflict within the group. Initiations are less likely to be successful in the conditions where we detected the highest HRs (i.e., when there is low directional agreement among initiators and individuals are in a minority[24]), suggesting that the highest costs are borne by unsuccessful leaders.

The effects of collective movements and initiations against directional and numerical conflicts were not only reflected as changes in HR but also corresponded to lower HRV. Although increased HR is linked to energy expenditure, lower HRV suggests that these situations also result in increased physiological stress. This aligns with our results showing large effects that could not be explained by greater mechanical effort (i.e., increased speed) alone. Surprisingly, we did not find evidence that failed initiation attempts also induce stress responses. However, the results on HRV might not be as robust as the HR measure, as there is no validated standardized protocol for measuring it, and calculating RMSSD from very short time windows (6 s of data) makes it more sensitive to irregularities, thereby weakening the strength of the signal in the data.

Although our study was conducted in only one group of one species, we expect the results to reflect general patterns across group-living species. Several factors suggest that the effects observed in our study are relatively weak compared with what may be possible in other social groups and/or other species. For example, for logistical reasons, we studied a relatively small group (n = 28; STAR Methods), whereas vulturine guineafowl typically form groups of up to 65 and sometimes over 90 individuals—conditions likely to exacerbate the challenge of making collective decisions and to amplify directional and numerical conflicts. Further, vulturine guineafowl exhibit higher levels of agreement during collective movements,[24] and lower rates of agonistic interactions,[34] than other species that make similar collective movements (e.g., olive baboons, *Papio anubis*).[28] Thus, the cost of being more surrounded, initiating, or failing to lead may be substantially greater in primates and other mammals that live in cohesive groups than what we observed in vulturine guineafowl. Because we were limited to studying a single group, our findings may not capture the full range of variation

in leadership dynamics or physiological responses across different groups or populations. Nevertheless, the study offers a proof of principle that leadership—even when seemingly beneficial—carries measurable physiological costs.

Overall, our results help to explain why individuals express a range of different social strategies within social groups over time, sometimes acting as leaders to secure benefits, and sometimes acting as followers to avoid costs. Ultimately, the asymmetric benefits of group living are accompanied by asymmetric costs for individuals, and social interactions can introduce proximate (physiological) constraints shaping evolutionary trade-offs. These findings support the idea that leadership is not a fixed trait but may emerge as a conditional strategy, dynamically negotiated among group members and shaped by internal states, social feedback, and cost-benefit assessments.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to, and will be fulfilled by, the lead contact, Damien Farine (damien.farine@anu.edu.au).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All original data are available from Edmond respository: https://doi.org/10.17617/3.RQP42F.
- All original code is available from Edmond repository: https://doi.org/10.17617/3.RQP42F.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, D.R.F.; methodology, H.B.B., J.A.K.-I., D.Z., C.H.W., C.C., F.O., C.N., W.C., B.N., and D.R.F.; investigation, H.B.B., J.A.K.-I., C.C., and D.R.F.; visualization, H.B.B., J.A.K.-I., C.C., and D.R.F.; funding acquisition, D.R.F. and C.H.W.; project administration, F.O., C.N., D.R.F., and C.H.W.; supervision, D.R.F.; writing – original draft, H.B.B. and D.R.F.; writing – review and editing, H.B.B., J.A.K.-I., D.Z., C.H.W., C.C., F.O., C.N., W.C., B.N., and D.R.F.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2025.06.065.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data and Code for reproducing all analyses	This paper	Edmond repository: https://doi.org/10.17617/3.RQP42F
Experimental models: Organisms/strains		
Vulturine guineafowl (*Acryllium vulturinum*)	wild	N/A
Software and algorithms		
R 4.3.0	R Core Team[59]	https://www.R-project.org/

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Study system and selection of social group

We conducted our study on wild vulturine guineafowl (*Acryllium vulturinum*) at the Mpala Research Centre in Laikipia county, Kenya (0.292 N, 36.898 E). The environment at our study site consists of mixed acacia bushland, with dense scrub interspersed with dirt roads and open glades, with seasons defined by rainfall (typically two wet and two dry seasons per year). Vulturine guineafowl are active during daylight hours (ca. 06:00-19:00), moving between dense brush and glades, which is where the majority of foraging and observable social interactions take place, and roosting in stands of acacia trees in the evening. This study took place from February-July 2021, with the early parts of the study taking place under intermediate seasonal conditions and slowly drying out due to the onset of what would eventually become a severe drought in 2022 and early 2023.

Several factors make vulturine guineafowl a good model for such a study. First, they are large, and their body mass (1.3 – 1.8 kg) means that they can carry equipment capable of collecting high resolution data over several months. Second, they are almost exclusively terrestrial, flying only to cross rivers or to go into trees (e.g. to roost in the evening), or when making short-distance, rapid escapes during predator attacks.[60] Third, they are seasonal breeders meaning that by studying outside of this period we avoided any confounds arising from reproductive behaviors. Fourth, groups are extremely cohesive, often touching each other while making collective movements (see Video S1). Previous work on the system has also demonstrated that their society is relatively egalitarian.[23]

We had initially aimed to collect data from two social groups, our reported group (N=28) and a second, similar-sized group (N=29). However, delays in permitting and worsening drought caused the second group to merge with another, much larger group, and when trapping we only captured half of that group's members. Hence, we could not collect sufficient data from the second group to include them, and our strategy of targeting two groups meant that our deployments were limited to smaller groups. Because these two groups were the smallest in our population at the time, we expect that our results are relatively conservative.

METHOD DETAILS

ECG logger implantation and data collection

ECG loggers (ECG-tag 1AA2, e-obs GmbH, Grünwald, Germany) were sterilized using ethylene oxide and subsequently implanted into the thoraco-abdominal cavity of 6 males and 7 females between February 25 and March 2 2021. Birds were anesthetized with isoflurane 5% and oxygen (1-3 L/min); butorphanol 1.5 mg/ml was injected in the pectoral muscle to provide analgesia during surgery and ringer solution (20 ml/kg, SC) was injected for fluid maintenance. An incision was made in the linea alba (~2 cm length) where the ECG loggers were implanted. The longer electrode was placed close to the heart and after confirming visually (QRS complex) that the live ECG signal was of good quality, the logger was fixed to the abdominal wall using an absorbable suture (Monosyn 4/0, B. Braun AG, Melsungen, Germany). Post-operative pain was managed with meloxicam IM 0.5 mg/kg and Marblofloxacin 5 mg/kg IM was injected as infection prophylaxis. Loggers weighed 25 g or about 2% of the body mass of the smallest vulturine guineafowl tagged (1.3 kg). We used data starting from March 10 2021 onward, to give individuals time to recover from the implantation.

ECG tags were programmed to operate at the same time as the GPS tags (every fourth day, see "GPS data collection" below). Because ECG tags were not rechargeable, they were limited to collecting only a fixed amount of data. We used a lifetime calculator provided by e-obs to design a data sampling strategy that would maximize the sampling frequency, the coverage of the periods in which birds were predominately active, and the total length of the data collection period. We opted for collecting a 6 s burst of HR data (at 180 Hz) with a 14 s inter-sample interval to capture the physiological state of birds approximately 30% of the time. We also

chose to collect data for the morning period (from when birds begin leaving the roost at 6 am to midday) because this was the period in which we were most certain that GPS tags had enough charge to be collecting 1 Hz GPS data and because this is when the birds are most active.[61] This strategy was designed to ensure that tags could collect data over several months (nominally 10 months), thus ensuring that data collection would cover periods outside of the breeding season (when groups split up to breed[62]). As it eventuated, the data collection occurred during a period of drought, meaning that birds did not breed but that we observed unusually high mortality rates (across the whole population), which ultimately limited the overall sampling period that we used in this study.

We did not include the first 30mins of each day (6am to 6.30am) into our analyses, because this is the period where individuals come down from their nightly roosts, which was accompanied with higher HRs than during the rest of the day, and thus did not seem representative of their 'normal' behavior. Because of clock drift, tags started collecting data progressively earlier over the course of the study, allowing us to use the pre-6 am data to extract the daily resting (baseline) HR of each individual.

GPS data collection

We fitted solar-powered GPS loggers (e-obs 15 g solar) to the majority of vulturine guineafowl in a social group. Tags were fitted using a backpack harness using Teflon ribbon and elevated using several layers of rubber matting. The total weight of the GPS logger plus backpack and harness is less than 2% of the body mass of all individuals (mean adult weights: females 1410 g, males 1625 g). For birds individuals fit with both GPS and ECG loggers, combined weight of all materials (ECG, GPS, harness, and rings) was less than 4% body mass (mean 3.3%, range 2.8-3.8%). Positional error of the GPS tags is typically less than 5 m, reduces with higher data collection frequency, and relative error between tags at the same location is generally lower than absolute error.[31] Previous testing of relative error suggests that distances between individuals was accurate to within 1 m for over 95% of the data.[33]

GPS tags were programmed to collect data for all daylight hours when birds were active—i.e., from 6 am to 7 pm (birds typically come down from the roost around 6:15 am and return around 6:45 pm). Tags collected data at two resolutions, depending on their level of battery charge—either at continuous 1Hz (one GPS location per second) when at high charge or else in a 10-second burst of 10 GPS locations every 5th minute when at a lower charge. For this study (following the design of recent studies[24]), we ensured that all tags within the focal group would collect simultaneous high-resolution GPS data (continuous 1Hz) by programming tags to collect data every fourth day (the same day for all tags), ensuring that loggers had sufficient time to fully recharge batteries, allowing us to collect 1 Hz data for the majority of the day (from 6am until the battery dropped to the lower threshold, which was always later than the ECG loggers switched off). Data were downloaded every second night using a VHF antenna, as part of a long-term study in this population.

Ethics statement

The study was conducted under a research authorization (KWS/BRP/5001) and capture permit from the Kenyan Wildlife Service (KWS/SCM/5705), the National Commission for Science, Technology and Innovation of Kenya (NACOSTI/P/21/6996), the National Environment Management Authority (NEMA/AGR/68/2017). All the research was done in collaboration with the Ornithology Section of the National Museums of Kenya. Capture and GPS fitting was reviewed by the Max Planck Ethikrat Committee. Implantations were reviewed by the Animal Welfare Officer at the University of Zurich and performed under the supervision of a Kenyan Wildlife Service Vet (Dr. Maureen Kamau). The procedure was reviewed and DZ was approved to perform the surgeries by the Kenya Veterinary Board (KVB/FVS/VolI/6).

QUANTIFICATION AND STATISTICAL ANALYSIS

ECG-based measures

The ECG data was analyzed with a custom-made peak detection algorithm designed to detect the R-peaks from the ECG signals, in the R environment.[59] We automatically filtered the data for artifacts, removing data windows with unusual gaps or anomalous R-R intervals or RMSSD (Root Mean Square of Successive Differences) values. After the automated error checking procedure, we also visually inspected 20 random ECG windows per individual per day to ensure correct R peak identification. In the quality control pipeline, we removed 8,2% of originally 206,835 data windows. We then calculated the HR (heart rate) in beats per minute from the 6 seconds of collected data windows every 20 seconds. We averaged all HR measures taken before 6am while birds were still on their roost per individual, after removing outliers, to obtain each birds' daily resting HR. We then subtracted the daily resting HR, which ranged between 111 and 165 bpm, from that day's absolute HR values for each individual to obtain a measure of HR increase relative to their resting HR, i.e. their baseline-corrected HR. We also obtained the root mean square of successive differences (RMSSD) by first calculating each successive time difference between heart beats (R-peaks) in milliseconds, squaring each of these values, and taking the square root of their mean as a measure of HRV (heart rate variability). RMSSD is a commonly used proxy for physiological stress, particularly in short-term measurements.[42]

Synchronization and correcting for ECG logger clock drift

As the two loggers (ECG and GPS) were not directly connected, we needed an additional step to synchronize their clocks. GPS tags maintain high clock accuracy (sub-second) from the GPS signal. However, the clocks on the ECG tags were programmed during the manufacturing process, and the signal of these clocks can drift (estimated 1 to 2 s per day according to e-obs). To calibrate the ECG data to the same time as the GPS data, we first designed our data collection to download the ECG data on the same evening as the

ECG collected data. Using a separate GPS clock (using the app "GPS clock"), we then carefully noted the time when the base station connected to an ECG tag to initiate the downloads (n = 810 download events across n=105 unique nights). This step gave us the GPS time (from the app) and the time on the logger (from the download log files) at exactly the same time point. We then modelled and plotted the difference between the GPS time and the logger time across the whole data collection period. The slope of this line (the GPS clock drift) was perfectly linear within each logger, and was on average 3.63 seconds per day (SD=0.44 across the different loggers). We therefore used the slope and intercept of the fitted lines to correct the timestamps for the ECG data on a per logger basis. These corrected timestamps were then used to align ECG data with data collected from GPS tags.

GPS-based measures

We extracted a range of group- and individual-level metrics from all GPS-tagged individuals (i.e., including those not implanted with an ECG logger). At the group level, we first extracted the position of the group centroid (mean of all individual positions) as a proxy for the group's location. We then calculated the speed (in meters per second) and bearing of the group movements from the displacement of the group centroid. Finally, we calculated the mean dyadic distance (i.e., the mean inter-individual distance for all possible pairs of group members) as a measure of how tightly packed the group was. At the individual level, we first calculated movement speed (in meters per second) and position relative to the group centroid. Position relative to the centroid is the distance in meters, where a positive y-axis value indicated their distance from the centroid in the direction of group movement, and a positive x-axis value indicated their distance to the right-hand side of the centroid. We calculated two additional measures of each individual's spatial positions within the group—a surroundedness value (1-CV, where CV is the circular variance of the vectors from group members to the focal individual[48]) and their nearest-neighbor distance (i.e., distance in meters to the next closest individual). The former is a reliable measure of centrality (how enclosed an individual is within the group), and the latter provides a measure of how isolated they are. In order to align GPS-derived metrics (calculated at 1Hz) with our ECG data, we calculated a summary value corresponding to each ECG window for each focal individual, such that all metrics were summarized into 20 s bursts, with each burst centered on one 6s burst of ECG data. For each GPS-derived metric, we took the mean of the 1Hz measures over each of our 20s windows as the summary value.

As some group members were not fitted with GPS tags (simply because we were unable to trap them), we used insights from the recent paper by He et al.[31] to select metrics that were robust to missing individuals. Specifically, He et al.[31] reported that the group centroid estimation is highly robust to missing individuals, with both empirical data and simulations suggesting with only 50% of group members tagged the error in the estimated group centroid is approximately 1 m (i.e. comparable to GPS error in the position of a single individual). Similarly, in terms of determining individual positions within the group, both surroundedness and nearest neighbor distances are highly robust (c. 0.05 error at 50% of the group tracked). Our coverage (~70% of group members) was—over the course of the study—comparable to previous studies. For example, the study by Strandburg-Peshkin et al.[28] on leadership in olive baboons (*Papio anubis*) was based on between 50% and 80% of group members being fitted with a GPS collar.

Identifying initiation events

To analyze the responses to movement initiation, we extracted successful and unsuccessful movement initiations from the raw GPS data, summarized the co-occurring initiations into events, and identified the level of agreement among initiators. This analysis was conducted using the code from a previously published study on collective decision-making in baboons and subsequently applied to vulturine guineafowl,[24] see below for more details.

The algorithm we used identifies sequences of initiations from an initial movement of one individual away from another (marked by a change from a minimum to a maximum in their dyadic distance). We defined the initiator as the individual responsible for the majority of the movement that contributed to the increase in dyadic distance. Initiations were considered as successful (a "pull") if the subsequent return to a minimum dyadic distance was predominately the result of movement by the individual initially left behind (i.e. the 'potential follower' followed), and as unsuccessful (an "anchor") if this was the result of movement by the individual originally identified as the initiator (i.e. the 'potential follower' did not follow and the initiator returned). Initiation attempts can take place over variable time scales, ranging from seconds to minutes (mean time for initiator to reach maximum distance: 144s, 95% range 15-557s; mean time to reach post-initiation outcome: 122s, 95% range 13-469s). For each initiation attempt, we summarized the number of potential followers as every individual for which there was a maximum within the same sequence of events for the given initiator (these could either become followers or could anchor the initiator after the point at which a maximum dyadic distance was reached, but all were counted as 'potential followers').

We also summarized the co-occurring initiations (those in which the "pull" phase of the movement overlapped for a portion of their duration) into initiation events. Then, we identified the level of agreement among the simultaneous initiators using the circular variance (CV) of the unit vectors pointing from the potential follower to each initiator (agreement = 1-CV, where 1 means that all vectors are pointing in the same direction and 0 means that all vectors initiate in opposing directions).[28] Note that the number of potential followers was always drawn from the individual-level data (i.e. calculated independently for each initiator) and not aggregated across simultaneous initiators. We used the same code and implementation of this algorithm as Strandburg-Peshkin et al.,[28] only reducing the minimum change in distance between individuals to 3.5 m (from 5 m in baboons) because guineafowl are substantially smaller and more cohesive. More details of our implementation can be found in Papageorgiou et al.[24]

We then cross-referenced the initiation data with each burst of ECG data, allowing us to determine whether the individual was initiating (or had recently initiated and either been successful or not), the number of potential followers (i.e. the number of group mates

that the individual would 'pull' if they were successful in the current initiation attempt) and the extent of the agreement among simultaneous initiators.

Statistical analyses

All analyses and data processing steps described here and above were performed in the R environment.[59] We fitted a total of eight LMMs (linear mixed models) using lme4 to test the hypotheses laid out in the main text (three models on change in HR relative to resting HR, models 1–3, and three models with the same structure but using HRV as response, models S1–S3). Briefly, model 1 tested the effects of movement and spatial positioning on HR, model 2 tested the effects of leadership and directional conflict (during initiations) on HR, model 3 tested the effect of leadership outcomes and directional conflict (post-initiating), and models S1–S3 repeated the same test with HRV as response variable, while maintaining the same model structures models 1–3, respectively. Two additional models were fit with individual speed as dependent variable to test how movement speed was affected by leading (initiating movements; model 4) and whether the attempts were successful (model 5). For all model structures and fixed terms, see Data S1. All LMMs included individual IDs and hour of the day as random effects. We only included data when the group was cohesive (~70% of the data), defined as the mean dyadic distance of individuals being below 25 meters, as it became difficult to determine group and individual-to-group dynamics when the group was more spatially dispersed. All of these decisions were made, and implemented, prior to analysing the data for our research questions.

Data from two individuals were excluded from the HR data because R peaks could not clearly be identified from their ECG profiles, probably due to poor electrode positioning. Five birds died, over the course of the study, most likely due to an ongoing drought and corresponding increase in predation, but their data until their disappearance was included in all analyses. The data collection resulted in 189,831 data windows; 118,586 of which we used for analyses, after passing data quality control and group cohesion criteria (full sample sizes for all models are given in Data S1 and in figure captions).