The physiological costs of spatial positioning and leadership in collective movements

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ABSTRACT

Forming collectives can generate substantial benefits, but much less is known about the costs that individuals incur in doing so. We simultaneously captured individual movement, within-group position, leadership, and heart rate for each member in a group of wild vulturine guineafowl. Individuals had significantly increased heart rates when moving collectively, occupying more central positions within the group, or attempting to initiate directional movement when consensus among group members was low. Such cardiac system activation can be indicative of physiological stress, entailing increased energy expenditure and long-term physiological damage. Thus, individuals paid the highest physiological costs in situations where theory predicts the benefits of collective behaviours should be greatest, revealing a hidden trade-off of social living.

INTRODUCTION

The benefits that individuals accrue from collective behaviours can vary with the spatial position or the specific role that they occupy within the group. A classic example of this is 'Hamilton's selfish herd', wherein maintaining a more central position within the group reduces the likelihood of being predated (*1, 2*). Individuals can also benefit from moving as a group, such as by selecting more efficient routes [through 'collective intelligence' (*3*) and 'the many wrongs' hypothesis (*4*)]. Within collective movements, leaders can also gain disproportionate benefits through earlier access to resources [the 'finder's share' (*5*)]. However, reaping these benefits can also come at a cost. For example, differences in preferences among group members can introduce conflicts over leadership (*6-8*), competition for better positions can provoke agonistic interactions (*9*), and collective movements can require individuals to forgo their own locomotor (*10*) and directional (*11*) preferences. Each of these challenges are likely to induce physiological costs. Determining how such costs change across different axes of social behaviour remains a core challenge for understanding the evolution of collective behaviour.

We studied the physiological consequences of collective movements, spatial positioning of individuals, and leadership in a group of wild vulturine guineafowl at the Mpala Research Centre 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 (*12*). Group sizes range from 15 to over 65 individuals (*13*) with an optimal group size of 33–37 individuals (*14*). Despite of having a steep dominance hierarchy (*15, 16*), groups maintain cohesion and reach consensus about where to go using shared decision-making (*15*). Specifically, individuals move in their preferred direction (i.e. initiate) and are either followed (successful initiations) or not (failed initiations) by other group members. All group members can lead, and the highly dynamic nature of group movements (Movie S1) means that all individuals occupy every position within the group over the course of the day.

To determine when, and for whom, costs arise from individual within-group positions and their different contributions to collective movements, we analysed data collected simultaneously from global positioning system (GPS) and electrocardiogram (ECG) loggers (Fig. 1; see methods for details). GPS loggers were fitted to ~70% of the members of a vulturine guineafowl group (N=20 of 28, collecting data at 1Hz, see (*17*) for further details) with an additional ECG logger fitted to 65% of the GPS birds (N=13, collecting data at 180Hz for 6 s in every 20 s window from 6 am to 12pm and corrected for the resting heart rate). Data were collected on 33 days spanning a 4.5-month period (by collecting data on every fourth day), providing simultaneous information about individual spatial position, group movements, leadership, and heart rate. Heart rate, the frequency of heart beats over time, is a reliable fine-scale proxy for the activity of the autonomic nervous system and is modulated during physical exercise or in response to physical or psychological stressors (*18, 19*). As heart rate is positively correlated with metabolic rate, increased heart rate is also a strong indicator for increased energy expenditure (*20, 21*). Consistently elevated heart rate can also lead to long-term physiological damage, such as oxidative stress (*22*). In addition, heart rate variability, which is calculated as the root mean square of successive differences (RMSSD) between heart beats (*23, 24*), can serve as a proxy for physiological stress. Reduced heart rate variability, indicated by lower RMSSD values, describes

the balance between sympathetic and parasympathetic nervous system activity, and is indicative of active physiological stress responses.

Our analyses focused on two distinct sets of questions: (1) the effects of movement and within-group spatial positioning, and (2) the effects of directional conflict and leadership outcomes on heart rate. Thus, for each ECG window, we used the GPS data to calculate (i) each individual's average speed (in m s^{-1}), (ii) the average speed of the group centroid (i.e., the mean of all individual positions), (iii) lead order, a scaled measure (0.05-1) of front-to-back position in the direction of group movement, (iv) surroundedness, which is a robust measure capturing how central each individual is relative to group members (*17, 25, 26*), (v) the mean dyadic distance between all group members as a measure of group density, and (vi) the distance of each individual to its nearest neighbour as a measure of isolation from the group. We then used data on the relative movements of individuals to extract leadership events [following (*8*)], and for each ECG window recorded (i) whether the individual was initiating, (ii) the number of simultaneous initiators, (iii) the agreement in directional preferences among simultaneous initiators and (iv) the success/failure of each initiator.

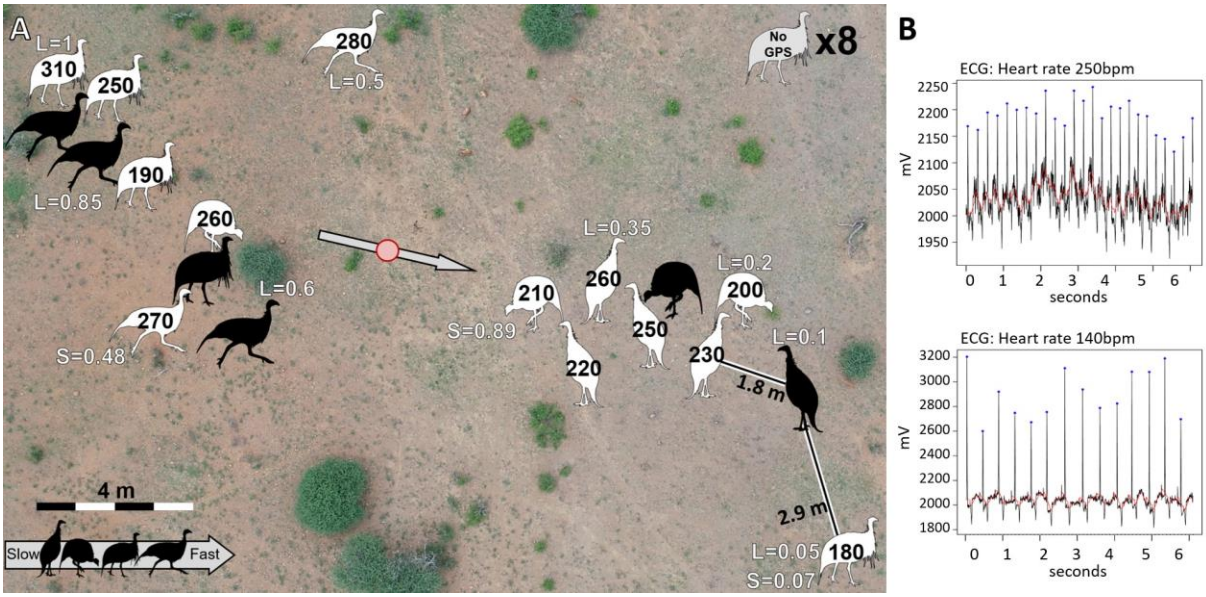

Fig. 1. Snapshot of GPS and ECG data collected from a social group of vulturine guineafowl. (A) GPS-based locations shown for individuals with only GPS loggers (black) or with both ECG and GPS loggers (white) from one ECG window. Black numbers within silhouettes indicate individual

heart rates. White text shows leadership order (L) and surroundedness (S) values for an exemplary subset of individuals. Nearest neighbour distances are also given for the two leading individuals (black and white bars, bottom right). Group centroid and direction of movement are represented by the red dot and grey arrow, respectively. (B) ECG data from one 6 second window for an individual with high (top) and low (bottom) heart rates (both of which have low heart rate variability). Note that individuals can occupy all positions within the group. Background image and permission to use provided by B. Costello.

RESULTS

Moving as a collective increases the physiological costs of movement

Studies of costs of movement in terrestrial animals typically consider effects such as the physical environment [e.g. 'energy landscapes' (*27*)], but only few studies have considered the role of the social environment in modulating movement costs [but see e.g. (*28, 29*)]. For example, studies have shown that individuals moving in groups change their locomotor patterns to match the collective (e.g. speeds (*30*) or gaits (*10*)). What remains unclear is how the activity of the group affects the movement costs borne by its members.

We addressed this gap by fitting a linear mixed model (LMM, model 1, table S1) to the baseline-corrected heart rate of vulturine guineafowl, revealing that collective movement has strong modulating effects on individual heart rate (Fig. 2A). Absolute heart rates of vulturine guineafowl ranged between 90 and 420 bpm with a mean of 183 bpm ± 32.8SD. As expected, we found that greater individual speeds corresponded to a higher heart rate (model 1: coefficient(individual speed)±SE=32.89±0.798, t=41.63, p<0.001; Fig. 2A), but that the effect of individual speed on heart rate was contingent on the speed of the group (model 1: coefficient(individual speed x group speed)±SE=-2.93±1.0, t=2.93, p=0.003; Fig. 2A). Specifically, the faster the group moved, the higher the individual heart rate for a given individual speed (Fig. 2A). A density plot showing the distribution of individual speeds in relation to different group speeds is provided in fig. S1. These results suggest that (i) group movements generate greater physiological costs and (ii) that conflicting preferences, which translate to differences in speed between individuals and the

group, can also generate greater physiological costs. Individual-level plots, showing raw data and reaction norms (fig. S2), confirm that these patterns are consistent across group members.

Being highly central or highly peripheral is physiologically costly

There are two competing hypotheses predicting how individuals should respond to their spatial position within the group. The first is based on Hamilton's selfish herd (*1*)—one of the most influential hypothesis in social evolution. It posits that individuals can gain safety from predators by positioning themselves between others to minimise their exposure. If the protection provided by a group is asymmetric, a peripheral position, and particularly moving at the front of a group (*2, 31*), is more dangerous and might thus induce stress (*32*). However, empirical evidence for the selfish herd is mixed, as protection for those in the centre might not be given, for example, when groups split during an attack (*33, 34*) and in moving animal groups, where alignment with neighbours might be a more effective strategy than selfish attraction (*35*). Another hypothesis speaking against central positions and close conspecific proximity being advantageous is that conflicts arise as groups become more tightly packed, requiring individuals to pay substantially more attention to other group members [e.g. in scramble competitions (*36*)], largely negating potential benefits arising from increased safety. Such resulting social interactions (*37, 38*) and crowding (*39, 40*) can themselves act as stressors, leading to physiological arousal, and considerable activation of the cardiac system [e.g. (*41-43*)], thereby contributing to energy expenditure (*44*).

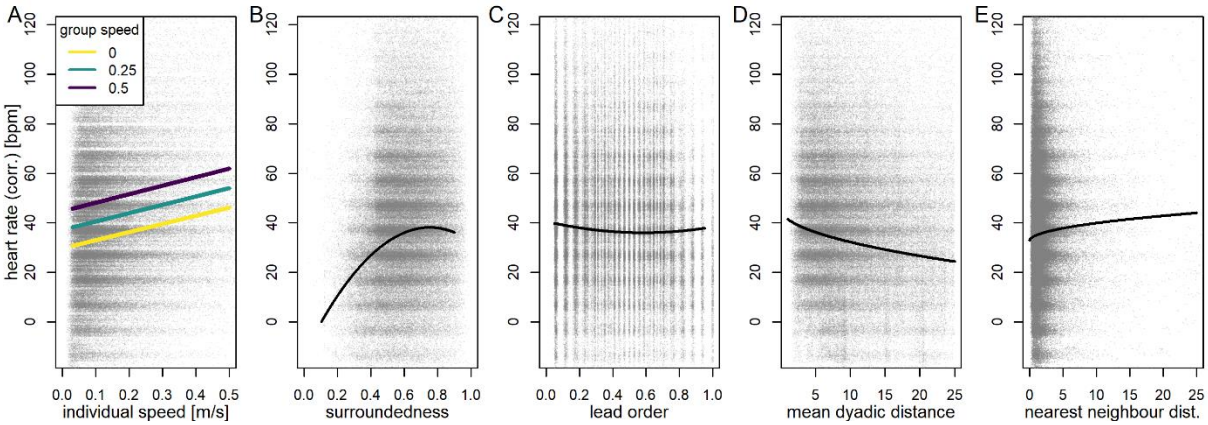

Fig. 2. Heart rate responses to group movement and different within-group positions. Collective

movement (A), being more surrounded (B), exposure to the front and back of the group (C), greater group density (D), or being isolated from other individuals (E) increases heart rate. Lines represent the model predictions from 130,438 ECG data windows. Corrected heart rates are the difference between individual absolute heart rate and their resting heart rate. All panels are from the same model (model 1, full results shown in table S1), and average values are used for all values not depicted in each panel. These are: individual speed=0.1 m s^{-1} and group speed=0.1 m s^{-1} (representing slow movements), surroundedness=0.5 (range 0.02–0.99), lead order=0.5 (range 0.05–1.0), mean dyadic distance=9.8 (range 1.13–25.0), nearest neighbour distance=2.11 (range 0.06–117.9). Semi-transparent grey points show 95% of the raw data points (upper and lower 2.5% not shown), jittered to reduce overlap. Data and model predictions are plotted separately for each individual in fig. S2.

Our data show that—from a physiological perspective—individuals pay a significantly greater cost when they are more central and when they are more peripheral (Fig. 2B–E). Specifically, heart rate was highest when individuals were more surrounded by others (i.e. more central), increasing by around 136 bpm on average for individuals that are fully surrounded by other group members (model 1: coefficient(surroundedness)±SE=136.78±3.35, t=40.51, p<0.001; coefficient(surroundedness^2)±SE=-90.42±2.64, t=-34.23, p<0.001; Fig. 2B and table S1). Individuals also had higher heart rates when at the front or back of the group (model 1: coefficient (lead order)±SE=-15.18±1.58, t=-10.01, p<0.001; FIG 2C), but the size of this effect is relatively small. At a group level, heart rate increased when group members were more tightly packed (model 1: coefficient (sqrt(mean dyadic distance))±SE=-4.27±0.09, t=-45.04, p<0.001; Fig. 2D). Lastly, we also found an increase in heart rate when individuals were more isolated (model 1: coefficient (sqrt(nearest neighbour distance))±SE=2.23±0.14, t=15.91, p<0.001; Fig. 2E), but again this effect was relatively weak. The same variables also affected heart rate variability in the opposite direction–it was lower when individuals were more surrounded (strongest effect), at the front or back of the group (weaker effect), when the group was tightly packed, or individuals were isolated. These results are consistent with stress arousal (see model 4, table S4, fig. S2). Our results therefore suggest that—on a moment by moment basis—vulturine guineafowl are substantially less sensitive to exposure to environmental stressors (e.g. potential predators) than

they are to the proximity to, and being surrounded by, other group members. These findings aligning with the hypothesis that while individuals are clearly benefiting from safety from predators by being in a group in such a predator-rich landscape, the resulting within-group interactions can offset reductions in physiological stress that such safety might confer.

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 (*45, 46*). In many group-living animal, including primates (*8*) and other mammals (*47*), fish (*48*), and birds (*15*), group members reach consensus through a process akin to voting. Some or all group members first initiate movement by moving away from others, in the desired direction of travel, and conflicts in preferences—when more than one directional preference exists—are resolved by selecting the direction of the majority (*49*). However, while leading can benefit individuals, for example by bringing the group to a more desirable resource for them [e.g. (*50, 51*)], almost nothing is known about the costs that leadership entails. While we found no strong effects (Fig. 2C) related to individuals having frontal positions in the group (which has long been associated with leading), the costs of leadership may instead be borne out of the degree of conflict that exists within the group when attempting to lead. That is, the social context in which an individual makes an initiation attempt may have stronger physiological implications than its position relative to the group or the direction of group movement.

To test the prediction that directional disagreement among group members (i.e. a leadership conflict) can be costly, we extracted successful and unsuccessful movement initiations from the GPS data [using the methods described in (*8*)]. We then summarised the co-occurring initiations into events and identified the level of directional agreement among co-initiators according to the distribution of their movement vectors. Fitting an LMM (model 2, table S2) to the corrected heart rate, together with group speed, directional agreement, and the number of potential followers (as a measure of behavioural disagreement), alongside other movement and position variables, supported our predictions. We first found that individuals had the highest heart rate when directional agreement was low and there were many potential followers (suggesting that the

initiator was acting against the majority group behaviour). This effect was strongest when the group was on the move (model 2: coefficient(directional agreement x group speed x N potential followers)±SE=-25.26±9.92, t=-2.55, p=0.011; Fig. 3A-B; see table S2 for individual effects and other interactions). These results suggest that initiations are particularly costly when disagreements arise during collective movements. Looking at heart rate variability, we found complementary, albeit weaker, statistical support for low agreement with high numbers of followers being linked to higher stress levels (i.e. lower heart rate variability; see model 5, fig. S4, table S5).

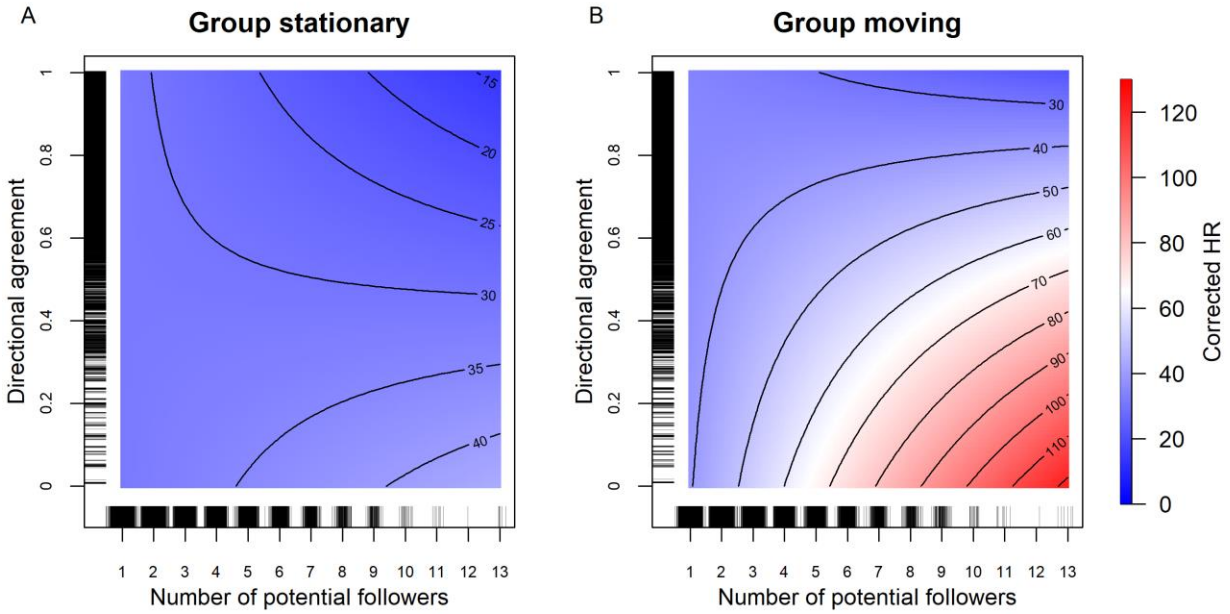

Fig. 3. The cost of leadership is greatest when there are more potential followers and directional agreement among initiators is low, especially when the group is moving. Plots show the model predictions from 69,506 ECG data windows (20 s each) in which the focal individual was detected making an initiation movement. The color-coded heart rate measure (HR) is corrected and thus shows the increase in heart rate, in beats per minute, relative to their resting heart rate. All panels are from the same model (model 2, table S2), 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 distribution of raw data points are shown along each of the axes.

Failed initiations are costly, especially when directional disagreement is high

While initiating itself is costly, a final question is whether the outcome of the initiation modulates these costs. We determined the outcome of these initiations (successful if the initiator was followed, and unsuccessful if it was not followed and subsequently returned) by investigating the period after the initiation, predicting that failed initiations would be more costly. Fitting an LMM (model 3, table S3) to the post-initiation outcomes, with an interaction between the outcome (whether the individual was successful or not) and the level of directional agreement among initiators prior to the event confirmed our prediction. Individuals had the highest heart rates (controlling for spatial position and movement) when their initiation failed, especially when agreement among the initiators was low (model 3: coefficient(successful x directional agreement)±SE=15.53±3.52, t=4.41, p=<0.001; Fig. 4; see table 3 for each individual effect). These results were not simply explained by movement, as individuals that were followed typically moved faster than those that were unsuccessful during the same period (fig. S5). These results further show how the social context in which an individual moves and contributes to collective outcome can have physiological consequences.

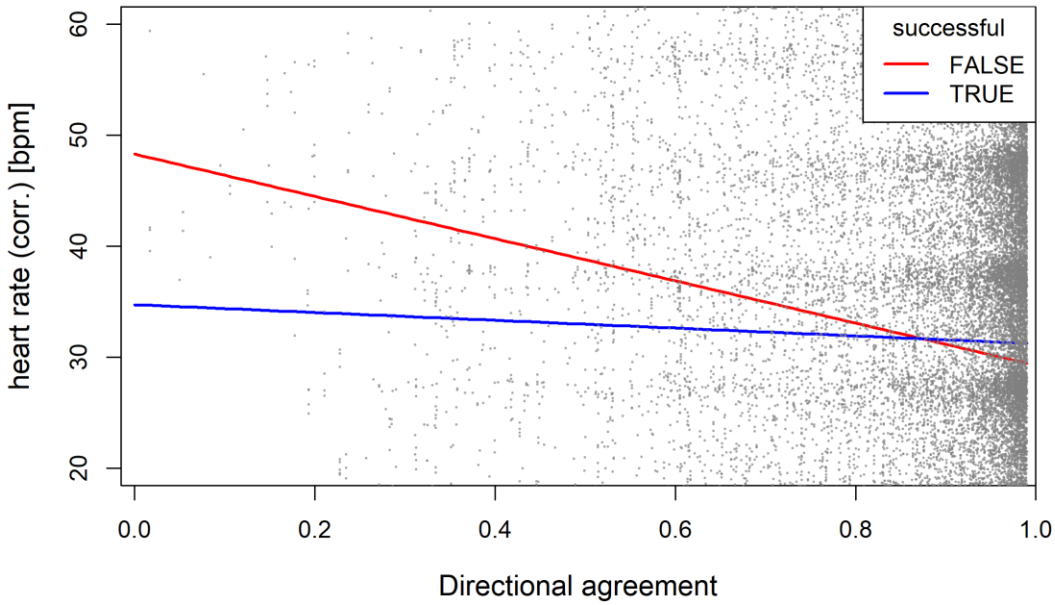

Fig. 4. Unsuccessful initiators have a higher heart rate than successful initiators, especially in the presence of directional conflict among initiators (low agreement). Lines show the model predictions from 23,317 ECG data windows (20 s each) where an individual was either successful (TRUE) or unsuccessful (FALSE) in initiating. The heart rate measure is corrected and thus shows the increase in heart rate, in beats per minute, relative to individual resting heart rates. The fits are from model 3 (table 3), with all other terms set to 0 as these only scaled the results up or down along the y-axis. Density distribution of raw data points are shown along each of the axes. We found little evidence for the outcome of initiations impacting heart rate variability (table S6, fig. S6).

DISCUSSION

While living in a group is an advantageous strategy for individuals across many animal species, the dynamics of collective behaviour can also have major physiological consequences. We found that heart rate when an individual moves at a given speed is higher during collective movements than when the group is stationary. We further found that tighter packing with conspecifics and being more surrounded by other group members increases individual heart rate, suggesting the physiological costs arising from spatial proximity (and resulting social interactions, see fig. S7 for examples) outweigh those arising from more direct exposure to potential environmental stressors (e.g. predators). The increases in heart rate related to individual spatial position within the group are mirrored by corresponding decreases in heart rate variability, suggesting that being in the centre of the group—and the social interactions taking place in a tightly packed group—can trigger stress responses. Nevertheless, while a dense social aggregation can lead to physiological arousal in individuals and may even be energetically costly, isolation from all other group members can also increase heart rate, albeit relatively weakly.

We also found that the costs of moving as a group are likely to be borne through directional conflict among group members, with initiators having the highest heart rates when the

directional agreement among initiators is low, initiators are trying to influence more group members, and the group is on the move. Failing to initiations also induces a higher heart rate, especially when this is the result of a low directional agreement among initiators. This result arises independently of differences in movement speed, as individuals that succeeded in initiating typically move faster post-initiation than those that fail. There was also support for some association between low directional agreement in the group and physiological stress (low heart rate variability), but surprisingly, we did not find evidence that failed initiation attempts induce a stress response. However, the results on heart rate variability might not be as robust as the heart rate measure, as calculating RMSSD from very short time windows (6s of data) makes it very sensitive to irregularities, thereby substantially increasing noise in the data.

While our study was conducted in only one species, we expect the results to reflect general patterns across group-living species. Several factors also suggest that the effects observed in our study are relatively weak compared to what may be possible in other social groups and/or in other species. For example, for logistical reasons we studied a relatively small group (N=28, see methods for details), whereas vulturine guineafowl group sizes are typically up to 65 individuals and can sometimes be temporarily much larger. Further, vulturine guineafowl have high levels of agreement in collective movements (*52*), and low rates of agonistic interactions, relative to species that make similar collective movements, such as savannah baboons (*8*). Thus, the cost of being more surrounded, initiating, or failing to lead may be substantially greater in some species than what we observed in vulturine guineafowl.

Together, our results can help to explain why we observe individuals expressing a range of different social strategies within social groups over time (*53*), sometimes vying for central positions that are hypothesised to be safer (*1*) [but see e.g. (*33, 35, 54*)] or acting as leaders [thereby potentially gaining greater access to resources (*55*)], and sometimes remaining peripheral or acting as followers (thereby paying lower socio-physiological costs). Ultimately, the asymmetric benefits of group living are accompanied with asymmetric costs for individuals and social interactions can introduce proximate (physiological) constraints shaping evolutionary trade-offs.

METHODS

Study system and selection of social group

We conducted our study on wild vulturine guineafowl 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 weight 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). Third, they are extremely cohesive, often touching each other while making collective movements (see Movie S1). Fourth, they form large groups that contain multiple breeding individuals (i.e. plural breeders), meaning that results are not confounded by effects arising from having a single breeding pair (e.g. differences in body size, life history strategies, etc.). Previous work on the system has also demonstrated that their society is relatively egalitarian (15).

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.

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 weight of the smallest vulturine guineafowl tagged.

The ECG loggers were programmed to record one 180 Hz burst of data for 6 seconds every 20 s. The raw data was stored on the battery-powered devices and was downloaded via radio antennas together with the GPS data. The sampling strategy was designed to maximise the longevity of the battery life of the ECG loggers while still collecting data for the majority of the sampling period. ECG tags were programmed to collect data from 6 am until 12 pm, as the activity of birds starts to decrease substantially after 10 am (56). 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 resting (baseline) heart rate of each individual, together with data from one overnight period.

ECG-based measures

The ECG data was analysed with a custom-made peak detection algorithm designed to detect the R-peaks from the ECG signals. We automatically filtered the data for artifacts, removing data windows with unusual gaps or anomalous R-R intervals or RMSSD 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 21.9% of originally 255,687 data windows. We then calculated the heart rate in beats per minute from the

6 seconds of collected data windows every 20 seconds, and subtracted the resting heart rate, which ranged between 111 and 165 bpm, for each individual to obtain a measure of heart rate increase relative to their resting heart rate. We also obtained the root mean square of successive differences (RMSSD) by first calculating each successive time difference between heart beats (R-peaks) in ms, squaring each of these values, and taking the square root of their mean as a measure of heart rate variability. RMSSD is a commonly used proxy for physiological stress, particularly in short-term measurements.

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 weight of all individuals (females are >1280 g, males are >1440 g). GPS loggers were programmed 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 (one GPS location per second) data for the majority of the day (from 6am until the battery depleted, which was always later than the ECG loggers switched off, see below). Data were downloaded every second night using a VHF antenna, as part of a long-term study in this population.

While we were unable to trap all group members, the coverage (~70% of group members) was—over the course of the study—comparable to previous studies. For example, the study by Strandburg-Peshkin, Farine, Couzin and Crofoot (8) on leadership in olive baboons (Papio anubis) was based on between 50% and 80% of group members being fitted with a GPS collar. Our prior testing suggests that estimations of relative positions are highly accurate with these tags, even when not all individuals are sampled in the group (e.g. median error in surroundedness is ~0.1 when 70% of the group is tracked and after accounting for GPS error (17)).

GPS-based measures

For each second of each day of logging, i.e. from 6am (birds leave the roost around 6:15am) until 7pm (birds enter the roost around 6:50pm), 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's movement from the rate and direction of displacement of the centroid, respectively. 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. From these relative positions, we then extracted the front-to-back order in the direction of group movement as the ranked order from highest to lowest relative-y values for each individual. 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, (26)) and their nearest-neighbour 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. Finally, we summarised these metrics for each ECG window for each focal individual, such that all metrics were summarised into 20 s bursts, with each burst centred on one 6s burst of ECG data. For all metrics, we took the mean over each 20s window as the summary value, except for the front-to-back order where we took the mode.

Identifying initiation events

To analyse the responses to movement initiation, we extracted successful and unsuccessful movement initiations from the raw GPS data, summarised 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 (8), see below for more details. Once collected, we then cross-referenced each burst of ECG data with the initiation data, allowing us to identify with each burst whether the individual was initiating (or had recently initiated and either been successful or not), and the extent of the agreement among simultaneous initiators.

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 was predominately the result of movement by the individual initially left behind, and as unsuccessful (an "anchor") if this was the result of movement by the individual originally identified as the initiator. We also summarised the co-occurring initiations (those in which the "pull" phase of the movement overlapped for some of the time) into initiation events, and 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) (8). We used the same code and implementation of this algorithm as (8), 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. in review.

Statistical analyses

We fitted a total of six LMMs (linear mixed models) using lme4 to test the hypotheses laid out in the main text (three models on change in heart rate relative to resting heart rate, models 1-3, and three models with the same structure but using heart rate variability as response, models 4-6). For all model structures and fixed terms, see tables S1 to S6. Briefly, model 1 tested the effects of movement and spatial positioning on heart rate, model 2 tested the effects of leadership and directional conflict (during initiations) on heart rate, model 3 tested the effect of leadership outcomes and directional conflict (post-initiating), and models 4-6 repeated the same test with heart rate variability a response while maintaining the same model structures models 1-3, respectively. 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. Data from two

individuals were excluded from the heart rate data because collection peaks could not clearly be identified from their ECG profiles, probably due to poor electrode positioning. Five additional birds died, most likely due to an ongoing drought and corresponding increase in predation taking place during the data collection period, but their data until their disappearance was included in all analyses. The data collection resulted in 199,817 data windows for analyses (full sample sizes for all models are given in tables S1 to S6 and in figure captions). All analyses and data processing steps described above were performed in the R environment (57).

Ethics statement

The study was conducted under a research authorisation (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/Voll/6).

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Supplementary materials for:

The physiological costs of spatial positioning and leadership in collective movements

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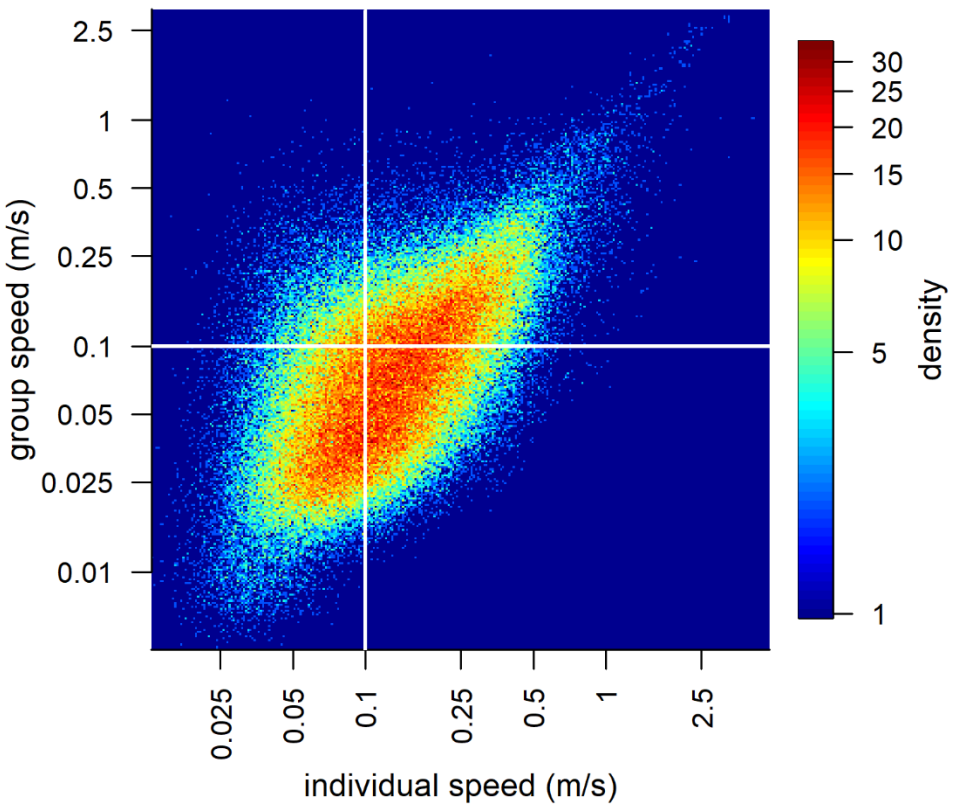


Fig. S1. Density plot of individual speeds at different group speeds.

The colours represent the density of data points of different individual speeds at different group speeds revealing that individuals mostly move faster than the group (measured as movement of the group centroid).

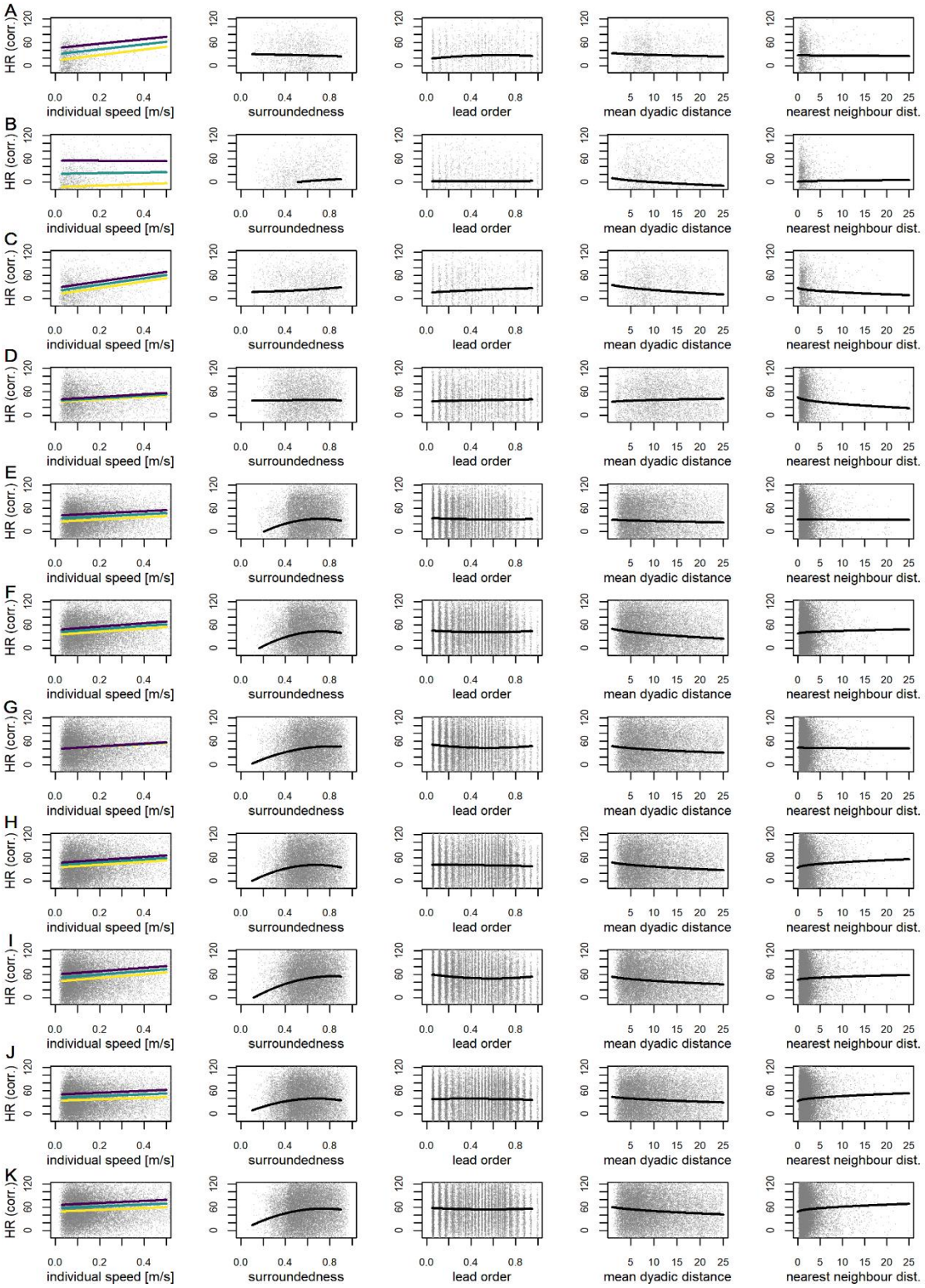
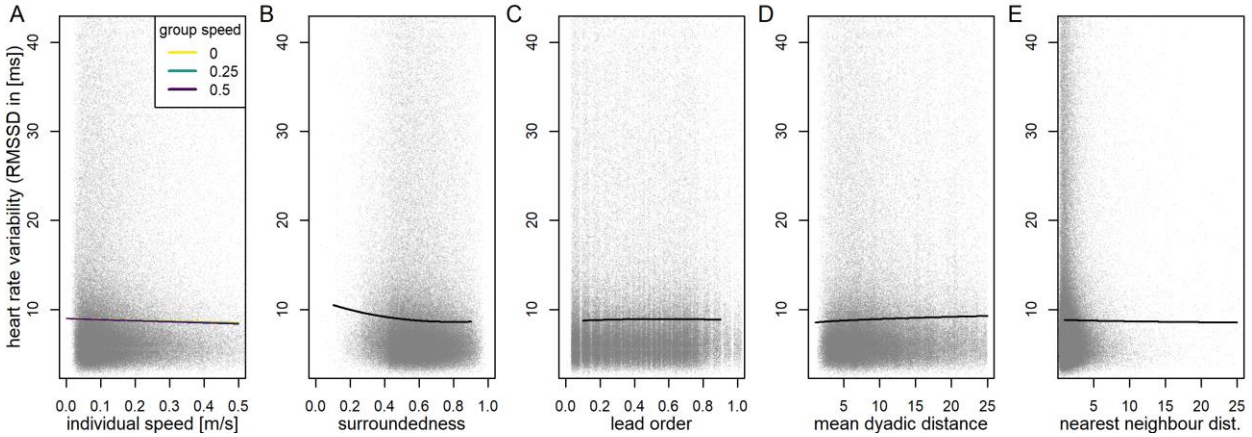


Fig. S2. Individual heart rate responses to group movement and different within-group positions showing data and reaction norms of 11 individuals with ECG loggers.

Each row of panels (A-K) shows the data points and model predictions (lines) of one individual (model structure same as in Fig 2 and table S1, where all individuals were fit in one model). “HR

(corr.)" represents the corrected heart rates as difference between an individual's absolute heart rate and their resting heart rate. From left to right: Collective movement, being more surrounded, exposure to the front and back of the group, greater group density, or being isolated from other individuals overall increases heart rate. Average values are used for all values not depicted in each panel (as given in Fig. 2). Semi-transparent grey points show 95% of the raw data points (upper and lower 2.5% not shown), jittered to reduce overlap. Note that individuals varied in the amount of data (rows are ordered from least to most).



S3. Heart rate variability in response to group movement and different within-group positions.

Collective movement (A), being more surrounded (B), exposure to the front and back of the group (C), being more proximate to others (D), or being isolated from other individuals (E) decreases the heart rate variability of vulturine guineafowl. Lines represent the model predictions from predictions from 130,438 ECG data windows (20 s each), back-transformed from the log-scale. Heart rate variability HRV was measured as the RMSSD in ms. All panels are from the same model (model 4, table S4), and biological average values were used for all values not depicted in each panel. These were: individual speed=0.1 m s-1 and group speed=0.1 m s-1 (representing slow movements), surroundedness=0.5 (range 0.02–0.99), lead order=0.5 (range 0.05–1.0), mean dyadic distance=9.8 (range 1.13–25.0), nearest neighbour distance=2.11 (range 0.06–117.9). Semi-transparent grey points show the raw data points.

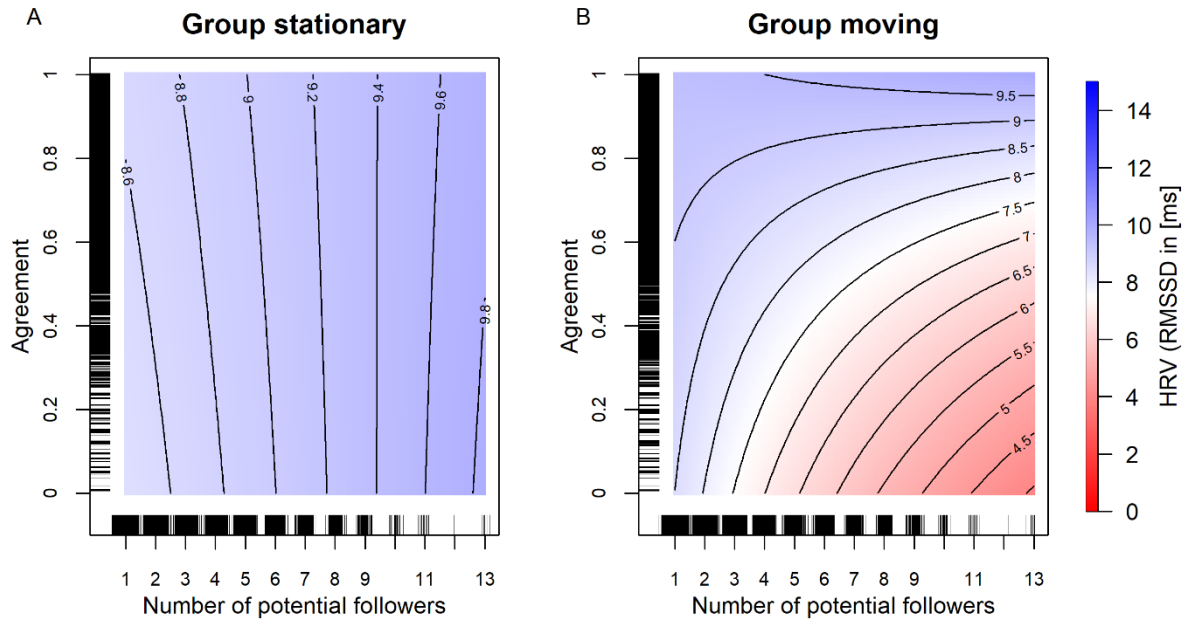


Fig. S4. Heart rate variability indicates the greatest signs of stress when there are more potential followers and agreement among initiators is low while the group is moving.

Plots show the model predictions from 65,782 ECG data windows (20 s each) back-transformed from the log-scale, in which the focal individual was detected making an initiation movement. The color-coded heart rate variability (HRV) was measured as RMSSD in ms. All panels are from the same model (model 5, table S5), 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. Rug plots along the axes show the distribution of raw data.

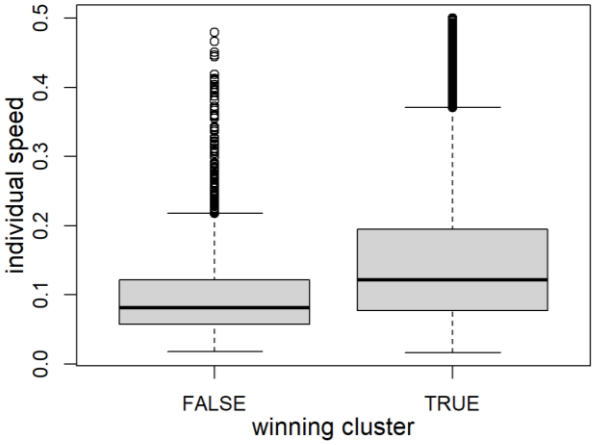


Fig. S5. Average individual speed of movement after an initiation attempt is higher for the successful than the unsuccessful initiators.

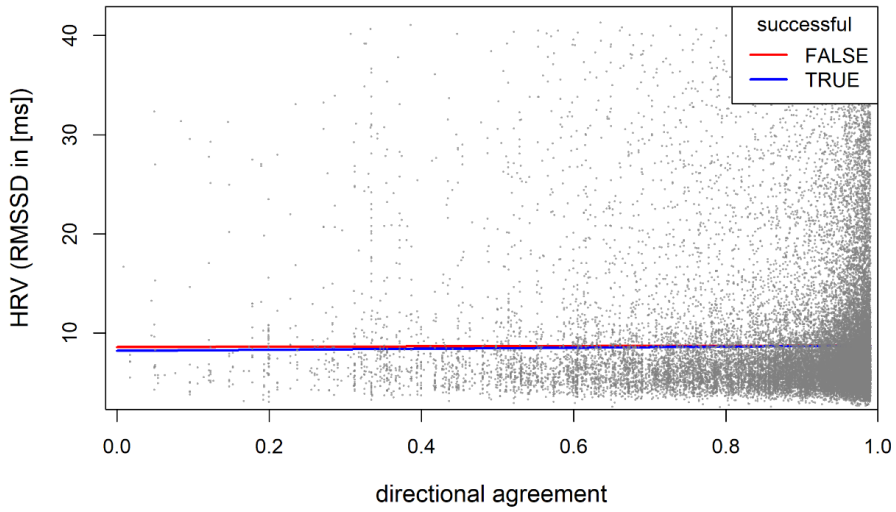


Fig. S6. Heart rate variability in response to group movement and different within-group positions.

Lines show the model predictions back-transformed from the log-scale from 30,083 ECG data windows (20 s each) where an individual was either successful (TRUE) or unsuccessful (FALSE) in initiating. Heart rate variability (HRV) was measured as the RMSSD in ms. The fits are from model 6 (table 6), with all other terms set to 0 as these only scaled the results up or down along the y-axis. Rug plots along the axes show the distribution of 95% of the raw data (not including lower and upper 2.5%).

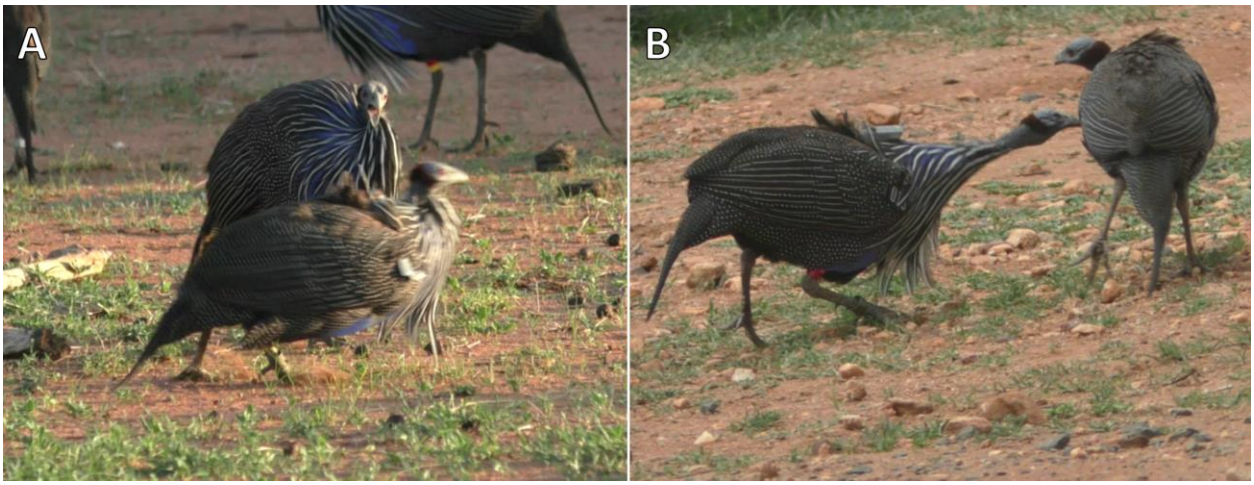


Fig. S7. Examples of typical agonistic interactions between group members.

Vulturine guineafowl express a number of agonistic interactions between members of the same social group including, but not limited to, displacing (A) or pecking (B) each other.

Table S1. Model 1 results – Effect of collective movement and spatial positioning on heart rate.

HR (corr.)	**Collective movement and spatial positioning**				
predictors	*Estimates*	*SE*	*t*	*CI*	*p*
(Intercept)	-4.53	5.35	-0.85	-15.02 – 5.95	0.397
surroundedness	135.78	3.35	40.51	129.21 – 142.35	**<0.001**
lead order	-15.83	1.58	-10.01	-18.93 – -12.73	**<0.001**
surroundedness2	-90.43	2.64	-34.23	-95.60 – -85.25	**<0.001**
lead order2	13.64	1.75	7.79	10.20 – 17.07	**<0.001**
ind speed	32.89	0.79	41.63	31.34 – 34.44	**<0.001**
group speed	29.98	1.15	26.06	27.73 – 32.24	**<0.001**
NN dist sqrt	2.23	0.14	15.91	1.96 – 2.51	**<0.001**
mean dyadic distance sqrt	-4.27	0.09	-45.04	-4.46 – -4.09	**<0.001**
ind speed × group speed	2.93	1.00	2.93	0.97 – 4.90	**0.003**
Random Effects					
σ^2	748.03				
$\tau_{00\ Ring}$	197.65				
$\tau_{00\ hour}$	57.33				
N_{Ring}	11				
N_{hour}	6				
Observations	130438				

Table S2. Model 2 results – Effects of leadership and directional conflict (during initiations) on heart rate.

HR (corr.)	**Leadership (during initiation)**				
predictors	*Estimates*	*SE*	*t*	*CI*	*p*
(Intercept)	30.15	7.75	3.89	14.96 – 45.34	**<0.001**
n potential followers	1.05	0.94	1.12	-0.79 – 2.88	0.263
agreement	2.63	1.93	1.36	-1.16 – 6.42	0.174
group speed	13.42	19.52	0.69	-24.85 – 51.68	0.492
x rel	0.58	0.11	5.04	0.35 – 0.80	**<0.001**
y rel abs	-2.62	0.11	-24.04	-2.83 – -2.41	**<0.001**
ind speed	37.06	1.12	33.16	34.87 – 39.25	**<0.001**
Sex [M]	-6.01	9.40	-0.64	-24.44 – 12.42	0.523
n potential followers × agreement	-2.50	1.01	-2.48	-4.47 – -0.52	**0.013**
n potential followers × group speed	27.79	9.62	2.89	8.94 – 46.64	**0.004**
agreement × group speed	10.75	20.22	0.53	-28.88 – 50.37	0.595
x rel × y rel abs	-0.10	0.07	-1.37	-0.24 – 0.04	0.170
group speed × ind speed	-2.09	1.40	-1.50	-4.83 – 0.64	0.134
(n potential followers × agreement) × group speed	-25.26	9.92	-2.55	-44.70 – -5.82	**0.011**
Random Effects					
σ^2	748.50				
$\tau_{00\ Ring}$	240.83				
$\tau_{00\ hour}$	51.66				
N_{Ring}	11				
N_{hour}	6				
Observations	69506				

Table S3. Model 3 results – Effects of leadership outcomes and directional disagreement (after initiation) on heart rate.

HR (corr.)		**Leadership (during initiation)**			
predictors	*Estimates*	*SE*	*t*	*CI*	*p*
(Intercept)	48.31	8.26	5.85	32.13 – 64.49	**<0.001**
winning clusterTRUE	-13.58	3.02	-4.50	-19.50 – -7.67	**<0.001**
agreement	-19.05	3.23	-5.89	-25.39 – -12.72	**<0.001**
x rel	0.65	0.19	3.41	0.28 – 1.03	**0.001**
y rel abs	-2.69	0.18	-15.14	-3.04 – -2.34	**<0.001**
ind speed	30.15	2.31	13.03	25.61 – 34.69	**<0.001**
group speed	18.73	3.25	5.76	12.36 – 25.11	**<0.001**
Sex [M]	-5.43	9.77	-0.56	-24.59 – 13.72	0.578
winning clusterTRUE × agreement	15.53	3.52	4.41	8.63 – 22.44	**<0.001**
x rel × y rel abs	-0.09	0.13	-0.74	-0.35 – 0.16	0.461
ind speed × group speed	12.68	5.89	2.15	1.13 – 24.22	**0.031**
Random Effects					
σ^2	705.29				
$\tau_{00\ Ring}$	259.66				
$\tau_{00\ hour}$	51.25				
N_{Ring}	11				
N_{hour}	6				
Observations	23317				

Table S4. Model 4 results – Effect of collective movement and spatial positioning on heart rate variability (measured as log(RMSSD) in ms).

log(RMSSD)	**Collective movement and spatial positioning**				
predictors	*Estimates*	*SE*	*t*	*CI*	*p*
(Intercept)	2.34	0.07	32.20	2.20 – 2.49	**<0.001**
surroundedness	-0.65	0.07	-9.19	-0.79 – -0.51	**<0.001**
lead order	0.10	0.03	2.87	0.03 – 0.16	**0.004**
surroundedness2	0.41	0.06	7.29	0.30 – 0.52	**<0.001**
lead order2	-0.08	0.04	-2.27	-0.16 – -0.01	**0.023**
ind speed	-0.10	0.02	-6.14	-0.14 – -0.07	**<0.001**
group speed	-0.01	0.02	-0.26	-0.05 – 0.04	0.798
NN dist sqrt	-0.01	0.00	-2.92	-0.01 – -0.00	**0.004**
mean dyadic distance sqrt	0.02	0.00	10.34	0.02 – 0.02	**<0.001**
ind speed × group speed	-0.07	0.02	-3.32	-0.11 – -0.03	**0.001**
Random Effects					
σ^2	0.34				
$\tau_{00\ Ring}$	0.04				
$\tau_{00\ hour}$	0.00				
N_{Ring}	11				
N_{hour}	6				
Observations	130438				

Table S5. Model 5 results – Effect of leadership and directional disagreement (during initiation) on heart rate variability (measured as log(RMSSD) in ms).

log(RMSSD)	**Leadership (during initiation)**				
predictors	*Estimates*	*SE*	*t*	*CI*	*p*
(Intercept)	2.12	0.12	18.16	1.89 – 2.35	**<0.001**
n potential followers	0.01	0.02	0.65	-0.03 – 0.05	0.515
agreement	0.03	0.04	0.67	-0.05 – 0.11	0.504
group speed	0.42	0.41	1.01	-0.39 – 1.23	0.310
x rel	-0.00	0.00	-1.37	-0.01 – 0.00	0.169
y rel abs	0.01	0.00	3.82	0.00 – 0.01	**<0.001**
ind speed	-0.11	0.02	-4.50	-0.15 – -0.06	**<0.001**
Sex [M]	0.03	0.14	0.23	-0.25 – 0.32	0.816
n potential followers × agreement	-0.00	0.02	-0.14	-0.04 – 0.04	0.890
n potential followers × group speed	-0.39	0.20	-1.89	-0.78 – 0.01	0.059
agreement × group speed	-0.33	0.43	-0.77	-1.17 – 0.51	0.440
x rel × y rel abs	-0.00	0.00	-0.75	-0.00 – 0.00	0.451
group speed × ind speed	-0.06	0.03	-1.98	-0.12 – -0.00	**0.048**
(n potential followers × agreement) × group speed	0.36	0.21	1.72	-0.05 – 0.77	0.086
Random Effects					
σ^2	0.34				
$\tau_{00\ Ring}$	0.06				
$\tau_{00\ hour}$	0.00				
N_{Ring}	11				
N_{hour}	6				
Observations	69506				

Table S6. Model 6 results – Effects of leadership outcomes and directional disagreement (after initiation) on heart rate variability (measured as log(RMSSD) in ms).

log(RMSSD)	**Leadership (post initiation)**				
predictors	*Estimates*	*SE*	*t*	*CI*	*p*
(Intercept)	2.15	0.12	17.44	1.91 – 2.39	**<0.001**
winning clusterTRUE	-0.05	0.06	-0.70	-0.17 – 0.08	0.482
agreement	0.02	0.07	0.27	-0.12 – 0.16	0.787
x rel	-0.01	0.00	-1.88	-0.02 – 0.00	0.060
y rel abs	0.01	0.00	1.49	-0.00 – 0.01	0.137
ind speed	-0.06	0.05	-1.26	-0.16 – 0.04	0.209
group speed	0.08	0.07	1.20	-0.05 – 0.22	0.230
Sex [M]	-0.01	0.14	-0.08	-0.29 – 0.27	0.935
winning clusterTRUE × agreement	0.04	0.08	0.57	-0.11 – 0.19	0.567
x rel × y rel abs	-0.00	0.00	-0.10	-0.01 – 0.01	0.921
ind speed × group speed	-0.24	0.13	-1.92	-0.49 – 0.01	0.055
Random Effects					
σ^2	0.33				
$\tau_{00\ Ring}$	0.06				
$\tau_{00\ hour}$	0.00				
N_{Ring}	11				
N_{hour}	6				
Observations	23317				

Movie S1. Example of collective movement by a group of vulturine guineafowl. This demonstrates the high cohesion among group members and the dynamic spatial positioning of individuals.