

# 1 **Locomotor compromises maintain group cohesion in baboon troops on the move**

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## 7 **Abstract**

8       When members of a group differ in locomotor capacity, coordinating collective  
9 movement poses a challenge: some individuals may have to move faster (or slower) than their  
10 preferred speed to remain together. Such compromises have energetic repercussions yet research  
11 in collective behavior has largely neglected locomotor consensus costs. Here we integrate high-  
12 resolution tracking of wild baboon locomotion and movement with simulations to demonstrate  
13 that size-based variation in locomotor capacity poses an obstacle to collective movement. While  
14 all baboons modulate their gait and move-pause dynamics during collective movement, the costs  
15 of maintaining cohesion are disproportionately borne by smaller group members. Although  
16 consensus costs are not distributed equally, all group-mates do make locomotor compromises,  
17 suggesting a shared decision-making process drives the pace of collective movement in this  
18 highly despotic species. These results highlight the importance of considering how social  
19 dynamics and locomotor capacity interact to shape the movement ecology of group-living  
20 species.

## 21 **Introduction**

22       Group-living animals incur consensus costs when they compromise their own preferred  
23 course of action to remain in contact with other members of their group (Conradt & Roper 2005;  
24 Pyritz *et al.* 2010). When group members vary in their physical characteristics (e.g., body size),

25 consensus costs may be particularly high, as physiological differences can introduce significant  
26 conflicts of interest among group-mates. Differences in locomotor capacity – the ability of an  
27 organism to move through its environment – may pose particularly severe challenges to  
28 behavioral coordination in heterogeneous groups. Locomotor capacity, which is dependent on a  
29 range of morphological features including body weight and limb length, affects the energetic  
30 costs of movement and therefore serves as a major driver of movement decisions (Perrigo 1987;  
31 Lees *et al.* 2012; Halsey 2016). Studies of several species of terrestrial animals revealed that  
32 individuals have a preferred travel speed (Pennycuik 1975) which is hypothesized to maximize  
33 energy efficiency (Hoyt & Taylor 1981).

34         Because physical characteristics, such as limb length and body mass, shape preferred  
35 travel speeds (Heglund & Taylor 1988), variation among individuals in body size will lead to  
36 differences in optimal stride frequencies and travel speeds within groups. How do groups  
37 maintain cohesion during collective movement when faced with such inter-individual  
38 differences?

39         The locomotor choices that individuals make with respect to stride frequency and length  
40 have important effects on their energetic cost of transport (bipeds: Muro-de-la-herran *et al.* 2014;  
41 Maculewicz *et al.* 2016; quadrupeds: Heglund *et al.* 1982; Dewhirst *et al.* 2017). Despite the  
42 obvious potential for differences in preferred travel speed and stride frequency to introduce  
43 behavioral and energetic conflicts of interest when individuals move together as a group, our  
44 understanding of the impact of locomotor capacity on collective movement is limited (Jolles *et*  
45 *al.* 2020). In social species, high inter-individual variation in locomotor capacity is expected to  
46 impose significant costs if group members must alter their patterns of movement in order to  
47 maintain group cohesion (Delgado *et al.* 2018; Sankey *et al.* 2019). Cohesion could be  
48 maintained in two ways: individuals with higher locomotor capacity can slow down or pause to  
49 allow other group members to catch up, or individuals with lower locomotor capacity can travel

50 faster or pause less frequently to keep up with their group-mates. In either case, some group  
51 members pay a cost. Faster animals who slow down or pause and wait pay an opportunity cost  
52 because they commit additional time to transit that could have otherwise been devoted to other  
53 activities such as feeding. Individuals who speed up to remain with their group, or who take  
54 fewer breaks during travel, increase their energetic cost of locomotion. On the other hand, if  
55 group members fail to coordinate, the resulting increase in group spread is expected to be costly,  
56 with individuals potentially experiencing greater exposure to predators and suffering from  
57 reduced information transfer (Lindström 1999; Ronget *et al.* 2018).

58 To test how members of heterogeneous groups maintain cohesion during collective  
59 movement, we fit GPS collars with integrated tri-axial accelerometers to the majority of  
60 members of a wild olive baboon (*Papio anubis*) group. Olive baboons live in cohesive groups of  
61 up to 150 individuals that travel together throughout the day in search of resources. Because they  
62 are sexually dimorphic and maintain stable mixed-age groups, they exhibit large within-troop  
63 variation in body size (Ray & Sapolsky 1992; Dunbar 2013).

64 We first tested whether differences in body size translated into differences in stride  
65 frequency, as well as vectorial dynamic body acceleration, an established proxy for energetic  
66 expenditure (Quasem *et al.* 2012, Wilson *et al.* 2020). We then investigated how fine-scale  
67 movements preserved group cohesion, and, in doing so, identified decision rules that might  
68 generate the observed patterns. Baboons group-mates do not benefit equally from their  
69 membership in their troop (Barton & Whiten 1993; Silk *et al.* 2009), and thus we hypothesized  
70 that individuals who had more to gain from group membership would be willing to incur  
71 additional locomotor costs to keep the group together. Specifically, due to their greater  
72 vulnerability to predators (Cowlshaw 1994), we predicted that smaller baboons would be more  
73 sensitive to their spatial positioning, make larger behavioral compromises, and bear more of the  
74 costs of maintaining group cohesion, compared to larger group members.

## 75 **Methods**

### 76 *Data collection*

77 Simultaneous tracking data were collected from 25 wild olive baboons (*Papio anubis*)  
78 belonging to a single group at the Mpala Research Centre in Laikipia, Kenya (Figure 1). The  
79 GPS data have formed the basis for several studies on individual positioning (Farine *et al.* 2017),  
80 collective movement (Farine *et al.* 2016; Strandburg-Peshkin *et al.* 2017) and consensus  
81 decision-making (Strandburg-Peshkin *et al.* 2015). Collar units recorded location estimates  
82 continuously at a 1 Hz sampling interval and tri-axial acceleration data at 12 Hz during daylight  
83 hours (06-18h) from August 1<sup>st</sup> to September 2<sup>nd</sup>, 2012. While individuals were chemically  
84 immobilized and being fit with telemetry collars (see Strandburg-Peshkin *et al.* 2015 for details  
85 on capture methodology), the length of each individual's front leg was measured (dorsal most  
86 point of the scapula to the carpus; hereafter referred to as "leg length"). Collared individuals  
87 consisted of 80% (23/29) of the adult (N = 13) and subadult (N = 10) members of the group, as  
88 well as two juveniles. Two of the adult individuals were removed from the analyses due to  
89 missing body measurements or inconsistencies in acceleration data. Focal video recordings of the  
90 behavior of collared individuals were collected and coded to identify periods of stationary and  
91 non-stationary behavior. In total, 20 minutes of non-stationary behavior and 180 minutes of  
92 stationary behavior was recorded in the field.

### 93 *Daily travel distance and displacement*

94 To assess how movement patterns, vary with body size, we calculated the daily travel  
95 distance and maximum displacement from the sleeping site of each group member, as well as of  
96 the group's centroid. Daily travel distance is a widely used measure of animal movement but is  
97 strongly affected by sampling frequency (Rowcliffe *et al.* 2012). For this reason, and to avoid the  
98 accumulation of GPS positional error inflating our estimates, we calculated daily travel distances  
99 after discretizing the data to 5-meter resolution (Strandburg-Peshkin *et al.* 2017). Maximum

100 displacement from the sleeping site was measured as a straight-line distance between the group's  
101 morning sleeping site and the most distant position visited on that day. We used linear mixed  
102 models (LMMs) to estimate the effects of leg length on (1) daily travel distance and (2) daily  
103 displacement, taking into account individual identity as a random effect and temporal  
104 autocorrelation between days using an autoregressive (AR1) component in both of the models  
105 (Pinheiro & Bates 2000).

#### 106 *Group movement parameters*

107 Group activity state was classified into two categories, stationary and non-stationary,  
108 based on changes in the displacement of the group centroid. Group travel bouts were classified  
109 using a change point detection algorithm (Lavielle 2005) on the centroid displacement speed.  
110 The speed and heading of the group's centroid were calculated at 10 second intervals.  
111 Individuals' relative positions within the group on the front-to-back axis were determined by  
112 multiplying their x-y locations by a rotation matrix based on the heading of the centroid. The  
113 resulting values were rescaled such that – regardless of group spread – 1 represents being at the  
114 front, 0 represents the center, and -1 represents the back of the group (Figure 1C). For some  
115 analyses, rather than front-to-back scaled values, individuals' positional rank relative to group  
116 mates were used.

#### 117 *Individual behavior and movement parameters*

118 Individual's activity state was inferred with a support vector machine following  
119 Fehlmann *et al.* 2017. Acceleration and location variables were time-matched with videos to  
120 obtain a labelled dataset. The most important features to classify the two activity states were  
121 heave peak frequency, and heave amplitude and the heave maximum power spectral density. We  
122 applied a Hampel filter to the acceleration data to remove spikes (Dewhurst *et al.* 2017) that were  
123 likely caused by direct physical strikes to the collar unit and trained the algorithm using ground-

124 truthed labels derived from the video recordings. The algorithm distinguished moving and non-  
125 moving activity states, exhibiting an accuracy of 0.92.

126 We then estimated stride frequency based on the timing of heave-axis (i.e. baboons'  
127 dorsal-ventral axis) peaks (Dewhirst *et al.* 2017) (Figure 1B). For each individual, we estimated  
128 a characteristic stride frequency by measuring her/his average stride frequency while moving  
129 alone, i.e. during periods when the individual was moving, but the rest of its group-mates were  
130 stationary, presumably engaged in foraging, socializing, or resting. Thus, the characteristic stride  
131 frequency of each individual represents the average stride frequency which she/he chooses,  
132 independent of social influences. We then tested for a correlation between individuals'  
133 characteristic stride frequencies and their leg lengths during both single-individual and group  
134 movement.

135 The vectorial dynamic body acceleration (VeDBA) of each group member was calculated  
136 using data from tri-axial accelerometers, following Halsey *et al.* 2009 and Wilson *et al.* 2020.  
137 Derivatives of dynamic body acceleration, such as VeDBA and ODBA (overall dynamic body  
138 acceleration), are proxy measures for movement-based energetic expenditure that has been  
139 validated for several quadrupedal taxa (Halsey *et al.* 2009; Qasem *et al.* 2012; Williams *et al.*  
140 2015; Wilson *et al.* 2020). We used a LMM to compare individuals' VeDBA values averaged  
141 over 10 second intervals during single-individual and group movement.

#### 142 *Modeling group spread and size-based segregation*

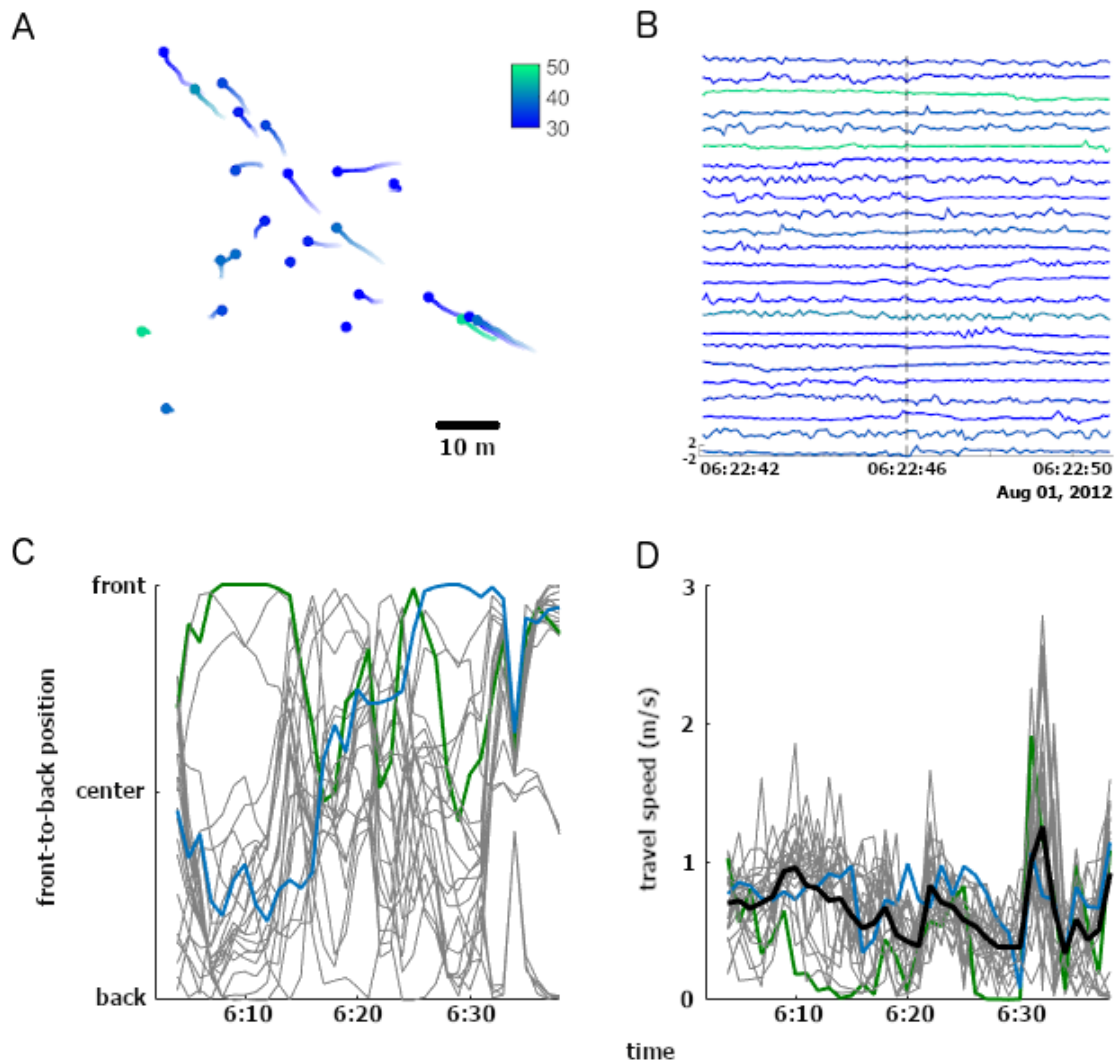
143 To assess how the simple decisions that individuals make with respect to modulating  
144 their travel speed change the collective properties of their group, we compared model  
145 simulations to our observed data. We modelled three alternative scenarios for a group moving in  
146 a single dimension (Video 1) and compared the results of these simulations to the observed  
147 patterns of group spread, measured as the total Euclidean distance between the front-most and  
148 back-most group member. In the modelled scenarios, individuals (1) moved at their preferred

149 speed (parameters included a characteristic speed for each agent drawn from the empirical data),  
150 (2) modulated their speed as function of their position in the group (parameters included a  
151 characteristic speed for each agent that varied as a function of their location in the group) or (3)  
152 moved at their preferred speed when group spread was low and modulated their speed as  
153 function of their position in the group when the spread exceeded a threshold value (parameters  
154 included a characteristic speed for each agent that varied as a function of their location in the  
155 group, and group spread). The durations of simulations were drawn from the distribution of the  
156 observed group travel bouts. We fit the parameters of speed modulation and the group spread  
157 threshold to find the values that best predict the observed data. Using these parameters, we then  
158 fit the models to the observed data and obtained an AIC (Akaike's Information Criterion) value  
159 for each model.

160         The effect of body size variation on the emergence of spatial segregation was assessed by  
161 sampling the relative location of large and small individuals and calculating the front-to-back  
162 positional rank difference between the two size categories (divided by the group mean leg  
163 length). We used a linear mixed model (LMM) to test the effect of body size on the positional  
164 rank difference with the group movement event as a random effect, for both simulated and  
165 observed movement tracks.

#### 166 *Individual behavior during group movement events*

167         We examined how individuals of different sizes adjust their locomotor behavior in the  
168 context of group movement, as well as the energetic consequences of these fine-scale movement  
169 decisions. We limited this analysis to group travel bouts when the group centroid was moving for  
170 at least two minutes and data were available for at least 15 baboons, ensuring a reliable  
171 representation of the group when estimating its activity state and the front-to-back rank position  
172 of group-members.



173  
174 *Figure 1.* Visualizing locomotor parameters of baboons during a segment of movement. A snapshot of (a) the  
175 locations of baboons at time  $t$ , represented by circles, with tails stretching back to individuals' locations at  $t-10$ s, and  
176 (b) the heave axis acceleration - with peaks representing footfalls - of all individuals, show variation in baboons'  
177 move and pause activity states, as well as in their stride frequencies. Over a 40-minute period, (c) individuals'  
178 position within the group, relative to the direction of group movement, as well as (d) individuals' speeds during  
179 group travel, are highly variable. In (a) and (b) individuals with longer leg length than average are represented in  
180 green, and shorter than average, in blue. The blue and green colored lines on (c) and (d) highlight the patterns of two  
181 individuals. The black line in (d) represents the travel speed of the group centroid.

182 Specifically, we assessed how a focal individual's leg length, its position within the  
183 group (as a linear and quadratic term), the difference in leg length between the focal individual  
184 and its nearest neighbor (for a subset of cases in which the nearest neighbour distance was under



185 5-m), group speed, and group spread affected focal individuals' (1) deviation in stride frequency  
186 from the characteristic stride frequency, and (2) VeDBA, measured in  $m/s^2$ . To account for the  
187 dynamic nature of both predictor and response variables within a travel bout, all measures were  
188 aggregated over 10 second intervals and each interval represented a single observation. The  
189 candidate generalized linear mixed models (GLMMs) included the above factors as main effects  
190 and also an interaction term between leg length and position in the group. All models accounted  
191 for individual identity and the cohesive group movement event as crossed random factors, and  
192 considered temporal autocorrelation by using an autoregressive moving average (ARMA)  
193 component. models were ranked according to AIC, a relative measure of parsimony, i.e. the  
194 balance between number of parameters and the fit of the model (Burnham & Anderson 1998).

195 We also examined how an individual's position in the group affected the variation in its  
196 activity states. We calculated individuals' ratio of time spent moving to time spent stationary,  
197 henceforth the "move:pause ratio." We used GLMMs, with the move:pause ratio as the response  
198 variable, and focal's leg length and its positions within the group as fixed effects. These models  
199 also accounted for individual identity and the group movement event as crossed random factors.  
200 Statistical analyses were performed in Matlab and R (R core team 2012) using the packages nlme  
201 and MuMin (Bartoń 2018; Pinheiro *et al.* 2018).

## 202 **Results**

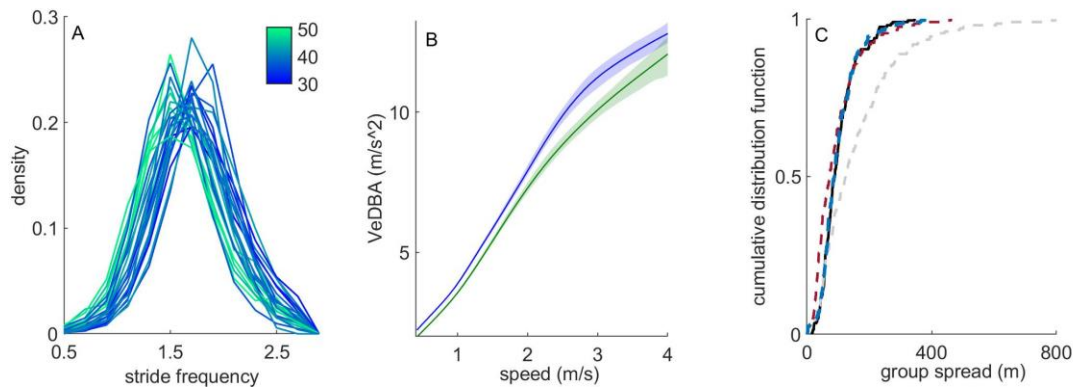
### 203 *Locomotor capacity varies with body size*

204 Baboons in the study group varied substantially in size (leg length: mean = 38 cm, range  
205 = 31 to 51 cm), stride frequencies, daily movement patterns, and energetic costs. Individuals  
206 displayed characteristic stride frequencies that varied as a function of body size (Figure 2A):  
207 when the group as a whole was stationary and individuals moved independently, stride frequency  
208 was negatively correlated with leg length (Pearson correlation,  $r = -0.53$ ,  $P = 0.01$ ). Preferences  
209 for particular stride frequencies extended to the context of collective movement. When the group

210 was moving cohesively ( $N = 96$  travel bouts lasting  $26 \pm 2$  minutes; mean + SE), larger  
211 individuals exhibited lower stride frequencies than smaller group-members (LMM,  $b \pm SE =$   
212  $0.013 \pm 0.002$  Hz, Wald  $t = 2.1$ ).

213 Baboons of different sizes also varied in their movement patterns; high-resolution GPS  
214 tracking revealed significant inter-individual variation in total daily distances travelled. The  
215 group as a whole – measured from the position of its centroid – traveled a mean of  $10.2 (\pm 2.7$   
216 SD) km per day, with most of that distance covered during long travel bouts, punctuated by  
217 periods when the group remained relatively stationary. Individual baboons travelled for  $142 \pm 25$   
218 minutes each day, during which they covered  $12.1 \pm 1.4$  (mean  $\pm$  SD) km. Individual's daily travel  
219 distance was negatively related to body size (Wald  $t = 1.91$ ), and decreased  $30 (\pm 10$  SD) m with  
220 each 1 cm increase in leg length. Only minor differences ( $\pm 1\%$ ) were found between individuals'  
221 daily maximum displacement from the sleeping site and that of the group's centroid, reflecting  
222 their shared route.

223 Differences in individual locomotion and movement patterns had energetic consequences  
224 that disproportionately impacted smaller individuals, particularly when the group engaged in  
225 collective movement. Overall, VeDBA decreased with increasing body size ( $b \pm SE = -0.13 \pm$   
226  $0.04$  m/s<sup>2</sup> for each 1 cm change in leg length; Wald  $t = 2.68$ ) and increased with travel speed ( $b$   
227  $\pm SE = 6.15 \pm 0.01$ , Wald  $t = 460.35$ , Figure 2B). Increases in travel speed had a larger impact on  
228 VeDBA of smaller baboons compared to their larger group-mates ( $b \pm SE = 0.14 \pm 0.03$ , Wald  $t$   
229  $= 3.89$ ). VeDBA values were higher when individuals moved together compared to when they  
230 were moving and the group was stationary ( $b \pm SE = 0.05 \pm 0.005$ , Wald  $t = 9.74$ ).



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*Figure 2.* Body size affects stride frequency, energetic expenditure, and locomotor modulation. (a) Variation in individuals' stride frequency while moving alone (i.e. during periods when the individual was moving, but the rest of its group-mates were stationary). Line color indicates leg length (in centimeters). (b) Differences in movement costs as estimated by VeDBA resulted in higher costs of movement for smaller individuals compared to large individuals travelling at the same speed. Individuals with longer leg length than average are represented in green, and shorter than average, in blue. (c) Cumulative distribution function for group spread under four alternative scenarios: observed (black solid), moving profile (gray dashed), position-dependent speed (green dashed), and position- and spread-dependent speed (blue dashed).

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### *Socially-mediated movement decisions maintain group cohesion*

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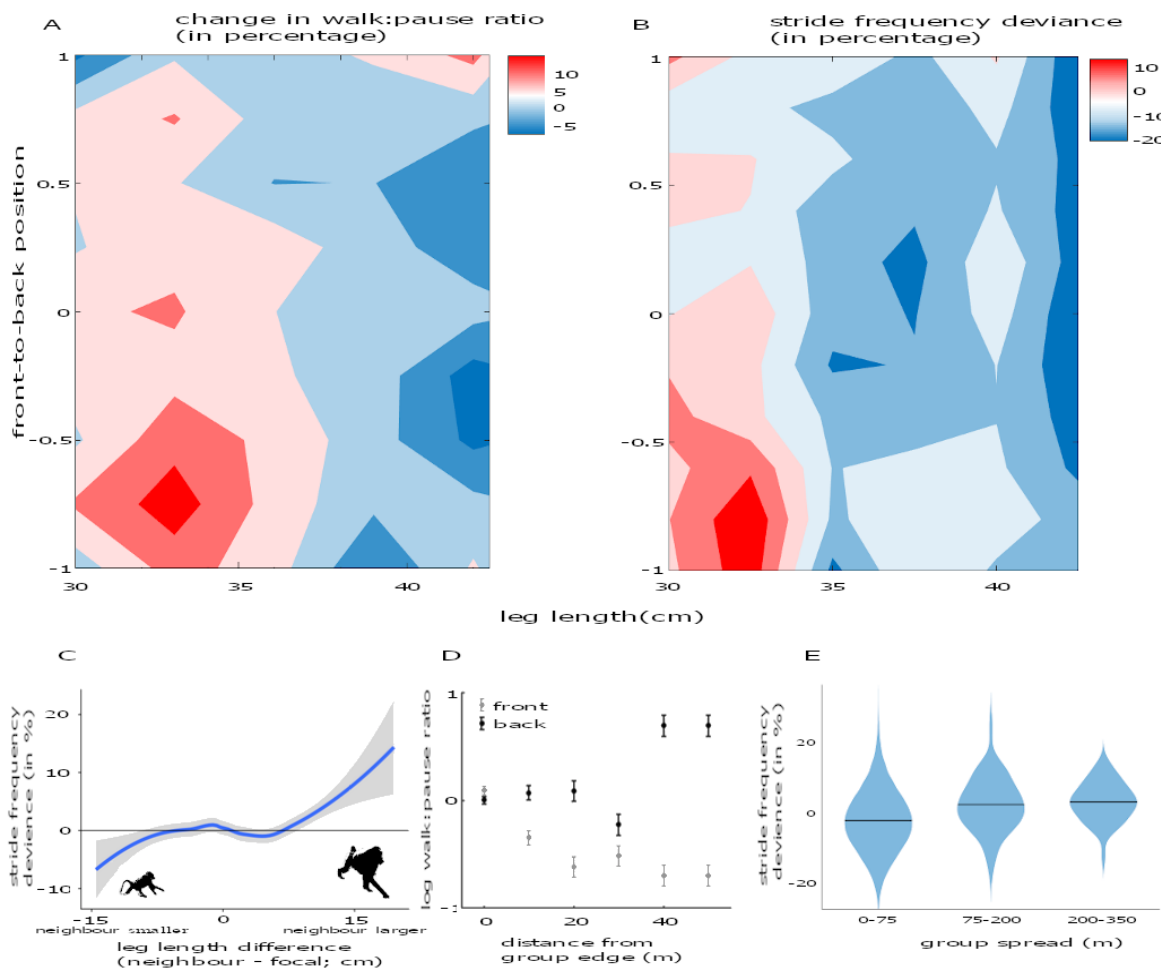
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We compared observed patterns of group spread and size-based spatial segregation to patterns predicted by agent-based models where individuals varied their stride frequency as a function of their leg length. Models in which individuals moved without any modulation to their characteristic stride frequency overestimated group spread by up to 800% [ $\Delta AIC = 260$ ]. In contrast, incorporation of simple socially-based decision rules improved model performance. The addition of a single rule in which individuals vary their speed as a function of their position within the group provided a good fit to our observed data for long travel bouts, but underestimated group spread for short travel bouts [ $\Delta AIC = 220$ ]. The best fitting model incorporated position-dependent modulation of speed when group spread was larger than a threshold value (estimated to be 80 meters), but allowed individuals to move at their characteristic stride frequency when the group was highly cohesive (Figure 2C). These patterns

252 align with our empirical data, where the mean deviation of group members from their  
253 characteristic stride frequency increased by a mean of  $0.7 (\pm 0.2 \text{ SD}) \%$  with 1 m increase in  
254 group spread (Wald  $t = 4.51$ ; Figure 3E). Our model predicts that size-based segregation will  
255 emerge if group members move at their characteristic stride frequency and do not modulate their  
256 stride frequency based on their position in the group; in simulated travel bouts, front-to-back  
257 positional rank was positively associated with body size (LM;  $b \pm \text{SE} = 2.71 \pm 0.90$ , Wald  $t =$   
258  $2.47$ ). In contrast, we found no evidence for size-based segregation in our empirical travel bouts;  
259 the mean rank difference between large and small individuals (mean =  $0.46$ ,  $\text{SD} = 0.85$ ) was not  
260 distinguishable from zero.



261

262 *Figure 3. Context-dependent decision rules support the emergence of cohesion. (a) The move:pause ratio and (b)*

263 *deviation of individuals' stride frequencies from their characteristic stride frequencies varied depending on an*

264 individual's leg length and front-to-back position in the group. (c) Differences in leg length between dyad members  
265 moving in proximity affects individuals' behavior. In proximity of a larger neighbor, the focal individual increased  
266 its stride frequency, whereas, in proximity of smaller neighbor the focal individual decreased its stride frequency,  
267 but to a lesser degree. (d) The decision to change activity state was dependent on the position in the group as  
268 apparent from the log of the move:pause ratio. In the front, individuals were more sensitive to being separated from  
269 the group, and were more likely to change their behavior at a shorter distance from the rest of the group, than when  
270 individuals were at the back and separated from the rest of the group. (e) The deviation from characteristic stride  
271 frequency was lower when group spread was small (0-75 m) compared to larger group spread (75-150 m, 150-350  
272 m) based on the trimodal distribution of group spread (Figure S1).

### 273 *Local decision rules support the emergence of cohesion*

274 Baboons modulate their travel speed by varying their stride frequency and their  
275 move:pause ratios. An individual's decision to adjust these fine-scale movement characteristics  
276 was sensitive to its social context. Individuals adjusted their stride frequency depending on the  
277 relative size of their nearest neighbor. Relative to their characteristic stride frequency, baboons  
278 increased their stride frequency when traveling in proximity (< 5 meters) to larger individuals,  
279 and decreased their stride frequency when in proximity to smaller individuals. However, the size  
280 of these behavioral adjustments was not equal; smaller individuals increased their stride  
281 frequency more than their larger neighbors decreased their stride frequency (LMM;  $b \pm SE =$   
282  $0.13 \pm 0.04 \%$ , Wald  $t = 2.68$ ; Figure 3A).

283 Position within the group also influenced baboons' movement decisions. While  
284 individuals in the front of the group maintained their characteristic stride frequency, baboons,  
285 regardless of size, increased their stride frequency when they were at the back ( $b \pm SE = 1.6 \pm$   
286  $0.3 \%$ , Wald  $t = 2.70$ ; Figure 3B). However, the behavioral strategies of small and large  
287 individuals differed at the center of the group. In these central positions, smaller individuals  
288 increased their stride frequencies but larger individuals did not deviate from their characteristic  
289 stride frequency (significant interaction between the quadratic term of group position and leg

290 length;  $2 \pm 0.2$  %, Wald  $t = 2.14$ ). Baboons changed their position within the group regularly  
291 (Figure 1C), maintaining the same positional rank along the front-back axis for an average of  
292 only  $54.0 \pm 14.1$  seconds. Overall, smaller individuals exhibited higher move:pause ratios than  
293 their larger group-members (binomial GLMM,  $b \pm SE = 0.46 \pm 0.10$ , Wald  $z = 4.41$ ), but this  
294 was especially true when they were at the back of the group (Figure 3A). All group members  
295 were less likely to move when they were at the front of the group, and more likely to move when  
296 they were at the back.

297         The spatial scale at which separation from the group prompted a change in an  
298 individual's move:pause ratio differed depending on whether an animal had outstripped or had  
299 fallen behind the rest of the group. At the front of the group, the increase in move:pause ratios  
300 occurred when individuals got 20 m ahead of their group-mates, whereas individuals had to fall  
301 at least 40 m behind the rest of their group before increasing their move:pause ratios (Figure 3D).

## 302 **Discussion**

303         In social species, variation in individual locomotor capacity complicates collective  
304 movement by forcing group members to modulate their speed in order to maintain group  
305 cohesion. Our agent-based models demonstrate that to replicate the levels of cohesion we  
306 observe in wild animal groups, group members need to dynamically adjust their patterns of  
307 movement in response to their social context. Simultaneous tracking of the majority of a group of  
308 wild baboons using GPS and accelerometer data loggers provided an opportunity to assess how  
309 individuals modulate their fine-scale behavior in response to changes in their social environment,  
310 and thereby maintain the spatial cohesion of their group. Individuals have a characteristic stride  
311 frequency that is related to their body size, but they adjust this stride to match the pace of  
312 movement of their nearest neighbors. Furthermore, individuals deviate more from their  
313 characteristic stride frequency when group spread increases. Individuals also balanced their  
314 tendency to pause during group movement as a function of their spatial position within the

315 group, waiting when they outstripped the group, and hustling to catch up when they fell behind.  
316 While all group members modulated their movement patterns in these ways, they did so to  
317 differing degrees. Compared to other members of their group, small baboons showed larger  
318 deviations from their characteristic stride frequency (Figure 3B). Consistent with previous work  
319 suggesting that changes in gait characteristics have important energetic consequences (Hoyt &  
320 Taylor 1981), smaller baboons also had higher VeDBA (i.e. a proxy for energetic expenditure)  
321 than their larger group-mates. Size-based differences in VeDBA were magnified as travel speed  
322 increased (Figure 2B). These results suggest that small individuals pay a disproportionate share  
323 of the energetic costs associated with maintaining group cohesion. Small individuals may incur  
324 additional costs if the effort required to keep up with their group-mates decreases their foraging  
325 efficiency — a likely outcome if small individuals are unable to pause to ‘forage on the go’.  
326 Because small individuals are more vulnerable to predators (Cowlshaw 1994), they may benefit  
327 more from the protection that group cohesion affords. Our results are thus consistent with the  
328 hypothesis that the costs of maintaining cohesion are largely borne by individuals that have the  
329 most to gain from group membership.

330 Baboons modulate their fine-scale movement decisions differently depending on their  
331 spatial position within their troop. We showed that individuals at the front of the group are more  
332 sensitive to group spread and pause often to let the rest of their group catch up, while individuals  
333 at the back of the group allow more separation from the group before increasing their  
334 move:pause ratios to catch up. This likely reflects context-dependent costs and benefits of  
335 different relative positions within the group. Differences in spatial positioning create variation in  
336 the ability of group members to influence group-level decisions (Couzin *et al.* 2005; Petit *et al.*  
337 2009; Farine *et al.* 2017; Mclean *et al.* 2018), which suggests that being at the back of the group  
338 may compromise an individual’s opportunity to contribute to the group’s consensus decisions.  
339 However, the willingness of individuals at the back of the group to allow a larger separation

340 from other group-members may reflect the benefits incurred by pausing often for small foraging  
341 bouts (and thus falling behind), and may be enabled by a perceived lower risk of predation  
342 associated with this position. Conversely, when individuals outstrip their group, their decision to  
343 slow down likely reflects a tradeoff between the opportunity costs of delaying arrival at their  
344 destination and the benefits of pausing to forage, as well as maintaining proximity to group-  
345 mates while in this particularly risky position within the group (Hamilton 1971; Krause 1994;  
346 Ioannou *et al.* 2015, 2019).

347         While the baboon troop as a whole travelled an average of 10.2 km per day, individual  
348 group members had significant variation in their daily travel distances: on the same day, some  
349 baboons travelled up to 1.1 km further than other members of their troop. Because all members  
350 of the troop followed the same general route, these individual differences in travel distance result  
351 from variation in individuals' local, small-scale movements. In general, smaller individuals had  
352 longer daily travel distances, suggesting that body size may play a role in the sinuosity of an  
353 individual's track. Inter-group and inter-population differences in baboon troop daily travel  
354 distances are well studied and can be attributed to a range of social and environmental factors  
355 including group size, food availability, and local interactions with other baboon troops and other  
356 species (Dunbar 1992; Pebsworth *et al.* 2012; Johnson *et al.* 2015; Slater *et al.* 2018). However,  
357 study of fine-scale variation in the daily travel distances of individuals in heterogeneous, socially  
358 cohesive groups is lacking. To our knowledge, there is no theoretical framework that explains  
359 why such differences arise. A more in-depth study of the effects of group members' body size,  
360 age-sex class, social rank, and affiliative network on the fine-scale differences in their daily  
361 travel distances is needed to understand why some individuals travel farther, even along the same  
362 route.

363         The differences in VeDBA documented in this study suggest that the energetic  
364 consequences of collective movement vary among members of heterogeneous groups and that



365 moving as part of a group is, in general, more energetically costly than moving alone. It is well  
366 established that the ecological cost of transport is highly variable across species, ranging from  
367 0.19% to 28% of overall energy expenditure (Garland Jr. 1983; Husak & Lailvaux 2017), and  
368 that smaller animal species have higher energetic costs associated with locomotion (Taylor *et al.*  
369 1982). While less is known about intraspecific relationships between body size and the energetic  
370 costs of locomotion, studies suggest that the same holds within species (Sockol *et al.* 2007;  
371 Pontzer *et al.* 2011; Sankey *et al.* 2019). This is consistent with our results showing that VeDBA  
372 was higher for smaller individuals and that the relationship between increasing speed and  
373 increasing VeDBA scaled with body size, with smaller individuals having relatively higher  
374 increases in VeDBA over increasing speeds. Variation in energy expenditure can result not only  
375 from variation in travel speed, but also from differences in individuals' tendencies to move and  
376 pause (Kramer & McLaughlin 2001), as well as variation in the cost of turning while moving  
377 (Wilson *et al.* 2013). However, energy expenditure encompasses only a part of an individual's  
378 energy balance. It is yet to be revealed how metabolic rates, energy intake, endurance and  
379 recovery dynamics change with body size (Nagy 2005; Birat *et al.* 2018), but all could  
380 potentially impact the cost of collective motion in heterogeneous groups. Tri-axial accelerometry  
381 provides a promising new method of quantifying many such inter-individual differences and may  
382 afford new opportunities for studying the costs of sociality in wild animals.

383 Heterogeneity in locomotor capacities between group members can have implications on  
384 the energetic demands of its members and may constrain group size and composition. First,  
385 larger groups must travel farther each day to meet their energetic needs (Clutton-Brock &  
386 Harvey 1977; Majolo *et al.* 2008), yet longer daily travel distances exacerbate inequalities in the  
387 energetic costs of locomotion. Increasing group size would thus lead to increasing disparities in  
388 the energetic expenditures of group members. The maximum daily travel potential of the  
389 smallest individuals could therefore contribute to limiting group size within a given species.

390 Second, the magnitude of the differences in locomotor capacities between the smallest and  
391 largest individuals of a given species may constrain the extent to which heterogeneous social  
392 groups can be cohesive. If the smallest and largest age-sex classes of individuals have such great  
393 disparities in locomotor energy expenditure that smaller individuals simply can't keep up with,  
394 or travel as far as, larger individuals over the course of full days, this could cause a reduction in  
395 groups' spatial cohesion, or even fission-fusion social dynamics (e.g., Pontzer & Wrangham  
396 2006).

397         The compromises that individuals make to maintain group cohesion occur across many  
398 axes – including compromises related to dietary, safety, and social needs (Krause & Ruxton  
399 2002; Markham & Gesquiere 2017; Jolles *et al.* 2020). A holistic view that considers the  
400 interactions between these axes of compromise is necessary to understand how individuals  
401 balance the costs and benefits of group-living. In baboons, group movement trajectories are  
402 steered by a process of shared decision-making among group members, suggesting that  
403 individuals may often make compromises in the timing and direction of movement in order to  
404 stay with their group (Strandburg-Peshkin *et al.* 2015). In this study, we show that individuals  
405 modulate their fine-scale locomotor behaviors relative to their social context and spatial position  
406 within the group during collective movement. All group members thus make locomotor  
407 compromises to maintain group cohesion, suggesting that the *pace* of collective movement is  
408 also driven by a shared decision-making process. Our findings stress the importance of  
409 considering the interaction between social dynamics and locomotor capacity in shaping the  
410 movement ecology of group-living species, and illustrate an approach for accomplishing this  
411 under socially and ecologically relevant field conditions.

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#### 428 **Ethics Statement**

429 All procedures were subject to ethical review and were carried out in accordance with the  
430 approved guidelines set out by the National Commission for Science, Technology and  
431 Innovation of the Republic of Kenya (NACOSTI/P/15/5727/4608). Baboon tracking was  
432 approved by the Smithsonian Tropical Research Institute (IACUC 2012.0601.2015).

#### 433 **Competing Interests**

434 The authors declare that no competing interests exist.

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586 **Video legends**

587           Video 1. Observed and simulated groups moving in a single dimension. Individuals with  
588 longer leg length are represented in green, and shorter, in blue.

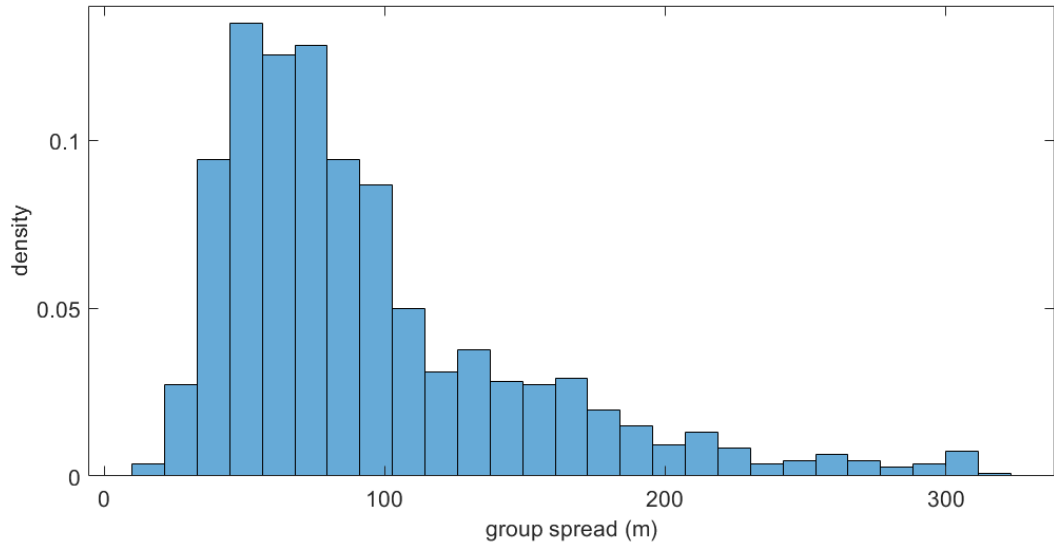


Figure S1. Group spread patterns. Group spread ranged between 35 and 320 meters.