Flexible group cohesion and coordination, but robust leader-follower roles, in a wild social primate using urban space

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ABSTRACT

Collective behaviour has a critical influence on group social structure and organisation, individual fitness, and social evolution, but we know little about whether and how it changes in anthropogenic environments. Here, we show multiple and varying effects of urban space-use upon group-level processes in a primate generalist – the chacma baboon (*Papio ursinus*) – within a managed wild population living at the edge of the city of Cape Town, South Africa. In natural space, we observe baboon-typical patterns of collective behaviour. In contrast, in urban space (where there are increased risks, but increased potential for high-quality food rewards), baboons show extreme flexibility in collective behaviour, with changes in spatial cohesion and association networks, travel speeds, and group coordination. However, leader-follower roles remain robust across natural and urban space, with adult males having a disproportionate influence on the movement of group members. Their important role in the group's collective behaviour complements existing research and supports the management tactic employed by field rangers of curbing the movements of adult males, which indirectly deters the majority of the group from urban space. Our findings highlight both flexibility and robustness in collective behaviour when groups are presented with novel resources and heightened risks.

INTRODUCTION

Due to the challenges involved in tracking the behaviours of many individuals simultaneously, we are only just beginning to understand the collective behaviour of wild social groups [1-3] and know little about whether and how it changes in anthropogenic environments. This is an important gap in knowledge given the critical influence collective behaviours exert on group dynamics, individual fitness, and social evolution [4-6] and the increasing levels of spatial overlap between wildlife and humans worldwide [7].

Here, we present a detailed field study of whether, and how, collective behaviour changes for a primate generalist when in urban space. We studied a group of chacma baboons (*Papio ursinus*) living at the edge of the City of Cape Town. The group's home-range includes natural space within Table Mountain National Park which is dominated by indigenous fynbos vegetation [8, 9], and urban space comprising residential suburbs. Urban spaces are established at lower altitudes with more productive soils and hence higher primary productivity [10] and include access to high-energy anthropogenic food sources [11]. Together these attractants provide a strong motivation for baboons to urban-forage [12], which can result in negative interactions between baboons and people [13-16].

The City of Cape Town contracts a private company that deploys field rangers whose objective is to deter baboons' from urban space using aversive conditioning [9, 15]. This management effort reduces the time the baboons spend in urban space [9, 17], but can contribute to significant within-group variation in behaviour and space-use [9, 13]. For example, in the group we study here, a combination of management effort and socioecological factors creates opportunities for individuals and small groups to break away from the main group and move into urban space more regularly [18]. However, the whole group does occasionally use urban space together, and these occasions offer the opportunity to directly compare baboon group coordination and collective behaviour in natural and urban space.

Previous research on chacma baboon collective behaviour has shown that individuals have strong and differentiated associations [19, 20] and high social cohesion [4, 21]. Groups also show high synchrony in activities [22] and high-ranking socially connected individuals (in particular adult males) have a large influence on group movement decisions [13, 23-26]. We therefore expected to see similar patterns of behaviour for our study group when in natural space but anticipated these patterns would alter when in urban space, for the following interconnected reasons.

First, urban space presents a fundamentally different resource and risk distribution compared to natural space [7, 27-30]. This affects individuals differently depending on their phenotype (e.g. sex and age: [31-33]), with consequences for group-level patterns of behaviour. For example, changes in resources and risks can prevent individuals from foraging together at specific locations [27, 34, 35], exaggerating differences in motivation or hunger among individuals and creating conflicts of interest [7, 36]. Specific to the Cape baboons, field rangers are also more likely to herd baboons in urban space [9, 12] with a focus on the core of the group, providing opportunities for more peripheral individuals to use urban space [18]. Second, urban space is both more noisy and fragmented (e.g., roads, buildings [37-39]) than natural space, which results in group members becoming visually and acoustically isolated, increasing inter-neighbour distances [40, 41]. Third, urban space can have reduced predation pressure (predators often avoid these environments: [42]) and provide opportunistic access to high-quality human food rewards [7] which can cause increased within-group competition [43, 44], with implications for group cohesion and stability [45]. Together, these factors can increase the costs for individuals achieving collective behaviour in urban space [1] forcing changes in social structure, organisation and functioning of groups [1, 46-48]. We therefore tested three connected hypotheses with respect to baboon collective behaviour in urban space using high-resolution GPS collar data for the majority of adults in the group.

We expected the baboons to show decreased social cohesion in urban space compared to natural space (Hypothesis 1) [46, 48, 49], due to high fission-fusion dynamics [18] along with a lack of natural predators [50] within the study troop, which we anticipated would heighten inter-individual conflicts of interest [51]. We predicted the group would be spread over a larger area when in urban space compared to natural space, resulting in increased modularity (i.e., greater clustering) of association networks [46]. To test these predictions we examined the area [52, 53], shape [54, 55], and spread [56-58] of the group when in natural and urban

space, and built networks describing patterns of spatial associations among individuals [46, 59]. If association networks are interrupted and modular then we expected poorer whole group coordination [24, 56, 60] in urban space compared to natural space (Hypothesis 2), as alignment in travel speed and direction would be difficult for individuals to maintain over large distances (though coordination among local neighbours in clusters' may be increased). We therefore predicted more variable group travel speeds, turning angles, and alignment across all individuals [56, 61-63] in urban space compared to natural space. Finally, we expected the influence of certain individuals on group members' movement to be reduced (Hypothesis 3). Specifically, previous studies of chacma baboon groups in this and other populations have highlighted the importance of adult males in influencing the movement patterns of group-members [13, 23, 25, 26]. Here, we expected male leadership to be reduced in urban space because of a limited opportunity to influence neighbour behaviour. To test this prediction, we used an automated procedure that quantifies local leadership events [64]. This is based on the relative movements of pairs of individuals where a successful "leader" initiates movement away from, and is followed by, another individual. An aggregation of all leader-follower events across dyads therefore represents each individual's relative 'influence' over group-member movement patterns at a defined spatial scale.

METHODS

Study site and subjects

We studied the 'Da Gama group', in the City of Cape Town, South Africa. The group comprised 2 adult males, 19 adult females, and approximately 30 subadults, juveniles and infants. The group was studied from July to November 2018, and for this study we use data collected mainly during the austral winter (July - September) when our GPS collars were active (see GPS data) and when the Peninsula baboons tend to use urban spaces more frequently [65]. Details on how we defined urban and natural space, and the time baboons spent within these are provided in the Supplementary Methods. Dominance ranks for all adult individuals were calculated from direct observations of aggressive interactions (displacements, chases and aggressive displays), following the clear submission of one individual, collected *ad libitum* over 78 days of group follows, as described in previous works [18, 66] and in the Supplementary Methods.

118   *GPS data*

119   We fitted n = 16 adult baboons with SHOAL group in-house constructed collars (F2HKv3),

120   recording GPS positions at 1 fix/second between 08:00 – 20:00 local time (GiPSy 5 tags,

121   TechnoSmArt, Italy). One collar was not found after automatic release and two collars failed

122   to record GPS data, resulting in data for n = 13 baboons (Table S1). To test our hypotheses,

123   we used GPS data collected between 08:00-18:00 local time, when 10 or more collars were

124   recording. Further details on why these criteria were used, and the accuracy and post-

125   processing of GPS data, are provided in the Supplementary Methods.

126   *Social cohesion (Hypothesis 1)*

127   To test for differences in social cohesion when baboons were in urban and natural space we

128   calculated 1) convex hull area and perimeter; 2) mean nearest neighbour distance; 3) mean

129   distance to the group centroid; and 4) group stretch and sphericity, using the package

130   "swaRm" in R [67]. Convex hull area may be particularly sensitive to missing individuals [68].

131   To test for differences in spatial association networks, we extracted two commonly used

132   metrics: eigenvector centrality and strength [46, 59], calculated based upon baboon

133   associations in urban and natural space. Association networks were constructed using the

134   "Spatsoc" package in R [69]. Baboon GPS fixes were grouped spatiotemporally, where

135   individuals within 5 metres and 1 minute of one another were assumed to be in association

136   using the "chain rule" [70]. Network edges were weighted using the simple ratio index. We

137   also used the walktrap community algorithm ("cluster_walktrap", "igraph" package, R [71]) to

138   identify clusters of densely-connected individuals in the networks using random walks, where

139   individuals within a cluster have stronger ties than between clusters [46]. A modularity score,

140   Q, is given for each cluster. Additionally, to identify the times when the baboons were

141   commonly within the vicinity of one another (or in discrete groups), we created spatiotemporal

142   groupings in either area of within 1 minute and 150 m, using the "Spatsoc" package in R [69].

143   A spatial threshold of 150 m was chosen as it is larger than common group spread on the

144   Cape Peninsula [10].

145   *Group coordination (Hypothesis 2)*

146   To test for differences in group coordination in urban and natural space we calculated 1)
147   speed of the group centroid; 2) mean linear speed across individuals; 3) standard error in
148   linear speed; 4) standard error in heading angle and, 5) polarization of the group (alignment
149   of individuals in direction of travel, going from 0: not aligned to 1: aligned), using the package
150   "swaRm" in R [67]. We also calculated polarization of identified subgroups (<150m; Fig. S4)
151   in urban space.

152   *Leadership (Hypothesis 3)*

153   To investigate the influence of certain individuals on group members' movement we
154   calculated leader-follower networks by identifying "pulls" between baboon dyads, using
155   functions as developed in [64] and made available at: http://crofoot.ucdavis.edu. These
156   functions identify sequences in which one individual (the "leader") initiates movement away
157   from another individual (the potential "follower"), who then either joins the first individual (this
158   would be a successful "pull") or remains where they are and the leader returns (an
159   unsuccessful "anchor"), within a predetermined distance threshold (see Fig. 2i). The
160   "disparity" and "strength" thresholds (outlined in the Supplementary Materials of [64]) were
161   both set at 0.1, as used in Strandburg-Peshkin *et al.* [64]. In our main results we present
162   analyses using 5 m thresholds, as used in [64], but also tested different distance thresholds;
163   these results are presented in the Supplementary Material. For each distance threshold, we
164   created N x N matrices (using successful "pulls" in natural and urban space), where "leaders"
165   are rows and "followers" are columns, with the frequency of dyadic pulls in a cell, for natural
166   and urban data. We then created directed leader-follower networks using the package
167   "igraph" in R [71] and extracted directed eigenvector centrality in the network as a measure
168   of the relative importance of individuals in influencing others movements and leading groups:
169   a measure used previously in studies investigating leader-follower dynamics [72, 73].

170   *Statistical analyses*

171   To examine differences in collective properties between urban and natural space (see
172   parameters above), we fitted linear models using generalised least squares ("gls" function in
173   "nlme" package, R [74]), whilst fitting a temporal autocorrelation structure to account for the
174   high resolution of the data. Because of the difference in sample sizes between urban and
175   natural space (natural dataset was 48x larger than urban dataset; see Supplementary

Methods), we bootstrapped all models with 48 repetitions, randomly sampling from the natural dataset for the number of minutes recorded in the urban dataset. We extracted model coefficients at each iteration, averaged each coefficient (across iterations) and calculated 95% confidence intervals for the bootstrapped data. We log-transformed (using the natural log) the following variables to meet normality criteria: convex hull area, convex hull perimeter, mean nearest neighbour distance, mean distance to the group centroid, speed of the group centroid, and mean linear speed, which was assessed using graphical procedures (Q-Q plots and standardised residuals vs. predicted values).

To examine differences between urban and natural space in association and leader-follower networks, we used linear mixed models ("lmer" function in "lme4" package, R [75]) and fitted network strength (association networks) and eigenvector centrality (both association and leader-follower networks) as response variables. We fitted individual baboon ID as a random effect, and standardised dominance rank as a fixed effect to control respectively for repeated values of individual and the effect of dominance rank (which is strongly correlated with association network metrics in natural space: [18], and leader-follower network metrics in both settings: Fig. 2h). Best-performing models were selected by Akaike Information Criteria (AIC). Model fit was checked using graphical procedures (Q-Q plot and standardised residuals vs. predicted values). Matrix correlations (Spearman's rank) were also conducted to test if dyadic associations/interactions were similar in natural and urban space.

RESULTS

Social cohesion (Hypothesis 1)

Baboons were farther apart from one another in urban compared to natural space (nearest neighbour distance: urban: 30.47 ± 1.21 m, natural: 11.96 ± 0.21 m (hereafter median ± SE), $p < 0.001$; Table 1; Fig. 1a) resulting in greater average distance to the group centroid (urban: 129.15 ± 3.63 m, natural: 36.11 ± 1.47 m, $p < 0.001$; Table 1), and increased group spread when in urban space (convex hull area: urban: 38379.36 ± 2511.88 m², natural: 3733.90 ± 233.68 m², $p < 0.001$; convex hull perimeter: urban: 947.26 ± 23.57 m, natural: 282.95 ± 7.74 m, $p < 0.001$; Table 1; Fig. 1c). In urban space baboons were rarely all found within 150m of each other (Fig. 1b) and were often in dispersed subgroups (Fig. 1d, Video S1). In contrast, in natural space baboons were often found within 150m of each other and rarely in dispersed

subgroups (Fig. 1be, Video S1). Moreover, where small subgroups or single individuals were identified within 150m in natural space, this was likely due to baboons travelling alone or in small groups in and out of urban space (Fig. S2). The group split into a maximum of 5 subgroups at any one time point in urban space (Fig. S4). Despite differences in group cohesion, group shape did not differ between urban and natural space, with the group having similar "sphericity" (i.e. closer to circle shape) (urban: 0.449 ± 0.010, natural: 0.382 ± 0.001, p = 0.098; Table 1), and "stretch" (urban: -0.344 ± 0.049, natural: -0.308 ± 0.007, p = 0.698; Table 1) in both spaces. Full model outputs are provided in Table 1.

214 **Table 1:** Results of a nonparametric bootstrap (48 iterations) of a generalised least squares
215 model for the effect of space (urban, natural) on each of eleven collective parameters of a
216 baboon group living on the urban edge in Cape Town, South Africa. Estimates, *t*-values, and
217 *p*-values are the mean average taken across bootstrap iterations. 95% confidence intervals
218 indicate the 95% distribution of the estimates, and standard errors represent the error around
219 the estimates. "Log" indicates the natural log scale. With the exception of "stretch", positive
220 estimates indicate a parameter increase in urban space and negative estimates indicate a
221 parameter decrease in urban space. "Stretch" decreases in urban space despite a positive
222 estimate.

Model	Estimate	SE	*t*	*p*	95% CI	
Social cohesion parameters						
Convex hull area (log)	2.295	0.015	17.262	**< 0.001**	2.108	2.481
Convex hull perimeter (log)	1.085	0.008	15.042	**< 0.001**	0.986	1.191
Mean nearest neighbour distance (log)	0.846	0.007	8.481	**< 0.001**	0.773	0.937
Mean distance to group centroid (log)	1.083	0.007	14.132	**< 0.001**	0.972	1.192
Sphericity	0.046	0.001	1.886	0.098	0.019	0.070
Stretch	0.036	0.006	0.316	0.698	-0.039	0.118
Group coordination parameters						
Speed of group centroid (log)	0.426	0.132	3.636	**0.005**	0.252	0.588
Mean speed (log)	0.655	0.007	7.712	**< 0.001**	0.567	0.746
Standard error in speed (log)	0.796	0.007	9.195	**< 0.001**	0.720	0.913
Standard error in heading	0.035	0.001	3.152	**0.009**	0.020	0.049
Polarization	-0.124	0.001	-6.353	**< 0.001**	-0.146	-0.108

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Figure 1. Reduced baboon group cohesion in urban compared to natural space. (a)
Frequency density plot for mean inter-baboon distances (natural log scale); (b) Frequency
density plot for number of baboons observed within 150m of each other; (c) Frequency
density plot for baboon group convex hull perimeter (natural log scale). In (a)-(c), data are
shown for baboons in natural (green) and urban (grey) space. (d) and (e) show satellite
images of baboons in a suburb of Cape Town, and in the natural space surrounding this
suburb, respectively. Baboon locations (identified by coloured dots) are overlaid, and white
circles of 150m diameter (as shown in (b)) illustrate differences in group cohesion at these
example moments.

Spatial association networks differed between urban and natural space (Fig. 2ac) with the
network in urban displaying lower density and higher modularity (density = 0.718; Q = 0.429)
compared to the network in natural (density = 1; Q = 0.118), reflecting lower cohesion in
urban space (Fig. 1) where baboons are further apart (Fig. 1ac) and more frequently in
subgroups (Fig. 1bd). These network differences result in different individual-level network
statistics. Individuals' association network strength was significantly lower in urban space
(median: 0.108, range: 0.048 – 0.245) compared to natural space (median: 0.339, range:
0.228 – 0.545) (GLMM: estimate ± SE = -0.214 ± 0.023, p < 0.001). Whilst individual
eigenvector centrality scores for the association network were similar in both urban and
natural space (GLMM: estimate ± SE = -0.055 ± 0.080, p = 0.504), the positive correlation
between eigenvector centrality and dominance rank was absent in urban space (Spearman's
rank correlation: natural: rho = 0.481, p = 0.096; urban: rho = 0.160, p = 0.603). Additionally,
dyadic relationships present in natural space were retained in urban space (Spearman's rank
correlation: rho = 0.445, p < 0.001).

Coordination (Hypothesis 2)

The speed of the group centroid was higher in urban space compared to natural space
(urban: 0.08 ± 0.01 m/s, natural: 0.05 ± 0.00 m/s (hereafter median ± SE), p = 0.005; Table
1). The group mean speed was also higher in urban space compared to natural space (urban:
0.16 ± 0.01 m/s, natural: 0.09 ± 0.00 m/s, p < 0.001; Table 1), and was more variable (urban:
0.07 ± 0.00, natural: 0.03 ± 0.00, p < 0.001; Table 1). Variation in baboons' headings was

greater in urban space compared to natural space (urban: 0.533 ± 0.006, natural: 0.505 ± 0.001, p = 0.009; Table 1) resulting in reduced polarization in urban space (urban: 0.290 ± 0.010, natural: 0.401 ± 0.002, p < 0.001; Table 1). The positive relationship between polarization and speed – where polarization increases when the group travels quickly towards a shared destination – was present in urban and natural space (Fig. S3ab) but this relationship was weaker in urban space (mean speed*urban space: estimate ± SE = -0.837 ± 0.108, t = -7.751, p < 0.001; Fig. S3a). Similarly, polarization increased with increasing standard error in speed (Fig. S3cd), but this relationship was weaker in urban space (standard error in speed*urban space: estimate ± SE = -2.631 ± 0.502, t = -5.204, p < 0.001; Fig. S3c). Finally, the increasing number of subgroups in urban space had no effect on whole group polarization (gls: estimate = -0.002, p = 0.867), though polarization within subgroups was greater than whole group polarization (Fig. S4). This was attributed to greater coordination between dyads (Fig. S5 & Fig. S6), rather than an artefact of calculating polarization over fewer individuals.

Figure 2. Interrupted networks in urban space, but retention of leader-follower roles.
(a) Baboon association network (undirected) and (b) leader-follower network (directed) in natural space; (c) Baboon association network (undirected) and (d) leadership network (directed) in urban space; In (a)-(d) high to low eigenvector centrality is represented by large to small circle sizes, and high to low dominance rank from dark to light colours. (e) Relationship (not statistically significant) between association network eigenvector centrality (undirected) for baboons when in natural and urban space; (f) Relationship (statistically significant) between leadership network eigenvector centrality (directed) for baboons when in natural and urban space; (g) Trend for higher dominance-ranked baboons being more central in the association network (undirected) in natural space, but not in urban space; (h) Higher-ranked baboons are more central in the leadership network (directed) in both urban and natural space; (i) Five baboons: the orange baboon is the blue baboon's closest spatial neighbour, within a 5m radius (shown by the light blue circle). If two baboons are often observed within 5m of each other they will have a strong link in (a) and (c). If the blue baboon (initiator) moves >5m away from a group member who then follows by >5m (orange baboon, follower), then this is considered a local leadership event, where one baboon influences the movement of another. Baboons with greatest influence on others' movements will have high eigenvector centrality in (b) and (d).

Leadership (Hypothesis 3)

Leader-follower networks differed between urban and natural space (Fig. 2bd) with the network in urban displaying a lower density (density = 0.942) than the network in natural (density = 1). Leadership eigenvector centrality was significantly correlated with dominance rank in natural space (Spearman's rank correlation: rho = 0.666, p = 0.013, n = 13; Fig. 2h), and this relationship was maintained in urban space (Spearman's rank correlation: rho = 0.792, p = 0.001, n = 13; Fig. 2h). Leadership eigenvector centrality scores were significantly lower in urban space (median: 0.621, range: 0.194 – 1.000) compared to natural space (median: 0.860, range: 0.448 – 1.000) (GLMM: estimate ± SE = -0.167 ± 0.031, p < 0.001). Leader-follower dyads that frequently interacted in natural space also interacted in urban space (Spearman's rank correlation: rho = 0.788, p < 0.001).

DISCUSSION

We provide evidence that chacma baboon social cohesion and coordination breaks down in urban space. Although the collared individuals of the Da Gama group only spend 2% of their daytime as a group in the urban space, their social behaviour is significantly altered when compared with their behaviour in natural space. In particular, the group was more spread out, less cohesive, with a higher clustering into subgroups when in urban space. The group also attained higher speeds, had a greater error in heading, and were less polarized in urban space. These findings therefore support our first two hypotheses regarding association networks being interrupted and interactions among individuals being constrained. However, we found only partial support for our third hypothesis regarding the disruption of leadership roles: though leader-follower networks were interrupted in urban space, dominance related leader-follower roles were retained. We discuss each of our findings in turn.

Baboon social cohesion and association networks were significantly reduced in urban space, supporting our first hypothesis. This finding is in line with recent research examining the influence of human proximity on social and spatial relationships in moor macaques [46], where groups are less cohesive, and individual social relationships constrained, when near to humans. Urban environments are heterogenous and unpredictable [76], with patchy food sources and high levels of contact with humans (in our group, this includes both residents and rangers). Previous research indicates that when there is high spatial variability in the environment (for example in food patches or predation risks), there is a greater scope for inter-individual conflicts of interest, and groups are predicted to fission into subgroups of individuals with similar requirements [13, 60]. It is likely that this is what we are seeing for the Da Gama group: conflicts in motivation between individuals when in the urban space cause a splitting of the group into subgroups and, with a lack of natural predators, this is preferential to social cohesion [7]. Indeed, we found greater inter-baboon distances, greater individual distances to the group centre, and a larger group spread in the urban space, as well as a retention of spatial associations and leader-follower interactions at the dyadic level in urban space. Moreover, the spread of the group in urban space had an uneven distribution. Individuals were often seen in dispersed subgroups, which translated into sparser urban spatial networks (network "strength" was significantly reduced in urban space) with a higher cluster modularity score than natural spatial networks. This is further evidenced by the multi-modal distribution of urban inter-individual distances, which has recently been used to determine "units" in multi-level societies [77], and here represents a greater clustering of individuals in urban space.

Baboon group coordination was disrupted because of fragmentation of the collective structure in urban space, providing support for our second hypothesis. The group was observed travelling at higher speeds and group members were more variable in their speed and heading, resulting in a less polarized group in urban as opposed to natural space. Since the group is spread out and clustered into subgroups in the urban space, it follows that travel direction and speed are highly variable across individuals. Previous research on the Cape baboons has found that, when using urban space, adult males adopt a "sit and wait strategy", spending a lot of time close to the urban edge and then making high-activity forays into urban space [11]. High speed in urban space is presumably indicative of high risk, and is likely the result of individuals quickly monopolising patchy high caloric food sources and subsequently being exposed to risks from residents, dogs, rangers, etc. Indeed, the relationship between speed and polarization (as group speed increases, so does group polarization: [78]), was significantly reduced in comparison to natural space (Fig. S3ab). This indicates that individuals are less polarized in travel direction whilst travelling at high speeds in urban space compared to natural space. This is likely due to group fragmentation in the urban space; here, within-subgroup polarization was greater than whole group polarization (Fig. S4), indicating that while subgroups align in collective motion, whole group alignment is reduced. Polarization also increased with increasing error in speed in natural space (Fig. S3d) and this relationship was reduced in urban space (Fig. S3c); higher values of standard error in speed were associated with lower values of polarization more commonly than in natural space. Together these results may be indicative of subgroups aligning in travel direction when moving off independently of one another – resulting in low whole group coordination in movement.

In the case of our third hypothesis, we found that, though leader-follower networks were interrupted, and leadership eigenvector centrality was significantly reduced in urban space, leadership roles as predicted by dominance rank remained stable. This finding therefore offers partial support for our final hypothesis. The retention of dominance-related leadership in urban space – where the group tended to be fragmented and poorly coordinated – is surprising but highlights the importance of high-ranked individuals upon the movement patterns of group members, which is seen throughout the species range. Indeed, in other populations, dominant individuals (namely, high-ranking adult males) have a strong influence on group movement, and therefore collective movement decisions [13, 23, 25, 26, 72, 79].

363 However, because our study troop has just two adult males, they may be afforded more
364 opportunity to elicit followers.

365 High-ranking individuals are more successful than other group members at making
366 movement initiations across both natural and urban space. Movement initiations are
367 extracted regardless of inter-individual distance within a dyad (see Methods), which means
368 that even if the group is fragmented and poorly coordinated, fine-scale movement is still
369 captured. In this way, we see that leadership is robust to other social changes seen in urban
370 space; or, put another way, leader-follower dynamics are density independent [5, 51, 60].
371 However, using different spatial criteria for identifying leadership "pulls" did reveal that in
372 urban space, the greater influence on group movements by dominant individuals is present
373 for movement initiations at up to 20m, whereas in natural space they only occur for
374 movements of up to 5m (Table S3). This shows that group members tend to follow high-
375 ranking individuals in urban space at a more global scale. In both cases group members are
376 responding to initiations, but in urban space, other individuals tend to be further away (mean
377 nearest-neighbour distances are more than doubled in urban space, and baboons tend to
378 only have a few neighbours even at distances of 20m: Fig. S8).

379 Our finding that this chacma baboon group exhibits leader-follower dynamics structured by
380 dominance rank differs to the findings in olive baboons (*Papio anubis*), where dominant
381 individuals do not strongly influence group movement decisions [64]. However, it is important
382 to note that we use the leader-follower data in a different way to the Strandburg-Peshkin *et*
383 *al.* [64] study. There, the authors took the leader-follower information and used this to explore
384 collective movement decisions when baboons were faced with different options regarding
385 where to travel. Here, we examined an individual's influence on other baboons' behaviour by
386 creating leader-follower networks based upon pulls across the whole dataset. It would
387 therefore be informative to compare both datasets at different scales (i.e., different threshold
388 distances with shorter or longer lag times between movement) and for different types of
389 movement events, to examine how collective movement is shaped by differences in context
390 or species.

391 Together, our results demonstrate how chacma baboons in the Cape Peninsula have
392 adapted to exploit urban space, adopting lower group cohesion and smaller group sizes,
393 which we expect reduces competition for high-quality, patchy food resources [27] and

increases their chance of evading rangers who attempt to deter them from urban space (pers. obs.). The current work therefore provides further evidence of how social flexibility allows animals to cope with accelerated human-induced changes to their environment [27, 46], and provides a basis for understanding these responses in other species. Future work could further examine leader-follower dynamics in wildlife groups inhabiting urban space, identifying when key decisions are made, how and when groups split and reform [80]. Alongside this, a more in-depth investigation into inter-individual differences in movement in urban environments may uncover how predictable individuals are when using these landscapes [81].

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