

Optimal group size in a highly social mammal

A. Catherine Markham^{a,b,1}, Laurence R. Gesquiere^{b,c}, Susan C. Alberts^{c,d}, and Jeanne Altmann^{b,d,1}

^aDepartment of Anthropology, Stony Brook University, Stony Brook, NY 11794; ^bDepartment of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544; ^cDepartment of Biology, Duke University, Durham, NC 27708; and ^dInstitute for Primate Research, National Museums of Kenya, Nairobi, Kenya 00502

Contributed by Jeanne Altmann, September 22, 2015 (sent for review April 5, 2015; reviewed by Colin A. Chapman and Marta B. Manser)

Group size is an important trait of social animals, affecting how individuals allocate time and use space, and influencing both an individual's fitness and the collective, cooperative behaviors of the group as a whole. Here we tested predictions motivated by the ecological constraints model of group size, examining the effects of group size on ranging patterns and adult female glucocorticoid (stress hormone) concentrations in five social groups of wild baboons (*Papio cynocephalus*) over an 11-y period. Strikingly, we found evidence that intermediate-sized groups have energetically optimal space-use strategies; both large and small groups experience ranging disadvantages, in contrast to the commonly reported positive linear relationship between group size and home range area and daily travel distance, which depict a disadvantage only in large groups. Specifically, we observed a U-shaped relationship between group size and home range area, average daily distance traveled, evenness of space use within the home range, and glucocorticoid concentrations. We propose that a likely explanation for these U-shaped patterns is that large, socially dominant groups are constrained by within-group competition, whereas small, socially subordinate groups are constrained by between-group competition and predation pressures. Overall, our results provide testable hypotheses for evaluating group-size constraints in other group-living species, in which the costs of intra- and intergroup competition vary as a function of group size.

glucocorticoid hormones | group size | *Papio cynocephalus* | ranging patterns | savanna baboons

The emergence and evolution of group living is a central topic in ecology and evolution (1, 2). According to theory, animals form groups when the benefits of aggregation—including decreased predation risk, facilitation of cooperative infant care, increased probability of winning intergroup competition, and information sharing—exceed the costs of maintaining close proximity with conspecifics (3–6). Conversely, costs are primarily derived from intragroup competition for limited resources, such as food and reproductive opportunities, and increased probability of disease transmission (5).

When group living does evolve, what size groups will form and what are the consequences for individuals living in groups of different sizes? Group size is a key aspect of group living that can have a pronounced effect on activity and travel patterns, and hence can have important fitness consequences for social animals (7–13). If group living is advantageous, do larger groups experience advantages relative to smaller groups, or do larger groups experience increasing costs that counter advantages? The ecological constraints model of group size posits that larger groups experience more intragroup competition for food resources than smaller groups; intragroup competition then drives larger home ranges and longer daily travel distances, imposing greater energetic costs on larger than on smaller groups (reviewed in ref. 13). Several studies have shown that foraging time increases as group size increases, supporting the ecological constraints model (13–15).

However, living in small groups may impose costs as well. Smaller groups are predicted to be more vulnerable to predation, and also to competition with conspecific groups because they may be more easily displaced or “pushed” than large groups, limiting access to key resources (3, 16, 17). Empirical evidence for the

fitness disadvantages of living in smaller groups has not been directly demonstrated, although one previous study in primates found that individuals in the smallest and the largest groups had longer daily travel than individuals in intermediate-sized groups, suggesting a travel cost of living in the smallest groups that was similar in magnitude to the cost of living in the largest groups (18).

Taken together, the tension between intragroup competition (more acute for large groups) versus intergroup competition and predation risk (particularly acute for small groups) is likely to be a key determinant of group size. Group size, in turn, is often an important source of variance in individual fitness: individuals in larger relative to smaller groups may experience longer interbirth intervals, delayed age at sexual maturity, lower fertility, and an increased prevalence of infectious disease (9–11). Less is known, however, about the physiological consequences of living in large versus small groups, such as levels of glucocorticoids (stress hormones) (10, 19, 20). Glucocorticoids are steroid hormones secreted in response to a stressor, which help restore homeostasis by diverting energy that normally supports growth, reproduction, and immune function. Whereas high glucocorticoid concentrations are beneficial under acute conditions, chronically elevated levels are detrimental to health and survival (21–23). When large groups experience greater feeding competition and increased travel distance, this will lead to energetic stress and should be reflected in elevated glucocorticoid levels in individuals in large groups. However, if these potential costs to larger groups are countered by significant advantages (e.g., if larger groups monopolize higher-quality patches of food than smaller groups), individuals may achieve an energetic balance (reflected in lower glucocorticoid levels) that is independent of group size or that even favors large groups.

Here we evaluated how ranging patterns and adult female fecal glucocorticoid concentrations (fGC) varied with group size within a

Significance

What are the costs and benefits for animals living in groups of different sizes? Balancing the trade-offs between within-group competition (which favors smaller groups) and between-group competition (which favors larger groups) suggests that intermediate-sized groups may be best, yet empirical support for this prediction has largely been lacking. Using long-term data on wild baboons, we provide novel evidence that individuals living in intermediate-sized groups have energetically optimal space-use strategies and lower glucocorticoid (stress hormone) concentrations than individuals in either large or small groups. Our results offer new insight into the costs and benefits of group living.

Author contributions: A.C.M., L.R.G., and J.A. designed research; A.C.M., L.R.G., S.C.A., and J.A. performed research; A.C.M. and L.R.G. analyzed data; and A.C.M., L.R.G., S.C.A., and J.A. wrote the paper.

Reviewers: C.A.C., McGill University; and M.B.M., University of Zurich.

The authors declare no conflict of interest.

Data deposition: Data underlying these analyses have been deposited in the Dryad repository ([dx.doi.org/10.5061/dryad.nh597](https://doi.org/10.5061/dryad.nh597)).

¹To whom correspondence may be addressed. Email: markham.catherine@gmail.com or altj@princeton.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1517794112/-DCSupplemental.

single population of wild baboons (*Papio cynocephalus*), a species characterized by highly cohesive and stable mixed-sex social groups ranging in size from ~20 to over 100 individuals (24). Our investigation provides an important extension of previous research on optimal group size, which has focused predominantly on fission-fusion species, in which group size changes frequently in response to immediate conditions (25). Within a baboon population, the home ranges of social groups overlap extensively, and foraging resources [primarily plant foods (26, 27)], are often located within regions of home range overlap (28). However, despite this home range overlap, groups rarely come in close proximity with one another, indicating that baboon groups temporally partition the landscape, using the same resources but at different times (29). When intergroup interactions do occur, differences in the number of adult males (a demographic component highly correlated with total group size) are a major predictor of the outcome of agonistic encounters: groups with more adult males have a competitive advantage over groups with fewer (30).

Based on the ecological constraints model, and on the commonly reported result that costs accumulate linearly with group size (13), we predicted that (i) larger groups would have larger home ranges and longer daily travel distances, and (ii) individuals in larger groups would spend a greater proportion of time foraging than those in smaller groups. As a reflection of local resource exhaustion, we also predicted that (iii) space use of large groups would be more evenly distributed throughout their home range [in the sense of refs. 31 and 32]. Finally, as a physiological response to decreased energy intake and increased traveling costs, we predicted that the average glucocorticoid concentrations of group members (iv) would increase with group size and (v) would increase with increased daily travel distances. We included measures of rainfall and temperature in all analyses because environmental factors can have a profound effect on space use and activity budgets in many species, and rainfall is the main limitation on tropical ecosystem primary productivity (33).

Results

Unexpectedly, group size was best represented as a quadratic predictor variable for annual home range [quasi-likelihood under the independence model criterion (QIC) with linear vs. quadratic

term: 16.095 vs. 13.031], monthly home range (57.835 vs. 22.762), average daily travel (29.988 vs. 21.632), and evenness of space use (45.581 vs. 25.507). Large and small groups had larger annual and monthly home ranges, longer average daily travel, and more even patterns of space use than intermediate-sized groups (Fig. 1 A–C and Table 1). Among environmental variables, only rainfall evenness had a significant effect: annual home range areas were larger when rainfall was less even (Table 1).

Again unexpectedly, group size was also best represented as a quadratic predictor variable for fGC concentrations: females in smaller and larger groups had higher fGC concentrations than females in intermediate-sized groups (QIC with linear vs. quadratic term: 25.045 vs. 23.656) (Fig. 1D and Table 1). Neither rainfall nor monthly maximum temperature significantly predicted female fGC concentrations (Table 1). Average daily travel distance positively predicted log-transformed fGC levels (Fig. 2 and Fig. S1): in months when groups traveled farther each day, average log-transformed fGC levels within groups were higher ($n = 131$ group months; $r^2 = 0.043$, $P = 0.017$).

Time spent foraging increased linearly with group size. Specifically, in a generalized estimating equation (GEE) model of annual proportion of time spent foraging, which included group size and environmental variables as predictors, only group size was a significant predictor of time spent foraging (group size: $\beta = 0.002$, $P < 0.001$) (Fig. 3 and Fig. S2; see Table S1 for full model results). We also tested a model with group size as a quadratic term, and the quadratic model had a slightly lower QIC than the linear one, but the difference was very small (QIC with linear vs. quadratic term = 6.800 vs. 6.739) and the curve appeared visually linear. Consequently, we judged the linear model—with fewer parameters—to be more appropriate. No environmental variables predicted the proportion of time spent foraging.

Discussion

Contrary to our predictions, we observed U-shaped relationships between group size and (i) home range area, (ii) average daily distance traveled, and (iii) evenness of space use within the home range, after taking into account environmental variables. Compared with both smaller and larger groups, groups intermediate

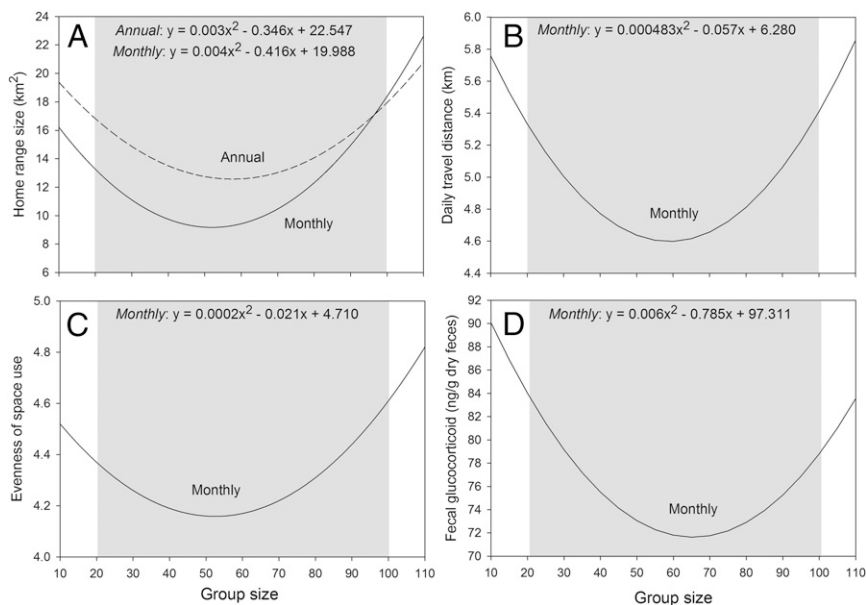


Fig. 1. Group size predicts ranging patterns (A–C) and fGC (D) in five baboon social groups. For simplicity of presentation, each panel represents the simple bivariate relationship between group size and the variable in question. See Table 1 for results of full statistical model incorporating weather parameters. Gray shading indicates the typical range of group size in wild baboons (24).

Table 1. Results from GEEs assessing the effect of group size and environmental variables on the home range size, daily distance traveled, evenness of space use, and fGC concentrations of five baboon social groups

Dependent variable	Estimate	Wald χ^2_1	P
Home range (annual)			
Intercept	2.888	4.443	0.035
Group size	-0.008	11.504	0.001
Group size²	8.21×10^{-5}	19.958	<0.001
Cumulative rainfall	3.37×10^{-5}	0.318	0.573
Rainfall evenness	-0.629	6.856	0.009
Average maximum temperature	-0.036	0.981	0.332
Home range (monthly)			
Intercept	1.272	21.344	<0.001
Group size	-0.016	13.863	<0.001
Group size²	1.43×10^{-4}	14.790	<0.001
Cumulative rainfall	-1.08×10^{-4}	0.176	0.675
Average maximum temperature	0.003	0.153	0.695
Average daily distance traveled (monthly)			
Intercept	0.125	5.209	0.022
Group size	0.002	3.045	0.081
Group size²	-1.61×10^{-5}	3.890	0.049
Cumulative rainfall	6.33×10^{-5}	2.398	0.122
Average maximum temperature	0.001	1.572	0.210
Evenness of space use (monthly)			
Intercept	4.918	63.899	<0.001
Group size	-0.023	7.638	0.006
Group size²	2.00×10^{-4}	8.551	0.003
Cumulative rainfall	1.49×10^{-4}	0.132	0.716
Average maximum temperature	-0.006	0.193	0.660
Fecal glucocorticoids (monthly)			
Intercept	2.002	744.619	<0.001
Group size	-0.004	9.234	0.002
Group size²	3.16×10^{-5}	14.898	<0.001
Cumulative rainfall	1.25×10^{-4}	0.030	0.863
Average maximum temperature	-0.001	0.418	0.518

Home range size and fGC were log-transformed and daily travel distance was inverse-transformed to approach normality. Statistically significant results are shown in bold.

in size had smaller home ranges, shorter daily travel distances, and used their home range less evenly (i.e., space-use was more temporally and spatially skewed). The finding that large groups use larger range areas than groups of intermediate size is consistent with the assumption that larger groups have high energetic demands. However, the finding that small groups also require larger range areas than groups of intermediate size differs from results reported by most previous studies, which have generally reported a positive linear relationship between group size and range area (e.g., refs. 34–36). As in our study, Stevenson and Castellanos (18) reported longer daily travel distance in both small and large groups than in intermediate-sized groups of Colombian woolly monkeys (*Lagothrix lagothricha*), suggesting that our results may be generalized rather than specific to baboons. In addition, our result showing a U-shaped relationship between group size and glucocorticoid levels suggests that being in a smaller or larger group may be more stressful or more energetically costly than being in an intermediate-sized group, and hence provides additional support for the idea that intermediate group sizes are ideal for baboons. Similar results—lower glucocorticoid levels in intermediate-sized groups—have been reported in ring-tailed lemurs (*Lemur catta*) by Pride (19). The higher stress hormone levels associated with small and large groups can negatively impact an animal's health and well-being and, ultimately, affect survival and reproduction.

Why did our study reveal ranging and activity disadvantages to small group size that have typically not been revealed before? We propose two possible reasons, the first biological and the second methodological. First, in our study population, group size is a significant predictor of group-level dominance, and smaller groups have a competitive disadvantage compared with larger groups (30). In addition, predation may represent a greater mortality risk for Amboseli baboons than it does for the arboreal primates that have been the subjects of many group-size studies. Significant populations of large predators have long been documented in Amboseli (37), and both successful and unsuccessful predation on baboons have been recorded throughout the baboon research in Amboseli (28), as well as in other baboon populations (e.g., ref. 38). Together, intergroup competition and predation may negatively impact the ranging patterns of smaller groups because smaller groups are more likely to be displaced by conspecific groups and predators, perhaps ultimately reducing fitness of individuals in small groups. For populations and species in which intergroup competition and predator pressure are less strong, small groups may not experience high costs. We predict that both the existence of an optimal group size (or range of sizes) and the placement of that optimum will depend on ecological conditions and density of conspecifics which, in turn, will influence the intensity of intergroup competition.

Second, absence of a U-shaped pattern in previous studies may also be explained by a bias toward studying intermediate and larger sized groups. Small groups are less available; they are subject to greater extinction, simply because of demographic stochasticity and perhaps also because of the costs revealed in the present study, and therefore may not be available for research. Even if they are available, researchers may choose to study somewhat larger groups to obtain larger sample sizes of individuals, a bias suggested by Sharman and Dunbar (39). Furthermore, in studies in which a range of group sizes are observed, researchers may have too few data points, particularly at the ends of the distribution, to test for significance of the quadratic term. As a result, significant variation contributed by points at the lower end of the relationship (i.e., smaller group sizes) may not be detected.

Taken as a whole, the results of our analyses of home range sizes, daily travel distances, evenness of space use, and glucocorticoid concentrations lead us to hypothesize that large (socially dominant) groups are constrained by within-group competition, whereas small (socially subordinate) groups are constrained by between-group competition and predation. Specifically, we propose that larger groups exhaust local food resources more rapidly than smaller groups, and therefore require more foraging

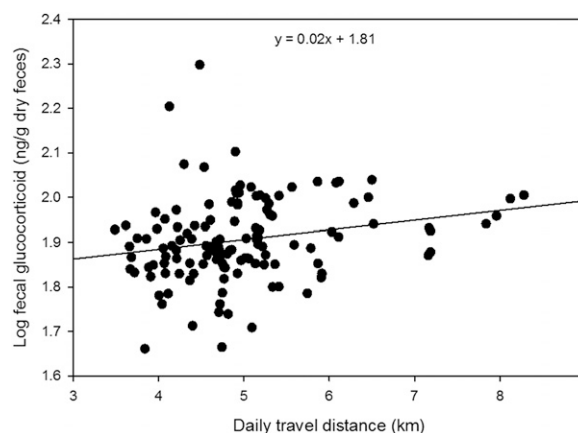


Fig. 2. Daily travel distance predicts monthly group fGC for five baboon social groups ($n = 131$ group-months). See Fig. S1 for a color version of this figure.

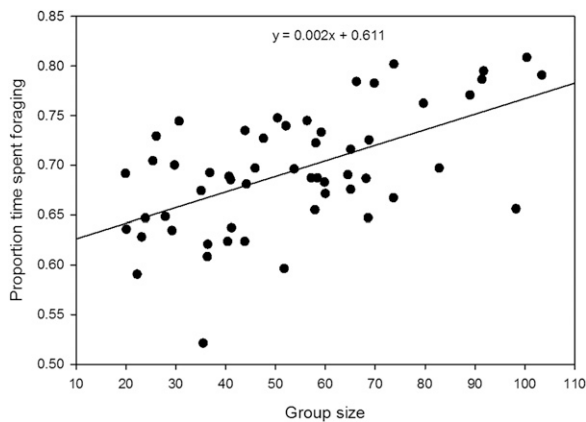


Fig. 3. Group size predicts annual proportion of time spent foraging for five baboon social groups. Data collected in hydrological years 2000–2010. Each point represents a single group-hydrological year, which begins in November each year and extends through the following October ($n = 55$ group years). See Fig. S2 for a color version of this figure.

time and greater daily distances traveled. In contrast, we propose that the increased range area and daily distance traveled in smaller groups results from the displacement of these groups by larger, socially dominant groups. Whatever the cause of the greater home range size and distance traveled by large and small groups, our result that daily travel distances had a positive linear relationship to glucocorticoid concentrations points to daily travel as one source of stress for animals living in both large and small groups. We predict that we would detect an even stronger correlation between glucocorticoid concentrations and daily travel if samples were paired for single individuals over shorter (i.e., daily) time intervals, as opposed to the monthly group averages presented in our study. Further study is needed to understand whether this pattern is influenced directly by the energetic costs of travel or indirectly by other factors that may independently influence both distance traveled and glucocorticoid concentrations.

Our study has several important implications. For fission-fusion species, characterized by fluidity in group size, changes in group size in response to ecological constraints and opportunities may be immediate. Consequently, realized group size in these species may often closely correspond to the predicted optimum (40). Particularly relevant to such species, Sibly (41) proposed that stable group size will usually be larger than the optimal group size because individuals are likely to join groups of optimal size to improve their own fitness, despite declines in the average fitness of existing group members. However, for species like baboons that are characterized by highly cohesive and relatively permanent social groups, optimal group size will reflect average long-term ecological conditions experienced by the group rather than short-term perturbations (19). This leads to the prediction that greater variability in group size will occur, even in these species, if ecological conditions are unstable over time and space. Baboons are among the most geographically and ecologically widespread of nonhuman primates, and group size variability may be an important mechanism of their adaptations to highly diverse conditions.

Materials and Methods

The study population of wild baboons lives within the Amboseli-Longido ecosystem, a semiarid short-grass savannah straddling the Kenya–Tanzania border (42). This region is characterized by a predictable 5-mo-long dry season (June–October) during which virtually no rain falls and the availability of food and drinking water declines as the season progresses (43). Rainfall is highly variable during the remaining 7 mo of the year, which is typically referred to as the “wet” season (November–May), and also varies tremendously between years (44).

Five social groups were the focus of detailed observations by the Amboseli Baboon Research Project (ABRP) several days each week, and all individuals were recognized by researchers on sight. Demographic events were typically accurate to within a few days. The mean (\pm SE) interval between consecutive censuses of a given group was 3.0 ± 0.02 d ($n = 6,780$ censuses). We calculated monthly group size as the total number of individuals present in each social group on the first day of every month, and annual group size as the average of these monthly values for all months within the hydrological year (November–October). During the 11-y period covered by the present study, average annual group size varied fivefold across groups, ranging from 19.9 individuals to 103.4 individuals (mean \pm SE: 53.5 ± 2.98 individuals) (Fig. S3). Complete details on ABRP monitoring effort and data-collection protocols can be accessed online (<https://amboselibaboons.nd.edu>). All protocols adhered to the laws and guidelines of Kenya (Research Permit MOEST 13/001/C351 Vol. II) and were approved by the Princeton University Institutional Animal Care and Use Committee (IACUC 1547).

To account for differences in the number of days in each calendar month for all monthly measures, we considered ranging patterns only on days 1–28 of each month; data from the 29–31 d of each month were excluded from analyses. To maintain even sampling of group-monitoring effort, only months in which all five social groups were tracked for days 1–28 were included in analyses [i.e., months in which collars were deployed or retrieved midmonth in at least one of the five groups ($n = 12$), were excluded from all monthly analyses].

Environmental Predictors of Ranging Patterns and Physiology. Previous research has revealed that weather fluctuations affect the quantity and distribution of food resources for baboons (32, 45), the ability of baboons to travel efficiently (46), their thermoregulatory stress (47, 48), and their metabolic demands (49). Weather conditions have also been shown to affect female baboon physiology; Amboseli baboon females had higher fGC levels during the dry season and in hotter months (50). To control for environmental variables in evaluating the effects of group size on ranging patterns and stress physiology, we used daily meteorological records collected at our research camp to calculate total cumulative rainfall and average maximum daily temperature for each hydrological year and each month. We also calculated rainfall evenness (the spread of rainfall across the months of a given hydrological year) as a measure of the patterning of rainfall within a year. The spread of rainfall across months was measured using the Shannon diversity index (51, 52). For months with no rainfall, we substituted 1×10^{-6} mm of rain to obtain a natural logarithm. By this approach, high values indicate hydrological years in which rainfall was relatively even across months (i.e., more similar rainfall each month) and low values indicate hydrological years in which rainfall was relatively uneven across months (e.g., all rainfall in 1 mo at the extreme). For consistency with our monthly ranging measures, only data from days 1–28 were used in the monthly weather calculations.

Ranging Patterns. To analyze the annual ranging patterns of each social group, we used data on group locations recorded by ABRP observers between November 1, 1999 and October 31, 2010 (i.e., the 2000–2010 hydrological years), a time period during which our recording of locational data were standardized and no group fissions occurred. On observation days, observers used hand-held global positioning system (GPS) units (model eTrex and GPSMAP 76, Garmin International) to record half-hourly GPS locations of focal groups. Groups rarely traveled in areas that were inaccessible to observers; therefore, GPS data were not spatially biased to times/locations for which observers were able to follow the animals. Furthermore, baboons spend almost all of their day on the ground in the largely level habitat of Amboseli (53), thereby minimizing research complications potentially arising from a 3D component of space use if animals were arboreal (54).

For a 900-d subset of this 11-y study period, we used GPS collars (model G2110B, Advanced Telemetry Systems) to remotely monitor the full-day ranging patterns of the five study groups. Specifically, we collared a single individual at a time within each study group. We preferentially collared adult females because females remain in their natal groups throughout their lives, eliminating the risk of dispersal. Males were collared in only two instances when there were no suitable female candidates at the time of collar deployment (i.e., all adult females in a given group were pregnant or had dependent young). We programmed each individual's collar to record hourly locations during the portion of the day that baboons are active (0600–1900 hours). Baboons are usually resting between 1900 and 0600 hours the following morning, and spatial displacement is minimal during these hours. Using GPS collar data from 5,649 paired 1900 and 0600 hour readings, we found that baboons moved 16.8 ± 0.61 m (mean \pm SE) between 1900 and 0600 hours the following morning. Collar data were used for the calculation of monthly home ranges and average daily travel distances. Collars were deployed in three sequential 300-d rounds, a time duration based

upon our monitoring frequency, manufacturer calculations for expected battery life, and ABRP field testing of equipment (55). For logistical reasons, collar deployment and subsequent retrieval date varied slightly between groups. To avoid analytical challenges of asynchronous monitoring, data included in our analyses were limited to the time window during which all groups were collared (April 1, 2008 to August 31, 2010: 883 d). Additional details on GPS collar deployment and monitoring efforts are provided in Markham et al. (29).

Annual and monthly home range size. Accurately estimating home range area is a major challenge in space-use studies because no single estimator is appropriate in all settings (56). Here we used two techniques to delineate ranges at the annual and monthly timescales, respectively. We selected each technique to maximize the strengths of the locational datasets available (observer-recorded vs. remotely recorded GPS data). For quantification of all ranging patterns, we used ArcGIS 9.2 (Environmental Systems Resource Institute) with the Home Range Extension (57) and XTools (Data East).

To most reliably capture intergroup and interyear variability in annual home ranges, we used observer-recorded locational data to construct home ranges by the adjusted polygon method (58). For each group-hydrological year, we first created 95% minimum convex polygons (95% MCPs) using the floating mean approach (57). The MCP method constructs home ranges by connecting the outer locations to form a convex polygon (59–61); percent MCPs extend this technique to generate an MCP for a specified subset of locations, thus minimizing biases of outlier locations and occasional excursions (56). Next, we calculated the distribution of locational data relative to a grid of 250×250 m (0.0625 km^2) cells overlaid on the study area. Grid cells that were never visited by any of the five social groups in a given hydrological year were considered to contain unsuitable habitat for baboons. Finally, we adjusted the 95% MCP home ranges by removing grid cells coded as unsuitable for that hydrological year. This technique eliminated portions of the landscape that baboons were unlikely to occupy (58), thereby avoiding the major failing that most traditional MCP assessments incorporate: large areas that are never used (62–64).

For the monthly timescale, we used data acquired remotely from GPS collars to construct home ranges by the digitized polygon method (29, 62, 65). When using locational data with high temporal resolution, this method is advantageous because it makes use of the temporal sequence of all locational points collected, thereby recognizing autocorrelated observations as an intrinsic and relevant property of movement data (66, 67). We first created daily travel paths with straight-line displacement that linked all temporally sequenced GPS positions captured for a group. We then added a buffer width of 250 m to represent the group's "area of influence" around the travel path; this buffer measure incorporates an estimate of the average spread of the group (see ref. 29 for further justification). Finally, we merged the buffered daily travel paths within each month.

Daily travel distance. We calculated daily travel distance by summing the straight-line distances between successive GPS locations for all hourly locations captured by the GPS collars from 0600 to 1900 hours.

Evenness of space use. Following Struhsaker (31), we used the Shannon–Weiner diversity index to quantify each group's monthly ranging patterns as an index of grid-cell-utilization diversity. Time spent by each group in each 250×250 m grid cell (see above) was assessed as the proportion of the total monthly GPS locations acquired for that group that were within a particular grid cell. By this approach, high diversity indices indicate months of relatively even grid cell use; that is, groups used all portions of their home range with similar relative intensity in contrast to low diversity indices which indicate that groups biased space use to a subset of grid cells within their home range.

Glucocorticoid Levels. Fecal sample collection, storage, and extraction were as described previously (68, 69). In brief, immediately after collection of freshly deposited fecal samples from known individuals, these samples were mixed and placed in 95% ethanol and transported back to our research camp within 8 h (after behavioral observations for the day ended). The samples were kept refrigerated at the camp for no longer than 2 wk before being shipped to the University of Nairobi, where they were freeze-dried, then sifted to remove the vegetative matter, and stored at -20°C . After transport to Princeton University, 0.2 g of fecal powder was extracted into 2 mL 90% (vol/vol) methanol using a multipulse vortexer for 30 min. Following extraction, samples were further purified using a prepped Oasis cartridge (Waters) and stored at -20°C . The samples were then assayed for glucocorticoids by RIA (50, 70) (full laboratory protocols also available at <https://amboselibaboons.nd.edu/>). The primary antibody in the Corticosterone kit for rats and mice (ICN Diagnostics) cross-reacts with major cortisol metabolites present in baboon feces (71). Interassay coefficients of variation were 13.6% and 10.7% ($n = 49$), respectively, for a low and high control. Intra-assay coefficients of variation were below 6% for both the low and high

control (any duplicate above 15% was reassayed). The hormone results are expressed as nanogram per gram of dry feces.

We had a total of 10,163 fecal samples from 157 adult females over the 11-y study period. Because fecal samples were collected ad libitum, sample numbers were variable across females and months (mean = 1.8 samples per female per month, range 0–16; some females were not sampled in particular months). To reduce the effect of uneven sampling, we first calculated for each female an average fGC within each month, resulting in 5,636 monthly values (mean 36 monthly values per female, range 1–93); we then calculated a monthly fGC concentration for the entire group that was the mean across individuals of each individual's monthly mean. To test whether the monthly distance traveled predicted group fGC concentrations, we used the hormone data from April 2008–August 2010 to match the distance traveled dataset collected when all groups were simultaneously collared.

Time Spent Foraging. The proportion of time spent foraging was determined using point sampling for adult females at 1-min intervals within 10-min focal samples (72). At each minute interval, observers recorded the activity of the focal baboon, categorized into four exhaustive and mutually exclusive behaviors with the following hierarchy: feeding (including both stationary food processing and feeding while moving), moving while not feeding, socializing, or resting (43). Observers selected a focal baboon for observation by random rotation among all adult females within a given group; this random rotation ensured that, within groups, each female was observed for approximately the same length of time each month. To obtain the foraging variable for testing the hypothesized relationships to group size, we first pooled feeding and moving while not feeding to produce the variable foraging time in the present analyses, following Bronikowski and Altmann (52) and Alberts et al. (43). As described in Alberts et al. (43), time spent moving occurs primarily as the baboons move to and between food and water resources, and most baboon feeding occurs as a continuous, fluid combination of walking and feeding. Thus, we most accurately capture the amount of time that the baboons in this ecosystem invest in obtaining food by combining time spent feeding with time spent moving. We calculated the proportion of time spent foraging as the number of sample points (pooled across animals within a given time period) when individuals were in the activity relative to the total sample number of points for which any activity was recorded.

Statistical Analyses. Accounting for repeated observations of each social group, we used GEEs to test whether group size and environmental variables predicted ranging patterns, glucocorticoid concentrations, and time spent foraging. In all annual models, we considered three environmental predictor variables: cumulative rainfall, evenness of rainfall across months, and average maximum temperature. Monthly models included two environmental predictor variables: cumulative rainfall and average maximum temperature. To approach normality, we used an arcsin-square root transform for the proportion of time spent foraging, a log-transform for home range areas and glucocorticoid levels, and an inverse-transform for daily travel distances. For all GEEs, group ID was entered as a repeated measure to account for multiple measures of the same group, and temporal autocorrelation in sequential indices of the dependent variable was controlled for by a first-order autoregressive structure (73, 74). We selected the single best model using QIC, which compares the adequacy of several models and identifies the model that best explains the variance of the dependent variable as that with the lowest QIC value (75, 76). We used a linear regression to test whether monthly distance traveled predicted log-transformed fGC concentrations. All statistical tests were performed in SPSS 22.0 with a significance value set to 0.05.

ACKNOWLEDGMENTS. We thank the government of the Republic of Kenya; the Kenya Wildlife Services; the staff and wardens of Amboseli National Park; the Institute for Primate Research, National Museums of Kenya; the local communities of the Amboseli region; Ker & Downey Safaris; Tortilis Camp in Amboseli; Amboseli Baboon Research Project researchers for their contributions to data and fecal sample collection and dedication in the field: R. Mututua, S. Sayialel, J. K. Warutere, G. Marinika, B. Oyath, and I. Longida; T. L. Wango, V. K. Oudou, M. C. M. Simao, K. Epstein, and P. Chen for the fecal sample processing and analyses; N. Learn, L. Maryott, P. Onyango, N. Rubenstein, and K. Pinc for their invaluable database assistance; and I. Couzin, A. Dobson, D. I. Rubenstein, and M. Wikelski for providing helpful comments on an earlier draft of this manuscript. This study was supported in part by the American Society of Primatologists (A.C.M.); the Animal Behavior Society (A.C.M.); the International Primatological Society (A.C.M.); National Institute on Aging Grants P01-AG031719 and R01AG034513 (to S.C.A. and J.A.); National Science Foundation Grants IBN-0322613 (to J.A. and S.C.A.), IOS-0919200 (to S.C.A.), and (BCS-0851750 (to J.A. and A.C.M.); and Sigma Xi (A.C.M.).

1. Maynard Smith J, Szathmáry E (1995) *The Major Transitions of Evolution* (Oxford Univ Press, Oxford, UK).
2. Wilson EO (1975) *Sociobiology: The New Synthesis* (Harvard Univ Press, Cambridge, MA).
3. Alexander RD (1974) The evolution of social behavior. *Annu Rev Ecol Syst* 5:325–383.
4. Rubenstein DI, Sundareshan SR, Fishchoff I, Saltz D (2007) in *Exploration into the Biological Resources of Mongolia*, eds Stubbe A, Kaczynski P, Wesche K, Samjaa R, Stubbe M (Martin Luther University Halle-Wittenberg, Halle, Germany), Vol 10, pp 159–176.
5. Krause J, Ruxton GD (2002) *Living in Groups* (Oxford Univ Press, Oxford).
6. Kerth G, Ebert C, Schmidtke C (2006) Group decision making in fission-fusion societies: Evidence from two-field experiments in Bechstein's bats. *Proc Biol Sci* 273(1602): 2785–2790.
7. Terborgh J (1983) *Five New World Primates: A Study in Comparative Ecology* (Princeton Univ Press, Princeton).
8. Rubenstein DI, Wrangham RW (1986) Socioecology: Origins and trends. *Ecological Aspects of Social Evolution*, eds Rubenstein DI, Wrangham RW (Princeton Univ Press, Princeton), pp 3–17.
9. Snaith TV, Chapman CA (2008) Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. *Behav Ecol* 19(6):1289–1296.
10. Snaith TV, Chapman CA, Rothman JM, Wasserman MD (2008) Bigger groups have fewer parasites and similar cortisol levels: A multi-group analysis in red colobus monkeys. *Am J Primatol* 70(11):1072–1080.
11. Altmann J, Alberts SC (2003) Variability in reproductive success viewed from a life-history perspective in baboons. *Am J Hum Biol* 15(3):401–409.
12. Pollard KA, Blumstein DT (2008) Time allocation and the evolution of group size. *Anim Behav* 76(5):1683–1699.
13. Chapman CA, Chapman LJ (2000) in *On the Move: How and Why Animals Travel in Groups*, eds Boinski S, Garber PA (Univ of Chicago Press, Chicago), pp 24–42.
14. Janson CH, van Schaik CP (1988) Recognizing the many faces of primate food competition: Methods. *Behaviour* 105(1/2):165–186.
15. Wrangham RW, Gittleman JL, Chapman CA (1993) Constraints on group size in primates and carnivores: Population density and day-range as assays of exploitation competition. *Behav Ecol Sociobiol* 32(3):199–209.
16. Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31(2):295–311.
17. van Schaik CP (1983) Why are diurnal primates living in groups? *Behaviour* 87(1):120–144.
18. Stevenson PR, Castellanos MC (2000) Feeding rates and daily path range of the Colombian woolly monkeys as evidence for between- and within-group competition. *Folia Primatol (Basel)* 71(6):399–408.
19. Pride RE (2005) Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behav Ecol* 16(3):550–560.
20. Raoof SA, Smith LC, Brown MB, Wingfield JC, Brown CR (2006) Glucocorticoid hormone levels increase with group size and parasite load in cliff swallows. *Anim Behav* 71(1):39–48.
21. McEwen BS (1998) Protective and damaging effects of stress mediators. *N Engl J Med* 338(3):171–179.
22. Sapolsky RM (2004) Social status and health in humans and other animals. *Annu Rev Anthropol* 33:393–418.
23. Sapolsky RM (2001) in *Coping with the Environment: Neural and Endocrine Mechanisms*, eds McEwen BS, Goodman HM, Handbook of Physiology (Oxford Univ Press, Oxford), Vol IV, pp 517–532.
24. Estes RD (1991) *The Behavior Guide to African Mammals* (Univ of California Press, Berkeley).
25. Grove M (2012) Space, time, and group size: A model of constraints on primate social foraging. *Anim Behav* 83(2):411–419.
26. Norton GW, Rhine RJ, Wynn GW, Wynn RD (1987) Baboon diet: A five-year study of stability and variability in the plant feeding and habitat of the yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. *Folia Primatol (Basel)* 48(1-2):78–120.
27. Altmann SA (1998) *Foraging for Survival: Yearling Baboons in Africa* (Univ of Chicago Press, Chicago).
28. Altmann SA, Altmann J (1970) *Baboon Ecology* (Univ of Chicago Press, Chicago).
29. Markham AC, Guttal V, Alberts SC, Altmann J (2013) When good neighbors don't need fences: Temporal landscape partitioning among baboon social groups. *Behav Ecol Sociobiol* 67(6):875–884.
30. Markham AC, Alberts SC, Altmann J (2012) Intergroup conflict: Ecological predictors of winning and consequences of defeat in a wild primate population. *Anim Behav* 82(2):399–403.
31. Struhsaker TT (1974) Correlates of ranging behavior in a group of red colobus monkeys (*Colobus badius tephrosceles*). *Am Zool* 14(1):177–184.
32. Barton RA, Whiten A, Strum SC, Byrne RW, Simpson AJ (1992) Habitat use and resource availability in baboons. *Anim Behav* 43(5):831–844.
33. Anonymous (1992) *Primary Productivity of Grass Ecosystems of the Tropics and Sub-Tropics* (Chapman and Hall, London).
34. Gillespie TR, Chapman CA (2001) Determinants of group size in the red colobus monkey (*Procolobus badius*): An evaluation of the generality of the ecological-constraints model. *Behav Ecol Sociobiol* 50(4):329–338.
35. Ganas J, Robbins MM (2005) Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: A test of the ecological constraints model. *Behav Ecol Sociobiol* 58(3):277–288.
36. Teichroeb JA, Sicotte P (2009) Test of the ecological-constraints model on ursine colobus monkeys (*Colobus vellerosus*) in Ghana. *Am J Primatol* 71(1):49–59.
37. Seyfarth RM, Cheney DL, Marler P (1980) Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Anim Behav* 28(4):1070–1094.
38. Cheney DL, et al. (2004) Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *Int J Primatol* 25(2):401–428.
39. Sharman M, Dunbar RIM (1982) Observer bias in selection of study group in baboon field studies. *Primates* 23(4):567–573.
40. Aureli F, et al. (2008) Fission-fusion dynamics: New research frameworks. *Curr Anthropol* 49(4):627–654.
41. Sibly R (1983) Optimal group size is unstable. *Anim Behav* 31(3):947–948.
42. Alberts SC, Altmann J (2012) The Amboseli Baboon Research Project: Themes of continuity and change. *Long-Term Field Studies of Primates*, eds Kappeler PM, Watts DP (Springer, Berlin), pp 261–287.
43. Alberts SC, et al. (2005) Seasonality and long-term change in a savanna environment. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*, eds Brockman DK, van Schaik CP (Cambridge Univ Press, Cambridge, UK), pp 157–195.
44. Altmann J, Alberts SC, Altmann SA, Roy SB (2002) Dramatic change in local climate patterns in the Amboseli basin, Kenya. *Afr J Ecol* 40(3):248–251.
45. Byrne RW, Whiten A, Henzi SP, McCulloch FM (1993) Nutritional constraints on mountain baboons (*Papio ursinus*): Implications for baboon socioecology. *Behav Ecol Sociobiol* 33(4):233–246.
46. Stelzner JK (1988) Thermal effects on movement patterns of yellow baboons. *Primates* 29(1):91–105.
47. Funkhouser GE, Higgins EA, Adams T, Snow CC (1967) The response of the savannah baboon (*Papio cynocephalus*) to thermal stress. *Life Sci* 6(15):1615–1620.
48. Brain C, Mitchell D (1999) Body temperature changes in free-ranging baboons (*Papio hamadryas ursinus*) in the Namib Desert, Namibia. *Int J Primatol* 20(4):585–598.
49. Henzi SP, Byrne RW, Whiten A (1992) Patterns of movement by baboons in the Drakensberg mountains: Primary responses to the environment. *Int J Primatol* 13(6):601–629.
50. Gesquiere LR, et al. (2008) Coping with a challenging environment: Effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons (*Papio cynocephalus*). *Horm Behav* 54(3):410–416.
51. Bronikowski A, Webb C (1996) Appendix: A critical examination of rainfall variability measures used in behavioral ecology studies. *Behav Ecol Sociobiol* 39(1):27–30.
52. Bronikowski AM, Altmann J (1996) Foraging in a variable environment: Weather patterns and the behavioral ecology of baboons. *Behav Ecol Sociobiol* 39(1):11–25.
53. Altmann J, Samuels A (1992) Cost of maternal care: Infant-carrying in baboons. *Behav Ecol Sociobiol* 29(6):391–398.
54. Milton K, May ML (1976) Body weight, diet and home range area in primates. *Nature* 259(5543):459–462.
55. Markham AC, Altmann J (2008) Remote monitoring of primates using automated GPS technology in open habitats. *Am J Primatol* 70(5):495–499.
56. Kenward RE (2001) *A Manual for Wildlife Radio Tagging* (Academic, San Diego).
57. Rodgers AR, Kie JG (2011) *HRT: Home Range Tools for ArcGIS* (Centre for Northern Forest Ecosystem Research: Ontario Ministry of Natural Resources, Ontario, Canada).
58. Grueter EC, Li D, Ren B, Wei F (2009) Choice of analytical method can have dramatic effects on primate home range estimates. *Primates* 50(1):81–84.
59. Hayne DW (1949) Calculation of size of home range. *J Mammal* 30(1):1–18.
60. Harris S, et al. (1990) Home-range analysis using radio-tracking data—A review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev* 20(2-3):97–123.
61. White GC, Garrott RA (1990) *Analysis of Wildlife Radio-Tracking Data* (Academic, San Diego).
62. Ostro LET, Young TP, Silver SC, Koontz FW (1999) A geographic information system method for estimating home range size. *J Wildl Manage* 63(2):748–755.
63. Powell R (2000) Animal home ranges and territories and home range estimators. *Research Techniques in Animal Ecology: Controversies and Consequences*, eds Boitani L, Fuller T (Columbia Univ Press, New York), pp 65–110.
64. Burgman MA, Fox JC (2003) Bias in species range estimates from minimum convex polygons: Implications for conservation and options for improved planning. *Anim Conserv* 6(1):19–28.
65. Pulliainen E (1984) Use of the home range by pine martens (*Martes martes* L.). *Acta Zool Fenn* 171:271–274.
66. Nathan R, et al. (2008) A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci USA* 105(49):19052–19059.
67. Boyce MS, et al. (2010) Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. *Philos Trans R Soc Lond B Biol Sci* 365(1550):2213–2219.
68. Khan MZ, Altmann J, Isani SS, Yu J (2002) A matter of time: Evaluating the storage of fecal samples for steroid analysis. *Gen Comp Endocrinol* 128(1):57–64.
69. Lynch JW, Khan MZ, Altmann J, Njahira MN, Rubenstein N (2003) Concentrations of four fecal steroids in wild baboons: Short-term storage conditions and consequences for data interpretation. *Gen Comp Endocrinol* 132(2):264–271.
70. Gesquiere LR, Onyango PO, Alberts SC, Altmann J (2011) Endocrinology of year-round reproduction in a highly seasonal habitat: Environmental variability in testosterone and glucocorticoids in baboon males. *Am J Phys Anthropol* 144(2):169–176.
71. Wasser SK, et al. (2000) A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. *Gen Comp Endocrinol* 120(3): 260–275.
72. Altmann J (1974) Observational study of behavior: Sampling methods. *Behaviour* 49(3):227–267.
73. Brockwell PJ, Davis RA (1991) *Time Series: Theory and Methods* (Springer, New York), 2nd Ed.
74. Box GEP, Jenkins GM, Reinsel GC (2008) *Time Series Analysis: Forecasting and Control* (John Wiley and Sons, New York).
75. Pan W (2001) Akaike's information criterion in generalized estimating equations. *Biometrics* 57(1):120–125.
76. Tsai M-Y, Wang J-F, Wu J-L (2011) Generalized estimating equations with model selection for comparing dependent categorical agreement data. *Comput Stat Data Anal* 55(7):2354–2362.