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Mean reversion over time to the optimal group size in a colobus monkey

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Abstract

The evolution of group living is a topic of enduring interest. While grouping has multiple benefits for individuals, such as decreased predation risk or an increased ability to find and defend food, it also leads to costs like within-group food competition and disease risk. Theorists have long argued that the balance of these costs and benefits should lead to a species-specific optimal group size for each set of environmental conditions where fitness is maximized, but this has proven difficult to test in the wild. No study has yet shown that group sizes within an animal population gravitate repeatedly to an optima over time. Here we test this hypothesis on a population of Rwenzori Angolan colobus monkeys in Uganda that live in a multilevel society with core units that are socially stable and spatially distinct.

Using three independent measures on eight years of data we show that core units show significant reversion back to a population-level attractor at a size of 10.02-10.50. We then assess whether there is support for better infant survival within this size range and find that infant survival peaks at the hazard minimizing size of 10.23-10.65. We thus provide robust support for optimal group size theory.

Main

Group living has been argued to be among the most important evolutionary transitions¹. Several animal lineages, including our own, evolved to be gregarious, but this has both benefits and costs². Major advantages to grouping include decreased predation risk, due primarily to dilution effects and better predator detection³, and feeding benefits, like increased discovery of resources because of shared ecological knowledge⁴, and group defence of territories⁵. The primary disadvantages of grouping are a concomitant rise in within-group scramble feeding competition with each additional group member⁶ and an increased likelihood of disease spread⁷. Since the 1960s, theorists have argued that the balance of costs and benefits should lead to a species-specific optimal group size for each set of environmental conditions where fitness is maximized⁸.

In 2002, Krause and Ruxton² contended that optimal group sizes should be common in nature and lamented the lack of empirical studies testing this hypothesis. The only convincing evidence at that time was that, in two large predators, hunting group sizes that optimize energy intake per hunter had been found for certain prey species (but not others)^{9,10}. In the intervening 25 years, some tantalizing support for optimal group sizes

have been found. Experimental manipulation of northern bobwhite (*Colinus virginianus*) coveys in outdoor plots demonstrated that small and large coveys had lower survival and mid-sized groups maximized survival and minimized energy expenditure¹¹. Evidence suggesting that mid-sized groups are the least energetically costly has been demonstrated in several wild long-term primate study systems, where quadratic U-shaped distributions are seen between group size and ranging variables¹²⁻¹⁴ or glucocorticoid (stress) levels^{13,15,16}. While in a gregarious terrestrial bird species (vulturine guinea fowl, *Acryllium vulturinum*), it was found that individuals in mid-sized groups used larger ranging areas than those in small or large groups and the resulting access to resources led to greater reproductive success¹⁷. However, up to this point, no study within a wild animal population has shown that groups revert back to an optimal size over time when they drift away from it.

There are several reasons that the optimal group size paradigm has proven difficult to test empirically. First, researchers often study too few groups of large, charismatic mammal species where manipulations to group size are not ethical². Second, there may be a bias towards studying large groups to increase sample size, leading to a dearth of comparative research on smaller groups¹³. Third, research studies need to be of long duration on many groups to capture pull over time towards an optimal group size. Fourth, in nature, group sizes may typically be greater than the optimal¹⁸. This was predicted by Sibly¹⁸ because groups close to optimal should be attractive to joiners, who do better by integrating into them than by being alone, but who inherently drive group size up and decrease the fitness benefits to all members. Giraldeau and Caraco^{19,20} and others^{21,2,22} expanded on this by noting that relationships among members of a group (e.g., kinship,

dominance) and the difficulty of dispersing and/or controlling immigration can prevent adjustments in group size that would bring it closer to optimum. To complicate matters, within the same group, males and females or differently ranked individuals may have different group sizes or compositions where their fitness is maximized²³⁻²⁶ and neighbouring groups may have variability in home range quality that select for different optimal sizes⁶.

Multilevel societies, where animals form distinct tiers of social groupings, are ideal to empirically test the optimal group size paradigm¹⁷. Core units, the first, base level of these societies, are numerous, socially stable, and spatially distinct and associate into higher-level tiers²⁷. Core units often share a home range, which allows testing for optimal group size without the confound of differing resource availability. Here, we examine whether core units within a band of Rwenzori Angolan colobus monkeys (*Colobus angolensis ruwenzorii*) in Uganda (Fig. 1a,b,f) show mean reversion to an optimal size over time and whether infant survival is maximized at this unit size. This species forms multilevel societies of at least three tiers (Fig. 1e). Core units fission and fuse to within about 20 m throughout the day, forming preferential associations called clans, which share a home range in a band tier^{28,29} (Fig. 1c,d). The Rwenzori colobus social structure is unique relative to other primate multilevel societies in that core units are either one-male, multifemale (OMUs) or multimale, multifemale (MMUs)^{27,30} (Table S1), which leads to high variability in core unit size (Range: 4-25). Further, since both sexes typically disperse from the natal core unit, but males tend to stay within the band and disperse between core units^{28,31}, there is a high degree of tolerance among core units and more flexibility in controlling core unit size than in a typical primate multilevel society made up of OMUs,

where one male or a kin-group of females aggressively control immigration into the unit. In two separate papers on our study band, ranging areas¹⁴ and female glucocorticoid levels¹⁶ have been shown to best fit quadratic U-shaped distributions relative to core unit size, and in both, the bottoms of the curve indicated that a size of 10-12 is energetically ideal; thus, providing a target for investigation of mean reversion and infant survival in this study.

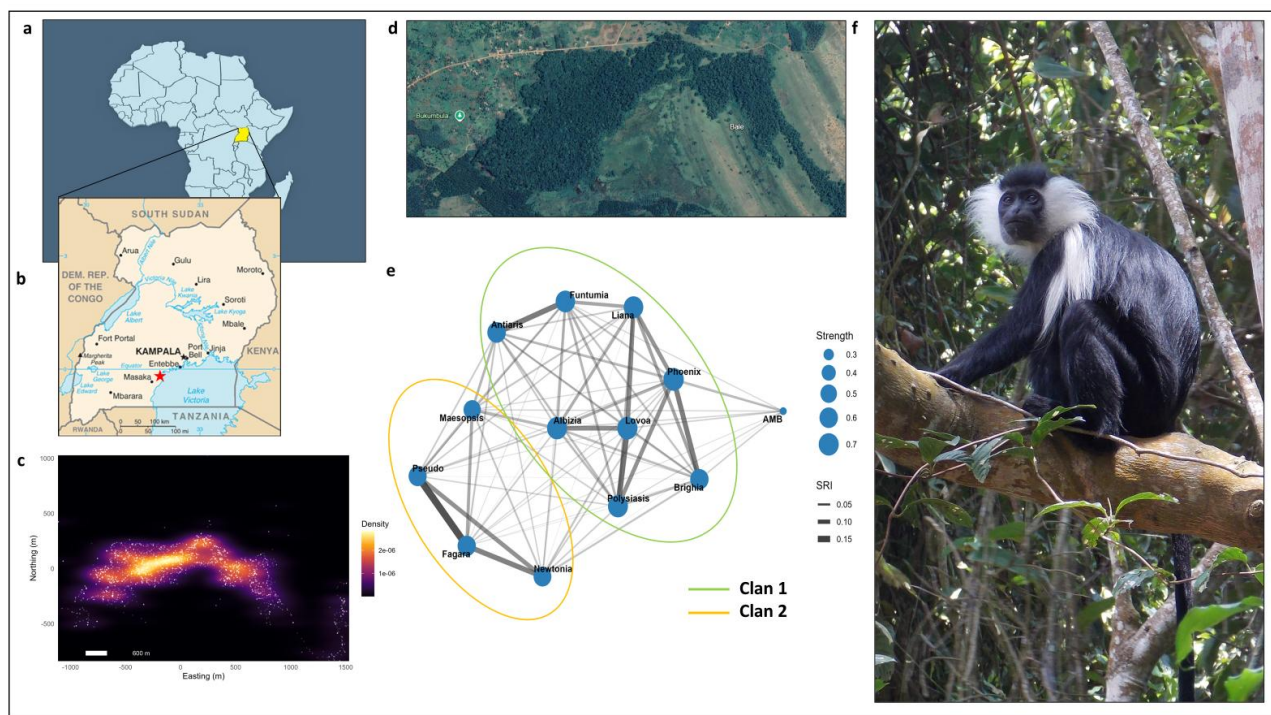


Fig. 1 **a**, Location of Uganda within Africa. **b**, Location of the study site, Nabugabo, indicated by the red star, within Uganda. **c**, A heat map showing overlapping GPS ranging data points for the 11 core units included in the analyses from the study band of Rwenzori Angolan colobus (*Colobus angolensis ruwenzorii*) at Nabugabo, demonstrating their shared home range. GPS points (N = 5,242) were collected every 15-min. during full-day follows of one core unit per day over a two-year period (2017-2019). **d**, The forest fragment where the study band resides at Nabugabo (downloaded from Google Earth, Aug. 4, 2026). **e**, A between-unit social network of the core units within the study band at the beginning of the study (2018-2019) calculated using Simple Ratio Indices (SRI) between all dyads. Scan samples were recorded of the ID of core units within 50 m of the focal unit at 2-hr. intervals during full-day follows. These data were used to calculate $SRI = N_{AB} / (N_A + N_B)$, where the number of times two core units were in association during scans is divided by the total number of scans where either was present. Note that though there was an All-Male Band (AMB) present at this time, they were not included in the analyses because they are ephemeral. Similarly, unit Antiaris was excluded from mean reversion analyses because they transferred to a neighboring band in 2020 for one month and in 2024

seemingly permanently. Circles show the clan associations where the SRI breakpoint was 0.05^{28,31}. **f**, Photo of a female Rwenzori Angolan colobus at Nabugabo, Uganda (credit: Edward Mujjuzi).

Over time group sizes are mean reverting

We used data collected over eight years from 11 core units where we had counts of individuals in each unit each month ($N = 1,034$ unit months). We used panel unit-root tests to determine if core unit sizes (Fig. 2) revert over time and test the null hypothesis that each size series wanders randomly (i.e., contains a unit root). The Levin-Lin-Chu Unit-Root Test (LLC), which assumes a common reversion rate across core units, did not reject this null in the intercept-only specification (statistic = -1.277, $p = 0.101$), but the Im-Pesaran-Shin Test (IPS), which allows each core unit to revert at its own rate, did reject the null ($Wtbar = -2.07$, $p = 0.019$). Results were robust to including a deterministic trend for each test (LLC statistic = -2.332, $p = 0.010$; IPS $Wtbar = -2.083$, $p = 0.019$), indicating the reversion is not an artifact of the mean specification. Together these tests show that core unit size is mean reverting in this population with reversion rates varying across units.

The speed of the reversion is slow but persistent

We estimated the speed of core unit reversion with a dynamic autoregressive panel (AR(1)) model, which regresses the monthly change in size on the lagged size across all unit-months. This demonstrated that the monthly change in core unit size depends negatively on current size, in that larger units tend to shrink and smaller units to grow (Table 1). The uncorrected within-unit autoregressive coefficient was 0.926, but because this estimator is downward-biased in dynamic panels (Nickell bias), we applied a Dhaene–Jochmans half-

panel jackknife correction, which raised the coefficient to 0.986. This corrected estimate implies gradual reversion by core units, with a deviation from equilibrium halving on a timescale of roughly four years (half-life of 47.0 months), rather than the 9.0 months implied by the uncorrected coefficient.

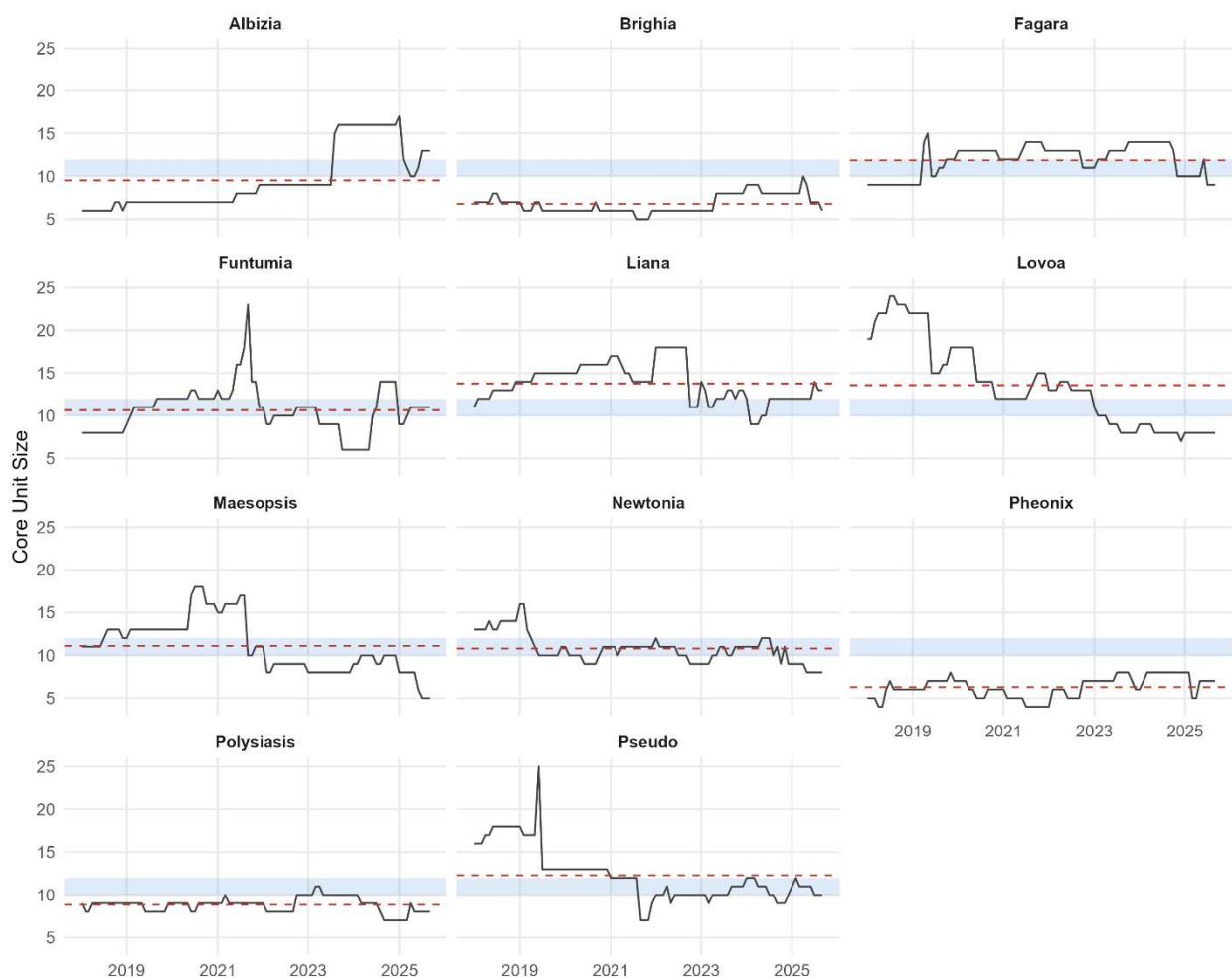


Fig. 2 Monthly variation in core unit size from Jan. 2018 – Dec. 2025 for each of the 11 Rwenzori Angolan colobus (*Colobus angolensis ruwenzorii*) units at Nabugabo, Uganda (N = 1,034 unit months) included in the panel regression. The blue bands show the hypothesized target range of 10-12 individuals from previous research on ranging areas¹⁴ and glucocorticoids¹⁶. The red dashed lines show each unit's mean size over time.

Table 1. The slope of change in core unit size per month and per year for Rwenzori Angolan colobus monkeys (*Colobus angolensis ruwenzorii*) at Nabugabo, Uganda

Core Unit	Mean Size	Slope (per month)	Slope (per year)
<i>Above the 10-12 target size - all showing declining slopes</i>			
Liana	13.8	-0.028	-0.337
Lova	13.6	-0.171	-2.060
Pseudo	12.3	-0.086	-1.030
<i>Within the 10-12 target size - mixed slopes</i>			
Fagara	11.9	0.021	0.256
Maesopsis	11.1	-0.076	-0.908
Newtonia	10.8	-0.038	-0.461
Funtumia	10.7	0.0004	0.005
<i>Below the 10-12 target size - all showing positive (growing) slopes – except one*</i>			
Brighia	6.8	0.018	0.214
Pheonix	6.3	0.020	0.238
Polysiasis*	8.8	-0.003	-0.035
Albizia	9.5	0.107	1.290

*Although below the 10-12 target, core unit Polysiasis has flat slopes indicating little to no change in size.

The group size equilibrium is just over 10

We located the equilibrium toward which core unit sizes revert to using three independent estimators that rest on different assumptions. First, we used a beta-convergence panel regression model with pooled data, which was significant for absolute convergence to a common equilibrium (Est. = -0.046, SE = 0.012, p = 0.0002) and calculated a pooled long-run mean ($\alpha/(1-\beta)$) at a core unit size of 10.17 (95% CI 8.82-11.52). The beta-convergence model was then run as a conditional model with unit-level fixed effects testing if each unit is reverting back to its own equilibrium, which was also significant (Est. = -0.074, SE = 0.024, p = 0.002). The Mean-Group estimator, which averages unit-specific long-run means and so permits heterogeneous equilibria, gave a target core unit size of 10.02 (95% CI 8.63–11.42). Finally, the simple between-unit mean of unit means was 10.50 (95% CI 9.04–11.97). Thus, all three metrics converge near 10 with overlapping confidence intervals and

all fall within or overlap the 10–12 range hypothesized from previous work (Fig. 3a)^{14,16}. A poolability test did not reject a common intercept across units ($F_{10,1000} = 1.50$, $p = 0.135$), consistent with a shared equilibrium. But notably, the Mean-Group estimate, which does not assume a common equilibrium, returned essentially the same value. The equilibrium of ≈ 10 is therefore best interpreted as a population-level attractor.

Infant survival is higher in optimally sized groups

The demographic attractor of ≈ 10 coincided with the core unit size that maximised infant survival (Fig. 3b). In a time-varying Cox proportional-hazards model based on 77 infants (up to three years of age) from 40 mothers in 12 core units, where 35 infant deaths had occurred, infant mortality was U-shaped with core unit size (quadratic term: Coef. = 0.031, SE = 0.013, $p = 0.015$) and was minimised near a unit size of 10.65 and elevated in both smaller and larger units (Fig. S1). This effect was robust to clustering by core unit ($N = 12$ clusters, quadratic term: Coef. = 0.031, SE = 0.013, $p = 0.031$) and by mother ($N = 40$ clusters, quadratic term: Coef. = 0.031, SE = 0.013, $p = 0.019$) and to a unit-level frailty term (quadratic term: Coef. = 0.042, SE = 0.015, $p = 0.005$). The frailty model gave a hazard-minimizing core unit size of 10.23. The population size toward which units demographically revert (≈ 10) therefore falls within the range that maximizes infant survival (≈ 10 –12; Fig. 3b shows infant survival to 12 months; Fig. S2 shows infant survival to 24 months), providing a selective basis for the demographic attractor.

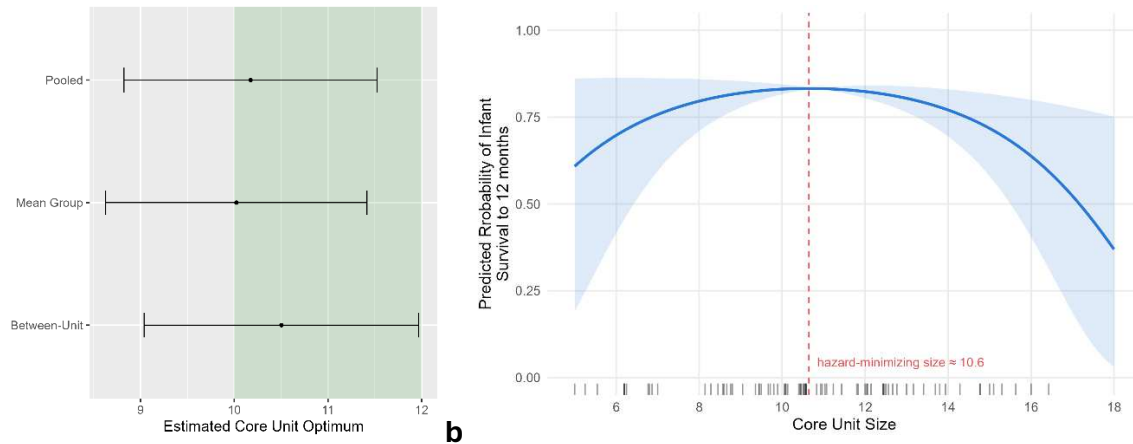


Fig. 3 a, The optimum core unit size estimated by three different methods with their 95% confidence intervals. Top, the pooled long-run mean, middle, the Mean-Group estimator, which averages unit-specific long-run means and permits heterogeneous equilibria, and bottom, the between-unit mean of unit means. The green band shows that fitness band of 10-12 predicted by previous work^{14,16}. **b**, Quadratic Cox model showing the predicted probability of an infant surviving to 12 months if it experienced a constant core unit size for Rwenzori Angolan colobus monkeys (*Colobus angolensis ruwenzorii*) at Nabugabo, Uganda. Data are from 77 infants born to 40 mothers in 12 core units. The shaded band shows 95% coefficient uncertainty and is wider at the extremes because estimates are based on fewer infants. Ticks mark show individual infants at their mean core unit size.

Discussion

Our results demonstrate, for the first time, mean reversion towards an optimal group size that maximizes infant survival in a wild animal population. In the Nabugabo Rwenzori Angolan colobus, there is population-level attraction over time to a target core unit size of ≈ 10 . Although, unit-specific long-run means were scattered (with only 5 of 11 core units falling inside the target indicated by previous work^{14,16} of 10–12), the Mean-Group average is robust to this scatter. The wide spread of observed unit sizes (6.3–13.8) thus reflects units observed at different points along their approach to a common central tendency, together with between-unit variation, rather than sustained divergence. Our Cox proportional-

209 hazard models demonstrate that infant survival is better at the size to which core units
210 revert to over time, providing a selective mechanism for this reversion.

211 Exactly why infant mortality is greater in smaller and larger core units in the
212 Nabugabo population needs to be investigated further. Theory would predict that small
213 units are suffering greater rates of predation³. While there are several predatory species in
214 the forest where the colobus reside³², we have rarely observed predatory attacks, so it is
215 difficult to assess if small units are targeted more. Additionally, because the multilevel
216 society allows core units to cluster in space (Fig. 1c,e), from a functional point-of-view,
217 small units can easily become part of a much larger group where inter-unit communication
218 warns others of any present threat³³.

219 When infants disappear, in the vast majority of cases, we do not know the cause of
220 death³⁴. However, we do know that infant mortality is increased in the months after male
221 immigration³⁴ and that males are more attracted to, and more likely to immigrate into, core
222 units with many females³⁵. Thus, a plausible reason for increased infant mortality in larger
223 core units could be male immigration. Our work has revealed that infants often die several
224 months after new males immigrate³⁴, a pattern that does not implicate high rates of
225 infanticide by males, because in primates infanticidal attacks tend to occur immediately
226 upon male immigration^{e.g.,36-38}. In Rwenzori colobus, former resident male(s) also emigrated
227 in the months following new male immigration. These former residents are the most likely
228 sires of the infants present and also provide a caregiving role in this species³⁹, so the loss of
229 invested caregivers may be the reason for infant death after changes to the adult male
230 composition of core units³⁴.

It is notable that previous work demonstrated that core units that are outside of the mid-sized optimum expend more energy in travel¹⁴ and that females within these units have higher fecal glucocorticoid levels¹⁶. In the case of larger core units, greater travel and more stress are likely indicative of higher levels of within-group scramble competition for food⁶, which has been previously demonstrated in this population¹⁶. Our infant data set included infants up to three years after birth. Weaning in this population is estimated at about 16 months of age³⁴, so weaned infants were included that would have needed to compete for food with many larger, more experienced individuals in large core units. This certainly could have contributed to greater infant mortality in these groups. For small core units though, the reasons for greater travel¹⁴ and higher female glucocorticoids¹⁶ are still opaque. We tested the idea that small core units are low-ranking and thus being displaced from high-quality food patches by larger units, but this was not supported⁴⁰. Some of the highest-ranking units in our study band were small⁴⁰, so why infants are dying at higher rates in these groups remains mysterious.

We were able to demonstrate mean reversion to an optimal group size in our study population because it is a multilevel society and thus allowed us to avoid some of the common pitfalls that make optimal group size theory so difficult to test^{2,13,18-22}. We were able to follow many groups over a long period of time, that represent the full breadth of sizes that this species demonstrates, and that shared a home range (Fig. 1c,d) and thus allowed the confound of differing resource availability to be controlled for. Intriguingly, we did not find support for Sibly's supposition that in nature group sizes should typically be greater than the optimal¹⁸. Indeed, our between-unit mean of unit means was 10.50 for the

eight-year study period, which is almost exactly the hazard-minimizing size where our analyses showed the best infant survival (10.23-10.65). We suggest that a larger “Sibly-size”², where groups are usually above optimal, may not be an issue for Rwenzori colobus because they can control group sizes more easily than many other species; both sexes can disperse from the natal core unit and both can disperse secondarily, dispersal is often in parallel, where several individuals move together^{28,31}, and core units have been observed to split and merge, although rarely³⁵. This extreme flexibility may also be possible because Rwenzori colobus are folivores and units share a home range, so there is little selective pressure to stay with kin to aid one another in food defense⁵. Nonetheless, it is still probable that there is between-individual variation in preferred group sizes or compositions (e.g., where the fitness of the sexes or of differently ranked individuals is maximized)²³⁻²⁶ and this is what leads to the variation that we see around the optimal and the slow reversion time.

Methods

Study Site and Subjects

We study Rwenzori Angolan colobus monkeys (*Colobus angolensis ruwenzorii*) on the west side of Lake Nabugabo, Masaka District, Uganda (0° 22' - 12° S and 31° 54' E, elevation of 1,134 - 1167 m a.s.l.) (Fig. 1a,b). The landscape is a mix of primary and secondary forest fragments, seasonally flooded forests, papyrus swamp, grassland, farmer's fields, tourist camps, and two villages⁴¹ (Fig. 1d). There are two rainy seasons annually from February to

May and September to November, with an average annual rainfall from 2017-2023 of 1,217 mm (range: 953-1,477 mm) and mean annual temperature of 21.9°C (21.6-22.2°C)³⁴.

We began habituating the study band (TR band) in 2015 and since 2017 we have recognized all individuals and understood the unique multilevel society²⁸. The core units within TR band share a forest fragment of ~1.4 km² (Fi. 1c,d) that is partly made up by the Manwa Forest Reserve¹⁴ and their range abuts that of two other unhabituated bands. Over the course of the study, TR band has been made up of 12-16 core units at any one time, that preferentially cluster into two clans (Fig. 1e). All-male units are only sometimes present in this band. Core unit composition within the band is >50% multi-male, multi-female and <50% one-male, multi-female (Table S1).

Data Collection

The data used for this study were collected during weekly demographic censuses that we have conducted since 2017, when we first identified all the monkeys in TR band, and during our routine full day follows, where one core unit is followed as the focal (typically N = 24 days per month). In weekly censuses, each core unit is contacted to count all visible individuals to track any births, deaths, immigrations or emigrations; these counts are further confirmed during full day follows. Here, to assess mean reversion in unit size, we utilize these data as monthly counts for 11 bisexual core units from January 2018 to December 2025 (N = 1,034 unit months). We censored the first year of data to ensure that we knew each individual well and we chose to include only those 11 core units that stayed within TR band for the entire duration of the study to maximize the timeline of changes in

their size. We did not utilize counts of core units that formed or dissolved during the study (N = 6), or those that transferred for periods of time to a neighboring band (N = 2).

To assess the impact of core unit size on infant survival, we used data on survival outcomes for 77 infants up to 3 years of age. These infants were born in 12 core units to 24 mothers from October 2017 to August 2023, and the dataset included 35 deaths. Infant birth and death dates were estimated as the mid-point between when the core unit was last seen with or without an infant and the day of observation of the missing or new infant (unless it was clear that the infant had been born that day because it was still wet with umbilical cord attached). Mean error in infant birth dates was 9.5 days (range: 0-47 days, N = 77) and for infant death dates it was 15.0 days (range: 0-52.5 days, N = 35). Core unit size was recorded monthly over the course of infants' lives up to three years. If the core unit size changed during a month, for that month we used the size that the core unit was for the majority of the month (over half). Weaning is estimated to occur when infants are about 17 months of age in this population¹⁶. All infant disappearances were treated as deaths because pre-weaned infants could not survive without their mothers, and dispersal by a lone infant, before the age of three years, to a core unit outside our study band where we could not track them is highly unlikely (unpubl. data).

Statistical Analyses

We conducted all analyses in R⁴² and plotted graphs with the tidyverse⁴³, igraph⁴⁴, and ggplot2⁴⁵ packages. We assessed mean reversion in core unit size, the speed of reversion, slopes of change, and equilibrium unit sizes using the packages tidyverse⁴³, plm⁴⁶, lmtest⁴⁷,

sandwich⁴⁸, and dplyr⁴⁹. We examined the impact of core unit size on infant survival using the readxl⁵⁰, dplyr⁴⁹, and survival⁵¹ packages. Statistics were two-tailed and an alpha level of ≤ 0.05 was considered significant.

Panel unit-root tests

To test whether the monthly core unit size series were mean-reverting rather than following a random walk we used two panel unit-root tests. The Levin–Lin–Chu (LLC) test assumes a common autoregressive reversion rate across units⁵², whereas the Im–Pesaran–Shin (IPS) test fits a separate augmented Dickey–Fuller regression to each unit and averages the resulting statistics, allowing units to revert at different rates⁵³. We ran each test with unit-specific intercepts and, separately, with unit-specific intercepts plus a deterministic trend. We selected lag orders using Akaike Information Criterion (AIC). As a robustness check, we also assessed cross-unit dependence, which was weak and compositional (mean pairwise $r \approx 0$), so a second-generation cross-sectionally augmented IPS test (CIPS)⁵⁴ yielded the same conclusion.

Reversion speed

We estimated within-unit reversion speed from a fixed-effects first-order autoregressive model ($\text{Size}_{it} = \alpha_i + \beta \text{Size}_{i,t-1} + \varepsilon_{it}$) fitted by the within estimator, with core unit fixed effects removing between-unit differences in mean size. We clustered standard errors by core unit using the Arellano heteroskedasticity- and autocorrelation-consistent estimator⁵⁵. Because the within estimator of β is downward-biased in dynamic panels of finite length (Nickell bias, of order $1/T$), we applied the Dhaene–Jochmans half-panel jackknife

correction⁵⁶ ($\beta_{\text{corrected}} = 2\beta_{\text{full}} - \frac{1}{2}(\beta_{\text{first-half}} + \beta_{\text{second-half}})$). We did not use difference or system GMM (Arellano–Bond) estimators, which are designed for panels with many units and few time periods and are unreliable and heavily over-instrumented with only 11 units. The half-life of a deviation from equilibrium was computed as $\ln(0.5)/\ln(\beta)$.

Equilibrium size

We first used two beta-convergence panel regressions, which regress the monthly change in core unit size on the lagged size level across all unit months, to determine if there was support for absolute convergence to a common equilibrium (pooled data) and/or each unit reverting back to its own equilibrium (conditional model with unit-level fixed effects). The long-run equilibrium size toward which core units revert was estimated using three independent measures. First, we computed the pooled long-run mean, $\alpha/(1-\beta)$, from a pooled autoregressive model, with a 95% confidence interval obtained by the delta method using cluster-robust (Arellano) covariances. Second, we computed a Mean-Group estimate by fitting a separate autoregressive model to each unit, deriving each unit's implied long-run mean $\alpha_i/(1-\beta_i)$, and averaging these across units, with the Pesaran–Smith standard error⁵⁷. Third, we computed the between-unit mean of observed unit-level mean sizes as a model-free cross-check. Whether a single common equilibrium was tenable was assessed with an F-test comparing the fixed-effects and pooled specifications. However, given the limited power of this test in dynamic panels, we treated it as supportive rather than decisive.

Infant survival

We modeled the relationship between core unit size and infant mortality with a time-varying Cox proportional-hazards model in counting-process form, using infant age in months as the time scale and core unit size as a monthly time-varying covariate. Size was mean-centered and entered as both linear and quadratic terms to allow a non-monotonic relationship. The quadratic term was assessed by a likelihood-ratio test, and the hazard-minimizing size was obtained from the fitted quadratic as its vertex. Tied event times were handled by the Efron approximation⁵⁸. Infants were followed from birth until death or censoring. To account for non-independence among infants, inference was repeated with cluster-robust standard errors clustered by core unit and, separately, by mother, and the model was refitted with a gamma-distributed shared frailty by core unit⁵⁹.

Data and Code Availability

The data analyzed for the current study and the R code used for the analyses are available at: <https://borealisdata.ca/previewurl.xhtml?token=6b98e8fa-c49f-4a52-9719-6adaefc9d09c>

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Julie A. Teichroeb – Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review and editing; Edward Mujjuzi – Data curation, Investigation, Project administration, Writing – review and editing; Samantha M. Stead – Data curation, Investigation, Methodology, Writing – review and editing.

The authors declare no competing interests.

Supplementary Information is available for this paper.

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