RESEARCH ARTICLE

PRIMATOLOGY WILEY

Golden-bellied mangabeys (*Cercocebus chrysogaster*) exhibit a larger home range and longer travel distances than those of bonobos (*Pan paniscus*) at LuiKotale, Democratic Republic of the Congo

Edward McLester[1] | Barbara Fruth[1,2,3]

[1]Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, Germany

[2]Centre for Research and Conservation, Royal Zoological Society of Antwerp, Antwerp, Belgium

[3]Department of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK

Correspondence
Edward McLester, Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Bücklestraße 5a, 78467 Konstanz, Germany.
Email: emclester@ab.mpg.de

Abstract

Primate ranging behavior is associated with numerous social and ecological correlates. Interspecific comparisons of ranging behavior can therefore provide insight into the socio-ecological conditions that characterize a species' niche within its community. We provide the first description of ranging behavior in golden-bellied mangabeys (*Cercocebus chrysogaster*), using sympatric bonobos (*Pan paniscus*) as a comparison. Over 6 months, we recorded GPS tracks at 1- and 5-min intervals from one habituated golden-bellied mangabey group and two habituated bonobo communities at LuiKotale, central Democratic Republic of the Congo. We compared estimates of home range size, time spent at different elevations, and hourly travel distances between species. We modeled daily travel distances against total monthly rainfall to investigate seasonal variation in daily ranging. The golden-bellied mangabey home range was similarly sized or larger than each of the two bonobo communities at LuiKotale across estimation methods. Mangabeys visited more of their range per day and spent more time in *terra firma* forest and less time in swamps than bonobos. Mangabeys traveled significantly farther per day and during midday hours than bonobos, but travel distances did not relate to monthly rainfall in either species. Golden-bellied mangabeys exhibited wide daily ranging behavior that more closely resembled that of sympatric bonobos than other *Cercocebus* species. Large homes ranges in mangabeys are likely influenced by food availability in *terra firma* forest, especially as groups appear to travel long distances between fruit trees and terrestrial food patches. Maximizing daytime activity may help mangabeys avoid competition from heterospecifics and indicates temporal niche partitioning in this primate community.

KEYWORDS
community ecology, feeding competition, primate ranging, travel patterns

1 | INTRODUCTION

An animal's niche is a theoretical concept that describes the unique set of social and ecological conditions in which a species lives and maintains a stable population (Bergmüller & Taborsky, 2010; Holt, 2009; Hutchinson, 1959). Understanding an animal's niche is a useful framework under which hypotheses of ecosystem structure, speciation, and behavioral flexibility can be developed (Schreier et al., 2009). As such, collecting evidence against which to build and test such hypotheses not only provides broad insight into the ecology of species but is increasingly important given the urgent need to understand behavioral and ecosystem responses to accelerating anthropogenic disturbance (Holt, 2009).

Investigating ranging behavior is a useful first step toward establishing a species' niche. How individuals and groups use their environment is associated with a variety of socio-ecological factors, including food availability (Chapman & Chapman, 2000a, 2000b; Janson & Goldsmith, 1995), predation risk (Boinski et al., 2000; Willems & Hill, 2009), and abiotic conditions such as temperature and rainfall (Ganas & Robbins, 2005; Hill, 2006; Johnson et al., 2015). For example, spatio-temporal variation in food availability is associated with several key ranging metrics, including the area of habitat used by groups (i.e., home range size) and how far individuals travel each day (i.e., daily travel distances [DTD]). Groups or individuals should be more likely to travel farther and expand home ranges to find new food patches and meet nutritional requirements when food availability is low. Mountain gorillas (Gorilla beringei beringei) exhibit longer DTD and larger home range sizes in areas of lower fruit availability (Ganas & Robbins, 2005), while guenons living in highly seasonal environments exhibit larger home ranges and greater travel distances in food-scarce vegetation or when resources are seasonally unavailable (e.g., samango monkeys, C. albogularis schwarzi—Parker et al., 2020; red-tailed monkeys, C. ascanius—McLester et al., 2019). Alternatively, individuals may reduce travel distances and switch to fallback foods to conserve energy when food is scarce (Chapman & Chapman, 2000a, 2000b; Hemingway & Bynum, 2005). When fruit is less abundant, chimpanzees (Pan troglodytes) and western gorillas (Gorilla gorilla gorilla) consume more leaves and reduce travel distances (Doran, 1997; Doran-Sheehy et al., 2004; Green et al., 2020) and L'Hoest's monkeys (Allochrocebus lhoesti) reduce home ranges and consume more seeds (Kaplin, 2001). Diet switching may also mean primates range into alternative habitat types to obtain food if staple dietary items are seasonally scarce. For example, chimpanzees are more likely to forage in higher elevation habitat in response to shifts in fruit availability (Green et al., 2020).

Ranging responses to food availability should be influenced by species-specific behavior and morphology. Primates that feed on more patchily distributed foods should also range farther to acquire sufficient food than primates with more generalized or flexible diets (Chapman & Chapman, 2000a, 2000b; Harvey & Clutton-Brock, 1981). Western lowland gorillas (G. gorilla gorilla) and mountain gorillas that seasonally consume fruit spend more time traveling and have larger home ranges than groups that consistently feed on folivorous foods (Doran-Sheehy et al., 2004; Ganas & Robbins, 2005; Masi et al., 2009). Larger-bodied primates should also exhibit greater home ranges and travel distances than smaller-bodied primates with lower metabolic demands (Milton, 1993). This discrepancy is often observable in tropical forests between large African apes and smaller monkeys. For example, ripe-fruit specialist chimpanzees typically have larger home ranges than sympatric cercopithecine monkeys that are similarly frugivorous but smaller-bodied (e.g., at Taï, Ivory Coast—Boesch & Boesch, 1989; Buzzard, 2006; at Nyungwe, Rwanda—Green et al., 2020; Kaplin, 2001).

Primates in large, cohesive groups may also range farther as food decreases because of greater intragroup feeding competition and faster rates of food patch depletion (Chapman & Chapman, 2000a, 2000b; Olupot et al., 1994). Alternatively, if intragroup competition is high and individuals cannot range far enough per day to obtain sufficient food, groups may fission temporarily or permanently into smaller subgroups that have smaller home ranges (Chapman et al., 1995; Cords & Rowell, 1986; Struhsaker & Leland, 1988). Groups may also need to travel and forage over longer distances to meet nutritional demands if intergroup competition is high, especially in small groups that are less able to aggressively defend resources from competing con- or heterospecifics (M. Brown, 2013).

Interspecific comparisons of ranging behavior can help disentangle the extent to which primates are responding to different, intersecting socio-ecological factors. Moreover, comparing group movements of sympatric species living under the same environmental conditions can indicate the extent to which animals have evolved similar or overlapping niches (Schreier et al., 2009; Struhsaker, 2017). For poorly known species, interspecific comparisons therefore provide a useful starting point from which hypotheses of niche partitioning can be developed.

One primate for which there are few behavioral and ecological data is the golden-bellied mangabey (Cercocebus chrysogaster). The largest of the Cercocebus mangabeys, these medium-sized, predominantly terrestrial monkeys are endemic to central Democratic Republic of the Congo (DRC) and are patchily distributed across a relatively small area (ca. 96,000 km²) of swamp forest habitat south of the Congo River (McLester et al., 2022). Groups are relatively large and typically comprise 50–70 individuals, but can total as many as >100 individuals (Ehardt & Butynski, 2013). Social organization and reproductive behavior is unknown, but groups include multiple adult males that disperse as solitary individuals (EM personal observation). Listed as "Data deficient" by the IUCN as recently as January 2020, this species is now classified as "Endangered" (Hart & Thompson, 2020). There are no detailed behavioral studies of this species, with only limited anecdotes from encounters with unhabituated groups reported previously (Ehardt & Butynski, 2013; Inogwabini & Thompson, 2013).

To provide a first empirical investigation into golden-bellied mangabey behavioral ecology, we describe the group composition and ranging behavior of a single group of habituated mangabeys at the LuiKotale study site. We compare these results with equivalent

data collected during the same period from two sympatric bonobo communities. Specifically, for each species we investigated: (1) home range size, (2) home range use (extent of home range visited per *n* follow days; time spent at different elevations), (3) hourly travel distances (HTD), and (4) DTD. Without previous behavioral data from golden-bellied mangabeys or cercopithecine monkeys in general at LuiKotale, we expected mangabeys to exhibit smaller home ranges and shorter travel distances than bonobos that live in similarly sized groups and have larger body masses (27–61 kg for bonobos vs. 8–15 kg for mangabeys—Ehardt & Butynski, 2013; Reinartz et al., 2013). Assuming golden-bellied mangabeys were primarily frugivorous as suggested by Kingdon (1997), we also expected both mangabeys and bonobos to travel farther per day in months with less rainfall, given fruit productivity at LuiKotale is lowest during dry seasons (B. Fruth & G. Hohmann unpublished data).

## 2 | METHODS

2.1 | Study site

We collected data at the LuiKotale study site, which comprises four adjacent community-owned forest blocks in the southwest buffer zone of Salonga National Park, DRC. All blocks are bisected by the Lokoro River, the largest river in the study area. In agreement with local communities, hunting and human disturbance are prohibited in each of these blocks south of the Lokoro River (Figure 1). The Lompole forest block, where the Bompusa East (BPE) bonobo study group (see below) ranges, has been protected since 2002 (Hohmann

& Fruth, 2003). The Bekombo and Mbungusani forest blocks, where the Bompusa West (BPW) bonobo and M2 mangabey study groups range, have been protected since 2016 and 2020, respectively.

Elevation at LuiKotale ranges from 324 to 481 m. Vegetation is a mosaic of mostly *terra firma* rainforest with open understory (71% cover), and temporarily and permanently inundated swamp forest along riverine valleys (29% cover; Beaune et al., 2013; Mohneke & Fruth, 2008). Annual rainfall is typically bimodal with short and long dry seasons around January–February and June–August, respectively. From 2003 to 2009, annual rainfall averaged 2132 mm (±SD 546 mm) and the mean monthly temperature range was 18–29°C (Fruth et al., 2014).

In addition to golden-bellied mangabeys and bonobos, five cercopithecine monkeys (red-tailed monkey, *Cercopithecus ascanius*; Wolf's monkey, *Cercopithecus wolfi*; de Brazza's monkey, *Cercopithecus neglectus*; Allen's swamp monkey, *Allenopithecus nigroviridis*; black mangabey, *Lophocebus aterrimus*) and two colobine monkeys (red colobus, *Piliocolobus tholloni*; black and white colobus, *Colobus angolensis*) are found at the study area. During this study, golden-bellied mangabeys frequently (typically 2–4 times daily) encountered groups of all these species except de Brazza's monkeys. These other species were not habituated and fled on noticing researchers. Potential predators of mangabeys and bonobos at LuiKotale include leopards (*Panthera pardus*) and African rock pythons (*Python sebae*), and, for mangabeys only, African golden cats (*Caracal aurata*) and raptors (e.g., crowned eagles, *Stephanoaetus coronatus*). Bonobos also prey upon golden-bellied mangabeys (B. Fruth & G. Hohmann unpublished data; L. Carvajal personal communication).

FIGURE 1 Estimated home range sizes for golden-bellied mangabeys (M2 group) and bonobos (Bompusa West [BPW] and Bompusa East [BPE] communities) at LuiKotale from January to June 2021. (a) Minimum convex polygon and 250 m grid cell analysis estimates. Grid cell colors indicate percentage of observation time spent in each cell. (b) 100%, 95%, and 50% isopleths for kernel density estimates. Black and white shading illustrates locations of rivers and swamp vegetation (typically <390 m; black shading) and is derived from the 30 m SRTM v3.0 digital elevation model (NASA, 2015).
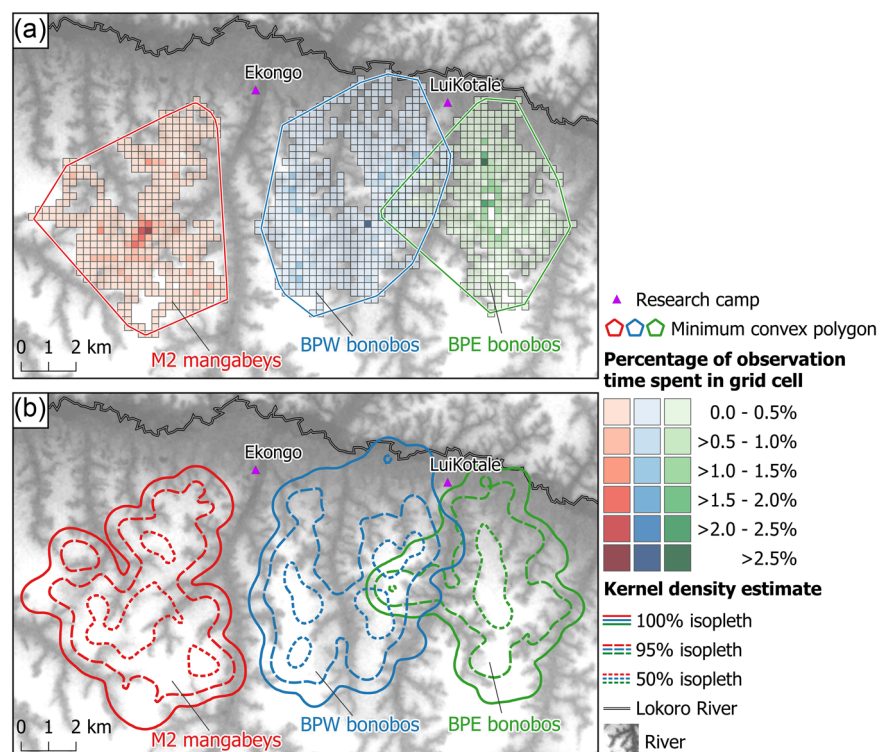
2.2 | Data collection

From March to June 2021, EM followed three golden-bellied mangabey groups (M1 through M3) typically from 05:30 h to 17:30 h (sunrise to sunset) daily in sets of 4 consecutive follow days. EM followed M2 golden-bellied mangabey group for 46 follow days in total (range = 14–15 days monthly from April–June), of which 37 were ≥8 h follows. EM followed M1 and M3 mangabey groups for 4 follow days each, in addition to brief encounters throughout the study as EM and field assistants followed M2 group and bonobos (Supporting Information: Figure S1). No group had been followed by researchers before this study and EM focused habituation efforts on M2 group. During the first 2 follow days each group traveled long distances (7–9 km) usually without stopping in what appeared to be attempts to avoid EM (see Results). After 3–7 follow days, most adult and subadult males in each group tolerated EM's presence up to 7–10 m away and groups no longer appeared to collectively flee from EM. After approximately 30 follow days, almost all individuals in M2 (except for adult females with infants) tolerated EM's presence within a few meters.

From January to June 2021, we also collected data from two communities of habituated bonobos (BPW and BPE communities) living adjacent to M2 group's home range. Bonobos from each study community were followed daily by one or two experienced field assistants collecting data for the long-term LuiKotale Bonobo Project. Field assistants followed the BPW bonobo community for 124 follow days (range = 17–26 days monthly from January-June; n = 105 ≥ 8 h follows) and the BPE bonobo community for 103 follow days (range = 8–24 days monthly from January–June; n = 77 ≥ 8 h follows). The range of the BPW community overlapped with that of M1 mangabey group, and BPE community had also been observed encountering unhabituated golden-bellied mangabeys (BF personal observation). M2 and M3 mangabey groups were also sympatric with unhabituated bonobos from at least one community (Supporting Information: Figure S1).

To estimate mangabey group sizes and compositions, EM counted individuals opportunistically as groups traveled in cohesive progressions in open understory vegetation or along researcher trails. EM positioned himself at the front of progressions and waited for all visible individuals to pass by, as far as was possible. EM also filmed progressions and reviewed footage to improve estimates, and photographed individuals throughout the study to differentiate animals based on facial features (camera: Canon 5D IV with 100–400 mm II lens). Sixteen individuals had been individually identified in M2 group by the end of the study. For bonobos, all individuals in the BPW and BPE communities were individually identified.

During follows, we used handheld Garmin GPSMAP 64s units to record GPS coordinates automatically (1-min intervals for mangabeys; 5-min intervals for bonobos). M2 mangabeys traveled as a relatively cohesive group, and we positioned ourselves in the group center as far as possible when not collecting data on specific individuals. Because bonobos exhibit a fluid fission-fusion social systems in which communities form subgroups of varying size and composition, we collected data on all adult and adolescent individuals using focal animal sampling (1-h focal follows—Altmann, 1974). To estimate bonobo party size and age-sex class composition, we defined a party as comprising all individuals observed during a given time period while following a focal individual, following Mulavwa et al. (2008). At 30-min intervals, we recorded individual identities of all bonobos observed during the preceding 30 min. We defined age-sex classes as: adult (≥15 years), adolescent (9–14 years), juvenile (5–8 years), and infant (0–4 years), following Hashimoto (1997).

To provide a simple index of seasonality against which to compare DTD, we followed mangabey and bonobo groups in all types of weather and measured rainfall twice daily (at 6 and 18 h) using two BRESSER multi-sensor weather stations with rain gauges located in open-canopy clearings at the LuiKotale and Ekongo research camps (Figure 1).

2.3 | Data analyses

We estimated home range size for each group using three methods: (1) 100% minimum convex polygon (MCP), (2) grid cell analysis (GCA; both calculated in QGIS 3.22.3—QGIS Development Team, 2022), and (3) kernel density estimate (KDE; calculated with the *adehabitatHR* package in R 4.1.2—Calenge, 2006; R Core Team, 2021). For GCA, we overlaid a grid of 250 × 250 m cells over the study area and summed the total area of grid cells entered by each group. For kernel density estimates, we calculated the 50%, 75%, 80%, 90%, 95%, 98%, 99%, and 100% isopleths based on a grid of 250 × 250 m cells. We calculated the area under the curve for each kernel density estimate, which provides a goodness of fit measure that reflects how closely the estimate matches the observed GPS coordinates (scale: 0–1, with numbers closer to 1 indicating better fits; following Martínez-Íñigo et al., 2021).

To estimate time spent at different elevations, we extracted elevation data using NASA's Shuttle Radar Topography Mission (SRTM) digital elevation model (Farr et al., 2007; NASA, 2015), which measures elevation for 30 m grid cells across the study site. We counted the percentage of coordinates recorded for each group in grid cells binned at 10-m intervals (e.g., percentage of coordinates recorded at 350–359 m, 360–369 m etc.).

We calculated DTD as the cumulative Euclidean distance between GPS coordinates for each follow day. We calculated HTD as the cumulative Euclidean distance between GPS coordinates for each follow hour (at least 50 min of consecutive coordinates). When calculating both DTD and HTD, we used only consecutive GPS fixes separated by ≥25 m to minimize overestimation of path length due to (1) shorter time intervals between coordinates for mangabeys versus bonobos, and (2) variation in GPS accuracy (typically ≤5 m).

In analyses of time spent at different elevations and DTD, we used only follows lasting ≥8 h. When analyzing HTD and DTD for golden-bellied mangabeys, we excluded the initial 7 follow days because the group appeared to flee from researcher presence during this period (see Section 2.2 above).

2.4 | Statistical analyses

We conducted statistical tests in JASP v16.0 (JASP Team, 2021) and R v4.1.2 (R Core Team, 2021), using a Bayesian framework to infer statistical significance. We used analysis of variance (ANOVA) with post-hoc *t*-tests to compare the variability (standard deviation) of HTD between groups, and ANOVA only to compare monthly variation in DTD between groups. In these tests, the resulting Bayes Factor (BF_{10}) indicates the relative probability that the data support the alternative hypothesis (here, that HTD variability and DTD differed significantly between groups and months, respectively).

To test if DTD related to changes in monthly rainfall, and if this relationship differed between groups of either species, we built a simple linear model with a Gaussian error distribution using the R package *brms* (Bürkner, 2021). We fitted DTD (continuous variable in meters) as the response. For each estimate of DTD, we fitted an interaction (including main effects) between total rainfall averaged between research camps for that month (continuous variable in millimeters) and group (categorical variable) as a fixed effect predictor.

We accounted for variation in DTD caused by differences in bonobo party size, which we defined as the maximum number of individuals except infants recorded across all 30-min interval scans during each follow. Party size was not relevant for mangabeys, which traveled in a relatively cohesive group. We categorized maximum party size and included it within our predictor for group. This resulted in a single categorical predictor with eight levels: M2 mangabeys; BPW 0–10 individuals; BPW 11–20 individuals; BPW 21–30 individuals; BPW ≥ 31 individuals; BPE 0–10 individuals; BPE 11–20 individuals; BPE 21–30 individuals.

We standardized continuous variables to a mean of zero and one standard deviation to improve model fitting and interpretation of continuous main effects in interactions, following Schielzeth (2010). There were no confounding effects of predictor multicollinearity (maximum variance inflation factor = 1.04). We fitted the model with the relatively weakly informative default *brms* priors for fixed effects and the default half student-t prior for the residual standard deviation. We ran eight Markov chains (Monte Carlo) for 8000 iterations with a warm-up of 2000 iterations each. We checked trace plots to confirm autocorrelation was not an issue and that effective sample sizes were adequate (minimum = 32,700, mean = 46,734). Gelman-Rubin diagnostics for each fixed effect indicated no issues with chain convergence (maximum point estimate = 1.0).

To test the significance of fixed effects, we used a leave-one-out cross-validation to compare the predictive performance of a null model with no fixed effects against models with each combination of fixed main and interaction effects. For each model, we calculated the expected log pointwise predictive density (ELPD), for which higher values indicate better model predictive accuracy (Vehtari et al., 2017). We selected the model with the highest ELPD score compared to the null model and inferred the likelihood fixed effects were associated with the response by calculating posterior probabilities from the percentage of samples in each posterior distribution with the same sign as the mean (i.e., the extent to which a posterior distribution overlapped zero).

3 | RESULTS

3.1 | Group sizes and composition

M2 group comprised approximately 65 individuals (12 adult males, 30–40 adult females and subadult males and females, and 15–25 juveniles). Throughout the study, EM typically observed around 6-8 adult females with dependent infants.

From January to March, BPW bonobos comprised 62 individuals (7 adult males, 16 adult females, 18 adolescents, 12 juveniles, and 9 infants) and BPE bonobos comprised 34 individuals (6 adult males, 10 adult females, 7 adolescents, 4 juveniles, and 7 infants). In mid-March, one adolescent female emigrated from the BPW to the BPE community, where she remained for the rest of the study.

3.2 | Home range sizes and overlap

Over the entire study, M2 golden-bellied mangabeys exhibited a total home range size of 21.5 km^2 (250 m GCA) to 27.6 km^2 (95% KDE; Figure 1; Table 1). Depending on estimation methods, the mangabey home range was similar to or smaller than that of the BPW bonobo community (250 m GCA = 31.1 km^2; 95% KDE = 26.2 km^2) and slightly larger than that of the BPE bonobo community (250 m GCA = 22.6 km^2; 95% KDE = 20.7 km^2). *Per capita* home ranges (250 m GCA and 95% KDE divided by the total number of individuals in each group) were 0.33–0.42 km^2 per individual for M2 mangabeys, 0.43–0.51 km^2 per individual for BPW bonobos, and 0.62–0.67 km^2 per individual for BPE bonobos.

Using 250 m GCA estimates, BPW and BPE bonobo home ranges overlapped by 2.3 km^2, which was 7.2% of BPW's and 9.9% of BPE's estimated range. Using 95% KDE estimates, bonobo home ranges overlapped by 1.4 km^2, which was 5.4% of BPW's and 6.8% of BPE's estimated range. Mangabey groups encountered bonobos on 20 of 51 (40%) follow days either through vocalizations or direct observations. Responses of adult mangabeys to bonobos varied substantially and included changing travel direction or immediately leaving fruit trees at which bonobos were arriving, to no observable reaction (EM personal observation).

3.3 | Home range use

In a single follow day, golden-bellied mangabeys visited a mean of 6% and a maximum of 11% of their home range, while BPW and BPE bonobos visited a mean of 3% and 4% and a maximum of 8% and 7% of their home range, respectively (Figure 2). As the number of successive follow days increased, mangabeys used a larger percentage of their home range than both bonobo communities. For moving windows of 7 successive

TABLE 1 Estimated home range size for golden-bellied mangabey and bonobo groups at LuiKotale from January to June 2021.

Group (total individuals)	100% minimum convex polygon (km²)	250 × 250 m grid cell analysis (km²)	Kernel density estimate (km²)								
			50%	75%	80%	90%	95%	98%	99%	100%	Area under curve
M2 golden-bellied mangabeys (ca. 65)	38.9	21.5	6.4	13.5	15.7	22.0	27.6	33.6	37.2	46.6	0.994
Bompusa West (BPW) bonobos (61–62)	43.2	31.1	5.7	11.6	13.5	19.9	26.2	34.3	39.7	51.7	0.993
Bompusa East (BPE) bonobos (33–34)	32.4	22.6	3.3	8.5	10.3	15.7	20.7	26.3	29.5	37.3	0.994

Note: Kernel density estimates are stratified by percentage isopleth and presented alongside the corresponding area under curve goodness-of-fit metric (scale: 0–1).
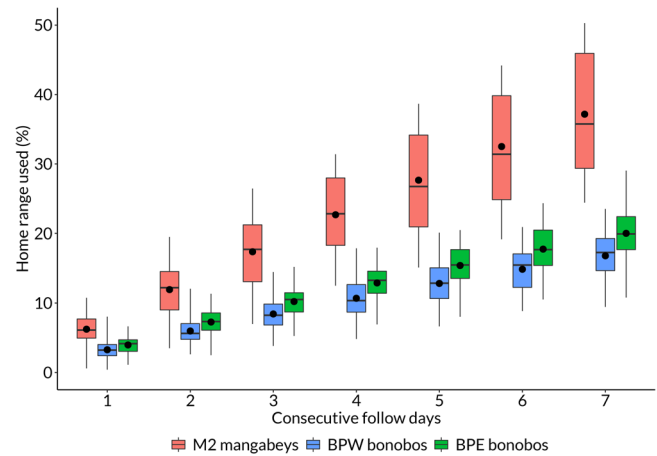
FIGURE 2 Percentage of home range visited by M2 group at LuiKotale from January to June 2021, calculated for moving windows of 1–7 successive follow days. Percentages are calculated by dividing the number of unique 250 m grid cells visited per day by the total number of unique grid cells visited during the study (bars = median values; dots = mean values; boxes = interquartile range; whiskers = minimum and maximum values).

follow days, M2 mangabey group visited a mean of 37% (range = 24%–50%) of their home range; about double the percentage used by BPW (mean = 17%; range = 9%–24%) and BPE (mean = 20%; range = 11%–29%) bonobos. Home range size estimates did not reach an asymptote for any study group; that is, groups consistently visited new areas throughout the study (Supporting Information: Figure S2).

Mangabeys spent most observation time in *terra firma* forest and did not spend long periods in riverine areas, typically quickly crossing small streams once per 2–3 follow days and avoiding large expanses of swamp. Rivers and seasonally inundated vegetation were usually located in valleys below 390 m, and mangabeys spent 89% of observation time above 390 m (Figures 1 and 3). Mangabeys did not travel within 2 km of the Lokoro River, while both bonobo communities foraged directly adjacent to the river. Unlike mangabeys, bonobos frequently crossed major rivers in the study area. BPW bonobos spent most observation time in higher, dry *terra firma* forest (85% time spent at ≥390 m), while BPE bonobos spent around twice as much observation time in riverine and swamp areas than BPW bonobos and M2 mangabeys (29% time spent at <390 m vs. 15% and 11%, respectively).

3.4 | HTD

Golden-bellied mangabey HTD varied throughout the day, with a roughly linear increase in HTD from 6:00 to 9:00 h and peak travel distances from 11 to 14 h (Figure 4). Mangabey HTD decreased in the late afternoon from 15:00 to 17:00 h. Both bonobo communities exhibited roughly the opposite trend, with peak HTD in mornings and afternoons (7–9 h; 13–17 h) and lowest HTD during the middle of the day (10:00–13:00 h).

Mangabey HTD was significantly less variable and exhibited a more consistent pattern than bonobo HTD (ANOVA: BF_{10} vs. null
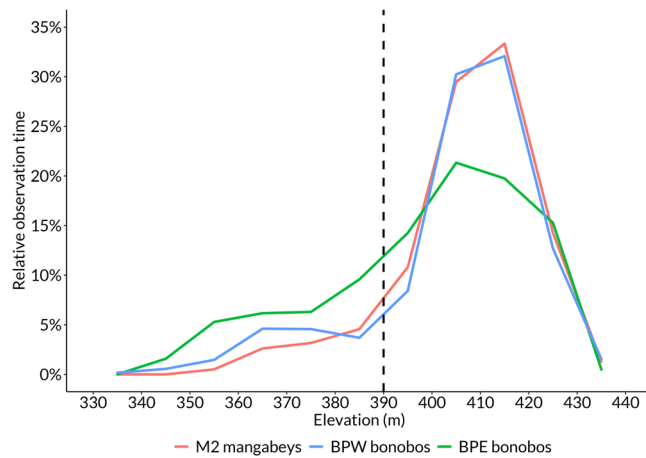
FIGURE 3 Percentage of observation time spent at different elevations (10 m bins) by golden-bellied mangabey and bonobo groups at LuiKotale from January to June 2021 (≥8 h follows only). The vertical dashed line indicates typical elevation of vegetation (≥390 m = *terra firma* forest; <390 m = seasonally and permanently inundated forest).
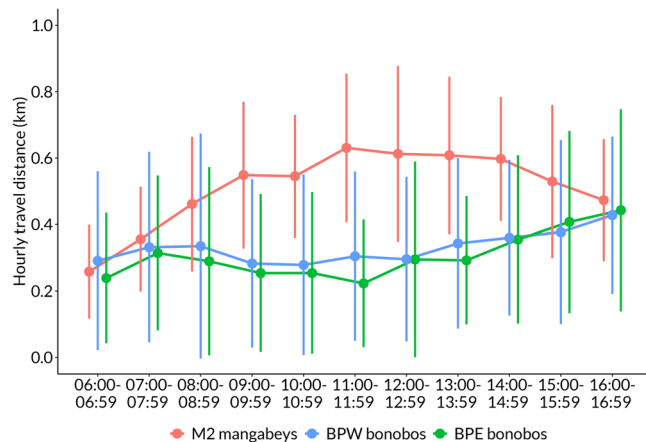
FIGURE 4 Estimated hourly travel distance of golden-bellied mangabey and bonobo groups at LuiKotale from January to June 2021 (horizontal lines = mean values; vertical error bars = standard deviation).

model = 38.125); that is, the standard deviation of HTD for each hour of the day was significantly lower for M2 mangabeys compared to BPW (post-hoc *t*-test: BF_{10} = 100.765) and BPE bonobos (BF_{10} = 3.552). The standard deviation of HTD did not differ significantly between BPW and BPE bonobo communities (BF_{10} = 0.722).

## 3.5 | DTD

The best-fitting model of golden-bellied mangabey and bonobo DTD included group and party size as predictors, but not rainfall (ELPD vs. null model = 34.303—Table 2). On average, M2 mangabeys traveled significantly farther per day than either bonobo community, irrespective of maximum party size (posterior means = −1.118 to

TABLE 2 Model selection for predictors of daily travel distance (DTD) based on expected log predictive density (ELPD) scores, where higher numbers indicate better predictive performance.

Model	ELPD score	ELPD score Δ null model
DTD ~ 1 (null model)	−231.350	-
DTD ~ rainfall	−232.007	−0.657
DTD ~ group	*−197.047*	*34.303*
DTD ~ rainfall + group	−198.034	33.316
DTD ~ rainfall × group	−204.214	27.136

Note: Models comprise a null model with no fixed effects and each possible combination of fixed interaction and main effects (interaction terms "×" = main and interaction terms "x + y + x:y"; bold italics = selected best fitting model).
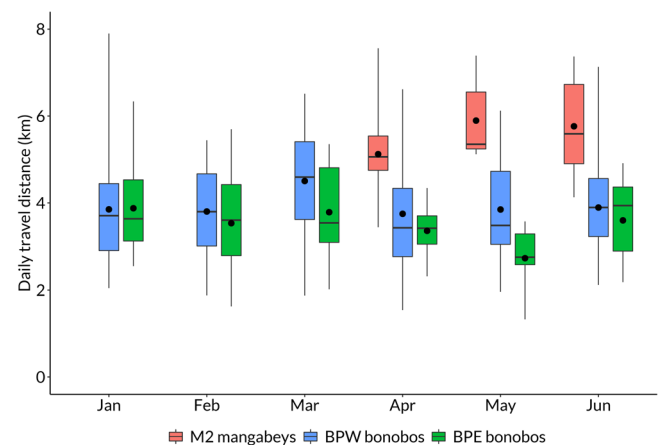
FIGURE 5 Estimated daily travel distance for golden-bellied mangabey and bonobo groups at LuiKotale from January to June 2021 (bars = median values; dots = mean values; boxes = interquartile range; whiskers = minimum and maximum values).

−1.805; posterior probabilities = 99.6%–100%—Figure 5; Table 3). Mangabeys traveled a mean of 5.53 km per day (range = 3.44–7.56 km; Figure 6; Table 4) versus means of 3.91 and 3.59 km for BPW and BPE bonobos, respectively. Maximum DTD for mangabeys was greater than that estimated for the BPE bonobo community (7.56 vs. 6.34 km). Only the BPW bonobo community with a party size of over 21 individuals traveled farther than the mangabey group (7.90 vs. 7.56 km).

DTD did not differ significantly between months in mangabeys (ANOVA: BF_{10} vs. null model = 0.640; Figure 5) or in either bonobo community (BPW—BF_{10} vs. null model = 0.079; BPE—BF_{10} vs. null model = 0.246).

4 | DISCUSSION

We compared the ranging behavior of sympatric golden-bellied mangabeys and bonobos to describe and contextualize the basic ecology of a poorly known cercopithecine monkey. These are the

TABLE 3 Fixed effect posterior distributions and probabilities for the best fitting model of daily travel distance (DTD), as selected in Table 2 (CI = credible interval).

Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI	Posterior probability
Intercept	1.147	0.876	1.423	100.0
Group: Bompusa West (BPW) bonobos (maximum party of 0–10 individuals)[a]	−1.528	−2.674	−0.387	99.6
Group: Bompusa East (BPE) bonobos (maximum party of 11–20 individuals)[a]	−1.627	−2.034	−1.220	100.0
Group: BPW bonobos (maximum party of 21–30 individuals)[a]	−1.118	−1.529	−0.713	100.0
Group: BPW bonobos (maximum party of >31 individuals)[a]	−1.120	−1.547	−0.690	100.0
Group: BPE bonobos (maximum party of 0–10 individuals)[a]	−1.805	−2.554	−1.048	100.0
Group: BPE bonobos (maximum party of 11–20 individuals)[a]	−1.679	−2.063	−1.295	100.0
Group: BPE bonobos (maximum party of 21–30 individuals)[a]	−1.530	−2.184	−0.868	100.0

[a]Reference = "Group: M2 mangabeys."
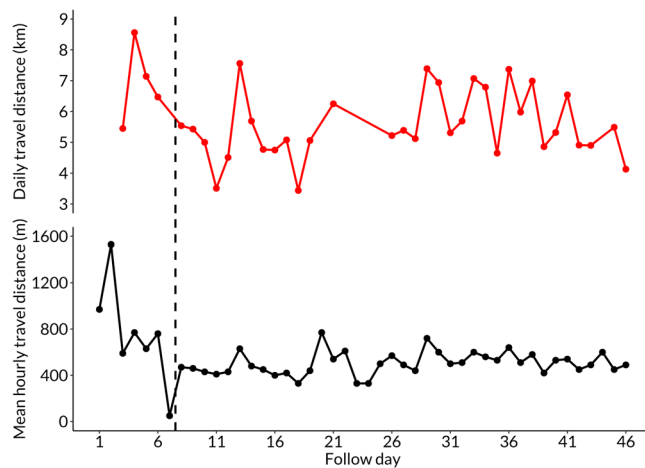
FIGURE 6 Estimated daily travel distance of M2 golden-bellied mangabey group at LuiKotale from January to June 2021 (n = 46 follow days): mean distance traveled per hour (black line) and absolute distance traveled on ≥8 h follows (red line). After 7 follow days (vertical dashed line), habituation of adult and subadult males had improved noticeably and the group as a whole no longer appeared to flee from researchers.

first detailed behavioral data collected from habituated golden-bellied mangabeys.

4.1 | Spatial patterns of mangabey and bonobo ranging

Estimates of home range size and DTD for golden-bellied mangabeys were substantially higher than those reported for other *Cercocebus* mangabeys, irrespective of estimation method, group size, and study length. M2's home range was approximately double the next highest estimate reported from the genus (21.5–27.6 km² vs. 12.7 km² for agile mangabeys, *C. agilis*—Table 5). Golden-bellied mangabeys also traveled around twice as far per day than agile mangabeys and three to four times farther than other *Cercocebus* species (Table 5). Against our prediction, golden-bellied mangabey home range and DTD estimates were therefore closer to or exceeded those of bonobos at LuiKotale than other *Cercocebus* mangabeys, even after accounting for group size. The size of M2 golden-bellied mangabey group was consistent with medium to large group sizes reported for other *Cercocebus* species (e.g., averaging 60–90 individuals for red-capped mangabeys, *C. torquatus*, Sanje mangabeys, *C. sanjei*, and sooty mangabeys, *C. atys*—Table 5). Even relatively large groups of *Cercocebus* mangabeys typically exhibit smaller ranges and travel shorter distances than sympatric apes (e.g., red-capped mangabeys and sooty mangabeys, *C. atys* vs. chimpanzees—Lehmann & Boesch, 2003; Martínez-Íñigo et al., 2021; agile mangabeys versus western lowland gorillas—Remis, 1997). For M2 mangabey group, however, the *per capita* home range (0.33–0.42 km²) was similar or slightly smaller than that of the largest bonobo community at LuiKotale and bonobos observed for 6–24 months at other sites (Table 6).

Variation in food availability between different habitat types is a key driver of group ranging. We could not compare golden-bellied mangabeys and bonobos with directly overlapping home ranges, which would have comprised the same spatial composition of habitat against which to compare ranging behavior for both species. Nonetheless, across all five of our study groups, mangabeys almost exclusively used *terra firma* forest, where they mostly consumed fruit. In contrast, bonobos foraged in both *terra firma* forest and seasonally inundated swamps, where they fed on terrestrial herbaceous vegetation (THV) including species found only in inundated environments (e.g., *Aframomum* spp.). THV is typically less patchily distributed than fruit and bonobos at LuiKotale consume more THV species when fruit availability is low (BF unpublished data). For bonobos, exploiting diverse dietary items from multiple habitat types may be an effective alternative to increasing travel distances to obtain fruit. Similarly, red-capped mangabeys that exhibit relatively

TABLE 4 Estimated daily travel distance for M2 golden-bellied mangabey (ca. 65 individuals) and Bompusa West (BPW) (61–62 individuals) and Bompusa East (BPE) (33–34 individuals) bonobo groups at LuiKotale from January to June 2021 (≥8 h follows only).

Group (party size)	Mean daily travel distance (DTD) (km)	Minimum (DTD)	Maximum DTD (km)
M2 golden-bellied mangabeys	5.53	3.44	7.56
Bompusa West (BPW) bonobos (0–10 individuals)	3.43	2.05	4.63
BPW bonobos (11–20 individuals)	3.56	1.54	6.41
BPW bonobos (21–30 individuals)	4.26	1.87	7.90
BPW bonobos (>31 individuals)	4.21	2.35	6.60
BPW bonobos (any party size)	3.91	1.54	7.90
Bompusa East (BPE) bonobos (0–10 individuals)	3.26	2.18	4.49
BPE bonobos (11–20 individuals)	3.40	1.33	4.99
BPE bonobos (21–30 individuals)	4.03	2.99	5.70
BPE bonobos (any party size)	3.59	1.33	6.34

Note: For bonobos, party size indicates the maximum party size (total number of individuals excluding infants) recorded during the daily follow. Estimates with any party size include daily follows when party size could not be estimated at any point during the day.

small home ranges at Sette Cama spend most time in *terra firma* forest but also forage in mangrove swamps and coastal forest where they consume a diversity of foods (e.g., crabs, fungi, insects—Cooke, 2012, 2014). Conversely, agile mangabeys at Mondika, which also live almost exclusively in *terra firma* forest and avoid rivers and large swamps, exhibit the second largest home range among *Cercocebus* (Shah, 2003). Compared to bonobos and *Cercocebus* mangabeys that exploit multiple habitat types, golden-bellied mangabeys restricted to *terra firma* forest may therefore range farther per day to obtain sufficient food and meet nutritional requirements.

The vertical distribution of food may also explain wide daily ranging. Golden-bellied mangabeys at LuiKotale traveled and foraged terrestrially, where they consumed THV (e.g., *Haumania* spp.) and foraged in leaf litter for insects, abscised fruit, and hard seeds (particularly *Irvingia*-like sp.; EM personal observation). In general, mangabeys only foraged arboreally in large fruit trees, during which around half of the group ascended trees to consume ripe or unripe fruit (predominantly *Ficus*, *Irvingia*, *Pancovia*, and *Synsepalum* spp.), while remaining individuals consumed abscised or dropped fruit from the ground. This behavior is similar to that of sooty mangabeys at Taï, which also spend most time (76% of observations) foraging and traveling terrestrially (McGraw, 1998). Sooty mangabey diet comprises a narrow range of fruit and terrestrial hard foods (nuts, seeds, and insects), and groups exhibit relatively large home ranges (McGraw et al., 2011; Table 5). In contrast, red-capped mangabeys with small home ranges are the least terrestrial of the *Cercocebus* mangabeys, spending substantially more time traveling and foraging arboreally (61% of observations) than agile, sooty, and likely golden-bellied mangabeys (Cooke, 2012; Mitani, 1989). In *terra firma* forest frequented by golden-bellied mangabeys, staple foods may not be available in all strata and instead may be concentrated at ground level and the upper canopy where most fruit is present. Subsequent

studies should investigate whether golden-bellied mangabeys therefore need to travel longer horizontal distances between patches than other *Cercocebus* species for which food may be more abundant across multiple strata.

When food is scarce or patchily distributed, primates should either exhibit larger home range sizes and DTD as groups travel farther to find resources, or form smaller groups (Chapman & Chapman, 2000a, 2000b). Golden-bellied mangabeys consistently traveled farther per day and visited larger percentages of their home range over time than bonobos, even where these species exhibited similar home range sizes. Moreover, golden-bellied mangabeys generally traveled as a cohesive group and only formed subgroups during peak foraging activity (2–4 subgroups separated by <100 m for 1–3 h daily—EM personal observation). Bonobos and other *Cercocebus* mangabeys (e.g., agile mangabeys—Shah, 2003; red-capped mangabeys—Dolado et al., 2016; Mitani, 1989) frequently fission into smaller parties, which should reduce intragroup competition (Dolado et al., 2016; Furuichi, 2009). For golden-bellied mangabeys, our preliminary observations suggest both intra- and intergroup competition may influence ranging behavior. Intergroup encounters between M2 and neighboring groups involved high rates of aggression (n = 3 encounters; EM unpublished data), and M2 group also fed mostly on relatively patchy foods (e.g., fruit, seeds, and insects) that should increase contest competition (Isbell, 1991). Conversely, conspecific groups of agile and Tana River mangabeys forage together in aggregations of >200 individuals, suggesting intergroup competition in these species may be lower (Homewood, 1976; Kinnaird, 1992; Shah, 2003). Whereas bonobos and some *Cercocebus* mangabeys may respond to decreases in food availability by forming subgroups, golden-bellied mangabeys may instead travel farther per day in more cohesive groups to obtain sufficient food while maintaining large enough groups to defend resources from competitors (M. Brown, 2013).

TABLE 5 Comparison of group sizes and ranging behavior reported for *Cercocebus* mangabeys, ordered by distribution from West to East Africa.

Species	Country	Site	Population density Individuals (km²)	Groups (km²)	Study duration (months)	Group size (total individuals)	Home range size (km²) (method)	Daily travel distance (km)	Reference
Sooty mangabey (*Cercocebus atys*)	Côte d'Ivoire	Taï NP	10.5–11.9	0.64	-	-	4.92	2.20	Rutte (1998; in Janmaat, 2006, McGraw et al., 2007); McGraw and Zuberbühler (2007); N'Goran et al. (2012)
					2	93–96	-	-	Janmaat, Byrne, et al. (2006)
					32	-	7.00–8.00	-	Bergmüller (1998; in Janmaat, 2006)
					-	45	4.00–6.00 (personal observation)	-	Galat and Galat-Luong (1985)
					-	115	5.00–7.00	-	McGraw (1998); McGraw et al. (2011); Shultz and Noë (2002)
	Sierra Leone	Tiwai Island	38.5	-	-	-	-	-	Oates et al. (1990)
White-naped mangabey (*C. lunulatus*)	Burkina Faso	Comoé-Léraba Reserve	5	-	-	6–13	>2.00	-	G. Galat & A. Galat-Luong personal communication in Butynski (2013)
	Côte d'Ivoire	Comoé NP	-	-	-	3–23	-	-	
Red-capped mangabey (*C. torquatus*)	Cameroon	Campo Reserve	-	0.51	15	14–38	2.47 (100% MCP)	-	Mitani (1989); Matthews and Matthews (2002)
	Gabon	Loango NP	15–17	0.97	-	-	-	-	Morgan (2007)
		Moukalaba-Doudou NP	62.4	-	-	-	-	-	Mangama-Koumba et al. (2016)
		Sette Cama	-	-	5	>70	1.44 (100% MCP) 0.99 (100 m GCA) 2.54 (personal observation)	1.00–1.10	Cooke (2012)
			-	-	4	90	1.40 (MCP)	-	Dolado et al. (2016)
Agile mangabey (*C. agilis*)	Central African Republic	Bai Hokou	-	-	6	130–136	12.70 (100% MCP) 9.50 (95% KDE)	$\bar{x} = 3.09$ (range = 2.74–3.44)	Devreese (2011); Devreese et al. (2013)
		Mondika	6.9	-	12	21–22	3.03 (100 m GCA)	$\bar{x} = 1.12$ (range = 0.39–1.99)	Shah (2003)
		Ngotto Forest	18.9	0.92	-	-	-	-	D. Brugière personal communication in Shah (2013)

TABLE 5 (Continued)

Species	Country	Site	Population density Individuals (km²)	Groups (km²)	Study duration (months)	Group size (total individuals)	Home range size (km²) (method)	Daily travel distance (km)	Reference
	Democratic Republic of the Congo	Ituri Forest	2–38.3	0.25	-	-	-	-	Thomas (1991); Kambale Saambili (1998; in Shah, 2013)
	Gabon	Makokou	6.7–12.5	-	17	8–18	1.98	1.22–1.40	Quris (1975)
	Republic of Congo	Odzala-Kokoua NP	10–40	0.50–2	-	-	-	-	Maisels (1996; in Maisels et al., 2020)
Golden-bellied mangabey (C. chrysogaster)	Democratic Republic of Congo	LuiKotale	-	-	4	Ca. 65	21.50 (250 m GCA) 27.63 (95% KDE)	$\bar{x}$ = 5.54 (range = 3.44–7.56)	This study
Sanje mangabey (C. sanjei)	Tanzania	Udzungwa Mountains	-	0.15–0.29	7	59	3.01 (95% MCP) 3.53 (95% KDE)	$\bar{x}$ = 1.76 (range = 0.84–2.13)	Mwamende (2009); Paddock et al. (2020)
					25	63–65	≥2.00	-	Ehardt et al. (2005); McCabe (2012)
Tana River mangabey (C. galeritus)	Kenya	Tana River	45	1.83	7	36	0.17 (50 m GCA)	Median = 1.04 (range = 0.70–1.51)	Homewood (1976); Butynski and Mwangi (1995)
					14	17	0.53 (50 m GCA)	Median = 1.13 (range = 0.62–1.48)	
					15	14–29	0.70 (100% MCP) 0.18–0.19 (50 m GCA)	$\bar{x}$ = 1.19 (range = 0.59–2.04)	Kinnaird (1990); Kinnaird (1992)
					12	$\bar{x}$ = 50	0.47 (50 m GCA)	$\bar{x}$ = 1.40	Wieczkowski (2005)

Note: Adapted in part from Cooke (2012), Devreese et al. (2013).
Abbreviations: GCA, grid cell analysis; KDE, kernel density estimate; MCP, minimum convex polygon; NP, national park.

TABLE 6 Comparison of group and home range sizes reported for bonobos.

Site	Study duration (months)	Group	Group size (total individuals) (adult individuals)	Home range (km²) (method)	Home range size (km² per individual)	Reference
Kokolopori	42	Ekalakala	- (11)	35.0 (95% KDE)	3.18 (adults only)	Samuni et al. (2020)
		Kokoalongo	- (26)	40.0 (95% KDE)	1.54 (adults only)	
LuiKotale	6	BPW	61–62 (22–23)	31.1 (250 m GCA)	0.43–0.51	This study
				26.2 (95% KDE)		
		BPE	33–34 (16–17)	22.6 (250 m GCA)	0.62–0.67	
				20.7 (95% KDE)		
Manzano	24	-	22–24 (9–10)	13.0 (500 m GCA)	0.40–0.57	Pennec et al. (2020)
				9.3 (100% KDE)		
Wamba	6	E1	25–31	14.0 (9500 m GCA)	0.45–0.56	Hashimoto et al. (1998)
		E2	35–52	25.0–31.5 (9500 m GCA)	0.48–0.90	

Abbreviations: GCA, grid cell analysis; KDE, kernel density estimate.

4.2 | Temporal patterns of mangabey and bonobo ranging

To investigate temporal variation in mangabey and bonobo ranging, we modeled DTD against rainfall as a proxy for changes in fruit availability. Against our prediction, neither mangabeys nor bonobos traveled farther per day in certain months or in response to variation in rainfall. Of the ripe fruit consumed by mangabeys that we could identify, several frequently consumed species were also fed on by bonobos (e.g., *Ficus*, *Synsepalum*, and *Irvingia* spp.), and the availability of these species varied during the study (EM personal observation). Nonetheless, any shifts in fruit availability during our relatively short study may not have been large enough to influence group ranging. Furthermore, mangabeys and bonobos may have responded to changes in fruit availability by switching to more generalized diets, instead of ranging farther, to meet nutritional demands. For example, mangabeys frequently consumed unripe fruit (predominantly *Phyllantus* spp.), which was not generally eaten by bonobos. *Cercocebus* mangabeys also typically exploit nutrient-rich hard foods that do not readily decompose and are therefore relatively abundant throughout the year (Fleagle & McGraw, 2002). Sooty mangabeys frequently consume *Coula* and *Sacoglottis* nuts and travel relatively far per day (>2 km) between patches (McGraw et al., 2011; Table 5). Similarly, individuals in M2 group spent long periods (30–60 min) feeding terrestrially on hard-shelled seeds surrounding large trees, which may provide a relatively stable food source over time. Moreover, we observed a relatively high rate of meat-eating by mangabeys in M2 group, including preying on medium-sized mammals such as duikers (McLester, 2022). Vertebrate meat is an important source of protein, as well as micronutrients that are otherwise scarce in plant foods, and may help mangabeys meet nutritional requirements if staple plant foods are unavailable. Future researchers should collect detailed phenological and dietary data to systematically compare how mangabeys and bonobos balance dietary flexibility against ranging longer distances in response to seasonal variation in food availability.

Our estimates of mangabey and bonobo HTD also highlighted a possible temporal dimension to niche partitioning by these species. Balancing foraging effort and resting time is crucial for primates to minimize energy loss to adverse environmental conditions. In tropical forests, primates therefore typically reduce activity during peak midday temperatures and are most active in early mornings and late evenings (Korstjens et al., 2010). Although bonobo HTD matched this expectation, golden-bellied mangabeys rarely rested during the day and usually traveled fastest from midday to late afternoon when temperatures were highest (Figure 4; BF unpublished data). Increased foraging at times when temperatures were high could be a direct response to bonobos and other heterospecific competitors that are more likely to be resting. M2 group also ceased activity immediately following sunset and remained almost entirely silent and stationary until sunrise, except for individuals briefly producing alarm calls typically once per night (n = 4 nocturnal follows). On starting each follow day, we never observed the group to have moved away from a sleeping site during the night. Predation risk, particularly from predominantly nocturnal leopards and golden cats, may be higher at night for smaller-bodied mangabeys than bonobos (Corredor-Ospina et al., 2021). Predators should be easier to detect when group members are resting silently, meaning mangabeys may be more likely to travel throughout the day and remain stationary overnight (C. H. Brown & Waser, 2017). Subsequent studies should compare activity budgets and dietary data between mangabeys and bonobos to build on these early results and provide further insight into the niches these animals occupy.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Edward McLester ![ORCID icon] http://orcid.org/0000-0002-9283-906X

REFERENCES

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–266.

Beaune, D., Fruth, B., Bollache, L., Hohmann, G., & Bretagnolle, F. (2013). Doom of the elephant-dependent trees in a Congo tropical forest. *Forest Ecology and Management*, 295, 109–117.

Bergmüller, R. (1998). *Die Nahrungsökologie der Rauchgrauen Mangabe (Cercocebus torquatus atys): Schlüssel zur socialen Organisation?* [MSc dissertation]. Universität Erlangen-Nürnberg.

Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, 25, 504–511.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, 78, 547–573.

Boinski, S., Treves, A., & Chapman, C. A. (2000). A critical evaluation of the influence of predators on primates: Effects on group travel. In S. Boinski, & P. A. Garber (Eds.), *On the move: How and why animals travel in groups* (pp. 43–72). The University of Chicago Press.

Brown, C. H., & Waser, P. M. (2017). Primate habitat acoustics. In R. M. Quam, M. A. Ramsier, R. R. Fay, & A. N. Popper (Eds.), *Primate hearing and communication* (pp. 79–107). Springer.

Brown, M. (2013). Food and range defence in group-living primates. *Animal Behaviour*, 85, 807–816.

Bürkner, P.-C. (2021). Bayesian item response modeling in R with brms and Stan. *Journal of Statistical Software*, 100, 1–54.

Butynski, T. M. (2013). White-naped mangabey, *Cercocebus lunulatus*. In T. M. Butynski, J. Kingdon, & J. Kalina (Eds.), *Mammals of Africa, Volume 2: Primates* (pp. 182–185). Bloomsbury.

Butynski, T. M., & Mwangi, G. (1995). Census of Kenya's endangered red colobus and crested mangabey. *African Primates*, 1, 8–10.

Buzzard, P. J. (2006). Ranging patterns in relation to seasonality and frugivory among *Cercopithecus campbelli*, *C. petaurista*, and *C. diana* in the Taï forest. *International Journal of Primatology*, 27, 559–573.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519.

Chapman, C. A., & Chapman, L. J. (2000a). Constraints on group size in red colobus and red-tailed guenons: Examing the generality of the ecological constraints model. *International Journal of Primatology*, 21, 565–585.

Chapman, C. A., & Chapman, L. J. (2000b). Determinants of group size in primates: The importance of travel costs. In S. Boinski, & P. A. Garber (Eds.), *On the move: How and why animals travel in groups* (pp. 24–42). The University of Chicago Press.

Chapman, C. A., Chapman, L. J., & Wrangham, R. W. (1995). Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, 36, 59–70.

Cooke, C. A. (2012). *The feeding, ranging, and positional behaviors of Cercocebus torquatus, the red-capped mangabey, in Sette Cama Gabon: A phylogenetic perspective*. [Doctoral thesis]. The Ohio State University.

Cooke, C. A. (2014). Crab predation by red-capped mangabeys (*Cercocebus torquatus*) in Sette Cama, Gabon. *African Journal of Ecology*, 53, 378–380.

Cords, M., & Rowell, T. E. (1986). Group fission in blue monkeys of the Kakamega Forest, Kenya. *Folia Primatologica*, 46, 70–82.

Corredor-Ospina, N., Kreyer, M., Rossi, G., Hohmann, G., & Fruth, B. (2021). First report of a leopard (*Panthera pardus*)-bonobo (*Pan paniscus*) encounter at the LuiKotale study site, Democratic Republic of the Congo. *Primates*, 62, 555–562.

Devreese, L. (2011). *Many hands make light work: Foraging strategies of agile mangabeys (Cercocebus agilis) exhibiting a permanent large grouping pattern at Bai Hokou, Central African Republic*. [MSc thesis]. University of Antwerp.

Devreese, L., Huynen, M. C., Stevens, J. M. G., & Todd, A. (2013). Group size of a permanent large group of agile mangabeys (*Cercocebus agilis*) at Bai Hokou, Central African Republic. *Folia Primatologica*, 84, 67–73.

Dolado, R., Cooke, C., & Beltran, F. S. (2016). How many for lunch today? Seasonal fission-fusion dynamics as a feeding strategy in wild red-capped mangabeys (*Cercocebus torquatus*). *Folia Primatologica*, 87, 197–212.

Doran, D. (1997). Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. *International Journal of Primatology*, 18, 183–206.

Doran-Sheehy, D. M., Greer, D., Mongo, P., & Schwindt, D. (2004). Impact of ecological and social factors on ranging in Western gorillas. *American Journal of Primatology*, 64, 207–222.

Ehardt, C. L., & Butynski, T. M. (2013). Golden-bellied mangabey, *Cercocebus chrysogaster*. In T. M. Butynski, J. Kingdon & J. Kalina, (Eds.), *Mammals of Africa, Volume 2: Primates* (pp. 174–177). Bloomsbury.

Ehardt, C. L., Jones, T. P., & Butynski, T. M. (2005). Protective status, ecology and strategies for improving conservation of *Cercocebus sanjei* in the Udzungwa Mountains, Tanzania. *International Journal of Primatology*, 26, 557–583.

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., & Alsdorf, D. (2007). The shuttle radar topography mission. *Reviews of Geophysics*, 45, RG2004.

Fleagle, J. G., & McGraw, W. S. (2002). Skeletal and dental morphology of African papionins: Unmasking a cryptic clade. *Journal of Human Evolution*, 42, 267–292.

Fruth, B., Ikombe, N. B., Matshimba, G. K., Metzger, S., Muganza, D. M., Mundry, R., & Fowler, A. (2014). New evidence for self-medication in bonobos: *Manniophyton fulvum* leaf- and stemstrip-swallowing

from LuiKotale, Salonga National Park, DR Congo. *American Journal of Primatology*, 76, 146–158.

Furuichi, T. (2009). Factors underlying party size differences between chimpanzees and bonobos: A review and hypotheses for future study. *Primates*, 50, 197–209.

Galat, G., & Galat-Luong, A. (1985). La communauté de primates diurnes de la forêt de Taï, Côte-d'Ivoire. *Revue d'Écologie (La Terre et La Vie)*, 40, 3–32.

Ganas, J., & Robbins, M. M. (2005). Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: A test of the ecological constraints model. *Behavioral Ecology and Sociobiology*, 58, 277–288.

Green, S. J., Boruff, B. J., Niyigaba, P., Ndikubwimana, I., & Grueter, C. C. (2020). Chimpanzee ranging responses to fruit availability in a high-elevation environment. *American Journal of Primatology*, 82, e23119.

Hart, J. A., & Thompson, J. (2020). *Cercocebus chrysogaster*. The IUCN Red List of Threatened Species 2020. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T4207A17956177.en

Harvey, P. H., & Clutton-Brock, T. H. (1981). Primate home-range size and metabolic needs. *Behavioral Ecology and Sociobiology*, 8, 151–155.

Hashimoto, C. (1997). Context and development of sexual behavior of wild bonobos (*Pan paniscus*) at Wamba, Zaire. *International Journal of Primatology*, 18, 1–21.

Hashimoto, C., Tashiro, Y., Kimura, D., Enomoto, T., Ingmanson, E. J., Idani, G., & Furuichi, T. (1998). Habitat use and ranging of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology*, 19, 1045–1060.

Hemingway, C. A., & Bynum, N. (2005). The influence of seasonality on primate diet and ranging. In D. K. Brockman, & C. P. Schaik (Eds.), *Seasonality in primates: Studies of living and extinct human and non-human primates* (pp. 57–104). Cambridge University Press.

Hill, R. A. (2006). Thermal constraints on activity scheduling and habitat choice in baboons. *American Journal of Physical Anthropology*, 129, 242–249.

Hohmann, G., & Fruth, B. (2003). Lui Kotal—A new site for field research on bonobos in the Salonga National Park. *Pan Africa News*, 10, 25–27.

Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences*, 106, 19659–19665.

Homewood, K. M. (1976). *Ecology and Behaviour of the Tana Mangabey, Cercocebus galeritus galeritus*. [Doctoral thesis]. University College London.

Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals. *The American Naturalist*, 93, 145–159.

Inogwabini, B.-I., & Thompson, J. A. M. (2013). The golden-bellied mangabey *Cercocebus chrysogaster* (Primates: Cercopithecidae): Distribution and conservation status. *Journal of Threatened Taxa*, 5, 4069–4075.

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, 2, 143–155.

Janmaat, K. R. L. (2006). *Fruits of enlightenment: Fruit localisation strategies in wild mangabey monkeys*. [Doctoral dissertation] University of St Andrews.

Janmaat, K. R. L., Byrne, R. W., & Zuberbühler, K. (2006). Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Animal Behaviour*, 72, 797–807.

Janson, C. H., & Goldsmith, M. L. (1995). Predicting group size in primates: Foraging costs and predation risks. *Behavioral Ecology*, 6, 326–36.

JASP Team. (2021). *JASP (Version 0.16)*. https://jasp-stats.org

Johnson, C., Piel, A. K., Forman, D., Stewart, F. A., & King, A. J. (2015). The ecological determinants of baboon troop movements at local and continental scales. *Movement Ecology*, 3, 14.

Kambale Saambili, H. (1998). *Comparative feeding ecology of sympatric mangabeys (Lophocebus albigenaCercocebus galeritus agilis and) in relation to crop raiding in the Okapi Wildlife Reserve, Democratic Republic of Congo*. [MSc dissertation] Makerere University.

Kaplin, B. A. (2001). Ranging behavior of two species of guenons (*Cercopithecus lhoesti and C. mitis doggetti*) in the Nyungwe Forest Reserve, Rwanda. *International Journal of Primatology*, 22, 521–548.

Kingdon, J. (1997). *The kingdon field guide to African mammals*. Academic Press.

Kinnaird, M. F. (1990). *Behavioral and demographic responses to habitat change by the Tana River crested mangabey (Cercocebus galeritus galeritus)*. [Doctoral thesis] University of Florida.

Kinnaird, M. F. (1992). Variable resource defense by the Tana River crested mangabey. *Behavioral Ecology and Sociobiology*, 31, 115–122.

Korstjens, A. H., Lehmann, J., & Dunbar, R. I. M. (2010). Resting time as an ecological constraint on primate biogeography. *Animal Behaviour*, 79, 361–374.

Lehmann, J. (2003). Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Tai National Park, Cote d'Ivoire. *Behavioral Ecology*, 14, 642–649.

Maisels, F., Hicks, T. C., Hart, J., & Shah, N. (2020). *Cercocebus agilis*. The IUCN Red List of Threatened Species 2020. https://doi.org/10.2305/IUCN.UK.2020-1.RLTS.T136615A167735266.en

Maisels, F. G. (1996). *Synthesis of information concerning the Parc National d'Odzala, Congo. Projet Ecofac Composante Congo*. AGRECO- CTFT, Brazzaville.

Mangama-Koumba, L. B., Yoshihiro, N., Mavoungou, J. F., Akomo-Okoue, E. F., Yumoto, T., Yamagiwa, J., & M'Batchi, B. (2016). Estimating diurnal primate densities using distance sampling method in Moukalaba-Doudou National Park, Gabon. *Journal of Applied Biosciences*, 99, 9395.

Martínez-Íñigo, L., Baas, P., Klein, H., Pika, S., & Deschner, T. (2021). Home range size in central chimpanzees (*Pan troglodytes troglodytes*) from Loango National Park, Gabon. *Primates*, 62, 723–734.

Masi, S., Cipolletta, C., & Robbins, M. M. (2009). Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. *American Journal of Primatology*, 71, 91–100.

Matthews, A., & Matthews, A. (2002). Distribution, population density, and status of sympatric cercopithecids in the Campo-Ma'an area, southwestern Cameroon. *Primates*, 43, 155–168.

McCabe, G. M. (2012). *Reproductive ecology of the Sanje mangabey in the Udzungwa Mountains, Tanzania*. [Doctoral thesis]. The University of Texas at San Antonio.

McGraw, W. S. (1998). Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology*, 105, 493–510.

McGraw, W. S., Vick, A. E., & Daegling, D. J. (2011). Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (*Cercocebus atys*) in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology*, 144, 140–153.

McGraw, W. S., & Zuberbühler, K. (2007). The monkeys of the Taï Forest: An introduction. In W. S. McGraw, K. Zuberbühler & R. Noë, (Eds.), *Monkeys of the Taï Forest: An African primate community* (pp. 1–48). Cambridge University Press.

McGraw, W. S., Zuberbühler, K., & Noë, R. (2007). *Monkeys of the Taï Forest: An African primate community*. Cambridge University Press.

McLester, E. (2022). Golden-bellied mangabeys (*Cercocebus chrysogaster*) consume and share mammalian prey at LuiKotale, Democratic Republic of the Congo. *Journal of Tropical Ecology*, 38, 254–258.

McLester, E., Brown, M., Stewart, F. A., & Piel, A. K. (2019). Food abundance and weather influence habitat-specific ranging patterns in forest- and savanna mosaic-dwelling red-tailed monkeys (*Cercopithecus ascanius*). *American Journal of Physical Anthropology*, 170, 217–231.

McLester, E., Hart, J. A., & Myers Thompson, J. A. (2022). Golden-bellied mangabey, *Cercocebus chrysogaster*. In R. A. Mittermeier, K. E. Reuter, A. B. Rylands, L. Jerusalinsky, C. Schwitzer, K. B. Strier, J. Ratsimbazafy & T. Humle, (Eds.), *Primates in Peril: The World's 25 Most Endangered Primates 2022–2023*. IUCN SSC Primate Specialist Group, International Primatological Society.

Milton, K. (1993). Diet and primate evolution. *Scientific American*, *269*, 86–93.

Mitani, M. (1989). *Cercocebus torquatus*: Adaptive feeding and ranging behaviors related to seasonal fluctuations of food resources in the tropical rain forest of south-western Cameroon. *Primates*, *30*, 307–323.

Mohneke, M., & Fruth, B. (2008). Bonobo (*Pan paniscus*) density estimation in the SW-Salonga National Park, Democratic Republic of Congo: Common methodology revisited. In T. Furuichi & J. Thompson, (Eds.), *The Bonobos: Behavior, ecology, and conservation* (pp. 151–166). Springer.

Morgan, B. J. (2007). Group size, density, and biomass of large mammals in the Réserve de Faune du Petit Loango, Gabon. *African Journal of Ecology*, *45*, 508–518.

Mulavwa, M., Furuichi, T., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Idani, G., & Mwanza, N. (2008). Seasonal changes in fruit production and party size of bonobos at Wamba. In T. Furuichi, & J. Thompson (Eds.), *The bonobos: Behavior, ecology, and conservation*. Springer.

Mwamende, K. A. (2009). *Social organisation ecology and reproduction in the Sanje mangabey in the Udzungwa Mountains National Park, Tanzania*. [MSc thesis]. Victoria University of Wellington.

N'Goran, P. K., Boesch, C., Mundry, R., N'Goran, E. K., Herbinger, I., Yapi, F. A., & Kühl, H. S. (2012). Hunting, law enforcement, and African primate conservation. *Conservation Biology*, *26*, 565–571.

NASA. (2015). *Shuttle Radar Topography Mission GL1 SRTM v3.0 digital elevation model, downloaded from NASA Earthdata*. https://earthdata.nasa.gov

Oates, J. F., Whitesides, G. H., Davies, A. G., Waterman, P. G., Green, S. M., Dasilva, G. L., & Mole, S. (1990). Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology*, *71*, 328–343.

Olupot, W., Chapman, C. A., Brown, C. H., & Waser, P. M. (1994). Mangabey (*Cercocebus albigena*) population density, group size, and ranging: A twenty-year comparison. *American Journal of Primatology*, *32*, 197–205.

Paddock, C. L., Bruford, M. W., & McCabe, G. M. (2020). Estimating the population size of the Sanje mangabey (*Cercocebus sanjei*) using acoustic distance sampling. *American Journal of Primatology*, *82*, e23083.

Parker, E. J., Hill, R. A., Allan, A. T. L., Howlett, C., & Koyama, N. F. (2020). Influence of food availability, plant productivity and indigenous forest use on ranging behavior of the endangered samango monkey (*Cercopithecus albogularis schwarzi*), in the Soutpansberg Mountains, South Africa. *Integrative Zoology*, *15*, 385–400.

Pennec, F., Gérard, C., Meterreau, L., Monghiemo, C., Ngawolo, J.-C. B., Laurent, R., & Narat, V. (2020). Spatiotemporal variation in bonobo (*Pan paniscus*) habitat use in a forest–savanna mosaic. *International Journal of Primatology*, *41*, 775–799.

QGIS Development Team. (2022). *QGIS geographic information system*. Open Source Geospatial Foundation Project. http://www.qgis.org/

Quris, R. (1975). Ecologie et organisation sociale de *Cercocebus galeritus agilis* dans le nord-est du Gabon. *La Terre et La Vie, Revue d'Histoire naturelle*, *29*, 337–398.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reinartz, G. E., Ingmason, E. J., & Vervaecke, H. (2013). Gracile chimpanzee (Bonobo, Pygmy Chimpanzee), *Pan paniscus*. In T. M. Butynski, J. Kingdon & J. Kalina, (Eds.), *Mammals of Africa, Volume 2: Primates* (pp. 64–69). Bloomsbury.

Remis, M. J. (1997). Ranging and grouping patterns of a Western lowland gorilla group at Bai Hokou, Central African Republic. *American Journal of Primatology*, *43*, 111–133.

Rutte, C. (1998). *Strategien der Nahrungssuche bei der Rauchbrauen Mangabe (Cercocebus torquatuss atys)*. [MSc dissertation]. Universität Erlangen-Nürnberg, Germany.

Samuni, L., Wegdell, F., & Surbeck, M. (2020). Behavioural diversity of bonobo prey preference as a potential cultural trait. *eLife*, *9*, e59191.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*, 103–113.

Schreier, B. M., Harcourt, A. H., Coppeto, S. A., & Somi, M. F. (2009). Interspecific competition and niche separation in primates: A global analysis. *Biotropica*, *41*, 283–291.

Shah, N. (2013). Agile mangabey, *Cercocebus agilis*. In T. M. Butynski, J. Kingdon & J. Kalina, (Eds.), *Mammals of Africa, Volume 2: Primates* (pp. 170–174). Bloomsbury.

Shah, N. F. (2003). *Foraging strategies in two sympatric mangabey species (Cercocebus agilis, Lophocebus albigena)*. [Doctoral thesis] Stony Brook University.

Shultz, S., & Noë, R. (2002). The consequences of crowned eagle central-place foraging on predation risk in monkeys. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*, 1797–1802.

Struhsaker, T. T. (2017). Dietary variability in redtail monkeys (*Cercopithecus ascanius schmidti*) of Kibale National Park, Uganda: The role of time, space, and hybridization. *International Journal of Primatology*, *38*, 914–941.

Struhsaker, T. T., & Leland, L. (1988). Group fission in redtail monkeys (*Cercopithecus ascanius*) in the Kibale Forest, Uganda. In A. Gautier-Hion, F. Bourlière, J.-P. Gautier & J. Kingdon, (Eds.), *A primate radiation: Evolutionary biology of the African Guenons* (pp. 364–388). Cambridge University Press.

Thomas, S. C. (1991). Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. *Biotropica*, *23*, 68–83.

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, *27*, 1413–1432.

Wieczkowski, J. (2005). Examination of increased annual range of a Tana mangabey (*Cercocebus galeritus*) group. *American Journal of Physical Anthropology*, *128*, 381–388.

Willems, E. P., & Hill, R. A. (2009). Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology*, *90*, 546–555.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.