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RESEARCH ARTICLE

Food abundance and weather influence habitat-specific ranging patterns in forest- and savanna mosaic-dwelling red-tailed monkeys (*Cercopithecus ascanius*)

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Abstract

Objectives: Primates that live in predominantly forested habitats and open, savanna mosaics should exhibit behavioral responses to differing food distributions and weather. We compared ecological constraints on red-tailed monkey ranging behavior in forest and savanna mosaic environments. Intraspecific variation in adaptations to these conditions may reflect similar pressures faced by hominins during the Plio-Pleistocene.

Methods: We followed six groups in moist evergreen forest at Ngogo (Uganda) and one group in a savanna-woodland mosaic at the Issa Valley (Tanzania). We used spatial analyses to compare home range sizes and daily travel distances (DTD) between sites. We used measures of vegetation density and phenology to interpolate spatially explicit indices of food (fruit, flower, and leaves) abundance. We modeled DTD and range use against food abundance. We modeled DTD and at Issa hourly travel distances (HTD), against temperature and rainfall.

Results: Compared to Issa, monkeys at Ngogo exhibited significantly smaller home ranges and less variation in DTD. DTD related negatively to fruit abundance, which had a stronger effect at Issa. DTD and HTD related negatively to temperature but not rainfall. This effect did not differ significantly between sites. Home range use did not relate to food abundance at either site.

Conclusions: Our results indicate food availability and thermoregulatory constraints influence red-tailed monkey ranging patterns. Intraspecific variation in home range sizes and DTD likely reflects different food distributions in closed and open habitats. We compare our results with hypotheses of evolved hominin behavior associated with the Plio-Pleistocene shift from similar closed to open environments.

KEYWORDS

guenon, hominin adaptation, movement ecology, resource distribution, savanna-woodland mosaic

1 | INTRODUCTION

Hominin evolution is characterized by responses to environmental shifts that resulted in drier, more heterogeneous landscapes during Mio-Pliocene cooling. Specifically, behavioral and morphological adaptations such as obligate bipedalism (Isbell & Young, 1996; Rodman & McHenry, 1980), increased encephalization (Potts, 1998; Stanley, 1992), and changes in dental morphology (Grine, Sponheimer, Ungar,

Lee-Thorp, & Teaford, 2012; Teaford & Ungar, 2000) have been ascribed to hominin adaptations to the retraction of forests and a transition to open mosaics (White et al., 2009; Cerling et al., 2011; reviewed in Potts, 2013). Compared to the closed, more homogeneous forests they replaced, these open mosaic environments were hotter and more arid (Bromage & Schrenk, 1995; Passey, Levin, Cerling, Brown, & Eiler, 2010; Potts, 1998), more seasonal (Foley, Ulijaszek, & Strickland, 1993), and exhibited a wider, less abundant distribution of food (Isbell & Young, 1996). Establishing the extent to which these changes in environmental conditions could have selected for hominin adaptations is of primary interest (Antón, Potts, & Aiello, 2014).

Comparisons of extant primate behavior in closed, primarily forested habitats (hereafter, "forests") and open, savanna-woodland mosaic (hereafter, "savanna mosaic") habitats can be used to reconstruct environmental pressures under which hominins likely would have evolved because these environments resemble the two extremes of the Miocene paleoclimate (Hernandez-Aguilar, 2009; Moore, 1996; Pickering & Domínguez-Rodrigo, 2010). For forest primates that also live in savanna mosaic habitats, such studies are rare, however, and still fewer studies have directly compared habitat-specific behavior. Nonetheless, where behavioral comparisons can be made between these habitat types, ranging patterns can provide evidence of adaptations to ecological conditions (Boinski, 1987; Doran-Sheehy, Greer, Mongo, & Schwindt, 2004). These adaptations include feeding strategies (Kaplin, 2001), social and grouping patterns (Wrangham, Gittleman, & Chapman, 1993), and physiological and energetic adaptations (Nunn & Barton, 2000); all of which inform on how primates utilize and respond to the environment. Ranging patterns are also quantifiable using several well-established metrics (e.g., home range size, daily and hourly travel distances—DTD and HTD—and home range use) that can be directly compared between forests and savanna mosaic habitats.

Variation in a number of biotic (e.g., food abundance; predation risk; polyspecific associations) and abiotic (e.g., temperature; rainfall) factors between habitat types should influence ranging patterns. For example, when key foods are scarce, primates may increase home range size and/or DTD to locate high-quality foods (Chapman & Chapman, 2000b; Hemingway & Bynum, 2005). Chimpanzees (*Pan troglodytes*) in forest at Taï, Côte d'Ivoire, reduce DTD when concentrated patches of dietary important nuts are ripe and switch to feeding on leaves when both fruit and nuts are scarce (Doran, 1997). Alternatively, instead of increasing search effort, primates may reduce travel and spend more time feeding on lower quality foods. For primates with flexible diets or in comparatively food-rich environments, fallback foods may still be diverse or abundant enough that ranging patterns do not alter significantly (Alberts et al., 2005; Buzzard, 2006). For example, forest mangabeys and guenons do not adjust DTD (*Lophocebus albigena* at Kibale, Uganda, Olupot, Chapman, Waser, & Isabirye-Basuta, 1997; *Cercopithecus mitis* and *C. lhoesti* at Nyungwe, Rwanda, Kaplin, 2001) or range use (*C. campbelli*, *C. petaurista*, and *C. diana* also at Taï, Buzzard, 2006) in response to changes in fruit availability.

Food abundance should have a greater influence on ranging behavior for forest primates in savanna mosaic habitats given the wider spatio-temporal distribution of resources in these environments (Chapman & Chapman, 2000a; Copeland, 2009). This is particularly the case where the quality and diversity of available resources is low enough that diet switching is a less effective alternative than expanding home ranges or increasing DTD, even for species with diverse diets. For example, Piel et al. (2017) observed chimpanzees in savanna-woodland at the Issa Valley, Tanzania, to consume only 77 plant species compared to mean 112 species for forest populations. As such, a narrow diet and the low density of resources in open savanna mosaics is associated with extremely large home range sizes for chimpanzees (e.g., 80–200 km^2 in savanna mosaics, Baldwin, McGrew, & Tutin, 1982; Pruetz & Bertolani, 2009; Rudicell et al., 2011; Samson & Hunt, 2012; compared to 6–20 km^2 in forests, Newton-Fisher, 2003; Nakamura et al., 2013). Wide seasonal variation in resource abundance between different vegetation types in savanna mosaic habitats has also been implicated in patterns of home range use. Chimpanzees in savanna mosaics range farther and preferentially exploit woodland species during dry seasons when fruit is most abundant in woodland compared to other vegetation types (Hernandez-Aguilar, 2009; Piel et al., 2017).

Interactions with sympatric taxa should also affect group ranging. Groups should avoid areas of high predation risk, which can vary substantially throughout home ranges depending on predator density and diversity and habitat type (Willems & Hill, 2009). Polyspecific associations can reduce predation risk, as well as increase foraging efficiency (reviewed in Teelen, 2007). Because these benefits are not always conferred equally by each species within an association, some species preferentially seek out heterospecifics. Maintaining associations may therefore require increasing DTD (Chapman & Chapman, 1996) or adjusting patterns of home range use (Cords, 1987) to coordinate group movements. Similarly, groups may divert travel routes toward or away from conspecifics to initiate or avoid intergroup competition (e.g., over food patches; access to heterospecifics, Brown, 2013).

Abiotic factors influence ranging (Baoping, Ming, Yongcheng, & Fuwen, 2009; Hill & Dunbar, 2002) as individuals thermoregulate to avoid overheating in hot temperatures and energy loss from cold during rainfall (Stelzner & Hausfater, 1986). Across habitats, high temperatures are associated with reduced travel speeds and duration (yellow baboons, *P. cynocephalus*, Stelzner, 1988; Johnson, Piel, Forman, Stewart, & King, 2015; white-faced capuchins, *Cebus capucinus*, Campos & Fedigan, 2009) and determine activity schedules (yellow baboons, Hill, 2005; Hill, 2006; chimpanzees, Kosheleff & Anderson, 2009). DTD relates negatively to rainfall in both forests (red colobus, *Piliocolobus tephrosceles*, Isbell, 1983; gorillas, *Gorilla beringei beringei*, Ganas & Robbins, 2005; proboscis monkeys, *Nasalis larvatus*, Matsuda, Tuuga, & Higashi, 2009; siamangs, *Hylobates syndactylus*, and lar gibbons, *H. lar*, Raemaekers, 1980) and more heterogeneous mosaic habitats (baboons, *Papio* spp., Johnson et al., 2015). Given that temperature and rainfall ranges are more seasonally variable in savanna mosaic habitats that exhibit longer, hotter dry seasons than forests (McGrew, Baldwin, & Tutin, 1981), these conditions should be

especially strong constraints on primate movement in open environments (Hill, 2005; Wessling, Kuhl, Mundry, Deschner, & Pruetz, 2018).

Previous investigations of primate ranging support the hypothesis that ranging patterns are shaped by food distribution and weather. As such, species living in both forests and savanna mosaic habitats should exhibit intraspecific variation in ranging. We tested this hypothesis in the red-tailed monkey (*Cercopithecus ascanius*), a forest guenon that lives in wide expanses of forest as well as forest-scarce fragments and mosaics (Sarmiento, Stiner, & Brooks, 2001). Specifically, we investigated red-tailed monkeys living in two contrasting environments: a predominantly forested landscape at Ngogo, Uganda; and a comparatively heterogeneous savanna-woodland mosaic at the Issa Valley, Tanzania. First, we predicted that red-tailed monkeys at Issa exhibit larger home range sizes than at Ngogo. Second, we predicted that although food abundance and rainfall and temperature should constrain HTD and DTD at both sites, these effects are stronger at Issa than at Ngogo. Specifically, we expected Issa monkeys to exhibit shorter DTD in dry seasons and longer DTD in wet seasons compared to Ngogo monkeys in all months. Finally, we predicted that home range use at Issa is more strongly associated with spatio-temporal changes in food abundance than at Ngogo.

2 | METHODS

2.1 | Study sites

The Ngogo study site is located in the approximate center of Kibale National Park in southwestern Uganda at elevations spanning 1,110–1,590 m. The site comprises about 40 km^2 mosaic of mostly primary forest (ca. 60% cover, Wing & Buss, 1970) interspersed with isolated patches of secondary forest, woodland, swamp, and grassland (Struhsaker, 1997). Rainfall varies substantially between months and years (1977–1984 yearly $\bar{x}$: 1500 mm, Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999). Consequently, wet and dry seasons are inconsistent between years, which make identifying other seasonal patterns difficult (e.g., plant phenology, Struhsaker, 1997). Predators of red-tailed monkeys at Ngogo include raptors (e.g., crowned hawk-eagles, *Stephanoaetus coronatus*, Mitani, Sanders, Lwanga, & Windfelder, 2001) and chimpanzees (Watts & Mitani, 2002). African golden cats (*Profelis aurata*) are presumed predators but are rarely encountered (Struhsaker, 1981). We followed six habituated red-tailed monkey groups at Ngogo: groups R1 through R6 comprised between 10 and about 35 individuals including one adult male per group, except for R6 which included two adult males (see Supplementary Table S1 for detailed demographics). All six groups frequently formed polyspecific associations (≥2 heterospecifics within the periphery of the study group) with habituated gray-cheeked mangabeys (*Cercocebus albigena*) and blue monkeys (*C. mitis*; except for R5 who we never observed to associate with blue monkeys during the study period) and infrequently with unhabituated black and white colobus (*Colobus guereza*), L'Hoest's monkeys (*C. lhoestii*), and olive baboons (*P. anubis*).

The Issa Valley is located about 668 km from Ngogo in the north of the Greater Mahale Ecosystem in western Tanzania (Piel et al., 2017). Research centers around 60 km^2 area of five major valleys and surrounding flat plateaus at elevations spanning 1,150–1,712 m. Vegetation is a mosaic of mostly deciduous *Brachystegia* and *Julbernadia* spp. miombo woodland, grassland, swamp, and minimal evergreen riparian forest (4% cover, EM unpublished data). Compared to the relatively continuous expanse of forest at Ngogo, forest at Issa is restricted to riverine strips that measure <10 m wide at some locations. The region is characterized by two distinct seasons: wet from November to April and dry (<100 mm monthly rainfall) from May to October (Piel et al., 2017; see Results). Chimpanzees also prey upon red-tailed monkeys at Issa (C. Giuliano unpublished data), and possible predators include both crowned-hawk eagles and five large carnivores: leopards (*Panthera pardus*), lions (*P. leo*), African wild dogs (*Lycaon pictus*), East Africa black-backed jackal (*Canis mesomelas schmidti*), and spotted hyenas (*Crocuta crocuta*; McLester, Sweeney, Stewart, & Piel, 2018). We followed one habituated group at Issa: K0 included between one and four adult males at any one time and increased from about 35–55 total individuals during the study. Red-tailed monkeys at Issa form polyspecific associations with three unhabituated species, although associations are rare compared to Ngogo (red colobus, *P. tephrosceles*; yellow baboons, *P. cynocephalus*, n = 2 observations; vervet monkeys, *Chlorocebus pygerythrus*, n = 2 observations; EM unpublished data).

2.2 | Data collection

2.2.1 | Ranging data

We collected ranging data at Ngogo from January 2008 to December 2008 (R1–R4), March to June 2017 (R6), and July to October 2017 (R5) and at Issa from January 2013 to March 2016 (K0). At Ngogo, we followed R1–R4 for 6 consecutive days separated by 5 days (see Brown, 2011), and we followed R5 and R6 every day as far as was possible. At Issa, we followed K0 for 5 consecutive days twice monthly from January 2013 to May 2015 and for 10 consecutive days each month from June 2015 to March 2016. For each group, one researcher or at least two trained field assistants arrived at the sleeping site and followed the group from 0700 to 1900 hr. During follows at Ngogo, we recorded group locations by estimating the group center-of-mass within a 50 × 50 m gridded map at 30-min intervals (see Brown, 2013) or by recording GPS coordinates automatically at 1-min intervals using a Garmin Rino 650 GPS unit (R6 and R5). At Issa, we recorded GPS coordinates automatically at 5-min intervals using Garmin Rino 650 and Garmin Rino 520 GPS units. To account for the difference in location intervals for R1–R4 compared to R5 and R6, we analyzed these groups separately. Unless otherwise stated, we used only all-day follows (≥9 hr continuous duration) in analyses, as per Kaplin (2001).

2.2.2 | Climate data

At Ngogo, temperature and rainfall data were collected daily by the Ngogo Chimpanzee Project using an analogue mercury thermometer and an Onset digital rain gauge, respectively. At Issa, we recorded temperature at 30-min intervals using a HOBO H8 Pro logger in forest vegetation. We recorded rainfall continuously from January 2013 to July 2014 and September 2014 to March 2016 using a HOBO RG3 rain gauge in woodland.

2.2.3 | Food abundance

In 2009, 2012, and 2013 at Ngogo, we sampled 272 50 × 50 m plots located at 50 m intervals in primary forest across the extent of R6, R5, and four neighboring group home ranges. Within each plot, we identified stems of 34 plant species that were ≥1% of the red-tailed monkey or gray-cheeked mangabey diet (see Brown, 2013) and recorded the number of stems for each plant species and diameter at breast height (DBH) of each stem. We ignored stems of diameter <10 cm, except for lianas which were measured regardless of size.

Plant phenology data at Ngogo were collected from March to October 2017 by trained field assistants from the Ngogo Chimpanzee Project who walked trails monthly (see Potts, Chapman, & Lwanga, 2009; Watts, Potts, Lwanga, & Mitani, 2012). Marked plants (n = 511 stems; Supplementary Table S2) identified to species level were examined for the presence–absence of the following: ripe and unripe fruit; new, young, and mature leaves; flowers.

From 2013 to 2016 at Issa, we sampled 155 20 × 20 m plots located randomly across the extent of the study site and in both forest and woodland vegetation classes (n = 90 forest plots; n = 57 woodland plots; n = 8 forest-woodland boundary plots). Without data on red-tailed monkey diet at Issa, within each plot, we identified all stems >10 cm to species level where possible and recorded the number of stems for each plant species and DBH of each stem. Unidentifiable stems were sampled and identified by a trained botanist—Yahya Abeid—at the National Herbarium of Tanzania.

Plant phenology was sampled at Issa by trained field assistants. Three trails (lengths: 623–2,608 m; n = 2 woodland trails; n = 1 forest trail) were walked monthly in 2013–2015. From 2016, trails were replaced with marked stems distributed across the site identified as the 15 plant species most consumed by chimpanzees. Observers examined marked plants of at least 10 cm DBH and 1 m tall (n = 1,431 total stems; Supplementary Table S3) identified to species level and counted the following: ripe and unripe fruit; new, mature and old leaves; flower buds; and mature flowers.

2.3 | Data analyses

2.3.1 | Home range size

We used QGIS 2.18.6 (QGIS Development Team, 2018) to calculate paths of Euclidean distance between GPS coordinates for each follow day. For R1–R6, we used follows of any duration (minimum: R1 = 1 hr; R2 = 0.5 hr; R3 = 2 hr; R4 = 0.5 hr; R5 = 1.5 hr; R6 = 2.25 hr) to increase the sample size relative to K0. To provide parity with previous studies of primate home range sizes, we then calculated (1) 100% minimum convex polygon (MCP) of these paths and (2) the number of grid cells intersected by these paths and the sum of this area (grid cell analysis—GCA). For GCA, we used 50 × 50 m cells for R6 and R5 and 75 × 75 m cells for K0 to account for increased group spread with larger group sizes, as per Kaplin (2001).

2.3.2 | HTD and DTD

To calculate DTD, we measured DTD as the total path length for each all-day follow. To control for overestimation of path length due to variation in GPS accuracy, for R5, R6, and K0, we used only GPS coordinates at 5-min intervals (mean of 1-min interval coordinates for R5 and R6) and minimum 5 m traveled between consecutive coordinates.

We calculated HTD for K0 as the cumulative Euclidean distance between all GPS points for each complete follow hour (≥50 min). To model HTD, we calculated mean temperature and binary occurrence of rain per follow hour. To model DTD, we calculated maximum temperature and total rainfall per day.

2.3.3 | Range use and food abundance

We calculated range use as the proportion of GPS points in each grid cell across each group's home range each month (combined across years for K0). We used only all-day follows with consistent 1-min (for R6 and R5) or 5-min (for K0) intervals between GPS points in this analysis. Only one all-day follow of K0 in October met this criterion, which we excluded from the analysis.

We calculated two indices of food abundance for primary forest at Ngogo and forest and woodland at Issa. In both indices, we used only plant species for which both phenology and density data were available (n = 27 species at Ngogo; n = 65 species at Issa). For each sample plot, we converted DBH into basal area for each stem and calculated total basal area density for each species within each plot (unit: m^2 basal area/m^2 area sampled). We used these measurements as an initial index of site-wide variation in basal area density for each species. To create a second, spatially explicit index of basal area density, we then used a spatial interpolation in GRASS GIS 7.4 to interpolate home range-wide distributions of basal area density for each plant species in each vegetation class (see Supplementary Material S1; Tables S2 and S3).

We categorized phenology observations into three plant parts (fruit; flowers; leaves, as per Bryer, Chapman, & Rothman, 2013). We used binary presence–absence measures of each plant part (1) to remove observer error relating to absolute counts and (2) because fruit crop size and number of flowers and leaves are typically proportional to basal area (e.g., Rimbach et al., 2014). For both our site-wide and spatially explicit indices of basal area density, we multiplied basal area densities for each species in sample plots and grid cells, respectively, at each site by monthly proportions (0–1; at Issa, the mean monthly proportion) of stems with each plant part present. For our

spatially explicit index, we summed these weighted measurements for each plant part across all species and resampled the resulting distributions to the grids of range use for each group (Ngogo: 50 m cells, Issa: 75 m cells) using maximum plant part abundance for each species (see Supplementary Material S1).

2.3.4 | Statistical analyses

We conducted all statistical analyses in R v3.5.1 (R Core Team, 2018; see Supplementary Table S4 for a summary of model formulas). To investigate the relationship between HTD and DTD and temperature and rainfall, we used the package *nlme* (Pinheiro, Bates, Debroy, & Sarkar, 2019) to build generalized linear mixed models (GLMM) with Gaussian error distribution. To analyze HTD, we fitted HTD as the response; mean hourly temperature and hourly rainfall (binary) as predictors; and month as a random intercept effect. To analyze DTD, we fitted DTD as the response; interactions between site and maximum daily temperature and daily rainfall (binary), alongside individual main effects, as predictors; and group ID as a random intercept effect to control for variation in group size and composition. We visually inspected the correlogram and plotted residuals of HTD over time to confirm that temporal autocorrelation was not present.

To investigate the relationship between DTD and food abundance, we built a linear model with DTD as the response and interactions, including individual main effects, between group ID and monthly mean fruit and flower abundance in primary forest at Ngogo and riparian forest and woodland combined at Issa, as predictors. We did not include leaf abundance as a predictor because it was collinear with group ID (see below).

To investigate the relationship between home range use and food abundance, we used the package *spaMM* (Rousset, Ferdy, & Courtiol, 2018) to build a GLMM with negative binomial distribution to account for overdispersion. We fitted count of GPS points per grid cell as the response; total number of GPS points per month as a log-transformed offset; and interactions, including individual main effects, between group ID and fruit, flower, and leaf abundance, as predictors. To control for spatial autocorrelation in range use, we fitted a binary adjacency matrix for grid cells used each month as a random intercept effect.

For all models, we manually checked plots of residuals and fitted values and QQ-plots to check that assumptions of normally distributed residuals and homogeneity of variance had been met. We tested predictors for collinearity by calculating variation inflation factors (VIF) using the package *car* (Fox, Weisberg, & Price, 2018) in an equivalent linear model including only the fixed effects from each model. Multicollinearity was not present in any model (maximum VIF: HTD = 1.05; DTD vs. weather = 1.23; DTD vs. food abundance = 7.35, after removing leaf abundance; range use = 2.06). We centered all predictors to a mean of zero and scaled continuous predictors to a standard deviation of one to improve interpretation of main effects included in interactions, as per Schielzeth (2010). For the mixed models, we used likelihood ratio tests to test significant differences between full and null models without fixed effects, and we interpreted *t* values as *z*-scores to calculate *p* values for individual effects.

3 | RESULTS

At Ngogo, we followed R1–R4 for 1–71 days for each month across the follow period, including days on which multiple groups were followed; except R1 and R3 which we did not follow in December (Table 1). We followed R5 and R6 for four consecutive months each (R6: 9–24 days per month; R5: 14–27 days per month). At Issa, we followed K0 for 1–11 days per month, except for 3 months in which we could not locate the group.

3.1 | Home range sizes

Home range estimates approached an asymptote after about 60 days for Ngogo groups and about 110 days for K0 at Issa (Figure 1). The Ngogo groups exhibited total home ranges of 0.44–0.65 km^2 (MCP) and 0.46–0.65 km^2 (50 m GCA), respectively (Figure 2; Table 1). Compared to home ranges reported from forest environments, all six

TABLE 1 Follow periods, home range sizes calculated using 100% minimum convex polygon (MCP) and grid cell analysis (GCA) methods and daily travel distances (DTD) for each group

Study site	Group	Follow period [follow days; all-day follows]	Home range size (km^2)		DTD	
			MCP	GCA [cell size]	Mean [range] (km)	Location interval
Ngogo	R1	Jan 2008–Sep 2018 [*n* = 225; 123]	0.58	0.52 [50 m]	0.97 [0.35–2.04]	30 min
	R2	Jan 2008–Aug 2016 [*n* = 352; 250]	0.44	0.56 [50 m]	1.01 [0.27–2.01]	
	R3	Jan 2008–Aug 2016 [*n* = 255; 159]	0.54	0.52 [50 m]	0.98 [0.34–1.71]	
	R4	Jun 2008–Aug 2016 [*n* = 158; 99]	0.59	0.46 [50 m]	1.04 [0.51–1.99]	
	R5	Jul–Oct 2017 [*n* = 89; 64]	0.65	0.65 [50 m]	1.70 [0.80–2.55]	5 min; minimum 5 m
	R6	Mar–Jun 2017 [*n* = 71; 50]	0.58	0.56 [50 m]	1.76 [0.94–2.54]	
Issa Valley	K0	Jan 2013–Mar 2016 [*n* = 237; 175]	16	3.93 [75 m]	1.90 [0.36–4.13] (wet season); 1.55 [0.68–3.42] (dry season)	

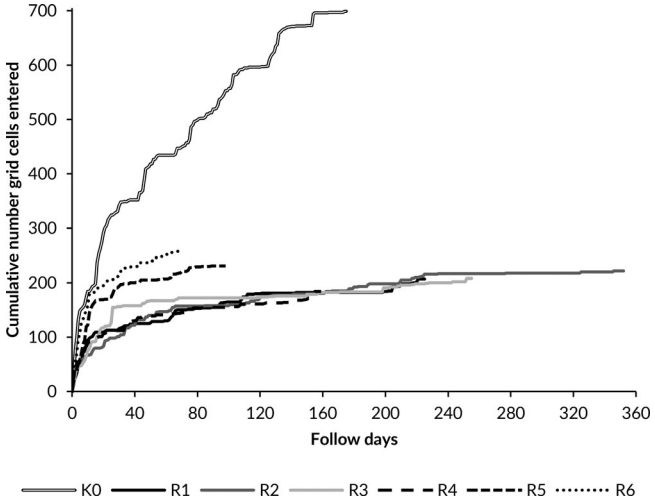

FIGURE 1 Cumulative use of home range by groups at Ngogo and Issa, calculated as number of unique 50 × 50 m grid cells and 75 × 75 m grid cells, respectively, entered per follow day

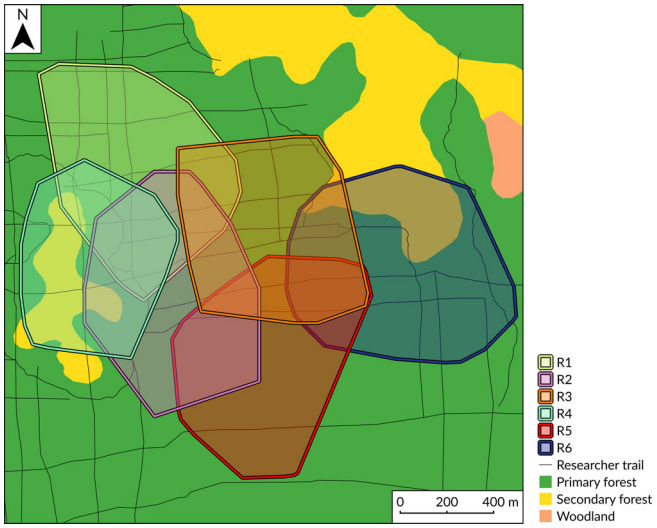

FIGURE 2 Home range sizes for Ngogo groups for the entire study period, calculated using 100% minimum convex polygons. Colored shading indicates vegetation cover. Black lines indicate selected researcher trails, included for reference

Ngogo groups exhibited home ranges larger than the average, but only R5 exhibited a home range larger than the maximum ($\bar{x}$: 0.27 km^2; maximum: 0.63 km^2 also at Ngogo; Table 2).

Compared to the Ngogo groups, K0 exhibited a substantially larger total home range of 3.93 km^2 (75 m GCA) and 16.0 km^2 (MCP; Figure 3). K0 exhibited a GCA measure 14.1 times greater than the average and 6.2 times greater than the maximum home range sizes reported from any other previous study (Table 2).

The extent of home range used per month for R6 and R5 ranged from 0.38 to 0.51 km^2 for R6 and 0.34 to 0.43 km^2 for R5 (59–79% of R6 home range; 60–76% of R5 home range; Figure 4). For K0, monthly home range use ranged from 0.06 to 1.02 km^2 (1.5–26% of K0 home range; Figure 4). K0 used a significantly greater monthly extent of its home range during the wet seasons compared to the dry seasons (Mann–Whitney: $U = 93.5$, $p = 0.036$).

3.2 | Daily travel distances

At Ngogo, DTD did not differ significantly between groups for R1–R4 (Kruskal-Wallis: $H = 4.851$, $p = 0.183$) or R5 and R6 (t-test: –0.916, $p = 0.362$). DTD differed significantly between months for R1–R4 pooled (Kruskal-Wallis: $H = 82.616$, $p < 0.001$; Figure 5) but not for R5 and R6 pooled (one-way ANOVA: $F_{7,106} = 1.178$, $p = 0.322$). K0 exhibited a significantly wider range of DTD in both wet and dry seasons than R5 and R6 (Kruskal-Wallis: $H = 16.006$, $p < 0.001$; Figure 5; Table 1) and R1–R4 (Kruskal-Wallis: $H = 214.620$, $p < 0.001$), although minimum DTD for R1–R4 was shorter than that for K0 in both seasons.

Mean DTD for R5 and R6 was longer than those reported in other studies for this species in forests, but maximum DTD was not (R5 and R6 $\bar{x}$ 1.72 km cf. $\bar{x}$ 1.28 km; R5 and R6 maximum 2.55 km cf. maximum 2.8 km at Buyangu, Kenya; Table 1; Table 2). In contrast, mean wet and dry season DTD and maximum DTD for K0 were all substantially longer (1.5, 1.2, and 1.5 times longer, respectively) than the mean and maximum DTD reported from previous studies (Table 1; Table 2).

3.3 | HTD and DTD in response to weather

During the study period at Ngogo, annual rainfall averaged 1,409 mm (mean monthly rainfall range: 33–207 mm). At Issa, annual rainfall averaged 1,012 mm (mean monthly rainfall range: 0–204 mm). Ngogo temperatures ranged from 14 to 34 °C, with a mean daily maximum temperature of 24.4 °C across all months. Issa temperatures ranged from 9.9 to 33.2 °C, with a mean daily maximum temperature of 24.7 °C in wet seasons and 28.0 °C in dry seasons.

On average, HTD for K0 peaked during from 7 to 10 a.m. and 6 to 7 p.m., corresponding with the highest daily temperatures from 1 to 4 p.m. (Figure 6). Temperature had a significant negative effect on HTD, but rainfall did not (GLMM: n = 1,228 hr; temperature, estimate = –25.075, $p < 0.001$; rainfall, estimate = –32.004, $p = 0.062$; Supplementary Table S5). Similarly, on average across both sites, temperature had a significant negative effect on DTD, but rainfall did not (GLMM: n = 425 days at Ngogo; n = 158 days at Issa; temperature, estimate = –69.222, $p < 0.001$; rainfall, estimate = –11.444, $p = 0.770$; Supplementary Table S6). Neither the effect of temperature nor rainfall on DTD differed significantly between sites (GLMM: temperature, $\chi^2 = 3.353$, df = 1, $p = 0.143$; rainfall, $\chi^2 = 0.644$, df = 1, $p = 0.422$).

3.4 | DTD and home range use in response to food abundance

Fruit, flowers, and leaves were substantially more abundant in primary forest at Ngogo than in forest or woodland at Issa, except for

TABLE 2 Comparison of red-tailed monkey ranging patterns, population densities, and group sizes from previous studies with the results of this study (CI = confidence interval; SD = standard deviation; SE = standard error; adapted in part from Tapper et al., 2019)

						Home range size			Population density			
Country	Study site	Primary vegetation	Number of study groups	Follow duration (months/group)	Mean DTD (km) [range]	Mean area (km^2) [range]	Method	% of Issa Valley GCA	Individuals/km^2	Groups/km^2	Group size [range]	Reference[a]
Central African Republic	Bangui	Lowland degraded deciduous rain forest	1	23		0.15	GCA (50 m)	3.8	117		17–23	1
Democratic Republic of Congo	Ituri Forest	Medium-altitude primary and secondary evergreen rain forest	Results from transects	6					18.9 [±4.4SE]	5.4 [±0.9SE]	3–11	2
Kenya	Kakamega (Buyangu)	Lowland primary and degraded semi-deciduous rain forest and scrub	2	12	1.80 [1.10–2.80]	0.23 [0.19–0.26]	GCA (50 m)	5.9	176	5.9	31 [30–32]	3
	Kakamega (Isecheno)	Lowland primary and regenerating semi-deciduous rain forest	4	11	1.50 [0.90–2.40]	0.36 [±0.13SD]	GCA (50 m)	9.2	72	5.2	23–26 [±9SD]	4; 5
Tanzania	Issa Valley	Medium-altitude primary woodland and evergreen riparian forest	1	39	1.75 [0.36–4.13]	3.93 16	GCA (75 m) MCP	— —	32 [25.5–40.9 95% CI]	4.5 [3.6–5.7 95% CI]	35–55	This study; 6
Uganda	Budongo (N15)	Medium-altitude primary semi-deciduous rain forest	1	4	0.96	0.2	GCA (25 m)	5.1	4.2	19.2	14 [12–18; n = 3]	7
	Budongo (N15; KP11; KP13)	Medium-altitude primary semi-deciduous rain forest	2	16	2.50 [2.43–2.56]	0.45 [0.40–0.49]	MCP	11.5	8.3		$\bar{x}$ = 13	8; 9
	Budongo (N3)	Medium-altitude logged semi-deciduous rain forest	1	4	1.3	0.2	GCA (25 m)	5.1	13.3	60	16 [13–18; n = 3]	7
	Budongo (N3; N11; B1; B4; W21; K4)	Medium-altitude logged semi-deciduous rain forest	3	16	2.25 [2.16–2.42]	0.21 [0.19–0.22]	MCP	5.3	46.4		$\bar{x}$ = 16 [14–18]	8; 9
	Kibale (K-15 & Mikana)	Medium-altitude logged evergreen rain forest	3	13	0.64	0.37 [±0.12]	Unknown	9.4	38.1	1	15 [±1]	10; 11
	Kibale (K-30)	Medium-altitude primary evergreen rain forest	3	13	0.62	0.26 [±0.04]	Unknown	6.6	135.1	4.8	28 [±1]	10; 11
	Kibale (Kanyawara)	Medium-altitude primary and secondary evergreen rain forest	>1		1.45	0.24 [0.2–0.28]	GCA (50 m)	6.1		$\bar{x}$ = 4.6	$\bar{x}$ = 35 [30–35]	12; 13; 14
			1–7	13–23	1.45 [1.09–2.03]	0.2–0.28	GCA (50 m)	5.1–7.1	140–175	4.5	$\bar{x}$ = 33 [28–35]	15; 16; 17; 18
			3	4–16		0.21 [0.16–0.25]	MCP	5.3	70–158	2.8–6.3	23 [19–29]	19; 20; 21

(Continues)

TABLE 2 (Continued)

Country	Study site	Primary vegetation	Number of study groups	Follow duration (months/group)	Mean DTD (km) [range]	Home range size			Population density			Reference[a]
						Mean area (km^2) [range]	Method	% of Issa Valley GCA	Individuals/km^2	Groups/km^2	Group size [range]	
	Kibale (Ngogo)	Medium-altitude primary and secondary evergreen rain forest	4[b]	37–63	1.57 [1.12–2.3]	0.23 [0.28–0.57]	GCA (50 m)	5.9	131.5		26 [14–35]	16; 17
			3		1.69 [±0.38]					2	$\bar{x}$ = 37 [35–40]	T. Struhsaker (unpublished data—see 4; 18)
			2[c]	29	1.00 [0.77–1.41]	0.55 [0.47–0.63]	Unknown	14			$\bar{x}$ = 36 [25–50]	22
			6	4–37	1.72 [0.80–2.55; R5 and R6]	0.56 [0.44–0.65]	MCP	14.2			$\bar{x}$ = 17 [10–35]	This study; 23

[a]1, Galat-Luong (1975); 2, Thomas (1991); 3, Gathua (2000); 4, Cords (1987); 5, Cords (1990); 6, EM unpublished data; 7, Sheppard (2000); 8, Plumptre and Reynolds (1994); 9, Plumptre, Reynolds & Bakuneeta (1997); 10, Rode, Chapman, McDowell, and Stickler (2006); 11, Chapman and Lambert (2000); 12, Struhsaker (1975); 13, Struhsaker (1978); 14, Struhsaker and Leland (1979); 15, Struhsaker (1980); 16, Struhsaker (1988); 17, Struhsaker and Leland (1988); 18, Butynski (1990); 19, Struhsaker (1997); 20, Treves (1998); 21, Wrangham, Crofoot, Lundy, and Gilby (2007); 22, Windfelder and Lwanga (2002); 23, Brown (2013).

[b]After one group (size: 35–50 individuals) fissioned during the study.

[c]After one group (size: 50 individuals) fissioned during the study.

woodland flower abundance in the dry season (Figure 7). Mean fruit and flower, but not leaf, abundance differed significantly between months in all three vegetation classes (Supplementary Table S7). At Issa, fruit and flower abundance exhibited substantial monthly variation, with peak abundance in the mid and late dry season.

On average across all groups, fruit abundance had a significant negative effect on DTD (linear model: n = 114 days at Ngogo; n = 158 days at Issa; fruit, estimate = –453.550, $p < 0.001$; Supplementary Table S8). More specifically, fruit had a significantly stronger negative effect on DTD for K0 compared to R5, but not R6 (interactions between fruit and group ID: R5, estimate = 858.250, $p < 0.001$; R6, estimate = 549.160, $p = 0.090$). Flower abundance had no effect on DTD across all groups on average (estimate = –41.020, $p = 0.481$).

GPS intervals were consistent enough for analysis of home range use in 46 all-days follows of R6 (range = 5–19 per month), 57 all-day follows of R5 (range = 10–20 per month), and 92 all-days follows of K0 (range = 4–15 per month). We did not find the effects of fruit, flower, or leaf abundance on range use to differ significantly between either group (GLMM: n = 1,017 grid cells at Nggo; n = 964 grid cells at Issa; interactions between food and group ID: fruit, $\chi^2 = 4.122$, df = 2, $p = 0.127$; flowers, $\chi^2 = 0.139$, df = 2, $p = 0.933$; leaves, $\chi^2 = 0.187$, df = 2, $p = 0.911$), nor did we find these predictors to have a significant effect on range use on average across all groups (fruit, estimate = 0.053, $p = 0.465$; flowers, estimate = –0.004, $p = 0.916$; leaves, estimate = –0.026, $p = 0.473$).

4 | DISCUSSION

4.0.1 | Home range sizes and DTD reflect food abundance

Our results indicate substantial intraspecific variation in red-tailed monkey ranging patterns between primarily forested and savanna mosaic habitats in response to both food abundance and weather. As predicted, Issa monkeys exhibited a significantly larger home range than either Ngogo group or any previously studied group. The lower abundance of at least two major dietary components in riparian forest at Issa compared to Ngogo (fruit and leaves, Figure 7) should be a primary explanation for this difference. Although Issa monkeys use both riparian forest and woodland, they are dependent on forest foods for longer periods of the year due to the relative paucity of woodland foods outside of dry months (e.g., time spent in forest cf. woodland: adult males 46% cf. 35%; adult females, subadults, juveniles 77% cf. 9%; n = 25 follow days November–December 2017, EM unpublished data). As such, the irregular spatial geometry of forest at Issa alone should lead to a larger estimate of home range size. This effect is clearly illustrated by the bias in the MCP estimate for K0, which is far larger than the GCA estimate due to including areas of woodland that the group did not use (Figure 3). Nonetheless, even when measured at a finer spatial scale (75 m grid cells), Issa monkeys still exhibited a far larger home range than forest groups. Similarly, with only a single group at Issa against which to compare, the larger group size of K0 compared to the Ngogo study groups could be

expected to explain a larger home range. However, in a previous study of K0 in 2012 when the group comprised about 35 individuals, Tapper et al. (2019) reported a home range of 0.78–1.93 km^2 after only 3 months of follows—already disproportionately larger than estimates for forest groups of similar sizes (Table 1).

In addition to a larger home range, Issa monkeys also exhibited a longer maximum DTD compared to the Ngogo groups. Reduced, more heterogeneous forest cover at Issa may result in smaller patches of fruit and flowers (Chapman & Chapman, 2000b) that are also less food-rich than at Ngogo. These patches are likely to be more rapidly depleted by monkeys at Issa—particularly given the larger group size of K0—resulting in greater daily search effort and a larger home range to meet subsistence needs (Wrangham et al., 1993). Similar to other sites, insects likely comprise an important component of red-tailed monkey diet at Issa (Bryer, Chapman, Raubenheimer, Lambert, & Rothman, 2015; AP unpublished data). Insects are typically more uniformly distributed but harder to locate than fruit, flowers, and leaves (Chapman & Chapman, 2000b). Increasing DTD may be the most efficient strategy for obtaining insects in narrow forest strips at Issa if alternatives such as expanding group spread are not possible (Isbell, 2012).

Increased food abundance should result in shorter DTD as intergroup feeding competition and rates of food depletion are reduced (Chapman & Chapman, 2000b; Janson & Goldsmith, 1995). Unlike previous studies (e.g., Buzzard, 2006; Kaplin, 2001), we found a negative effect of fruit abundance on DTD across both sites that corroborates this hypothesis. Specifically, fruit was significantly more abundant in dry seasons, which also likely explains the smaller proportions of home range used in these months. Moreover, this effect was only significantly stronger for K0 at Issa compared to the smaller Ngogo group (R5). Similar effect sizes for the two larger study groups across both sites supports the hypothesis that increased intragroup feeding competition with larger group sizes influences primate DTD to a greater extent than variation in food abundance alone.

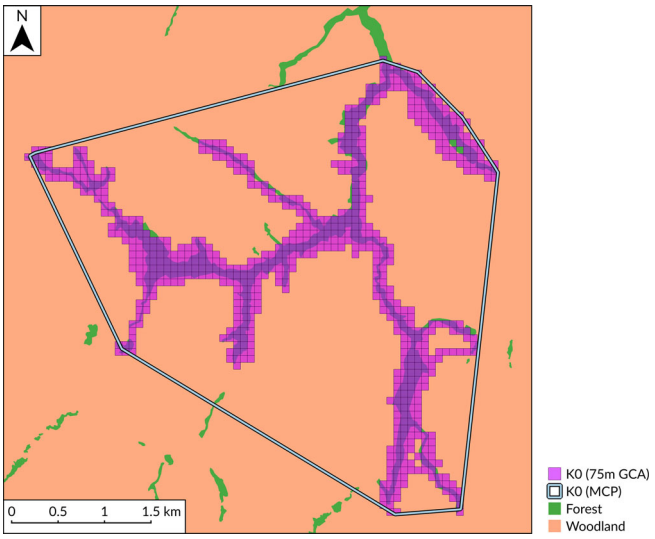

FIGURE 3 K0 home range size at Issa for the entire study period, calculated using 100% minimum convex polygon and 75 m grid cell analysis methods. Colored shading indicates vegetation cover

4.0.2 | Thermal constraints on travel distances

We also found evidence that temperature negatively influences HTD and DTD. Issa monkeys exhibited smallest monthly DTD ranges in dry season months when maximum temperatures were the highest and lowest travel speeds during highest hourly temperatures at 13–16 hr. These patterns corroborate the hypothesis that temperature should

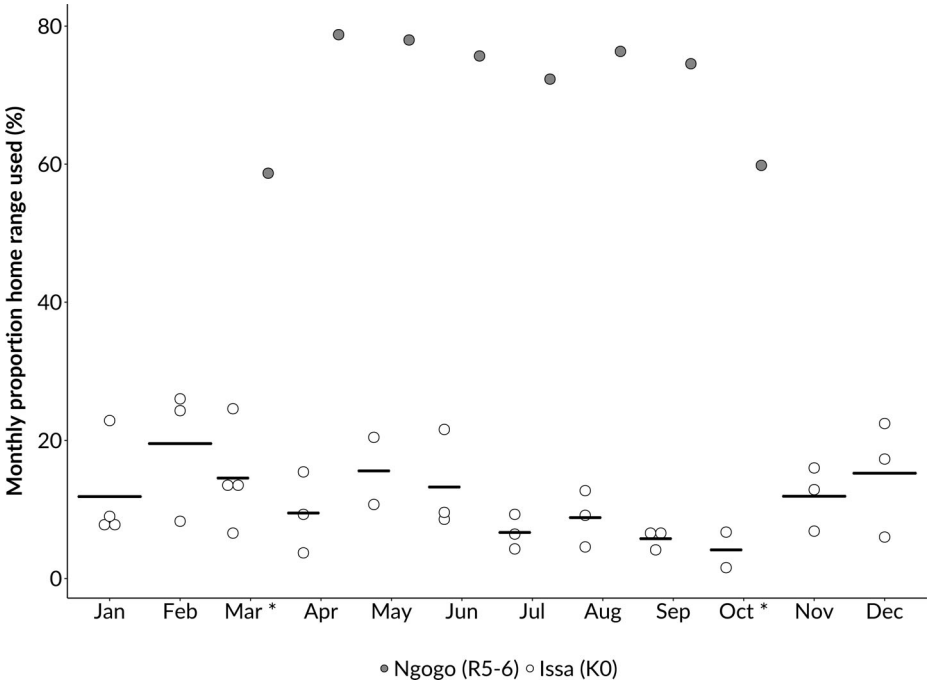

FIGURE 4 Monthly proportion of home range used by groups at Ngogo and Issa. Proportions calculated using 50 m GCA method for R6 and R5 at Ngogo and 75 m GCA method for K0 at Issa. Black bars indicate mean values. Asterisks indicate half months for follows for Ngogo groups

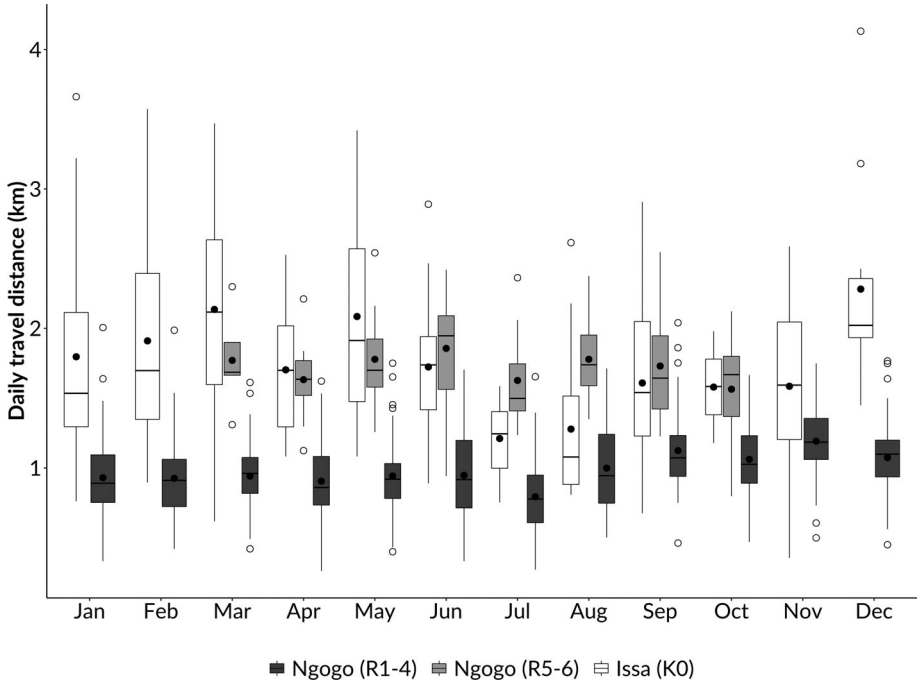

FIGURE 5 Group mean daily travel distance at Ngogo and Issa by month. Values are grouped by site and GPS interval (R1–R4: 30-min intervals; R5, R6, and K0: 5-min intervals). Black dots and circles indicate mean and outlying values, respectively

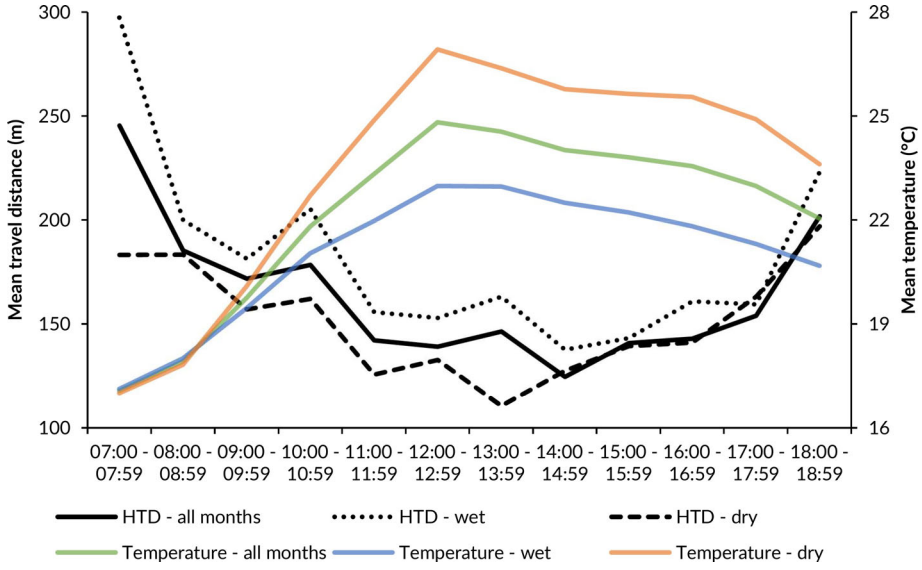

FIGURE 6 Mean hourly travel distance exhibited by K0 in wet and dry seasons and in all months combined. Colored lines indicate mean hourly temperature in wet and dry seasons and in all months combined

constrain the utilization of open vegetation (e.g., woodland) for forest primates (Pruetz, 2018; Wessling et al., 2018). As such, behavioral responses (e.g., seeking shade; reducing time spent traveling) should vary between forests and savanna mosaics (Hill, 2005). For example, savanna chimpanzees at Fongoli, Senegal, shelter in caves when temperatures are hottest (Pruetz, 2007) and preferentially utilize forest patches that provide the only sources of shade and water (Pruetz & Bertolani, 2009). Although fruit may provide most water, red-tailed monkeys drink from streams and arboreal water holes at both Ngogo and Issa. Given the lack of rain and drying up of streams for substantial periods (ca. 3 months) in the late dry season at Issa, water requirements could also limit monkey ranging. In the absence of higher resolution weather data from Ngogo, behavioral responses to heat stress at small temporal scales (e.g., hourly or minute by minute variation) remain to be compared between forest and savanna mosaic habitats.

In contrast to our third prediction, neither HTD nor DTD related to rainfall. At Issa, microhabitat variation in rainfall means that light rainfall measured in one part of the study area may not reflect heavy rainfall elsewhere that results in localized flooding (AP personal observation). Flooding rivers can restrict access to forest patches that are only reachable to monkeys by traveling terrestrially through woodland (EM, unpublished data). Conversely, in patches with more continuous canopy cover red-tailed monkey groups travel in all but the heaviest of rainfall, when visibility and vocal communication between individuals are likely limited (EM personal observation). Although primates

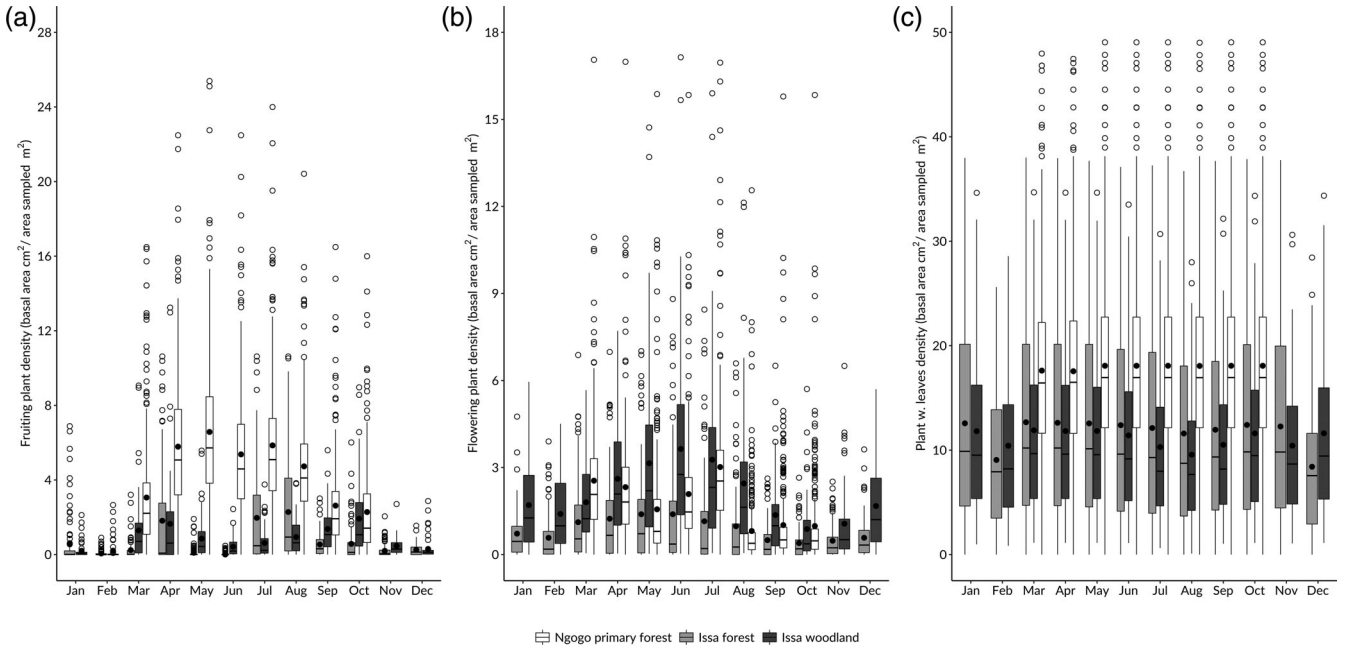

FIGURE 7 Site-wide indices of food abundance measured in sample plots at Ngogo and Issa. Shown are fruiting plant density (a), flowering plant density (b), and plant with leaves density (c) by vegetation class and month. Black dots and circles indicate mean and outlying values, respectively

should reduce travel in rain to minimize energy loss (Stelzner, 1988), in savanna mosaics, the difficulty of meeting daily nutritional requirements may mean that in food-rich areas monkeys prioritize traveling and foraging during rainfall only until maintaining group cohesion becomes difficult.

4.0.3 | Determinants of home range use

Although home range sizes and DTD reflected differences in food availability between sites, range use did not relate to food abundance at Ngogo or Issa despite significant monthly variation in fruit and flower availability. At Ngogo, the relatively high availability of food may mean that resource depletion does not significantly limit time spent at a patch; similar to the consistent patterns of DTD and proportions of home range used. At Issa, higher resolution data on diet composition may be needed to investigate the effect of other foods, such as insects. Insects comprise an important component of red-tailed monkey diet at Ngogo (Struhsaker, 2017), particularly as fall-back foods (Rothman, Raubenheimer, Bryer, Takahashi, & Gilbert, 2014). If insects are distributed more heterogeneously than fruit, flowers, and leaves, then insect abundance should influence range use to a greater extent than these plant parts. This relationship should also vary between forests and more open environments given inter-habitat differences in insect availability. At Issa, for example, insect abundance likely varies between vegetation types given that monkeys are known to exploit woodland locusts driven into riparian forest by dry season fires (FS personal observation).

We included all identifiable plant species in our measures of food abundance at Issa because the species that comprise monkey diet are not yet identified. This approach could have led to overestimations of food availability, masking an effect on range use. At Ngogo, food abundance indexed with similar phenology methods does not relate to energy balance (urinary c-peptide levels) in red-tailed monkeys either (MB unpublished data), suggesting that controlling for species-specific diet composition is also important even in food-rich forests. For example, although we averaged variation in plant part presence for each species per month, future studies should account for intra-specific phenological variation across even relatively small spatial scales at Ngogo (Brown, 2011). Competition from six other larger-bodied primates may also have negated the influence of plant parts that we identified as present but were consumed by other species or ignored due to diet switching (Brown, 2013).

Range use may also be influenced by factors other than food abundance. In our models, we considered all patches (grid cells) equally regardless of vegetation type or position in the home range (periphery vs. core). At Issa, however, forest configuration and a large home range mean that monkeys may not travel to distant patches if reducing DTD and increasing group spread are more efficient alternatives (Ganas & Robbins, 2005). Potential predators are frequently encountered by red-tailed monkeys at both sites (e.g., chimpanzees; crowned-hawk eagles, Mitani et al., 2001; Watts & Mitani, 2002; McLester et al., 2018). Anti-predator responses include hiding or changing group travel direction (Cords, 1987), which affect time spent in an area. Moreover, predation risk should differ between savanna mosaic and forest habitats (Dunbar, 1988). For example, Issa monkeys use isolated forest patches that are only accessible by traveling terrestrially through woodland. Groups pause travel at forest peripheries for substantial periods of time while scanning the immediate area or

waiting for predators to leave before moving between patches, typically running without stopping (EM personal observation). Similarly, intergroup encounters—frequently over access to blue monkeys and gray-cheeked mangabeys (Brown, 2011)—occur along home range peripheries, which can result in abrupt changes of direction depending on the outcome or preemptive avoidance (Brown, 2013).

4.0.4 | Hominin adaptations to savanna mosaic environments

Our results provide insight into environmental pressures that hominins (e.g., *Ardipithecus*, *Paranthropus*, and early *Homo* spp.) would have faced in similar paleoenvironments (Antón et al., 2014; Leonard & Robertson, 1997). Furthermore, although red-tailed monkeys are phylogenetically distant to hominins, our results indicate similarities between strategies exhibited by monkeys and those predicted for later hominins (e.g., *Homo*) in coping with these pressures. For example, thermoregulation has been implicated as an important driver of hominin evolution (e.g., Passey et al., 2010; Wheeler, 1992; Wheeler, 1994). Exploiting open vegetation (e.g., woodland) foods should have resulted in increased thermal stress due to reduced shade and greater travel distances to obtain scarcely distributed resources (Ruxton & Wilkinson, 2011). Although monkeys primarily use riparian forest at Issa, we found temperature still negatively affected travel speed. This relationship is similar to that predicted for hominins, which should have reduced activity and sought shade during peak daily temperatures (Wheeler, 1994).

Food distribution should also have been a significant determinant in the behavior of early *Homo* species, given the substantial increase in energy expenditure in *H. erectus* compared to the australopithecines (Leonard & Robertson, 1997). We ascribed the larger home range size and range of DTD for Issa monkeys to the less abundant and more seasonally variable distribution of food in a savanna mosaic habitat. These results reflect hypothesized increases in hominin home range sizes and DTD that would have been necessary to support foraging effort for scarcer resources in savanna mosaic environments (Rose & Marshall, 1996). Such differences in spatial requirements for primates in forests and savanna mosaics also support predicted decreases in hominin population density with the expansion of open environments (Grove, Pearce, & Dunbar, 2012), as illustrated by extant variation (Table 1).

In addition to increasing home range, primates may also expand dietary breadth to cope with the wide distribution of resources that characterize drier, mosaic habitats. In a comparative study of hominin dietary niches, Nelson and Hamilton (2018) showed that early hominins (e.g., *Ardipithecus*) most closely resemble modern chimpanzee niche-space in the types and amounts of resources they consume, whereas later hominin species may have exploited aquatic sources (see also Braun et al., 2010) to meet subsistence requirements, expanding their dietary niche and gradually becoming more generalist over time (Roberts & Stewart, 2018). Subsequent analyses that incorporate red-tailed monkey food source distribution and diversity should reveal whether dietary composition, in addition to home range sizes, also differs between forest and savana mosaic populations. Moreover, dental microwear and isotopic comparison of the available plants in these forests should provide extant analogues for comparisons of especially contemporaneous fossil hominins (sensu Lee-Thorp, Sponheimer, & van der Merwe, 2003). Comparing these data from more groups across a finer vegetation, gradient should further clarify the extent to which ecological conditions have influenced both extant and extinct primate behavioral adaptations.

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DATA AVAILABILITY STATEMENT

The data analyzed in this study are available from the corresponding author on reasonable request and with consent from other authors as appropriate.

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SUPPORTING INFORMATION

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

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