



LJMU Research Online

McLester, E, Brown, M, Stewart, FA and Piel, AK

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

<http://researchonline.ljmu.ac.uk/id/eprint/11193/>

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

McLester, E, Brown, M, Stewart, FA and Piel, AK (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 (2). pp. 217-231. ISSN 1096-8644

LJMU has developed [LJMU Research Online](#) for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact researchonline@ljmu.ac.uk

<http://researchonline.ljmu.ac.uk/>

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

3

4 Running title: Red-tailed monkey ranging patterns

5

6 Edward McLester ^{a*}, Michelle Brown ^b, Fiona A. Stewart ^{a, c} & Alex K. Piel ^{a, c}

7

8 ^a School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK

9 ^b Department of Anthropology, University of California, Santa Barbara, USA

10 ^c Greater Mahale Ecosystem Research and Conservation Project, Box 60118, Dar es Salaam, Tanzania

11

12 * Corresponding author

13

14 Correspondence to: Edward McLester, School of Natural Sciences and Psychology, Liverpool John
15 Moores University, Byrom Street, L33AF, UK

16

17 Email: e.mclester@2016.ljmu.ac.uk

18

19 **Abstract**

20
21 **Objectives:** Primates that live in predominantly forested habitats and open, savanna mosaics should
22 exhibit behavioral responses to differing food distributions and weather. We compared ecological
23 constraints on red-tailed monkey ranging behavior in forest and savanna mosaic environments. Intra-
24 specific variation in adaptations to these conditions may reflect similar pressures faced by hominins
25 during the Plio-Pleistocene.

26
27 **Methods:** We followed six groups in moist evergreen forest at Ngogo (Uganda), and one group in a
28 savanna-woodland mosaic at the Issa Valley (Tanzania). We used spatial analyses to compare home
29 range sizes and daily travel distances (DTD) between sites. We used measures of vegetation density
30 and phenology to interpolate spatially explicit indices of food (fruit, flower, and leaves) abundance. We
31 modeled DTD and range use against food abundance. We modeled DTD and at Issa hourly travel
32 distances (HTD), against temperature and rainfall.

33
34 **Results:** Compared to Issa, monkeys at Ngogo exhibited significantly smaller home ranges and less
35 variation in DTD. DTD related negatively to fruit abundance, which had a stronger effect at Issa. DTD
36 and HTD related negatively to temperature but not rainfall. This effect did not differ significantly
37 between sites. Home range use did not relate to food abundance at either site.

38
39 **Conclusions:** Our results indicate food availability and thermoregulatory constraints influence red-
40 tailed monkey ranging patterns. Intra-specific variation in home range sizes and DTD likely reflects
41 different food distributions in closed and open habitats. We compare our results with hypotheses of
42 evolved hominin behavior associated with the Plio-Pleistocene shift from similar closed to open
43 environments.

44
45 Key words: guenon; movement ecology; resource distribution; savanna-woodland mosaic; hominin
46 adaptation

47
48 **Introduction**

49
50 Hominin evolution is characterized by responses to environmental shifts that resulted in drier, more
51 heterogeneous landscapes during Mio-Pliocene cooling. Specifically, behavioral and morphological
52 adaptations such as obligate bipedalism (Rodman & McHenry, 1980; Isbell & Young, 1996),
53 increased encephalization (Stanley, 1992; Potts, 1998), and changes in dental morphology (Teaford &
54 Ungar, 2000; Grine, Sponheimer, Ungar, Lee-Thorp, & Teaford, 2012) have been ascribed to hominin
55 adaptations to the retraction of forests and a transition to open mosaics (White et al., 2009; Cerling et
56 al., 2011; reviewed in Potts, 2013). Compared to the closed, more homogeneous forests they
57 replaced, these open mosaic environments were hotter and more arid (Bromage & Schrenk, 1995;
58 Potts, 1998; Passey, Levin, Cerling, Brown, & Eiler, 2010), more seasonal (Foley, Ulijaszek, &
59 Strickland, 1993), and exhibited a wider, less abundant distribution of food (Isbell & Young, 1996).
60 Establishing the extent to which these changes in environmental conditions could have affected
61 selection pressures that drove hominin adaptations is of primary interest (Antón, Potts, & Aiello,
62 2014).

63 Comparisons of extant primate behavior in closed, primarily forested habitats (hereafter,
64 “forests”) and open, savanna-woodland mosaic (hereafter, “savanna mosaic”) habitats can be used to
65 reconstruct environmental pressures under which hominins likely would have evolved because these
66 environments resemble the two extremes of the Miocene paleoclimate (Moore, 1996; Hernandez-
67 Aguilar, 2009; Pickering & Domínguez-Rodrigo, 2010). For forest primates that also live in savanna
68 mosaic habitats, such studies are rare, however, and still fewer studies have directly compared
69 habitat-specific behavior. Nonetheless, where behavioral comparisons can be made between these
70 habitat types, ranging patterns can provide evidence of adaptations to ecological conditions (Boinski,
71 1987; Doran-Sheehy, Greer, Mongo, & Schwindt, 2004). These adaptations include feeding strategies
72 (Kaplin, 2001), social and grouping patterns (Wrangham, Gittleman, & Chapman, 1993), and
73 physiological and energetic adaptations (Nunn & Barton, 2000); all of which provide insight into how
74 primates utilize and respond to their immediate environment. Ranging patterns are also quantifiable
75 using several well-established metrics (e.g. home range size, daily and hourly travel distances – DTD
76 and HTD – and home range use); the determinants of which can then be directly compared between
77 forests and savanna mosaic habitats.

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

92 Food abundance should have a greater influence on ranging behavior for forest primates in
93 savanna mosaic habitats given the wider spatio-temporal distribution of resources in these
94 environments (Chapman & Chapman, 2000a; Copeland, 2009). This is particularly the case where the
95 quality and diversity of available resources is low enough that diet switching is a less effective
96 alternative than expanding home ranges or increasing DTD, even for species with diverse diets. For
97 example, Piel et al. (2017) observed chimpanzees in savanna-woodland at the Issa Valley, Tanzania,
98 to consume only 77 plant species compared to mean 112 species for forest populations. As such, a
99 narrow diet and the low density of resources in open savanna mosaics is associated with extremely
100 large home range sizes for chimpanzees (e.g. 80-200km² in savanna mosaics – Baldwin, McGrew, &
101 Tutin, 1982; Pruett & Bertolani, 2009; Rudicell et al., 2011; Samson & Hunt, 2012; compared to 6-
102 20km² in forests – Newton-Fisher, 2003; Nakamura et al., 2013). Wide seasonal variation in resource
103 abundance between different vegetation types in savanna mosaic habitats has also been implicated
104 in patterns of home range use. Chimpanzees in savanna mosaics range farther and preferentially
105 exploit woodland species during dry seasons when fruit is most abundant in woodland compared to
106 other vegetation types (Hernandez-Aguilar, 2009; Piel et al., 2017).

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

117 Abiotic factors such as temperature and rainfall influence ranging (Hill & Dunbar, 2002;
118 Baoping, Ming, Yongcheng, & Fuwen, 2009) as individuals thermoregulate to minimize energy loss
119 (Stelzner & Hausfater, 1986). Groups should adjust travel activity to optimal temperatures to avoid
120 overheating or excessive cold (e.g. due to rain). Across habitats, high temperatures are associated
121 with reduced travel speeds and duration (yellow baboons, *P. cynocephalus* – Stelzner, 1988;
122 Johnson, Piel, Forman, Stewart, & King, 2015; white-faced capuchins, *Cebus capucinus* – Campos &
123 Fedigan, 2009) and determine activity schedules (yellow baboons – Hill, 2005; Hill, 2006;
124 chimpanzees – Kosheleff & Anderson, 2009). DTD relates negatively to rainfall in both forests (red
125 colobus, *Piliocolobus tephrosceles* – Isbell, 1983; gorillas, *Gorilla beringei beringei* – Ganas &
126 Robbins, 2005; proboscis monkeys, *Nasalis larvatus* – Matsuda, Tuuga, & Higashi, 2009; siamangs,
127 *Hylobates syndactylus*, and lar gibbons, *H. lar* – Raemaekers, 1980) and more heterogeneous mosaic
128 habitats (baboons, *Papio* spp. – Johnson et al., 2015). Given that temperature and rainfall ranges are
129 more seasonally variable in savanna mosaic habitats that exhibit longer, hotter dry seasons than
130 forests (McGrew, Baldwin, & Tutin, 1981), these conditions should be especially strong constraints on
131 primate movement in open environments (Hill, 2005; Wessling, Kuhl, Mundry, Deschner, & Pruett,
132 2018).

133 Previous investigations of primate ranging support the hypothesis that ranging patterns are
134 shaped and constrained by food distribution and climate. As such, species living in both forests and
135 savanna mosaic habitats should exhibit intra-specific variation in ranging. We tested this hypothesis in
136 the red-tailed monkey (*Cercopithecus ascanius*), a forest guenon that lives in predominantly forested
137 habitats as well as forest-scarce fragments and mosaics (Sarmiento, Stiner, & Brooks, 2001).

138 Specifically, we investigated red-tailed monkeys living in two contrasting environments: a mainly
139 forested landscape at Ngogo, Uganda; and a comparatively heterogeneous savanna-woodland
140 mosaic at the Issa Valley, Tanzania. First, we predicted that red-tailed monkeys at Issa exhibit larger
141 home range sizes than at Ngogo. Second, we predicted that while food abundance and rainfall and
142 temperature should constrain HTD and DTD at both sites, these effects are stronger at Issa than at
143 Ngogo. Specifically, we expected Issa monkeys to exhibit shorter DTD in dry seasons and longer DTD
144 in wet seasons compared to Ngogo monkeys in all months. Finally, we predicted that home range use
145 at Issa is more strongly associated with spatio-temporal changes in food abundance than at Ngogo.
146

147 **Methods**

148 **Study sites**

149 The Ngogo study site is located in the approximate center of Kibale National Park in southwestern
150 Uganda at elevations spanning 1110 – 1590m. The site comprises a ca. 40km² mosaic of mostly
151 primary forest interspersed with isolated patches of secondary forest, woodland, swamp, and
152 grassland (Struhsaker, 1997). Rainfall varies substantially between months and years (1977 – 1984
153 yearly \bar{x} : 1500mm – Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999). Consequently, wet
154 and dry seasons are inconsistent between years, which makes identifying other seasonal patterns
155 difficult (e.g. plant phenology – Struhsaker, 1997). Predators of red-tailed monkeys at Ngogo include
156 raptors (e.g. crowned hawk-eagles, *Stephanoaetus coronatus* – Mitani, Sanders, Lwanga, &
157 Windfelder, 2001) and chimpanzees (Watts & Mitani, 2002). African golden cats (*Caracal aurata*) are
158 presumed predators but are rarely encountered (Struhsaker, 1981). We followed six habituated red-
159 tailed monkey groups at Ngogo: groups R1 through R6 comprised between 10 and ca. 35 individuals
160 in total including one adult male per group, except for R6 which included two adult males (see
161 supplementary Table S1 for detailed demographics). All six groups frequently formed polyspecific
162 associations (≥ 2 heterospecifics within the periphery of the study group) with habituated gray-cheeked
163 mangabeys (*Cercocebus albigena*) and blue monkeys (*C. mitis*; except for R5 who we never
164 observed to associate with blue monkeys during the study period) and infrequently with unhabituated
165 black and white colobus (*Colobus guereza*), L'Hoest's monkeys (*C. lhoestii*), and olive baboons (*P.*
166 *anubis*),
167

168 The Issa Valley is located ca. 668km from Ngogo in the north of the Greater Mahale
169 Ecosystem in western Tanzania (Piel et al., 2017). Research centers around a ca. 60km² area of five
170 major valleys and surrounding flat plateaus at elevations spanning 1150 – 1712m. Vegetation is a
171 mosaic of mostly deciduous *Brachystegia* and *Julbernardia* spp. miombo woodland, grassland,
172 swamp, and minimal evergreen riparian forest (4% cover – EM unpublished data). Compared to the
173 relatively continuous expanse of forest at Ngogo, forest at Issa is restricted to riverine strips that
174 measure <10m wide at some locations. The region is characterized by two distinct seasons: wet from
175 November to April and dry (<100mm monthly rainfall) from May to October (Piel et al., 2017; see
176 Results). Chimpanzees also prey upon red-tailed monkeys at Issa (C. Giuliano unpublished data) and
177 possible predators include both crowned-hawk eagles and five large carnivores: leopards (*Panthera*.
178 *pardus*), lions (*P. leo*), African wild dogs (*Lycaon pictus*), East Africa black-backed jackal (*Canis*
179 *mesomelas schmidtii*), and spotted hyenas (*Crocuta crocuta*; McLester, Sweeney, Stewart, & Piel,
180 2018). We followed one habituated group at Issa: K0 included between one and five adult males at
181 any one time and increased from ca. 35 to 55 total individuals over the study period. Red-tailed
182 monkeys at Issa form polyspecific associations with three unhabituated species, although
183 associations are rare compared to Ngogo (red colobus, *P. tephrosceles*; yellow baboons, *P.*
184 *cynocephalus* – $n = 1$ observation; vervet monkeys, *Chlorocebus pygerythrus* – $n = 2$ observations;
185 EM unpublished data).
186

187 **Data collection**

188 **Ranging data**

189 We collected ranging data at Ngogo from January 2008 to December 2008 (R1 – R4), March to June
190 2017 (R6), and July to October 2017 (R5), and at Issa from January 2013 to March 2016 (K0). At
191 Ngogo, we followed R1 – R4 for six consecutive days separated by five days (see Brown, 2011), and
192 we followed R5 and R6 every day as far as was possible. At Issa, we followed K0 for 5 consecutive
193 days twice monthly from January 2013 to May 2015, and for 10 consecutive days each month from
194 June 2015 to March 2016. For each group, one researcher or at least two trained field assistants
195 arrived at the sleeping site and followed the group from 0700 – 1900 h. During follows at Ngogo, we
196 recorded group locations by estimating the group center-of-mass within a 50 x 50 m gridded map at
197 30-minute intervals (see Brown, 2013) or by recording GPS coordinates automatically at 1-minute

198 intervals using a Garmin Rino 650 GPS unit (R6 and R5). At Issa, we recorded GPS coordinates
199 automatically at 5-minute intervals using Garmin Rino 650 and Garmin Rino 520 GPS units. To
200 account for the difference in location intervals for R1 – R4 compared to R5 and R6, we analyzed
201 these groups separately. Unless otherwise stated, we used only all-day follows (≥ 9 hour continuous
202 duration) in analyses, as per Kaplin (2001).

203

204 *Climate data*

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

210

211 *Food abundance*

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

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

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

229 Plant phenology was sampled at Issa by trained field assistants. Three trails (lengths: 623 –
230 2608m; $n = 2$ woodland trails; $n = 1$ forest trail) were walked monthly in 2013 – 2015. From 2016,
231 trails were replaced with marked stems distributed across the site identified as the fifteen plant
232 species most consumed by chimpanzees. Observers examined marked plants of at least 10cm DBH
233 and one meter tall ($n = 1431$ total stems; supplementary Table S3) identified to species level and
234 counted the following: ripe and unripe fruit; new, mature and old leaves; flower buds and mature
235 flowers.

236

237 *Data analyses*

238 *Home range size*

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

247

248 *Hourly and daily travel distances*

249 To calculate DTD, we measured DTD as the total path length for each all-day follow. For R5, R6 and
250 K0, we used only GPS coordinates at 5-minute intervals to control for overestimation of path length
251 due to variation in GPS accuracy, which is exacerbated by short time intervals between recording
252 coordinates. For R6 and R5, we averaged coordinates recorded every minute by 5-minute intervals.

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

257

258 *Range use and food abundance*

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

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

272 We categorized phenology observations of plant parts into three foods (fruit; flowers; leaves –
273 as per Bryer, Chapman, & Rothman, 2013). We used binary presence-absence measures of each
274 plant part 1) to remove observer error relating to absolute counts, and 2) because fruit crop size and
275 number of flowers and leaves are typically proportional to basal area (e.g. Rimbach et al., 2014). For
276 both our site-wide and spatially explicit indices of basal area density, we multiplied basal area
277 densities for each species in sample plots and grid cells, respectively, at each site by monthly
278 proportions (0-1; at Issa, the mean monthly proportion) of stems with each plant part present. For our
279 spatially explicit index, we summed these weighted measurements for each plant part across all
280 species and resampled the resulting distributions to the grids of range use for each group (Ngogo:
281 50m cells, Issa: 75m cells) using maximum plant part abundance for each species (see
282 supplementary material S1).

283
284 *Statistical analyses*

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

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

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

307 For all models, we manually checked plots of residuals and fitted values, and QQ-plots to
308 check that assumptions of normally distributed residuals and homogeneity of variance had been met.
309 We tested predictors for collinearity by calculating variation inflation factors (VIF) using the package
310 *car* (Fox, Weisberg, & Price, 2018) in an equivalent linear model including only the fixed effects from
311 each model. Multicollinearity was not present in any model (maximum VIF: HTD = 1.05; DTD vs.
312 weather = 1.48; DTD vs. food abundance = 6.07, after removing leaf abundance; range use = 8.73).
313 We centered all predictors to a mean of zero and scaled continuous predictors to a standard deviation
314 of one to improve interpretation of main effects included in interactions, as per Schielzeth (2010). For
315 the mixed models, we used likelihood ratio tests to test significant differences between full and null
316 models without fixed effects, and we interpreted t values as z-scores to calculate p values for
317 individual effects.

318
319
320
321
322
323
324
325
326
327
328
329
330
331
332
333
334
335
336
337
338
339
340
341
342
343
344
345
346
347
348
349
350
351
352
353
354
355
356
357
358
359
360
361
362
363
364
365
366
367
368
369
370
371
372
373
374
375
376
377

Results

At Ngogo, we followed R1 – R4 for between 71 – 352 days (1 – 71 days for each month across the follow period, including days on which multiple groups were followed; except R1 and R3 which were not followed in December; Table 1). We followed R5 and R6 continuously for four months each (R6: 9 – 24 days per month; R5: 14 – 27 days per month). At Issa, we followed K0 for a total of 237 days (1 – 11 days per month). We could not locate K0 in 3 out of 39 months.

Home range sizes

The cumulative number of unique grid cells entered by the Ngogo groups approached an asymptote after ca. 40 days (Figure 1). For K0, this rate began to slow after ca. 110 days, although the group still entered ca. 100 more unique grid cells on two further occasions.

The Ngogo groups exhibited total home ranges of 0.44 – 0.65km² (MCP), and 0.46 – 0.65km² (50m GCA), respectively (Figure 2; Table 1). In comparison to other home range sizes reported for this species in forest environments, all six Ngogo groups exhibited home ranges larger than the average, but only R5 exhibited a home range larger than the maximum (\bar{x} : 0.27km²; maximum: 0.63km² also at Ngogo; Table 2).

Compared to the Ngogo groups, K0 exhibited a substantially larger total home range of 3.93km² (75m GCA) and 16.0km² (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 0.38km² to 0.51km² for R6 and 0.34km² to 0.43km² 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 – 1.02km² (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: $U = 93.5$, $p = 0.036$).

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: -0.717 , $p = 0.475$). 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: $F_{7, 106} = 1.255$, $p = 0.280$). K0 exhibited a significantly wider range of DTD in both wet and dry seasons than R5 and R6 (Kruskal-Wallis: $H = 13.672$, $p = 0.001$; Figure 5; Table 1) and R1 – R4 (Kruskal-Wallis: $H = 270$, $p < 0.001$), 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} 1.83km cf. \bar{x} 1.28km; R5 and R6 maximum 2.62km cf. maximum 2.8km at Buyangu, Kenya; Table 1; Table 2). In contrast, mean wet and dry season DTD and maximum DTD for K0 were all substantially longer (1.6, 1.3, and 1.5 times longer, respectively) than the mean and maximum DTD reported from previous studies (Table 1; Table 2).

Hourly and daily travel distances in response to weather

During the study period at Ngogo, annual rainfall averaged 1409mm (mean monthly rainfall range: 33 – 207mm). At Issa, annual rainfall averaged 1012mm (mean monthly rainfall range: 0 – 204mm). Ngogo temperatures ranged from 14 – 34°C, with a mean daily maximum temperature of 24.4°C across all months. Issa temperatures ranged from 9.9 – 33.2°C, with a mean daily maximum temperature of 24.7°C in wet seasons and 28.0°C in dry seasons.

Annually and in both wet and dry seasons, HTD for K0 peaked during the early morning (7 – 10am) and late evening (6 – 7pm) on average (Figure 6). HTD was shortest between 1 – 4pm, corresponding with a plateau in daily temperature at that time. Temperature had a significant negative effect on HTD but rainfall did not (GLMM: $n = 1228$ hours; 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: $n = 583$ days; temperature – estimate = -64.860 , $p = 0.002$; rainfall – estimate = -19.337 , $p = 0.628$; supplementary Table S6). Neither the effect of temperature nor rainfall on DTD differed significantly between sites (GLMM: temperature – estimate = -65.266 , $p = 0.143$; rainfall – estimate = 53.204 , $p = 0.567$).

Daily travel distances and home range use in response to food abundance

378 Fruit, flowers, and leaves were substantially more abundant in primary forest at Ngogo than in forest
379 or woodland at Issa, except for woodland flower abundance in the dry season (Figure 7). Mean fruit
380 and flower, but not leaf, abundance differed significantly between months in all three vegetation
381 classes (supplementary Table S7). At Issa, fruit and flower abundance exhibited substantial monthly
382 variation, with peak abundance in the mid and late dry season.

383 On average across all groups, fruit abundance had a significant negative effect on DTD
384 (linear model: $n = 272$ days; fruit – estimate = -375.470 , $p < 0.001$; supplementary Table S8). More
385 specifically, fruit had a significantly stronger negative effect on DTD for K0 compared to R5, but not
386 R6 (linear model interactions between fruit and group ID: R5 – estimate = 691.970 , $p < 0.001$; R6 –
387 estimate = 301.800 , $p = 0.324$). Flower abundance did not relate significantly to DTD for any group
388 (linear model: estimate = 7.240 , $p = 0.922$).

389 GPS intervals were consistent enough for analysis of home range use in 46 all-days follows of
390 R6 (range = 5 – 19 per month), 57 all-day follows of R5 (range = 10 – 20 per month), and 92 all-days
391 follows of K0 (range = 4 – 15 per month). We did not find the effects of fruit, flower, or leaf abundance
392 on range use to differ significantly between either group (GLMM: $n = 1032$ grid cells at Ngogo; $n = 969$
393 grid cells at Issa; interactions between food and group ID: fruit – $\chi^2 = 0.638$, $df = 2$, $p = 0.727$; flowers
394 – $\chi^2 = 1.667$, $df = 2$, $p = 0.435$; leaves – $\chi^2 = 1.230$, $df = 2$, $p = 0.541$), nor did we find these
395 predictors to have a significant effect on range use on average across all groups (GLMM: fruit –
396 estimate = -0.002 , $p = 0.991$; flowers – estimate = 0.024 , $p = 0.726$; leaves – estimate = -0.001 , $p =$
397 0.986).

398

399 Discussion

400

401 *Home range sizes and DTD reflect food abundance*

402

403 Our results indicate substantial intra-specific variation in red-tailed monkey ranging patterns between
404 primarily forested and savanna mosaic habitats in response to both food abundance and weather. As
405 predicted, Issa monkeys exhibited a significantly larger home range than either Ngogo group or any
406 previously studied group. The lower abundance of at least two major dietary components in riparian
407 forest at Issa compared to Ngogo (fruit and leaves – Figure 7) should be a primary explanation for this
408 difference. While Issa monkeys use both riparian forest and woodland, they are dependent on forest
409 foods for substantial periods of the year due to the relative paucity of woodland foods outside of dry
410 months (e.g. time spent in forest cf. woodland: adult males 45.6% cf. 35.1%; adult females, subadults,
411 juveniles 77.5% cf. 8.7%; $n = 25$ follow days November – December 2017 – EM unpublished data).
412 As such, the irregular spatial geometry of forest at Issa alone should lead to a larger estimate of home
413 range size. This effect is clearly illustrated by the bias in the MCP estimate for K0, which indicates a
414 far larger home range than the GCA estimate as a result of including areas of woodland that the
415 group did not use (Figure 3). Nonetheless, even when measured at a finer spatial scale (75m grid
416 cells), Issa monkeys still exhibited a far larger home range than forest groups. Similarly, with only a
417 single group at Issa against which to compare, the larger group size of K0 compared to the Ngogo
418 study groups could be expected to explain a larger home range. However, in a previous study of K0 in
419 2012 when the group comprised ca. 35 individuals, Tapper et al. (2019) reported a home range of
420 $0.78 - 1.93\text{km}^2$ after only three months of follows – already disproportionately larger than estimates
421 for forest groups of similar sizes (Table 1).

422 In addition to a larger home range, Issa monkeys also exhibited a longer maximum DTD
423 compared to the Ngogo groups. For discretely distributed fruit and flowers, reduced, more
424 heterogeneous forest cover at Issa may result in smaller patches (Chapman & Chapman, 2000b) that
425 are also less food-rich than at Ngogo. These patches are likely to be more rapidly depleted by
426 monkeys at Issa – particularly given the larger group size of K0 – resulting in greater daily search
427 effort and a larger home range to meet subsistence needs (Wrangham et al., 1993). Similar to other
428 sites, insects likely comprise an important component of red-tailed monkey diet at Issa (Bryer,
429 Chapman, Raubenheimer, Lambert, & Rothman, 2015; AP unpublished data). Insects are typically
430 more uniformly distributed but harder to locate than fruit, flowers, and leaves (Chapman & Chapman,
431 2000b). Increasing DTD may be the most efficient strategy for obtaining insects in narrow forest strips
432 at Issa if alternatives such as expanding group spread are not possible (Isbell, 2012).

433 Increased food abundance should result in shorter DTD as inter-group feeding competition
434 and rates of food depletion are reduced (Janson & Goldsmith, 1995; Chapman & Chapman, 2000b).
435 Unlike previous studies (e.g. Kaplin, 2001; Buzzard, 2006), we found a negative effect of fruit
436 abundance on DTD across both sites that corroborates this hypothesis. Specifically, fruit was
437 significantly more abundant in dry seasons, which also likely explains the smaller proportions of home

438 range used in these months. Moreover, this effect was only significantly stronger for K0 at Issa
439 compared to the smaller Ngogo group (R5). Similar effect sizes for the two larger study groups across
440 both sites supports the hypothesis that increased intra-group feeding competition with larger group
441 sizes influences primate DTD to a greater extent than variation in food abundance alone.

442

443 *Thermal constraints on travel distances*

444

445 We also found evidence that temperature negatively influences HTD and DTD. Issa monkeys
446 exhibited smallest monthly DTD ranges in dry season months, when maximum temperatures were
447 highest, and highest hourly temperatures and lowest travel speeds converged between 13 – 16h.
448 These patterns corroborate the hypothesis that temperature should be an important constraint on the
449 utilization of open vegetation (e.g. woodland) for forest primates (Pruetz, 2018; Wessling et al., 2018).
450 As such, behavioral responses (e.g. seeking shade; reducing time spent travelling) should vary
451 between forests and savanna mosaics (Hill, 2005). For example, savanna chimpanzees at Fongoli,
452 Senegal, shelter in caves when temperatures are hottest (Pruetz, 2007) and preferentially utilize
453 forest patches that provide the only sources of shade and water (Pruetz & Bertolani, 2009). Although
454 fruit may provide most water, red-tailed monkeys drink from streams and arboreal water holes at both
455 Ngogo and Issa. Given the near complete absence of rain and drying up of streams for substantial
456 periods (ca. three months) in dry seasons at Issa, water may be a similarly limiting factor for monkey
457 ranging. In the absence of higher resolution data from Ngogo, the effects of such ecological variables
458 on behavioral responses to heat stress at small temporal scales (eg. hourly or minute by minute
459 variation) remain to be compared between forest and savanna mosaic habitats.

460 In contrast to our third prediction, rainfall did not relate to HTD or DTD. Monkey responses to
461 rainfall may be confounded by other factors. For example, at Issa microhabitat variation in rainfall
462 means that light rainfall measured in one part of the study area may not reflect heavy rainfall
463 elsewhere that results in localized flooding (AP personal observation). Flooding rivers can restrict
464 access to forest patches that are only reachable to monkeys by travelling terrestrially through
465 woodland (EM unpublished data). Conversely, in patches with more continuous canopy cover red-
466 tailed monkey groups travel in all but the heaviest of rainfall, at which point visibility and vocal
467 communication between individuals are likely limited (EM personal observation). Although primates
468 should reduce travel in rain to minimize energy loss (Stelzner, 1988), in savanna mosaics the difficulty
469 of meeting daily nutritional requirements may mean that in food-rich areas monkeys prioritize
470 travelling and foraging during rainfall only until maintaining group cohesion becomes difficult.

471

472 *Determinants of home range use*

473

474 While site-specific DTD and home range sizes suggest food availability can influence group
475 movements, range use at Ngogo did not relate to food abundance despite significant monthly
476 variation in fruit and flower availability. Similar to the consistent patterns of DTD and proportions of
477 home range used, the relatively high availability of food in forests may mean that resource depletion
478 does not significantly limit time spent at a patch. Despite this, and contrary to our fourth prediction,
479 food abundance did not relate to range use at Issa either. Higher resolution data on diet composition
480 are needed to investigate the effect of other foods, such as insects. Insects comprise an important
481 component of red-tailed monkey diet at Ngogo (Struhsaker, 2017), particularly as fallback foods
482 (Rothman, Raubenheimer, Bryer, Takahashi, & Gilbert, 2014). If insects are distributed more
483 heterogeneously than fruit, flowers, and leaves then insect abundance should influence range use to
484 a greater extent than these plant parts. This relationship should also vary between forests and more
485 open environments given inter-habitat differences in insect availability. At Issa for example, insect
486 abundance likely varies between vegetation types given that monkeys are known to exploit woodland
487 locusts driven into riparian forest by dry season fires (FS personal observation).

488 Unlike at Ngogo, we included all identifiable plant species in our measures of food abundance
489 at Issa because the species that comprise monkey diet are not yet identified. This approach may have
490 led to overestimations of food availability, which could partly explain why we did not find the effect of
491 these plant parts on range use to differ between sites. Additionally, although we only modeled dietary-
492 important plant species at Ngogo, phenology may only partially reflect food availability for monkeys.
493 For example, while we averaged variation in plant part presence for each species per month when
494 modeling use of two home ranges, future studies that consider more home ranges should account for
495 intra-specific phenological variation that can occur across even relatively small spatial scales at
496 Ngogo (Brown, 2011). Compared to Issa, competition from six other larger-bodied primates at Ngogo
497 may also reduce the availability of resources that we identified as present, but were in fact consumed

498 by other species or not influential due to highly flexible diet switching (Brown, 2013). Food abundance
499 indexed with the same phenology methods also does not relate to energy balance (urinary c-peptide
500 levels) in red-tailed monkeys at Ngogo (MB unpublished data), suggesting that controlling for species-
501 specific dietary variation is equally important when quantifying food abundance in food-rich, forests as
502 in savanna mosaic habitats.

503 Range use may also be influenced by factors other than food abundance. In our models we
504 considered all patches (grid cells) equally regardless of vegetation type or position in the home range
505 (periphery vs. core). At Issa however, forest configuration and a large home range mean that
506 monkeys may not travel to distant patches if reducing DTD and increasing group spread are more
507 efficient alternatives (Ganas & Robbins, 2005). Potential predators are frequently encountered at both
508 sites (e.g. chimpanzees; crowned-hawk eagles – Mitani et al., 2001; Watts & Mitani, 2002; McLester
509 et al., 2018). Anti-predator responses in red-tailed monkeys include hiding or changing group travel
510 direction (Cords, 1987), which affect time spent in an area at both sites. Furthermore, predation risk
511 should differ between savanna mosaic and forest habitats (Dunbar, 1988). For example, Issa
512 monkeys use isolated forest patches that are only accessible by travelling terrestrially through
513 woodland. Groups pause travel at forest peripheries for substantial periods of time while scanning the
514 immediate area or waiting for predators to leave before moving between patches, typically running
515 without stopping (EM personal observation). Similarly, inter-group encounters – frequently over
516 access to blue monkeys and grey-cheeked mangabeys (Brown, 2011) – also occur along home range
517 peripheries, which can result in abrupt changes of direction depending on the outcome or preemptive
518 avoidance (Brown, 2013).

519

520 *Hominin adaptations to savanna mosaic environments*

521

522 By comparing ranging behavior across a vegetation gradient that mirrors the Mio-Pliocene transition
523 from forests to open savanna mosaics our results provide insight into environmental pressures that
524 hominins (e.g. *Ardipithecus*, *Paranthropus*, and early *Homo* spp.) would have faced in similar
525 paleoenvironments (Leonard & Robertson, 1997; Antón et al., 2014). Furthermore, while red-tailed
526 monkeys are phylogenetically distant to hominins, our results nonetheless indicate similarities
527 between strategies exhibited by monkeys and those predicted for later hominins (e.g. *Homo*) in
528 coping with these pressures. For example, thermoregulation has been implicated as an important
529 driver of hominin evolution (e.g. Wheeler, 1992; Wheeler, 1994; Passey et al., 2010). Exploiting open
530 vegetation (e.g. woodland) foods should have resulted in increased thermal stress due to reduced
531 shade and greater travel distances to obtain scarcely-distributed resources (Ruxton & Wilkinson,
532 2011). While monkeys primarily use riparian forest at Issa, we found temperature still negatively
533 affected travel speed. This relationship is similar to that predicted for hominins, which should have
534 reduced activity and sought shade during peak daily temperatures (Wheeler, 1994).

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

545 In addition to increasing home range, primates may also expand dietary breadth to cope with
546 the wide distribution of resources that characterize drier, mosaic habitats. In a comparative study of
547 hominin dietary niches, Nelson & Hamilton (2018) showed that early hominins (e.g. *Ardipithecus*)
548 most closely resemble modern chimpanzee niche-space in the types and amounts of resources they
549 consume, whereas later hominin species may have exploited aquatic sources (see also Braun et al.,
550 2010) to meet subsistence requirements, expanding their dietary niche and gradually becoming more
551 generalist over time (Roberts & Stewart, 2018). Subsequent analyses that incorporate red-tailed
552 monkey food source distribution and diversity should reveal whether dietary composition, in addition
553 to home range sizes, also differs between forest and savanna mosaic populations. Moreover, dental
554 microwear and isotopic comparison of the available plants in these forests should provide extant
555 analogues for comparisons of especially contemporaneous fossil hominins (sensu Lee-Thorp,
556 Sponheimer, & van der Merwe, 2003). Comparing these data from more groups across a finer

557 vegetation gradient should further clarify the extent to which ecological conditions have influenced
558 both extant and extinct primate behavioral adaptations.

559

560 **Data Availability Statement**

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

563

564 **Acknowledgements**

565 We thank the Uganda Wildlife Authority and the Uganda National Council for Science and Technology
566 for permission to conduct research at Ngogo, and the Tanzanian Wildlife Research Institute and the
567 Commission for Science and Technology for permission to conduct research at the Issa Valley. EM's
568 data collection was funded by the American Society of Primatologists and Liverpool John Moores
569 University. The GMERC Project is supported by the UCSD / Salk Center for Academic Research and
570 Training in Anthropogeny (CARTA). At Ngogo, we thank the Ngogo Monkey Project field team for
571 assistance with botanical plots, Sylvia Amsler for sharing geospatial data from the Uganda Biomass
572 Study, and David Watts, John Mitani, Kevin Langergraber, and the Ngogo Chimpanzee Project for
573 collecting and sharing phenology and weather data. At Issa, we thank Sebastian Ramirez-Amaya,
574 Eden Wondra, Noémie Bonnin, Camille Vitet, Michael Kimaro, and field assistants for additional data
575 collection, and Yahya Abeid for plant species identification. Finally, we thank Francis Gilbert for
576 statistical advice.

577

578

References

- 579 Alberts, S. C., Hollister-Smith, J. A., Mututua, R. S., Sayialel, S. N., Muruthi, P. M., Warutere, J. K., &
580 Altmann, J. (2005). Seasonality and long-term change in a savanna environment. In D. K.
581 Brockman, & C. P. van Schaik (Eds.), *Seasonality in Primates: Studies of Living and Extinct*
582 *Human and Non-Human Primates* (pp. 157-196). Cambridge, UK: Cambridge University Press.
- 583 Antón, S. C., Potts, R., & Aiello, L. C. (2014). Human evolution. Evolution of early *Homo*: an
584 integrated biological perspective. *Science*, 345, 1236828.
- 585 Baldwin, P. J., McGrew, W. C., & Tutin, C. E. G. (1982). Wide-ranging chimpanzees at Mt. Assirik,
586 Senegal. *International Journal of Primatology*, 3, 367-385.
- 587 Baoping, R., Ming, L., Yongcheng, L., & Fuwen, W. (2009). Influence of day length, ambient
588 temperature, and seasonality on daily travel distance in the Yunnan snub-nosed monkey at
589 Jinsichang, Yunnan, China. *American Journal of Primatology*, 71, 233-241.
- 590 Boinski, S. (1987). Habitat use by squirrel monkeys (*Saimiri oerstedii*) in Costa Rica. *Folia*
591 *Primatologica*, 49, 151-167.
- 592 Braun, D. R., Harris, J. W., Levin, N. E., McCoy, J. T., Herries, A. I., Bamford, M. K., Bishop, L. C.,
593 Richmond, B. G., & Kibunja, M. (2010). Early hominin diet included diverse terrestrial and aquatic
594 animals 1.95 Ma in East Turkana, Kenya. *Proceedings of the National Academy of Sciences*, 107,
595 10002-10007.
- 596 Bromage, T. G., & Schrenk, F. (1995). Biogeographic and climatic basis for a narrative of early
597 hominin evolution. *Journal of Human Evolution*, 28, 109-114.
- 598 Brown, M. (2011). *Intergroup encounters in grey-cheeked mangabeys (Lophocebus albigena) and*
599 *redtail monkeys (Cercopithecus ascanius): Form and function*. Doctoral thesis, Columbia
600 University, USA.
- 601 Brown, M. (2013). Food and range defence in group-living primates. *Animal Behaviour*, 85, 807-816.
- 602 Bryer, M. A. H., Chapman, C. A., Raubenheimer, D., Lambert, J. E., & Rothman, J. M. (2015).
603 Macronutrient and energy contributions of insects to the diet of a frugivorous monkey
604 (*Cercopithecus ascanius*). *International Journal of Primatology*, 36, 839-854.
- 605 Bryer, M. A. H., Chapman, C. A., & Rothman, J. M. (2013). Diet and polyspecific associations affect
606 spatial patterns among redtail monkeys (*Cercopithecus ascanius*). *Behaviour*, 1-17.
- 607 Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-
608 density subpopulations. *Ecological Monographs*, 60, 1-26.
- 609 Buzzard, P. J. (2006). Ranging Patterns in Relation to Seasonality and Frugivory Among
610 *Cercopithecus campbelli*, *C. petaurista*, and *C. diana* in the Tai Forest. *International Journal of*
611 *Primatology*, 27, 559-573.
- 612 Campos, F. A., & Fedigan, L. M. (2009). Behavioral adaptations to heat stress and water scarcity in
613 white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. *American*
614 *Journal of Physical Anthropology*, 138, 101-111.
- 615 Cerling, T. E., Wynn, J. G., Andanje, S. A., Bird, M. I., Korir, D. K., Levin, N. E., Mace, W., Macharia,
616 A. N., Quade, J., & Remien, C. H. (2011). Woody cover and hominin environments in the past 6
617 million years. *Nature*, 476, 51-56.
- 618 Chapman, C. A., & Chapman, L. J. (1996). Mixed-species primate groups in the Kibale Forest:
619 Ecological constraints on association. *International Journal of Primatology*, 17, 31-50.
- 620 Chapman, C. A., & Chapman, L. J. (2000a). Constraints on group size in red colobus and red-tailed
621 guenons: Examining the generality of the ecological constraints model. *International Journal of*
622 *Primatology*, 21, 565-585.
- 623 Chapman, C. A., & Chapman, L. J. (2000b). Determinants of group size in primates: The importance
624 of travel costs. In S. Boinski, & P. A. Garber (Eds.), *On the Move: How and Why Animals Travel in*
625 *Groups* (pp. 24-42). Chicago, USA: The University of Chicago Press.
- 626 Chapman, C. A., & Lambert, J. E. (2000). Habitat alteration and the conservation of African primates:
627 Case study of Kibale National Park, Uganda. *American Journal of Primatology*, 50, 169-185.
- 628 Chapman, C. A., Wrangham, R. W., Chapman, L. J., Kennard, D. K., & Zanne, A. E. (1999). Fruit and
629 flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*, 15,
630 189-211.
- 631 Copeland, S. R. (2009). Potential hominin plant foods in northern Tanzania: Semi-arid savannas
632 versus savanna chimpanzee sites. *Journal of Human Evolution*, 57, 365-378.
- 633 Cords, M. (1987). Mixed species association of *Cercopithecus* monkeys in the Kakamega Forest,
634 Kenya. *University of California Publications in Zoology*, 117, 1-109.
- 635 Cords, M. (1990). Mixed-species association of East African guenons: General patterns or specific
636 examples? *American Journal of Primatology*, 21, 101-114.

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

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

641 Dunbar, R. I. M. (1988). *Primate Social Systems*. London, UK: Croom Helm.

642 Foley, R. A., Ulijaszek, S. J., & Strickland, S. S. (1993). The influence of seasonality on hominid
643 evolution. *Seasonality and Human Ecology* (pp. 17-37).

644 Fox, J., Weisberg, S., & Price, B. (2018). car: Companion to Applied Regression, available from
645 <https://cran.r-project.org/web/packages/car>.

646 Galat-Luong, A. (1975). Notes préliminaires sur l'écologie de *Cercopithecus Ascanius schmidti* dans
647 les environs de Bangui (R.C.A.). *Revue d'Écologie (La Terre et la Vie)*, 29, 288-297.

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

651 Gathua, J. M. (2000). *Intraspecific Variation in Foraging Patterns of Redtail Monkeys (Cercopithecus*
652 *ascanius) in the Kakamega Forest, Kenya*. Doctoral dissertation, Columbia University, USA.

653 Grine, F. E., Sponheimer, M., Ungar, P. S., Lee-Thorp, J., & Teaford, M. F. (2012). Dental microwear
654 and stable isotopes inform the paleoecology of extinct hominins. *American Journal of Physical*
655 *Anthropology*, 148, 285-317.

656 Grove, M., Pearce, E., & Dunbar, R. I. (2012). Fission-fusion and the evolution of hominin social
657 systems. *Journal of Human Evolution*, 62, 191-200.

658 Hemingway, C. A., & Bynum, N. (2005). The influence of seasonality on primate diet and ranging. In
659 D. K. Brockman, & C. P. van Schaik (Eds.), *Seasonality in Primates: Studies of Living and Extinct*
660 *Human and Non-Human Primates* (pp. 57-104). Cambridge, UK: Cambridge University Press.

661 Hernandez-Aguilar, R. A. (2009). Chimpanzee nest distribution and site reuse in a dry habitat:
662 Implications for early hominin ranging. *Journal of Human Evolution*, 57, 350-364.

663 Hill, R. (2005). Day length seasonality and the thermal environment. In D. K. Brockman, & C. P. van
664 Schaik (Eds.), *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human*
665 *Primates* (pp. 197-214). Cambridge, UK: University of Cambridge Press.

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

668 Hill, R. A., & Dunbar, R. I. M. (2002). Climatic determinants of diet and foraging behaviour in baboons.
669 *Evolutionary Ecology*, 16, 579-593.

670 Isbell, L. A. (1983). Daily ranging behavior of red colobus (*Colobus badius tephrosceles*) in Kibale
671 Forest, Uganda. *Folia Primatologica*, 41, 34-48.

672 Isbell, L. A. (2012). Re-evaluating the Ecological Constraints model with red colobus monkeys
673 (*Procolobus rufomitratus tephrosceles*). *Behaviour*, 149, 493-529.

674 Isbell, L. A., & Young, T. P. (1996). The evolution of bipedalism in hominids and reduced group size in
675 chimpanzees: Alternative responses to decreasing resource availability. *Journal of Human*
676 *Evolution*, 30, 389-397.

677 Janson, C. H., & Goldsmith, M. L. (1995). Predicting group size in primates: foraging costs and
678 predation risks. *Behavioral Ecology*, 6, 326-336.

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

681 Kaplin, B. A. (2001). Ranging behavior of two species of guenons (*Cercopithecus lhoesti* and *C. mitis*
682 *doggetti*) in the Nyungwe Forest Reserve, Rwanda. *International Journal of Primatology*, 22, 521-
683 548.

684 Kosheleff, V. P., & Anderson, C. N. (2009). Temperature's influence on the activity budget,
685 terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. *American Journal*
686 *of Physical Anthropology*, 139, 172-181.

687 Lee-Thorp, J. A., Sponheimer, M., & van der Merwe, N. J. (2003). What do stable isotopes tell us
688 about hominid dietary and ecological niches in the pliocene? *International Journal of*
689 *Osteoarchaeology*, 13, 104-113.

690 Leonard, W. R., & Robertson, M. L. (1997). Comparative primate energetics and hominid evolution.
691 *American Journal of Physical Anthropology*, 102, 265-281.

692 Matsuda, I., Tuuga, A., & Higashi, S. (2009). Ranging behavior of proboscis monkeys in a riverine
693 forest with special reference to ranging in inland forest. *International Journal of Primatology*, 30,
694 313-325.

695 McGrew, W. C., Baldwin, P. J., & Tutin, C. E. G. (1981). Chimpanzees in a hot, dry and open habitat:
696 Mt. Assirik, Senegal, West Africa. *Journal of Human Evolution*, 10, 227-244.

- 697 McLester, E., Sweeney, K., Stewart, F. A., & Piel, A. K. (2018). Leopard (*Panthera pardus*) predation
698 on a red-tailed monkey (*Cercopithecus ascanius*) in the Issa Valley, western Tanzania. *Primates*,
699 60, 15-19.
- 700 Mitani, J. C., Sanders, W. J., Lwanga, S. J., & Windfelder, T. L. (2001). Predatory behavior of
701 crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behavioral*
702 *Ecology and Sociobiology*, 49, 187-195.
- 703 Moore, J. (1996). Savanna chimpanzees, referential models and the last common ancestor. In W. C.
704 McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great Ape Societies* (pp. 275-292). Cambridge, UK:
705 Cambridge University Press.
- 706 Nakamura, M., Corp, N., Fujimoto, M., Fujita, S., Hanamura, S., Hayaki, H., Hosaka, K., Huffman, M.
707 A., Inaba, A., Inoue, E. et al. (2013). Ranging behavior of Mahale chimpanzees: A 16 year study.
708 *Primates*, 54, 171-182.
- 709 Nelson, S. V., & Hamilton, M. I. (2018). Evolution of the human dietary niche: Initial transitions. In M.
710 N. Muller, R. W. Wrangham, & D. R. Pilbeam (Eds.), *Chimpanzees and Human Evolution* (pp. 286-
711 310). Boston, USA: Harvard University Press.
- 712 Newton-Fisher, N. E. (2003). The home range of the Sonso community of chimpanzees from the
713 Budongo Forest, Uganda. *African Journal of Ecology*, 41, 150-156.
- 714 Nunn, C. L., & Barton, R. A. (2000). Allometric slopes and independent contrasts: A comparative
715 test of Kleiber's Law in primate ranging patterns. *The American Naturalist*, 156, 519-533.
- 716 Olupot, W., Chapman, C. A., Waser, P. M., & Isabirye-Basuta, G. (1997). Mangabey (*Cercocebus*
717 *albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale
718 National Park. *American Journal of Primatology*, 43, 65-78.
- 719 Passey, B. H., Levin, N. E., Cerling, T. E., Brown, F. H., & Eiler, J. M. (2010). High-temperature
720 environments of human evolution in East Africa based on bond ordering in paleosol carbonates.
721 *Proceedings of the National Academy of Sciences*, 107, 11245-11249.
- 722 Pickering, T. R., & Domínguez-Rodrigo, M. (2010). Chimpanzee referents and the emergence of
723 human hunting. *The Open Anthropology Journal*, 3, 107-113.
- 724 Piel, A. K., Strampelli, P., Greathead, E., Hernandez-Aguilar, R. A., Moore, J., & Stewart, F. A. (2017).
725 The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) in the Issa valley, western
726 Tanzania. *Journal of Human Evolution*, 112, 57-69.
- 727 Pinheiro, J., Bates, D., Debroy, S., & Sarkar, D. (2019). nlme: Linear and Nonlinear Mixed Effects
728 Models, available from <https://cran.r-project.org/web/packages/nlme>.
- 729 Plumptre, A. J., & Reynolds, V. (1994). The effect of selective logging on the primate populations in
730 the Budongo Forest Reserve, Uganda. *Journal of Applied Ecology*, 31, 631-641.
- 731 Plumptre, A. J., Reynolds, V., & Bakuneeta, C. (1997). *The effects of selective logging in*
732 *monodominant tropical forests on biodiversity*. Report submitted to Overseas Development
733 Administration (ODA), Wildlife Conservation Society and National Geographic Society.
- 734 Potts, K. B., Chapman, C. A., & Lwanga, J. S. (2009). Floristic heterogeneity between forested sites in
735 Kibale National Park, Uganda: Insights into the fine-scale determinants of density in a large-bodied
736 frugivorous primate. *Journal of Animal Ecology*, 78, 1269-1277.
- 737 Potts, R. (1998). Environmental hypotheses of hominin evolution. *Yearbook Of Physical*
738 *Anthropology*, 41, 93-136.
- 739 Potts, R. (2013). Hominin evolution in settings of strong environmental variability. *Quaternary Science*
740 *Reviews*, 73, 1-13.
- 741 Pruett, J. D. (2007). Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at
742 Fongoli, Senegal: Implications for thermoregulatory behavior. *Primates*, 48, 316-319.
- 743 Pruett, J. D. (2018). Nocturnal behavior by a diurnal ape, the West African chimpanzee (*Pan*
744 *troglodytes verus*), in a savanna environment at Fongoli, Senegal. *American Journal of Physical*
745 *Anthropology*, 166, 541-548.
- 746 Pruett, J. D., & Bertolani, P. (2009). Chimpanzee (*Pan troglodytes verus*) behavioral responses to
747 stresses associated with living in a savanna-mosaic environment: Implications for hominin
748 adaptations to open habitats. *PaleoAnthropology*, 2009, 252-262.
- 749 R Core Team (2018). R: A language and environment for statistical computing. Vienna, Austria: R
750 Foundation for Statistical Computing <https://www.R-project.org/>
- 751 Raemaekers, J. (1980). Causes of variation between months in the distance traveled daily by
752 gibbons. *Folia Primatologica*, 34, 46-60.
- 753 Rimbach, R., Link, A., Montes-Rojas, A., Di Fiore, A., Heistermann, M., & Heymann, E. W. (2014).
754 Behavioral and physiological responses to fruit availability of spider monkeys ranging in a small
755 forest fragment. *American Journal of Primatology*, 76, 1049-1061.

- 756 Roberts, P., & Stewart, B. A. (2018). Defining the 'generalist specialist' niche for Pleistocene *Homo*
757 *sapiens*. *Nature Human Behaviour*, 2, 542-550.
- 758 Rode, K. D., Chapman, C. A., McDowell, L. R., & Stickler, C. (2006). Nutritional correlates of
759 population density across habitats and logging intensities in redtail monkeys (*Cercopithecus*
760 *ascanius*). *Biotropica*, 38, 625-634.
- 761 Rodman, P. S., & McHenry, H. M. (1980). Bioenergetics and the origin of hominid bipedalism.
762 *American Journal of Physical Anthropology*, 52, 103-106.
- 763 Rose, L., & Marshall, F. (1996). Meating eating, sociality and home bases revisited. *Current*
764 *Anthropology*, 37, 307-338.
- 765 Rothman, J. M., Raubenheimer, D., Bryer, M. A., Takahashi, M., & Gilbert, C. C. (2014). Nutritional
766 contributions of insects to primate diets: implications for primate evolution. *Journal of Human*
767 *Evolution*, 71, 59-69.
- 768 Rousset, F., Ferdy, J.-B., & Courtiol, A. (2018). spaMM: Mixed-Effect Models, Particularly Spatial
769 Models, available from <https://cran.r-project.org/web/packages/spaMM>.
- 770 Rudicell, R. S., Piel, A. K., Stewart, F., Moore, D. L., Learn, G. H., Li, Y., Takehisa, J., Pinteá, L.,
771 Shaw, G. M., Moore, J. et al. (2011). High prevalence of simian immunodeficiency virus infection in
772 a community of savanna chimpanzees. *Journal of Virology*, 85, 9918-9928.
- 773 Ruxton, G. D., & Wilkinson, D. M. (2011). Avoidance of overheating and selection for both hair loss
774 and bipedality in hominins. *Proceedings of the National Academy of Sciences*, 108, 20965-20969.
- 775 Samson, D. R., & Hunt, K. D. (2012). A thermodynamic comparison of arboreal and terrestrial
776 sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki
777 Wildlife Reserve, Uganda. *American Journal of Primatology*, 74, 811-818.
- 778 Sarmiento, E. E., Stiner, E. O., & Brooks, E. G. E. (2001). Red-tail monkey *Cercopithecus ascanius*
779 distinguishing characters and distribution. *African Primates*, 5, 18-24.
- 780 Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods*
781 *in Ecology and Evolution*, 1, 103-113.
- 782 Sheppard, D. J. (2000). *Ecology of the Budongo Forest Redtail: Patterns of Habitat Use and*
783 *Population Density in Primary and Regenerating Forest Sites*. Master's thesis, University of
784 Calgary, Canada.
- 785 Stanley, S. M. (1992). An ecological theory for the origin of *Homo*. *Paleobiology*, 18, 237-257.
- 786 Stelzner, J. K. (1988). Thermal effects on movement patterns of yellow baboons. *Primates*, 29, 91-
787 105.
- 788 Stelzner, J. K., & Hausfater, G. (1986). Posture, microclimate, and thermoregulation in yellow
789 baboons. *Primates*, 27, 449-463.
- 790 Struhsaker, T. T. (1975). *The Red Colobus Monkey*. Chicago, USA: University of Chicago Press.
- 791 Struhsaker, T. T. (1978). Food habits of five monkey species in the Kibale Forest, Uganda. In D. J.
792 Chivers, & J. Herbert (Eds.), *Recent Advances in Primatology, Vol 1, Behaviour* (pp. 225-248).
793 New York, USA: Academic Press.
- 794 Struhsaker, T. T. (1980). Comparison of the behaviour and ecology of red colobus and redtail
795 monkeys in the Kibale Forest, Uganda. *African Journal of Ecology*, 18, 33-51.
- 796 Struhsaker, T. T. (1981). Polyspecific associations among tropical rain-forest primates. *Zeitschrift für*
797 *Tierpsychologie*, 57, 268-304.
- 798 Struhsaker, T. T. (1988). Male tenure, multimale influxes, and reproductive success in redtail
799 monkeys (*Cercopithecus ascanius*). In A. Gautier-Hion, F. Bourlière, J.-P. Gautier, & J. Kingdon
800 (Eds.), *A Primate Radiation: Evolutionary Biology of the African Guenons* (pp. 340-363).
801 Cambridge, UK: Cambridge University Press.
- 802 Struhsaker, T. T. (1997). *Ecology of an African Rainforest*. Gainesville, Florida, USA: University of
803 Florida Press.
- 804 Struhsaker, T. T. (2017). Dietary variability in redtail monkeys (*Cercopithecus ascanius schmidtii*) of
805 Kibale National Park, Uganda: the role of time, space, and hybridization. *International Journal of*
806 *Primatology*, 38, 914-941.
- 807 Struhsaker, T. T., & Leland, L. (1979). Socioecology of five sympatric monkey species in the Kibale
808 Forest, Uganda. *Advances in the Study of Behavior*, 9, 159-228.
- 809 Struhsaker, T. T., & Leland, L. (1988). Group fission in redtail monkeys (*Cercopithecus ascanius*) in
810 the Kibale Forest, Uganda. In A. Gautier-Hion, F. Bourlière, J.-P. Gautier, & J. Kingdon (Eds.), *A*
811 *Primate Radiation: Evolutionary Biology of the African Guenons* (pp. 364-388). Cambridge, UK:
812 Cambridge University Press.
- 813 Tapper, S., Johnson, C., Lenoël, A., Vining, A., Stewart, F., & Piel, A. (2019). Riverine red-tails:
814 Preliminary data on forest guenons in a savanna woodland habitat in the Issa Valley, Uganda,

815 western Tanzania. In K. Nowak, A. Barnett, & I. Matsuda (Eds.), *Primates in Flooded Habitats: Ecology and Conservation* (pp. 270-275). Cambridge, UK: Cambridge University Press.

816

817 Teaford, M. F., & Ungar, P. S. (2000). Diet and the evolution of the earliest human ancestors.

818 *Proceedings of the National Academy of Sciences*, 97, 13506-13511.

819 Teelen, S. (2007). Influence of chimpanzee predation on associations between red colobus and red-

820 tailed monkeys at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, 28,

821 593-606.

822 Thomas, S. C. (1991). Population densities and patterns of habitat use among anthropoid primates of

823 the Ituri Forest, Zaire. *Biotropica*, 23, 68-83.

824 Treves, A. (1998). The influence of group size and neighbors on vigilance in two species of arboreal

825 monkeys. *Behaviour*, 135, 453-481.

826 Watts, D. P., & Mitani, J. C. (2002). Hunting behavior of chimpanzees at Ngogo, Kibale National Park,

827 Uganda. *International Journal of Primatology*, 23, 1-28.

828 Watts, D. P., Potts, K. B., Lwanga, J. S., & Mitani, J. C. (2012). Diet of chimpanzees (*Pan troglodytes*

829 *schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity.

830 *American Journal of Primatology*, 74, 114-129.

831 Wessling, E. G., Kuhl, H. S., Mundry, R., Deschner, T., & Pruetz, J. D. (2018). The costs of living at

832 the edge: Seasonal stress in wild savanna-dwelling chimpanzees. *Journal of Human Evolution*,

833 121, 1-11.

834 Wheeler, P. E. (1992). The thermoregulatory advantages of large body size for hominids foraging in

835 savannah environments. *Journal of Human Evolution*, 23, 351-362.

836 Wheeler, P. E. (1994). The thermoregulatory advantages of heat storage and shade-seeking

837 behaviour to hominids foraging in equatorial savannah environments. *Journal of Human Evolution*,

838 26, 339-350.

839 White, T. D., Ambrose, S. H., Suwa, G., Su, D. F., DeGusta, D., Bernor, R. L., Boisserie, J. R., Brunet,

840 M., Delson, E., Frost, S. et al. (2009). Macrovertebrate paleontology and the Pliocene habitat of

841 *Ardipithecus ramidus*. *Science*, 326, 87-93.

842 Willems, E. P., & Hill, R. A. (2009). Predator-specific landscapes of fear and resource distribution:

843 Effects on spatial range use. *Ecology*, 90, 546-555.

844 Windfelder, T. L., & Lwanga, J. S. (2002). Group fission in red-tailed monkeys (*Cercopithecus*

845 *ascanius*) in Kibale National Park, Uganda. In M. E. Glenn, & M. Cords (Eds.), *The Guenons: Diversity and Adaptation in African Monkeys* (pp. 147-159). New York, USA: Kluwer Academic Publishers.

846

847

848 Wrangham, R., Crofoot, M., Lundy, R., & Gilby, I. (2007). Use of overlap zones among group-living

849 primates: A test of the risk hypothesis. *Behaviour*, 144, 1599-1619.

850 Wrangham, R. W., Gittleman, J. L., & Chapman, C. A. (1993). Constraints on group size in primates

851 and carnivores: Population density and day-range as assays of exploitation competition.

852 *Behavioral Ecology and Sociobiology*, 32, 199-209.

853

854 **Table 1** Follow periods, home range sizes calculated using one hundred percent minimum convex polygon (MCP) and grid cell analysis (GCA) methods, and
 855 daily travel distances (DTD) for each group.
 856

Study site	Group	Follow period [follow days; all-day follows]	Home range size (km ²)		Daily travel distance		Location interval (minutes)
			MCP	GCA [cell size]	Mean [range] (km)		
Ngogo	R1	Jan 2008 – Sep 2018 [<i>n</i> = 225; 123]	0.58	0.52 [50m]	0.97 [0.35 – 2.04]		30
	R2	Jan 2008 – Aug 2016 [<i>n</i> = 352; 250]	0.44	0.56 [50m]	1.01 [0.27 – 2.01]		
	R3	Jan 2008 – Aug 2016 [<i>n</i> = 255; 159]	0.54	0.52 [50m]	0.98 [0.34 – 1.71]		
	R4	Jun 2008 – Aug 2016 [<i>n</i> = 158; 99]	0.59	0.46 [50m]	1.04 [0.51 – 1.99]		5
	R5	Jul – Oct 2017 [<i>n</i> = 89; 64]	0.65	0.65 [50m]	1.81 [0.94 – 2.62]		
	R6	Mar – Jun 2017 [<i>n</i> = 71; 50]	0.58	0.56 [50m]	1.85 [1.03 – 2.58]		
Issa Valley	K0	Jan 2013 – Mar 2016 [<i>n</i> = 237; 175]	16	3.93 [75m]	2.04 [0.45 – 4.22] (wet season); 1.72 [0.87 – 3.92] (dry season)		

857

858
859
860
861

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 (CI = confidence interval; SD = standard deviation; SE = standard error; adapted in part from Tapper et al., 2019).

Country	Study site	Primary vegetation	Number of study groups	Follow duration (months/group)	Mean DTD (km) [range]	Home range size			Population density			Reference
						Mean area (km ²) [range]	Method	% of Issa Valley GCA	Individuals/km ²	Groups/km ²	Group size [range]	
Central African Republic	Bangui	Lowland degraded deciduous rain forest	1	23		0.15	GCA (50m)	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 (50m)	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 (50m)	9.2	72	5.2	23-26 [±9SD]	4; 5
Tanzania	Issa Valley	Medium-altitude primary woodland and evergreen riparian forest	1	39	1.90 [0.45-4.23]	3.93	GCA (75m)	-	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 (25m)	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 (25m)	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]	Unkown	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]	Unkown	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 (50m)	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 (50m)	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
Kibale (Ngogo)	Medium-altitude primary and secondary evergreen rain forest	4 [†]	37-63	1.57 [1.12-2.3]	0.23 [0.28-0.57]	GCA (50m)	5.9	131.5		26 [14-35]	16; 17	
		3		1.69 [±0.38]					2	\bar{x} = 37 [35-40]	T. Struhs	

												aker (unpu blishe d data – see 4; 18)	
			2 †	29	1.00 [0.77- 1.41]	0.55 [0.47- 0.63]	Unkn own	14				$\bar{x} = 36$ [25-50]	22
			6	4-37	1.40 [±0.32SE]	0.56 [±0.03SE]	MCP	14.2				$\bar{x} = 17$ [10-35]	This study; 23

862

863 † After one group (size: 35 – 50 individuals) fissioned during the study.

864 ‡ After one group (size: 50 individuals) fissioned during the study.

865

866 ¹ Galat-Luong (1975); ² Thomas (1991); ³ Gathua (2000); ⁴ Cords (1987); ⁵ Cords (1990); ⁶ EM unpublished data; ⁷ Sheppard (2000); ⁸ Plumtre & Reynolds
867 (1994); ⁹ Plumtre, Reynolds & Bakuneeta (1997); ¹⁰ Rode, Chapman, McDowell & Stickler (2006); ¹¹ Chapman & Lambert (2000); ¹² Struhsaker (1975); ¹³
868 Struhsaker (1978); ¹⁴ Struhsaker & Leland (1979); ¹⁵ Struhsaker (1980); ¹⁶ Struhsaker (1988); ¹⁷ Struhsaker & Leland (1988); ¹⁸ Butynski (1990); ¹⁹ Struhsaker
869 (1997); ²⁰ Treves (1998); ²¹ Wrangham, Crofoot, Lundy & Gilby (2007); ²² Windfelder & Lwanga (2002); ²³ Brown (2013)

870 **Figure 1** Cumulative use of home range by groups at Ngogo and Issa, calculated as number of
871 unique 50 x 50m grid cells and 75 x 75m grid cells, respectively, entered per follow day
872

873 **Figure 2** Home range sizes for Ngogo groups for the entire study period, calculated using one
874 hundred percent minimum convex polygons (MCP). Colored shading indicates vegetation cover.
875 Black lines indicate selected researcher trails, included for reference
876

877 **Figure 3** K0 home range size at Issa for the entire study period, calculated using one hundred
878 percent minimum convex polygon (MCP) and 75m grid cell analysis (GCA) methods. Colored shading
879 indicates vegetation cover
880

881 **Figure 4** Monthly proportion of home range used by groups at Ngogo and Issa. Proportions
882 calculated using 50m GCA method for R6 and R5 at Ngogo and 75m GCA method for K0 at Issa.
883 Black bars indicate mean values. Asterisks indicate half months for follows for Ngogo groups
884

885 **Figure 5** Group mean daily travel distance at Ngogo and Issa by month. Values are grouped by site
886 and GPS interval (R1 – R4: 30-minute intervals; R5, R6, and K0: 5-minute intervals). Black dots and
887 circles indicate mean and outlying values, respectively
888

889 **Figure 6** Mean hourly travel distance exhibited by K0 in wet and dry seasons and in all months
890 combined. Colored lines indicate mean hourly temperature in wet and dry seasons and in all months
891 combined
892

893 **Figure 7** Site-wide indices of food abundance measured in sample plots at Ngogo and Issa. Shown
894 are fruiting plant density (A), flowering plant density (B), and plant with leaves density (C) by
895 vegetation class and month. Black dots and circles indicate mean and outlying values, respectively