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RESEARCH ARTICLE

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Social and ecological correlates of space use patterns in Bwindi mountain gorillas

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Space use patterns determine access to resources necessary for survival and reproduction. Although it is recognized that the interplay between social and ecological variables shapes spacing patterns, few studies in group-living animals have simultaneously assessed their importance in a comprehensive approach using different spatiotemporal space use measures. In territorial species, such patterns are strongly determined by between-group competition, but its impact in non-territorial species is poorly understood. To better understand the role of social and ecological variables in non-territorial mountain gorillas (*Gorilla beringei beringei*), we simultaneously evaluated the impact of between-group competition (local gorilla population density and frequency of intergroup encounters) and within-group competition (group size) on space use patterns in 13 gorilla groups in Bwindi Impenetrable National Park, Uganda, while also examining variation in food availability (herbaceous food availability and level of frugivory). We found evidence of between-group competition, indicated by a decline of both monthly home range size and frequency of revisits to each part of the home range as the local gorilla population density increased and by an increase in daily travel distance on days when intergroup encounters occurred. Within-group feeding competition was inferred by a decrease in the frequency of revisits as group size increased. Lastly, food availability influenced the gorillas' spacing patterns, as indicated by a decline in monthly home range size as herbaceous food availability increased and by an increase in daily travel distance as the degree of frugivory increased. In sum, our results suggest that Bwindi gorillas adapted their space use according to the constraints of intraspecific competition and the availability of food resources. We provide some of the first evidence of between-group competition influencing spacing patterns in a non-territorial species. This study suggests a gradient between territoriality and non-territoriality, along which the level of between-group competition varies.

KEYWORDS
daily travel distance, *Gorilla beringei beringei*, intraspecific competition, monthly home range size, revisit frequency

1 | INTRODUCTION

Space use patterns are an important component of the behavioral ecology of animals because they regulate access to resources, which is a key determinant of fitness (Morales et al., 2010). These patterns are dynamic responses to social and ecological conditions that vary on different temporal and spatial scales (Börger, Dalziel, & Fryxell, 2008) and are often manifested in an animal's home range (*sensu* Burt, 1946) size and patterns of use (Benhamou & Riotte-Lambert, 2012; Börger et al., 2008). Although the interplay between social and ecological factors has been shown to determine space use patterns (Börger et al., 2008; Campos et al., 2014; Markham, Guttal, Alberts, & Altmann, 2013), comprehensive approaches that simultaneously assess the effect of between-group competition, within-group competition and food availability using different spatial and temporal measures of spacing patterns in social species are largely lacking.

For territorial species, in which territory owners actively exclude conspecifics from their home range (Brown & Orians, 1970), between-group competition is a major determinant of spacing patterns (reviewed by Adams, 2001). In contrast, for non-territorial species, between-group competition is expected to play a weaker role in influencing space use (Potts & Lewis, 2014) but has received little attention so far (but see Anderson, 1981; Kitchen, Cheney, & Seyfarth, 2004; Markham et al., 2013; Robinson, 1988). Competition between groups can be reflected by the density of conspecific individuals or by intergroup encounter frequencies. For species with non-overlapping home ranges, range size generally decreases as population density increases (Adams, 2001; Efford, Dawson, Jhala, & Qureshi, 2016). This relation has been shown in a variety of territorial species (e.g., Aronsson et al., 2016; Bogdziewicz, Zwolak, Redosh, Rychlik, & Crone, 2016; Schoepf, Schmohl, König, Pillay, & Schradin, 2015) and indicates that territoriality constrains space use of neighbors. In contrast, in the absence of territoriality, increasing conspecific density should increase the degree of shared space (Caillaud, Ndagijimana, Giarrusso, Vecellio, & Stoinski, 2014; Grant, Chapman, & Richardson, 1992), which may decrease the availability and predictability of food resources in shared areas (Grant et al., 1992). Hence, for non-territorial species, an increase in density should lead to an increase in home range size due to the energy requirements of additional neighboring individuals (Kjellander et al., 2004).

As population density increases, the frequency of encounters between groups is expected to increase (Caillaud et al., 2014; Vander Wal, Yip, & McLoughlin, 2012; but see Barrett & Lowen, 1998). Accordingly, for territorial species, home range size decreases as the number of intergroup encounters increases (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2003), whereas daily travel distance may increase on days of encounters (Bravo & Sallenave, 2003; Fashing, 2001). Despite recent studies investigating the effect of the outcome of intergroup encounters on spacing patterns in both territorial and non-territorial species (e.g., Crofoot, 2013; Markham, Alberts, & Altmann, 2012; Mosser & Packer, 2009; Roth & Cords, 2016), the impact of different measures of between-group competition, namely density of conspecifics and intergroup encounters, on space use patterns is largely unknown in non-territorial species.

In addition to between-group competition, competition within social units can be a key factor in determining space use (Campos et al., 2014; Snaith & Chapman, 2008). The ecological constraints model predicts that an increase in group size increases within-group feeding competition, forcing groups to expand home range size and daily travel distance to accommodate the greater foraging requirements of additional group members, thereby causing higher energetic costs for individuals in larger groups (Chapman & Chapman, 2000; Janson & Goldsmith, 1995). Additionally, groups may increase group spread to avoid within-group feeding competition (Chapman & Chapman, 2000; Snaith & Chapman, 2008). In contrast to home range size and day range, the revisit frequency to particular areas should be inversely related to group size as there is greater resource depletion with increasing group size (Cody, 1971; Davies & Houston, 1981).

Furthermore, ecological resource availability is an important influence on space use (McLoughlin & Ferguson, 2000). As food abundance increases, individuals need less space to obtain adequate energy (Saïd et al., 2005), resulting in the commonly observed inverse relationship between food abundance and both home range size and daily travel distance, but a positive relationship with revisit rates (e.g., Bartlam-Brooks, Bonyongo, & Harris, 2013; Boyer, Crofoot, & Walsh, 2012; Jedrzejewski, Schmidt, Theuerkauf, Jedrzejewska, & Okarma, 2001). These relationships may be altered by the spatial and temporal variability of food resources, such that species feeding on meat or fruit have larger home ranges and longer daily travel distances than those feeding on more evenly distributed and abundant resources (Clutton-Brock & Harvey, 1977; Gittleman & Harvey, 1982).

To better understand the role of social factors and their interplay with ecological variability in determining spacing patterns in a non-territorial species, we investigated these patterns in Bwindi mountain gorillas. To do so, we simultaneously assessed the impact of between-group competition, indicated by local gorilla population density and frequency of intergroup encounters, and within-group competition, reflected by group size, on space use patterns in wild mountain gorillas while also considering variation in food availability, that is, herbaceous food availability and level of frugivory. Mountain gorillas are a good model to investigate the interplay of social and ecological factors because they are non-territorial but face within- and between-group competition for access to food and mates and they live in an environment with spatiotemporally variable, yet highly abundant food resources. The two populations in the Virunga Volcanoes and in Bwindi Impenetrable National Park, Uganda, live in cohesive social groups (mean group size ± SD: 11 ± 8.0), consisting of at least one adult male, several adult females, and their offspring (Gray et al., 2013; Kalpers et al., 2003; Roy et al., 2014). Gorillas in Bwindi consume abundant herbaceous vegetation, which is available throughout the year, and seasonally available and dispersed fruit (Ganas, Robbins, Nkurunungi, Kaplin, & McNeilage, 2004). Within Bwindi, groups exhibit intra-population variation in access to herbaceous food resources and the degree of frugivory (Ganas, Nkurunungi, & Robbins, 2009; Nkurunungi, Ganas, Robbins, & Stanford, 2004), which makes them ideal to test the effect of variability in food availability on intraspecific variation in space use patterns.

Between-group competition in mountain gorillas has been considered to be low, as reflected by a high degree of home range overlap among neighboring groups (Caillaud et al., 2014; Ganas & Robbins, 2005; Watts, 1998a). However, groups appear to use particular areas less as neighbors increasingly used these areas (Seiler, Boesch, Mundry, Stephens, & Robbins, 2017). Furthermore, intergroup encounters may influence space use because they are strongly linked to female mate choice and male–male competition since they are the only time when females disperse to neighboring groups (Harcourt, Stewart, & Fossey, 1976; Robbins & Sawyer, 2007; Sicotte, 1993). Although a previous study found a tendency of longer travel distances on days with intergroup encounters (Watts, 1991), between-group competition and its impact on different spatiotemporal measures of spacing patterns in gorillas are still poorly understood.

The dynamics of within-group feeding competition in mountain gorillas remain unresolved (Ganas & Robbins, 2005; Watts, 1998a). One study in Bwindi found a positive effect of group size on home range size and daily travel distance (Ganas & Robbins, 2005), yet two studies in the Virungas did not observe these patterns (Caillaud et al., 2014; Watts, 1998a). However, these studies did not control for several other variables, such as food availability, which are likely to influence space use patterns. Furthermore, the effect of group size on other space use metrics, such as revisit rates that reflect depletion of food resources and within-group competition, remains unclear (Watts, 1998b).

In this study, we investigated how social and ecological factors influenced three different spatiotemporal measures of space use in Bwindi mountain gorillas: monthly home range size, daily travel distance and revisit frequencies to each part (i.e., grid cells) of the home range. Specifically, we made the following predictions for the effect of social factors:

(i) Because of between-group competition for food (Grant et al., 1992; Jetz, Carbone, Fulford, & Brown, 2004), we expected that a higher local gorilla population density would lead to an increase in monthly home range size and daily travel distance but to a reduction in revisit frequencies. (ii) We predicted that on days when intergroup encounters occur, groups would have longer daily travel distances and as the number of encounters increases, groups would have smaller home ranges but higher revisit frequencies to avoid male-male competition. (iii) Following the ecological constraints model, we predicted that larger groups would have larger monthly home range sizes and longer daily travel distances due to greater within-group feeding competition. As resource depletion increases with group size, we expected that larger groups would have lower revisit frequencies.

Concerning the effect of ecological factors, we had the following predictions:

(iv) We expected that an increase in herbaceous food availability would lead to a decrease in both monthly home range size and daily travel distance but to an increase in revisit frequencies. (v) As fruit trees in Bwindi are widely dispersed (Nkurunungi et al., 2004), we predicted that an increase in the level of fruit consumption (frugivory) would lead to an increase in monthly home range size, daily travel distance, and revisit frequencies.

2 | METHODS

2.1 | Study site and data collection

We studied 13 habituated groups of mountain gorillas, varying in size from five to 24 individuals (Table 1; Supplementary Information; see also Seiler & Robbins, 2016), in Bwindi Impenetrable National Park, Uganda, between May 2012 and July 2013. Using handheld global positioning system (GPS) units (GPSmap 60CSx and 62), we recorded the locations of each gorilla group. On each observation day, we collected location data at 30 s intervals by walking along the trails used by the majority of the group. These trails are easy to detect because gorillas create obvious trails by trampling vegetation, discarding food items and defecating as they move through the forest (Ganas & Robbins, 2005; Watts, 1991). We recorded part of the location data while following the group during the daily observation period, which was limited to 4 hr per day according to park authority regulations. Data for all groups were collected in the morning to mid-day and hence the timing of data collection did not differ much among the study groups. NS and 12 field assistants who were intensively trained collected data for a mean of 16 days (range: 4–31 days) per month and group (3–14 months per group; Table 1). The variation in the number of observation days and months per group was mainly due to two group fissions during the study period. NS visited each assistant every other month and ensured data collection quality by checking the assistants' GPS usage, location data collection, scan sampling data collection, gorilla behavior, and food species identification. We also recorded crop raiding behavior (Seiler & Robbins, 2016). Rainfall was measured daily by the Uganda Wildlife Authority at stations located in the four general locations where the study groups ranged (Supplementary Information). This research was conducted in compliance with the regulations of the Uganda National Council for Science and Technology and the Uganda Wildlife Authority, and adhered to the American Society of Primatologists' principles for the ethical treatment of primates.

2.2 | Test predictor variables

2.2.1 | Local gorilla population density

We calculated local gorilla population density (Table 1) for each group by weighting the mean group sizes of all other gorilla groups in the study area by the inverse distance between the respective home range centers. Using both our and the Bwindi gorilla census 2011 location data (Roy et al., 2014), we determined minimum convex polygon (MCP) home ranges of the study groups and of 26 unhabituated groups (mean group size = 7; range: 2–17 individuals) in ArcGIS 9.3 (ESRI Inc., Redlands CA). We then identified the centroid of points that form the MCP centers applying Hawth's Tool (Beyer, 2004) or used the only location point available (Figure S1 and Table S1). Because a mean of only three location points (range: 1–11) were available for the unhabituated groups from the Bwindi census 2011 (Table S1), the MCP was the most appropriate method to determine home range centroids. Although the MCP method has been criticized for overestimating

TABLE 1 Summary statistics for the predictor and response variables of the 13 Bwindi mountain gorilla study groups

Group	Monthly number of grid cells entered[a,c]	Monthly home range size (km^2)[a,d]	Daily travel distance (m)[a]	Mean group size[e]	Mean group composition	Monthly number of intergroup encounters[b]	Local gorilla population density[f]	Monthly FDR[b]	Total sampling effort (days)	Sampling effort (days)[a]
Bitukura (Bi)	80.9 ± 45.2 (11–163)	0.8 ± 0.5 (0.1–1.6)	951.4 ± 872.0 (107.9 –6455.4)	9	4 SB, 1 BB, 4 ADF, 3 JUV, 1 INF	0 (0, 1.75) (0–3)	7.9	8.4 (3.1, 17.0) (0–175.2)	162	11.6 (2–16)
Kyagurilo (Ky)	169.9 ± 68.0 (71–316)	1.7 ± 0.7 (0.7–3.1)	957.0 ± 462.4 (284.0 –2968.6)	11	2 SB, 2 BB, 7 ADF, 1 JUV, 7 INF	0 (0, 1) (0–1)	7.6	3.5 (1.0, 7.9) (0 –16.7)	394	28.1 (11–31)
Oruzogo (Or)	73.5 ± 7.7 (69–85)	0.7 ± 0.1 (0.7–0.9)	760.8 ± 355.5 (143.7 –1453.5)	14	2 SB, 5 BB, 7 ADF, 2 JUV, 6 INF	0 (0, 0) (0–0)	7.6	0.4 (0.2, 1.9) (0.1–5.8)	75	15.0 (15–15)
Nshongi (Ns)	60.8 ± 15.9 (38–73)	0.6 ± 0.2 (0.4–0.7)	952.9 ± 547.6 (306.4 –2636.8)	13	3 SB, 4 BB, 6 ADF, 5 JUV, 2 INF	0 (0, 0.25) (0–1)	6.9	10.2 (8.7, 11.3) (5.1–13.5)	57	14.3 (12–15)
Kakono (Kak)	70.1 ± 10.5 (61–93)	0.7 ± 0.1 (0.6–0.9)	794.3 ± 447.7 (154.2 –2451.3)	5	1 SB, 4 BB	0.5 (0, 1.25) (0–2)	8.0	38.4 (8.9, 69.8) (0.5–119.8)	104	14.9 (14–15)
Bweza (Bw)	88.3 ± 49.0 (17–170)	0.9 ± 0.5 (0.2–1.7)	993.4 ± 584.4 (234.6 –2999.3)	4	1 SB, 3 ADF, 1 JUV, 2 INF	0 (0, 0) (0–1)	8.4	2.3 (0, 17.1) (0 –71.6)	128	12.8 (4–15)
Kahungye (Kah)	109.0 ± 24.7 (67–167)	1.1 ± 0.3 (0.7–1.7)	1000.9 ± 585.3 (224.4–3563.4)	13	2 SB, 4 BB, 7 ADF, 6 JUV, 5 INF	0 (0, 2) (0–5)	6.4	1.2 (0.1, 4.1) (0 –9.6)	191	13.6 (4–16)
Busingye (Bu)	105.7 ± 29.9 (70–156)	1.1 ± 0.3 (0.7–1.6)	918.5 ± 578.2 (251.0 –4201.8)	4	1 SB, 3 ADF, 1 JUV, 2 INF	0 (0, 2) (0–5)	7.7	0.4 (0.3, 0.6) (0 –13.8)	204	17.0 (14–18)
Mishaya (Mi)	87.5 ± 36.5 (50–184)	0.9 ± 0.4 (0.5–1.8)	887.3 ± 607.0 (213.5 –4025.0)	5	1 SB, 1 BB, 3 ADF, 2 JUV	0 (0, 2) (0–3)	8.6	1.8 (0, 10.5) (0 –48.9)	202	14.4 (6–16)
Nkuringo (Nk)	82.1 ± 27.8 (25–122)	0.8 ± 0.3 (0.3–1.2)	790.8 ± 460.0 (193.9 –2284.1)	7	4 SB, 3 ADF, 3 JUV, 3 INF	0 (0, 0) (0–1)	7.0	26.2 (18.2, 31.0) (5.1–52.9)	194	16.2 (10–18)
Habinyanja (Ha)	110.3 ± 28.7 (67–167)	1.1 ± 0.3 (0.7–1.7)	1146.7 ± 627.3 (301.5–3689.8)	13	1 SB, 2 BB, 10 ADF, 4 JUV, 2 INF	0 (0, 0) (0–1)	7.2	5.4 (0.9, 26.8) (0.5–89.1)	195	15.0 (10–17)
Mubare (Mu)	95.0 ± 24.6 (54–140)	1.0 ± 0.3 (0.5–1.4)	944.2 ± 485.6 (202.8 –2729.6)	7	1 SB, 1 BB, 5 ADF, 1 JUV	1.0 (0, 1) (0–2)	6.6	0 (0, 0.2) (0–43.2)	205	15.8 (15–17)
Rushegura (Ru)	103.6 ± 36.6 (53–173)	1.0 ± 0.4 (0.5–1.7)	1335.1 ± 710.0 (207.8–3248.7)	7	1 SB, 2 BB, 4 ADF, 4 JUV, 4 INF	0 (0, 1) (0–2)	6.4	1.3 (0.2, 2.9) (0 –25.5)	198	14.1 (6–16)

SB = silverback (≥12 years); BB = blackback (8–12 years); ADF = adult female (≥8 years); JUV = juvenile (3.5–8 years); INF = infant (0–3.5 years); FDR = fruit:dung ratio.

[a] Mean ± SD (range).

[b] Median (quartiles) (range).

[c] Number of unique 100 × 100 m grid cells entered.

[d] Based on the number of 100 × 100 m grid cells entered.

[e] Number of weaned group members.

[f] Weighted mean size of the gorilla population outside the group; the larger the estimate, the more neighboring gorillas are located near a group.

home range size (Börger et al., 2006; Worton, 1989), there is no reason to assume that this bias would vary among groups. Using very few data points to determine MCPs of the unhabituated groups might displace the home range centroids to some extent. However, given an average annual MCP home range size of 26 km^2 (Ganas & Robbins, 2005), the maximum displacement would be about 2.9 km. As it is very unlikely that all location data from all unhabituated groups were sampled from the periphery of the groups' home ranges and hence that the centroids of all unhabituated groups were misplaced to the maximum extent, we believe that the imprecision of the centroids' locations will not have a notable impact on our density variable. The local gorilla population density for each study group represents the weighted size of the gorilla population except the group. Hence, the larger the estimate, the more neighboring gorillas are located near a group (Figure S2).

2.2.2 | Intergroup encounters

Throughout the daily observation period we recorded all visual and auditory encounters (hearing chest beats of a non-group member) with other groups and solitary silverbacks on an ad libitum basis to determine the number of intergroup encounters per group (Table 1). It was not possible to determine winners and losers of such encounters. Although the variation in sample days (range: 57–394; Table 1) may underestimate the number of intergroup encounters, there was no reason to expect that the frequency of intergroup encounters would differ among groups.

2.2.3 | Group size

We determined mean group size for each group, defined as the average number of weaned individuals per month and group (range: 4–14 individuals; Table 1).

2.2.4 | Availability of herbaceous food

Our measure of food availability was based on the energy density of the most important herbaceous food species ($N = 24$) in the gorillas' diet. Energy density of herbaceous foods was determined by combining both biomass density estimates and nutritional analyses of the plant parts consumed. We defined the most important herbaceous food species as those contributing to >1% of the diet recorded over the study period (Ganas et al., 2009). To determine those species, we estimated dietary composition of groups by recording foods consumed by each individual in view during instantaneous scan sampling at 5 min intervals throughout the daily observation period (Ganas et al., 2004). We directly observed 167 gorillas with a mean total observation time of 214 hr (range: 46–1383 hr) per group.

To get biomass estimates, we sampled 490 transects of 200 m length placed within 500 × 500 m grid cells overlaid onto the study area (Figure S1). The transects were sampled once because there is only little seasonal variability in herbaceous food availability despite large spatial variation (Ganas et al., 2009). Along each transect, we sampled ten 1 m^2 plots placed in 20 m intervals on alternate sides and measured stem length and counted leaves of herbaceous gorilla food species (Ganas et al., 2009; Seiler & Robbins, 2016). We estimated biomass of the most important herb species using regression equations relating the respective measure (stem length or number of leaves) recorded in the vegetation transects to the dry weight of sampled plants (Ganas et al., 2009). We first calculated biomass of the herb species in a plot and then summed all species' biomasses to get biomass density per plot. We calculated biomass density (g/m^2) per 500 × 500 m grid cell by summing the biomass of all plots in each cell divided by the number of plots sampled in each cell (Ganas et al., 2009; Supplementary Information).

Nutritional data were available for 76 herbaceous food species (which included 67% of the most important herbaceous food species; Ganas, Ortmann, & Robbins, 2008) and eight additional gorilla food species were analyzed for their nutritional content in the same laboratory applying the same methods. We calculated the herbaceous vegetation energy density of each 500 × 500 m grid cell by multiplying the predicted metabolic energy (kcal/g) of each herb species from the nutritional analysis by its biomass density (g/m^2) and summing all species' energy contents ($kcal/m^2$; Figure S3 and for more details Seiler et al., 2017). The herbaceous vegetation energy density of each monthly home range per group was determined using the mean energy density of all 500 × 500 m grid cells entered in a month, weighted by the distance traveled in each cell for each month and group. The herbaceous vegetation energy density for each day was equal to the mean value for all 500 × 500 m grid cells entered during the day, weighted by the distance travelled within each 500 × 500 m cell. We also determined the mean herbaceous vegetation energy density per group by averaging all monthly energy density estimates per group. As a post-hoc test, we correlated the mean herbaceous vegetation energy density per group with local gorilla population density using a Pearson correlation to investigate whether areas with more food could host a higher local gorilla population density or whether between-group competition for food would decrease food availability in areas with a high local gorilla population density.

2.2.5 | Level of frugivory

To determine the relative frugivory of each group (Table 1), we collected two randomly selected fecal samples from the night nests of each group on each observation day (number of samples $N = 4703$) and estimated the fruit:dung ratio (FDR; Head, Boesch, Makaga, & Robbins, 2011):

$$\mathrm{FDR} = \mathrm{FC}/\text{wet weight of fresh fecal sample, and}$$
$$\mathrm{FC} = \Sigma_{i=1}^{n}\ \mathrm{FW}_i \times \mathrm{SD}_i/\mathrm{SF}_i,$$

where FC is the estimated amount of fruit consumption that had contributed to the fecal sample that was collected, FW_i represents the weight of one fruit of species i (without seeds), SD_i equals the number of seeds of species i in the sample collected that day, and SF_i equals the mean number of seeds in one fruit of species i. To get both the mean number of seeds in a fruit and the weights per fruit of each species, we collected 20 specimens from each fruit species ($N = 23$) consumed by the gorilla groups during the study period. For the monthly FDR, we combined the samples found on each day in a month. We also calculated the relative mean frugivory of each gorilla group by averaging the monthly FDR per group across the study period. As gorillas might feed on fruit only for a small proportion of the day (Robbins, 2008), using the FDR method will give a more realistic measure of the gorillas' fruit consumption than using scan sampling during the 4-hr daily observation period.

2.3 | Response variables

2.3.1 | Monthly home range size (model 1)

Using the location data, we defined the monthly home range size for each group by adapting the digitized polygon method (Ostro, Young, Silver, & Koontz, 1999) and determined the number of unique 100 × 100 m grid cells entered per month and group (Table 1), with the cell size being an estimated maximum group spread of Bwindi gorillas (NS and MMR, personal observation). We did not apply a home range estimation method based on point densities, such as kernel density estimates (Worton, 1989), as we could not assess the gorillas' temporal use when following only their trails. Applying the digitized polygon method (Ostro et al., 1999), paths originating from autocorrelated location data are buffered with a pre-defined distance that reflects the area of influence of a group or individual, in our case maximum group spread (50 m spread on either side of the travel path) and hence a biologically meaningful distance.

2.3.2 | Daily travel distance (model 2)

Using all-day location data and by connecting the subsequent location points, we measured the cumulative lengths of the trails between two night nests to determine daily travel distance (Ganas & Robbins, 2005; Watts, 1991). A function developed in R (R Core Team, 2015) smoothed the daily tracks to improve accuracy (Supplementary Information) because considerable location error can be obtained when data are taken from roughly the same location (while gorillas are resting or feeding, see also Janmaat, Ban, & Boesch, 2013). We calculated the length of 1,301 cleaned travel paths (mean number of travel paths per group ± SD: 100 ± 68.4; range: 29–301). Additionally, we tested for a correlation between the monthly total of the daily travel distances and monthly home range size per group (Supplementary Information). The correlation was positive ($\text{Est} \pm \text{SE} = 0.250 \pm 0.045$, $p < 0.001$, $R^2 = 0.508$), but the R^2 value was low enough to warrant investigating the two variables independently.

2.3.3 | Revisit frequency per grid cell (model 3)

Using the daily location data, we determined the number of times that each gorilla group entered each 500 × 500 m grid cell during the study period. The second visit to a grid cell by each group was considered as the first revisit (i.e., we did not include the first visit). Cases when a group left and re-entered the same grid cell on the same day were not counted as a revisit. We could not include grid cells that had not been revisited (only one recorded visit) because no data for a control variable (i.e., previous visit; see below) were available.

2.4 | Models and statistical analyses

2.4.1 | Monthly home range size model (model 1)

To quantify the effects of local gorilla population density, number of intergroup encounters per month, group size, herbaceous food availability per monthly home range, and monthly level of frugivory on the monthly home range size ($N = 140$ observations from 13 groups), we used a linear mixed model (LMM; Baayen, 2008). As a control predictor we included monthly rainfall as it negatively influenced monthly home range size of Virunga gorillas (Vedder, 1984). Additionally, we included whether gorillas crop raided during that month as a factor with two levels (yes/no) to control for the possible effect of the gorillas having smaller home ranges when feeding on crops (Campbell-Smith, Campbell-Smith, Singleton, & Linkie, 2011). Lastly, we included the number of observation days per month to control for the scaling relationship between sampling effort and home range size. Although the number of observation days per month is not expected to scale linearly with home range size but should be asymptotic (Gautestad & Mysterud, 1993), this was the best fit to our data as shown by model selection (Burnham & Anderson, 2002; Supplementary Information). To ensure that the model controlled for the variation in observation days per month (range: 4–31), we fitted the full model using a reduced dataset only comprising months with at least 15 observation days, which confirmed that the model can control for this variation (Supplementary Information, Table S2).

2.4.2 | Daily travel distance model (model 2)

We fitted a LMM (Baayen, 2008) to examine the impact of the five test predictors (local gorilla population density, occurrence of an intergroup encounter on that day [yes/no], group size, herbaceous food availability per daily travel path, and daily level of frugivory) on the daily travel distance (log-transformed; $N = 1301$ days from 13 groups and 10 groups of origin; i.e., the original group that subsequently fissioned). As a control predictor we included daily rainfall as it negatively influenced the daily travel distance of Bwindi gorillas (Ganas & Robbins, 2005).

2.4.3 | Revisit frequency model (model 3)

We used a Generalized Linear Mixed Model (GLMM; Baayen, 2008) to examine the influence of the test predictors (local gorilla population density, mean number of intergroup encounters, group size, herbaceous food availability per 500 × 500 m grid cell, and mean level of frugivory) on the revisit frequency per 500 × 500 m grid cell per group

($N = 369$ observations from 13 groups, 10 groups of origin, and 266 grid cells). As Virunga gorillas adjust their revisit patterns to the extent of previous use (Watts, 1998b), we controlled for this effect by including mean intensity of previous use as a control predictor (Supplementary Information). To control for varying sample days per group, we included the number of observation days per group (log-transformed) as an offset term in the model.

2.4.4 | Statistical analysis

All models were fitted in R (R Core Team, 2015) and implemented using the functions glmer or lmer of the lme4 package (Bates, Mächler, Bolker, & Walker, 2015). All LMMs were fitted with Gaussian error structure and identity link (models 1 and 2) (Baayen, 2008), whereas the GLMM was fitted with Poisson error structure and log link function (model 3) (McCullagh & Nelder, 1989). For all models and where applicable, we included (i) the mean of the test predictors per group (=between-groups effect) and (ii) the test predictors centered to a mean of zero per group (=within-groups effect) to account for potential dissimilar effects of the predictors within and among groups (van de Pol & Wright, 2009; Supplementary Information). We included group ID ($N = 13$) as a random-effects variable (random intercept) in all models to control for repeated observations. For the daily travel distance (model 2) and the revisit frequency model (model 3), we included the ID of the group of origin ($N = 10$) to control for the possible dependent ranging of recently fissioned groups. Because the home range size model (model 1) became too complex when including this random-effects variable, we conducted additional analyses showing that its exclusion did not bias the results (Supplementary Information). Additionally, we included grid cell ID ($N = 266$) as an additional random-effects variable in the revisit frequency model (model 3). Furthermore, we included random slopes terms allowing for the effects of the fixed-effects predictors to randomly vary among the levels of the random-effects variables (hereafter called random slopes; see Supplementary Information) to keep error I rate at the nominal level of 5% (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009). We controlled for potential temporal and spatial autocorrelation in the residuals (Supplementary Information; Fürtbauer, Mundry, Heistermann, Schülke, & Ostner, 2011) using the following equation to determine the autocorrelation term:

$$\mathrm{ac}_i = \frac{\sum_{j=1}^{n|j \neq i}\left(\mathrm{residual}_j \times \mathrm{dnorm}(\mathrm{dist}(j,i),\mathrm{mean} = 0,\mathrm{sd} = D)\right)}{\sum_{j=1}^{n|j \neq i}\mathrm{dnorm}(\mathrm{dist}(j,i),\mathrm{mean} = 0,\mathrm{sd} = D)},$$

with ac_i being the value of the autocorrelation term for the ith data point, $residual_j$ being the residual of the jth data point (determined from a model lacking the autocorrelation term), and dnorm(dist(i, j), *mean* = 0, sd = D) being the density of a Gaussian distribution function (with a mean of zero and a standard deviation of D) for a quantile being the spatial distance or time lag between data points i and j. The value of D was optimized such that the log-likelihood of the full model with the autocorrelation term included was maximized.

We checked for model assumptions and no violations were found (Supplementary Information). To assess collinearity we determined Variance Inflation Factors (VIFs; Field, 2005) for all models using the function vif of the package car (Fox & Weisberg, 2011) applied to corresponding standard linear models lacking random-effects terms (intercept and slopes). Partially high VIFs (maximum VIF across all models: 5.7) suggested potential problems (Zuur, Ieno, & Elphick, 2010). Hence, we fitted additional reduced models excluding the potentially collinear predictors one at a time (for all predictors with VIFs > 3; Supplementary Information) and compared the estimates of these reduced models with those obtained from the full model. Because estimates of the reduced home range size (model 1) and revisit frequency model (model 3) changed and due to a low variation in the respective predictor variables, we conducted multi-model inference to confirm the importance of the significant predictor variables in the full models (Burnham & Anderson, 2001, 2002). We determined the probability of each predictor variable to be in the truly best model by summing Akaike weights for all models including a given variable (Supplementary Information).

We checked for model stability for each model by excluding each level of the random-effects variables from the data one at a time and comparing the estimates for these subsets of the data to those obtained from a model based on the full data set; no influential cases were found. For all models, we tested the significance of the test predictors by comparing the full model with a null model excluding the test predictors using a likelihood ratio test (Forstmeier & Schielzeth, 2011). For more details of model implementation, please see Supplementary Information.

2.5 | Post-hoc analysis: Direction of travel paths on days with intergroup encounters

To further investigate whether groups avoided each other on days with intergroup encounters, we visually inspected travel paths ($N = 76$) of the study groups on days with encounters and qualitatively compared them to travel paths on days when no encounter was observed ($N = 76$). For both, we determined the percentage of travel paths that was characterized by a sharp turn in the travel direction, defined as a change in the travel direction of at least 90°, involving backtracking and complete reversals. Additionally, we determined the percentage of travel paths, in which a group's travel direction was heading towards their home range centroids (see section 2.2.1) on days with intergroup encounters. As we did not have data on the exact location and timing of encounters for most days, we could not assess whether the change in travel direction occurred after an intergroup encounter.

3 | RESULTS

3.1 | Monthly home range size (model 1)

Bwindi gorilla groups entered 101 ± 44.2 (mean ± SD) 100 × 100 m grid cells per month (range: 17–316; Table 1). We found a significant effect of the test predictors on monthly home range size (likelihood ratio test:

χ^2 = 20.698, df = 8, p = 0.008). Monthly home range size decreased as both local gorilla population density and the between-groups effect of herbaceous food availability increased (Table 2). Due to potential collinearity issues and a low variation in the respective predictor variables (local gorilla population density, group size, and between-groups effect of herbaceous food availability), we determined summed Akaike weights for each test predictor. Akaike weights were highest for local gorilla population density and herbaceous food availability, confirming the results of the full model (Table 3). The post-hoc analysis, which investigated whether areas with more food hosted a higher local gorilla population density or whether between-group competition for food decreased food availability in areas with a higher local gorilla population density, revealed the correlation between mean herbaceous vegetation energy density per group and local gorilla population density to be non-significant (r = −0.202, N = 13 groups, p = 0.509).

3.2 | Daily travel distance (model 2)

Bwindi gorilla groups travelled for a mean of 975 ± 593.0 m per day (range: 108–6,455 m; Table 1). The test predictors showed a significant impact on daily travel distance (χ^2 = 20.553, df = 7, p = 0.004). Groups had longer daily travel distances on days when intergroup encounters occurred. Within groups, we found an increase in daily travel distance as the amount of fruit consumption increased (Table 2).

TABLE 2 Summary of mixed model results investigating space use behavior of Bwindi mountain gorillas

Response variable	Monthly home range size (model 1)				Daily travel distance (model 2)				Revisit frequency per 500 × 500 m grid cell (model 3)			
Predictor variable[a]	Est	SE	χ^2	p	Est	SE	χ^2	p	Est	SE	χ^2	p
Intercept	16.964	9.297	[c]	[c]	0.637	0.016	[c]	[c]	−3.746	0.077	[c]	[c]
Local gorilla population density	**−11.473**	**5.294**	**4.544**	**0.033**	−0.033	0.030	1.121	0.290	−0.216	0.097	3.955	0.047
Intergroup encounters (w)	5.099	3.213	2.364	0.124	**0.170**	**0.041**	**7.824**	**0.005**		[e]		
Intergroup encounters (b)	−0.549	3.016	0.033	0.856		[d]			0.135	0.081	2.799	0.094
Group size	1.844	5.019	0.134	0.714	−0.003	0.034	0.006	0.940	**−0.194**	**0.079**	**6.247**	**0.012**
Herbaceous food availability (w)	−3.874	2.539	2.247	0.134	−0.001	0.009	0.025	0.875	0.013	0.036	0.143	0.705
Herbaceous food availability (b)	**−9.335**	**4.473**	**4.247**	**0.039**	<0.001	0.033	0.107	0.744	0.148	0.129	1.211	0.271
Frugivory (w)	7.668	4.281	2.881	0.090	**0.032**	**0.010**	**8.104**	**0.004**		[e]		
Frugivory (b)	2.305	3.214	0.513	0.474	−0.014	0.014	0.867	0.352	−0.200	0.090	3.730	0.053
Rainfall (w)	−7.380	3.641	3.602	0.058	−0.022	0.008	5.070	0.024				
Rainfall (b)	13.794	4.137	10.559	0.001	0.016	0.019	0.664	0.4156				
Crop raiding	−11.079	8.587	1.622	0.203								
Mean intensity of previous use (w)									0.174	0.044	9.028	0.003
Mean intensity of previous use (b)									−0.210	0.091	4.218	0.040
Number of observation days	5.403	0.529	54.691	<0.001						[f]		
Autocorr[b]					0.062	0.013	12.795	<0.001	0.452	0.049	21.438	<0.001

For all models, the comparison of the full model versus the null model that excluded the test predictors revealed significance. Significant test predictors (p < 0.05) are indicated in bold. (w) indicates the within-groups effect and (b) indicates the between-groups effect of this predictor. Empty cells indicate variables not included in a model. The results for the random-effects terms are shown in Table S3.

[a] We show the estimates (Est), standard error (SE), the chi-square value (χ^2; df were generally 1) and p values for each test predictor.

[b] The autocorrelation term (Autocorr) represents temporal autocorrelation for the daily travel distance model (model 2) and spatial autocorrelation for the revisit frequency model (model 3). The temporal autocorrelation term was removed from the home range size model (model 1) because the estimate was negative.

[c] Not shown because of having a very limited interpretation.

[d] Daily intergroup encounters was included as a factor with two levels (no/yes) in the daily travel distance model (model 2), hence no between-groups effect.

[e] Mean frugivory and the mean number of intergroup encounters were used as test predictors in the revisit frequency model (model 3), hence no within-groups effect.

[f] Please note, to control for the variation in the number of sampling days, we included number of sampling days as an offset-term in the model and hence no Est, SE, χ^2, or p value are available.

TABLE 3 Summed Akaike weights for the test predictor variables

Response variable	Monthly home range size (model 1)	Revisit frequency per 500 × 500 m grid cell (model 3)
Predictor variable		
Local gorilla population density	0.73	0.84
Intergroup encounters	0.22	0.35
Group size	0.48	0.84
Herbaceous food availability	0.62	0.18
Frugivory	0.32	0.47

3.3 | Revisit frequency per grid cell (model 3)

During the study period, the mean number of revisits per group and 500 × 500 m grid cell was 4 ± 3.8 (range: 1–28 revisits per grid cell). The test predictors revealed a significant effect on the revisit frequency per grid cell within the home range ($\chi^2 = 13.567$, df = 6, $p = 0.035$). We found that the revisit frequency declined significantly as both local gorilla population density and group size increased (Table 2). Akaike weights were highest for local gorilla population density and group size, confirming the results of the full model (Table 3).

3.4 | Direction of travel paths on days with intergroup encounters

To further assess whether groups avoided each other, we visually investigated the travel paths of groups on days with intergroup encounters compared to days when no encounters were observed. We found that the travel paths were characterized by a sharp turn in the travel direction (change in direction of >90°; Figure S4) on 81.6% of days that intergroup encounters occurred ($N = 76$). In contrast, we observed a sharp turn in travel direction on 47.4% of days when no encounters were observed ($N = 76$). Groups moved towards the centroid of their home range on 56.6% of the days that intergroup encounters occurred.

4 | DISCUSSION

Using a dataset on 13 wild mountain gorilla groups, which represents more than one third of the social units and individual gorillas in the whole population (Roy et al., 2014), we provide some of the first evidence of between-group competition in mountain gorillas, indicated by an adjustment of all three spatiotemporal measures of spacing patterns. Additionally, revisit patterns indicated within-group feeding competition in this mainly folivorous great ape (Ganas et al., 2004). This highlights the importance of investigating space use metrics other than the commonly used daily travel distance and monthly home range size to make inferences about within-group feeding competition (see also Snaith & Chapman, 2005). Furthermore, our study shows that groups adjusted their space use patterns to the energetic value of food resources.

4.1 | Between-group competition

Daily travel distance increased on days with intergroup encounters, whereas local gorilla population density had a negative effect on monthly home range size and revisit frequencies. The increase of the daily travel distance on days with intergroup encounters, as also observed in the Virunga gorillas (Watts, 1991) and colobus monkeys (Fashing, 2001), may reflect males wanting to keep away from other groups to prevent their females from dispersing, to avoid infanticide, and/or to follow groups in order to attract more females (Harcourt et al., 1976; Sicotte, 1993). The inverse relationship between local population density and home range size, typical for territorial species (e.g., Bogdziewicz et al., 2016; Schoepf et al., 2015), suggests that neighboring gorilla groups represent a social barrier constraining movements (Barrett & Lowen, 1998). Such an avoidance-based spacing pattern (i.e., reducing monthly home range size and revisit frequency as local gorilla population density increases) may reduce the frequency of intergroup encounters, which are strongly linked to mate competition in gorillas (Harcourt et al., 1976; Robbins & Sawyer, 2007). Similarly, territorial species have lower encounter rates than expected by random walks (Barrett & Lowen, 1998; Hutchinson & Waser, 2007) to actively avoid neighbors and/or mate competition (Aronsson et al., 2016; Kjellander et al., 2004). Although we could not assess whether groups changed their travel direction following an intergroup encounter, we found that they did so on most days with intergroup encounters in contrast to days when no encounter occurred, during which such turns were clearly less common. This has also been found in territorial species (Asensio, Brockelman, Malaivijitnond, & Reichard, 2011) and further suggests that groups avoided each other (see also Byrne, Whiten, & Henzi, 1987; Chapman & Valenta, 2015; Mehlman & Parkhill, 1988).

Mountain gorillas have considerable intergroup home range overlap (Caillaud et al., 2014; Ganas & Robbins, 2005; Watts, 1998a) and a higher local gorilla population density should increase the unpredictability of food availability in the shared areas (Grant et al., 1992). Hence, groups may restrict their movements to avoid areas that have been depleted by neighbors. Constraining movements with increasing density (e.g., Aronsson et al., 2016; Schoepf et al., 2015) may have important long-term costs because animals might limit themselves by reducing the use of potentially available space, thereby lowering the carrying capacity in the long-term (see also Wrangham, Crofoot, Lundy, & Gilby, 2007).

4.2 | Within-group competition

We found evidence of within-group feeding competition when investigating revisit frequencies. As group size increased, the gorillas decreased revisit frequencies, presumably to avoid previously used areas with reduced herbaceous food availability due to depletion (Cody, 1971; Davies & Houston, 1981). The primary indicators of within-group feeding competition in primates, referred to as the ecological constraints model, has been an increase in daily travel distance and home range size with increasing group size (Chapman & Chapman, 2000; Janson & Goldsmith, 1995; for carnivores see Wrangham, Gittleman, & Chapman, 1993), yet we did not find such an effect. A previous study of the Bwindi gorillas found support for the ecological constraints model (Ganas & Robbins, 2005), but that study did not control for repeated observations on the same groups, which can lead to an erroneous significance of a predictor variable (Jenkins, 2002). Instead of increasing travel distance, individuals may have increased group spread to avoid within-group feeding competition as found in colobus monkeys (Snaith & Chapman, 2008) and suggested for the Virunga gorillas (Watts, 1991). This strategy seems most likely as daily travel distance was also not obviously affected by variation in herbaceous food availability.

4.3 | Food availability

On a daily basis, gorillas showed short-term adjustments to the availability of fruit by increasing travel distance. However, daily travel distance was not affected by herbaceous food availability, which suggests that its variation was too small to have a significant effect or that groups increased group spread in areas with low resource abundance (Snaith & Chapman, 2008). Additionally, gorillas may adapt their daily travel distances to the quality of food patches within an area. On a monthly basis, gorilla groups reduced home range size with increasing availability of abundant herbaceous food, which does not vary temporally (Ganas et al., 2009). However, we found no effect of frugivory on monthly home range size or revisit frequency. The spatial distribution of fruit trees might be a key factor in determining these long-term spacing patterns. Overall, we observed behavioral adaptations to the value of food resources: groups reduced energy expenditure with increasing abundance of an evenly distributed resource (Bartlam-Brooks et al., 2013; Saïd et al., 2005) but were willing to travel further to gain foods that offer easily digestible energy (Ganas & Robbins, 2005; Masi, Cipolletta, & Robbins, 2009).

5 | CONCLUSIONS

In sum, this study exemplifies how mountain gorillas adjusted their space use to competition with conspecifics and variability in food availability. Gorillas responded to social and ecological variability across all spatiotemporal measures of spacing patterns, though different social and ecological factors were not equally important. Hence, important factors affecting space use may go unnoticed when not examining different spatiotemporal measures of space use (Campos et al., 2014; Markham et al., 2013).

Bwindi gorillas appeared to be constrained in their movements by neighbors, resembling the avoidance response typical for territorial species (Adams, 2001; Brown & Orians, 1970). We suggest that non-territorial species, like mountain gorillas, may use spacing mechanisms that elicit such an avoidance response to reduce or avoid between-group competition (see also Seiler et al., 2017). The importance of neighbors in influencing spacing patterns in a species that does not actively defend its home range suggests a gradient between territoriality and non-territoriality, along which the level of between-group competition varies (see also Bartlett, 2003; Nowicki, Searcy, Krueger, & Hughes, 2002; Richard, 1985). Together, our research highlights the importance of investigating several space use metrics while integrating both social and ecological factors, which provides a more comprehensive understanding of how social animals adapt to the dynamics of intraspecific competition and ecological variability.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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