



RESEARCH ARTICLE

Ecological correlates of space use patterns in wild western lowland gorillas

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Abstract

The distribution of resources is a crucial determinant of animals' space use (e.g., daily travel distance, monthly home range size, and revisitation patterns). We examined how variation in ecological parameters affected variability in space use patterns of western lowland gorillas, *Gorilla gorilla gorilla*. They are an interesting species for investigating this topic because key components of their diet are nonfruit items (herbaceous vegetation and tree leaves) that occur at low density and are sparsely distributed, and fruits, which show high spatiotemporal variation in availability. We estimated how availability of nonfruit foods and fruit, frugivory (proportion of feeding time consuming fruit), and swamps in areas used by the gorillas influenced daily travel distance, monthly home range size, and revisit frequency to grid cells in the home range of one habituated gorilla group in Loango National Park, Gabon. Using location data from 2015 to 2018, we found that the gorillas decreased their daily travel distance as both the density of nonfruit foods and the proportion of swamps in areas used increased. Daily travel distances were shorter when both frugivory and availability of fruit were higher, yet, daily travel distances were longer when availability of fruit was low but frugivory was still high. Furthermore, monthly home range size increased as frugivory increased and monthly revisit frequencies to an area increased as fruit availability of an area increased. In conclusion, the availability of both nonfruit and fruit influenced the gorillas' space use patterns. Gorillas decreased foraging effort when food availability was high but were willing to incur increasing foraging costs to feed on fruit when availability was low. This study highlights how animals have to adjust their space use with changing resource availability and it emphasizes the value of examining multiple parameters of space use.

KEYWORDS

daily travel distance, frugivory, home range size, ranging behavior, revisit frequency

[Correction added on 15 July 2020, after first online publication: Projekt Deal funding statement has been added.]

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1 | INTRODUCTION

Space use, or the parameters measuring how animals use space such as daily travel and home range, is an important topic in animal ecology because it regulates species' ability to obtain sufficient nutrients and energy, influences reproduction, survival and fitness, affects interspecies interactions, and has implications for conservation management strategies (Morales et al., 2010; Pearce, Carbone, Cowlshaw, & Isaac, 2013). Food distribution fundamentally influences space use. According to optimal foraging theory, animals should spend more time in areas that yield the highest average rate of energy intake and both resource depletion and regeneration rates should influence decisions about when to return to an area (Charnov, 1976; Pyke, Pulliam, & Charnov, 1977). Variation in space use within and among species may be influenced by food availability, diet, dimensionality in feeding (terrestrial vs. arboreal), cognitive abilities, and patterns of group living (Chapman, Rothman, & Lambert, 2012; Harris & Chapman, 2007; Janmaat, Ban, & Boesch, 2013; Pearce et al., 2013).

Space use occurs at various temporal and spatial scales (e.g., monthly vs. annual patterns; Börger, Dalziel, & Fryxell, 2008). Daily travel distance is an important short-term measure of space requirements (Carbone, Cowlshaw, Isaac, & Rowcliffe, 2005; Isbell, 1991). A home range is defined as the total area used by an animal or group over a particular period and it is generated by daily movement trajectories (Börger et al., 2008; Van Moorter, Rolandsen, Basille, & Gaillard, 2016). Animals do not use all parts of their range equally; areas of intense utilization are commonly referred to as the core areas, which are assumed to contain the biologically most relevant resources (Asensio, Lusseau, Schaffner, & Aureli, 2012; Börger et al., 2006). Furthermore, home range owners exhibit area-restricted space use and hence repeatedly return to areas within their home range with various frequencies (Benhamou & Riotte-Lambert, 2012; Van Moorter et al., 2016).

As food resources increase in abundance, animals require less space to acquire appropriate amounts of energy (Saïd et al., 2005; Tufto, Andersen, & Linnell, 1996). As a result, a common occurrence is an inverse relationship between food abundance and both home range size and daily travel distance (e.g., *Cebus capucinus*, Campos et al., 2014; *Canis lupus*, Jedrzejewski, Schmidt, Theuerkauf, Jedrzejewska, & Okarma, 2001; *Panthera leo*, Loveridge et al., 2009), but a positive relationship between food abundance and revisit frequencies (e.g., *C. capucinus*, Boyer, Crofoot, & Walsh, 2012). Species feeding on foods that are less abundant in space and time, such as fruit or meat, are expected to have larger home ranges and longer daily travel distances than those feeding on abundant resources that are more readily available (Clutton-Brock & Harvey, 1977; Gompper & Gittleman, 1991). Primates exhibit an array of dietary patterns, with many species considered as primarily frugivores or folivores (Chapman et al., 2012). Despite these broad classifications, most species consume many dietary items, so they may respond differently to how food availability varies in space and time depending on to what degree they consume different types of food.

To better understand the role of ecological variability in determining space use patterns, we conducted a comprehensive study of space use

patterns in wild western lowland gorillas in Loango National Park, Gabon. Western lowland gorillas, living in tropical lowland forests of Central Africa, are an interesting species in which to investigate space use because two key components of their diet vary greatly in abundance and distribution in both time and space. Terrestrial herbs and tree leaves consumed by western gorillas are available year-round but at low densities, whereas fruits show high spatial and temporal variation in availability (Doran-Sheehy, Mongo, Lodwick, & Conklin-Brittain, 2009; Remis, Dierenfeld, Mowry, & Carroll, 2001). Western gorillas have larger home ranges and longer daily travel distances than mountain gorillas, likely reflecting a greater dietary dependence on widely dispersed fruit and lower availability of evenly distributed herbaceous vegetation (Robbins & Robbins, 2018). Some studies have shown that fruit consumption, which may make up as much as 70% of feeding time in some months, has a major effect on space use in western lowland gorillas (Bermejo, 2004; Cipolletta, 2004; Doran-Sheehy, Greer, Mongo, & Schwindt, 2004; Salmi, Presotto, Scarry, Hawman, & Doran-Sheehy, 2020), but the relationship among the abundance of nonfruit foods, fruit availability, and space use is not well understood.

Both fruit availability and the amount of time spent feeding on fruit should be important determinants of western gorillas' space use. Daily travel distance increases as the amount of fruit in the gorillas' diet increases in western gorillas and Bwindi mountain gorillas (Cipolletta, 2004; Doran-Sheehy et al., 2004; Seiler et al., 2018), suggesting that gorillas are willing to travel further to consume these foods. However, the effect of fruit availability on the daily travel distance has not been investigated, nor whether the effect of frugivory on daily travel distance might be dependent on the availability of ripe fruit. Furthermore, the observed positive relation between daily travel distance and frugivory suggests that home range size may increase as fruit intake increases, yet one study found a negative relationship (Doran-Sheehy et al., 2004). Overall, the relationship among space use, fruit availability, and frugivory requires further study in western gorillas.

The availability of terrestrial herbaceous vegetation and tree leaves may also influence space use of western gorillas (Doran et al., 2002). Monthly home range size in Bwindi mountain gorillas is negatively correlated with the availability of herbs in areas used (Seiler et al., 2018). Therefore, the longer daily travel distances of western lowland gorillas compared with mountain gorillas may reflect the lower density of herbaceous foods (Doran et al., 2002; Head, Boesch, Makaga, & Robbins, 2011; Table 2). Although most herbaceous vegetation occurs at low density in lowland forests, swamps contain high densities of some important terrestrial herb species that play an important role in shaping space use patterns of western gorillas (Doran et al., 2002; Doran-Sheehy et al., 2004; Magliocca & Gautier-Hion, 2002). Given the high variability of herbaceous vegetation (i.e., very low densities in most habitat types with the exception of high densities in swamps), the impact of availability of both herbaceous vegetation and swamps on gorillas' space use should be empirically tested in conjunction with frugivory and fruit availability.

In this study, we investigated how the density of nonfruit foods (terrestrial herbs and tree leaves), the availability of fruit, frugivory, and swamps influenced daily travel distance, monthly home range size, and revisit frequencies in one group of wild western gorillas. We

also compared annual home range and core area size with other study sites. Specifically, using 4 years of data from a group of habituated western gorillas, we made the following predictions:

We predicted that a higher density of nonfruit foods would lead to shorter daily travel distances and monthly home range sizes, but an increase in the revisit frequency. Second, because swamps (defined as terra firma habitat permanently inundated with water) in Loango National Park contain a frequently consumed herb species (*Cyperaceae*; Head et al., 2011), we predicted that when gorillas used areas with more abundant swamp habitat, they had shorter daily travel distances, smaller monthly home range, and core area sizes, but higher monthly revisit frequencies. Lastly, as fruits vary in availability in both time and space, we predicted that greater frugivory would lead to longer daily travel distances and larger monthly

home range sizes, but the effect would be weaker when more fruits were available and frugivory was high (Doran et al., 2002).

2 | METHODS

2.1 | Study site and data collection

One habituated group (Atananga Group) of western lowland gorillas in Loango National Park, Gabon, was studied from January 2015 to November 2018 (Figure 1). The group had 10–16 members during this time, including one adult male, 3–6 adult females, 1 blackback male, and 5–8 immature individuals. Field assistants collected data on the group for a total of 811 days and for an average of 203 days per

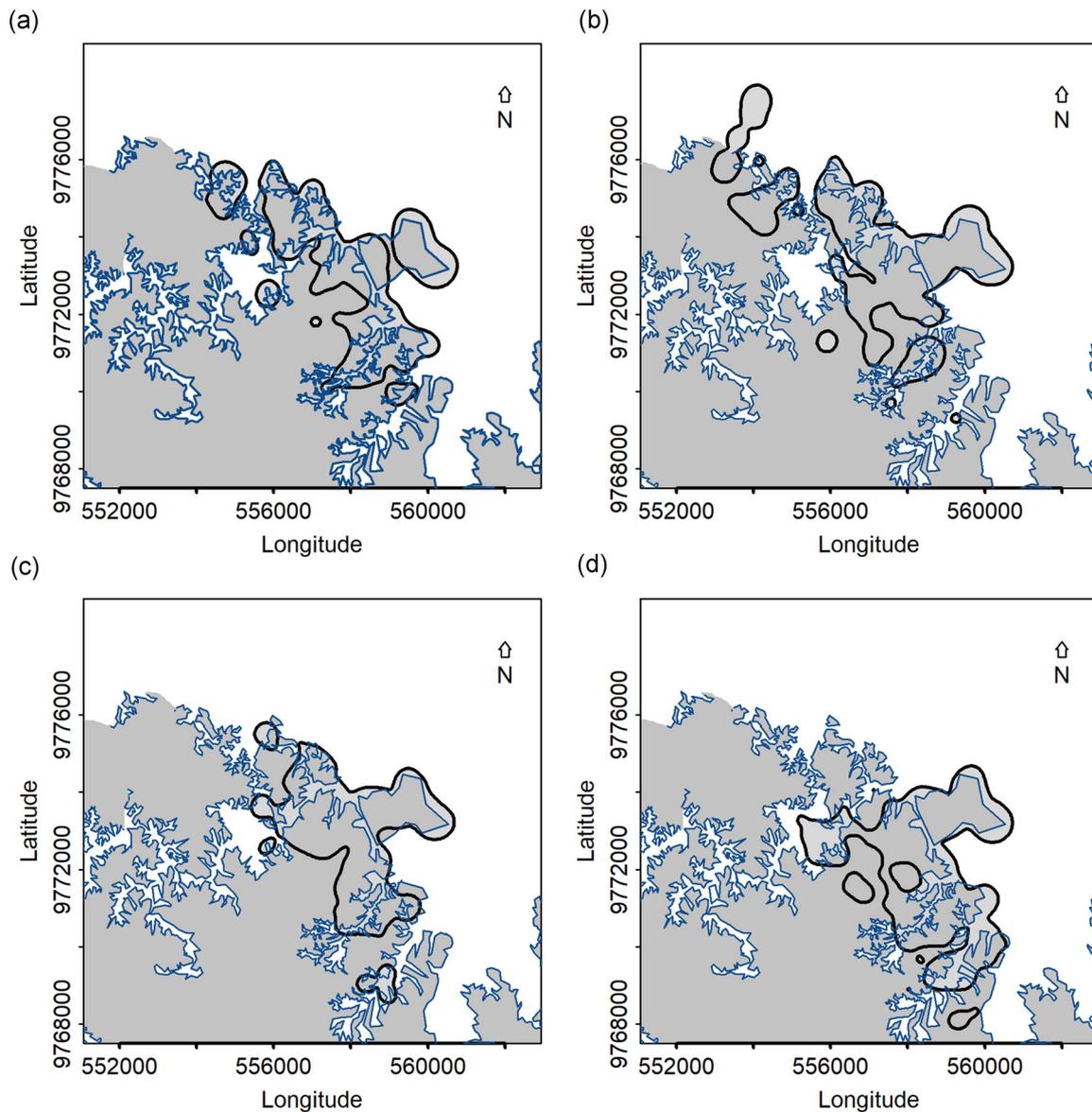


FIGURE 1 Annual home range of Atananga group of western lowland gorillas from 2015 to 2018 in Loango National Park, Gabon. The black lines indicate the 90% kernel home range; the blue lines show the edge of the swamps and the lagoon. (a–d) Annual home range for 2015–2018, respectively

year (range: 175–231 days). Using handheld global positioning system (GPS) units (GARMIN 64S), field assistants collected location data every 30–60 s on each observation day. Some of the location data were recorded by following the gorillas when they were in view and some of the data were collected when observers followed the trails left where the gorillas had walked (assessed by bent vegetation, discarded plant remains, hand and footprints, and feces). This study was conducted in compliance with the regulations of the Agence Nationale des Parcs Nationaux and the Centre National de la Recherche Scientifique et Technique of Gabon, and adhered to the American Society of Primatologists' principles for the ethical treatment of primates. Data used in this study are available upon request.

2.2 | Data analysis

To test the predictions, we used generalized additive models (GAMs) and a generalized additive mixed model (GAMM), which are extensions of generalized linear models (GLMs) and generalized linear mixed models (GLMMs). These additive models include a priori unspecified nonlinear variables (a smoothing function), which enables greater flexibility than GLMs and GLMMs and allows nonlinear responses (Hastie & Tibshirani, 1986; Wood, 2011). This is similar to including a quadratic or cubic term in GLM but it is even more flexible. Specifically, we used two GAMs to examine the impact of the test predictors on the responses daily travel distance (log-transformed to achieve an approximately symmetrical distribution; $N = 239$) and monthly home range size ($N = 43$). Furthermore, we used a GAMM to examine the impact of the test predictors on the response revisit frequency per 500×500 m grid cell per month ($N = 1,273$ observations from 98 grid cells).

The test predictors were density of nonfruit foods, proportion of each occupied grid cell comprising swamp, frugivory, and availability of fruit per day (see next section). For the models investigating daily travel distance and monthly home range size, we also added an interaction term between frugivory and availability of fruit. The interaction between these two variables tested whether the effect of frugivory on the response was dependent on the availability of fruit. We did not include frugivory in the revisit frequency model as it is a nonspatial measure (Seiler et al., 2018). To control for differences in sampling effort, we included observation time per day as a control predictor in the daily travel distance model, the square root-transformed observation time per month in the home range size model (Gautestad & Myrseter, 1993) and the monthly observation time (log-transformed) as an offset term in the revisit frequency model. Lastly, we included smoothed terms in the additive models (Hastie & Tibshirani, 1986; Wood, 2011), which can be used to model patterns of seasonal variation, such as rainfall or temperature that can be a priori unspecified and nonlinear. As daily travel distance in gorillas was highly temporally autocorrelated (Seiler et al., 2018), we also included temporal autocorrelation using a smoothed term in this model. We included the smoothed term of date as a cyclic variable to control for any seasonal effects on monthly home range size (see Supporting Information). For the monthly revisit

frequency model, we controlled for potential spatial autocorrelation by including a smoothed term of the location coordinates.

2.3 | Test predictor variables

2.3.1 | Density of nonfruit foods

We estimated the density of the most important nonfruit foods (terrestrial herbaceous vegetation and tree leaves) in the study area. First, we estimated the composition of the diet using instantaneous scan sampling at 10 min intervals throughout the daily observation period, during which the field assistants recorded the food species and parts consumed by each individual in view (Seiler et al., 2018). We identified the most important nonfruit foods as species that contributed $>1\%$ of instantaneous feeding records for the study group ($N = 14$ most important nonfruit foods) as measured over the whole study period of on average 1,608.0 hr per year ($N = 4$, range: 1,173.9–1,966.2 hr).

To estimate the density of these important nonfruit foods across the group's home range, we calculated their stem density by sampling 99 vegetation transects of 200 m length, which were systematically placed in 500×500 m grid cells that covered the group's home range. Each transect was started in the southwest corner of each grid cell and ran due north. Along each transect, we counted the number of stems of the most important herb species in 10 equally spaced 2×2 m plots and measured the abundance of tree leaves by counting the number of food trees in 10 equally spaced 10×10 m plots, with consecutive plots located on alternate sides of the transect. We then extrapolated the density of nonfruit foods per 500×500 m grid cell by using data from all the plots within that cell. Mean density of nonfruit foods per 500×500 m grid cell was 0.22 nonfruit foods/m² (range: 0–3.05 nonfruit foods/m²; $N = 99$ transects).

The density of nonfruit foods per monthly home range was estimated using the mean density in all 500×500 m grid cells entered in a month, weighted by the distance traveled in each cell for a given month (to account for the different extents the grid cells were used). We calculated the density of nonfruit foods for each day by averaging the density in all 500×500 m grid cells entered during the day, again weighted by the distance traveled within each grid cell. Because we focused only on the area entered per month, this is a measure of local density of nonfruit foods, not overall density in the entire home range or nearby parts of the forest. For processing and analyzing the spatial data, we used the packages spatstat (Baddeley & Turner, 2006), splancs (Bivand, Rowlingson, Diggle, Petris, & Eglén, 2016), and SDMTtools (VanDerWal, Falconi, Januchowski, Shoo, & Storlie, 2014) in R (R Core Team, 2017).

2.3.2 | Swamps

Swamps were permanently inundated areas surrounded by terra firme forest (Doran-Sheehy et al., 2004; Head et al., 2011). We estimated the proportion of swamp per 500×500 m grid cell as

measured on the study site map. We used ArcGIS 9.3 (ESRI Inc., Redlands CA) to determine how much area of a given 500 × 500 m grid cell was covered by swamp and how much area was covered by terra firme to determine the proportion of swamp per cell. We determined the proportion of swamp per monthly home range by calculating a weighted mean across all 500 × 500 m grid cells that were used by the gorillas in a given month, with the weighting reflecting the distance traveled in a cell in a given month. To get the daily estimate, we averaged the proportion of swamp of all 500 × 500 m grid cells entered during the day, weighted by the distance traveled within each grid cell. Because these are measures of only the area entered per day or per month, this is a measure of local swamp use, not overall density in the entire home range or nearby parts of the forest.

2.3.3 | Spatial fruit availability index

To measure the availability of fruit per month and per grid cell, we monitored an average of 284 trees per month (range: 60–487) from 29 different species from January 2015 to November 2018, including only species whose fruits were consumed by the study group based on direct observations and fecal analysis (Robbins, unpublished data). We monitored on average 10 individual trees per species (range: 3–32) and recorded the presence of ripe fruit per tree (Head et al., 2011). We estimated a spatial monthly fruit availability index per 500 × 500 m grid cell using the formula:

$$\sum_{k=1}^n D_k * B_k * P_{km}$$

where D_k is the density of species k per km² for each 500 × 500 m grid cell, B_k is the mean basal diameter of species k (using the trees in the phenology study), P_{km} is the percentage of trees of species k with ripe fruits in a month m , and n is the total number of fruit species (Head et al., 2011; Seiler & Robbins, 2016). The density of tree species per grid cell was derived from the same 99 transects that we used to estimate density of nonfruit foods. The mean spatial fruit availability index per month and grid cell was 3 (median: 0.3; range: 0–236; $N = 5,443$). The availability of fruit per daily travel path and monthly home range and core area was based on the mean fruit availability of all grid cells traversed by a daily track or encompassed in an area, respectively, weighted by the distance traveled within each grid cell or by the size of overlap with a cell, respectively. Because this is a measure of only the area entered per month, not the overall home range, this is a measure of local fruit availability, not overall availability in the entire home range or nearby parts of the forest.

2.3.4 | Frugivory

We measured daily frugivory as the proportion of daily feeding scan records that included fruit feeding. We averaged all daily proportions

for the monthly value ($N = 47$ months, mean number of daily values per month: 22, range: 3–31).

2.4 | Response variables

2.4.1 | Daily travel distance

In contrast to other studies (Ganas & Robbins, 2005; Seiler et al., 2018; Watts, 1991), we did not measure the lengths of the trails between two night nests to estimate daily travel distance, but measured the cumulative lengths of travel paths on all days with more than 5 hr observation time from January 2017 to November 2018. We chose this method because it is difficult to get full nest to nest daily travel distances. Using a function we developed in R (R Core Team, 2017), we smoothed the daily tracks to remove location errors and improve accuracy (Seiler et al., 2018). We measured the length of 239 cleaned travel paths and included observation time as a control predictor in the analysis. Mean observation time for the daily travel distances included was 7.7 hr (range: 5.0–9.5 hr) and there is a potential bias toward observations in the afternoon, accounting for days when more time was needed to find the gorillas in the morning.

2.4.2 | Monthly home range size

We measured monthly home range sizes by counting the number of unique 100 × 100 m grid cells entered per month (embedded within the 500 × 500 m grid cells used for estimating food availability), which is an adaptation of the digitized polygon method. This method buffers the travel path of a group, originating from autocorrelated location data, with a predefined distance. This predefined distance should reflect the area used by a group adjacent to a travel path (Ostro, Young, Silver, & Koontz, 1999). We chose a grid cell size of 100 × 100 m and hence reflecting 50 m on either side of the travel path to make the monthly home range size comparable with that of mountain gorillas that used the same method (Seiler et al., 2018). To measure monthly home range size ($N = 43$ monthly home ranges), we used on average 18 days per month (range: 3–29). Models can control for variation in the number of observation days when including number of observation days as a control predictor to account for varying sampling effort, as shown by a previous home range analysis on mountain gorillas using less data than the current study (Seiler et al., 2018).

2.4.3 | Monthly revisit frequency

Using the location data, we measured the number of times each 500 × 500 m grid cell was used by the study group per month. We treated the second visit to a grid cell as the first revisit and considered several visits on the same day to the same grid cell as one visit (Seiler et al., 2018).

2.4.4 | Annual home range and core area size

We estimated annual home ranges (90% kernel home ranges) and core areas (50% kernel home ranges) applying the fixed kernel density estimation (Worton, 1989) with the *adehabitatHR* package (Calenge, 2006) in R 3.4.3 (R Core Team, 2017). The kernel method produces utilization distributions, which are based on location point densities (Worton, 1989) and reflect a group's relative use of space (Van Winkle, 1975). To reduce biases from different sampling frequencies among years (Börger et al., 2006), we restricted the annual home range analysis to one randomly selected location point per day (Seiler, Boesch, Mundry, Stephens, & Robbins, 2017). We used on average 203 days per year (range: 175–231) to measure annual home range and core area size. Using sensitivity analysis, we estimated the bandwidth h that produces kernel home ranges with relatively little fragmentation (Caillaud, Ndagijimana, Giarrusso, Vecellio, & Stoinski, 2014; Seiler et al., 2017) and chose to fix the bandwidth to $h = 400$ (Figure S1). In addition, for comparative reasons, we measured annual home range and core area size using the bandwidth $h = 200$ to make the results directly comparable with those from two mountain gorilla populations (Caillaud et al., 2014; Seiler et al., 2017).

2.5 | Statistical analysis

We fitted all models in R (R Core Team, 2017) and implemented them using the functions *gam* of the *mgcv* package (Wood, 2011) or *gamm4* of the *gamm4* package (Wood & Scheipl, 2017). All GAMs were fitted with Gaussian error structure and identity link, whereas

the GAMM was fitted with Poisson error structure and log link function. The test predictors were transformed (log, square root, and 5th root) to achieve approximately symmetrical distributions (Supporting Information) and then z-transformed to a mean of 0 and a standard deviation of 1 (Schielzeth, 2010). To control for repeated observations in the revisit frequency model, we included grid cell ID ($N = 98$) as a random effect. In addition, we included the random slope of fruit availability within grid cell ID (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009) to keep Type I error rate at the nominal level of 5%.

We checked for various diagnostics of model validity and stability (DFBetas, leverage and variance inflation factors [VIFs]; distribution of residuals, visual inspection of QQ plots residuals plotted against fitted values, Table S1). We did not find any violations or deviations from the assumptions of normality and homogeneity of residuals (Field, 2005; Quinn & Keough, 2002). In the revisit frequency model (Model 3), we checked for the absence of overdispersion (dispersion parameters = 1.98). To assess collinearity among the test predictor variables we used 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 and smoothed terms. No collinearity issues were found (maximum VIF = 1.96). For the mixed model, we assessed model stability by excluding each level of the random effects one at a time and compared the estimates for each predictor with those from the full data set (Table S2). For the GAMs, we established significance of the full model by comparing it with the null model lacking the test predictors using a F test, whereas for the GAMM, we used a likelihood ratio test (Forstmeier & Schielzeth, 2011).

TABLE 1 Summary of the statistical analysis of the impact of resource availability on three space use parameters across several spatial and temporal scales in Atananga group of western lowland gorillas in Loango National Park, Gabon

Response variable	Daily travel distance (Model 1, GAM)			Monthly home range size (Model 2, GAM)			Monthly revisit frequency per 500 × 500 m grid cell (Model 3, GAMM)		
	Est	SE	<i>p</i>	Est	SE	<i>p</i>	Est	SE	<i>p</i>
Intercept	7.788	0.032	a	296.698	16.257	a	−4.569	0.040	a
Density of nonfruit foods	−0.084	0.030	.005	−5.789	14.037	.682	−0.096	0.050	.053
Proportion of swamp	−0.067	0.032	.039	28.425	14.384	.059	−0.042	0.058	.475
Availability of fruit	−0.028	0.041	a	20.009	19.196	.304	0.083	0.042	.048
Frugivory	−0.041	0.035	a	41.172	19.453	.041			
Frugivory and availability of fruit ^b	−0.130	0.032	<.001	c	c	c			
Observation time	0.118	0.030	<.001	96.030	14.777	<.001	d	d	d

Note: For each model, we show the estimates (Est), standard errors (SE), and p values for each test predictor. Significant test predictors ($p < .05$) are indicated in bold. Empty cells indicate variables not included in a model. Mean and standard deviation of the original values of the predictor variables are shown in Table S4.

Abbreviations: GAM, generalized additive model; GAMM, generalized additive mixed model.

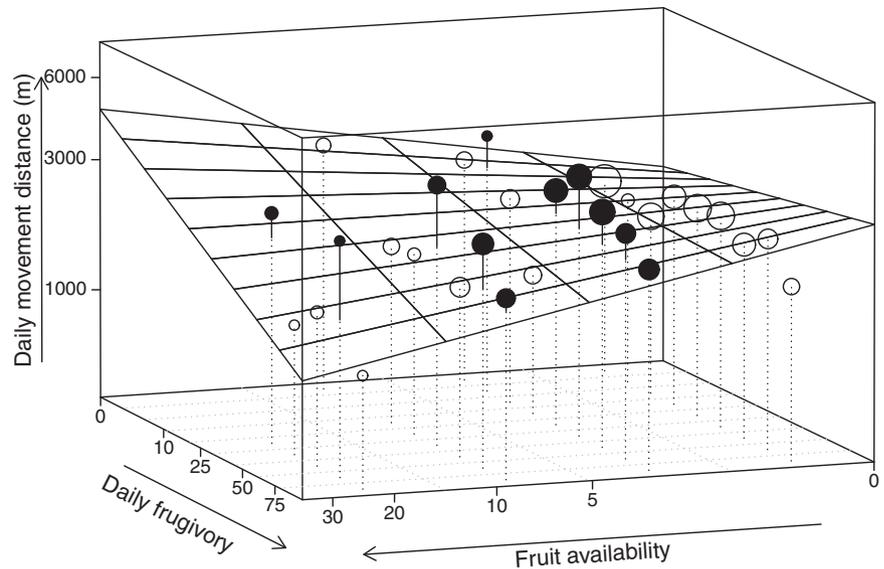
^aNot shown because the terms are included in an interaction and therefore have a very limited interpretation.

^bWe tested for an interaction between these two test predictor variables.

^cInteraction term was not significant and hence removed from the model.

^dIncluded as an offset term and hence no estimates.

FIGURE 2 Impact of daily frugivory on daily travel distance (log-transformed) depends on the availability of fruit in western lowland gorillas. The surface represents the fitted daily travel distance as a function of daily frugivory and fruit availability. The height of the sphere represents the actual travel distances per combination of frugivory and fruit availability. Spheres above the fitted surface are in black; spheres below the surface are in white. The volume of the spheres is proportional to the number of data points



3 | RESULTS

3.1 | Daily travel distance (Model 1)

The mean daily travel distance of the study group was 2,562 m ($N = 239$, range: 354–7,575 m). A comparison of the full model to the null model lacking the test predictors (density of nonfruit foods, amount of swamp in area used, and an interaction term between daily frugivory and availability of fruit per day) revealed that the test predictors significantly influenced the daily travel distances ($F = 5.789$, $df = 5.722$, $p < .001$). Daily travel distance decreased as the density of nonfruit foods and the amount of swamps in area used increased (Table 1). Furthermore, we found that the interaction term between daily frugivory and availability of fruit was significant. Specifically, daily travel distance was shorter when both frugivory and availability of fruit were higher. However, daily travel distances were longer when fruit availability was low but frugivory was high (Figure 2).

3.2 | Monthly home range size (Model 2)

The study group entered on average 297 100×100 m grid cells per month (range: 82–659), which corresponds to an average monthly home range size of 2.97 km^2 ($N = 43$ monthly home ranges, range: $0.82\text{--}6.59 \text{ km}^2$). A comparison of the full model to the null model lacking the test predictors (density of nonfruit foods, amount of swamp in area used, and an interaction term between frugivory and availability of fruit) revealed only a weak and nonsignificant association between the test predictors on the monthly home range size ($F = 2.421$, $df = 3.803$, $p = .070$). The interaction term testing whether the effect of frugivory on monthly home range size depended on fruit availability was not significant and we dropped it. In a simpler model we then found that monthly HR were larger in months with higher levels of frugivory (Table 1).

3.3 | Monthly revisit frequency model (Model 3)

The study group revisited each 500×500 m grid cell on average twice per month ($N = 1,273$ revisits, range 0–14 per month and grid cell). A comparison of the full model to the null model lacking the test predictors (density of nonfruit foods, amount of swamp in area used, and availability of fruit) revealed only a weak and nonsignificant association between the test predictors on the monthly revisit frequency ($\chi^2 = 7.556$, $df = 3$, $p = .056$). Specifically, the group increased its revisit frequency as fruit availability in a grid cell increased. (Table 1).

3.4 | Annual home range and core area size

Using the kernel density estimation, mean annual home range size the gorilla group was 14 km^2 (range: $12.31\text{--}15.34 \text{ km}^2$). Mean annual core area size was 3.6 km^2 (range: $3.41\text{--}3.79 \text{ km}^2$, Table S3).

4 | DISCUSSION

Using a multiyear data set, we provide some of the first evidence that the abundance of nonfruit foods (herbaceous vegetation and tree leaves), in addition to both frugivory and fruit availability, is a significant determinant of space use by western gorillas. Previous studies testing the effect of ecological resource availability on space use in western gorillas focused primarily on the impact of frugivory and did not include measures of herb availability (Bermejo, 2004; Cipolletta, 2004; Doran-Sheehy et al., 2004). Social factors, such as the frequency of intergroup encounters and density of animals may also influence space use (e.g., *Colobus guereza*, Harris & Chapman, 2007; *Gorilla beringei beringei*, Seiler et al., 2018), but we were unable to test for such influences because we studied only one group. Overall, western gorillas in Loango showed behavioral adaptations to

TABLE 2 Variability in space use parameters across different gorilla populations

Subspecies and study site	Annual home range size km ²	Annual core area size km ²	Monthly home range size km ²	Daily travel distance (km)	Herb density per m ²	Gorilla density per km ²
Western lowland gorillas (<i>Gorilla gorilla gorilla</i>)						
Loango National Park, Gabon ^a	14 (12.3–15.3)	4 (3.4–3.8)	3.0 (0.8–6.6)	2.6 (0.4–7.6)	0.22	0.82–1.06 ^b
Bai Hokou, Central African Republic	15.9 (13.1–18.1) ^b		3.0 (2.0–5.1) ^c	1.5 (0.3–3.0) ^c	1.11 ^d	0.9 ^d
Mondika, Central African Republic ^e	15.4		6.4 (4.6–8.3)	2.0 (0.1–4.9)	0.78 ^e	4.48 ^f
Mountain gorillas (<i>Gorilla beringei beringei</i>)						
Bwindi Impenetrable National Park, Uganda	10.0 (4.1–22.9) ^g	3.0 (1.1–7.2) ^g	1.0 (0.2–3.2) ^g	1.0 (0.1–6.5) ^g	4.4–10.6 ^h	1 ⁱ
Virunga Massif, Rwanda	8.1 (3.2–23.6) ^j	2.5 (0.8–7.5) ^j		0.8 ^d	8.8 ^k	1 ⁱ

Note: Each cell gives the mean and the range in parentheses. Empty cells indicate space use parameters that were not estimated for a respective site.

^aThis study ($h = 200$).

^bArandjelovic et al. (2010).

^cCipolletta (2004).

^dWright et al. (2015).

^eDoran-Sheehy et al. (2004)

^fHead et al. (2011).

^gSeiler et al. (2018).

^hGanas, Robbins, Nkurunungi, Kaplin, and McNeilage (2004).

ⁱRobbins and Robbins (2018).

^jCaillaud et al. (2014).

^kWatts (1984).

the distribution of ecological resources: they reduced energy expenditure in areas that offered a higher abundance of major dietary items (herbaceous vegetation, tree leaves, and fruit), yet they were willing to travel further to obtain fruit when it was less available.

4.1 | Daily travel patterns

The mean daily travel distance of the Loango gorillas fell at the upper end of the values traveled per day across sites, even though we considered all tracks that lasted longer than 5 hr, which should lead to a lower overall estimate of the daily travel distance than full days (Table 2). This might reflect the particularly low densities of herbaceous vegetation and trees found in Loango (Head et al., 2011), forcing the gorillas to move longer distances and to increase foraging costs.

The gorillas showed short-term adjustments of decreasing daily travel distance as both the density of nonfruit foods (herbs and tree leaves) and the amount of swamp in their local area increased. It is notable that even with a very low herb density (Table 2), the density and distribution of herbs influenced western gorillas' space use. In Loango and elsewhere, the density of herbs is spatially clumped and swamps are highly localized (Doran et al., 2002), which might allow gorillas to spend several days in the same area characterized by high herb densities and swamps, leading to short daily travel paths. Gorillas appear to use swamps in Loango mainly to feed on a herb species that is not available elsewhere (*Cyperaceae*; Head et al., 2011). However, at Mondika, a positive relation between daily travel

distance and frequency of swamp use was found, largely explained by the availability of certain ripe fruits (*Nauclea* sp. and *Grewia* sp.) found only on the edge of the swamps (Doran-Sheehy et al., 2004). These fruits are very rare at Loango. Together, all these findings suggest that the impact of nonfruit foods depends on the spatial distribution of the food resources and that different plant species seem to be important determinants of the gorillas' space use at different sites.

This study goes beyond examining the simple relationship between daily travel distance and the amount of fruit in the gorillas' diet (Cipolletta, 2004; Doran-Sheehy et al., 2004; Seiler et al., 2018), by testing for an interaction between fruit consumption and local fruit availability. Daily travel distances were short when both fruit consumption and fruit availability were high. In contrast, when fruit consumption was high but little fruit was available, the gorillas increased their daily travel distances (Figure 2). The presumed increase in energy expenditure with increasing fruit consumption when it was low in availability, suggests that gorillas are willing to travel further to gain foods that offer easily digested energy, as also observed in other species (*Saimiri oerstedii*, Boinski, 1987; *Pan troglodytes*, Carbone et al., 2005; Normand, Ban, & Boesch, 2009; *G. gorilla gorilla*, Masi, Cipolletta, & Robbins, 2009; *G. beringei beringei*, Seiler et al., 2018; *Pongo pygmaeus wurmbii*, Vogel et al., 2017).

4.2 | Monthly space use

The local density of nonfruit foods did not influence monthly space use (home range size and revisit frequencies), which might reflect low

consumption of herbs during months with high fruit availability and high levels of frugivory (Doran-Sheehy et al., 2009; Masi et al., 2009). Swamp use also did not influence monthly home range size, which is in contrast to results from Mondika, where gorillas decreased their monthly home range size as the frequency of swamp use increased (Doran-Sheehy et al., 2004). Spatial variation in herb availability negatively influences monthly home range size of Bwindi mountain gorillas, which had a much higher herb density (Seiler et al., 2018; Table 2). The influence of density of nonfruit foods on home range size may be more apparent in species that are primarily folivorous, such as *C. guereza* (Harris & Chapman, 2007).

We provide the first evidence of the positive relationship between monthly home range size and frugivory in western gorillas, which may be explained by the low density of fruit trees in Loango compared with other sites where this relationship was not observed (Doran-Sheehy et al., 2004; Head et al., 2011). This relationship also was not observed in Bwindi mountain gorillas, but their habitat has an even lower density of fruit trees and fruit consumption is also lower than for western gorillas (Ostrowsky & Robbins, 2020; Seiler et al., 2018). The distribution of fruiting trees also affected monthly revisit patterns. As the availability of fruit in an area increased, revisits to that area increased, suggesting that Loango gorillas returned more frequently to areas with high food abundance. This pattern follows the predictions of optimal foraging theory (Charnov, 1976; Pyke et al., 1977) and has been supported in studies on other species (*C. capucinus*, Boyer et al., 2012; Kohler, 1984).

4.3 | Annual space use

Variation in annual home range size and core area was very low, despite annual variation in fruit availability (Table 2; Supporting Information). High fidelity of annual home range between consecutive years also suggests high stability in the annual home range, which should improve fitness via increased foraging efficiency by allowing the gorillas to know the distribution and predictability of fruiting trees within their range (Bermejo, 2004). Gorillas and other primates may have mental representations of the location for major food sources, thereby benefitting from stable home ranges (e.g., *Ateles belzebuth* and *Lagothrix poeppigii*, Di Fiore & Suarez, 2007; *P. troglodytes*, Janmaat et al., 2013; Normand et al., 2009; *G. gorilla gorilla*, Salmi et al., 2020). Annual home range size of western gorillas at three sites is larger than that at two mountain gorilla sites, which could be due to both lower herb density and greater reliance on widely distributed fruit trees (Table 2).

5 | CONCLUSION

This study provides additional evidence of the importance of fruit for western gorillas (Doran-Sheehy et al., 2004; Masi et al., 2009; Salmi et al., 2020). Fruit appears to play a more influential role in affecting space use than nonfruit foods (herbaceous vegetation

and tree leaves) in western gorillas because it influenced space use patterns on the monthly and daily scale whereas nonfruit food availability was important on the daily scale only. Even in Bwindi mountain gorillas, whose diet is only ~15% fruit, space use is influenced by both food categories (Ostrowsky & Robbins, 2020; Seiler et al., 2018).

All animals have to adapt their behavior to changes in food availability and distribution and consequently many show large seasonal variation in foraging and space use (e.g., *S. oerstedii*, Boinski, 1987; *C. capucinus*, Campos et al., 2014; *P. pygmaeus wurmbii*, Vogel et al., 2017). This study highlights that the impact of food resources on animals' space use patterns is highly dependent on the respective scale (i.e., daily, monthly, or annually) and on the type of food resource investigated. Space use by primates and other animals has implications for many topics ranging from cognitive abilities to conservation management strategies, emphasizing the importance of using multiscale approaches when investigating animal's space use patterns (Börger et al., 2006; *C. capucinus*, Campos et al., 2014; *G. beringei beringei*, Seiler et al., 2018).

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DATA AVAILABILITY STATEMENT

Data used in this study are available upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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