ORIGINAL ARTICLE

Influence of food availability, plant productivity, and indigenous forest use on ranging behavior of the endangered samango monkey (*Cercopithecus albogularis schwarzi*), in the Soutpansberg Mountains, South Africa

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Abstract

Understanding the determinants of ranging patterns in species susceptible to habitat fragmentation is fundamental for assessing their long-term adaptability to an increasingly human-dominated landscape. The aim of this study was to determine and compare the influence of ground-based food availability, remotely sensed plant productivity, and indigenous forest use on the ranging patterns of the endangered samango monkey (*Cercopithecus albogularis schwarzi*). We collected monthly ranging data on two habituated samango monkey groups, from February 2012 to December 2016, from our field site in the Soutpansberg Mountains, South Africa. We used linear mixed models to explore how food availability, plant productivity, and indigenous forest use influenced monthly ranging patterns, while controlling for group size, number of sample days and day length. We found that as more areas of high plant productivity (derived from remotely sensed EVI) were incorporated into the ranging area, both total and core monthly ranging areas decreased. In addition, both total ranging area and mean monthly daily path length decreased as more indigenous forest was incorporated into the ranging area. However, we found no effect of either ground-based food availability or remotely sensed plant productivity on ranging patterns. Our findings demonstrate the behavioral flexibility in samango monkey ranging, as samangos can utilize matrix habitat during periods of low productivity but are ultimately dependent on access to indigenous forest patches. In addition, we highlight the potential of using remotely sensed areas of high plant productivity to predict ranging patterns in a small ranging, forest-dwelling guenon, over ground-based estimates of food availability.

Key words: food availability, forest use, plant productivity, ranging patterns, remote sensing, samango monkey

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INTRODUCTION

Habitat loss and fragmentation are the most significant causes of global biodiversity loss (Fahrig 2003; Lindenmayer & Fischer 2006). Within forest biomes, loss and fragmentation of habitat has accelerated at an unprecedented rate due to the anthropogenic conversion of land for agriculture and urbanization (Haddad *et al.* 2015). Many species rely on continuous natural forest patches for foraging, reproduction, and shelter (Saunders *et al.* 1991; Fischer & Lindenmayer 2007). Fragmentation of these patches increases the likelihood of population declines through genetic isolation, microclimate change, decreased availability of resources, increased predation risk, and increased competition (Saunders *et al.* 1991; Fahrig 2003; Haddad *et al.* 2015). Understanding how animals use space in fragmented habitats is central to animal behavioral ecology and is key to determining the extent to which they can persist in an increasingly fragmented and human-dominated landscape (Fahrig 2007; Wilson *et al.* 2016).

Resources are often distributed unevenly in time and space across the landscape, which is exacerbated in fragmented environments (Fairgrieve 1995; Fahrig 2003). As a result, animals may modify their home range size and use in order to access sufficient resources (Law & Dickman 1998). Primates, in particular, have been shown to have considerable flexibility in their ranging patterns in response to fluctuations in resource availability (Clutton-Brock 1975; Di Bitetti 2001; Bartlett 2009). Furthermore, this relationship is more pronounced in frugivorous primates than in folivorous primates (Clutton-Brock 1977) due to the higher spatiotemporal fluctuations in fruit availability compared to leaves (Janson & Chapman 1999), and owing to the fact that fruit has a shorter digestion time than leaves (Demment & Laca 1991). The ability of a species to adapt to habitat fragmentation may therefore depend on their ability to exploit resources within suitable matrix habitat (Law & Dickman 1998; Fahrig 2007).

Studies exploring ranging patterns in small ranging species, such as primates, typically use ground-based phenology to determine the influence of resource availability (Di Bitetti 2001; Kaplin 2001; Twinomugisha & Chapman 2007; Albert *et al.* 2013; Gabriel 2013; Campera *et al.* 2014; Santhosh *et al.* 2015). Ground-based phenology provides detailed and accurate information on the availability of specific food items, yet often lacks spatial coverage (Studer *et al.* 2007). One of the most significant advances in ecological and conservation studies, however, has been the application of remotely sensed estimates of plant productivity, which has greatly enhanced our understanding of animal movement patterns (Kerr & Ostrovsky 2003; Turner *et al.* 2003; Pettorelli *et al.* 2011; Neumann *et al.* 2015).

The Enhanced Vegetation Index (Huete *et al.* 2002) (EVI) is a remotely sensed correlate of photosynthetic activity and has consistently been used as an indicator of primary productivity (Paruelo *et al.* 1997), plant phenology (Justice *et al.* 1985) and canopy structure (Gamon *et al.* 1995). EVI represents the difference in earth surface reflectance patterns between the red and near-infrared parts of the electromagnetic spectrum, while taking into account the reflectance of the blue band (Eidenshink & Faundeen 1994). Values range from -1.0 (indicating non-vegetated areas) to $+1.0$ (densely vegetated areas) (Huete *et al.* 2002). Although remotely sensed estimates of plant productivity appear to have a complex relationship with ground-based estimates of food availability (Willems *et al.* 2009), the strong linear relationship with leaf cover has led to its application in ranging studies as an indirect measure of food availability, particularly in species which consume large proportions of leaves (Leimgruber *et al.* 2001; Ito *et al.* 2006; Willems *et al.* 2009; Villamuelas *et al.* 2016).

One of the main advantages of remotely sensed productivity over ground-based phenology, however, is the ability to monitor plant productivity over vast geographical scales and at regular time intervals (Huete *et al.* 2006; Lu *et al.* 2015). Because of this, the majority of studies applying remotely sensed productivity to animal ecology have been biased toward wide-ranging species (birds: Evans *et al.* 2006, carnivores: Nilsen *et al.* 2005, ungulates: Leimgruber *et al.* 2001; Ito *et al.* 2006). While the potential benefits of applying remotely sensed productivity to smaller-ranging species in fragmented habitats are vast, studies on primates, where there are pressing conservation concerns (Estrada *et al.* 2017), are almost entirely lacking (Zinner *et al.* 2002; Willems *et al.* 2009). However, remotely sensed productivity often lacks the spatial resolution and detail of ground-based phenology (Studer *et al.* 2007), meaning that regions sampled often include areas of lower productivity which may rarely be utilized or even inaccessible to forest-dwelling species (Lawes 1992). Despite this, the potential of remote sensing to identify areas of the habitat which are highest in plant productivity may provide valuable information on the ranging ecology of forest specialists capable of consuming large proportions of leaves. While each method of sampling phenology has its advantages, studies directly comparing their effectiveness are lacking (but see Gordo 2007; Willems *et al.* 2009; Villamuelas *et al.* 2016).

The samango monkey (*Cercopithecus albogularis* subsp.: Dalton *et al*. 2015), a forest specialist, is threatened in South Africa (Linden *et al*. 2016). Their distribution is largely restricted to areas of tall-canopy, evergreen indigenous forests such as Afromontane/mistbelt, scarp, and coastal belt forests (Lawes 1990; Skinner & Chimimba 2005), which are becoming increasingly fragmented as a result of anthropogenic disturbance (Lawes 1992; Friedmann & Daly 2004; Kingdon *et al*. 2008). They are primarily arboreal and form single-male, multifemale groups (Henzi & Lawes 1987), averaging around 30 individuals (Lawes *et al*. 2013; Coleman & Hill 2014a). Unlike most other forest guenons, which are predominantly frugivorous (Lambert 2004), samango monkeys display considerable dietary flexibility and are able to consume large amounts of leaves (Coleman & Hill 2014a; Linden *et al*. 2015; Parker 2019). This is largely owing to their gut morphology and longer caecum (Bruorton & Perrin 1991), which facilitates the extraction of protein by breaking down cellulose in plant cell walls (Lawes *et al*. 1990; Bruorton & Perrin 1991; Lawes 1991). This dietary flexibility may account for the geographic range of the samango monkey extending to more southerly latitudes in comparison to other forest guenons (Wolfheim 1982; Coleman & Hill 2014a), and also facilitates the ranging of samangos into matrix habitat during periods of fruit scarcity (Lawes 1990; Skinner & Chimimba 2005; Nowak *et al*. 2017; Wimberger *et al*. 2017). Despite this, they are heavily reliant on food items located within patches of indigenous forest (Nowak *et al*. 2017; Wimberger *et al*. 2017) and are therefore reluctant to disperse over large stretches of open ground and inhabit small or isolated forest fragments (Lawes 1992, 2002; Lawes *et al*. 2000; Madisha *et al*. 2018). Understanding the factors that influence ranging patterns of the samango monkey is critical, therefore, for assessing the extent to which they can persist in an increasingly fragmented and human-dominated landscape.

The main aim of this study was to determine the influence of food availability (sampled locally), plant productivity (sampled remotely), and indigenous forest use on the monthly ranging patterns of the samango monkey. Secondly, in order to broaden the potential applicability of remotely sensed plant productivity to other small ranging guenons, we aimed to directly compare the effectiveness of each of these methods in explaining samango monkey ranging patterns. As the time available for ranging each day (Hill *et al*. 2003), and group size (Takasaki 1981), are both known to influence ranging patterns, we also collected data on this information to include as control variables in our analysis. Similarly, we included the number of days used to estimate monthly ranging patterns in our analysis to control for sample size (Getz *et al*. 2007). We predicted that the monthly ranging area, monthly core area and mean monthly daily path length of samango monkeys would increase during periods of low food availability and plant productivity, as resources become more spatially dispersed (Kaplin 2001; Boyle *et al*. 2009). We also predicted that monthly ranging patterns would increase when samango monkeys utilized less indigenous forest, as a result of monkeys ranging further into matrix habitat in order to access alternate food resources during periods of low productivity (Nowak *et al*. 2017; Wimberger *et al*. 2017). While remotely sensed plant productivity may provide an indirect measure of food availability in species which consume large proportions of leaves, we predicted that the phenological detail afforded by ground-based food availability would more accurately predict ranging patterns in a small ranging species.

MATERIALS AND METHODS

Study site

We conducted fieldwork at the Lajuma Research Centre in the western Soutpansberg Mountains, South Africa (23°02′23″S, 29°26′05″E) over a period of five years between February 2012 and December 2016. The isolated subpopulation of samango monkeys (*C. a. schwarzi*; Dalton *et al*. 2015) living on the mountain range is currently listed as Endangered (Linden *et al*. 2016), and represents the most vulnerable of the three samango monkey subspecies within South Africa (Linden *et al*. 2016). Across the mountain range there is substantial seasonal variation with cool, dry winters (mean seasonal temperature 16°C and mean seasonal total rainfall 16 mm) and hot, wet summers (mean seasonal temperature 20°C and mean seasonal total rainfall 561 mm), resulting in substantial variation in the spatial and temporal distribution of resources (Willems 2007). The south-facing cliffs also trap moisture resulting in fragmented patches of tall-canopy, evergreen indigenous mistbelt forest (Mucina & Rutherford 2006). These forests have extremely diverse plant communities, but prominent tall trees include lemonwood (*Xymalos monospora*), real yellowwood (*Podocarpus latifolius*), mountain wild-quince (*Cryptocarya transvaalensis*), forest waterberry (*Syzygium gerrardii*), and black ironwood (*Olea capensis* subsp. *macrocarpa*) (Mucina & Geldenhuys 2006). These forests are separated both naturally and anthropogenically by a mosaic of riparian forests, semi-deciduous woodlands, thicket, montane grasslands, farmland, and residential gardens, creating a

diverse matrix habitat (Mostert *et al.* 2008). Altitude at the field site ranges from 1150 to 1750 m.

Data collection

We followed two well-habituated groups of samango monkeys; "Barn" (30–40 individuals) and "House" (60–70 individuals), for an average of nine complete days (max: 17, min: 2) every month across the study period. Complete days were defined as days where a group was followed from morning sleep site to evening sleep site, without losing audio-visual contact for more than 60 minutes (Coleman & Hill 2014b). Only months containing a minimum of five complete days were used in subsequent analyses, which appeared to be the minimum number of days which was representative of the areas visited by each group for that month (Seaman *et al.* 1999). This resulted in 97 "complete" months across the study period (Barn: 53, House: 44). During each full day we collected instantaneous scan samples (Altmann 1974), using a handheld PDA (Psion Teklogix Workabout Pro 3), on as many individuals as possible ($n = 36625$, mean: 6.2, max: 24, min: 1) within a five-minute window, at 20 minute intervals. General information collected during each scan sample included date, time and group ID, while we also recorded data on specific behaviors including feeding (chewing or ingesting food) and foraging (searching for food, picking/handling food) which were used to determine the diet preferences of the study groups. In addition, a GPS point (Garmin GPSmap 64S) of the group's location was taken from the group's centroid to coincide with the start of each scan sample, to within an accuracy of 5 m. This resulted in 113,373 locations for Barn group and 113,458 locations for House group.

Environmental monitoring in the field

We counted the number of leaves, fruit, and seed pods for 20 individually marked trees of 24 different species (480 trees in total) (Parker 2019) within the first two weeks of every month, over the five-year study period (Coleman & Hill 2014b). Trees were selected to give a representation of various habitat types, while also being considered important species in the samango monkey diet (Coleman 2013; Linden *et al.* 2015). Items were counted on an individually marked branch on each tree and then scaled up to give an estimate for each tree based on the estimated number of branches for that tree (Coleman & Hill 2014b). Where there were no items on the marked branch but items on the tree, either the total number of items were counted on the tree where possible, or esti-

mates were made for the whole tree based on the number of items on another branch and the estimated number of branches for that tree (Coleman & Hill 2014b). In addition, we used randomly generated 5 m^2 vegetation plots across the study area ($n = 702$) to estimate the relative abundance of the 24 tree species monitored. Within each vegetation plot, all trees with a diameter at breast height >10 cm (Chapman *et al.* 1994; Clark & Clark 1999) were counted and identified where possible.

Remote sensing of the environment

We downloaded EVI composites for each month across the study period (2012–2016), at a resolution of 30 m^2, from the Landsat 7 & 8 databases from Google Earth Engine (https://earthengine.google.com). Images were downloaded for the entire western Soutpansberg Mountains. Monthly composites were used for comparability with the scale of ground-based food availability estimates. We used EVI in this analysis as it is more sensitive to changes in areas of high biomass, canopy differences, canopy structure, and plant phenology compared to other vegetation indices such as the Normalized Difference Vegetation Index (NDVI) (Huete *et al.* 2002), factors which are known to be important for space use in forest-dwelling species (Emerson *et al.* 2011; Coleman & Hill 2014b).

Estimation of ranging area and daily path length

To estimate the monthly ranging area of each group, we used adaptive localized convex hulls (*a*-LoCoH: Getz & Wilmers 2004; Getz *et al.* 2007), due to its superior ability of dealing with hard boundaries and its compatibility of coping with temporally close data points compared to other home range estimation methods (Getz & Wilmers 2004; Ryan *et al.* 2006; Getz *et al.* 2007). Ranging areas were created within the "*t*-LoCoH" package (Lyons *et al.* 2013) in R 3.4 (R Core Team 2017), using the maximum distance between monthly GPS points for each group as the *a*-value to allow correct construction of isopleths (Getz *et al.* 2007). We estimated two measures of ranging area (in hectares) for each group, for each month across the study period. Total monthly ranging area (monthly ranging area hereafter) was delineated by the 95% volume isopleth (Silverman 1986; Worton 1989; Getz *et al.* 2007), while monthly core ranging area (monthly core area hereafter) was delineated by the 50% volume isopleth (Börger *et al.* 2006; Getz *et al.* 2007). We defined ranging patterns in this way instead of more common terminology such as "home range" and "core home

range," as a home range is typically determined over a yearly or multiyear period (Fleming *et al*. 2015). As such, monthly "home ranges" may not be representative of the actual home range. These ranging areas were then loaded into QGIS 2.18 (QGIS Development Team 2017) to extract estimates of plant productivity and indigenous forest use. Using the same method, we also estimated the overall home range size (overall home range hereafter) of each group using all GPS points collected across the study period, which was used to calculate estimates of food availability. Monthly mean daily path length (monthly DPL hereafter) was calculated by summing the straight-line distance (in km) between sequential GPS points from each scan sample across a complete day, using the distanceTrack function in the "argosfilter" package in R, and averaging across DPLs for each month.

Ground-based food availability estimates

We calculated monthly food availability estimates for leaves, fruit, and seed pods based on the five species for each food item which collectively contributed to over 60% of the samango monkey diet (Parker 2019). To do this, we averaged the number of leaves, fruit, and seed pods counted each month for each tree ($n = 20$) across each species ($n = 24$). This resulted in a monthly mean value per food item for each species across the study period. Flowers and other food items were excluded from analysis as they comprised such a small proportion of the diets of both groups across the study period (Table S1). We then scaled these values up to give representative values across the overall home range of each group. To do this, we multiplied these values by the estimated number of trees of each species (derived from the vegetation plots) within each group's overall home range, thus giving a representative monthly food availability estimate per food item (leaves, fruit and seed pods) for each of the 24 species sampled. The estimated number of trees within each group's range was calculated by dividing the area of each group's overall home range by the area of a vegetation plot (5 m^2), and then multiplying this figure by the mean number of trees per species across all plots ($n = 702$). To determine the five species which contributed over 60% of the samango monkey diet for each food item respectively, we summed the total number of scans recorded feeding and foraging on each food item of a particular species and then calculated this as a proportion of the total number of scans recorded feeding and foraging over the study period. Finally, we summed the total monthly food availability estimates for the five most

consumed species of each food item respectively, thus giving an estimate of the monthly availability of the most commonly eaten fruits, leaves and seed pods respectively. As only four species of seed were eaten with any regularity across the study period (contributing 98% of all seed species eaten), we only included four seed species in our seed availability estimates.

Remotely sensed plant productivity and indigenous forest use estimates

Monthly EVI composites where cloud cover did not impede the study area by >30% were used in all analyses. For months where cloud cover exceeded this threshold, we selected the clearest image from the 16-day EVI composites. Composites were loaded into QGIS and a mean EVI value across each group's monthly ranging area was calculated for each sample month using the "zonal statistics" plugin, thus giving an indirect estimate for mean leaf availability across each group's range. EVI was run with a zero, 1- and 2-month time lag in subsequent analyses to allow for any possible lag in leaf availability between that sampled remotely and that which was available on the ground (Willems *et al*. 2009). EVI values for months where data were missing completely were estimated by averaging the values between the previous and following month. While estimating missing values in this way does not account for other factors that predict variation in EVI (e.g. ecological or physical factors), only 11 out of 118 sample months were missing and, as such, estimated values are likely to be representative. As using mean plant productivity across the ranging area in this way may mask areas or periods of particularly high or low productivity, we also identified the areas of each group's monthly range which were highest in plant productivity. To do this, we clipped EVI rasters by values >0.5, a value which represents dense vegetation (Huete *et al*. 2006), within the monthly ranging area using the "Raster Calculator." We then calculated these areas as a proportion of each group's monthly ranging area using the "LecoS" (Landscape ecology Statistics) (Jung 2016) plugin in QGIS, for each month across the study period. Finally, to calculate the proportion of monthly ranging area that included indigenous forest, we used the "indigenous forest" layer of the 2014 SANBI (South African National Biodiversity Institute) landcover map (30 m^2 resolution) and calculated this as a proportion of each group's monthly ranging area using the "LecoS" (Jung 2016) plugin in QGIS. The SANBI indigenous forest layer is derived from a combination of seasonal maximum NDVI values (from images

taken between April 2013 and April 2014), forest biome boundaries (from the SANBI database), and shadow and altitude terrain parameters (from NASA's Shuttle Radar Topography Mission database).

Data analysis

We used linear mixed-effects models with a Gaussian error structure to determine the effects of food availability, plant productivity, and indigenous forest use on the ranging patterns of samango monkeys. For each of the home range variables (monthly ranging area, monthly core area, and mean monthly daily path length), we used separate models to determine the effect of ground-based food availability, remotely sensed plant productivity, and proportion of indigenous forest and areas of high plant productivity incorporated into the monthly ranging area. We ran separate models in this way due to collinearity between multiple variables (Bolker *et al.* 2008), while also allowing for comparison in explanatory power between methods. We included day length, group size, and number of "complete" days used to estimate monthly ranging patterns as control variables, while month and year were included as random variables. Models were fitted in R 3.4 (R Core Team 2017) using the lmer function of the "lme4" package (Bates *et al.* 2014). We checked for normality and homogeneity of residuals by visually inspecting histograms and qqplots of the residuals, and the residuals plotted against fitted values. Collinearity between fixed effects were inspected using Variance Inflation Factors (VIF) from the vif function within the "car" package. VIF values were derived from a standard linear model excluding the random effects, with all values <1.5 indicating no collinearity between variables (Hair *et al.* 2014). *P*-values for the individual effects were based on likelihood ratio tests comparing the full model with respective reduced models, dropping one fixed effect at a time (R function drop1), with significance inferred at the 5% level. To allow for likelihood ratio tests we fitted the models using Maximum Likelihood (Bolker *et al.* 2008) and used Akaike's Information Criterion (Burnham & Anderson 2002) to infer goodness of fit between separate models.

Ethical statement

All behavioral data collection followed the Association for the Study of Animal Behavior (ASAB) Guidelines for the Treatment of Animals in Behavioral Research and Teaching (ASAB 2012) and were covered by the Liverpool John Moores University's use of Live Animals in Unregulated Research Protocol (NK_EP/2016-10). All fieldwork was approved by the Life Sciences Ethical Review Process Committee and the Department of Anthropology Ethics Committee at Durham University, UK and was conducted with approved permits from Limpopo Province Department of Economic Development and Tourism (LEDET).

RESULTS

Overall home range size across the study period was considerably larger for House (123.9 ha) group compared to Barn (89.7 ha), with home ranges between the groups overlapping significantly (Fig. 1). Visualization of the home ranges also highlights a clear avoidance of large open areas, cliff faces, and hard boundaries, with the core areas focused within the indigenous forest. While monthly ranging area varied considerably within each group, ranges were fairly consistent between groups (Barn group max: 52.0 ha, min: 11.4 ha; House group max: 58.1 ha, min: 14.3 ha).

We found no effect of ground-based food availability (Table 1) or remotely sensed plant productivity (Table 2) on the monthly ranging area, monthly core area, or mean monthly DPL. This also held when introducing a 1- and 2-month time lag into the analysis to account for possible delays in remotely sensed plant productivity (Table S2). We found that both monthly ranging area and mean monthly DPL significantly decreased as more areas of high plant productivity were included within the monthly ranging area, but found no effect on the monthly core area (Table 3). Similarly, we found that both monthly ranging area and monthly core area significantly decreased as more indigenous forest was incorporated into the monthly ranging area (Fig. 2, Table 4). However, the proportion of monthly ranging area comprising indigenous forest was not related to mean monthly DPL. The proportion of indigenous forest within the monthly ranging area was also positively correlated with areas of high plant productivity (likelihood ratio test: $t = 4.20$, df = 1, $P < 0.001$).

Proportion of monthly ranging area containing indigenous forest best explained variation in monthly ranging patterns compared to ground-based food availability and remotely sensed plant productivity, based on log likelihood ratio tests and model information criterion. In addition, proportion of areas of high plant productivity within the monthly ranging area was a better predictor of total monthly ranging area and mean monthly DPL than food availability or plant productivity sampled across the ranging area (Table 5).
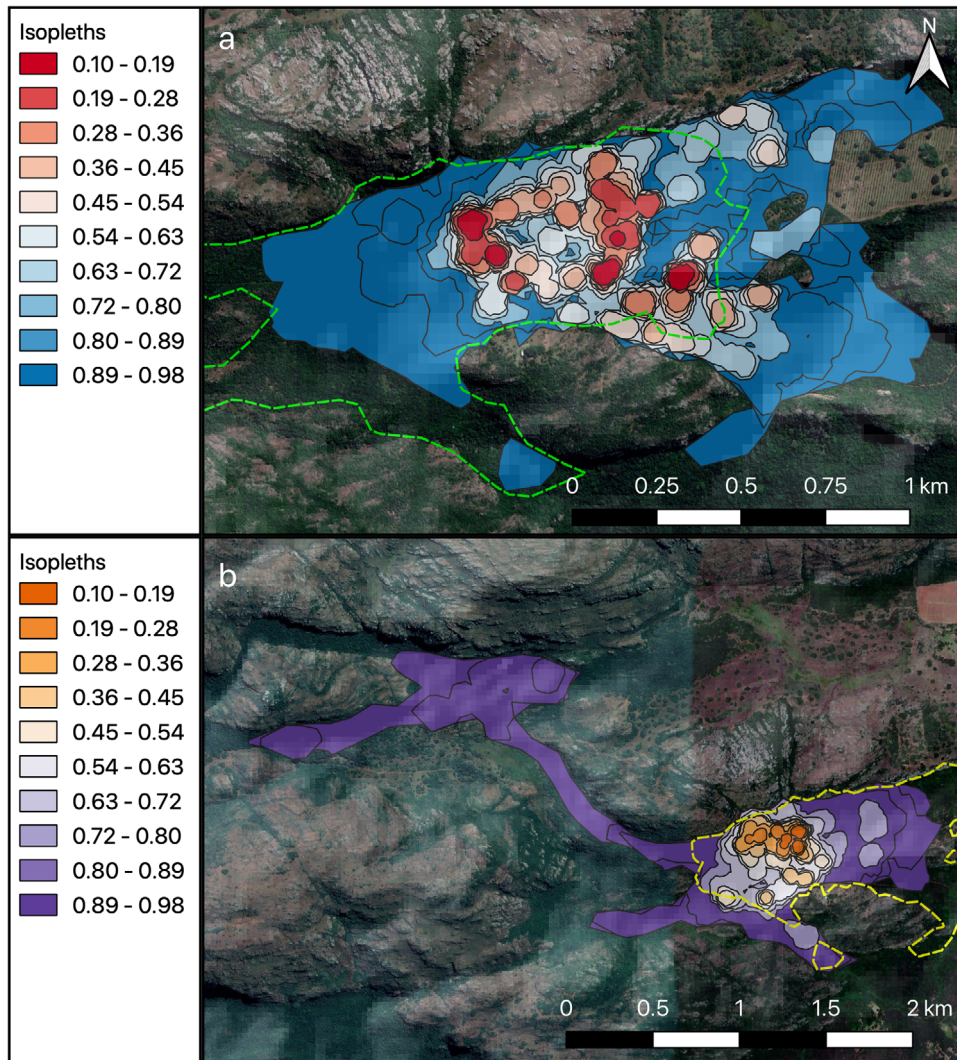
Figure 1 Utilization distributions (UDs) showing the overall home range size and location for both (a) Barn and (b) House groups in the Soutpansberg Mountains, South Africa, across the study period (2012–2016). Outline of House group's (green dotted line, image a) and Barn group's (yellow dotted line, image b) home range are shown to highlight the proximity of each group in relation to each other and to indicate that home ranges overlapped. Total home range is delineated as isopleths ≤ 0.98. Core home range is delineated as isopleths ≤ 0.5.

DISCUSSION

Understanding the influence of resource availability on space use is central to assessing the adaptability of a species to habitat fragmentation (Fahrig 2007; Wilson *et al*. 2016). Here, we explored the influence of food availability, plant productivity, and indigenous forest use on the monthly ranging patterns of the endangered samango monkey in the Soutpansberg Mountains, South Africa. While we found no effect of ground-based food availability or remotely sensed plant productivity sampled across the ranging area on monthly ranging patterns, we found that utilization of both areas high in plant productivity and indigenous forest were significantly associated with a reduction in some aspects of monthly ranging.

Both total and core monthly ranging area significantly decreased as more indigenous forest was incorporated into the ranging area, suggesting that by utilizing more of this habitat type samango monkeys can increasingly focus their ranges on this highly productive habitat. Reliance on natural forest fragments is commonly observed in frugivorous species, such as bats (Ripperger *et al*. 2015) and
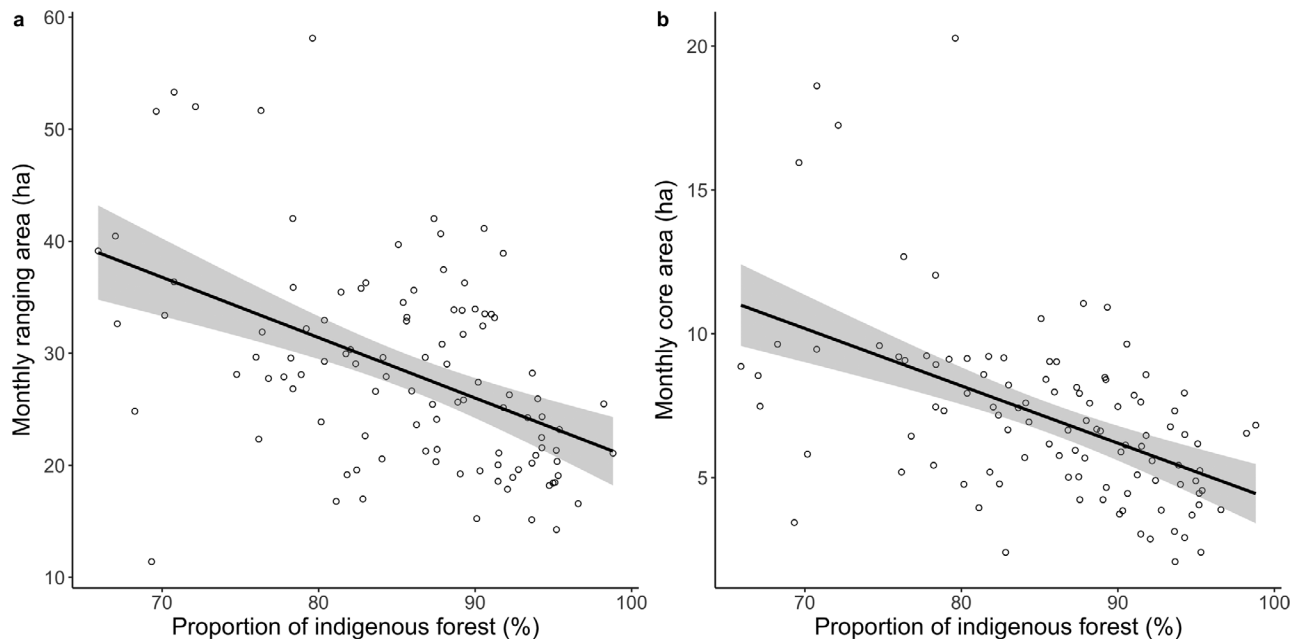
Figure 2 Effect of proportion of monthly ranging area including indigenous forest on (a) size of monthly ranging area and (b) monthly core area.

primates (Estrada & Coates-Estrada 1996; Nowak *et al.* 2017), which typically reduce their ranging area by incorporating more natural forest fragments into the home range (Chaverri *et al.* 2007; Palminteri & Peres 2012; Campera *et al.* 2014). Similarly, our results demonstrate the importance of the indigenous forest as a highly productive habitat to samango monkeys and that in order to live at reasonable population densities, access to indigenous forest patches is key for this species (Linden *et al.* 2016; Nowak *et al.* 2017). The indigenous forest contains important indigenous fruits, such as figs (Linden *et al.* 2015), which contribute significantly to the samango monkey diet (Coleman 2013; Linden *et al.* 2015; Parker 2019). For example, samango monkeys in the Eastern Cape preferentially forage on indigenous fruits and seeds when available regardless of the availability of exotic species which provide a higher calorific content (Nowak *et al.* 2017; Wimberger *et al.* 2017). Similarly, while samangos at Lajuma are capable of utilizing matrix habitat to access alternate resources during periods of low productivity, access to these natural forest fragments is clearly key (Wimberger *et al.* 2017). By incorporating more indigenous forest into the ranging area, samangos are able to reduce their ranging and access more preferred food items in the indigenous forest (Coleman 2013; Linden *et al.* 2015), thereby reducing the need to exploit the habitat matrix as intensively.

In contrast, mean monthly DPL was not influenced by indigenous forest use. While indigenous forest may be important for daily ranging patterns in terms of connectivity between forest patches (Swart & Lawes 1996), the daily distance travelled appears to be more influenced by the time available for foraging (indicated by day length) in this study (Hill *et al.* 2003). However, other factors such as weather (Isbell 1983; Hill 1999), intergroup encounters (Yamagiwa & Mwanza 1994), predator avoidance (Willems & Hill 2009; Coleman & Hill 2014b), mating season dynamics (Erlinge *et al.* 1990), and sleep site location (Albert *et al.* 2011) may also be important. Furthermore, daily path length may not be a reliable measure when exploring ranging patterns in samango monkeys, as their reluctance to traverse open ground (Lawes 1992, 2002; Lawes *et al.* 2000) may superficially increase travel paths when going around, rather than through, open areas.

We also found that as samango monkeys incorporated more areas of high plant productivity into the ranging area, both the total monthly ranging area and mean monthly DPL significantly decreased. These areas represent the most densely vegetated parts of the ranging area (Huete *et al.* 2002) which are highest in plant biomass (Paruelo *et al.* 1997; Willems *et al.* 2009). Therefore, while these areas may include important fruit species (Nowak *et al.* 2017; Wimberger *et al.* 2017), the ability

Table 1 Coefficient estimates and key statistics of models predicting effect of availability of leaves, fruit, and seed pods on total monthly ranging area, core ranging area, and daily path length

Variable	Estimate	SE	CI$_{lower}$	CI$_{upper}$	t-value	P
Ranging area						
Intercept	0.291	0.153	−0.024	0.623	(1)	(1)
Leaves	−0.011	0.011	−0.034	0.012	−1.023	0.329
Fruit	−0.005	0.007	−0.020	0.010	−0.673	0.502
Seed pods	−0.005	0.008	−0.022	0.012	−0.603	0.554
Day length	−0.007	0.013	−0.034	0.019	−0.572	0.568
Days	**0.007**	0.002	0.002	0.012	2.840	0.006
Group	0.003	0.015	−0.026	0.032	0.183	0.857
Core area						
Intercept	0.124	0.051	0.020	0.237	(1)	(1)
Leaves	−0.007	0.004	−0.015	0.001	−1.758	0.103
Fruit	0.001	0.003	−0.005	0.007	0.336	0.738
Seed pods	−0.004	0.003	−0.010	0.003	−1.153	0.271
Day length	−0.005	0.004	−0.014	0.003	−1.266	0.213
Days	0.001	0.001	−0.001	0.003	0.815	0.431
Group	0.003	0.006	−0.009	0.014	0.491	0.630
DPL						
Intercept	−0.365	0.251	−0.861	0.130	(1)	(1)
Leaves	−0.016	0.023	−0.061	0.029	−0.705	0.483
Fruit	−0.023	0.019	−0.061	0.015	−1.217	0.225
Seed pods	−0.013	0.021	−0.056	0.029	−0.626	0.535
Day length	**0.150**	0.020	0.110	0.190	7.464	<0.001
Days	0.007	0.007	−0.007	0.021	1.033	0.321
Group	0.012	0.037	−0.062	0.086	0.316	0.753

Ranging area, total monthly ranging area; core area, monthly core area; DPL, mean monthly daily path length. (1) not shown because of having no meaningful interpretation.

Table 2 Coefficient estimates and key statistics of models predicting effect of mean plant productivity across the ranging area on total monthly ranging area, core ranging area, and daily path length

Variable	Estimate	SE	CI$_{lower}$	CI$_{upper}$	t-value	P
Ranging area						
Intercept	0.387	0.155	0.062	0.719	(1)	(1)
Productivity	0.057	0.059	−0.062	0.177	0.958	0.346
Day length	−0.018	0.013	−0.047	0.010	−1.346	0.187
Days	**0.008**	0.002	0.003	0.013	3.410	0.001
Group	−0.005	0.013	−0.031	0.021	−0.385	0.701
Core area						
Intercept	0.166	(1)	0.054	0.054	(1)	(1)
Productivity	0.015	0.406	0.023	−0.031	0.061	0.524
Day length	−0.009	3.648	0.005	−0.020	0.000	0.056
Days	0.001	1.128	0.001	−0.001	0.003	0.288
Group	−0.001	0.016	0.005	−0.011	0.010	0.900
DPL						
Intercept	−0.294	0.231	−0.750	0.163	(1)	(1)
Productivity	−0.085	0.133	−0.351	0.184	−0.636	0.532
Day length	**0.148**	0.021	0.105	0.190	6.960	<0.001
Days	0.007	0.007	−0.006	0.021	1.125	0.284
Group	−0.007	0.034	−0.075	0.061	−0.208	0.836

Ranging area, total monthly ranging area; core area, monthly core area; DPL, mean monthly daily path length. Productivity, mean plant productivity (indexed by enhanced vegetation index) sampled across the total monthly ranging area. (1) not shown because of having no meaningful interpretation.

of samangos to incorporate a large proportion of leaves in their diet (Coleman & Hill 2014a; Parker 2019) may serve to reduce some aspects of ranging patterns by utilizing more areas which are high in plant productivity. The lack of relationship observed with the monthly core area is likely a result of the consistency in the spatial and temporal availability and distribution of high plant productivity areas within the core range, in addition to the location of important resources such as sufficient sleeping trees (Kaplin 2001). We also found that the proportion of areas high in plant productivity and indigenous forest within the ranging area were positively correlated, indicating that the most productive areas of the landscape are disproportionately found within this habitat type.

In contrast, neither ground-based food availability nor remotely sensed plant productivity sampled across the ranging area influenced samango monkey ranging patterns, which contradicted our predictions. However, this is perhaps unsurprising given our previous findings, in that by utilizing more areas high in plant productivity, which are disproportionately located within the indigenous forest, samangos can reduce aspects of ranging patterns owing to their dietary flexibility (Coleman & Hill 2014a; Linden *et al*. 2015; Wimberger *et al*. 2017) (Table S1). By focusing ranging on these areas, samangos can access sufficient resources either by consuming indigenous fruits when available, or by increasing consumption of leaves, which are readily available and easily located (Hemingway & Bynum 2005), when fruit is

Table 3 Coefficient estimates and key statistics of models predicting effect of proportion of areas of high plant productivity within the ranging area on total monthly ranging area, core ranging area, and daily path length

Variable	Estimate	SE	CI$_{lower}$	CI$_{upper}$	*t*-value	*P*
Ranging area						
Intercept	0.320	0.131	0.044	0.600	(1)	(1)
High productivity	**−0.006**	0.003	−0.011	−0.001	−2.309	0.029
Day length	−0.005	0.011	−0.029	0.018	−0.451	0.652
Days	**0.007**	0.002	0.002	0.011	2.815	0.006
Group	−0.005	0.013	−0.031	0.021	−0.400	0.690
Core area						
Intercept	0.151	0.047	0.051	0.256	(1)	(1)
High productivity	−0.001	0.001	−0.003	0.001	−1.086	0.323
Day length	−0.007	0.004	−0.016	0.002	−1.636	0.110
Days	0.001	0.001	−0.001	0.003	0.826	0.419
Group	−0.001	0.005	−0.011	0.010	−0.121	0.904
DPL						
Intercept	−0.321	0.219	−0.754	0.112	(1)	(1)
High productivity	**−0.013**	0.006	−0.024	−0.001	−2.156	0.033
Day length	**0.157**	0.019	0.119	0.194	8.300	<0.001
Days	0.005	0.007	−0.008	0.019	0.821	0.429
Group	−0.005	0.034	−0.071	0.062	−0.135	0.893

Ranging area, total monthly ranging area; core area, monthly core area; DPL, mean monthly daily path length. High productivity, proportion of areas of high plant productivity within the total monthly ranging area. (1) not shown because of having no meaningful interpretation.

Table 4 Coefficient estimates and key statistics of models predicting effect of proportion of ranging area containing indigenous forest on total monthly ranging area, core ranging area, and daily path length

Variable	Estimate	SE	CI$_{lower}$	CI$_{upper}$	*t*-value	*P*
Ranging area						
Intercept	0.564	0.141	0.264	0.854	(1)	(1)
Forest use	**−0.004**	0.001	−0.006	−0.002	−4.237	<0.001
Day length	−0.004	0.011	−0.027	0.019	−0.357	0.722
Days	**0.007**	0.002	0.003	0.012	3.413	0.001
Group	0.008	0.013	−0.016	0.034	0.677	0.502
Core area						
Intercept	0.248	0.047	0.149	0.344	(1)	(1)
Forest use	**−0.002**	0.000	−0.002	−0.001	−4.780	<0.001
Day length	−0.004	0.004	−0.012	0.003	−1.178	0.248
Days	0.001	0.001	−0.001	0.002	0.984	0.335
Group	0.005	0.005	−0.004	0.015	1.101	0.277
DPL						
Intercept	−0.038	0.256	−0.545	0.468	(1)	(1)
Forest use	−0.004	0.002	−0.009	0.001	−1.618	0.110
Day length	**0.149**	0.018	0.113	0.186	8.124	<0.001
Days	0.009	0.006	−0.004	0.022	1.369	0.192
Group	0.008	0.035	−0.062	0.077	0.218	0.828

Ranging area, total monthly ranging area; core area, monthly core area; DPL, mean monthly daily path length. Forest use, proportion of monthly ranging area containing indigenous forest. (1) not shown because of having no meaningful interpretation.

scarce. The ability to utilize a range of resources in these areas may reduce the need to exploit the habitat matrix as intensively, thereby masking any influence of food availability and plant productivity across the ranging area. Similarly, plant productivity sampled across the ranging area was also uninformative. This was likely a consequence of the arboreal nature of samango monkeys, which are reluctant to disperse over large stretches of open ground or non-forested habitat (Lawes 1992, 2002; Lawes *et al.* 2000), areas which would have influenced this productivity estimate. Interestingly, Willems *et al.* (2009) also found no correlation between NDVI (another remotely sensed estimate of plant productivity) and either home range or core home range size in vervet monkeys

(*Chlorocebus pygerythrus*) at the same field site, but found a negative association with DPL. However, unlike samangos, vervets are not predominantly forest-dwelling (Willems *et al.* 2009) and so daily ranging patterns may be suitably explained by productivity across the home range as vervets are more capable of utilizing open habitats which are largely avoided by samangos (Lawes 2002). Although plant productivity across the ranging area was uninformative, our findings demonstrate the capacity of remote sensing to identify areas of the habitat which are highest in plant productivity, and that these areas appear much more informative when exploring ranging patterns in small ranging, forest-dwelling guenons.

Contrary to our predictions, we found that the proportion of indigenous forest within the monthly ranging area best explained monthly ranging patterns, based on log likelihood ratio tests and model information criterion. While ground-based estimates of food availability

Table 5 Candidate model set and model selection results for total ranging area, core ranging area, and daily path length

Ranging variable	Model	Fixed effects	LogLik	ΔLogLik	AIC	ΔAIC$_c$	w
Ranging area	4	Forest use + Day length + Days + Group	133.3	7.8	−250.5	0.0	1.00
	3	High productivity+ Day length + Days + Group	127.5	2.0	−238.9	11.6	0.00
	1	Productivity + Day length + Days + Group	125.5	0.0	−235.1	15.4	0.00
	2	Leaves + Fruit + Seeds + Day length + Days + Group	125.9	0.4	−231.8	18.7	0.00
Core area	4	Forest use + Day length + Days + Group	236.3	9.9	−456.5	0.0	1.00
	3	High productivity + Day length + Days + Group	226.7	0.3	−437.4	19.1	0.00
	1	Productivity + Day length + Days + Group	226.4	0.0	−436.9	19.6	0.00
	2	Leaves + Fruit + Seeds + Day length + Days + Group	227.7	1.3	−435.5	21.0	0.00
Daily path length	3	High productivity + Day length + Days + Group	31.3	1.5	−46.6	0.0	0.24
	4	Forest use + Day length + Days + Group	30.3	0.5	−44.6	2.0	0.08
	1	Productivity + Day length + Days + Group	29.2	−0.6	−42.4	4.2	0.03
	2	Leaves + Fruit + Seeds + Day length + Days + Group	30.1	0.3	−40.3	6.3	0.02

ΔLogLik, difference in log likelihood compared to the best model; AIC$_c$, Akaike information criterion corrected for small sample size; ΔAIC$_c$, difference in AIC$_c$ compared to the best model; w, Akaike weight. Ranging area, total monthly ranging area; core area, monthly core area; DPL, mean monthly daily path length. Forest use, proportion of monthly ranging area containing indigenous forest; High productivity, proportion of areas of high plant productivity within the total monthly ranging area; Productivity, mean plant productivity (indexed by enhanced vegetation index) sampled across the total monthly ranging area.

offer greater phenological detail, the dietary flexibility and reliance of samangos on the indigenous forest ultimately determines the variation in monthly ranging patterns. Conversely, when focusing their range less on these areas, samangos can exploit alternate resources in the surrounding matrix habitat. This flexibility may help to mitigate the effects of habitat loss and fragmentation by facilitating movement between forest fragments. However, access to indigenous forest is clearly key to samango monkey ranging patterns (Nowak *et al*. 2017). In order for samango monkeys to persist in an increasingly fragmented and human-dominated landscape, proper management of these forests is essential (Swart & Lawes 1996). Across South Africa, metapopulations are declining owing to increasing habitat loss and a lack of corridors connecting suitable habitats (Lawes 2002). This is particularly relevant for the subpopulations in the Soutpansberg Mountains which are isolated from neighboring populations (Linden *et al*. 2016). Management plans should therefore focus on expanding protected areas of indigenous forest through reclaiming and restoring non-viable areas (Linden *et al*. 2016). In addition, minimizing disturbance in and around large forest patches (Lawes *et al*. 2000) and continuing to connect forest fragments is also crucial in order to facilitate movement between patches and ensure the long-term viability of subpopulations (Swart & Lawes 1996).

The results from our study highlight the potential of using remote sensing to identify areas of the habitat which are particularly high in plant productivity, and demonstrate the applicability of using this measure to explore ranging patterns in a small ranging, forest-dwelling guenon. The ability of samango monkeys to utilize a range of food items within these areas, which are predominantly located within the indigenous forest, appears key to explaining monthly ranging patterns. Therefore, effective management of these forests is essential in order to ensure the long-term persistence of the samango monkey in an increasingly fragmented and human-dominated landscape.

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SUPPLEMENTARY MATERIALS

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

Table S1 Monthly range and average time spent feeding (%) on different food items by each samango monkey group at Lajuma between 2012 2016. Average values from Coleman & Hill, 2014 (also collected from Barn group) also shown to demonstrate values are characteristic of the groups.

Table S2 Coefficient estimates and key statistics of models predicting effect of mean plant productivity across the ranging area, with a one and two-month lag, on total monthly ranging area.

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