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Spatial Ecology of the Endangered Milne-Edwards' Sifaka (*Propithecus edwardsi*): Do Logging and Season Affect Home Range and Daily Ranging Patterns?

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Abstract Primates often live in human-altered habitats; Malagasy lemurs are no exception. It is important to understand if habitat alteration affects primates' space use patterns across multiple spatial and temporal scales, as this drives population density. We quantified the daily, seasonal, and annual space-use of seven groups of Milne-Edwards' sifaka (*Propithecus edwardsi*) living in unlogged and logged rain forest in Ranomafana National Park, Madagascar between December 2002 and November 2003. Concurrent data showed that sifakas consumed higher quality foods in the unlogged than in logged forests; thus we explored how space use patterns were related to energy use strategies. Sifaka groups in the logged rain forest traveled 7–13% less per day than groups in the unlogged rain forest, despite their larger home ranges (median: 46.12 and 23.52 ha, in the logged and unlogged forests, respectively). Sifakas may thus use an energy-minimizing strategy at the scale of the individual day but an energy-maximizing strategy at the annual home range scale. Sifakas exhibited fidelity to the home range across seasons, but their core area of use shifted considerably with season. We found no difference in population density between sites. However, given the

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interannual variability in sifaka foods, a multiyear study is needed to assess if energy strategies observed in this study are consistent across longer time periods. Our findings suggest that lemurs may persist in logged habitats by altering spatial use patterns; future work should attempt to quantify the threshold level of forest regeneration from logging that will allow lemurs to persist at similar densities as in unlogged forest.

Keywords Daily path length · Home range · Lemur · Logging · Rain forest

Introduction

Primate movement patterns are highly influenced by resource availability (Clutton-Brock 1977; Milton and May 1976; Mitani and Rodman 1979). Thus, factors affecting resource availability, such as season (Hemingway and Bynum 2005; Li *et al.* 2000), sociality, e.g., group composition and range overlap (Ganas and Robbins 2005; Takasaki 1981), and logging (Chapman *et al.* 2000; Wieczkowski 2005), often directly alter the spatial distribution of primates and, as a consequence, their population dynamics (Morales *et al.* 2010). Animal resource selection varies with the time and spatial scale considered (Kernohan *et al.* 2001); therefore, it is important to assess how annual home range size, core areas within the home range, seasonal home range size, and daily movement vary across habitats with different disturbance histories to understand fully how the environment influences animal movement and thus population structure and regulation (Morales *et al.* 2010).

Primates respond to altered resource availability, whether due to season or human activities, in two general ways. When preferred high-quality resources become limited in abundance or become more patchy in their distribution, primates may 1) increase their home range or daily distance traveled to seek additional resources (energy-maximizing strategy; Ganas and Robbins 2005; Li and Rogers 2005; Li *et al.* 2000; Wieczkowski 2005) or 2) reduce their home range or daily distance traveled as a means to reduce energy expenditure and the need for additional resources (energy-minimizing strategy; Fan *et al.* 2008; Strier 1992; Wright 1999). Although daily distance traveled and home range are often considered independent from each other, they need not be so. Animals perceive and interact with the environment at multiple spatial scales simultaneously (Nams 2005), such that behaviors may vary by scale but are connected hierarchically (Senft *et al.* 1987). Daily movement and home range can be considered hierarchical patterns of space use or resource selection (Johnson 1980; Moorcroft and Lewis 2006). Strategies of resource acquisition, which we broadly classify as energy-minimizing or -maximizing, can be understood as scale-dependent selection behaviors, wherein daily path length is selection within the home range and home range is selection within the landscape (Johnson 1980).

Whether a primate species behaves in a way to maximize energy intake or minimize energy use is related to diet and the distribution of preferred resources (Milton and May 1976). Frugivores often increase their home range and daily distance traveled to procure additional patchily distributed fruit (Ganas and Robbins 2005), whereas folivores are more likely to reduce home range and daily distance traveled to conserve energy, as foliage is often evenly distributed in the environment (Koenig *et al.* 1998; Norscia *et al.* 2006). Many primate studies have hypothesized a causal relationship between reduced resources and larger groups expanding their home range and traveling further per day to compensate for the increased competition among individuals (Clutton-Brock and Harvey 1977; Steenbeek and Schaik 2001; van Schaik and van Hooff 1983). If reduced resource availability cannot be compensated for by either strategy, individuals may lose body mass or condition, which may affect fecundity and survival, and ultimately the population dynamics of the species (Hemingway and Bynum 2005; Lewis and Kappeler 2005).

We studied the IUCN-endangered Milne-Edwards' sifaka, *Propithecus edwardsi* (hereafter sifaka; IUCN 2011), to understand how 1) daily distance traveled, home range, core area of the home range, and intergroup spatial overlap differed between a previously logged and unlogged rain forest site, and 2) whether any variation in spatial use might have population-level implications, such as altered density. Sifakas are diurnal, sexually monomorphic, strepsirrhine primates (5–6 kg; Pochron *et al.* 2004) that inhabit the central-southeastern rain forests of Madagascar. Their diet consists mainly of foliage, fruits, and seeds and varies seasonally, with a preference for fruits and seeds when available and leaves when fruits and seeds are not available (Hemingway 1998; Meyers and Wright 1993; Wright *et al.* 2005). As with other Malagasy primates, sifakas experience high variability in intraannual rainfall that leads to unpredictability and scarcity of food resources, especially in the austral winter (Dewar and Richard 2007; Wright *et al.* 2005). Historic and continued logging throughout their range has altered forest structure and plant species composition, thus affecting resource availability (Brown and Gurevitch 2004).

In a concurrent study of these same sifakas, Arrigo-Nelson (2006) found that groups in the unlogged forest consumed calorie- and nutrient-rich fruits and seeds 15.6% more than sifakas in the previously logged forest, which consumed more leaves. In addition, fruits and seeds were more available in the unlogged forest vs. the logged forest, and at both sites fruits and seeds were more available and thus consumed more during the warm-wet season than the cool-dry season (Arrigo-Nelson 2006; Arrigo-Nelson and Randriamahaleo 2006). Similar to previous studies, Arrigo-Nelson (2006) also found that the leaves of *Bakerella clavata*, which thrive in disturbed areas, were used by sifakas at both sites; however, sifakas in the logged forest consumed more than twice as much *Bakerella* as sifakas in the unlogged forest.

Given that sifakas are neither strict folivores nor frugivores (Hemingway 1998), we predicted sifakas may exhibit a combination of energy-minimizing and -maximizing tactics in response to altered resource availability between seasons and between the logged and unlogged sites. We tested the hypotheses that 1) annual home range size and core areas of sifaka groups did not differ between the unlogged and logged rain forest sites, 2) home range size and core areas did not differ between seasons, and 3) seasonal home range size and core areas did not differ within or between sites. Sifakas of the logged rain forest may move less per day to conserve energy, especially when fruit is least available during the austral winter, but maintain a larger home range compared to groups in the unlogged rain forest as a means to acquire all necessary resources to survive and reproduce. Because resource defense (territoriality) is important in shaping intergroup relationships and thus the spatial structure of the population, we predicted that adjacent groups would exhibit low home range or core overlap or both, especially when resources were limited, e.g., within the austral winter or in the logged forest site. We expected that the logged rain forest would have a more diffuse distribution of primates to compensate for altered resources, and thus a lower primate density.

Methods

Study Sites and Seasons

We conducted this research within Ranomafana National Park (RNP) in central-eastern Madagascar (21°02′–21°25′S and 47°18′–47°37′E; Fig. 1) between December 2002 and November 2003. RNP protects 416 km^2 of mostly submontane tropical rain forest, ranging in elevation from 559 to 1396 m. RNP experiences two seasons based on temperature and rainfall: a warm-wet (December–March) and a cool-dry (June–September) season, with two transitional periods (April–May, October–November; Arrigo-Nelson 2006). Mean daily rainfall during the warm-wet season was 19±SD 21 mm (range 0–112 mm) and its mean minimum and maximum daily temperatures were 18±SD 1 and 23±SD 2°C, respectively. Mean daily rainfall during the cool-dry season was 6±SD 10 mm (range 0–48 mm) and its mean minimum and maximum daily temperatures were 11±2 SD and 17±SD 3°C, respectively. Annual rainfall in RNP ranges between 2300 and 4000 mm.

We sampled sifakas within the logged rain forest of the Talatakely trail system (logged site) and the unlogged rain forest of Valohoaka trail system (unlogged site). A small village and market occupied the logged site during the 1930s and 1940s. This site encompassed 2.1 km^2 and ranged in elevation from 835 to 1116 m, and experienced selective logging of commercially valuable hardwoods by timber exploiters from 1986 to 1989 (Wright 1997; Wright and Andriamihaja 2003). The unlogged rain forest site was located 3.9 km southeast of the logged forest, but connected to it by contiguous forest; it was never commercially logged (Balko and Underwood 2005) and has experienced minimal human disturbance, mostly in the form of day visits by tourists and passage by local people. This site encompassed 1.4 km^2 and ranged in elevation from 834 to 1205 m. At both sites a network of mostly low-impact trails were laid out explicitly to follow sifaka groups. The logged rain forest trail network was started in 1986 and consisted of a total length of 46.8 km of trails, while the unlogged forest trail network was started in 1988 and consisted of 27.1 km of trails. At both trail networks, a series of markers every 25 m indicated the trail name and location. The logged site had reduced structural complexity vs. the unlogged site, e.g., a reduced basal area, tree height, crown volume, and a more open canopy, but similar tree density and species richness (Arrigo-Nelson 2006; Balko and Underwood 2005).

Data Collection and Sifaka Groups

We observed a total of 15 adult sifakas; we sampled 4 groups (9 adults) in the logged site and 3 groups (6 adults) in the unlogged site (hereafter individual groups are referenced as Logged-group no. and Unlogged-group no.). Detailed sex and age composition for each group for the study year is described by Arrigo-Nelson (2006), while a long-term history of the groups in the logged forest is described by Morelli *et al.* (2009). In both areas, sifakas were habituated to human observers and

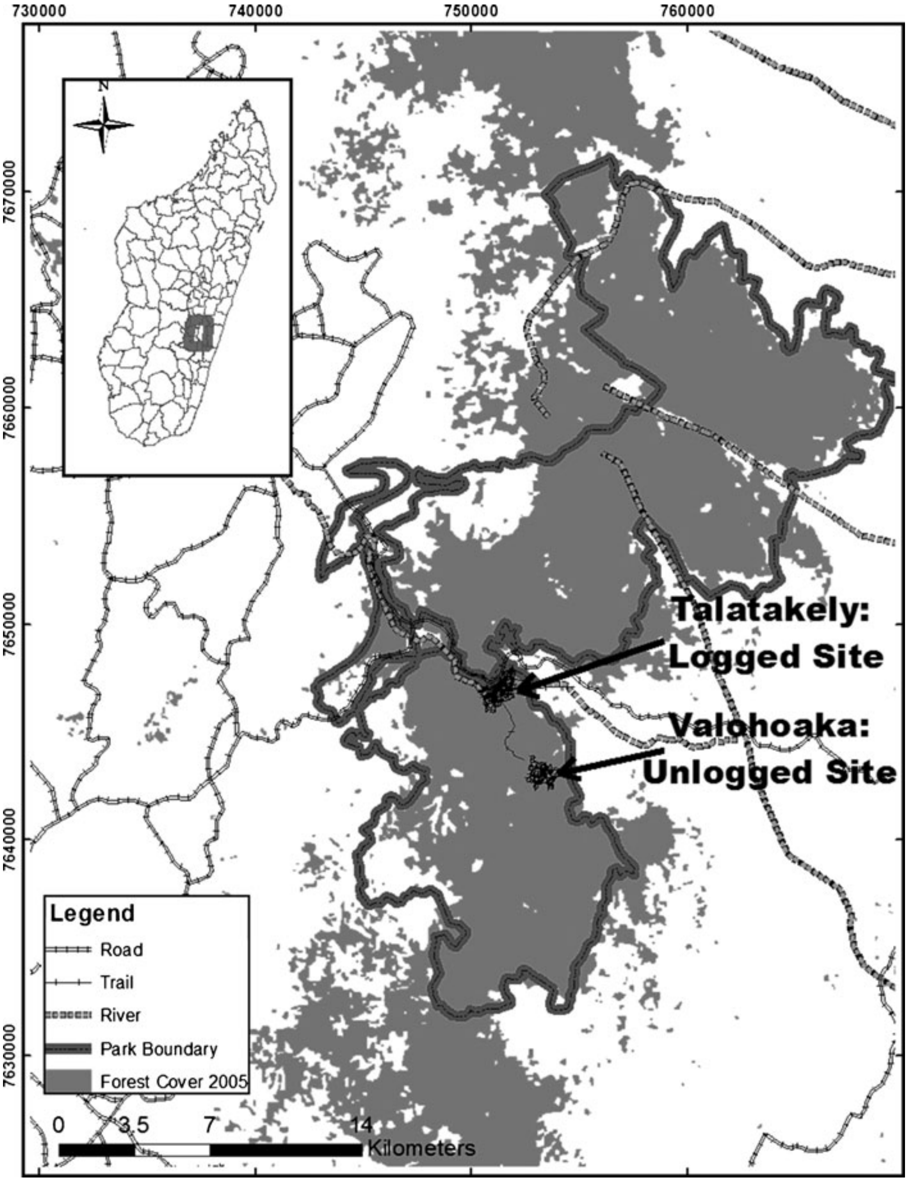

Fig. 1 Spatial dynamics of groups of *Propithecus edwardsi* at an unlogged (Valohoaka trail system) and logged site (Talatakely trail system) within Madagascar's central-eastern rainforests from December 2002 to November 2003. Top insert map shows political provinces and location on the island of Madagascar. Rain forest extent from Conservation International (2011).

were individually identified by colored neck collars and tags. We captured sifakas under veterinary supervision and followed procedures as in Glander *et al.* (1992). Between December 2002 and November 2003, two research teams observed each sifaka group for ≥5 consecutive days each month, collecting instantaneous scan samples at 10-min intervals (Altmann 1974). Each scan sample included the activity of every adult group member and the nearest trail location.

Data Analyses

We calculated daily path lengths (DPL) for each sifaka group as the sum of the Euclidean distances between consecutive trail locations taken every 10 min. We included only day follows for which locations were recorded completely between morning and evening sleep trees, or data collection started before 07:00 h with >9 h of observation and <5% missing observations. We used a generalized linear mixed-effects model in the R package lme4 (R Development Core Team 2010) to evaluate multiple fixed effects on the response variable DPL. Fixed effects included day light length (DayLength), rainfall (Rain), cool-dry vs. warm-wet seasons (Season), and logged vs. unlogged rain forest (Site). To account for variation among sifaka groups, Group was a random variable nested within Site. To avoid multicollinearity, we examined correlations among variables and did not include variables with $r>0.6$ in the same model (Graham 2003). We constructed biologically meaningful *a priori* models that included additive and interactive variables and evaluated model parsimony using Akaike's information criterion with a small sample size bias correction (AIC_c). We model-averaged parameter estimates to incorporate model selection uncertainty (Burnham and Anderson 2002).

We used all location data to estimate the home range of sifaka groups. Although some studies have subsampled data to reduce autocorrelation among successive sampling locations, this appears only to reduce the accuracy and precision of home range estimates (Blundell *et al.* 2001; De Solla *et al.* 1999). More importantly, we based our home range estimates on fixed time periods that were biologically meaningful, e.g., annual and seasonal as defined previously and collected location data systematically with 10-min scan samples (Fieberg 2007; Otis and White 1999). By using trail locations as animal locations, our data were naturally discretized with an inherent spatial rounding error of half the distance between potential trail locations of 12.5 m. We incorporated this error into our home range estimates by randomly shifting all locations to a distance between 0 and the rounding error of 12.5 m (Laver 2005). We expect our use of trail locations to have little to no bias in our results because of the extensive trail systems in our study area and observations that sifakas consistently use traditional travel routes over which trails were laid out (Erhart and Overdorff 2008).

There are many models available to estimate home range (Kernohan *et al.* 2001). Using our data, we evaluated two commonly applied nonparametric kernel models (fixed-kernel and adaptive-kernel) with an information-theoretic approach (Horne and Garton 2006). We determined the model with the lower AIC_c the most parsimonious with our data and thus used it to estimate home range. We performed home range analyses with home-range tools (HRT; Rodgers *et al.* 2007) for ArcGIS (ESRI, Redlands, CA). We calculated kernel home ranges using a bivariate normal distribution, rescaling x–y coordinates to unit variances. We set raster cell size to 12.5 m × 12.5 m to reflect the spatial resolution of the data. We evaluated home range size using 95% isopleths. Kernel home range estimators are well known to be sensitive to bandwidth selection (Silverman 1986). We used the root-n bandwidth estimate, as it has been found to be robust with simulated and empirical data and overcomes common issues of larger sample sizes and spatial clumping caused by animal site fidelity that routinely cause other bandwidth estimators to fail or oversmooth (Steury *et al.* 2010).

For each home range, we also estimated a core area within the home range using an objective Bayesian analysis for evaluating the optimal isopleth(s) by categorizing the utilization distribution structure into ≥0 separate completely random point patterns (Wilson *et al.* 2010). This method does not rely on an assumed 50% isopleth as a core area, but instead evaluates the underlying internal home range space-use patterns to delineate highly clustered or core areas. To estimate the posterior distribution of core area isopleths, we used 60,000 Monte Carlo simulations and evaluated and removed appropriate burn-in periods. We conducted analyses in R (R Development Core Team 2010) with freely available code (http://warnercnr.colostate.edu/~hooten/other/, Accessed 6 October, 2011).

To evaluate site fidelity of sifaka groups between seasons and space-use overlap between adjacent sifaka groups, we estimated home range and core overlap. We calculated overlap using a utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005) implemented in the R package adehabitat (Calenge 2006). The UDOI makes use of the product of the two groups' utilization distributions being compared and is recommended for quantifying space-use sharing. A UDOI of 0 indicates no home range overlap, while 1 indicates home ranges are uniformly distributed and overlap is 100%.

We used multi-response permutation procedures (MRPP) implemented in Blossom (Cade and Richards 2005) to test for differences between and within the unlogged and logged rain forest sites. We ran permutation tests using ranked data, such that they are analogous to the KruskalW allis test; we treated intrasite comparisons as paired data, as observations were repeated measures. MRPP is a class of multivariate permutation tests of group differences that is useful for small sample sizes and is robust to nonnormally distributed data and heterogeneous error variances (Mielke and Berry 2001). We used $\alpha=0.05$ to indicate statistically significant difference.

Results

We found that DPL of sifaka groups was positively related to increasing day length. For every 1 h of increase in day length, sifaka groups in both the unlogged and logged forests traveled an estimated additional 161±SE 31 m. Sifaka groups in the logged site traveled less per day than groups at the unlogged site (Table I; Fig. 2; the model Daylength + Site had 3 times (0.57/0.19) the support vs. the Daylength model without the Site variable). There was >2 times the weight of support for an additive effect ($w_i=0.57$) between day length and study site, vs. an interaction effect ($w_i=0.23$), suggesting day length influences DPL similarly among all sifaka groups. On average, sifaka groups in the logged rain forest moved 92±SE 46 m less per day than groups in the unlogged forest (Table II). At a day length of 12 h, we estimated sifaka groups in the logged rainforest traveled 747±SE 43 m/d, while sifaka groups in the unlogged forest traveled 818±SE 39 m/d; across all day lengths, site level differences ranged from 7.5% to 13% (Fig. 2). We found no evidence that either season, other than its relationship to day length, or rainfall affected sifakas' DPL (models including the variables season or rainfall had no model weight).

We estimated home range size for six of the seven sifaka groups for the entire sampling year and by season separately; the range of group Logged-3 extended

Table I Top models (likelihood >0.125) using a generalized linear mixed-effects model to estimate daily path length of groups of *Propithecus edwardsi* in a logged and unlogged rain forest site within Ranomafana National Park, Madagascar

Model[a]	K[b]	AIC_c	ΔAIC_c	Model likelihood	Model weight (w_i)	Deviance
DayLength + Site(group)	5	2320.82	0.00	1.00	0.57	2309.43
DayLength*Site(group)	6	2322.67	1.85	0.40	0.23	2310.41
DayLength	4	2322.97	2.16	0.34	0.19	2314.41

Sampling occurred from December 2002 to November 2003.

[a] Fixed effect variables include daylight length (DayLength), rainfall (Rain), a difference among the cool-dry season, warm-wet season, and the two transitional periods (Season), and logged rain forest vs. unlogged rain forest (Site). To account for variation between sifaka groups, group was a random variable nested within Site.

[b] The number of parameters per model.

beyond the trail network and was, therefore, removed from analyses. Across all home ranges calculated, e.g., by year, warm-wet season, and cool-dry season, for all sifaka groups, we selected the fixed-kernel estimator as the most parsimonious model; thus we estimated all home ranges using a fixed-kernel. We found that the 95% home range of sifaka groups were statistically different between the unlogged and logged sites across the entire year (δ_1=–2.44, df=1, p=0.03) and cool-dry season (δ_1=–2.44, df=1, p=0.03); in the warm-wet season, the directionality of the relationship between the sites was the same, but the differences were not significant (δ_1=–1.64, df=1, p=0.08). Across the entire year and all seasons, we found larger sifaka home ranges in the logged site than the unlogged site (Table III). Despite differences in annual and cool-dry season home range sizes by site, sifaka density was not different between the unlogged and logged sites across the entire year (δ_1=0.81, df=1, p=0.79), cool-dry

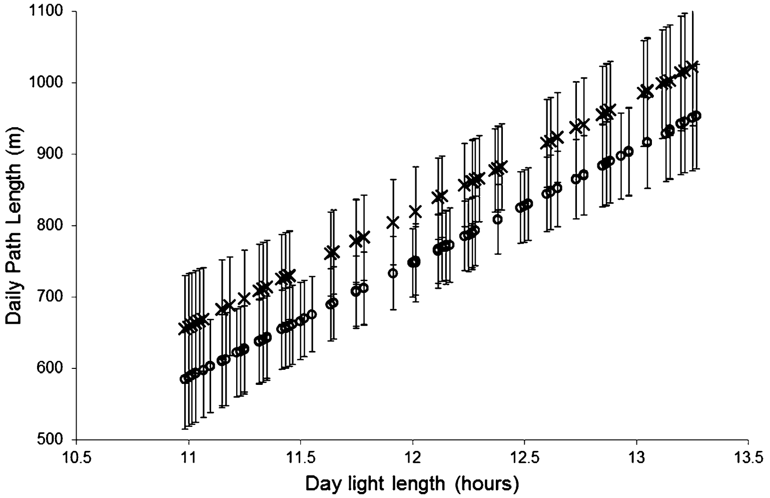

Fig. 2 Daily path length variation (model-averaged mean±95% confidence limits) by day light length and difference between an unlogged (X; Valohoaka) and logged (O; Talatakely) rain forest site within Ranomafana National Park, Madagascar (Sample Days: N_{logged}=94 and N_{unlogged}=69).

Table II Model averaged regression coefficients of supported variables that influence *Propithecus edwardsi* daily path length

Variable	Estimate (m)	SE	95 % Unconditional confidence interval
Intercept	1183.68	371.1	456.34–1911.02
Site	92.19	40.90	12.03–172.18
DayLength	161.1	30.54	101.23–220.97

season (δ_1=0.813, df=1, p=0.79), or warm-wet season (δ_1=0.81, df=1, p=0.79, Table III). We did not explicitly test for an effect of group size on home range, but only group Logged-4 had more than two to three adults and its home range was similar to group Logged-1 with only two adults (Table III).

We found that the core area of sifaka home ranges did not differ between logged and unlogged sites by year (δ_1=–1.14, df=1, p=0.13), cool-dry season (δ_1=–0.16, df=1, p=0.35), or warm-wet season (δ_1=–1.14, df=1, p=0.13). We also found core home range size to not differ by season within either the logged (δ_1=–0.163, df=1, p=0.35) or unlogged (δ_1=0.49, df=1, p=0.63) sites (Table III).

Annual and seasonal home range overlap between adjacent sifaka groups was low at both sites (Fig. 3), with the highest overlap index of 0.11 between Unlogged-1 and Unlogged-2 during the warm-wet season (Table IV). Annual and seasonal core area overlap was 0 between all groups, except for Logged-1 and Logged-4, with a very small annual and warm-wet season home range overlap index of <0.05 (Table IV). We found greater seasonal site fidelity at the home range (δ_1=–2.4, df=1, p=0.03) and core area (δ_1=–2.4, df=1, p=0.03) levels at the unlogged than logged site (Table IV). The median home range overlap between the cool-dry and warm-wet seasons was 0.68 for logged site sifaka groups, while it was 0.76 for the unlogged site sifaka groups. The median core area overlap between the cool-dry and warm-wet seasons was much less vs. the home range overlap, at an index of 0.11 for logged site sifaka groups and 0.21 for unlogged site sifaka groups.

Discussion

As predicted, sifaka groups in the logged rain forest site appeared to exhibit a combination of energy minimizing and maximizing tactics, at different scales, to compensate for altered resource availability. Larger home range sizes in the logged site vs. the unlogged site suggest an energy intake maximizing strategy at the annual and landscape scales. By contrast, shorter DPL in the logged site are more consistent with an energy loss minimizing strategy at the daily and home range scales. Perhaps to compensate for more dispersed and smaller patches of high-quality resources, groups living in logged rain forest travel less per day to minimize energy use, but cover a larger area overall to acquire necessary and highly patchy quality resources. Sifaka groups in the unlogged rain forest appear to need less area to acquire necessary resources due to increased availability, but move more per day throughout the year to obtain higher-quality but patchily distributed resources, such as fruit.

Our findings are consistent with those of other studies of sifakas living in altered habitats. For example, sifaka groups living in degraded rain forest fragments *ca.*

Table III Home range, core area, and density estimates of six *Propithecus edwardsi* groups by year and season in a logged and unlogged rain forest site within Ranomafana National Park, Madagascar. Sampling occurred from December 2002 to November 2003

Sampling period[a]	Sifaka group[b]	No. of individuals per group[c]	Total location samples	Total no. of sample days	95% Fixed kernel home range (ha)	Standardized smoothing parameter (Root-N)	Core area (95% credible intervals; ha)	Density (individuals/km^2)[c]
Year	L1	2	7029	58	46.13	0.167	11.51 (11.10–11.76)	7.95
	L3	3	7010	60	32.74	0.169	7.44 (7.30–7.48)	10.04
	L4	8	21275	69	46.12	0.253	12.33 (11.20–12.75)	20.34
	UL1	3	9672	24	23.52	0.168	3.75 (3.60–3.79)	13.27
	UL2	3	6521	56	23.26	0.175	5.05 (4.90–5.51)	13.42
	UL4	2	2698	58	33.19	0.169	9.43 (8.69–9.59)	6.03
Warm-wet	L1	2	2582	20	46.46	0.2	12.16 (11.73–12.67)	7.90
	L3	3	1757	17	27.53	0.187	2.26 (2.18–2.55)	12.13
	L4	8	5475	25	40.02	0.198	7.68 (7.31–7.96)	23.32
	UL1	3	2124	18	18.37	0.231	2.65 (2.56–2.78)	18.78
	UL2	3	1432	18	18.11	0.215	3.2 (3.10–3.46)	18.61
	UL4	2	907	22	31.52	0.179	8.01 (7.95–8.79)	6.60
Cool-dry	L1	2	1903	19	35.11	0.225	13.16 (11.30–13.70)	6.53
	L3	3	2534	21	27.11	0.2	5.26 (5.01–5.91)	11.06
	L4	8	7459	24	39.75	0.194	14.36 (14.34–15.47)	20.86
	UL1	3	3245	19	19.33	0.203	3.4 (3.24–4.78)	16.63
	UL2	3	2794	18	19.84	0.182	8.93 (8.93–8.62)	16.20
	UL4	2	912	20	26.41	0.18	11.08 (9.21–11.50)	7.738

[a] Year: December 2002–November 2003; warm-wet season: December 2002–March 2003; cool-dry season: June 2003–September 2003.

[b] L no. and UL no. indicates sifaka groups at the logged and unlogged rain forest site, respectively.

[c] The number of individuals included all nondependent sifakas (adults, subadults, and juveniles). Density was corrected for overlapping home ranges.

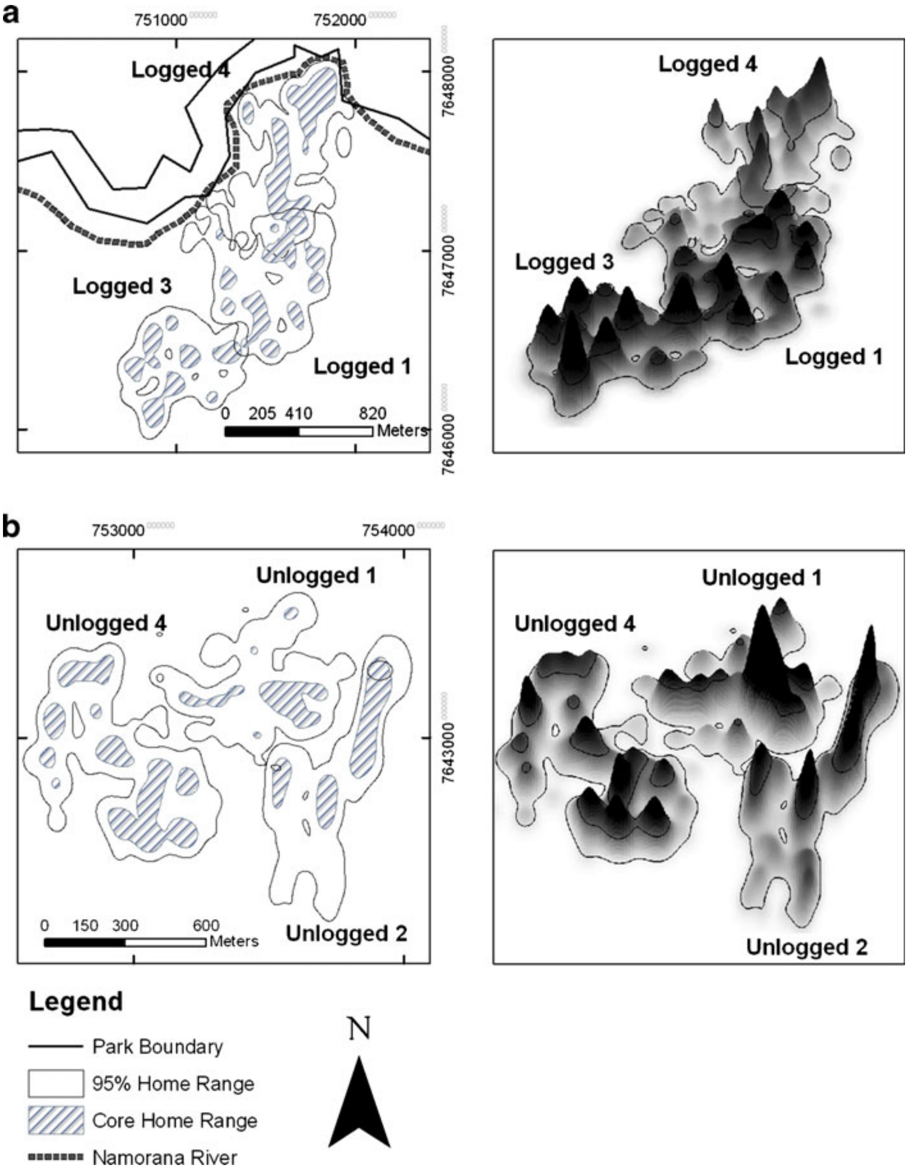

Fig. 3 *Propithecus edwardsi* annual home range (left) and equivalent 3-dimensional utilization distribution (right) from December 2002 to November 2003 at the logged (**a**, three groups) and unlogged (**b**, three groups) rain forests within Ranomafana National Park, Madagascar. Note that the scale is slightly different between the two sites.

25 km from our study site have home ranges of 32–61 ha (Foltz 2009), which are similar to or larger than sifaka groups living at the logged site in RNP. Further, groups of diademed sifakas (*Propithecus diadema*) living in rain forest fragments similarly had shorter DPL, but also smaller home ranges than conspecifics living in nearby continuous forest; these differences were hypothesized to be a strategy of minimizing energy loss adopted by the fragment-dwelling *Propithecus diadema*, which feed

Table IV Annual and seasonal home range overlap in terms of the UDOI index (Fieberg *et al.* 2005) between groups of *Propithecus edwardsi* in a logged and unlogged rain forest within Ranomafana National Park, Madagascar

		95% Home range			Core area		
Comparison	Site[a]	Year	Warm-wet	Cold-dry	Year	Warm-wet	Cold-dry
Between sites and groups, within seasons	L1:L3	0.02	0.03	0.00	0.00	0.00	0.00
	L1:L4	0.06	0.07	0.02	0.05	0.03	0.00
	L3:L4	0.00	0.00	0.00	0.00	0.00	0.00
	UL1:UL2	0.02	0.11	0.06	0.00	0.00	0.00
	UL1:UL4	0.00	0.01	0.01	0.00	0.00	0.00
	UL2:UL4	0.00	0.00	0.00	0.00	0.00	0.00
Between seasons, within a site and group	L1		0.49			0.11	
	L3		0.69			0.16	
	L4		0.68			0.05	
	UL1		0.74			0.30	
	UL2		0.81			0.21	
	UL4		0.76			0.17	

A UDOI of 0 indicates no home range overlap, while 1 indicates home ranges are uniformly distributed and overlap is 100%.

[a] L no. and UL no. indicates sifaka groups at the logged and unlogged rain forest site, respectively.

heavily on the relatively abundant leaves of *Bakerella clavata*, which is of relatively low nutritional value (Irwin 2008).

Contrary to our predictions, there was very little difference in cool-dry season home range size vs. the warm-wet season home range. When food resources were most limited during the austral winter, sifakas still used a similar-sized area as to when preferred food resources were more plentiful. In addition, we did not observe sifakas increasing or decreasing their DPL between seasons, beyond what was expected with changing day length. It has often been reported that primate DPL varies seasonally owing to resource availability and diet, including studies of *Propithecus* sp. (Irwin 2008; Norscia *et al.* 2006; Powzyk 1997), without explicitly modeling the constraint that available day length may have on movement of diurnal species. By accounting for the number of daylight hours, we found that there was otherwise no seasonal effect on DPL. It is clear that sifakas move more in the warm-wet season than in the cool-dry season, but they appeared to move no more than expected by the increase in available daylight hours.

Our home range estimates of sifaka groups at the logged site are similar to previous estimates of *ca.* 38 ha for these groups from a decade earlier (Powzyk 1997; Wright 1995), despite changes in group composition over this period (Morelli *et al.* 2009). In addition, a 2008 cold-dry season study of groups Unlogged-1 and 2 showed similar home range size and shape to the estimates reported in this article (B. Gerber *unpubl data*; Kotschwar 2010). A separate 2008 cold-dry season study also found group Logged-4, with five individuals, to have a home range size (difference of 5 ha) and shape (Bannar-Martin 2009) similar to those of our estimate reported here when the group contained eight individuals. Although a more comprehensive long-term analysis is warranted, such consistency in spatial-use across a decade or more suggests that even with individual turnover and environmental stochasticity, sifaka home range size and boundaries may be stable for long periods of time. If true, changes in group size could cause significant variation in density that may be unrelated to resource availability. One mechanism for long-term home range stability, proposed by Isbell (2004), is that targeted aggression and subsequent dispersal of females may curb increasing group size and not increase resource competition due to a fixed home range size. However, for sifakas living in the logged forest, dispersal appears to be similar between sexes and largely driven by mate availability (Morelli *et al.* 2009). Alternatively, home range stability may reflect stability of resources, the advantage of familiarity with those resources, and the costs of expanding or moving due to neighboring groups.

The most meaningful difference between primate groups living in forests of different resource availability may have less to do with the total amount of area they use on a daily or annual basis than with how they distribute their use within their range (Ostro *et al.* 1999). At both sites, sifaka groups exhibited a strong nonuniform distribution of use within their home range. Site fidelity between seasons was higher for groups living in the unlogged forest, suggesting groups may maintain smaller home ranges owing to adequate yearly resources in the same patch of forest. In contrast, seasonal resources may not be as abundant within the same area at the logged forest, which may explain why logged forest sifakas generally had a larger number of core areas than sifakas living in unlogged forest. These core areas in the logged site were generally smaller in size than those in the unlogged site, leading to the lack of difference in total core area between sites. This provides additional support that quality resources in the logged areas are more diffuse, thus the need for larger home ranges.

Across seasons, regardless of forest, sifakas appear to concentrate their activity within different parts of their annual range, while generally maintaining the same overall home range. The very small home range overlap observed in this study suggests that sifakas may maintain spatial structuring with few intergroup encounters, thus minimizing conflict; home range boundaries may thus be maintained by scent-marking (Pochron *et al.* 2005). Such low home range overlap appears unique for a relatively large mammal, as other mammals of similar body size have been predicted to have exclusivity to only *ca.* 40% of their home range (Jetz *et al.* 2004). Among primates, such low home range overlap also appears unusual, as this is more likely to occur with species whose diet is *ca.* only 30% leaves (Grant *et al.* 1992); the annual diet of our focal individuals in 2003 was 49% leaves in the unlogged forest and 66% in the logged forest (Arrigo-Nelson 2006). The consequence of such spatial exclusivity may be a limitation on sifaka population density.

Primates with low reproduction, low ecological flexibility, or a narrow niche space, such as frugivores, are less tolerant to habitat disturbances that reduce resource availability (Cowlishaw *et al.* 2009; Johns and Skorupa 1987). Despite the low fecundity of our focal species (Dunham *et al.* 2008), sifaka population density does not appear to differ between logged and unlogged rain forest sites in this study. In recent years, there have been several predation events that have likely reduced sifaka density in the logged rain forest site, although these events are unlikely to be due to habitat effects on the primates. There is also some suggestion that average intrinsic rate of population growth is similar in the logged and unlogged sites (Dunham *et al.* 2008). However, there is also evidence that female sifakas living in the logged rain forest can weigh *ca.* 11% less than females in the unlogged rain forest (Arrigo-Nelson 2006). Female body mass is known to affect interbirth interval and infant survival in primates (Lewis and Kappeler 2005; van Schaik and van Noordwijk 1985), which suggests potential differences in population viability of sifakas between the rain forest sites if a lower fecundity was not compensated by an increase in survival rate. Even given a lack of density differences between the two sites, it is important to better understand all components of population dynamics, including immigration/emigration and birth/death rates, before concluding that logging does or does not have an effect on sifakas at the population level.

Similar densities of sifakas in logged and unlogged areas of the southeastern rain forest, and the possible energy intake-maximizing at the home range level and loss-minimizing strategy at the daily movement level used by sifaka groups in degraded areas, provide encouraging evidence that sifakas are able to persist in and adapt to lower resource quality habitats. Given the potential variability in sifaka resources between years (Wright *et al.* 2005), a thorough study that tracks both resource availability and the spatial patterns of sifakas across multiple years is needed. Further examination of changing seasonal core areas within group home ranges for this and other primate species threatened by human habitat disturbance, with particular attention to differences in plant species composition and phenology, may provide deeper insight to the resources essential to persistence in degraded habitats. This information will be useful in broadening conservation efforts to include partially degraded forests and investigating forest restoration goals that will enable primate population reestablishment in previously cleared and heavily degraded areas.

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