

Seasonally Consistent Small Home Range and Long Ranging Distance in *Presbytis rubicunda* in Danum Valley, Borneo

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Abstract Seasonal fluctuation in food availability is a universal problem for wild animals. One common response to dietary changes is to modify ranging patterns. We studied the ranging pattern of one group (8–12 individuals) of red leaf monkeys (*Presbytis rubicunda*) in the lowland dipterocarp forest of Danum Valley, Borneo from December 2006 to December 2008. The seasonal availability of fruits varies significantly in this forest because of mast fruiting. We tested the hypothesis that changes in ranging pattern are linked with seasonal changes in diet in this species. We recorded activity, foods eaten, and location every 10 min from around 06:00 until 16:00 h, 5–10 days/mo. The home range size was 21.4 ha over the 25-mo study (95% kernel contour). There were no statistically significant relationships between feeding times on the four major nonexclusive dietary components (all species of seeds, all species of young leaves, young leaves of *Spatholobus macropterus*, and other species of young leaves) and either the home range (95% kernel contour) or the core area (50% kernel contour). The areas used in the seed-eating and non-seed-eating seasons overlapped to a large extent. The daily path length was 1160 ± 340 m (mean \pm SD, range: 550–2140 m). Neither daily path length nor monthly mean travel rate was significantly related to feeding time on any of the four major dietary components. The group's ranging patterns may be related to the unusual fallback strategy of this population, which depends on the young leaves of an abundant liana (*S. macropterus*), which are available in small patches. The monkeys need only a small home range because of the high abundance

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of these leaves. However, they range a relatively long distance because the patches of *S. macropterus* are easily depleted; thus the ranging distance does not decrease in non-seed-eating periods.

Keywords Colobus monkey · Daily path length · Home range · Mast fruiting · *Spatholobus macropterus*

Introduction

Animals cope with seasonal fluctuations in food availability in various ways (Hanya *et al.* 2013; van Schaik *et al.* 1993). For example, many primates change their diet to lower quality but consistently available foods, such as leaves, in response to a decrease in their preferred foods (Hemingway and Bynum 2005; Tsuji *et al.* 2013). Primates may also modify their home range to use different habitats in response to seasonal patterns in food availability (Buij *et al.* 2002; Jose-Dominguez *et al.* 2015). Although ranging patterns are key to understanding primate responses to seasonality in food availability, the relationships among the seasonality of food availability, diet, and ranging patterns are not straightforward. For example, preferred high-quality foods are usually found only in a limited space, so some primates move a long distance to secure such high-quality foods but range less when they eat abundant low-quality foods (Agetsuma 1995; Agostini *et al.* 2010; Hill and Agetsuma 1995; Milton 1981). Many studies report a positive correlation between fruit-feeding and ranging distance (Bennett 1986; Campera *et al.* 2014; Jose-Dominguez *et al.* 2015; O'Brien and Kinnaird 1997). In contrast, the daily path length of guerezas (*Colobus guereza*) did not correlate with their diet, although their main food changes seasonally from leaves to fruits (Fashing 2001a, b). Similarly, ranging patterns by Indo-Chinese gray langurs (*Trachypitecus crepusculus*) do not vary with seasonal changes in diet (Fan *et al.* 2015). Even where changes in diet and ranging patterns are linked, the direction of association can vary among populations or species. For example, hoolock gibbons (*Hoolock leuconedys*) in Gaoligongshan, China decrease their ranging distance when fruit becomes scarce (Zhang *et al.* 2014), but Francois' langurs (*Trachypitecus francoisi*) in Fusui, China increase their ranging distance when fruit and young leaves are scarce, and eat many different species of plant (Zhou *et al.* 2007). Blue-eyed black lemurs (*Eulemur flavifrons*) enlarge their home range when fruit availability decreases (Volampeno *et al.* 2011), but the home range of Japanese macaques is the largest in fruit-rich autumn to accumulate fat to survive winter (Hanya *et al.* 2006). These examples of variable responses in the ranging patterns to dietary changes indicate that a deep understanding of the feeding strategy of a species and the characteristics of its habitat is necessary to explain the ranging patterns of a primate species.

The lowland dipterocarp forest of Southeast Asia is particularly interesting for investigating the habitat characteristics of animal ranging patterns owing to the pronounced seasonality in fruiting phenology. In this type of forest, general flowering and subsequent mast fruiting events occur at unpredictable and multiyear intervals, when trees of Dipterocarpaceae and other families bear fruits simultaneously. Fruit production outside the mast fruiting period is lower than the African and American tropics (Sakai 2002; Wich and van Schaik 2000). The severe seasonality of fruit availability affects the diet and nutritional status of the animals living there (Hanya and Bernard

2012, 2013; Kanamori *et al.* 2010; Wong *et al.* 2005), but few studies have investigated the effects of this on primate ranging patterns.

Red leaf monkeys (*Presbytis rubicunda*, also called red langurs), in the lowland dipterocarp forest of Danum Valley, Borneo, have an unusual fallback strategy that makes them a particularly interesting subjects for the study of ranging patterns. In response to increased fruiting, they increase seed consumption. Outside of the fruiting period, they rely on the young leaves of a single species of a legume liana, *Spatholobus macropterus*, as a fallback food (Hanya and Bernard 2012). This species has high available protein content and high stem density (Hanya and Bernard 2015).

We tested the hypothesis that seasonal changes in the diet are linked with changes in the ranging patterns (home range size and ranging distance) in a population of red leaf monkeys experiencing pronounced variation in the availability of their preferred foods (seeds) because of mast fruiting. We investigated the relationship between ranging patterns and four major nonexclusive food categories (seeds, young leaves, young leaves of *Spatholobus macropterus*, and young leaves other than those of *S. macropterus*). In particular, we predict that ranging distance and home range size correlate positively with seed consumption because seed availability is more limited in space than their fallback foods (young leaves of *S. macropterus*) (Hanya and Bernard 2015). Alternatively, if home range size and daily path length are not correlated with seed consumption, red leaf monkeys may expand their home range when seed consumption increases. We have no predictions for the other food categories.

Methods

Study Site

We conducted our study in a primary lowland dipterocarp forest around Danum Valley Field Centre (4°57'N, 117°48'E, 300 m above sea level) in the Danum Valley Conservation Area (438 km²) in eastern Sabah, northern Borneo. Hanya and Bernard (2012, 2013) describe the details of the study site.

Behavioral Observation

We observed one habituated group of red leaf monkeys with 8–12 individuals from around 06:00 until 16:00 h, 5–10 days/mo from December 2006 to December 2008, during which one clear peak of fruiting was observed in May–October 2007. We recorded their activity and foods eaten by scan sampling every 10 min. Over the 25 mo of the study period, their diet was composed of seeds (including whole-fruit feeding, 50% of the feeding time), young leaves (46%), and other foods (flowers, bark, and pith, 4% in total). When we followed the group, we recorded its location every 10 min by a GPS device (GPSmap 60CSx). The total observation time was 1141 h, and the monthly observation time was 16–87 h (mean: 46 h). Observation times for the first 2 mo were short (27 and 16 h) because we were not accustomed to following the group. Monthly observation time decreased after May 2007, as we also started following other species of primates. The number of location points was 6578, and the monthly number was 103–516 (mean: 263).

Analysis

We determined home range size using a fixed kernel density method with an *ad hoc* estimation of smoothing factor h (Schuler *et al.* 2014). We regarded 95% kernel density contours as the home range and 50% as the core area. For comparative purposes, we also report the minimum convex polygon (MCP) for the entire period.

We examined the minimum number of locations required to estimate the home range using data from the month with the greatest number of locations (April 2007, $N = 516$). The home range reached an asymptote at 450 locations (Fig. 1). As the number of locations was <450 for most months, we used 2 mo as the minimum unit of analysis to estimate home range. As the number of locations was small for the first two and the last months, we discarded the data for those 3 mo, leaving eleven 2-mo periods, beginning with February–March 2007 and ending with October–November 2008, with 416–796 location points per 2-mo period (mean: 555).

We calculated a “similarity index” defined as $D = \sum S_i$ (Krebs 1999), where D is the similarity index and S_i is the percentage of each food category (seeds, young leaves of *Spatholobus macropterus*, and young leaves other than those of *S. macropterus*) common to 2 mo. The similarity index between two consecutive months was significantly larger than that of nonconsecutive months ($F = 8.01$, $t = 2.83$, $df = 460$, $P = 0.0049$), indicating that the diet composition in each month resembled that of previous or subsequent months.

To test whether the group used different areas when they eat different foods, we designated each 2-mo period as either a seed-eating or non-seed-eating period. Seed-eating periods included February/March 2007, June/July 2007, August/September 2007, October/November 2007, and August/September 2008, when seed-eating accounted for 64–82% of the total feeding time (five 2-mo periods). In non-seed-eating periods, seed eating accounted for only 23–39% of the feeding time (six 2-mo periods).

We calculated home range overlap between all possible combinations of 2-mo periods ($N = 55$). These data were not statistically independent of each other because home range data from each period was compared to that of many other periods. To avoid statistical problems associated with nonindependence, we performed an analysis

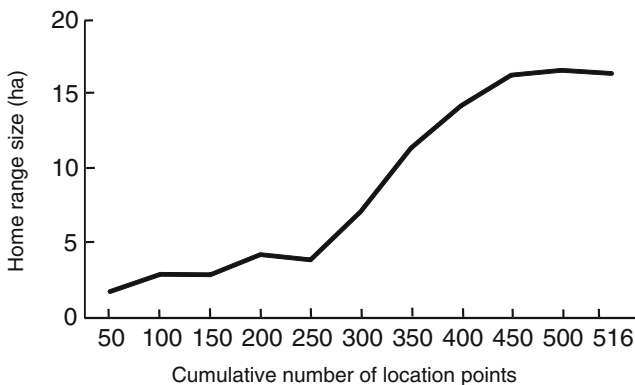


Fig. 1 Relationship between cumulative number of location points and home range area in red leaf monkeys in Danum Valley using data for April 2007.

of similarity (ANOSIM) test using the *anosim* function of *vegan* in R v.3.2.1. ANOSIM examines whether there is a significant difference between groups of sampling units based on similarity/dissimilarity within and between the sampling units (Clarke 1993). We examined whether or not home range overlap between like periods was larger than that between unlike periods. We set the number of permutations used in the analysis at 999.

We calculated the ranging distance as the sum of the distance between the location points recorded every 10 min. When the distance was <20 m, we assigned it to 0 m because the group was likely to have remained in the crown of the same tree, whose maximum width was 20 m. We evaluated ranging distance in two ways: daily path length and monthly mean travel rate. We calculated the daily path length (m/day) using data for days when we followed the group for >7 h ($N = 86$ days). We assumed that the group continued to range at the observed rate for 12 h. This may over- or underestimate “true” daily path length, as the ranging distance for 06:00–08:00 h was significantly longer than for later 2-h periods during the day (using a 10-min ranging distance as the unit of analysis: $F = 5.82$, $df = 4330$, $P < 0.001$). However, the proportion of early morning data to the total ranging distance data was not significantly different among the 25 study months ($\chi^2 = 28.7$, $P = 0.23$). Therefore, it is unlikely that we over- or underestimated the daily path length in particular months. We calculated the monthly mean travel rate (m/h) using all data. Because ranging distance is affected by the time of day, we divided the data into four 2-h periods (06:00–08:00, 08:00–10:00, 10:00–12:00, 14:00–16:00) and divided the total observed distance that the group traveled during the 2-h period in the month by the observation time for that 2-h period. We used the mean of the values for the four 2-h periods for each month ($N = 25$ mo).

We examined the effect of diet on ranging using general linear models (GLMs), with the proportion of feeding time on the four main food categories relative to the total feeding time (seed, including whole fruit-feeding, young leaves, young leaves of *Spatholobus macropterus*, and young leaves other than those of *S. macropterus*) as independent factors and ranging parameters (home range size, core area size, monthly mean travel rate, and daily path length) as dependent variables. We examined the effects of the four dietary parameters in different models because they correlate with each other. The unit of analysis was day for the daily path length, month for the mean travel rate, and 2 mo for the home range and core area size. For each analysis, we used the same units as the ranging parameters for the corresponding dietary data.

We analyzed location data using QGIS 2.4.0 (© 1989, 1991 Free Software Foundation, Inc.), R 3.2.1; (© The R Foundation for Statistical Computing) and Kashmir 3D 8.0.9 (© Tomohiko Sugimoto). We used R 3.2.1 for all statistical analyses. We set the α level at $P < 0.05$.

Ethical Note

The research complied with the “Guidelines for field research on non-human primates” of the Primate Research Institute, Kyoto University. The research adhered to the legal requirements of Malaysia and Japan.

Results

Home Range

The home range of the study group for the entire study period was 21.4 ha by 95% kernel contour (Electronic Supplementary Material [ESM] Fig. S1) and 32.6 ha by MCP.

We found no effect of feeding time on seeds, young leaves, the young leaves of *S. macropterus*, and young leaves other than those of *Spatholobus macropterus* on the 2-mo home range or core area sizes (Table I; ESM Figs. S2 and S3).

The red leaf monkeys used similar areas in the seed-eating and non-seed-eating seasons. The mean overlap in home range between two different 2-mo periods was 15.0 ha (± 1.81 SD, range 11.5–18.8 ha), which was 78% of the mean 2-mo home size range (19.1 ± 2.93 ha). Home range overlap between like periods, e.g., seed-eating and seed-eating periods, was not significantly different from that between unlike periods, i.e., seed-eating and non-seed-eating periods (ANOSIM test, $R = -0.013$, $P = 0.61$).

Ranging Distance

The daily path length was 1160 ± 340 m (range: 550–2140 m) and was not significantly affected by diet (Table I; ESM Fig. S4). Similarly, the monthly mean travel rate (m/h) was not significantly affected by feeding time on the four major food categories for that month (Table I; ESM Fig. S5).

Table I Results of GLM analysis of the effect of diet of red leaf monkeys in Danum Valley on home range size and ranging distance from December 2006 to December 2008

Independent variable	Response variable	<i>F</i>	df	<i>t</i>	<i>P</i>
Home range (95% kernel) <i>N</i> = 11	Seed feeding time	1.32	9	7.15	0.28
	Young leaf feeding time	1.75	9	1.32	0.22
	<i>S. macropterus</i> young leaf feeding time	0.84	9	0.92	0.38
	Non- <i>S. macropterus</i> young leaf feeding time	0.02	9	0.13	0.90
Core area (50% kernel) <i>N</i> = 11	Seed feeding time	0.19	9	0.44	0.67
	Young leaf feeding time	0.31	9	0.56	0.59
	<i>S. macropterus</i> young leaf feeding time	0.32	9	0.57	0.58
	Non- <i>S. macropterus</i> young leaf feeding time	0.02	9	0.13	0.90
Daily path length <i>N</i> = 86	Seed feeding time	0.05	83	0.23	0.82
	Young leaf feeding time	0.07	83	0.26	0.80
	<i>S. macropterus</i> young leaf feeding time	1.19	83	1.09	0.30
	Non- <i>S. macropterus</i> young leaf feeding time	0.67	83	0.82	0.42
Monthly mean travel rate <i>N</i> = 23	Seed feeding time	0.03	23	0.18	0.86
	Young leaf feeding time	0.21	23	0.46	0.65
	<i>S. macropterus</i> young leaf feeding time	1.26	23	1.12	0.27
	Non- <i>S. macropterus</i> young leaf feeding time	0.50	23	0.71	0.49

Discussion

Small Home Range and Long Daily Path Length

The ranging patterns of the red leaf monkeys in Danum Valley were characterized by a small home range size (21 ha) and a long daily path length (1160 m/day), with little seasonal variation. Rigorous comparison is difficult owing to the differences in the methods used to estimate home range, but only 7 of 33 populations belonging to 22 different species of colobines have smaller home ranges than those in this study (Table II). Some colobines with particularly small home ranges (<10 ha) live in modified habitats, such as forest fragments (Harris and Chapman 2007) or plantations (Kool 1993). Our results suggest that the home range of red leaf monkeys in Danum Valley is one of the smallest for colobines living without considerable artificial habitat alterations. It is smaller than other populations of this species: 70–84 ha in the lowland dipterocarp forest of Sepilok (Davies 1991) and 33–99 ha in the peat swamp forest of Tanjung Puting (Supriatna *et al.* 1986), 108 ha in the peat swamp forest of Sabangau (Ehlers Smith *et al.* 2013). We should be cautious in generalizing these findings because we have data for only one group. However, this small home range is unlikely to be exceptional for this population owing to the high group density in this area (7.7 groups/ha; Hanya and Bernard).

Although it has one of the smallest home ranges, the daily path length of our study group was one of the longest among 33 colobus populations of 23 different species (Table I). Colobus monkeys with a ranging distance longer than 1000 m/day live in high mountains (Bleisch *et al.* 1993; Fan *et al.* 2015; Grueter *et al.* 2008; Kirkpatrick *et al.* 1998; Sayers and Norconk 2008). Although they do not live in such habitats, red leaf monkeys in Sabangau (Ehlers Smith *et al.* 2013) and Danum Valley (this study) have equally long ranging distances. Ehlers Smith *et al.* (2013) suggest that long ranging distances in Sabangau are related to heavy and seasonally consistent reliance on seeds. However, this is not the case for Danum Valley, because seed eating was seasonally variable (Hanya and Bernard 2013), but the monkeys maintained a long daily path length irrespective of season.

Based on a review of 33 species of nonhuman primates, Mitani and Rodman (1979) found that territorial species have a longer daily path length in relation to home range size than nonterritorial species. This suggests that the small home range and long ranging distance of red leaf monkeys in Danum Valley may be related to territorial defense against neighboring groups. We observed other groups or heard vocalizations only on the periphery of the home range of the study group, suggesting that the home range was mutually exclusive. However, we never observed an intergroup encounter and our study group did not respond actively to vocalizations by monkeys in other groups. Thus, territorial defense seems to be an unlikely explanation for the long ranging distance.

The dietary characteristics of our study population may explain its ranging pattern. Red leaf monkeys in Danum Valley rely on the young leaves of a single species of liana, *Spatholobus macropterus*, as a fallback food (Hanya and Bernard 2012). This species has high available protein content (Hanya and Bernard 2012, 2015). The flushing stem of this species is quite abundant (75/ha; Hanya and Bernard 2015). However, most of the patches are small and few monkeys can feed in the same patch.

Table II Home range size and day range length of colobus monkeys

Species	Site	Region/ country	Habitat	Number of individuals in the study group(s)	Number of groups studied	Home range (ha)	Estimation method	Day range length (m)	References
<i>Presbytis comata</i>	Kamojang	Java	Montane tropical	6–7	3	35–40	Grid	500	Ruhayat (1983)
<i>P. comata</i>	Patenggang	Java	Montane tropical	10	1	14	Grid		Ruhayat (1983)
<i>P. femoralis</i>	Kuala Lompat	Malay Peninsu- la	Dipterocarp	16	3	14–31	Grid	682	Bennett (1986)
<i>P. hosei</i>	Lipad	Borneo	Dipterocarp		Unknown	35		740	Mitchell (1994) cited by Ehlers Smith <i>et al.</i> (2013)
<i>P. potenziani</i>	Betumonga	Mentawai	Dipterocarp	2–5	5	25–40		540	Fuentes (1996)
<i>P. rubicunda</i>	Danum Valley	Borneo	Dipterocarp	8–12	1	21	Kernel	1160	This study
<i>P. rubicunda</i>	Sabangau	Borneo	Peat Swamp	5–7	1	33	MCP		
<i>P. rubicunda</i>	Septlok	Borneo	Dipterocarp	6	1	108	Kernel	1645	Ehlers Smith <i>et al.</i> (2013)
<i>P. rubicunda</i>	Tanjung Puting	Borneo	Peat Swamp	3–8	9	134	MCP		Davies (1991)
<i>Trachypithecus auratus</i>	Pangandaran	Java	Plantation	13–14	2	70–84			Supriatna <i>et al.</i> (1986)
<i>T. crepusculus</i>	Wuliangshan	China	Semi-humid and mid-mountain	81–90	1	2.5–8			Kool (1993)
<i>T. francoisi</i>	Fusui	China	Limestone hill	6	1	344	Kernel	1101	Fan <i>et al.</i> (2015)
<i>T. francoisi</i>	Nonggang	China	Limestone hill	11	1	376	MCP		
						19	Grid	438	Zhou <i>et al.</i> (2007)
						69	Grid	541	Zhou <i>et al.</i> (2007)

Table II (continued)

Species	Site	Region/ country	Habitat	Number of individuals in the study group(s)	Number of groups studied	Home range (ha)	Estimation method	Day range length (m)	References
<i>T. geei</i>	Goalpara	India		10–20	8			750	Mukherjee and Saha (1974)
<i>T. johnii</i>	Kakachi	India	Evergreen	16–18	1	24			Oates <i>et al.</i> (1980)
<i>T. leucocephalus</i>	Fusui	China	Limestone hill	6–14	4	28–48	MCP		Li and Rogers (2005)
<i>T. obscurus</i>	Kuala Lompat	Malay Peninsula	Dipterocarpaceae		Unknown	17–33		560	Curtin (1976), (1980) cited by Ehlers Smith <i>et al.</i> (2013)
<i>T. pileatus</i>	Madhupur	Bangladesh	Moist deciduous	12	5	23		450	Islam and Husain (1982), Stanford (1991)
<i>Nasalis larvatus</i>	Kinabatangan	Borneo	Riverine	16	1	138	Grid	799	Matsuda <i>et al.</i> (2009)
<i>N. larvatus</i>	Samunsam	Borneo	Mangrove	16	8	770		485	Bennett and Sebastian (1988)
<i>Rhinopithecus bieti</i>	Samage	China	Subtropical to temperate	410	1	2475	Grid	1620	Grueter <i>et al.</i> (2008)
<i>R. bieti</i>	Wuyapiya	China	Conifer	175	1	2500	Grid	1310	Kirkpatrick <i>et al.</i> (1998)
<i>R. brelichi</i>	Fanjingshan	China	Temperate	436	1	3500		1290	Bleisch <i>et al.</i> (1993)
<i>Semnopithecus dassumieri</i>	Orcha	India	Moist deciduous		Unknown	375			Dolhinow (1972) cited by Ehlers Smith <i>et al.</i> (2013)
<i>S. entellus</i>	Kanha	India	Moist deciduous	20	1	75	Grid		Newton (1992)
<i>S. entellus</i>	Langtang	Nepal	Subtropical	30	1	1275		1500	Sayers and Norconk (2008)
<i>S. schistaceus</i>	Junbesi	Nepal	Conifer/ broadleaf		Unknown				Curtin (1975) cited by Ehlers Smith <i>et al.</i> (2013)
	Nyungwe	Rwanda	Mixed tropical	300	1	2440	Kernel	1700	Fashing <i>et al.</i> (2007)

Table II (continued)

Species	Site	Region/ country	Habitat	Number of individuals in the study group(s)	Number of groups studied	Home range (ha)	Estimation method	Day range length (m)	References
<i>Colobus angolensis</i>						2070	MCP		
<i>C. guereza</i>	Kanyawara	Uganda	Moist high	9	1	32	Grid	535	Oates (1977)
<i>C. guereza</i>	Kanyawara	Uganda	Moist high		8	5–12	Kernel		Harris and Chapman (2007)
						7–33	MCP		
<i>C. guereza</i>	Kakamega	Kenya		7–21	5	12–20	Grid	434–708	Fashing (2001a)
<i>C. satanas</i>	Douala-Edea	Cameroon		16	1	60	Grid	458	McKey <i>et al.</i> (1981)
<i>C. satanas</i>	Foret des Abelles	Gabon	Mixed tropical	16–19	3	573	Grid	510	Fleury and Gautier-Hion (1999)

Adapted from Ehlers Smith *et al.* (2013).

The number of individuals cofeeding in *S. macropterus* feeding events was smaller than in seed-feeding events (Hanya and Bernard 2015) and individual patches were small and depleted quickly. As a consequence, red leaf monkeys in Danum Valley may need to move relatively longer distances to visit many patches of *S. macropterus*. This is the situation predicted by the ecological constraints model (Wrangham *et al.* 1993). More rigorous tests are necessary to assess the potential for scramble competition over patches of *S. macropterus* by comparing different-sized groups (Kurihara and Hanya 2015). We predict that smaller groups will have a shorter daily path length.

We suggest that the small home range of red leaf monkeys is related to the abundance of *Spatholobus macropterus* and their long daily path length is related to the quick depletion of the food patches. Although these two explanations seem contradictory, they are compatible if the plant regenerates (flushes) quickly after feeding by animals (Ito and Takatsuki 2005). Data are needed on feeding pressure from the monkeys and the flushing behavior to test this.

Seasonally Consistent Ranging Pattern

The other important characteristic of this population is the lack of seasonality in its ranging patterns, in spite of the strong seasonality due to mast fruiting. Our hypothesis that seasonal changes in the diet are linked with changes in the ranging patterns was not supported; the monkeys did not increase their home range size or ranging distance and they did not shift their home range in response to increased fruit availability. Unlike the Sabangau population (Ehlers Smith *et al.* 2013), this was not related to a seasonally invariable diet. Seasonal variation in the diet was quite large in our study site; seed-feeding time varied as much as 18 times over the study period (Hanya and Bernard 2013). Because fallback foods are usually abundant, monkeys may not need to move around to find patches (Hanya and Chapman 2013). However, in this population, individuals move a long distance to eat *Spatholobus macropterus*. More monkeys stay in seed feeding patches than in young leaf feeding patches, and they stay for a longer time (Hanya and Bernard 2015). As a consequence, the number of seed feeding patches the monkeys visit is smaller than the number of young leaf feeding patches (Hanya and Bernard 2015). The daily path length is approximately the product of the number of patches and the interpatch distance. Thus, the effect of the short interpatch distance when eating young leaves of *S. macropterus* may have been canceled out by the larger number of patches visited in one day.

The size of the home range did not differ with diet, and the overlap was large (78%) between two different 2-mo periods. As a proximate factor, monkeys may not be able to enlarge their home range owing to the presence of neighboring groups. The group density in this area seems high (Hanya and Bernard *unpubl. data*), but we cannot test this possibility because of the lack of obvious intergroup interactions. As an ultimate factor, we can explain seasonal variation in home range size as a response to fluctuation in the availability of main foods (Hanya and Chapman 2013). In Japanese macaques, for example, the home range is large when they eat fruits, which are limited in abundance, and small when they eat abundant leaves (Hanya *et al.* 2006). This example suggests that monkeys enlarge their home range only when they are likely to exhaust its resources. As a result of forestomach fermentation (Lambert 1998), red leaf monkeys can probably live on leaves alone. In contrast, Japanese macaques cannot live solely on

leaves for an extended period (Hanya 2004; Nakagawa *et al.* 1996); they survive during the fruit-scarce periods by metabolizing the fat accumulated in fruit-rich seasons (Hanya *et al.* 2004). The home range size of Japanese macaques varies seasonally because the area they need is large in fruit-rich seasons and small in fruit-scarce ones. Unlike fruits for Japanese macaques, seeds may not be indispensable for the survival of red leaf monkeys, so they may not need to enlarge their home range to secure enough seed resources in fruit-rich seasons.

In conclusion, the ranging of red leaf monkeys in Danum Valley is characterized by small home range size and long daily path lengths, and does not correlate with seasonal variation in diet. We explain this pattern by the unusual fallback strategy of this population that depends on the abundant young leaves of a liana (*Spatholobus macropterus*), which are available in small patches. The monkeys need only a small home range because of the high abundance of this liana, but they range a relatively long distance because patches are easily depleted. Even in seasons when their diet changes from seeds to young leaves, which requires only short interpatch movement, the ranging distance does not decrease because they visit many patches of *S. macropterus*.

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References

- Agetsuma, N. (1995). Foraging strategies of Yakushima macaques (*Macaca fuscata yakui*). *International Journal of Primatology*, 16(4), 595–609.
- Agostini, I., Holzmann, I., & Di Bitetti, M. S. (2010). Ranging patterns of two syntopic howler monkey species (*Alouatta guariba* and *A. caraya*) in northeastern Argentina. *International Journal of Primatology*, 31(3), 363–381.
- Bennett, E. L. (1986). Environmental correlates of ranging behavior in the banded langur, *Presbytis melalophos*. *Folia Primatologica*, 47(1), 26–38.
- Bennett, E. L., & Sebastian, A. C. (1988). Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in Sarawak. *International Journal of Primatology*, 9(3), 233–255.
- Bleisch, W., Song, C. A., Ren, X. D., & Xie, J. H. (1993). Preliminary results from a field study of wild Guizhou snub-nosed monkeys (*Rhinopithecus brelichii*). *Folia Primatologica*, 60(1–2), 72–82.
- Buij, R., Wich, S. A., Lubis, A. H., & Sterck, E. H. M. (2002). Seasonal movements in the Sumatran orangutan (*Pongo pygmaeus abelii*) and consequences for conservation. *Biological Conservation*, 107(1), 83–87.
- Campera, M., Serra, V., Balestri, M., Barresi, M., Ravaolaha, M., Randriatafika, F., & Donati, G. (2014). Effects of habitat quality and seasonality on ranging patterns of collared brown lemur (*Eulemur collaris*) in littoral forest fragments. *International Journal of Primatology*, 35(5), 957–975.
- Clarke, K. R. (1993). Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18(1), 117–143.

- Davies, G. (1991). Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of northern Borneo. *International Journal of Primatology*, 12(2), 119–144.
- Ehlers Smith, D. A., Ehlers Smith, Y. C., & Cheyne, S. M. (2013). Home-range use and activity patterns of the red langur (*Presbytis rubicunda*) in Sabangau tropical peat-swamp forest, central Kalimantan, Indonesian Borneo. *International Journal of Primatology*, 34(5), 957–972.
- Fan, P. F., Garber, P., Chi, M., Ren, G. P., Liu, C. M., Chen, X. Y., & Yang, J. X. (2015). High dietary diversity supports large group size in Indo-Chinese gray langurs in Wuliangshan, Yunnan, China. *American Journal of Primatology*, 77(5), 479–491.
- Fashing, P. J. (2001a). Activity and ranging patterns of guerezas in the Kakamega Forest: intergroup variation and implications for intragroup feeding competition. *International Journal of Primatology*, 22(4), 549–577.
- Fashing, P. J. (2001b). Feeding ecology of guerezas in the Kakamega Forest, Kenya: the importance of Moraceae fruit in their diet. *International Journal of Primatology*, 22(4), 579–609.
- Fashing, P. J., Dierenfeld, E. S., & Mowry, C. B. (2007). Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of *Colobus guereza* in Kakamega Forest, Kenya. *International Journal of Primatology*, 28(3), 673–703.
- Fleury, M. C., & Gautier-Hion, A. (1999). Seminomadic ranging in a population of black colobus (*Colobus satanas*) in Gabon and its ecological correlates. *International Journal of Primatology*, 20(4), 491–509.
- Fuentes, A. (1996). Feeding and ranging in the Mentawai island langur (*Presbytis potenziani*). *International Journal of Primatology*, 17(4), 525–548.
- Grueter, C. C., Li, D. Y., van Schaik, C. P., Ren, B. P., Long, Y. C., & Wei, F. W. (2008). Ranging of *Rhinopithecus bieti* in the Samage Forest, China. I. Characteristics of range use. *International Journal of Primatology*, 29(5), 1121–1145.
- Hanya, G. (2004). Diet of a Japanese macaque troop in the coniferous forest of Yakushima. *International Journal of Primatology*, 25(1), 55–71.
- Hanya, G., & Bernard, H. (2012). Fallback foods of red leaf monkeys (*Presbytis rubicunda*) in Danum Valley, Borneo. *International Journal of Primatology*, 33(2), 322–337.
- Hanya, G., & Bernard, H. (2013). Functional response to fruiting seasonality by a primate seed predator, red leaf monkey (*Presbytis rubicunda*). *Tropical Ecology*, 54(3), 383–395.
- Hanya, G., & Bernard, H. (2015). Different roles of seeds and young leaves in the diet of red leaf monkeys (*Presbytis rubicunda*): comparisons of availability, nutritional properties, and associated feeding behavior. *International Journal of Primatology*, 36(1), 177–193.
- Hanya, G., & Chapman, C. A. (2013). Linking feeding ecology and population abundance: a review of food resource limitation on primates. *Ecological Research*, 28(2), 183–190.
- Hanya, G., Yoshihiro, S., Zamma, K., Matsubara, H., Ohtake, M., Kubo, R., Noma, N., Agetsuma, N., & Takahata, Y. (2004). Environmental determinants of the altitudinal variations in relative group densities of Japanese macaques on Yakushima. *Ecological Research*, 19(5), 485–493.
- Hanya, G., Kiyono, M., Yamada, A., Suzuki, K., Furukawa, M., Yoshida, Y., & Chijiwa, A. (2006). Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. *Primates*, 47(3), 275–278.
- Hanya, G., Tsuji, Y., & Grueter, C. C. (2013). Fruiting and flushing phenology in Asian tropical and temperate forests: implications for primate ecology. *Primates*, 54(2), 101–110.
- Harris, T. R., & Chapman, C. A. (2007). Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates*, 48(3), 208–221.
- Hemingway, C., & Bynum, N. (2005). The influence of seasonality on primate diet and ranging. In D. K. Brockman & C. P. van Schaik (Eds.), *Seasonality in primates: Studies of living and extinct human and non-human primates* (pp. 57–104). Cambridge: Cambridge University Press.
- Hill, D. A., & Agetsuma, N. (1995). Supra-annual variation in the influence of *Myrica rubra* fruit on the behavior of a troop of Japanese macaques in Yakushima. *American Journal of Primatology*, 35(3), 241–250.
- Islam, M. A., & Husain, K. Z. (1982). A preliminary study on the ecology of the capped langur. *Folia Primatologica*, 39(1–2), 145–159.
- Ito, T. Y., & Takatsuki, S. (2005). Relationship between a high density of sika deer and productivity of the short-grass (*Zoysia japonica*) community: a case study on Kinkazan Island, northern Japan. *Ecological Research*, 20(5), 573–579.
- Jose-Dominguez, J. M., Savini, T., & Asensio, N. (2015). Ranging and site fidelity in northern pigtailed macaques (*Macaca leonina*) over different temporal scales. *American Journal of Primatology*, 77(8), 841–853.

- Kanamori, T., Kuze, N., Bernard, H., Malim, T. P., & Kohshima, S. (2010). Feeding ecology of Bornean orangutans (*Pongo pygmaeus morio*) in Danum Valley, Sabah, Malaysia: a 3-year record including two mast fruitings. *American Journal of Primatology*, 72(9), 820–840.
- Kirkpatrick, R. C., Long, Y. C., Zhong, T., & Xiao, L. (1998). Social organization and range use in the Yunnan snub-nosed monkey *Rhinopithecus bieti*. *International Journal of Primatology*, 19(1), 13–51.
- Kool, K. M. (1993). The diet and feeding behavior of the silver leaf monkey (*Trachypithecus auratus sondaicus*) in Indonesia. *International Journal of Primatology*, 14(5), 667–700.
- Krebs, C. J. (1999). *Ecological methodology*. San Francisco: Benjamin/Cummings.
- Kurihara, Y., & Hanya, G. (2015). Comparison of feeding behavior between two different-sized groups of Japanese macaques (*Macaca fuscata yakui*). *American Journal of Primatology*, 77(9), 986–1000.
- Lambert, J. E. (1998). Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology*, 7(1), 8–20.
- Li, Z. Y., & Rogers, M. E. (2005). Habitat quality and range use of white-headed langurs in Fusui, China. *Folia Primatologica*, 76(4), 185–195.
- Matsuda, I., Tuuga, A., & Higashi, S. (2009). Ranging behavior of proboscis monkeys in a riverine forest with special reference to ranging in inland forest. *International Journal of Primatology*, 30(2), 313–325.
- McKey, D. B., Gartlan, J. S., Waterman, P. G., & Choo, G. M. (1981). Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biological Journal of the Linnean Society*, 16(2), 115–146.
- Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental-development. *American Anthropologist*, 83(3), 534–548.
- Mitani, J. C., & Rodman, P. S. (1979). Territoriality: relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioral Ecology and Sociobiology*, 5(3), 241–251.
- Mukherjee, R. P., & Saha, S. S. (1974). The golden langurs (*Presbytis geei* Khajuria, 1956) of Assam. *Primates*, 15(4), 327–340.
- Nakagawa, N., Iwamoto, T., Yokota, N., & Soumah, A. G. (1996). Inter-regional and inter-seasonal variations of food quality in Japanese macaques: Constraints of digestive volume and feeding time. In J. E. Fa & D. G. Lindburg (Eds.), *Evolution and ecology of macaque societies* (pp. 207–234). New York: Cambridge University Press.
- Newton, P. (1992). Feeding and ranging patterns of forest hanuman langurs (*Presbytis entellus*). *International Journal of Primatology*, 13(3), 245–285.
- O'Brien, T. G., & Kinnaird, M. F. (1997). Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18(3), 321–351.
- Oates, J. F. (1977). The guereza and its food. In T. H. Clutton-Brock (Ed.), *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes* (pp. 275–321). London: Academic Press.
- Oates, J. F., Waterman, P. G., & Choo, G. M. (1980). Food selection by the south Indian leaf monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia*, 45(1), 45–56.
- Ruhiyat, Y. (1983). Socio-ecological study of *Presbytis aygula* in West Java. *Primates*, 24(3), 344–359.
- Sakai, S. (2002). General flowering in lowland mixed dipterocarp forests of South-east Asia. *Biological Journal of the Linnean Society*, 75(2), 233–247.
- Sayers, K., & Norconk, M. A. (2008). Himalayan *Semnopithecus entellus* at Langtang National Park, Nepal: diet, activity patterns, and resources. *International Journal of Primatology*, 29(2), 509–530.
- Schuler, K. L., Schroeder, G. M., Jenks, J. A., & Kie, J. G. (2014). Ad hoc smoothing parameter performance in kernel estimates of GPS-derived home ranges. *Wildlife Biology*, 20(5), 259–266.
- Stanford, C. B. (1991). The diet of the capped langur (*Presbytis pileata*) in a moist deciduous forest in Bangladesh. *International Journal of Primatology*, 12(3), 199–216.
- Supriatna, J., Manullang, B. O., & Soekara, E. (1986). Group composition, home range, and diet of the maroon leaf monkey (*Presbytis rubicunda*) at Tanjung Puting Reserve, Central Kalimantan, Indonesia. *Primates*, 27(2), 185–190.
- Tsuji, Y., Hanya, G., & Grueter, C. C. (2013). Feeding strategies of primates in temperate and alpine forests: comparison of Asian macaques and colobines. *Primates*, 54(3), 201–215.
- van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, 24, 353–377.
- Volampeno, M. S. N., Masters, J. C., & Downs, C. T. (2011). Home range size in the blue-eyed black lemur (*Eulemur flavifrons*): a comparison between dry and wet seasons. *Mammalian Biology*, 76(2), 157–164.
- Wich, S. A., & van Schaik, C. P. (2000). The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology*, 16, 563–577.

- Wong, S. T., Servheen, C., Ambu, L., & Norhayati, A. (2005). Impacts of fruit production cycles on Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. *Journal of Tropical Ecology*, *21*, 627–639.
- Wrangham, R. W., Gittleman, J. L., & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day range as assays of exploitation competition. *Behavioral Ecology and Sociobiology*, *32*(3), 199–209.
- Zhang, D., Fei, H. L., Yuan, S. D., Sun, W. M., Ni, Q. Y., Cui, L. W., & Fan, P. F. (2014). Ranging behavior of eastern hoolock gibbon (*Hoolock leuconedys*) in a northern montane forest in Gaoligongshan, Yunnan, China. *Primates*, *55*(2), 239–247.
- Zhou, Q. H., Huang, C. M., Li, Y. B., & Cai, X. W. (2007). Ranging behavior of the francois' langur (*Trachypithecus francoisi*) in the Fusui Nature Reserve, China. *Primates*, *48*(4), 320–323.