Cohabitation Study of the Leaf Monkey and Bornean White-Bearded Gibbons in Gunung Palung National Park, West Kalimantan

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Diet and habitat overlaps were studied for the leaf monkey (*Presbytis rubicunda*) and bornean white-bearded gibbons (*Hylobates albibarbis*) in tropical forest of Cabang Panti Research Station (CPRS), Gunung Palung National Park, West Kalimantan. Systematic data on feeding and ranging behaviour were collected from August 2009 up to February 2010 for the three groups of two sympatric primate species that shared two neighbouring patches. Our results showed that seven types of habitat in CPRS were affected to both primates, particularly in plant utilization for feed and the use of vertical space patterns. If the leaf monkeys were present in the same forest patch, the Bornean white-bearded gibbons showed a reduced within-group dispersal and significantly less foraging time in a given forest patch. This might be due to the bornean white-bearded gibbons were more selective in their diet selection. When fruits were scarce, bornean white-bearded gibbons spent most of their foraging time in many types of forest ecosystem, while leaf monkey foraged within one or two types of forest ecosystem. At this period, diet and habitat overlaps between the two species were low. When the availability of fruits increased, leaf monkeys shifted their foraging range and both species became confined to the forest habitat. Consequently, the overlaps of diets and habitats were increased while the peak was at the end of the fruit season.

Key words: Cohabitation, *Presbytis rubicunda*, *Hylobates albibarbis*, sympatric species, CPRS

INTRODUCTION

Cabang Panti Research Station (CPRS) locates in the core zone of Gunung Palung National Park (GPNP). It provides as a special area reserved for research activities, since forest ecosystems at CPRS are home to seven primate species: leaf monkey (*Presbytis rubicunda*), bornean white-bearded gibbons (*Hylobates albibarbis*), orangutan (*Pongo pygmaeus*), proboscis monkey or *bekantan* (*Nasalis larvatus*), long tailed macaque (*Macaca fascicularis*), horsfield's tarsier (*Tarsius bancanus borneanus*) and slow loris (*Nycticebus coucang*). Both leaf monkey and bornean white-bearded gibbons are endemic in Kalimantan and confined to several places in Gunung Palung National Park (Marshall 2004), while the other species are abundant elsewhere, except orangutan and *bekantan*.

The leaf monkey (*P. rubicunda*) is a folivorous primate that generally forages at the high canopy level (Davies 1991). Apart from proboscis monkey (*N. larvatus*) which is folivorous, other primates live sympatric with leaf monkey are largely frugivorous. They rely to a greater extent on foods other than fruits, hence tend to be more evenly distributed in space and time (Snaith & Chapman

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2005, 2007; García & Arroyo 2005). *Presbytis rubicunda* and *H. albibarbis* are widely distributed throughout primarily forest ecosystems that include coastal, lowlands, and 1.500-2.200 m asl montane (Payne 2000). Leaf monkey shows a flexible foraging strategy that enables to exploit food sources in fragmented forest close to human (Supriatna & Hendras 2000). In contrast, *H. albibarbis* generally only live in undisturbed primary forests, but sometimes found in exploited habitat such as logging and forest plantations. Curran *et al.* (2004), Dennis and Colfer (2006) showed a 38 percent loss in lowland forest within GPNP between 1988 and 2002 and >70 percent loss in the 10-km wide buffer zone around the park during the same period.

Leaf monkeys and bornean white-bearded gibbons live in same habitat in CPRS. Both types of primates are thought to use the same resources in meeting their needs and are sympatric (that is, species that have different ecological niches and living in the same area). As described by Odum (1971) and Schreier *et al.* (2009) species that live in the same area will utilize the space in accordance with ecological niches. Currently, only few field spatial studies used on primate species (Davies 1991), therefore, little quantitative information related to behavioral mechanisms and the utilization of space by primates are provided (van Schaik *et al.* 2009). Primate life history data from CPRS are limited, and suggest that gibbon life histories are roughly

half to that of leaf monkey (Marshall *et al.* 2008; Marshall 2009).

Vertical distribution, feeding behavior and movement patterns are three factors that distinguish the ecological niches of sympatric species (Marshall *et al.* 2008; Schreier *et al.* 2009). Resource partitioning involves differ-ential utilization of the three niche components by different species (Schoener 1971), which in turn allow cohabitation. Niche overlap refers to the utilization of some of the same resource types by two or more species (Abrams 1980). McArthur and Levins (1967) suggested that competition coefficients could be considered as measures of ecological overlap. Gibbons are frugivorous; their diet at CPRS comprise mainly the pulp of ripe fruits (65% of the diet on average, range 0-95%, based on data collected between 1985 and 1992), increased by ripe figs (23%, range 0-75%), flowers (6%, range 0-28%), leaves (3%, range 1-25%), and seeds (3%, range 0-8%; Marshall & Leighton 2006). On the other hand, leaf monkeys are seed and leaf specialists (seeds: 52%, range 25-95%; leaves: 25%, range 0-42% during the same period as the gibbon data), and also consume unripe fruit pulp (13%, range 2-72%; confined to plant taxa that are dispersed by bats and whose nutritional quality is similar to that of leaves), figs (5%, range 0-25%), and flowers (5%, range 0-20%; Marshall 2004; Marshall *et al.* 2009a). The similarity between types of food such as fruit and leaves, allowing the overlap in resource use, should be exist some form of ecological separation in order to avoid competition. Ecological separation can arise from breakdown of one habitat type into several microhabitats. Such microhabitats in the case of these two primate species could differ with respect to foraging habitat, feeding level, time of eating, food type and plant part actually ingested. However, Rusterholz (1981), Kreuzer and Huntly (2003) observes that an important element in the relationship between niche overlap and competition is the degree of availability of the environmental resources.

In order to study the habitat and diet interactions between the two primate species, the following objectives were set: (i) to determine the extent of overlap in food and habitat utilization between leaf monkey and the bornean white-bearded gibbons, (ii) to assess abundance of fruits shared by both species, and (iii) to predict the potential for the two primate species to compete for resources using indices of niche overlap and resource abundance.

MATERIALS AND METHODS

Time and Study Area. The study was conducted from August 2009 to February 2010. The study was carried out on Cabang Panti Research Station. CPRS is located between the valley of Palung Mountain and Panti Mountain, Gunung Palung National Park, West Kalimantan 1^0 13ʹ S, 110^0 7ʹ E. The reserve was establish in 1937, covering 1.500 ha study site that includes seven distinct, contiguous forest types, determined by elevation, soils, and drainage: (i) peat swamp forest on nutrient poor, bleached white soils overlain by variable amounts of organic matter (5-100 m asl); (ii) freshwater swamp forest on nutrient rich, seasonally flooded, poorly drained gleyic soils (5-10 m asl); (iii) alluvial forest on rich sandstone-derived soils recently deposited from upstream sandstone and granite parent material (5-50 m asl); (iv) lowland sandstone forest on well drained sandstone-derived soils with a high clay content and sparse patches of shale (20-200 m asl); (v) lowland granite foreston well-drained, granite-derived soils (350-800 m asl); (vi) upland granite forest on well drained, granite-derived soils (350-800 m asl); (vii) montane forest on largely granite-derived soils (750-1100 m asl). These forest types differ substantially in their floristic composition, temporal patterns of food availability, structure, and temperature (Cannon *et al.* 2007a,b). Most areas in the east range at altitude below 100 m asl, the highest peak is at altitude of 1116 m asl (Palung mountain) and 1050 m asl (Panti mountain). Mean monthly temperaturs were ranged from 24.8 to 29 ^{o}C with mean rainfall in this region year is about 3.000 mm.

Daily Activity of Primate. Three groups each of *P. rubicunda* and *H. albibarbis* were located at their sleeping site each morning and followed on foot from 06.00 to 18.00 h. Group of *P. rubicunda* consisted of BC, SK, and BK groups, while the group of *H. albibarbis* consisted of AP, MB, and DT groups. On average, 8 h of observational data per day were collected using binoculars and spotting scopes (35-60x). The leaf monkey study group consisted of 8-10 individuals and 5 individuals of the bornean white-bearded gibbons. Each study group was observed independently for 20 days every month with observations being alternated at weekly intervals between August 2009 and February 2010. The leaf monkey and bornean white-bearded gibbons groups were habituated and studied for various lengths of time since the mid 1980's (e.g., Knott 1998; Curran & Leighton 2000; Marshall & Leighton 2006; Cannon *et al.* 2007b; Marshall *et al.* 2008).

Five-minute focal animal samples (Altmann 1974a) were collected at 15 minute intervals throughout the day with subjects chosen according to a fixed rotation between age and sex classes. For each scan, the following records were: (i) feeding time, (ii) the individual feeding position level above the ground, (iii) the plant species or diet, (iv) the specific part of the food item actually ingested, (v) height, diameter, and canopy of species plant for diet and sleeping trees, (vi) pattern of daily movement and home range, (vii) numbers, age and sex of other individuals of the group presently utilizing the same fruit tree, and the activities of all visible animals.

The activity categories were defined as: (i) resting: stationary or sleeping, (ii) moving: traveling, (iii) feeding: actively manipulating potential food items, ingesting or masticating food, and (iv) social: a category which included activity such as grooming, mounting, copulating, playing, fighting, hiding from predators and episodes when an infant was embraced by the other monkeys or ape in the troop.

Using this sampling regime, the total time spent in visual contact during systematic sampling were 190.58 h for leaf monkey and 192.58 h for bornean white-bearded

gibbons. The mean were 115 and 134 focal records per month for leaf monkey and bornean white-bearded gibbons, respectively.

Phenology. To quantify temporal variation in food availability, 81 individual trees from eighteen species were ranked as important for the leaf monkey and bornean white-breaded gibbons diet, and were selected and monitored for phenological condition. From every species, two individuals were monitored in each forest.

Food Preference. Food preference was calculated with Struhsaker (1974) method, and used selection ratios as the measurement of food preference. This method assumed that the amount of feeding time, the number of individuals feeding and the feeding frequency on a particular tree species may be influenced by stem density and crown size (potential fruit producing area). Stem density was determined at random of 0.04 ha plots with 2% sampling intensity of each primate species home range and cover all species over 5 m tall. An index of crown size was computed as the sum of maximum crown depth and maximum crown diameter. This index makes the fewest assumptions about crown shape. A cover index that is an estimate of the relative food producing area was calculated as the product of stem density and mean crown size (Struhsaker 1974) from a sample of six trees per species. A selection ratio was calculated by dividing the percentage feeding observations by the cover index for a particular tree species. It was not possible to weight the cover index by availability of food items because this scale is only a rough indication of food production biased towards fruits, leaf and flower. It does not include other items such as invertebrates, flowers, gum and other species-specific items consumed by primates.

The use of Vertical Space. Daily activities related to the utilization of both primate tree heights were analyzed with chi-square test (the confidence interval 95%). Tree height divided by the interval 5 m. In a chi-square test was performed testing the hypothesis: H_0: distribution of animal activity does not differ according to altitude; H_1: distribution of animal activity does differ according to altitude.

Niche Overlap. Analysis of niche overlaps used approach of two variables, i.e. food (diet) resource and habitat resources (Krebs 1989). Calculation of the similarity of food plant species and the ecological niche overlap was calculated by Simplified Morisita Index (Horn 1966) and the percentage of niche overlap values:

Niche overlap index (Simplified Morisita Index):

$$C_H = \frac{2\sum_{i=1}^{n} p_{ij} \cdot p_{ik}}{\sum_{i=1}^{n} p_{ij}^2 + \sum_{i=1}^{n} p_{ik}^2}$$

Niche overlaps percentage:

$$P_{jk} = [\sum_{j=1}^{n} (\min p_{ij}, p_{ik})] \, 100\%$$

Home Range. Points of coordinates sample were collected using a GPS receiver and analysize using the software Arc View 3.3. Analyses were performed by connecting the outermost point of coordinates (maximum convex polygon) where leaf monkey and White-bearded Gibbons movement. Based on group analysis results will be obtained extensive use of spatial horizontally or individual home ranges and home ranges that are used together.

Niche Width. The niche width for the two species was calculated on: (i) the number of plant species eaten (Bruggeman & Breanndán 2000) and (ii) on the proportion of time spent feeding on different plant species of the feeding time during the seven months of the study. In the latter case, the Shannon Index of Diversity (Shannon 1948) was implemented.

RESULTS

Daily Activity of Primate. Average of group size of leaf monkey ranged from 8-10 individual; the largest number in population was the infants; female had more percentage than male. On the other hand, female and male were in the same group size of bornean white-bearded gibbons (Table 1). All group in both primates lived in lowland sandstone habitat. This habitat type was associated with the availability of food and the height of trees where appropriate activities were compared to habitat types (Marshall & Leighton 2006).

The activities of leaf monkey were started at 05:35 until 18:25, began with feeding behavior after moving from sleep tree in the morning. If the sleep tree was a food tree, the

Table 1. Group size of leaf monkey and bornean white-bearded gibbons

Group	Old		Adult		Juvenile		Infant	Number of individual
	♂	♀	♂	♀	♂	♀		
Leaf monkey group								
BC group	1	1	0	2	0	1	3	8
SK group	1	1	0	3	1	0	4	10
BK group	1	1	0	2	1	0	2	7
Bornean white-bearded gibbons group								
AP group	1	1	0	1	1	0	1	5
MB group	1	1	0	1	0	1	1	5
DT group	1	1	0	1	1	0	1	5

Each group of *P. rubicunda* and *H. albibarbis* are named based on research pioneered the path around the home range.

activity began with feeding behavior at the sleep tree. Activities of the bornean white-bearded gibbon was started slightly earlier i.e. at 05:15 and ended up at 18:35. Bornean white-bearded activity began with gibbon locomotion behaviour moved from the sleep tree. Movements of individuals out of the sleeping tree were initiated by adult males followed by the other group members. Bornean white-bearded movement in the early morning was preceded by loud vocalizations among males and females. When male and female were vocalized at the same time, the female voice was louder and more dominant. The percentage of the daily activities of each groups were described at Figure 1.

Phenology. For every plant species, a maximum index of 29 (from two individuals each) was expected under ideal fruiting conditions. Monthly fruit indices varied between 4.73 and 7.8 (mean = 5.96) (Table 1). Within the study period, between four and 18 species were in fruit at any given month (Table 2).

Diet Selection. Koompasia excelca that comprised about 7.29% of the leaf monkey feeding diet was in the sixth ranked in the selection ratio although it was the most utilized food species. The low rank status was resulted of its high density and cover index values, therefore reduced its selection ratio value. *Piper* spp., contributing only about 1.01% of leaf monkey feeding time, scored the highest selection ratio. *Myristica* spp. comprised about 7.35% of the bornean white-bearded gibbon diet.

Amount of niche overlaps related diet selection was presented in Table 2, considered highly selected to its relatively low density. For all 18 top species shared by both primates, there were no significantly differences between the selection ratios (Wilcoxon-paired sample test, d.f. = 18, P < 005). *Piper* spp. was however, excluded from the analysis, because it was very highly selected by leaf monkey and its high value had a very strong singular effect on the outcome of the test.
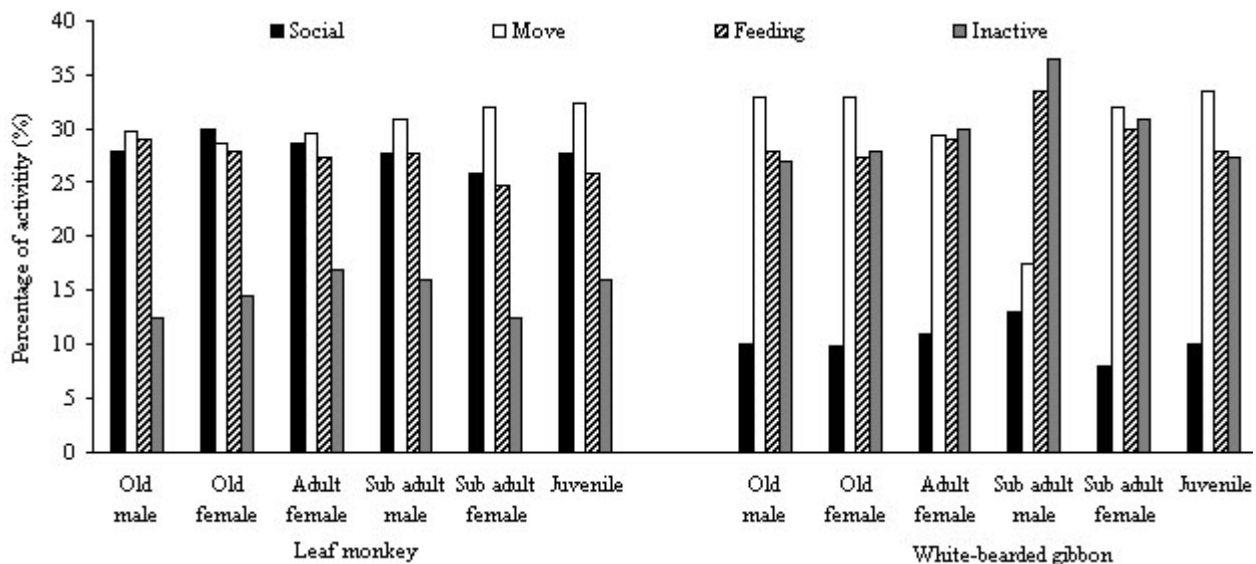

Figure 1. Average of daily activity percentage on leaf monkey and white-bearded Gibbon base on age class and sex.

Table 2. Selection ratios of *P. rubicunda* and *H. albibarbis* for some major fruit tree species shared by both primates

Species	% in diet			Selection ratio	
	Cover index	P.s	H.a	P.s	H.a
Irvingia malayana	352.2	6.34	3.76	41.90	9.70
Neoscortechinia spp.	342.6	1.09	0.89	5.46	9.24
Bauhinia spp.	67.1	7.09	7.10	38.63	18.87
Xanthophyllum spp.	157.3	5.54	1.19	13.78	1.69
Baccaurea spp.	247.8	5.69	4.99	41.60	4.76
Koompasia excelca	537.9	7.29	3.87	38.10	18.13
Freisodielsia spp.	108.2	0.09	0.88	0.32	20.24
Willughbeia spp.	44.5	1.15	1.34	10.89	11.15
Austrobuxus spp.	109.8	2.37	3.78	1.60	11.60
Hydnocarpus spp.	62.9	1.67	2.98	2.42	0.33
Desmos spp.	98.1	0.50	0.35	4.01	4.13
Ficus callocecy	576.5	6.89	2.80	49.90	67.53
Myristica spp.	689.9	7.35	10.01	116.24	16.17
Blumeodendron spp.	11.1	4.56	1.18	8.13	1.21
Derris spp.	67.0	2.54	1.90	3.39	0.41
Scaphlum spp.	217.4	2.86	2.70	3.11	12.66
Canarium spp.	189.7	7.18	6.00	23.74	7.48
Gymnocranthera spp.	278.4	3.88	7.44	35.00	30.01

P.s.: *P. rubicunda;* H.a: *H. albibarbis.*

Table 3. Distribution of fruit production in some selected tree species eaten by both *P. rubicunda* and *H. albibarbis*

Tree species	Distribution of fruiting between 2009 and 2010						
	Aug	Sep	Oct	Nov	Dec	Jan	Feb
Irvingia malayana	--------------------						
Neoscortechinia spp.	------------------						
Bauhinia spp.			------------			------------	
Xanthophyllum spp.	-------------						
Baccaurea spp.		------------			-------------------		
Koompasia excelca		------------			-------------------		
Freisodielsia spp.	--------------------						
Willughbeia spp.	--------------	-------------------					
Austrobuxus spp.	--------------	-------------------					
Hydnocarpus spp.	--------------						
Desmos spp.			-------------				
Ficus callocecy	--------------						
Myristica spp.	--------------						
Blumeodendron spp.	--------------						
Derris spp.				---------------------------			
Scaphlum spp.	--------------------						
Canarium spp.	--------------						
Gymnocranthera spp.	--------------						

Table 4. Average height position of each activity *P. rubicunda* and *H. albibarbis*

Activity	Average of height position (m)	
	Leaf monkey	White-bearded gibbon
Move	25.11	28.86
Feeding	26.73	26.34
Inactive	26.65	27.84
Social	24.99	28.22

Table 5. Result of comparative differences based on the height position between *P. rubicunda* and *H. albibarbis* with the Chi-Square test

Activity	Average of height position (m)	
	Leaf monkey	White-bearded gibbon
Move vs feeding	0.010*	0.010*
Move vs inactive	0.010*	0.020*
Move vs social	0.783ns	0.348ns
Feeding vs inactive	0.050ns	0.000*
Feeding vs social	0.020*	0.000*
Inactive vs social	0.018*	0.552 ns

*significant (Asymp Sig < α = 0.05), ns: no significant (Asymp Sig > α = 0.05).

Table 6. Monthly habitat and diet overlaps in relation to fruit indices between August 2009 and February 2010

Season	Month	Habitat overlap	Diet overlap	Fruit index
Dry	August	0.15	0.29	4.73
	September	0.24	0.12	7.18
Dry-Wet	October	0.37	0.34	6.84
Wet	November	0.43	0.39	5.36
	December	0.40	0.25	4.98
	January	0.80	0.48	6.93
Wet-dry	February	0.93	0.74	6.11

The use of Vertical Space. The height position of all activities of leaf monkey and bornean white-bearded gibbon on the tree was m and 25.91 and 27.84 m, respectively. The analysis of average height positions and activities of leaf monkey and bornean white-bearded gibbon using a Chi-Square test showed a significantly different results [(Asymp Sig = 0.000, or <α (0.025)]. This showed that there were differences in the use of space vertically between the leaf monkey and the white-bearded gibbon. Average of height position and the testing of activity differences based on the height position between *P. rubicunda* and *H. albibarbis* with the Chi-Square test (α = 0.05) on the tree are presented in Tables 4 and 5.

Niche Overlaps. In this research, niche overlap can be defined as a variety of diet shared and habitat resources (Krebs 1989), while habitat overlap is only refer to the overlap in ranging space. Monthly habitat overlap between the two primates were varied from 0.15 up to 0.93 (Median = 0.43, Table 6), while diet overlap were varied from 0.12 up to 0.74 (Median = 0.34) during the seven months from August 2009 to February 2010. Diet and habitat overlaps were low in the dry season (August-October, Table 6) but increased in the wet season (November-January, Table 6). The highest overlap in diet and habitat were observed in the period immediately following the wet season (February, Table 6). Food plant species similarity between *P. rubicunda* and *H. albibarbis* were 53.29% and the Morisita index was 0.53, meaning that 53.29% of food plant were eaten by both species.

Home Range. The use of horizontal space (home range) of bornean white-bearded gibbon was larger (26.34 Ha) than that of leaf monkey (17.87 Ha). Extensive overlap of home ranges for both species was 34.21% in the average (Table 7, Figure 2).

Niche Width. Based on number of plant species taken as diet source, monthly niche widths was varied from 17 to 37 (Mean = 27) and from 15 to 31 (Mean = 23) for leaf monkey and bornean white-bearded gibbon, respectively (Table 8). The Shannon Index H', for niche width was varied from 1.58-2.67 and 1.60-3.28 in the leaf monkey and bornean white-bearded gibbon, respectively. Although the niche of bornean white-bearded gibbon was wider than the leaf monkey, the differences between them were not significantly different (P > 0.05). This might be due to they often found in habitat that has been exploited in areas such as logging and forest plantations. The correlation between monthly niche widths H' with the corresponding diet overlaps was not significantly different either for leaf monkey (r_s = 0.107; P > 0.05) or bornean white-bearded gibbon (r_s = 0.179; P > 0.05), suggesting that diet overlap varied independently of niche widths for all of diet species.

Table 7. Area of overlapping home ranges between there groups of *P. rubicunda* and *H. albibarbis*

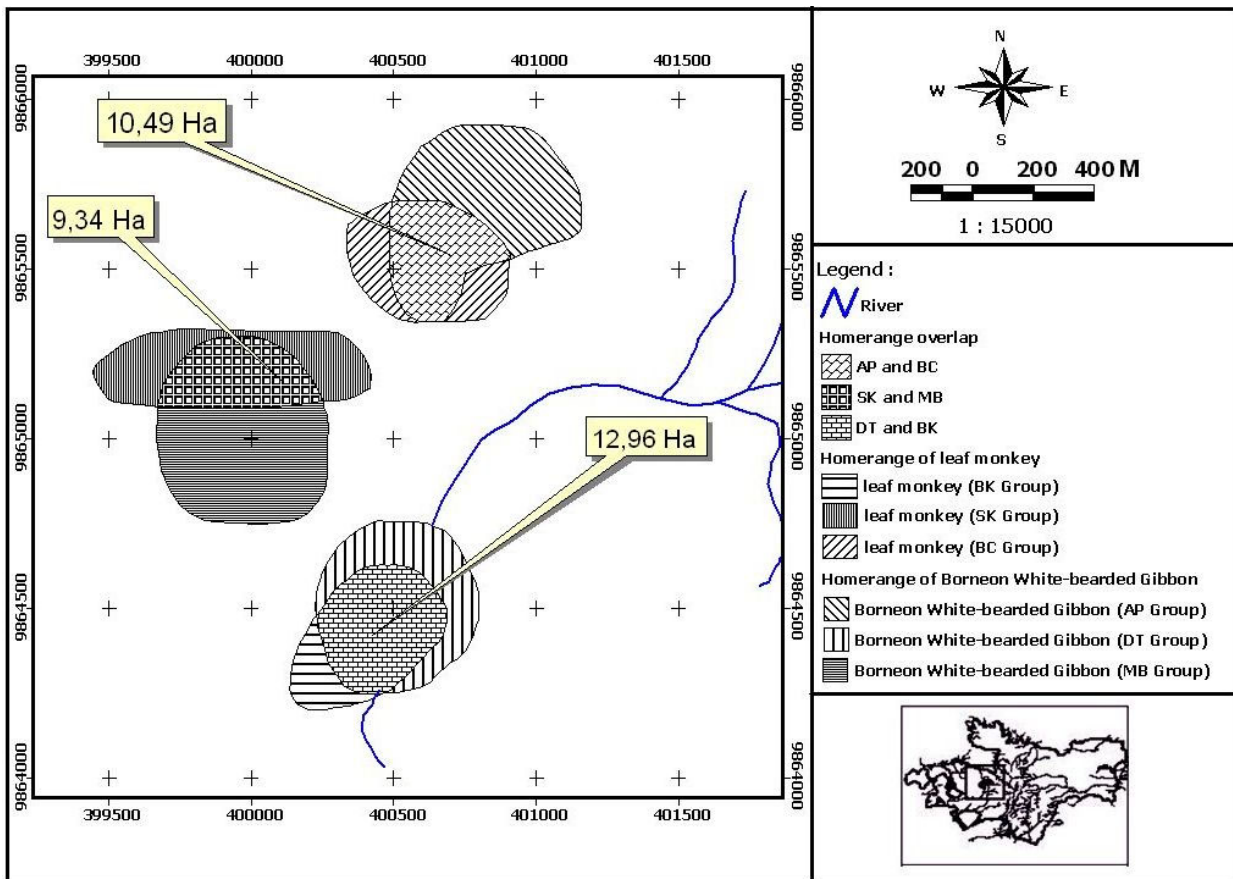| Area of overlapping	Size overlap (ha)	Percentage (%)
Leaf monkey (BC) & bornean white-bearded gibbon (AP group	10.49	31.21
Leaf monkey (SK) & bornean white-bearded gibbon (MB group)	9.34	24.02
Leaf monkey (BK) & bornean white-bearded gibbon (DT group)	12.96	47.42
Average of overlapping	10.93	34.21

Figure 2. Overlap areas between leaf monkey (*P. rubicunda*) and white-bearded Gibbon (*H. albibarbis*).

Table 8. Monthly niche widths for *P. rubicunda* and *H. albibarbis* between August 2009 - February 2010

Month	Number of plant species eaten within the forest			Niche width H'	
	P. rubicunda	*H. albibarbis*	common to both	*P. rubicunda*	*H. albibarbis*
August	27	10	4	2.18	1.87
September	22	16	5	2.14	1.58
October	24	30	13	1.61	2.77
November	30	30	14	2.57	2.79
December	37	31	14	2.59	3.18
January	17	15	8	2.14	2.08
February	23	28	13	2.41	2.28

DISCUSSION

Daily activity of bornean white-bearded gibbon was started earlier than the leaf monkey. At the beginning of the activity, bornean white-bearded gibbon always begins with a vocalization, while the leaf monkey was rarely initiated by the vocalizations of their daily activities. Vocalizations by male leaders meant as alarm call to the other group members when they are in threat. This behavior occurred within a relatively short time i.e. $\pm$ 1 minute, before they finally move away. Bornean white-bearded gibbon prefers to run away if they see predators (including humans). This strategy was different with the leaf monkeys that prefer to hide for a long period of time.

In the SPCP, bornean white-bearded gibbon tends to avoid confrontation with the leaf monkeys. During two times of observation, the bornean white-bearded gibbons shared on the same tree or in adjacent trees with the leaf

monkey for less than five minutes. The bornean white-bearded gibbon was almost ahead in the tree than the leaf monkeys. When the leaf monkeys arrived then the bornean white-bearded gibbon group moved to other place. This result is supported with of Singh *et al.* (1998) and Porter (2001), mentioned that the cohabitation primates are tend to avoid a confrontation. The same resource use among leaf monkeys and bornean white-bearded gibbon occurs in the SPCP but in different range of times. This is due to the leaf monkey has more aggressive nature, larger in population size and body size. Basic ecological theory predicts that behavior of territorial defends strongly associated with social system. In polygynous systems where females are relatively sedentary (e.g., leaf monkeys), the quality of the defended territory by a male will dictate by the number of females that he is able to attract (Pearson 2002). However, different social behaviour occurred in the bornean white-bearded gibbons which are a monogamous

territorial species and the social constraints prohibit females from freely assorting themselves (Cheyne 2010).

Fruit phenology displayed temporal variation, the pattern observed during this study indicated that the peak of fruit production generally lagged behind the peak off rainfall periods. In the dry period of August there was lack of fruit production, leaf monkeys spent most of their foraging time in the dry woodland plains, and returned back to the forest at late afternoon. The fruit diet of leaf monkeys then mainly constituted fruits of *Koompasia exelsa* and *Syzygium* spp. which were in peak season in the dry woodland plains. In contrast, the bornean white-bearded gibbon foraged in the forest throughout the study period. Within the forest, bornean white-bearded gibbons fed mainly on fruits of *Dialium* spp. and foraged for scanty and irregularly distributed fruits of *Syzygium* spp., *Bauhinia* spp., *Alangium* spp., and *Baccaurea* spp.

When fruits were scarce, both species increased their consumption of leaf and invertebrates and fed mostly at lower height position fed and sometimes at ground level. The leaf monkey spent considerable time eating for leaf, insects, and dry seeds within the forest. The bornean white-bearded gibbon spent time to dig the soil searching for insect, leaf, and liana. General descriptions and detailed data on the plant composition of each forest type are provided by Cannon and Leighton (2004), Marshall (2004), Paoli *et al.* (2006), and Cannon *et al.* (2007a,b).

Although the two species had similar niche widths, they exploited different habitats and feeding heights, hence reduced overlap values. Therefore, this period would have presented the lowest potential for competition. As well as with the research result of Snaith and Chapman (2008), it is not clear whether the resultant habitat segregation during low levels of fruit availability implied a mechanism of competition avoidance. There is growing empirical evidence and widening conceptual realization that distinct classes of foods allow different effects on primate populations on ecological and evolutionary time scales (McConkey *et al.* 2002; Lambert *et al.* 2004; Laden & Wrangham 2005; Lambert 2007; Marshall *et al.* 2008; Vogel *et al.* 2008). Marshall (2004) states that leaf monkey are open-country species whose ranging patterns are determined by the essential localized resources such as water and sleeping sites, and that home ranges of primates might overlap most at areas containing resources with a restricted spatial distribution. It was possible then that the overlap in diet observed in this period was either a consequence of a direct effort by leaf monkey to search for food within the forest, or that the overlap may have resulted because leaf monkeys were adopting a typical 'refuging system' in their ranging pattern.

The high peak in fruit production following a few months of increased rainfall was characterized by high values of habitat and diet overlap, resulting from a major shift in habitat utilization by leaf monkeys from woodland plains into a forest-restricted range. Synecologists consider stratigraphic separation in the canopy to be an important method by which primates partition their resources (Ungar 1996). Despite the increased overlaps,

the two primate species did not show significantly different in their feeding levels owing to the fact that they selected similar food species. Between leaf monkey and bornean white-bearded gibbon had 46.71% different type of diet. Diet overlaps were varied independently from habitat overlap may suggest that there exist mechanisms to partition food resources even when habitat overlap is high. Two possible hypotheses are put forward here to explain this situation. First, the two species had distinct microhabitats that could only have been uncovered by measuring 'finer' divisions within food and habitat components. Second hypothesis was the limited woodland foraging range at the forest utilized by leaf monkeys provided sufficient food supply that increased habitat overlap need not resulted in increased competition.

High level of fruit production at the time suggested that food were not a limiting factor. Most of the fruit trees were productive at this time and although the two species had similar preferences for a few species, these species were either synchronous, fruiting throughout the study period such as *Irvingia malayana*, *Neoscortechinia* spp., *Baccaurea* spp., and *Atuna* spp., or retained fruits for a long period like *Dracontomelon* spp.

As in the dry season, the unclear mechanisms governed habitat choice in wet season in bornean white-bearded gibbon and consequently the level of overlaps were also not clear. The possibility patterns in range use are affected by distribution and abundance of resources (Janson & Schaik 1987; Davies *et al.* 1988; Chapman & Chapman 1999; Wasserman & Chapman 2003; Hanya *et al.* 2004), the optimal use of these resources (Menzel 1973; Pyke *et al.* 1977) and potential dangers (Altmann 1974b). It was observed that bornean white-bearded gibbon did not exploit the habitat towards the end of the wet season, yet there was a superabundance of succulent herbs as well as fruits. It is also likely that in this season, habitat choice was a trade-off between foraging rewards and predation risk, as observed for bornean white-bearded gibbon in Gunung Palung National Park by Marshall (2004).

Animal cohabitate by division of canopy strata for the use of vertical space in the sleeping trees and food trees (Singh *et al.* 1998), i.e. 27.84 and 25.91 m respectively for bornean white-bearded gibbon activity either alone or together with leaf monkey and for leaf monkey activity either alone or together with white-bearded gibbon. Analysis of average height positions and activities of leaf monkey and bornean white-bearded gibbon using Independent-Samples T Test showed significantly different suggested that there were differences in the use of vertical space between the leaf monkey and bornean white-bearded gibbon. The highest frequency of absolute height of the leaf monkey was in the height range of 21-25 m, whereas 26-30 m for bornean white-bearded gibbons.

Bornean white-bearded gibbon home range (horizontal space) was larger than that of leaf monkey. The largest overlap (12.96 ha out of 16.61 ha or 47.42%) was found between BK group of leaf monkey group with DT group of bornean white-bearded gibbon. These conditions

indicate the presence of food niche segregation and niche space between the two primates. Niche segregation occurs as a result of competition or an increase in feed efficiency of the search area and the difference in the edible parts of plants (Beaudrot & Marshall 2011). In this case, the niche separation can reduce the level of competition and increase the chance that the two primates have cohabitation to utilize an area overlapping the home ranges (Garcia & Arroyo 2005).

The findings of this study agree with Schoener's (1982) observation that temporal variations do occur in overlap values. These also in agreement with that of Pekarrinen (1984) and Charnov (1976) that competition may not be continuous but may only occur at certain times. However, overlap in resource use would only result in more intense competition if the resources were limiting (Waser 1976; Camillo & Garofalo 1989). At the high period of fruit production, competition was less likely occurred. In addition, understanding how species respond to natural variation in habitat quality may provide insight into their responses to future habitat alteration, through either human-induced habitat degradation or climate change (Marshall *et al*. 2006; Meijaard *et al*. 2008).

Based on this research, we concluded that horizontal space utilized by bornean white-bearded gibbons was larger than that of the leaf monkeys. The utilization of vertical space for the bornean white-bearded gibbons was higher than that of the leaf monkey; therefore related to the presence of fruit or food source and behavior of these two different primates. There were shared resources used at different times (cohabitation) between leaf monkey and the bornean white-bearded gibbons.

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REFERENCES

Abrams P. 1980. Some comments on measuring niche overlap. *Ecology* 61:44-49. http://dx.doi.org/10.2307/1937153

Altmann J. 1974a. Observational study of behavior: sampling methods. *Behaviour* 49:227-267. http://dx.doi.org/10.1163/156853974X00534

Altmann SA. 1974b. Baboon, space, time, and energy. *Am Zool* 14:221-248. http://dx.doi.org/10.1093/icb/14.1.221

Beaudrot LH, Marshall AJ. 2011. Primate communities are structured more by dispersal limitation than by niches. *J Anim Ecol* 80:332-341. http://dx.doi.org/10.1111/j.1365-2656.2010.01777.x

Bruggeman J, Breanndán ÓN. 2000. A niche width model of optimal specialization. *J Comp & Math Organization Theory* 6:161-170. http://dx.doi.org/10.1023/A:1009633318912

Camillo E, Garofalo CA. 1989. Analysis of the niche of two sympatric species of bombus (*Hymenopthera, Apidae*) in South Eastern Brazil. *J Trop Ecol* 5:81-92. http://dx.doi.org/10.1017/S0266467400003242

Cannon CH, Curran LM, Marshall AJ, Leighton M. 2007a. Beyond mast-fruiting events: community asynchrony and individual dormancy dominate woody plant reproductive behavior across seven Bornean forest types. *Curr Sci* 93:1558-1566. http://dx.doi.org/10.1111/j.1461-0248.2007.01089.x

Cannon CH, Curran LM, Marshall AJ, Leighton M. 2007b. Long-term reproductive behavior of woody plants across seven Bornean forest types in the Gunung Palung National Park (Indonesia): suprannual synchrony, temporal productivity, and fruiting diversity. *Ecol Lett* 10:956-969. http://dx.doi.org/10.1111/j.1461-0248.2007.01089.x

Cannon CH, Leighton M. 2004. Tree species distribution across five habitats in a Bornean rain forest. *J Veg Sci* 15:257-266. http://dx.doi.org/10.1111/j.1654-1103.2004.tb02260.x

Chapman CA, Chapman LJ.1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40:215-231. http://dx.doi.org/10.1007/BF02557712

Charnov EL. 1976. Optimal foraging: The marginal value theorem. *Theor Pop Biol* 9:129-136. http://dx.doi.org/10.1016/0040-5809(76)90040-X

Cheyne SM. 2010. Behavioural ecology of gibbons (*Hylobates albibarbis*) in a degraded peat-swamp forest. In: Gursky S, Supriatna J (eds). *Indonesian Primates*. Developments in primatology: progress and prospects. New York: Springer. p 121-156. http://dx.doi.org/10.1007/978-1-4419-1560-3_8

Curran LM, Leighton M. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol Monogr* 70:101-128. http://dx.doi.org/10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2

Curran LM, Trigg SN, McDonald AK, Astiani D, Hardiono YM, Siregar P, Caniago I, Kasischke E. 2004. Lowland forest loss in protected areas of Indonesian Borneo. *Science* 303:1000-1003. http://dx.doi.org/10.1126/science.1091714

Davies AG, Bennett EL, Waterman PG. 1988. Food selection by two south-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biol J Linn Soc* 34:33-56. http://dx.doi.org/10.1111/j.1095-8312.1988.tb01947.x

Davies G. 1991. Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in Dipterocarp Forest of Northern Borneo. *Int J Primatol* 12:119-144. http://dx.doi.org/10.1007/BF02547577

Dennis RA, Colfer CP. 2006. Impacts of land use and fire on the loss and degradation of lowland forest in 1983-2000 in East Kutai District, East Kalimantan, Indonesia. Singapore. *J Trop Geogr* 27:30-48. http://dx.doi.org/10.1111/j.1467-9493.2006.00238.x

García JT, Arroyo BE. 2005. Food-niche differentiation in sympatric hen (*Circus cyaneus*) and montagu's harriers (*Circus pygargus*). *Ibis* 147:144-154. http://dx.doi.org/10.1111/j.1474-919x.2004.00377.x

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. *Ecol Res* 19:485-493. http://dx.doi.org/10.1111/j.1440-1703.2004.00662.x

Horn HS. 1966. Measurement of overlap in comparative ecological studies. *The American Naturalist* 100:419-424. http://dx.doi.org/10.1086/282436

Janson HC, van Schaik CP. 1987. Recognising the many faces of primate food competition: Methods. *Behaviour* 105:165-166..

Knott CD. 1998. Changes in orangutan diet, caloric intake, and ketones in response to fluctuating fruit availability. *Int J Primatol* 19:1061-1079. http://dx.doi.org/10.1023/A:1020330404983

Krebs CJ. 1989. Ecologycal Methodology. New York: Harper and Row Publishers.

Kreuzer MP, Huntly NJ. 2003. Habitat-specific demography: evidence for source-sink population structure in a mammal, the pika. *Oecologia* 134:343-349.

Laden G, Wrangham RW. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. *J Hum Evol* 49:482-498. http://dx.doi.org/10.1016/j.jhevol.2005.05.007

Lambert JE. 2007. Seasonality, fallback strategies, and natural selection: a chimpanzee and cercopithecoid model for interpreting the evolution of the hominin diet. In: Ungar PS (ed). *Evolution of the Human Diet: The Known, the Unknown, and The unknowable*. Oxford: Oxford Univ Pr. p 324-343.

Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *Am J Phys Anthro* 125:363-368. http://dx.doi.org/10.1002/ajpa.10403

Marshall AJ. 2004. *The Population Ecology of Gibbons and Leaf monkeys across a Gradient of Bornean Forest Types*. Cambridge MA: Harvard Univ Pr.

Marshall AJ. 2009. Are montane forests demographic sinks for bornean white-bearded gibbons (*Hylobates albibarbis*)?. *Biotropica* 41:257-267. http://dx.doi.org/10.1111/j.1744-7429.2008.00461.x

Marshall AJ, Ancrenaz M, Brearley FQ, Fredriksson GM, Ghaffar N, Heydon M, Husson SJ, Leighton M, McConkey KR, Morrogh-Bernard HC, Proctor J, van Schaik CP, Yeager CP, Wich SA. 2009a. The effects of habitat quality, phenology, and floristics on populations of Bornean and Sumatran orangutans: are Sumatran forests more productive than Bornean forests? In: Wich SA, Utami-Atmoko SS, Mitra ST, van Schaik CP (eds). *Orangutans: Geographic Variation in Ecology and Conservation*. Oxford: Oxford Univ Pr. p 97-117.

Marshall AJ, Cannon CH, Leighton M. 2008. Competition and niche overlap between gibbons (*Hylobates albibarbis*) and other frugivorous vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia. In: Lappan S, Whittaker D, Geissman T (eds). *Wild Gibbon Populations: New Understandings of Small Ape Socioecology, Population Biology and Conservation*. New York: Springer Publ.

Marshall AJ, Leighton M. 2006. How does food availability limit the population density of white-bearded gibbons?. In: Hohmann G, Robbins MM, Boesch C (eds). *Feeding Ecology of The Apes and Other Primates*. Cambridge: Cambridge Univ Pr. p 311-333.

Marshall AJ, Nardiyono LM, Engström B, Pamungkas J, Palapa J, Meijaard E, Stanley SA. 2006. The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan. *Biol Conserv* 129:566-578. http://dx.doi.org/10.1016/j.biocon.2005.11.025

McArthur RH, Levins R. 1967. The limiting similarity; Convergence and divergence of co-existing species. *Am Nat* 101:377-385. http://dx.doi.org/10.1086/282505

McConkey KR, Aldy F, Ario A, Chivers DJ. 2002. Selection of fruit by gibbons (*Hylobates muelleri* x *agilis*) in the rain forests of Central Borneo. *Internat J Primatol* 23:123-145. http://dx.doi.org/10.1023/A:1013253909046

Meijaard E, Sheil D, Marshall AJ, Nasi R. 2008. Phylogenetic age is positively correlated with sensitivity to timber harvest in Bornean mammals. *Biotropica* 40:76-85.

Menzel EW. 1973. Chimpanzee spatial memory organisation. *Science* 182:943-945. http://dx.doi.org/10.1126/science.182.4115.943

Odum EP. 1971. Fundamental of Ecology. Toronto: WB Saunders Company.

Paoli GD, Curran LM, Zak DR. 2006. Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: Evidence for niche partitioning by tropical rain forest trees. *J Ecol* 94:157-170. http://dx.doi.org/10.1111/j.1365-2745.2005.01077.x

Payne J. 2000. *The Field Guide of Mammalian in Kalimantan, Sabah, Sarawak and Brunei Darussalam*. Bogor: WCS-Indonesia Program.

Pearson T. 2002. Polygyny and extra-pair paternity in a population of southwestern willow flycatchers (*Empidonax traillii extimus*) [Thesis]. Northern Arizona: Northern Arizona Univ.

Pekkarinen A. 1984. Resource partitioning and coexistence in bumbe-bees (*Hymenopter, Bombinne*). *Ann Entomol fenn* 50:97-107.

Porter LM. 2001. Dietary differences among sympatric callitrichinae in Northern Bolivia: *Callimico goeldii*, *Saguinus fuscicollis,* and *S. labiatus*. *Internat J Primatol* 22:961-992. http://dx.doi.org/10.1023/A:1012013621258

Pyke GH, Pulliam HR, Charnov EL. 1977. Optimal foraging: a selective view of theory and tests. *Q Rev Biol* 52:137-154. http://dx.doi.org/10.1086/409852

Rusterholz KA. 1981. Competition and structure of an avian foraging guild. *Am Nat* 118:173-190. http://dx.doi.org/10.1086/283813

Schoener TW. 1971. Theory of feeding strategies. *Ann Rev Ecol System* 2:369-404. http://dx.doi.org/10.1146/annurev.es.02.110171.002101

Schoener TW. 1982. The controversy over interspecific competition. *Am Sci* 70:586-595.

Schreier BM, Harcourt AH, Coppeto SA, Somi MF. 2009. Interspecific competition and niche separation in primates: a global analysis. *Biotropica* 41:283-291. http://dx.doi.org/10.1111/j.1744-7429.2008.00486.x

Shannon CE. 1948. A mathematical theory of communication. *Bell system Tech J* 27:379-423.

Singh M, Singh M, Kumar MA, Kumar HN, D'Souza L, Anantha KSBA. 1998. Behavior of lion-tailed macaque (*Macaca silenus*) in vulnerable and relatively secure habitats in rainforest of Western Ghats, India. *Tigerpaper* 5:16-25.

Snaith TV, Chapman CA. 2005. Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus. *Behav Ecol Sociobiol* 59:185-190. http://dx.doi.org/10.1007/s00265-005-0023-x

Snaith TV, Chapman CA. 2007. Primate group size and interpreting socioecological models: Do folivores really play by different rules? *Evol Anthropol* 16:94-106. http://dx.doi.org/10.1002/evan.20132

Snaith TV, Chapman CA. 2008. Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. *Behav Ecol* 19:1289-1296. http://dx.doi.org/10.1093/beheco/arn076

Struhsaker TT. 1974. Correlates of ranging behaviour in a group of red colobus monkeys (*Colobus badius tephrosceles*). *Am Zool J* 14:177-184.

Supriatna J, Hendras EW. 2000. Indonesian Primate. Jakarta: Yayasan Obor Indonesia.

Ungar PS. 1996. Feeding height and niche separation in sympatric Sumatran monkeys and apes. *Folia Primatol* 67:163-168.

van Schaik CP, Marshall AJ, Wich SA. 2009. Geographic variation in orangutan behavior and biology: its functional interpretation and its mechanistic basis. In: Wich SA, Utami S, Mitra Setia T, van Schaik CP (eds). *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*. Oxford: Oxford Univ Pr. p 351-361.

Vogel ER, van Woerden JT, Lucas PW, Utami-Atmoko SS, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *J Hum Evol* 55:60-74. http://dx.doi.org/10.1016/j.jhevol.2007.12.005

Waser PM. 1976. Cercocebus albigena: site attachment, avoidance and intergroup spacing. *Am Nat* 110:911-935. http://dx.doi.org/10.1086/283117

Wasserman MD, Chapman CA. 2003. Determinants of colobine monkey abundance: the importance of food energy, protein, and fiber content. *J Anim Ecol* 72:650-659. http://dx.doi.org/10.1046/j.1365-2656.2003.00736.x