Activity budget, travel distance, sleeping time, height of activity and travel order of wild East Bornean Grey gibbons (*Hylobates funereus*) in Danum Valley Conservation Area

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Abstract. Activity budget, travel distance, sleeping time and height of activity of two wild East Bornean grey gibbon (*Hylobates funereus*) groups and travel order of one group were investigated during the dry and wet season at the Danum Valley Conservation Area, Sabah, Malaysia. One male showed seasonal change in his behaviors between the dry season (August) and wet season (December). He spent more time engaged in moving, playing and grooming, traveled longer and entered the sleeping tree later in the dry season when fruit was abundant but did the opposite in wet season. On the other hand, another male gibbon whose family had a new-born baby did not show a similar seasonal behavioural change between the dry season (May–June) and wet season (December). Fruit availability and gibbon family composition, especially whether the family had a new-born baby, may have an influence on the activity budget, movement and sleeping time of East Bornean grey gibbons. Early night-tree entry may be influenced by combined factors such as fruit availability, predator avoidance and fruit competition with other animals. The female gibbon's activities occurred at greater height above the ground compared to that of males in the early morning and the late afternoon. Similar to other gibbons, the female East Bornean grey gibbon led the group more often than the male. In addition, a rare observation was made of infant carrying by the adult male when the infant was 29 months old.

Key words. gibbon behavior, activity pattern, seasonal change, infant carrying by male

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INTRODUCTION

The East Bornean grey gibbon (*Hylobates funereus*) is a globally Endangered species (Geissmann & Nijman, 2008; Roos et al., 2014) found in the northern and eastern regions of Borneo (Grove, 1972; Marshall & Marshall, 1976). Although the songs of East Bornean grey gibbons have been often studied (Haimoff, 1985; Mitani, 1985a–c; Tenaza, 1985; Inoue et al., 2013), there has been little information concerning East Bornean grey gibbon behavior, especially with regard to activity patterns and time budgets except for the study of Leighton (1987). According to her study, East Bornean grey gibbons ate fruit 62% and leaves 32% of the diet. They spent 4% of their activity time singing, less than 1% grooming and less than 1% playing.

Gibbons (Family Hylobatidae) are arboreal apes restricted to the tropical and sub-tropical forests of Southeast Asia, South China, Bangladesh and Northeast India. Gibbons are frugivorous (Gittins & Raemaekers, 1980; Leighton, 1987). They eat mostly ripe fruits and also large amounts of figs, of which the latter provide a stable food source to meet their basic energetic requirements (Elder, 2009). Gibbons eat more fruit when it is available (Chivers, 1974; Ahsan, 1994; Bricknell, 1999), although, young leaves, flowers, insects (Ahsan, 1994; Chivers, 1984; Bartlett, 2007) and bird eggs (Carpenter, 1940) are also eaten. The daily path lengths of gibbons vary seasonally in response to the abundance of preferred food resources (Raemaekers, 1980; Bricknell, 1999; Bartlett, 2009). Gibbons arrive at sleeping trees several hours before nightfall (Chivers, 1974; Reichard, 1998; Ahsan, 2001; Cheyne, 2010). Gibbons usually live in monogamous social system consisting of a mated pair and their offspring. Monogamy is generally considered to evolve in response to a need for male care (Wittenberger & Tilson, 1980; Clutton-Brock, 1989; Gubernick et al., 1993). However, direct paternal care by male gibbons have hardly been reported other than in siamangs (*Symphylangus syndactylus*), except an anecdotal evidence of infant-carrying by a male western Hoolock gibbon (*Hoolock hoolock*) (McCann, 1933).

The Danum Valley Conservation Area (DVCA) in Sabah, Malaysian Borneo, where East Bornean grey gibbons are present, provides an opportunity to study this little known and endangered primate. There are seasonal fruit-rich and

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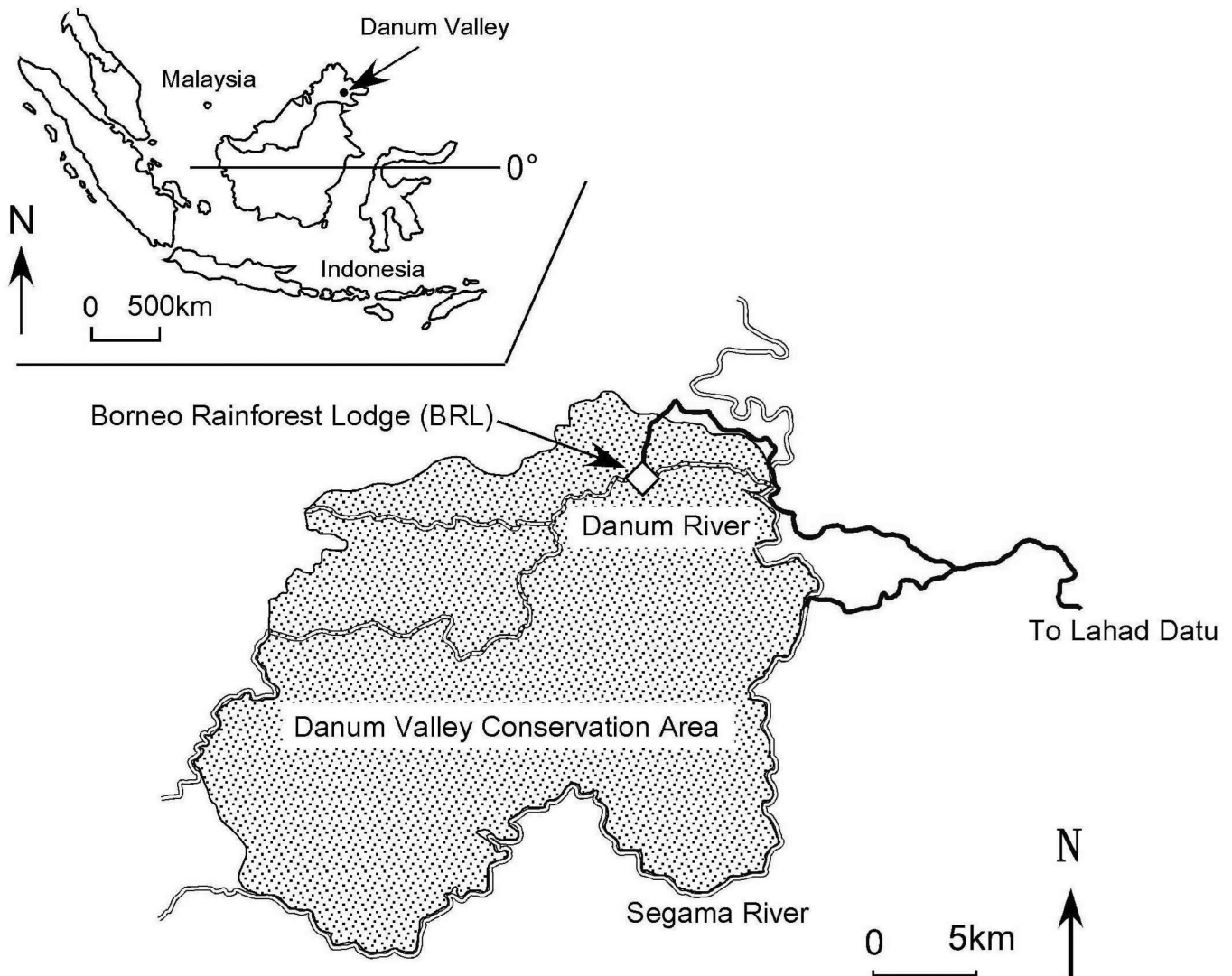
Fig. 1. Location of the Borneo Rainforest Lodge (BRL) in the Danum Valley Conservation Area (DVCA; arrow), Sabah, Malaysia.

fruit-poor periods in the DVCA (Kanamori et al., 2010). In this area, the dry season occurs during April to September and the wet season occurs during October to March (Yasuma & Andau, 1999). The fruit-rich period is often in the dry season and fruit-poor period is in both dry season and wet season. We hypothesized that East Bornean grey gibbons of the DVCA would show seasonal variation in activity patterns according to changes in weather conditions and fruit abundance. To test this hypothesis, we investigated their activity budgets and daily path lengths in both dry season (August and May–June) and wet season (December) from 2003 to 2008 and from 2011 to 2013. During the study period, fruit were abundant in August and scarce in May–June and December. The height where East Bornean grey gibbon activities occur and travel order of one group was also investigated. As we hypothesized that males of East Bornean grey gibbons, like siamangs and western Hoolock gibbons, also participate in infant carrying, we observed travel order of one group from 2009 to 2013.

METHODS

Study area and subjects. Our study was conducted around the Borneo Rainforest Lodge (BRL) in the Danum Valley Conservation Area (DVCA) located in Sabah, Malaysian Borneo (Fig. 1). This area consists of primary rainforest. The dry season in the area usually occurs during April to September and the wet season usually occurs during October to March (Yasuma & Andau, 1999).

The East Bornean grey gibbons we studied were members of the two groups. We named them the SAPA group and the JACUZZI group (Fig. 2). We collected activity data for 3 adult gibbons; the SAPA male, the JACUZZI male and the JACUZZI female. The SAPA group whose territory was close to the BRL had been exposed to many rangers, nature guides and tourists since the opening of the BRL in 1994, and had become habituated to humans. Although the JACUZZI group was not well habituated, it became fully habituated in June 2011 after we followed the group for 20 days since December 2009. The territories of the two groups were located near the BRL (5°01'N, 117°44'E; elevation: approx. 180 m a.s.l).
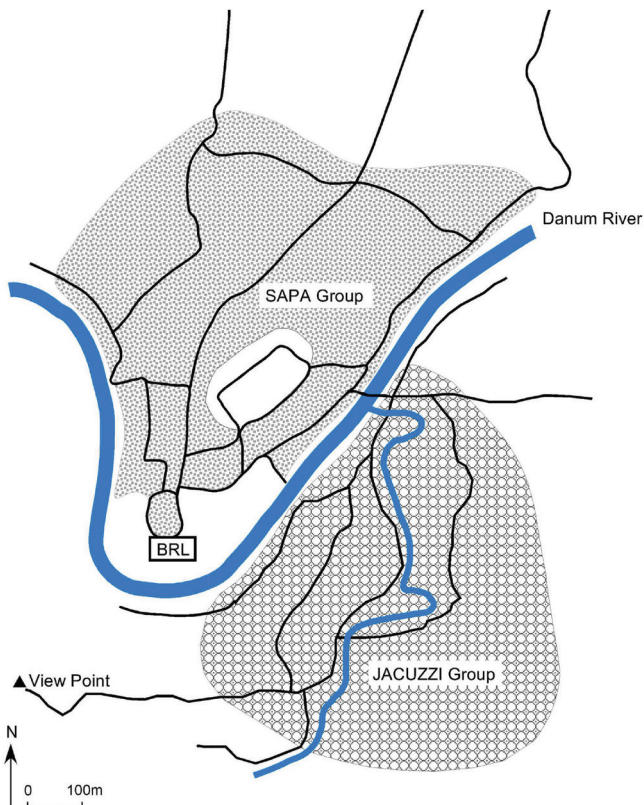
Fig. 2. Location of the BRL, the territory of the SAPA group and the territory of the JACUZZI group. The grey area represents the territory.

During our study period, the SAPA group initially consisted of four individuals: an adult male, an adult female, an adolescent female, and an immature male. However, the adult female disappeared in April 2005, the adolescent female left the SAPA group in October 2006, and the immature male died in April 2008. The SAPA male disappeared in August 2009 and the group disappeared. Therefore, the number of group members was reduced from four to one in our study period. It was unclear why family members disappeared or died. During our study period from 2011–2013, the JACUZZI group initially consisted of three individuals: an adult male, an adult female and a male infant. During our preliminary study period for the JACUZZI group from 2009 to 2010, a male infant was born in January 2010. We observed the infant from June 2010 (5 months old) to December 2012 (35 months old). He and his mother (the JACUZZI female) disappeared in March 2013. After the JACUZZI female disappeared in March 2013, a new adult female joined the JACUZZI group in April 2013. Therefore, the number of group members from 2009 to 2013 changed in the order of two, three and two. The study period included two mast fruiting events (July–August 2005 and May–September 2007). Species names of fruits eaten by the SAPA male in two mast fruiting events were shown in Appendix A.

Data collection and analysis. With the aid of field assistant, we conducted successive 4–7 days follow-up observations two times a year in August (dry season) and in December (wet season) for the SAPA male. We also conducted same observations two times a year in May–June (dry season)

and in December (wet season) for the JACUZZI adult pairs. All observations occurred between 0530–1600 hours. We recorded activity of the SAPA adult male every August and December from 2005 to 2008 and activities of the JACUZZI adult pairs every May–June and December from 2011 to 2013. Activity was focally observed every 10-minute. We recorded activity as sing, move (move and travel), feed (fig), feed (non-fig fruit), feed (leaves/flowers/others), play, groom, rest. As gibbons were occasionally screened from view by trees or leaves, we could not observe them all the time. Thus, we recorded 89.3% of the SAPA male's activities, 96.2% of the JACUZZI male's activities and 95.4% of the JACUZZI female's activities. Height of activity was measured using a Laser Rangefinder (Nikon Laser 550 AS) in addition to activity data. Height of activity of the SAPA male was observed from August 2007 to December 2008. For the JACUZZI male, it was observed from June 2011 to May 2013.

Boundary of home range was estimated from the cumulative day-range map of each group (Bartlett, 2008). When we followed gibbon groups, we traced subject's travel route on a map of the study site every 10-minute, using a handheld global positioning system unit (Garmin GPSMAP 60CSx, Kansas City, USA). As neighbour groups were not habituated, we could not follow them. So, it was not clear how much home range overlapped with the neighbouring groups. Thus, this home range approximation shows a total home range size including the overlap. The home ranges were estimated by using square-grid method. A grid with 100 m^2 (10×10 m) square cells was superimposed over the home range map, and the number of cells included in the area was counted. If more than one-half of any square was within the home range, we counted it as a full square and if less than one-half of any square was within the home range, we ignored it.

Travel distance and sleeping time (time of night-tree entry) were also recorded as often as possible. Travel routes were logged on a map of the study site by using a handheld GPS unit during the group follows, and travel distances were measured using a digital curvimeter (COMCURVE-9JR Koizumi Sokki Mfg. Co., Ltd. Japan). Sleeping time was defined as time entering sleeping tree. We recorded the time of subject's entering sleeping tree and then continued to observe it for at least 30 min until it went to sleep. At 0500 hours the next morning, we went under the sleeping tree and observed the animals waking up to confirm their sleeping tree. Travel distance and sleeping time of the SAPA male was recorded every August and December from 2003 to 2008. For the JACUZZI male, they were recorded every May–June and December from 2011 to 2013. We tested differences of travel distances and sleeping times of the SAPA male among seasons using the Student paired t-test. In order to elucidate the developmental process of the JACUZZI infant and how gibbon parents contact with their offspring, travel order of the JACUZZI group was recorded as often as possible in our 55 days' following from December 2009 to May 2013. Travel order was counted while the group was moving from one tree to another. When gibbons traveled over several trees without stopping, it was counted as one
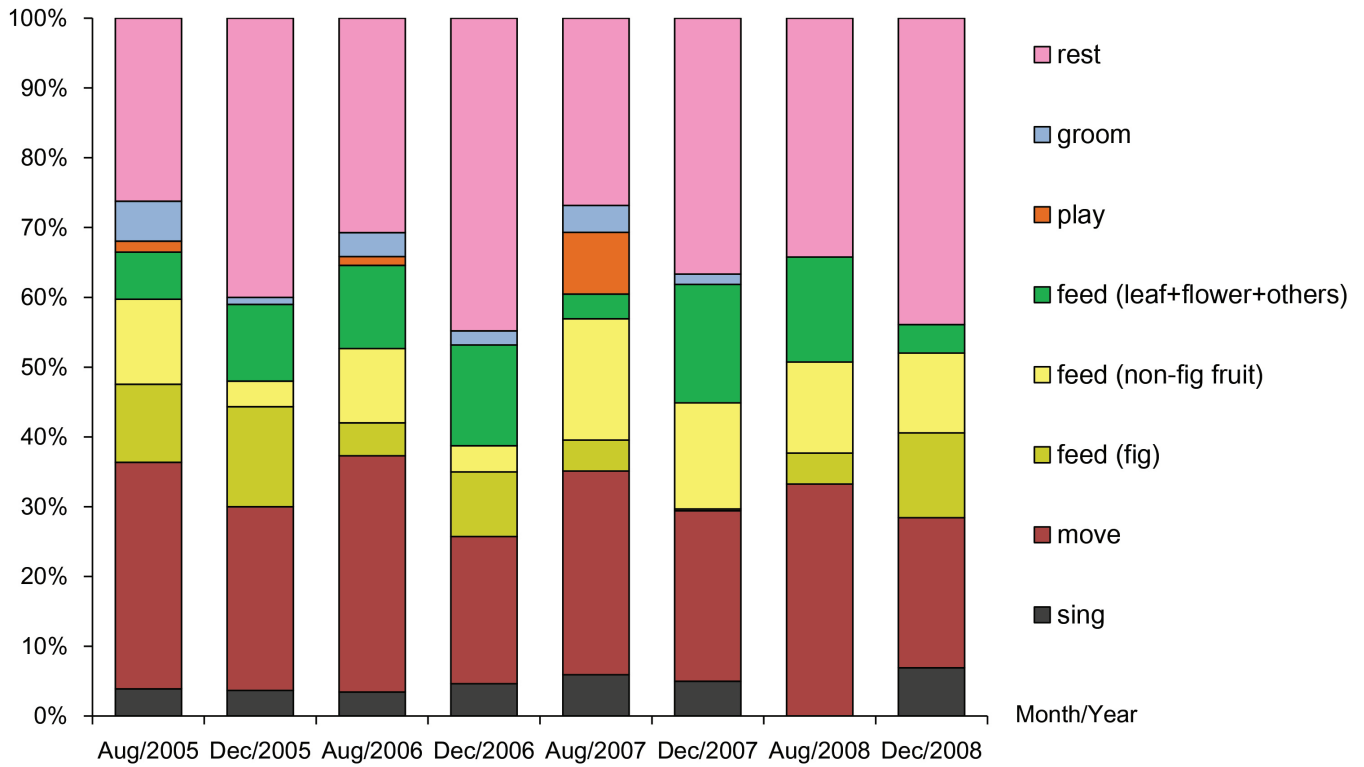
Fig. 3. Activity budget of the SAPA male in both wet season (December) and dry season (August) from 2005 to 2008.
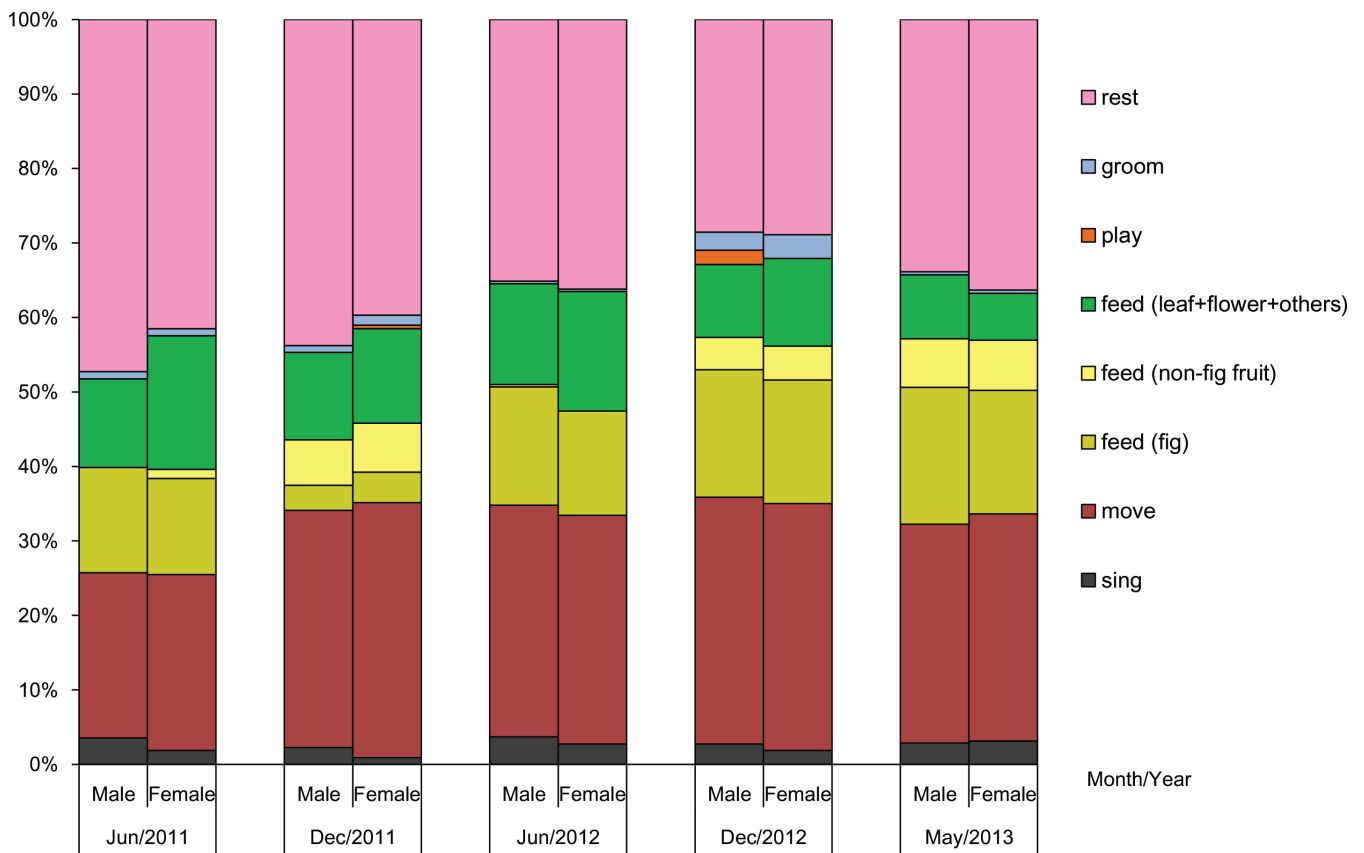

Fig. 4. Activity budget of the JACUZZI male and the JACUZZI female in both wet season (December) and dry season (May–June) from 2011 to 2013.
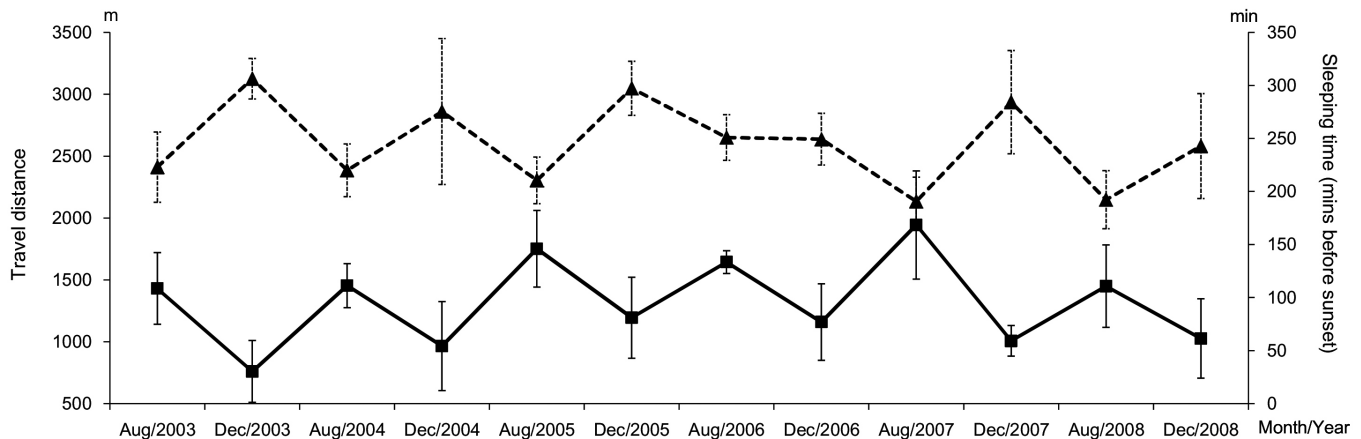
Fig. 5. Average daily travel distance and average sleeping time of the SAPA male for August (dry season) and December (wet season) from 2003 to 2008. Travel distance was counted for 38 days in August and for 35 days in December. Sleeping time was counted for 39 days in August and for 37 days in December. Solid line: travel distance. Dotted line: sleeping time.

RESULTS

We accumulated over 180 hours (16 days in August and 12 days in December) of observations from 2003 to 2004 and 544 hours (36 days in August and 29 days in December) of observations from 2005 to 2008 of the SAPA group. We accumulated over 247 hours (19 days in May–June and 16 days in December) of observations from 2011 to 2013 of the JACUZZI group.

Seasonal variations in activity budgets. Comparison of activity budget in dry season with wet season revealed that activity budget of the SAPA male varied seasonally (Fig. 3). He spent 32.2% (range: 29.2–33.9%) of the observation time moving, and 29.6% (range: 26.2–34.2%) resting in the dry season (August from 2005 to 2008). In contrast, he spent 23.2% (range: 21.1–26.3%) of the observation time moving, and 41.3% (range: 36.7–44.8%) resting in the wet season (December from 2005 to 2008). The percentage of time spent moving during the dry season was significantly higher compared to during the wet season (Student paired t-test: t_3=4.43, p<0.05), and the percentage of resting time in August was significantly lower compared to December (Student paired t-test: t_3=−9.80, p<0.01). The percentage of resting time was especially low during the dry season in 2005 and 2007 when mast fruiting occurred in the DVCA. He engaged in moving for a longer time and in resting for a shorter time during the dry season compared to the wet season. The percentage of time spent on social activity (playing plus grooming) was higher in August from 2005 to 2008 (average: 5.9%) than in December from 2005 to 2008 (average: 1.1%).

On the other hand, the activity budget of the JACUZZI male and the JACUZZI female did not differ between dry season (May–June) and wet season (December) (Fig. 4). Instead, the time spent moving gradually became longer from 2011 to 2012 (Fig. 4). The JACUZZI male's time spent moving increased from 22.2% in June 2011 to 33.2% in December

2012 and his time spent resting decreased from 47.3% to 28.5% during the same period when the infant of the JACUZZI group grew up from 17 months old to 35 months old. The JACUZZI female's time spent moving also increased from 23.6% in June 2011 to 33.2% in December 2012 and her time spent resting decreased from 41.5% in June 2011 to 28.9% in December 2012.

The mean feeding time of the SAPA male devoted to fruits was 19.6% (range: 15.4–23.4%) in the dry season (August from 2005 to 2008) and 17.7% (range: 13.0–23.6%) in wet season (December from 2005 to 2008). The mean feeding time of the JACUZZI male devoted to fruits was 18.0% (range: 14.1–24.9%) in dry season (May–June from 2011 to 2013) and 14.9% (range: 9.5–21.5%) in wet season (December from 2011 to 2013). The mean feeding time of the JACUZZI female devoted to fruits was 16.5% (range: 14.0–23.3%) in dry season (May–June from 2011 to 2013) and 15.5% (range: 10.7–21.1%) in wet season (December from 2011 to 2013). There was no appreciable difference between dry season and wet season in feeding time devoted to fruits in both two groups. The ratio between the feeding time devoted to figs and the feeding time devoted to non-fig fruits was not constant in each period. Feeding time of the female was longer than the male when the infant was from 17 months old (female; 32.1%, male; 26.0%) to 23 months old (female; 23.4%, male; 21.2%) (Fig. 4). Two males spent on average 0.13% of their time feeding on flowers.

Home range size, daily travel distance and sleeping time. Home range of the SAPA group covered approximately 34 ha, the boundaries of which were determined during >724 hours of observations from 2003 to 2008. Home range of the JACUZZI group covered approximately 33 ha, the boundaries of which were determined during >247 hours observations from 2011 to 2013.

A significant difference in travel distance of the SAPA male was found between dry season (August) and wet season (December) from 2003 to 2008 (Fig. 5, Student paired t-test: t_5=7.73, p<0.01). A significant difference in sleeping time of the SAPA male was also found between dry season
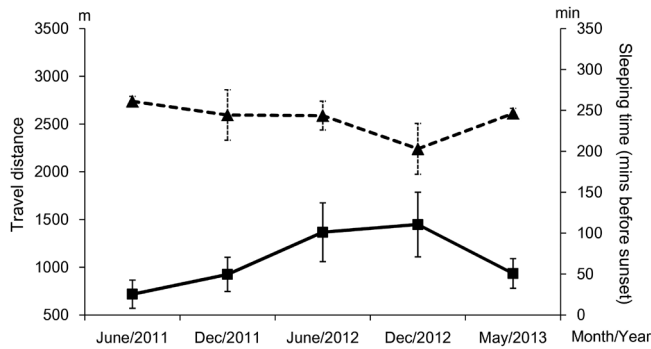
Fig. 6. Average daily travel distance and average sleeping time of the JACUZZI male for May–June (dry season) and December (wet season) from 2011 to 2013. Travel distance was counted for 13 days in August and for 13 days in December. Sleeping time was counted for 14 days in August and for 15 days in December. Solid line: travel distance. Dotted line: sleeping time.

(August) and wet season (December) during same period (Fig. 5, Student paired t-test: $t_5=-4.23$, $p<0.01$). On the other hand, we found no significant difference between dry season (May–June) and wet season (December) in travel distance and sleeping time of the JACUZZI male from 2011 to 2013 (Fig. 6). The two male gibbons showed the same tendency that travel distance was long when sleeping time was late, although it was not statistically significant. The mean daily path length for the SAPA male was 1.34 km per day (SD=0.44, range: 0.37–2.66, N=73) and it for the JACUZZI male was 1.10 km per day (SD=0.36, range: 0.61–1.84, N=26). The mean daily sleeping time for the SAPA male was 243 mins before sunset (SD=50, range: 156–384, N=76) and it for the JACUZZI male was 237 mins before sunset (SD=30, range: 172–307, N=29). In our

study area (Time zone; UTC/GMT +8 hours), sunrise time in August was ranged from 0603–0605 hours and sunset time was ranged from 1816–1826 hours. Sunrise time in May–June was ranged from 0555–0600 hours and sunset time was ranged from 1815–1825 hours. Sunrise time in December was ranged from 0602–0617 hours and sunset time was ranged from 1753–1807 hours.

Diurnal activity cycle. Analysis of diurnal activity cycles of three gibbons from 0530–1600 hours showed that male gibbons started singing solo songs before dawn, and the three gibbons sang duet songs until around noon (Fig. 7). The percentage of time spent moving was constant in the daytime. The percentage of time spent feeding slightly decreased (from an average of 39.3% to 33.7%) but the percentage of time spent resting slightly increased (from an average of 14.4% to 24.9%) from 0600–0950 hours to 1000–1350 hours. The percentage of time spent social activity (playing plus grooming) slightly increased (from an average of 1.6% to 4.0%) from 0600–0950 hours to after 1000–1350 hours.

Height of activity. The mean canopy height in the DVCA was approximately 45 m (Willott, 1999). The tallest tree we measured around the BRL was 85 m. The three gibbons typically stayed above 10 m in the early morning and in the evening and nearly half of the time was spent below 30 m from 0600 to 1350 hours (Fig. 8). They sometimes moved below the height of 20 m (Fig. 9). The percentage of time spent moving below the height of 20 m out of the total time spent moving was about half (SAPA male: 54.5%, JACUZZI male: 52.2%, JACUZZI female: 48.1%). Gibbons sang at heights from less than 10 m to 60 m. The SAPA male stayed at lower place than the JACUZZI gibbons in the daytime.
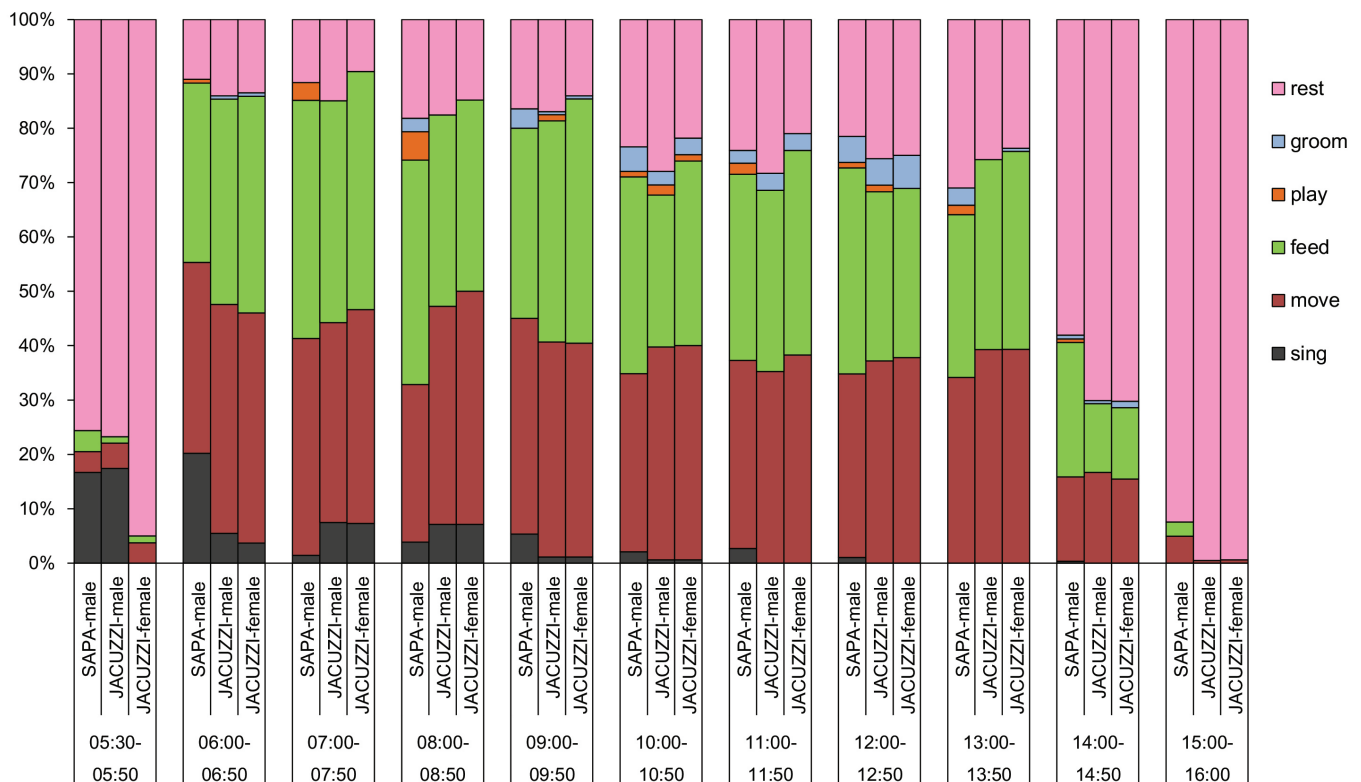

Fig. 7. Diurnal activity cycle of three gibbons (two males and one female) from 0530−1600 hours.
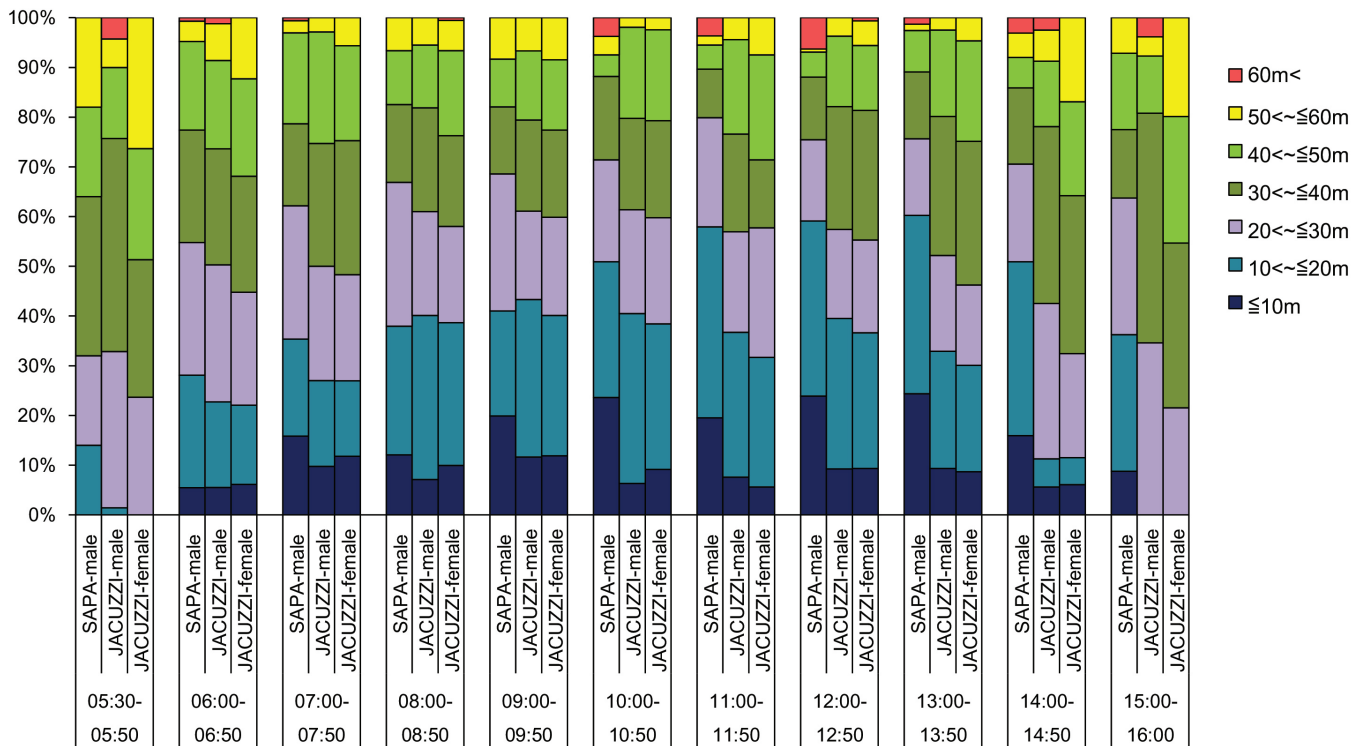
Fig. 8. Heights of diurnal activity of three gibbons (two males and one female) from 0530–1600 hours.
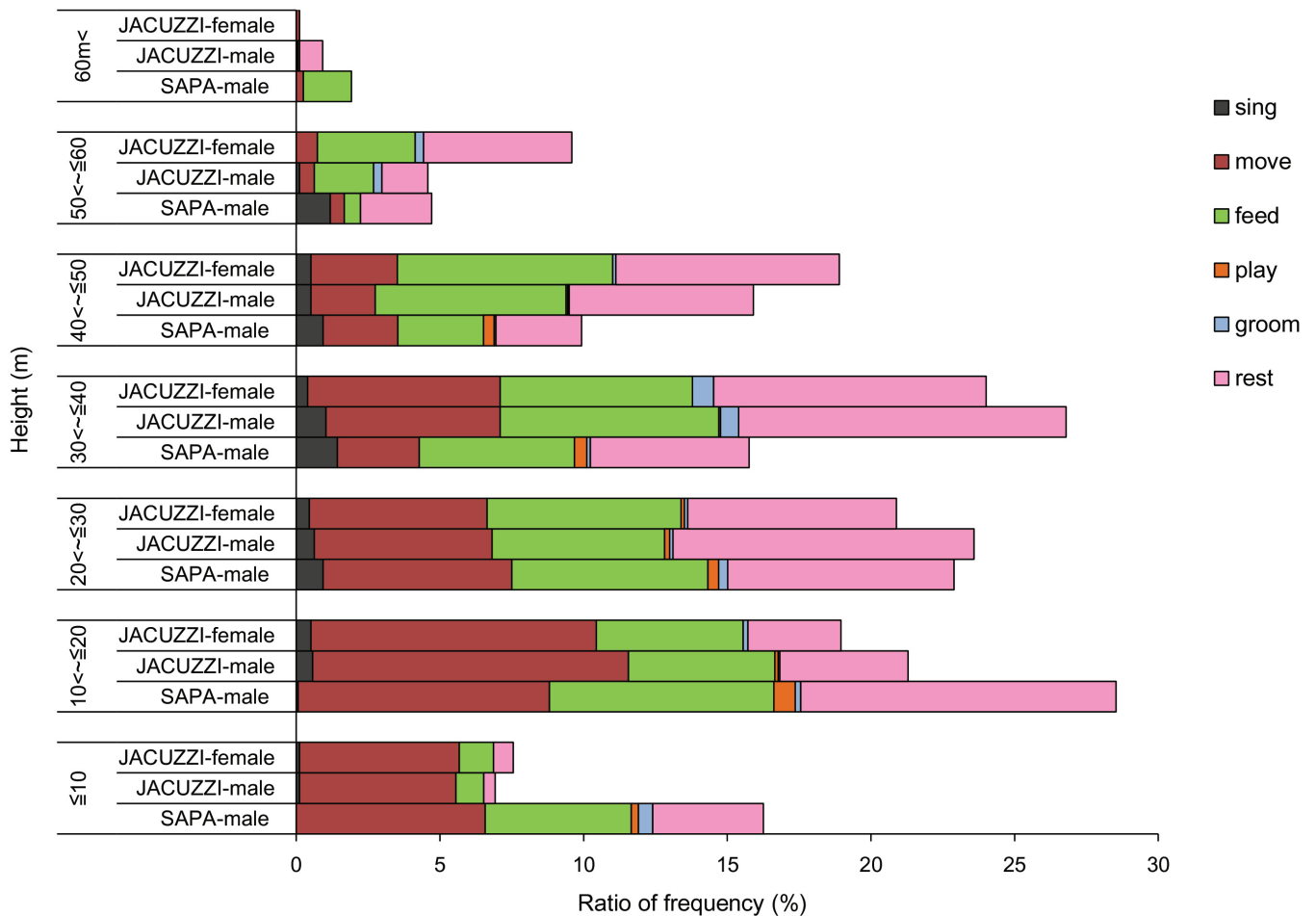

Fig. 9. Activity of three gibbons (two males and one female) at each height.

Table 1. Travel order of the JACUZZI group.

Observation Period		Dec 2009	June 2010	Dec 2010	June 2011	Dec 2011	June 2012	Dec 2012	May 2013
Age of Infant (month)		No Infant	5M	11M	17M	23M	29M	35M	No Infant
Travel order (%)	Male – Female	23.3	0.0	0.0	0.0	0.0	0.0	0.0	36.1
	Female – Male	76.7	0.0	0.0	0.0	0.0	0.0	0.0	63.9
	Male with Infant – Female	0.0	0.0	0.0	0.0	0.0	3.8	0.0	0.0
	Male – Female with Infant	0.0	40.5	32.7	25.0	10.3	1.9	0.0	0.0
	Female with Infant – Male	0.0	59.5	67.3	55.9	32.7	7.7	0.0	0.0
	Male – Female – Infant	0.0	0.0	0.0	0.0	3.2	4.8	11.0	0.0
	Male – Infant – Female	0.0	0.0	0.0	2.9	10.9	29.8	17.8	0.0
	Female – Male – Infant	0.0	0.0	0.0	0.0	1.3	1.0	11.0	0.0
	Female – Infant – Male	0.0	0.0	0.0	4.4	31.4	34.6	45.8	0.0
	Infant – Male – Female	0.0	0.0	0.0	1.5	0.0	1.0	0.8	0.0
	Infant – Female – Male	0.0	0.0	0.0	10.3	10.3	15.4	13.6	0.0
N		43	42	55	68	156	104	118	36
Total observation time (hour)		39.6	35.8	39.0	45.3	56.1	43.0	57.5	45.0

The JACUZZI female spent more of her time at higher up in the trees in the early morning and late afternoon compared to the male. We observed only once that the JACUZZI male climbed down to the ground in order to feed on mushrooms.

Travel order of the JACUZZI group. The female led travel more often than the male in every observation period (Table 1). The JACUZZI female led the group to sleeping trees 20 out of 26 times during the period of June 2011 to May 2013. In our observation period from December 2009 to May 2013, the infant started to travel independently from 17 months old and traveled completely by himself when he was 35 months old. Percentage of his travel clinging to his mother decreased from 80.9% to 0.0% between 17-month-old and 35-month-old. The infant often traveled between the male and the female. We observed infant carrying by male when the infant was 29 months old. In all four cases, it lasted about 10–20 seconds. All infant carrying by the male occurred above or along a small river where the height of the trees above or along the river was low (10 m or less). When the group came near to a small river and the female happened to be separated far back from the infant, the male held the infant and moved along or crossed the river carrying him.

DISCUSSION

Seasonal variations in activity budgets. In our study, one male (SAPA male) showed seasonal differences in the activity budget. He spent more time moving than resting during the dry season but did the opposite during the wet season, without a significant difference in feeding time. The percentage of time spent on social activity (playing plus grooming) in August was higher than that in December. Travel distance in August was longer than that in December and sleeping time in August was later than that in December. In the DVCA, there were usually few fruits available in December and an abundance of fruits in August (Kanamori et al., 2010). Our results might show that the SAPA male spent more time engaged in moving, playing and grooming, traveled longer and entered sleeping tree later when fruit was abundant. The other study male (JACUZZI male) did not show seasonal differences between seasons. It might be partly due to the fact that there were few fruiting trees in both dry season (May–June) and wet season (December) during the study period (pers. obs.). As we did not have rainfall, gibbon activity and fruiting data throughout the year, we could not conclude clearly about the relation between seasonality of rainfall and gibbon activity.

The percentage of time devoted to fruit-feeding by the East Bornean grey gibbons showed no appreciable difference between dry season and wet season. This result is consistent with studies that show that gibbons are frugivorous animal that are highly dependent upon fruits (Gittins & Raemaekers, 1980; Leighton, 1987). Less fruit dependent species, such as the orangutan are known to switch to other food items when fruits are scarce. Kanamori et al. (2010) reported that the percentage of fruit-feeding for orangutans living around the BRL changed from 11.7 to 100% across different months of the year in response to seasonal changes in fruit production.

Home range size, daily travel distance and sleeping time. Home range size of our study groups, which ranged from 33–34 ha, was consistent with a previous study by Leighton (1987) that showed that mean home range size of East Bornean grey gibbons was 36 ha (range: 33–43). We rarely observed intergroup encounters within 50 m during the study period; two times for the SAPA group and five times for the JACUZZI group. As encounters occurred in a limited area around range boundary except for one episode, the overlap in home range between groups was considered to be small. Rates of intergroup encounters of other East Bornean grey gibbon studies were as low as once a month (Mitani, 1985c; Leighton, 1987). Other studies on gibbons also report some degree of home range overlaps with the neighboring group (Reichard & Sommer, 1997). The overlap of the territories is about 15% in the Sabangau National Park, Central Kalimantan, Indonesia (Cheyne, 2010) and 64% in Khao Yai National Park, Thailand (Reichard & Sommer, 1997). The percentage of the overlap is significantly different depending on the species or the region.

The mean daily path length for the two groups was 1.27 km per day. Travel distance of gibbons may differ according to several factors such as species, climate and region. Leighton (1987) showed that average daily travel distance for East Bornean grey gibbons was 0.85 km. Bartlett (2007) showed that the normal daily travel distance for white-handed gibbons in Khao Yai was 1.30 km. On the other hand, Cheyne (2010) showed average daily travel distance for Bornean agile gibbons (*Hylobates albibarbis*) in the Sabangau National Park is 2.43 km and travel distances in dry season are higher than those in wet season. Raemaekers (1980) and Bartlett (2008) also stated that daily path length varies seasonally in response to the abundance of preferred resources. Daily path length of the SAPA male was shorter in the dry season compared to that in wet season. The SAPA male might decrease activity time and travel distance in December in order to decrease energy costs because he could not have sufficient nutrition intake from fruits in December. There was no clear pattern in the daily path length of the JACUZZI male across the dry and wet seasons. The travel distance of the JACUZZI male increased as the infant of his group grew older. According to Cheyne (2010), groups without infants travelled farther than groups with ventral infants. The JACUZZI male and his group members might have restricted most of their activity except feeding and resting, because female with ventral infant had to expend a great deal of energy through her lactation and carrying infant. We suppose that the female would affect the travel of the JACUZZI male. As the infant became heavier as he grew older, the female carrying a heavy infant may not be able to move long distances. In June 2011, the infant was 17 months old and was about one-third of an adult's body size. Then, the female carried him 80.9% of travels (Table 1). However, from 17 months old to 29 months old, the infant became more independent as he grew older. In this period, the percentage at which the infant traveled independently increased from 19.1% to 100.0% (Table 1). This might decrease the travel cost to the group. This was one reason that travel distance gradually increased. It was unclear why travel distance decreased after the infant and his mother disappeared in March 2013.

Gibbons usually retire to sleeping trees several hours before sunset. Our subjects entered night trees, 156 to 384 mins (mean 240 mins) before sunset. This result is similar to the Bornean agile gibbons in the Sabangau National Park, which entered the sleeping tree 219 to 297 mins (mean 257 mins) before sunset (Cheyne, 2010).

What factors may influence the time to enter sleeping trees? The SAPA male entered sleeping trees in the late afternoon in August (fruit rich; dry season) but he entered them in the early afternoon in December (fruit poor; wet season). However, the JACUZZI male did not show seasonal difference between May–June (fruit poor; dry season) and December (fruit poor; wet season) in entering time to sleeping trees. Chivers (1974) reported that siamangs entered night trees earlier when food availability decreased. Sleeping time of gibbons around the BRL might also be influenced by fruit abundance.

Reichard (1998) suggested that gibbons enter night trees early as an adaptive response to avoid predators. In the DVCA, predation pressure is considered to be high. Kanamori et al. (2012) reported that a juvenile orangutan was probably wounded by a Sunda clouded leopard (*Neofelis diardi*) near the BRL. Mr. Amshahri Sari who was a ranger of Imbak Canyon Conservation Area 80 km apart from the BRL, observed an infant gibbon that was attacked by an eagle. This eagle attacked an infant gibbon when it was separated far from its parents, caught it and flew away. In our study period, two infant gibbons and three adult gibbons disappeared or died. As predators such as clouded leopards, pythons and eagles were often observed around the BRL, some of them were likely to be attacked by predators. Hence, this hypothesis may also apply to gibbons around the BRL.

Cheyne (2010) suggested that the early entry to sleeping trees could be to avoid food competition with monkeys and orangutans, which were active up to and beyond sunset. If study gibbons encountered pig tailed macaques or orangutans at the feeding trees, the gibbons sometimes vacated the feeding tree, allowing them to take possession of the food tree. She indicated that gibbon species living with orangutans enter the sleeping tree significantly earlier than gibbon species living without orangutans. As we often observed that gibbons competed with these animals for feeding trees near the BRL, Cheyne's hypothesis may also be applicable to our subjects.

With regard to the relation between night-tree entry time and sunset time, Ahsan (2001) found that the start and end of the active day in the hoolock gibbon (*Hylobates hoolock*) was highly correlated with sunrise and sunset, but was also influenced by the weather. In the DVCA, there is little difference in sunset time between May–June and August. But night-tree entry time was different between May–June and August. As night-tree entry time was different between May–June (mean: 213 mins before sunset) and August (mean:

251 mins before sunset), this result might show that the end of the active day was not exactly correlated with sunset time. As a result, night-tree entry might be influenced by combined factors such as fruit amount, predator avoidance and fruit competition with other animals.

Diurnal activity cycle. Diurnal activity cycle showed males sang before and around dawn. It was consistent with the singing behavior of East Bornean grey gibbons (Mitani, 1984) and other gibbon species (Tenaza, 1976; Mitani, 1988; Geissmann & Nijman, 2006). After dawn, males and females sang duet songs during the morning hours. The percentage of time spent moving was constant in the daytime. The percentage of time spent feeding slightly decreased and the percentage of time spent resting increased after 1000 hours until night-tree entry. This pattern is not consistent with the activity pattern of other species that feeding had two peaks of high activity levels in the early-mid morning and in the mid-late afternoon, and resting had a peak of high activity level around noon (Bartlett, 2009; Fan et al., 2008). Gibbons in the DVCA might avoid prolonged resting in the middle of the day because of combined factors such as fruit amount, predator avoidance and fruit competition with other animals.

Height of activity. Gibbons did not always use high parts of forest trees for their activities. Gibbons stayed at high areas (predominantly above 30 m) in the early morning and in the late afternoon, but descended to lower areas (mostly below 30 m) to forage in between those time periods. In order to avoid terrestrial predators, gibbons might stay out of reach high up in the trees from dusk until dawn. The average height where the JACUZZI female conducted her activities was higher than that of the JACUZZI male at the sleeping trees. It was consistent with a previous study showing that adult females with infants selected significantly higher sleeping trees than adult males (Reichard, 1998). The SAPA male tended to stay at lower heights than the JACUZZI male. This probably reflects the difference in habituation level between two males. The SAPA male was well habituated and moved to lower areas near us but the JACUZZI male was sometimes afraid us and moved to higher spots away from us.

Travel order and infant carrying by male. The female of the JACUZZI group led group travel more often than the male. Many studies have shown that female gibbons lead most travel bouts (Chivers, 1974; Tenaza, 1975; Reichard & Sommer, 1997). It was also consistent with the previous study showing that females with infants usually went into a sleeping tree first (Reichard, 1998). Infant carrying by male had been hardly observed in the wild for most gibbon species (Hylobatidae) other than siamangs (*Symphalangus syndactylus*) (Chivers, 1974; Chivers & Raemaekers, 1980; Gittins & Raemaekers, 1980). Our observation was the second report of infant carrying by *Hylobates* male since McCann (1933). Our finding suggests that infant carrying by male occurs for only a short time within a limited period under a specific condition. Although this was only observed in one group, the observation of infant carrying by male may yield an important clue as to the relation between monogamous social system and male care.

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APPENDIX

Appendix A: Fruit list that the SAPA male ate during mast fruiting season (August 2005 and August 2007).

Family	Species
Alangiaceae	*Alangium javanicum*
Annonaceae	*Uvaria sarsogonensia*
Capparaceae	*Cratewa religiosa*
Dipterocarpaceae	*Parashorea tomentella*
Ebenaceae	*Diospyros marcrophylla*
Euphorbiaceae	*Neoscortechinia forbesii*
Maliaceae	*Aglaia* sp.
Moraceae	*Ficus* sp. *Ficus xylophylla* *Garcinia forbesii*
Sapindaceae	*Nephenium ramboutanake*
Sapotaceae	*Madhuca kunstleri*