



HOKKAIDO UNIVERSITY

Title	Feeding and Ranging Behaviors of Proboscis Monkey <i>Nasalis larvatus</i> in Sabah, Malaysia
Author(s)	Matsuda, Ikki; 松田, 一希
Degree Grantor	北海道大学
Degree Name	博士(地球環境科学)
Dissertation Number	甲第8718号
Issue Date	2008-03-25
DOI	https://doi.org/10.14943/doctoral.k8718
Doc URL	https://hdl.handle.net/2115/34633
Type	doctoral thesis
File Information	Matsuda.pdf



**Feeding and Ranging Behaviors of Proboscis
Monkey *Nasalis larvatus* in Sabah, Malaysia**

A Ph.D. Dissertation Submitted to
Graduate School of Environmental Earth Science,
Hokkaido University

By

Ikki Matsuda

2008

CONTENTS

SUMMARY	i - iv
INTRODUCTION	1 - 5
STUDY AREA	5 - 7
METHODS	
1. Surveys of topography and vegetation	7
2. Behavioral observation of BE-Group	8 - 10
3. Boat census along the river	10
RESULTS	
1. Number and composition of groups	11
2. Selection of sleeping sites	11 - 13
3. Activity budget	13 - 15
4. Food habits	
4. 1. <i>Vegetation and food menu</i>	16 - 17
4. 2. <i>Spatiotemporal distribution of food sources</i>	17
4. 3. <i>Food preference</i>	18 - 19
4.4. <i>High preference for fruits, especially seeds</i>	19 - 22
4. 5. <i>Seasonal trend of food menu diversity</i>	22
4. 6. <i>Consumption of tree barks, termite nests and water</i>	22 - 23
5. Ranging behavior	
5. 1. <i>Home range</i>	24
5. 2. <i>Travel distance</i>	24 - 25
5. 3. <i>Behavioral core trees</i>	25 - 26
5. 4. <i>Effects of water level on ranging</i>	26 - 27
DISCUSSION	
Feeding Behavior.....	27 - 33
Ranging Behavior and Predation Pressure	33 - 40
Conservation Implications	40 - 42
ACKNOWLEDGMENTS	43 - 44
REFERENCES	45 - 53
11 Tables, 37 Figures and 1 Appendix	

SUMMARY

A one-male group (BE-Group) of proboscis monkey *Nasalis larvatus* consisting of the -male Bejita, six adult females and some immatures was chosen and focal male and females in BE-Group were followed for a total of 1,968 and 1,539 hours, respectively, along the Menanggul River (which is a tributary of the Kinabatangan River), Sabah, Malaysia, focusing on feeding and ranging behaviors from May 2005 to May 2006. In order to determine the availability and seasonal changes of plant species consumed by the focal monkeys, vegetation surveys were carried out in 2.15 ha along 16 200-500 m trails set up in the forest. In addition, sleeping sites of all the groups in the area were surveyed in the evenings of 6-22 days per month using a boat along the river side. The main results were:

1) Sleeping sites of BE-Group were distributed in a wide range of overlap with those of other groups, suggesting no territoriality between different groups on the riverside trees. BE-Group seemed to select their sleeping sites on riverside trees at narrow river locations to reduce the predation chance of clouded leopard and/or to raise the probability of successful river crossing by females (often with infants) and juveniles to escape from predators.

2) As there was no difference in time budget between individuals excluding the category others (grooming + copulation) which contributed very little, the data of all focal monkeys were pooled, and its resting, feeding, moving and others accounted for 76.4%, 19.5%, 3.5% and 0.5%, respectively. In the feeding time, young leaves, fruits, flowers, mature leaves and other food sources constituted 65.9%, 25.9%, 7.7%, 0.03%

and 0.5%, respectively, indicating that the tendency of consuming young leaves was strong in terms of total food amount. However, monthly fruit production of plants positively correlated with monthly fruit-eating and feeding activity of proboscis monkeys, respectively, though young leaf production to young leaf-eating and flower production to flower-eating did not correlate with each other, respectively, and both young leaf and flower production did not correlate with feeding activity. These suggest that fruit production significantly affects the activity budget of proboscis monkeys.

3) In both the male and females, the ratio of feeding time was the highest at 15:00 - 17:00, i. e. shortly before sleeping. As proboscis monkeys require about 50 hours for processing leaves, they may feed on lots of foods in late afternoon to spend the night time not only for sleeping but also for digestion.

4) Total number of plant species consumed by focal monkeys was 188 (127 genera, 55 families). When the availability of each species was estimated from the vegetation survey in which 180 tree and vine species were described and monthly followed their phenology, the actual observed time for consuming them was significantly different from consumption time expected from availability in some species, suggesting that the proboscis monkey is the picky eater. For instance, *Mallotus muticus*, *Ficus binnendijkii*, *Crudia reticulate*, *Lophopyxis maingayi* and so on were positively preferred by proboscis monkeys.

5) The seven focal monkeys spent a total of 177.2 hours for fruit-eating, of which seed-eating constituted 97%, suggesting that the proboscis monkeys seemed to consume the fruits in favor of seeds. Whenever monkeys collected ripe fruits, they abandoned

flesh and consumed only seeds. They fed extensively on the seeds of *Mallotus muticus* trees and *Lophopyxis maingayi* vines which were the most abundant plant species in the study area, although some dominant and predominant species were not consumed or showed negative food preference. Because the proboscis monkeys almost completely grind and digest the seeds of these abundant plant species, in this study site, they may limit too much increase of the predominant species and permit minor plant species to survive in the community.

6) Nonetheless, some seeds of *Antidesma thawaitesianum*, *Nouclea subdita* and *Ficus* spp. remained undigested in the feces of proboscis monkeys. The undigested seeds were small and relatively hard and were found in intact shape. Especially seeds of *Ficus* spp. were often found in feces when the proboscis monkeys often fed on its fruits, and *Ficus* species have been thought to be one of the most important plant species for a lot of wildlife. There is a possibility that proboscis monkeys may play the role of seed dispersal for a few plant species.

7) During 1,968 hours, the BE-Group moved within the range of 138.3 ha. The ranging of proboscis monkey was affected by the location of river crossing points and the availability of foods, in particular fruits.

8) The daily path length of BE-Group ranged from 220 m to 1,734 m (mean: 799 m) which was negatively correlated with fruit availability. The proboscis monkeys were apt to stay within a small range in fruit-abundant seasons.

9) BE-Group sometimes stayed within a limited area to frequently visit a particular tree which produced their favorite foods. Out of positively preferred trees or vines, *Crudia reticulate*, *Cynometra ramiflora* and *Carallia brachiata* could be such

behavioral core trees.

10) Since the water level of the river had a statistically significant effect on the location of BE-Group's sleeping site, when more than 3 m deep water covered the forest floor more than 1 km from both sides of the riverbank towards the inland in seasonal flood, the group slept inside the forest. It may be that the proboscis monkeys are not restricted to the riverbank, which has an uncluttered view for easily finding predators, because of reduced predation pressure by terrestrial animals during times when high water levels prevent predators from hunting.

Thus, the feeding behavior of proboscis monkeys shows a high degree of fruit-eating (or seed-eating) in some seasons, and their extremely wide dietary diversity was demonstrated. Therefore, the ranging behaviors of proboscis monkeys were influenced by availability of fruits. The fruit-eating and fruit availability were one of the key factors to control the feeding and ranging behaviors of proboscis monkeys. In addition to those factors, ranging behaviors, including the sleeping sites selection of proboscis monkeys may be affected by predation pressure. In any case, the riverine forest of at least 800 m from the both river banks is evidently needed for the surviving of proboscis monkeys.

INTRODUCTION

The proboscis monkey (*Nasalis larvatus*) belongs to the subfamily Colobinae, distributed in Asia and Africa that includes 44 species of 7 genera and 15 species of 3 genera, respectively (Groves, 2001; Fashing, 2007; Kirkpatrick, 2007). The monkeys in this subfamily are characterized by a reduced thumb and an enlarged and sacculated forestomach (Napier and Napier, 1967 and 1985; Napier, 1985). The forestomach with fermenting bacteria enables the digestion of cellulose and deactivates toxins in leaves (Bauchop and Martucci, 1968; Kay et al., 1976; Bauchop, 1978; Chivers and Hladik, 1980; Waterman, 1984). The endemic proboscis monkeys in Borneo Island inhabit mangrove, peat swamp and riverine forests. They exhibit sexual dimorphism; that is, the body size of adult males, which have a long and hanging nose, is the largest among colobine species and their weight reaches about 20-24 kg, whereas adult females have a much shorter nose than that of the males and their weight is about 10 kg (Allen and Coolidge, 1940; Schultz, 1942; Napier and Napier, 1985). Furthermore, proboscis monkeys are adept at swimming in rivers and walking on soft mangrove because their hind feet have webbed toes (Napier and Napier, 1967; Napier, 1985). Even though earlier research on proboscis monkeys reported stable or loosely organized multi-male groups (Kern, 1964; Kawabe and Mano, 1972; Jeffrey, 1979; Macdonald, 1982), recent studies have revealed that the monkeys are evidently organized into stable one-male groups consisting of one adult male, several females and their offspring and all-male groups consisting of young males (Benett and Sebastian, 1988; Yeager, 1989 and 1995; Murai, 2004a, 2004b, 2006 and 2007).

Whereas substantial detailed research on Asian and African colobines has been conducted until now (Struhsaker, 1987; Fashing, 2007; Kirkpatrick, 2007), only a little information on proboscis monkeys has been reported because some of their favorite habitats are swampy and thus prevent the observation and tracking of the monkeys in inland forests. Nonetheless, since proboscis monkeys always come back to the riverbank for sleeping (Kern, 1964; Kawabe and Mano, 1972; Jeffrey, 1979; Bennett, 1986a; Bennett and Sebastian, 1988; Yeager, 1989) even though the reason why the riverbank is a preferred sleeping site has not yet been resolved, most earlier long and short-term research has been conducted by observing from a boat on the river while the monkeys are on the riverbank in the early morning and late afternoon.

In the previous boat-based studies on feeding behavior of proboscis monkeys, those conducted over shorter time periods conclude that food habits of proboscis monkeys show a high degree of folivory and low food diversity (Kern, 1964; Kawabe and Mano, 1972; Macdonald, 1982) whereas the importance of fruit-eating in their food habits and relatively higher food diversity is reported in longer term studies (Yeager, 1984 and 1989; Salter, et al. 1985; Bennett and Sebastian, 1988). Since Yeager (1989) reports that the monkeys seasonally changed their food parts (fruit, flower and young leaf), the short-term studies might not cover a long enough period of time to observe their various feeding behaviors, including their fruit-eating. However, in observing proboscis monkeys only from the river by boat for a limited time, there is a limit in the ability to determine their feeding behaviors and whether they have a strong tendency for fruit or leaf-eating because the monkeys spend daytime mostly in the forest. Similarly, it is difficult to estimate the amount of their feeding time in a day when observing from

a boat on the river, although one report on proboscis monkeys by Salter et al. (1985), is conducted both by boat and occasional foot survey, represents the activity budgets and the daily rhythm of feeding amount in a day. According to this report, proboscis monkeys spend most of their time resting, feeding or moving as the amount of these activities differs between forest types and the daily feeding rhythm fluctuates with a peak at 13:00-15:00.

In addition to the feeding behavior of proboscis monkeys, their ranging behavior has not yet been studied in detail as terrain problems also make it difficult to follow the monkeys in the forest. Their ranging behavior is usually investigated from the location of their observed sleeping site by boat survey. The sleeping sites of proboscis monkey's one-male groups overlapped each other (Benett and Sebastian, 1988; Yeager, 1989; Murai 2004a) and their home range sizes, which are estimated by the length of the riverbank used, differ between habitats in one male groups: 315 ha in mangrove forests (Boonratana, 1993); 900 ha in mixed mangrove and lowland forests (Benett and Sebastian, 1988); 137 ha in peat swamp forests (Yeager, 1989); 221 ha in riverine forests (Boonratana, 2000). Only Boonratana's figure of 221 ha in riverine forests is calculated by tracking the monkeys in the forest.

One report suggests that the ranging behavior of proboscis monkeys may be affected by spatial and temporal distribution of food availability (Boonratana, 2000), as reported from other primates (Clutton-Brock, 1975; Raemaekers, 1980; Oates, 1987; Bennett and Davies, 1994; Olupot et al., 1994; Koenig, 2000; Di Fiore, 2003; Kirkpatrick, 2007; Lambert, 2007). It is also said that predation pressures are an important factor affecting ranging behaviors and social systems of primates, although

the estimation of predation rates is difficult as predation events on any type of primate are rarely observed (Cheney and Wrangham, 1987; Miller and Treves, 2007). In proboscis monkeys, three accidental observations of predations on adult males by false gaviail (*Tomistoma schlegeli*) (Galdikas 1985) and by clouded leopard (*Neofelis nebulosa*) (Davis, 1962; Jackson & Nowell 1996) and one case of predation on an adolescent female by false gaviail has been reported (Yeager 1991a). Of the four reports, Yeager (1991a) suggests that the ranging behavior and social system of proboscis monkeys is affected by predation pressure when they cross the river, as this behavior exposes monkeys to a high risk of predation by aquatic predators such as crocodiles.

Compared with the research on feeding and ranging behavior of proboscis monkeys, the research on their social system is the most focused theme in former studies since it is relatively easy to observe the relationship between the groups even by boat from the river. Recent long-term studies suggest that the proboscis monkey has a multi-level society in which one-male groups regularly associate with each other at least along the riverbank (Benett and Sebastian 1988; Yeager 1991b and 1992; Boonratana 2002; Murai 2004a). The degree of association between one-male groups at the riverbank may be influenced by the water level of the river and/or predation pressure (Yeager 1993; Murai 2004a). However, it is still unknown whether the association between the groups is maintained even in the forest.

Because of the limited habitat of proboscis monkeys along the river, the World Conservation Union (IUCN) reported in 1978 that the major threat to their population is habitat loss through logging. Their conservation status has been classified as

“endangered” since 2000 by IUCN, and this species is listed on Appendix I by the Convention of International Trade in Endangered Species (CITES). To conserve this endangered species, several studies for population estimation have been conducted: < 300, 1000, 5000 and 6000 individuals in Brunei Bay, Sarawak, protected reserves in Kalimantan and Sabah, respectively (Bennett, 1986b; Yeager and Blondal, 1992; Sha 2006), while the ecological data for the preservation of proboscis monkeys (especially feeding and ranging data in the forest), which should be useful information when establishing new forest reserves and replanting plant species at logged areas is hardly known.

Thus, as there is a total lack of behavioral data on proboscis monkeys inside the forest in past studies, to understand their ecology and preserve this endangered species, information about this monkey inside the forest is needed in every category. The present study, which is the first systematic research on a one-male group of proboscis monkeys observed not only at the riverbank but also inside the forest throughout a day, provides information focusing on their feeding and ranging behaviors.

STUDY AREA

This study was made from January 2005 to May 2006 in riverine forests along the Menanggul River, a tributary of the Kinabatangan River, Sabah, Malaysia (Fig. 1). Whereas the southern area of the Menanggul River was extensively covered by natural forest, the northern area had been deforested for oil palm plantations except for a legally

protected zone along the river. The riverine forest was inhabited by not only proboscis monkeys but also long-tailed macaques (*Macaca fascicularis*), pig-tailed macaques (*Macaca nemestrina*), silver langurs (*Trachpithecus cristatus*), hose's langurs (*Presbytis hosei*), bornean gibbons (*Hylobates muelleri*) and orangutans (*Pongo pygmaeus*). Although the main objective of this study was to investigate the behavior and food habits of proboscis monkeys, the food habits of other primates were also described facultatively. This area is one of tourism resources, and many boats and tourists visited the Menanggul River (especially in June-September), with the peak in September when an average of 12 boats and 70 tourists were counted per day (Fig. 2).

The rainfall was measured every morning at base camp, using a tipping bucket rain gauge. The air temperature was automatically recorded by a HOBO Water Temp Pro deposited at a lodge near the mouth of the Menanggul River. I firmly stuck a 5 m tall board of Borneo ironwood *Eusideroxylon zwageri* which was scaled at intervals of 10 cm, with 0 cm at the river bottom, onto the floor of river mouth to measure the water level. Whenever I entered the Menanggul River 20-26 days per month, the water level was checked at 18:30-19:00. Mean minimum temperature was nearly constant at about 24°C throughout a year but mean maximum temperature fluctuated between 27.4°C in February and 32.5°C in September (Fig. 3). Annual precipitation from June 2005 to May 2006 was 2,509 mm (Fig. 4A). Although monthly rainfall fluctuated from 90.9 mm in August to 560.6 mm in February, the dry season was not as clear as in the Samunsam Wildlife Sanctuary, western Sarawak, Malaysia (Basiuk, 1985; Bennett and Sebastian, 1988). In parallel with the fluctuation of monthly rainfall, the mean water level at the river mouth was highest in February (345 cm) and lowest in August

(66 cm) (Fig. 4B).

METHODS

1. Surveys of topography and vegetation

Prior to the beginning of regular surveys from May 2005, I made a topographic map of the study areas by using GPS. Along the Menanggul River, datum points were located at intervals of 50 m over an area stretching from the river mouth to a point 6 km upstream. At intervals of 500 m and over an area stretching from the river mouth to a point 4,000 m upstream, 200-500 m long and 1 m wide trails were set up (Fig. 1) by cutting off the floor layer of vegetation for the ready observation and following of proboscis monkeys. Along the trail, I labeled the trees of DBH ≥ 10 cm and vines of diameter ≥ 5 cm which were located on the trail or within 1 m from the edge of the trail, i. e. surveyed width = 3 m. All of the labeled trees and vines were measured DBH and taxonomically identified with the support of the Forest Research Center of Sabah State Forestry Department. Since trails were set up on both riversides, the total number of trails was 16: TR 2 = 200 m long, TR 4 = 400 m, TR 6 = 400 m, TR 8 = 250 m, TR 10 = 400 m and other trails = 500 m each. From May 2005, the trees and vines were visited at the end of each month to follow their phenology, that is, presence or absence of flowers (including floral buds), fruits (including ripe and unripe fruits) and young leaves (including leaf buds).

2. Behavioral observation of BE-Group

Prior to following a particular one-male group, I made a preliminary observation of some one-male groups to choose a group which seemed appropriate for the present study. In the study area, all of the one-male groups were relatively habituated to tourists on the river. However, once researchers attempted to land on a riverbank, the proboscis monkeys became excited and escaped into the forest, but not BE-Group whose -male, Bejita, was unperturbed by the landing researchers and the other members of the group followed his attitude. Then, I carefully approached them almost everyday in the second half of April 2005 to habituate them to researchers. During this preliminary observation, I described some physical characteristics of BE-Group's -male and all adult-female members to identify them from proboscis monkeys of other one-male groups.

From the beginning of May 2005 to May 2006, the focal monkeys (which were all adults) in BE-Group were followed continuously from the time they were found until evening each day through a focal animal sampling method (Altman, 1974). At 06:00-06:30 a. m. of each sampling day, I and two research assistants arrived at the BE-Group's sleeping site which had been determined the previous evening. The -male Bejita was always focal and another focal monkey was chosen from the adult-female members by attempting to avoid the choice of the female followed on the last day. Of the three researchers, one followed the male, one followed the focal female and the other one supported the two followers. They followed the focal monkeys until the BE-Group set up their sleeping site and started sleeping at 18:30-19:00, though, if the focal female was lost from the researcher's sight for more

than 30 minutes, one of the other females was chosen as a new target. The monkeys were followed 11-17 days per month, except in February 2006 when the study area was totally flooded and BE-Group was not discovered for almost one month due to their migration in the forest. In March, when the forest floor was flooded but BE-Group was fortunately found, the focal monkeys were followed by using boat even in the deep forest.

During observations, activities of the focal monkeys were recorded in seconds. The researchers recorded the time the focal monkeys started and ended the following three activities, i. e. resting, moving and feeding, in seconds. Behaviors other than these three categories were treated as others. Resting includes all instances in which the subject was inactive, defecating or urinating. Moving includes any locomotor behaviors resulting in a change in spatial position. Feeding includes the acts of plucking, masticating, swallowing food or drinking water. Others include social and self grooming and copulation. When the focal monkeys were feeding, we recorded whether the food items consisted of young leaves (including leaf buds), flowers (including floral buds), fruits (ripe and unripe fruits), or others (including tree barks and termite nests). The food plants were taxonomically identified *in situ* and recorded, but if the food plant species was yet unidentified, leaves, flowers and/or fruits were collected from the plant for identification at the Forest Research Center. To certify that fruit-eating resulted in the seeds being defecated, some feces were examined *in situ*, though seeds of only a few plant species remained intact. While following Bejita, his geographical points were located by GPS at intervals of 10 minutes. The daily path length of Bejita from one sleeping site to the next sleeping site was considered as

BE-Group's daily path length in this paper, because all group members traveled almost the same route and the focal females rarely moved more than 50 m away from Bejita.

3. Boat census along the river

Proboscis monkeys have been thought to set up their sleeping sites on the riverside trees (Kern, 1964; Kawabe and Mano, 1972; Jeffrey, 1979; Bennett, 1986a; Bennett and Sebastian, 1988; Yeager, 1989) (Fig. 5). In order to observe the distribution of sleeping sites, membership of one-male groups, all-male groups and mixed groups and the number of these groups and solitary monkeys, a boat census was conducted starting from a point 6 km upstream of the river mouth in the evening of 6-13 days per month except in February 2006 when the boat census was carried out in the evening of 22 days partly in search of the lost BE-Group. At 16:00-16:30, we started the boat census from 6 km upstream, went down the river slowly to the river mouth, and finished before it got dark at 18:00-18:30. Whenever a group was found in each census, the member composition was recorded by categorizing the monkeys into five sex & growth stage groups (Table 1). In each boat census, because the survey was carried out traveling only one way on the river, the same groups were not counted double.

RESULTS

1. Number and composition of groups

In each boat census, 2-15 one-male groups were observed, except in February and March when the study area was entirely flooded and almost all of the groups traveled in the forest without returning to the riverbank for sleeping (Table 2). The size of the one-male groups was 2-29 individuals, with a mean number of about 5 females and 5-8 immatures (subadults, juveniles and infants). In addition to the one-male groups, there were a few mixed groups which referred to a loosely bonded predominantly male group with several females, all-male groups and solitary monkeys. The membership of mixed groups and all-male groups seemed unstable. The solitary monkeys were rarely observed and most of the monkeys found were males. Overall, 21-218 individuals of proboscis monkeys were observed in each census, i. e. with 3.5-29.8 individuals / km, suggesting that the number of proboscis monkeys which could be found in the study area at the riverbank fluctuates greatly from day to day due to the differing time each group would return to the riverbank.

2. Selection of sleeping sites

Figure 6 shows the temporal trends of the BE-Group's sleeping sites along riverbanks based on the data obtained from the 13-month observation of this one-male group. They occasionally moved more than 1,000 m per day but usually stayed within a limited range for several weeks or months, frequently crossing the Menanggul River. During the 13-month observation, 261 sleeping sites of BE-Group (confirmed by

full-day observation and boat census) were distributed between 1,500 m and 5,180 m from the river mouth (Fig. 7A). As for other groups, 621 sleeping sites (confirmed by boat census) were distributed between 150 m and 5,650 m from the river mouth (Fig. 7B), with a wide range of overlap with the distribution of BE-Group's sleeping sites, suggesting no territoriality between different groups at least on the riverside trees. The absence or inconspicuousness of between-group hostility is supported by Figure 8 representing that 100 sleeping sites of other one-male groups were located within 200 m from BE-Group's sleeping site. Thirty-seven sleeping sites were located within 50 m, with occasional occurrences in which the same tree was shared. The nearest sleeping sites of other one-male groups were frequently situated on the same riverside with BE-Group's sleeping site (Chi-square test: $\chi^2 = 16.49$ and $p < 0.0001$).

Over a total of 3,506 hours (Bejita: 1,968 hrs; females: 1,539 hrs), river crossings by Bejita and focal adult females were observed 90 times and 65, respectively. The frequency of pooled river crossings for Bejita and adult females was significantly higher at the parts of the river where the width was narrower, between 1,400 m and 5,250 m from the river mouth, which is the range of the riverbank used by BE-Group (Generalized linear models with Poisson error and log link: coefficient -0.053 ± 0.020 and $p(G) < 0.01$). As shown in Figures 6 and 7, BE-Group often (15 times or more) had sleeping sites at 2,650-2,700 m, 3,500-3,550 m and 4,200-4,250 m from the river mouth. At these locations, the Menanggul River was as narrow as 15-20 m in width (Fig. 9A) so that the α -male Bejita almost always successfully crossed the river from tree to tree (Fig. 9B). Whereas females often failed jumping between-trees and fell into the river, their success probability was higher at these locations than at others (Fig.

9B). The ratio of successful river crossings was 93% in the male, 53% in adult females with infants, 56% in adult females without infants and only 32% in juveniles (Fig. 10). Although I did not observe any deaths of the individuals which fell into the river, the Menanggul River is inhabited by estuarine crocodiles (*Crocodylus porosus*) which were thought to be one of the major predators for proboscis monkeys. In following BE-Group, I happened to observe an infant and a juvenile suddenly attacked and victimized by clouded leopard (*Neofelis nebulosa*) on 21 July 2005 and 8 April 2006, respectively (Fig. 11). BE-Group seemed to select their sleeping sites on riverside trees at narrow river locations to reduce the predation chance of clouded leopards and/or to raise the probability of successful river crossing by females (often with infants) and juveniles to escape from predators.

3. Activity budget

Six focal adults, Chi-J , Bul-J , Bul-I , Lun-J , Lun-I , Ara-J and Big-J survived and stayed in BE-Group throughout the 13 months, whereas a subadult female, Ranfan, transferred to another one-male group in April 2006, Chi-I disappeared for unknown reason in December 2005 and Ara-I (Fig. 11A) was victimized by a clouded leopard on 21 July 2005 (Fig. 12). In addition to these members, new infants Big-I and Ara-I were born by Bigmama on 15 March 2006 and Arare on 27 January 2006, respectively, and a new female adult member Midori and her daughter Mi-J transferred into BE-Group from another one-male group on 15 March 2006, though Mi-J was victimized by a clouded leopard on 8 April 2006 (Fig. 11B). In the observation of this group, the new member Midori was also treated as one

of focal members. During the 13 months, the adult male Bejita was followed for a total of 1967.8 hours and adult females were followed for 48.2 hours (Midori) to 681.7 hours (ChiChi) (Table 3). An average of 12.5 ± 1.6 hours per day made for a total of 3,506 hours

As depicted in Table 4, the difference in time budget among seven focal monkeys, even including the new member Midori, was not significant for resting (One-way ANOVA: $F = 1.03$ and $p = 0.40$), feeding ($F = 1.14$ and $p = 0.34$) and moving ($F = 1.35$ and $p = 0.23$) consisting 73.9-79.6%, 16.4-21.0% and 3.0-3.6%, respectively, but significant in others (grooming + copulation) (Kruskal-Wallis-test: $H = 45.5$ and $p < 0.01$) constituting 0.1-2.4%. Thus, as there was no difference in time budget between individuals excluding the category others which contributed very little, the data of all focal monkeys were pooled, and its resting, feeding, moving and others accounted for 76.4%, 19.5%, 3.5% and 0.5%, respectively (Total in Table 4). Including about 12-hour stays at night at sleeping sites, proboscis monkeys spent about 21 hours / day for resting and sleeping and only about 3 hours / day for activities. Sexual difference in time budget was significant for feeding (t-test: $t = 2.02$ and $p = 0.04$), moving (U-test: $U = 10003.5$ and $p = 0.04$) and others ($U = 16140$ and $p < 0.0001$) (Fig. 13). The male would spend more time on feeding than female to maintain his larger body. As the male frequently retraced the way he came to bring back the females separated from BE-Group, he would spend more time on moving than female. Females more frequently performed grooming to other females, infants and juveniles while the male more frequently performed copulation. Among activities, moving and others constituted only 2.3-4.3% and 0.05-1.3% per month, respectively, and therefore feeding

seemed a key factor which determined the activity budget of proboscis monkeys. To confirm the seasonal fluctuation of feeding activity, I examined the seasonal fluctuation of defecation frequency. The seasonal fluctuation of mean daily defecation frequency was significant in both the male (One-way ANOVA: $F = 7.96$ and $p < 0.01$) and females (Kruskal-Wallis-test: $H = 41.43$ and $p < 0.01$), with a high peak from June to August and another peak in November (Fig. 14A). As mentioned in the following section, monthly fruit production of plants positively correlated with monthly feeding activity (Pearson product-moment correlation coefficient: $r^2 = 0.37$ and $p = 0.04$) and fruit-eating ($r^2 = 0.61$ and $p = 0.003$) of proboscis monkeys, respectively, and fruit production and fruit-eating was the largest July to August. However, monthly young leaf and flower production of plants did not correlate with young leaf- and flower-eating, respectively (young leaf: $r^2 = 0.18$ and $p = 0.17$; flower: $r^2 = 0.01$ and $p = 0.74$) and feeding activity (young leaf: $r^2 = 0.08$ and $p = 0.38$; flower: $r^2 = 0.02$ and $p = 0.70$). These suggest that fruit production significantly affects the activity budget of proboscis monkeys. Figure 14 additionally shows the seasonal fluctuation of urination frequency, also with a peak in June-July. The fluctuations in daily feeding rhythm were statistically significant in both the male (One-way ANOVA: $F = 4.94$ and $p < 0.01$) and females ($F = 3.48$ and $p < 0.01$) (Fig. 15), with a peak at 15:00-17:00, i. e. shortly before sleeping.

4. Food habits

4. 1. Vegetation and food menu

In the survey of vegetation along 16 trails, 1,645 trees and 497 vines of 180 species (124 genera, 46 families) were described (Table 5). Predominant species were *Mallotus muticus*, *Excoecaria indica*, *Dillenia excelsa*, *Croton oblongus*, *Nauclea subdita*, *Xylosma sumatrana*, *Pternandra galeata*, *Vitex pinnata*, *Vatica rassak* and *Antidesma thwaitesianum* in trees and *Lophopyxis maingayi*, *Croton caudatus*, *Dalbergia parvifolia*, *Hydnocarpus sumatrana*, *Entada rheedei*, *Bridelia stipularis*, *Albizia corniculata*, *Artabotrys suaveolens*, *Bauhinia diptera* and *Millettia nieuwenhuisii* in vines. Since DBH markedly varied among species and growth stages, total basal area of each species is also shown in Table 5. Whereas the surveyed area reached as large as 2.15 ha (3 m width × 7,150 m length), the cumulative number of plant species did not plateau (Fig. 16) due to extremely high species diversity in tropical riverine forests. Accordingly, the total number of plant species consumed by focal monkeys during a total of 3,506 hours was 188 (127 genera, 55 families, Fig. 17 and Table 6), exceeding the total number of plant species described in the survey of vegetation (180 species). The proboscis monkeys frequently ingested young leaves, fruits and flowers and occasionally mature leaves and others (barks of *Eugenia* sp. 2 and nests of termite *Microcerotermes distans*), and the difference of the composition of each plant part among seven focal monkeys was not significant in young leaves (One-way ANOVA: $F = 0.78$ and $p = 0.58$), fruits ($F = 0.87$ and $p = 0.52$), flowers (Kruskal-Wallis-test: $H = 6.94$ and $p = 0.22$) and others ($H = 0.70$ and $p = 0.87$) (Table 7). Thus, as there was no difference in the composition of the plant parts consumed

between individuals, the data for the focal monkeys were pooled, and young leaves, fruits, flowers, mature leaves and others constituted 65.9%, 25.9%, 7.7%, 0.03% and 0.5%, respectively (Total in Table 7). The numbers of plant species providing young leaves, fruits and flowers were 182, 49 and 28, respectively, with overlaps as shown in Figure 18.

4. 2. Spatiotemporal distribution of food sources

Every month, excepting February, 2006, when the study area was flooded with 3-4 m deep water and the tagged trees and vines could not be identified, phenology of the 2,142 plants along the 16 trails was surveyed by examining whether each plant had young leaves, fruits and/or flowers. Out of the 2,142 plants, 1,902 were of species consumed by focal monkeys: 1,899 plants for young leaves; 919 for fruits; 469 for flowers (Fig. 19). Figure 20 represents the spatiotemporal distribution of plants with fruits, flowers or young leaves. Young leaves were highly available in all seasons and all trails (Fig. 20A) and flowering trees and vines showed relatively even distribution across the trails and seasons (Fig. 20B). In contrast, the abundance of fruiting plants was distorted to particular seasons and trails (Fig. 20C). Spatially, the fruiting plants were more abundant on the southern side (trail of odd numbers), especially on TR 13, than the northern side (trails of even numbers). Seasonally, the availability of fruits was higher in July-August and November but lower in May than in other months.

4. 3. *Food preference*

In 48 of 180 species described in the vegetation survey along the 16 trails, the number of plants exceeded 12 which was the mean number of plants per species, i. e. 2,142 plants / 180 species. Out of the 48 dominant species, 16 species had many fruits and flowers but proboscis monkeys did not consume their fruits or flowers at all for unknown reasons, whereas orangutan or long-tailed macaque was facultatively observed consuming fruits of five of those species (Table 8). Out of the five species, *Vitex pinnata*, *Microcos crassifolia* and *Dracontomelon dao* had seeds which seemed too hard for proboscis monkeys to consume. Fruits of *Entada rheedei* appeared too large and hard for proboscis monkeys to take the seeds out of the fruits. *Excoecaria indica* was one of the predominant tree species in the study area and produced a lot of fruits throughout a year but neither proboscis monkeys, orangutans or long-tailed macaques consumed any fresh fruits and flowers on the trees, though a group of long-tailed macaques was once observed taking some old and dry *E. indica* fruits floating in the river. Even young leaves of this plant species were rarely consumed by proboscis monkeys. This species may have some chemicals which are toxic or repellent for the nonhuman primates. The proboscis monkeys did not consume any fruits and flowers of the predominant species *Croton caudatus* and *C. oblongus*, with very rare consumption of young leaves. Their fruits and young leaves exerted a specific smell, suggesting the presence of some toxic or repellent chemicals.

To test the proboscis monkeys' preference for edible plant species, time spent for consuming each plant species was compared with time expected from its availability. The availability of each part (flowers, fruits and young leaves) was calculated using the

following formula. Availability = $B_k \cdot (n_{ki} / N_k) / 12$ where N_k is the total number of plants, n_{ki} is the number of tree or vine plants with flowers, fruits or young leaves in month i and B_k is total basal area per hectare in the species k . As shown in Table 9, the availability of each species was given by basal area, and G-test was conducted for trees and vines separately. Thus, the plant species were divided into six categories, i. e. (vine and tree) \times (fruits, flowers and young leaves), and observed data and expected values were compared by using G-test (Table 9) for each category. Accordingly, the difference between observed data and expected values was statistically significant in all of the six categories ($G = 31307$ and $p < 0.0001$ in tree fruits; $G = 4686$ and $p < 0.0001$ in vine fruits; $G = 5860$ and $p < 0.0001$ in tree flowers; $G = 2405$ and $p < 0.0001$ in vine flowers; $G = 56541$ and $p < 0.0001$ in tree young leaves; $G = 11259$ and $p < 0.0001$ in vine young leaves). In Table 9, the preferences of proboscis monkeys were categorized into positive (PO), negative (NG) and neutral (NU) preferences when the observed consumption was considerably larger, smaller than and nearly equal to the availability, respectively: observed or expected time is more than 180 minutes and the ratio of observed time to expected time is > 2.0 (PO), < 0.5 (NG) and $0.5 < 2.0$ (NU).

4.4. High preference for fruits, especially seeds

As shown in Figure 13, the percentage of time spent for feeding exhibits remarkable seasonal fluctuation. To examine the contribution of fruit, flower and young leaf consumptions, the seasonal fluctuations of the three factors are separately represented in Figure 21A. Flower consumption was constantly low throughout a year. Since the proboscis monkeys were primarily leaf eaters, young leaves almost constantly

contributed to their food habits at a high level. In contrast, fruit consumption was very low in some seasons but exceeded the percentage of young leaves in July and August, indicating the high contribution of fruits to the seasonal fluctuation of feeding activity. For young leaves, fruits and flowers, the male-female difference of seasonal fluctuation was not statistically significant (U-test: U = 10059 and p = 0.28; U = 11641 and p = 0.28; U = 10277 and p = 0.43, respectively) (Fig. 21B-D).

The seven focal monkeys spent a total of 177.2 hours for fruit-eating, of which unripe fruits constituted 90.4% (Fig. 22A). A fruit was composed of seed, flesh and calyx, and the proboscis monkeys spent 32.9%, 2.1% and 0.9% of 177.2 hours for consuming only seeds, flesh and calyxes, respectively (Fig. 22B). When the seeds and the flesh of the fruit firmly stuck to each other and seemed difficult to be separated, proboscis monkeys concurrently consumed both the seeds and flesh in most cases (64.1% of the time). Accordingly, seeds made up 97% of 177.2 hours, suggesting that the proboscis monkeys seemed to consume the fruits in favor of seeds. Whenever monkeys collected ripe fruits, they abandoned flesh and consumed only seeds.

Fruit consumption by the focal members of the BE-Group was observed for a total of 49 plant species (Table 10), and seeds were consumed in 48 species, excepting *Ziziphus borneensis* which had extremely hard seeds. On the other hand, calyxes were consumed in only *Alseodaphne insignis* (Table 10). The growth of *A. insignis* fruits could be divided into four stages (Fig. 23). In unripe stage 1, the calyx was fresh and larger than the flesh, in which the seed was indistinct (Fig. 23A). In unripe stage 2, the calyx was still fresh and the flesh became large, with an immature seed (Fig. 23B). In unripe stage 3, the flesh grew up to full size with a still immature seed, and the calyx

was withered (Fig. 23C). In the ripe stage, the flesh was juicy with a mature seed (Fig. 23D). Proboscis monkeys consumed only calyxes in unripe stage 1, calyxes and flesh in unripe stage 2 and only seeds in unripe stage 3 and ripe stage. *A. insignis* was so rare in the study area that no trees of this species were described in the vegetation survey along 16 trails. Nonetheless, the focal members repeatedly visited three ca. 20-25 m tall trees of *A. insignis* near TR 13. Of the three, two trees (I and II) were located near the riverside and the other tree (III) was about 100 m away from the riverside. Whereas trees I and III produced fruits for at least four months from October to January, proboscis monkeys frequently visited in only December and January (Fig. 24) when the fruits had seeds, indicating that the main targets of the monkeys were not calyxes or flesh but seeds. The consumption of calyxes in April may suggest that the phenology of *A. insignis* is not well synchronized among trees.

In the observation of BE-Group, feces content was examined in 400 feces samples of focal members, ranging from 19 feces in September to 71 in November. Seeds were contained in 23 of 71 feces in November, 15 of 38 feces in December and 5 of 21 feces in March. The indigested seeds were of *Antidesma thawaitesianum*, *Nouclea subdita* and *Ficus* spp. in November and December (Fig. 25A), which was consistent with the fact that focal members of the BE-Group consumed fruits of *A. thawaitesianum* and *N. subdita* mostly in November and December (Fig. 25B). Species of *Ficus*, *F. binnendijkii* and *F. globosa* were relatively abundant in the study area and their fruits were positively preferred by proboscis monkeys (Table 9). Although *F. binnendijkii* had fruits throughout a year, the monkeys consumed only their young fruits containing immature seeds which seemed digestible in their forestomach.

F. globosa had fruits from September to May and the monkeys consumed not only young fruits but also pre-ripe or ripe fruits containing mature seeds. Most of the seeds contained in the feces were probably of *F. globosa*. The mature seeds of *A. thawaitesianum*, *N. subdita* and *F. globosa* were probably too small and hard to be ground by teeth of proboscis monkeys.

4. 5. Seasonal trend of food menu diversity

The number of species consumed by the focal members of BE-Group seasonally fluctuated, ranging from 36 species in September to 82 species in December, excepting February when data was hardly obtained due to deep flooding (Fig. 26). The Shannon-Wiener index of Diversity (H') (Pielou, 1966) was used to calculate for food menu diversity. Identified plant species were used in the analysis; unidentified plants were not included. Except in February, food menu diversity H' ranged from 2.28 to 3.37, with a low in July, September and May 2006, whereas evenness (J') was nearly constant at 0.6-0.8 (Fig. 26). The months with low diversity corresponded to the seasons when the fruit consumption peaked (Fig. 21A). Stepwise regression analysis detected a significantly negative correlation between the seasonal fluctuations of time spent feeding on fruits and food menu diversity (H') ($p = 0.043$, see Table 11).

4. 6. Consumption of tree barks, termite nests and water

In addition to fruits, flowers and young leaves, tree barks and termite nests were consumed by proboscis monkeys (Fig. 27). In the study area, there were two species of papery bark trees, *Eugenia* sp. 2 and *Pternandra galeata*. Whereas *P. galeata* was

more dominant than *E. sp. 2*, proboscis monkeys consumed papery bark of *E. sp. 2* but not of *P. galeata*. Since fruits and young leaves were negatively and flowers were never consumed in *P. galeata* (Table 9), the trees of *P. galeata* might have some chemicals repellent for proboscis monkeys. The bark of *E. sp. 2* were consumed from September to March (Fig. 28A). Especially in females, the bark feeding season was restricted to three months from September to November. Although there were many species of termite nests in the study area, proboscis monkeys consumed nests of only arboreal species represented by *Microcerotermes distans*. Whereas the male Bejita consumed the nests almost throughout a year, females consumed them only from November to April (Fig. 28B).

In the study area, several 1-3 m wide streams were meandering through the forest and many temporary pools appeared on the forest floor after heavy rains. Because in leaf-eating monkeys, including proboscis monkeys, water is primarily supplied from leaves in the process of digesting cellulose in their stomach, they rarely drank water. Nonetheless, the focal male and female monkeys were observed drinking water 11 and 15 times, respectively. In addition, juveniles of BE-Group were facultatively observed drinking water 14 times. When they drank water, the male always went down to the forest floor to use such water sources as the river and small streams but juveniles almost always hand-dipped from tree holes without descending to the forest floor (Fig. 29). Females took water from the Menanggul River or small streams 12 times and from tree holes three times. At the river, small streams and temporary pools, the monkeys drank water for 21-80 seconds by putting their mouth into the water.

5. Ranging Behavior

5. 1. *Home range*

Over a total of 1,968 hours, BE-Group moved within a range of 138.3 ha, viz. 553 50 m × 50 m grids (Fig. 30). Because the group almost always had sleeping sites at riversides, the frequently used grids were distributed along the Menanggul River. The grids used 22 or more times were situated at 2,650-2,700 m, 3,500-3,550 m and 4,200-4,250 m where the Menanggul River was as narrow as 10-15 m in width and BE-Group often crossed the river (cf. also Fig. 9). The core ranging area was located around TR 13 where foods, in particular fruits, were most abundant from July to May (Fig. 20C). Thus, Figure 30 suggests that the ranging of proboscis monkey is affected by the location of river crossing points and the availability of foods, in particular fruits. Whereas sleeping sites of one-male groups were often close to each other and they exhibited less or no hostility near the riverside, different groups rarely encountered each other in the deep forest and, if encountered, they showed aggressive behavior. During the 13-month observation, the encounters (in which another one-male group was in a radius of less than 50 m from BE-Group) were observed only three times, and in all of the encounters Bejita drove off the rival -males.

5. 2. *Travel distance*

Excepting the missing period in February, BE-Group traveled a total of 128.8 km within the home range. The daily path length was from 220 m to 1,734 m, with a mean distance of 799 m (Fig. 31). Although the group traveled long distances when they moved along the Menanggul River, their daily path length rarely exceeded 1,000 m

when they traveled away from the river, evidently because they had to return to the riverside for sleeping before sunset.

Figure 32 demonstrates the seasonal fluctuation of mean daily path length and availability of fruits, flowers and young leaves. The daily path length significantly correlated with the availability of fruits (stepwise regression analysis: $p = 0.0028$ see Table 11) but not of flowers and young leaves. The negative correlation between the daily path length and fruit availability indicates that proboscis monkeys were apt to stay within a small range in fruit-abundant seasons. In addition, daily rainfall also seemed to reduce the daily path length, though the rainfall accounts for only 4.8% of the variation of daily path length (Spearman's rank correlation tests: $r^2 = 0.048$ and $p < 0.01$) (Fig. 33).

5. 3. Behavioral core trees

BE-Group sometimes stayed within limited areas to repeatedly visit particular trees which produced their favorite foods. Out of positively preferred trees or vines (Table 9), *Crudia reticulata*, *Cynometra ramiflora* and *Carallia brachiata*, which were repeatedly visited (five or more times on different days), could be such behavioral core trees. For instance, *C. ramiflora* had cigar like rolls of young leaves which seemed very attractive to the proboscis monkeys. From 16 to 21 July, BE-Group was frequently attracted to a large *C. ramiflora* tree near the riverside point which was about 300 m upstream from TR 16, and therefore the group traveled only 3,110 m during the five days (Fig. 34). Out of tree species which were not described in the vegetation survey but were observed to be consumed by proboscis monkeys, *Artocarpus* sp. 2 and

Garcinia rostrata could be behavioral core trees (cf. Table 6).

5. 4. *Effects of water level on ranging*

The ranging behavior of BE-Group dramatically changed when the study area was partly flooded in early to mid January and entirely flooded from early February to early March. The group came back to the riverside everyday until 10 January. However, from 11 January when the water level reached 238 cm at the mouth of the Menanggul River and the forest floor around trail 10 was covered by about 1 m deep water, BE-Group started wandering in the forest without coming back to the riverside until 17 January (Fig. 35A). While wandering in the forest, BE-Group had sleeping sites at small open gaps or near former tractor roads (Fig. 36). From 18 January when the water level was 185 cm at the river mouth and the water depth at TR 10 decreased to about 40 cm, BE-Group began returning to the riverside again for sleeping (Fig. 35B). Whereas BE-Group was lost in February, I happened to rediscover them on 3 March and resumed following them by boat. In the second flood, the water covered a wide range of forest including the southern area of the Menanggul River and the oil palm plantation (Fig. 35C). Nonetheless, their traveling range was limited to within about 800 m from the riverside as in the first flood, suggesting that proboscis monkeys can not be far away from the river even in the deep floods.

During the 13-month observation, 270 sleeping sites of BE-Group were located: 261 sites on the riverbank and 9 sites inside the forest. The water level at the river mouth ranged from 8 cm to 433 cm with a median 108 cm when the sleeping sites were located on the riverbank, and from 220 cm to 398 cm with a median 250 cm when the

sleeping sites were located inside the forest (Fig. 37). The water level had a statistically significant effect on the location of the sleeping site (logistic regression analysis: coefficient = 0.027 ± 0.006 ; likelihood ratio G-test: $p < 0.0001$).

DISCUSSION

Feeding Behavior

Although former studies on the feeding ecology of proboscis monkeys indicate a high degree of leaf-eating and low food menu diversity (Kern, 1964; Kawabe and Mano, 1972; Macdonald, 1982), recent studies show a relatively high degree of fruit-eating and food menu diversity: young leaves, fruits and flowers constitute 38%, 50% and 3% in Samunsam, respectively (Benett and Sebastian, 1988) and 52%, 40% and 3% in Natai Lengkus, respectively (Yeager, 1989); 90 plant species of 39 families in Bako (Salter et al., 1985) and Samunsam and 47 plant species of 19 families in Natai Lengkus (Yeager, 1989) are reported for proboscis monkeys' food habits. In this study, the feeding behavior of proboscis monkeys also showed a high degree of fruit-eating in some seasons although the tendency of consuming young leaves was strong in terms of total food amount, and their extremely wide dietary diversity was demonstrated.

There are two expected possibilities as to why the amount of proboscis monkeys' fruit-eating in Samunsam and Natai Lengkus is higher than this study site. One is that the habitat types are different; Samunsam: mixed mangrove and lowland forests; Natai Lengkus: peat swamp forests. The different habitat types between study sites may

have different food availability and induce different food preferences in proboscis monkeys. However, it is difficult to fairly compare the food availability between study sites as the estimation method in Natai Lengkus is different from the method used in this study and there is no food availability data in Samunsam. Nonetheless, Yeager (1989) suggests that the food availability in Natai Lengkus is higher than in Samunsam due to the higher density of proboscis monkeys in Natai Lengkus (62.6 individuals / km²) than Samunsam (5.93). As following the density calculation by Yeager (1989), the density of proboscis monkeys in the present study site is 29.8 individuals / km² (the highest density is used during the study period) which is higher than Samunsam and lower than Natai Lengkus. Thus, as the food availability expected by the density shows various values between study sites, the different amount of proboscis monkeys' fruit-eating (which, as previously showed, is largely dependant on fruit availability) in each study site appears to result in their different food preference in each study site.

Another reason may be the methodological difference between researchers. In Samunsam, the percentages of each food part are based on only 34 feeding observations which are not taken systematically for 16 months, and in Natai Lengkus, the percentages are based on 1,700 observation hours of data which were collected through a scan sampling every 5 minutes for 12 months. Both studies were conducted mostly by boat from the river while the monkeys were at the riverbank. Thus, the methodological difference seems to be one of the reasons to explain the different amount of fruit consumption between the studies. The observation time in the present study, which was conducted not only by boat but also by following the group on foot in the forest, was much longer than the two other studies, and thus the data in this study

would show the most exact tendency of feeding behaviors of proboscis monkeys. The difference in food menu diversity between habitats may also be explained with the same reasons, i. e. the difference of data collection method, observation hours and/or observed place (only from the river by boat or on foot following the monkeys in the forest). Detailed studies of proboscis monkeys that observe the monkeys in the forest are awaited for performing a fair comparison.

The proboscis monkey was observed consuming termites and/or its nests and bark of a specific tree, although it was a small amount in the present study, and the bark and termite feeding seasons were more restricted in females than in the male. Red leaf monkeys (*Presbytis rubicunda*) in Sabah, Malaysia feed on termite nests (*Macrotermes* sp.) to supplement mineral intake, to buffer forestomach pH and to absorb toxins (Davies and Baillie, 1988; Davis, 1991). In the howler monkey (*Alouatta belzebul discolor*), which is a leaf eater similar to the proboscis monkey, geophagy occurs when consumption of leaves increases considerably and bark-eating occurs in times of lower and higher frugivory (De Souza et al., 2002; Pinto and Setz, 2004). Although the hanuman langur (*Semnopithecus entellus*) is observed consuming insects such as larvae when they are available (Newton, 1992), in Asian colobines, it is very rare to consume animal matter due to their specific stomach structure (Kirkpatrick, 2007), and thus it seems unlikely that proboscis monkeys consume termites as a protein source. In proboscis monkeys, these specific food habits appear to serve different functions at different times as reported on red leaf monkeys by Davies and Baillie (1988): to supplement mineral nutrients, to absorb toxins and/or to assist digestion. The reason why the feeding frequency of these specific food habits is higher in the male than the

females is unknown, but the male may need them more to maintain the larger body size.

According to Salter et al. (1985), proboscis monkeys reveal their daily feeding rhythm with an active peak between 13:00 to 15:00. However, the feeding peak was shown to be between 15:00 to 1700 in the present study. Although the two studies indicate the same general trend: there is one feeding peak in the afternoon, the present study showed the peak two hours later. This inconsistency between the two studies may be a result of the small sample size of the study by Salter et al. (1985), which was collected from several groups ranging in various forest types of Bako National Park: tree mangrove, nipa swamp, riverine forest and dipterocarp / high kerangas forest. Feeding trials of the proboscis monkeys in captivity report that the transit time, defined as the elapsed time from feeding to the appearance of the marker in the feces is 14 hours and the retention time, defined as the time between the appearance of 5% and 80% of the markers, is 52 hours (Dierenfeld et al., 1992). As proboscis monkeys require a lot of time to digest the foods, it may be preferable that they feed on a lot of food several hours before they sleep to spend the night time not only for sleeping but also for digestion.

Among the activities of the proboscis monkeys, feeding may be a key factor which determines the seasonal fluctuation of their activity budget because moving and others (grooming + copulation) constituted very small amount (2.4-4.3%). In the feeding items of proboscis monkeys, they spent more time on feeding when they spent more time on fruit-eating than on young leaf-eating, suggesting that fruit-eating is the important factor to influence their activity budget. It also may indicate that the monkeys can digest the fruits faster than young leaves. The amount of feeding was

estimated considering not only the time but also frequency of feces in this study. The mean daily defecation of proboscis monkeys seasonally fluctuated with several peaks which mostly corresponded to the peaks in the fluctuation of spending time on fruit-eating, supporting that the fruits enable to be digested faster than other foods, especially young leaves which are their main food items. In two African colobines with a peculiar stomach which is suitable for leaf digestion as the proboscis monkey's is, the resting time of the white colobus monkey (*Colobus guereza*), which has a strong tendency for leaf-eating, is longer than the red colobus (*Colobus badius tephrosceles*) which has a strong tendency for fruit-eating (Dumber and Dumber, 1974; Clutton-Brock, 1975), and it suggests that digesting leaves takes more time compared with digesting fruits. Accordingly, this instance also supports that the proboscis monkeys can digest fruits faster than young leaves. In other words, they can digest larger amount of fruits compared with young leaves. Waterman (1984) reports that the colobine monkeys must either be able to exploit foliage highly favorable to their digestive system, or be able to top up their diet with concentrates such as seeds or fruits, and Yeager (1989) comments on Waterman's report by saying that proboscis monkeys appear to top up their diet with seeds. Although proboscis monkeys are suggested to be efficient digesters of cell wall constituents (Dierenfeld et al., 1992), they may prefer fruits, especially seeds, because seeds can be digested efficiently and contain rich carbohydrates such as starch, though less protein than young leaves (Davies et al., 1988). Proboscis monkeys may obtain enough protein from young leaves, which usually contain rich protein (Choo et al., 1981; Waterman, 1984; Lambert, 2007), but they may not obtain enough energy from young leaves alone, as young leaves are more difficult to

digest.

Regarding most plant species consumed by the proboscis monkeys, the actual time observed consuming them was quite different from what was expected based on food availability, suggesting that the proboscis monkey is a picky eater. Also, this monkey changed its preference for which part in a fruit to feed on: flesh, seeds and/or calyxes, in different months. The proboscis monkeys' favorite part was the unripe fruit seed, which it can easily consume by crunching with little effort. Seed predation is characteristic in colobine frugivory (Davies, 1991), and Yeager (1989) reports that the proboscis monkey is also a seed eater. Since proboscis monkeys feed especially on dominant plant seeds, Yeager (1989) suggests that they may increase equitability and permit a larger number of minor plant species to survive in the community. Proboscis monkeys fed extensively on the seeds of *Mallotus muticus* trees and *Lophopyxis maingayi* vines which were the most abundant plant species in this study area, although some dominant and predominant species were not consumed or were shown negative food preference. Ranglack and Yeager (1986), who examined over 100 proboscis monkeys feces samples, did not find any seeds inside those feces, although the undigested seeds of some plant species, which were small and relatively hard, were found in perfect shape in the proboscis monkey feces in the present study which examined 400 feces samples. This may be because of the difference of the sampling efforts between the two studies. In the present study, especially seeds of *Ficus* spp. were often found in feces when the proboscis monkeys often fed on its fruits. *Ficus* species are one of the most important plant species for a lot of wildlife, suggesting that proboscis monkeys play the seed dispersal role for some important plant species. If

proboscis monkeys assist proportion of some dominant or predominant plant species and play a role as a seed dispersal animal for some important minor plant species, they may be a key species in maintaining the forest and wildlife diversity in the areas they inhabit.

Ranging Behavior and Predation Pressure

Proboscis monkeys appeared to be non-territorial at least at their sleeping sites in this study, as all group types of proboscis monkeys overlapped their sleeping sites. Yeager (1989) reports that the home ranges of the proboscis monkey's one-male groups overlap an average of more than 95% and Boonratana (2000) confirms the non-territoriality of a one-male group using the formula devised by Mitani and Rodman (1979). To predict whether the one-male group would be territorial in this study, I also used Mitani and Rodman (1979)'s formula $D = d / (4A / \pi)^{0.5}$, where D is the index of defensibility, d is the daily path length (km) and A is the home range area (km²). If D is ≥ 1 , the primate group is expected to be territorial, and if D is < 1 , the primate group is expected to be non-territorial. The index of defensibility of a one-male group in this study is 0.60, indicating that the study group is non-territorial.

The home range size of proboscis monkeys is different between habitats: 315 ha (Abai) in mangrove forest (Boonratana, 1993); 900 ha (Samunsam) in mixed mangrove and lowland forests (Benett and Sebastian, 1988); 137 ha (Natai Lengkus) in peat swamp forest (Yeager, 1989); 221 ha (Sukau) in riverine forest (Boonratana, 2000). But, other than the figure of 221 ha by Boonratana (2000), all of the home range sizes are estimated by the river length used by the one-male groups. As some studies on the

home range size of primates show that the size decreases when the food availability becomes more abundant (Mckey and Waterman, 1982; Therborgh, 1983), the differences of home range size between habitats in proboscis monkeys may also be explained by food availability. Actually, Yeager (1989) proposes that the home range size in Natai Lengkus is smaller than in Samunsam because the food availability of Natai Lengkus is higher than that of Samunsam, and Boonratana (2000) also suggests that the smallest home range size in Natai Lengus is due to its high food availability throughout the year. However, the comparison of food availability between habitats is difficult as it is mentioned above. Nonetheless, according to Yeager (1989), over 70% of the stems located within the vegetational plots at Natai Lengkus are potential food sources of the proboscis monkeys at some point during her study, and it was 67% in the present study, suggesting that the food availability in these two study sites is similar as well as the home range sizes: 138.3 ha in the present study site and 137 ha in Natai Lengkus. The larger home range size of proboscis monkeys in Sukau (221 ha by Boonratana (2000)) than in the present study may also be explained by the food availability. The proboscis monkey group in Sukau (Sukau group) had home ranges in both a lower area of the Menanggul River and a western area of the Kinabatanga River (Boonratana, 2000). Since the present study indicated the low food availability in a lower area of the Menanggul River compared with the upstream area of the river in which the home range of BE-Group was located, the Sukau group may need a wider home range size than that of BE-Group, although the research time in the two studies is different and the food availability in the western area of the Kinabatanga River is unknown. Food availability may be a barometer to explain the difference in the home

range size of proboscis monkey.

Primates' ranging patterns are influenced by the spatial and temporal distribution of food availability (Clutton-Brock, 1975; Raemaekers, 1980; Oates, 1987; Bennett and Davies, 1994; Olupot et al., 1994; Boonratana, 2000; Koenig, 2000; Di Fiore, 2003; Kirkpatrick, 2007; Lambert, 2007). In the proboscis monkeys' home range area, the core areas are located at relatively high fruit availability areas, and also, the daily path length in each month showed a negative correlation with the amount of fruit availability. Boonlatana (2000) reports that daily path length of one proboscis monkey group increases on days when the group feeds more on young leaves, but the group does not travel far on days when the diet includes a high proportion of fruits and seeds, indicating the same general trend as found in this study. On the other hand, other Asian colobines such as the banded langurs (*Presbytis melalophos*), hanuman langurs (*Semnopithecus entellus*) and capped langurs (*Trachypithecus pileatus*) are reported to have traveled farther in months when diet is based on fruits and/or flowers rather than young leaves or mature leaves (Bennett, 1986c; Stanford, 1991; Newton, 1992), indicating the opposite results of the ranging behavior related to diets of proboscis monkeys. Whereas other colobines travel further to feed on the fruiting and/or flowering plant species which are scattered in forests, proboscis monkeys feed on fruits without traveling further distance because they prefer to feed on the fruits of dominant plant species in which the distance between patches may be shorter. Not only this study but also Yeager (1989) reports that proboscis monkeys prefer to feed on dominant plant species fruits, supporting why their daily path length decreases on days when they feed on fruits. On the other hand, Bonlatana (1993 and 2000) discusses the reason why the group of proboscis monkeys

travels farther each day during certain months when they tend to feed on young leaves. He suggests that it is because they need to consume young leaves of different plant species at different areas to reduce the risk of potential toxins they may ingest when they feed on specific plant species. In fact, Yeager (1989) also indicates that food menu diversity of proboscis monkeys increases when their preferred foods (fruits) are scarce, as well as this study. Thus, the decrease of their preferred fruits appears to induce the increase of their leaf-eating amount and of their daily path length. It is thought that fruit-eating, fruit availability and spatial and temporal distribution of major foods are the key factors to influence the ranging behavior of proboscis monkeys.

Two cases of predation events on an adolescent female and an adult male proboscis monkey by a crocodilian, false gavia (*Tomistoma schlegeli*) have been reported at the riverside in Natai Lengkus (Galdikas, 1985; Yeager, 1991), suggesting that the proboscis monkeys' river crossing behavior exposes them to a high risk of predation. Proboscis monkeys cross the river where the width is significantly narrower (Yeager, 1991), and in addition to this, when proboscis monkeys crossed the river, they often selected locations in which both genders of adult monkeys could safely cross to the other side of the river from tree to tree in this study. Proboscis monkeys appear unwilling to fall into the water, suggesting that those selections could be influenced by the predation threat by crocodiles. Apart from the two predation events by clouded leopards (*Neofelis nebulosa*) reported in this study, two additional observations of predations on adult males have been reported (Davis, 1962; Nowell and Jackson, 1996), indicating that not only crocodiles are possible predation threats for proboscis monkeys but clouded leopards in trees also can be a serious threat for them.

It has been thought that proboscis monkeys almost always come back to the riverbank to sleep for effective avoidance of predation, where predators can only approach them from the landward side (Kern, 1964; Jeffrey, 1979; Bismark, 1981; Onuma, 2002) although there is no certain data. However, this study showed that the proboscis monkeys tended to select sleeping sites where they could cross the river to the other side easily from tree to tree. This is thought to be a strategy to provide protection against predators both from land and in the river. At the selected sleeping site, attacks by the clouded leopard can be avoided by escaping to the other side of the river from tree to tree while not falling into the river where there may be crocodiles. It can be said that predation pressure is one of the important factors influencing why proboscis monkeys sleep at the riverbank almost every night.

Although proboscis monkeys have been thought to almost always come back to riverbanks for sleeping (Kern, 1964; Kawabe and Mano, 1972; Jeffrey, 1979; Bennett, 1986a; Bennett and Sebastian, 1988; Yeager, 1989) as mentioned above, the monkeys were observed sleeping in the deep forest on flooded days. In this study, the water level statistically influenced the ranging behavior of the proboscis monkeys, especially sleeping site selection. Since a large group may reduce the hunting success of predators by increasing the efficiency with which predators are detected through increased vigilance, predation pressure may influence social group formation (Alexander, 1974; Clutton-Brock and Harvey, 1977; van Schaik and van Hooff, 1983; Cheney and Wrangham, 1987; Miller and Treves, 2007). Kummer (1971) also considers that the multi-level society which has been reported in some primate species may be effective predation avoidance. At the sleeping site on the riverbank, the

proboscis monkey is one of the species which has been reported to form a multi-level society (Benett and Sebastian, 1988; Yeager, 1991b; Boonratana, 2002; Murai, 2004a), and Murai (2004a) suggests that this multi-level society is also for avoiding predators. The predation events on proboscis monkeys by crocodiles and clouded leopards listed above support the idea that the monkeys are certainly exposed to predation threat. It may be that the proboscis monkeys are not restricted to the riverbank, which has an uncluttered view for easily finding predators, because of reduced predation pressure by terrestrial animals during times when high water levels prevent predators from hunting. Although Boonratana (2000) and this study suggests that the ranging behavior of proboscis monkeys is affected by fruit-eating, fruit availability and spatial and temporal distribution of major foods, the water level and/or the predation pressure may also be important factors effecting their ranging behavior.

Yeager (1993) reports that the degree of association between one-male groups of proboscis monkeys in a multi-level society shows a negative correlation with water level because it may be that the monkeys sleep inside the forest as they are scared of tree falls and the phenomenon which undermines vegetation and breaks off land masses from the river's edge during the high water level season. According to Murai (2004a) who studied at the same site as the present study, the water level also negatively correlates with the degree of association between one-male groups, though it is a marginally insignificant correlation ($p = 0.056$). In this study, BE-Group solitarily slept inside the forest on flooded days, although the group often slept close to other one-male groups at riverside trees on non-flooded days, supporting the proposition that water level influenced the social system between one-male groups. The low degree of

association, which was observed only during high water level, may also result from the reduced predation pressure. Water level and/or predation pressure may influence not only the ranging behavior of proboscis monkeys but also their multi-level society.

Whereas agonistic behaviors between one-male groups was rarely observed at the sleeping site, even though they slept in the same tree, encounters with one-male groups were observed only several times in the forest during the study period, suggesting that one-male groups keep a certain distance in order to avoid encountering each other in the forest. The degree of association between one-male groups in the gelada baboon, which has the multi-level society the proboscis monkey has, may be influenced by food availability (Ohsawa, 1979). On the other hand, the degree of association of the proboscis monkeys' one-male groups may not be attributed to food availability because with their specialized physiology they appear to use widely available and abundant food sources, especially leaves, high in digestion inhibitors and low in nutrition (Yeager, 1993; Murai, 2004a). But as this study revealed, ranging behaviors of proboscis monkeys were influenced by the availability of fruits and various types of food parts (fruits, flowers and young leaves) were given strong preference, thus it can be suggested that food competition between one-male groups is high. As a result, there is a possibility that proboscis monkeys' one-male groups avoid encounters with each other in the forest to reduce the food competition between one-male groups, although the monkeys, as they have been reported, appear not to have territoriality or a high degree of association at the riverbank. Food competition may be one of the factors influencing ranging behaviors of proboscis monkeys if one-male groups avoid encounters with each other in the forest, although more systematic studies focusing on

their social system in the forest are needed to demonstrate this hypothesis.

Conservation Implications

In addition to the factors such as availability and distribution of food and predation pressure which influence feeding, ranging and social structures of the proboscis monkey, we may need to consider the possibility of environmental destruction by human activities affecting monkeys' behaviors. The major threat to the proboscis monkeys, which prefer to inhabit the vicinity of riverside forests, is habitat loss through logging and the spread of agriculture along river edges (IUCN, 1978; Jeffrey, 1982; Salter and Mackenzie, 1985). Murai (2004a and 2004b) suggests that the large size of the all-male group seems to be attributed to habitat fragmentation by the expansion of oil palm plantations. The places where proboscis monkeys slept inside the forest were the edge of open areas made by earlier logging or the edge of channels made by water removal and supply for oil palm plantations, demonstrating the effect of human activities on the ranging behaviors of proboscis monkeys in this study. As a general trend, the density of proboscis monkeys in riverine and peat swamp forests are higher than that of mangrove forests (Benett and Sebastian, 1988; Yeager, 1989; Boonlatana, 1993; Murai, 2004a; Sha, 2006) and the monkeys prefer the riverine forests to the mangrove forests (Bernard and Hamzah, 2006). Considering those reports, the riverine and peat swamp forests seem to be the areas where we need to put emphasis when considering the proboscis monkeys' conservation.

To estimate the populations of the proboscis monkey, the first step is to consider their conservation. In the lower Kinabatangan areas, including the present study area,

several population surveys of proboscis monkeys by boat have been conducted. The population numbers in each survey are different: Boonlatana (1993): 4.1 individuals / km; Goossens et al. (2002): 6.9; Sha (2006): 7.9. Whereas proboscis monkeys mostly sleep at the riverbank (Kern, 1964; Kawabe and Mano, 1972; Jeffrey, 1979; Bennett, 1986a; Bennett and Sebastian, 1988; Yeager, 1989), the number of the monkeys counted in each boat census in this study fluctuated by each day as the number of monkeys which came back to the riverbank depended on many factors. Especially in the flood season, often no monkeys were found through the boat censuses. When we discuss evaluation of the proboscis monkeys' population, it may be important to consider the factor of different population sizes estimated by different studies: whether the difference is based on the encounter ratio by day or the real decreases caused by the deforestation.

It has been difficult to say how large of an area the proboscis monkeys need to survive because most former researchers could not conduct studies on proboscis monkeys, specifically following them in the forest where the terrain was frequently swampy and impossible to walk on. Although only a little data has been obtained, proboscis monkeys moved into the forest about 750 m (Salter et al., 1985), 600 m (Benett and Sebastian, 1988; Boonlatana, 2000), 500 m (Yeager, 1989) and 800 m maximum from the riverbank in this study, suggesting that forests of at least 800 m from the both riverbanks are needed for proboscis monkeys' survival.

A lot of tourists visited the Mennenggul River, including the present study site, everyday by boat to enjoy the eco-tourism. In fact, the noisy boat engine sounds, and a lot of camera flashes created by tourists sometimes interfered with the river crossing of proboscis monkeys. Also, to attract the monkeys' attention so as to satisfying the

picture taking needs of the tourists, some of the tour guides often shouted at the monkeys. The excessive behavior of those guides and the behavior of tourists may be influence some behaviors of proboscis monkeys. The construction of new lodges around the study site is planned, and eco-tourism is becoming more popular as a leisure activity. For prospective conservation, it is not only important to protect the proboscis monkeys' habitat, but also to educate and train the tour guides to behave properly and the need to appeal to tourists to improve their manners around wildlife.

ACKNOWLEDGMENTS

The staff of the Economic Planning Unit in Malaysia, particularly Ms. M. Bt. A. Manan and Ms. G. Vu, who kindly arranged permission to conduct my research in Malaysia. The staff of the Sabah Wildlife Department, especially Mr. A. Tuuga (my counterpart) and Mr. E. Tangon, who supported my research in the lower Kinabatangan area. Mr. Haji H. Tukiman and Mr. L. Ruki in the Forestry Department, Sabah which lent me the comfortable house in Sukau village. Mr. J. Sugau, Ms. J. T. Pereira and Mr. P. Miun in the Forest Research Center of the Forestry Department, Sabah who identified all the plants species in this study. Dr. I. Lackman-Ancrenaz, Dr. M. Ancrenaz, Dr. B. Goossens, Dr. T. Tsubouti, Mr. A. Abulani, Mr. Z. A. Jaffer, Ms. A. B. Etin and all members of KOCP (Kinabatangan Orangutan Conservation Project) who were helpful with my research in Malaysia. Dr. M. Mohamed, Dr. H. Bernard who has been helpful with research. Dr. T. Murai gave me information about research sites. Dr. G. Hanya visited my research site before starting the project and provided useful information on data collection in this research. Dr. A. Nishimura, Dr. K. Hirota and Mr. A. Chijiwa also visited my research site during the study period and encouraged me. Dr. T. Miura assisted with the identification of the termite species. Dr. T. Kubo and Dr. Y. Akiyama assisted the statistical analysis in this paper. Mr. T. Ikeda, Mr. T. Sugimoto and all of the Higashi laboratory members provided useful discussion for me. All the Sukau villagers, especially Mr. N. Bin Mokhsen, Mr. Haji S. Bin Ahmad and Mr. P. Haji Mansor who are the leaders in the village, for assisting my peaceful and safe life in the village. The staff of Hotel City View in Sandakan, especially Mr. T. S. Heng, who

provided comfortable and warm service for me whenever I spent time there. Mr. M. N. Bin Hj. Siddek who is a bus driver from Sandakan to Sukau and Mr. L. M. Choi who is a taxi driver in Sandakan who provided the safe and comfortable trip for me. Mr. A. Bin Arsih, Mr. M. S. Bin A. Karim and Mr. M. Bin Ismail, who are my research assistants in the field and who always assisted my hard research. I could not complete my data collection without their assistance. Ms. H. Katsuta and Mr. R. Delatorre kindly undertook proofreading of this manuscript. Dr. K. Watanabe, Dr. J. Yamagiwa, Dr. T. Iwakuma and Dr. N. Agetsuma who took care of the deputy president of the board of examiners of my thesis and gave me their valuable comments on this thesis. I am grateful to all the people listed above.

My deepest appreciation goes to Dr. S. Higashi because, without his supervision from the time this study was started until its bound form this thesis would not have been possible. I am certainly indebted to Ms. Y. Katsuta who helped me to overcome a lot of difficulties throughout my study life. Lastly, I truly appreciate my family for supporting my research. I was able to be strong due to their encouragement every time when I was discouraged.

REFERENCES

- Alexander RD (1974) The evolution of social behaviour. *Ann Rev Ecol Syst* 5:325-383
- Allen GM, Coolidge HJ (1940) Mammal and bird collections of the Asiatic primate expedition. *Bull Mus comp Zool Harvard* 87:131-166
- Altmann J 1974 Observational study of behavior: Sampling methods. *Behaviour* 69: 227-267
- Basiuk R (1985) Samunsam Wildlife Sanctuary: A Management Plan, National Parks and Wildlife Office, Sarawak Forest Department, Kuching.
- Bauchop T (1978) Digestion of leaves in vertebrate arboreal folivores. In: Montgomery GG (eds) *The Ecology of Arboreal Folivores*, Smithsonian Institution Press, Washington D. C., pp 193-204
- Bauchop T, Martucci RW (1968) Ruminant-like digestion of the langur monkey. *Science* 161:698-700
- Bennett EL (1986a) Proboscis monkeys in Sarawak: Their ecology, status, conservation and management, World Wildlife Fund Malaysia, Kuala Lumpur, and New York Zoological Society, New York
- Bennett EL (1986b) Proboscis monkeys in Sarawak: Their ecology, status, conservation and management. WWF-Malaysia/NYZS. NTIS.
- Bennett EL (1986c) Environmental correlates of ranging behaviour in the banded langur, *Presbytis melalophus*. *Folia Primatol* 47:26-38
- Bennett EL, Sebastian AC (1988) Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in Sarawak. *Int J Primatol*

9:233-256

Bennett EL, Davies AG (1994) The ecology of Asian colobines. In Colobine Monkeys: Their Ecology, Behaviour and Evolution. A.G. Davies and J.F. Oates (eds). Cambridge University Press: Cambridge.

Bernard H, Hamzah Z (2006) Population size and distribution of the proboscis monkey (*Nasalis larvatus*) in the Klias Peninsula, Sabah, Malaysia. Malayan Nature J 59:153-163

Bismark M (1981) Preliminary survey of the proboscis monkey at Tanjung Putting Reserve, Kalimantan. Tigerpaper 8:26

Boonratana R (1993) The ecology and behaviour of the proboscis monkey (*Nasalis larvatus*) in the Lower Kinabatangan, Sabah. PhD Thesis. Faculty of Graduate Studies, Mahidol University

Boonratana R (2000) Ranging behavior of proboscis monkeys (*Nasalis larvatus*) in the lower Kinabatangan, Northern Borneo. Int J Primatol 21:497-518

Boonratana R (2002) Social organization of proboscis monkeys (*Nasalis larvatus*) in the Lower Kinabatangan, Sabah, Malaysia. Malayan Nature J 56:57-75

Cheney DL, Wrangham RW (1987) Predation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 227-239

Chivers DJ and Hladik CM (1980) Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. J Morphol 166:337-386

Choo GM, Waterman PG, Mackey DB, Gartlan JS (1981) A simple enzyme assay for dry matter digestibility and its value in studying food selection by generalist

- herbivores. *Oecologia* 49:170-178
- Clutton-Brock TH (1975) Ranging behaviour of red colobus (*Colobus badius tephrosceles*), in the Gombe National Park. *Anim Behav* 23:706-722
- Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. *J Zool Lond* 183:1-39
- Davis DD (1962) Mammals of the lowland rainforests of North Borneo. *Bulletin of the national museum of Singapore* 31:1-129
- Davies AG (1991) Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in the dipterocarp forest of northern Borneo. *Int J Primatol* 12:119-144
- Davies AG, Ballie IC (1988) Soil-eating by red leaf monkeys (*Presbytis rubicunda*) in Sabah, northern Borneo. *Biotropica* 20:252-258
- Davies AG, Bennett EL, Waterman PG (1988) Food selection by two South-east Asia colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biol J of the Linn Soc* 34:33-56
- De Souza LL, Ferrari SF, Costa ML, Kern DC (2002) Geophagy as a correlate of folivory in red-handed howler monkeys (*Alouatta belzebul*) from Eastern Brazilian Amazonia. *J Chem Ecol* 28:1613-1621
- Dierenfeld ES, Koontz FW, Goldstein RS (1992) Feed intake, digestion and passage of the proboscis monkey (*Nasalis larvatus*) in captivity. *Primates* 33:399-405
- Di Fiore A (2003) Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador. *Am J Primatol* 59:47-66
- Dumber RIM, Dumber P (1974) Ecology and population dynamics of *Colobus guereza*

- in Ethiopia. *Folia primatol* 21:188-209
- Fashing PJ (2007) African Colobine Monkeys: Patterns of Between-Group Interaction. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK (eds) *Primates in perspective*. Oxford University Press, New York, pp 201-224
- Galdikas BMF (1985) Crocodile predation on a proboscis monkey in Borneo. *Primates* 26:495-496
- Goossens B, Setchell JM, Abulani DMA, Jalil F, James SS, Aris SH, Lakim MH, Seventri AD, Sariningsih SS, Ancrenaz M (2002) A boat survey of primates in the Lower Kinabatangan Wildlife Sanctuary. In: Maryati M, Takano A, Goossens B, Indran R (Eds.) *Lower Kinabatangan scientific expedition*. Universiti Malaysia Sabah. pp 37-45
- Groves CP (2001) *Primate Taxonomy*. Smithsonian Institution Press, Washington DC
- IUCN (1978) Proboscis or long-nosed monkey. Draft data sheet for Red Data Book. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland
- IUCN (2000) *IUCN red list of threatened animals*. Gland, Switzerland/Cambridge, UK:IUCN
- Jeffrey SM (1979) The proboscis monkey: some preliminary observations. *Tigerpaper* 6:5-6
- Jeffrey SM (1982) Threats to the proboscis monkeys. *Oryx* 16:337-339
- Kawabe M, Mano T (1972) Ecology and behaviour of the wild proboscis monkey, *Nasalis larvatus* (wurbm.) in Sabah, Malaysia. *Primates* 13:213-227
- Kay RNB, Hoppe P, Maloiy GM (1976) Fermentative digestion of food in the colobus

- monkey, *Colobus polykomos*. *Experimentia* 32:485-487
- Kern JA (1964) Observations on the habits of the proboscis monkey, *Nasalis larvatus* (Wernb), made in the Brunai Bay area, Borneo. *Zoologica* 49:183-192
- Kirkpatrick RC (2007) The Asian Colobines Diversity Among Leaf-Eating Monkeys. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK (eds) *Primats in perspective*. Oxford University Press, New York, pp 186–200
- Koenig A (2000) Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). *Behav Ecol Sociobiol* 48:93–109
- Kummer H (1971) Immediate case of primate social structures. In *Proceeding 3rd International Congress of Primatology, Zurich 1970*, vol. 3, Basel: Kerger, pp. 1-11
- Lambert JE (2007) Primate Nutritional Ecology. Feeding biology and diet at ecological and evolutionary scales. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK (eds) *Primats in perspective*. Oxford University Press, New York, pp 482-495
- Macdonald DW (1982) Notes on the size and composition of groups of proboscis monkey (*Nasalis larvatus*). *Folia primatol* 37:95-98
- Makey D, Waterman PG (1982) Ranging behaviour of a group of black colobus (*Colobus satanas*) in the Douala-Edea Reserve, Cameroon. *Folia Primatol* 39:264-304
- Miller LE, Treves A (2007) Predation on primates. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK (eds) *Primats in perspective*. Oxford University Press, New York, pp 525–543
- Mitani JC and Rodman PS (1979) Territoriality: The relation of ranging patterns and

- home range size to defensibility, with an analysis of territoriality among primate species. *Behav Ecol Sociobiol* 5:241-251
- Murai T (2004a) Social structure and mating behavior of proboscis monkey *Nasalis larvatus* (Primates; Colobinae). PhD Thesis. Graduate School of Environmental Earth Science, Hokkaido University
- Murai T (2004b) Social behaviors of all-male proboscis monkeys when joined by females. *Ecological Research* 19:451-454
- Murai T (2006) Mating behaviors of the proboscis monkey (*Nasalis larvatus*). *Am J Primatol* 68:832-837
- Murai T, Mohamed M, Bernard H, Mahedi PA, Saburi R, Higashi S (2007) Female transfer between one-male groups of proboscis monkey (*Nasalis larvatus*). *Primates* 48:117-121
- Napier PH (1985) Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the Subfamily Colobinae. British Museum (Natural History), London
- Napier JR, Napier PH (1967) A Handbook of Living Primates. Academic Press, London
- Napier JR, Napier PH (1985) The Natural History of the Primates, MIT Press: Cambridge, Massachusetts, pp: 158
- Newton PN (1992) Feeding and ranging patterns of forest hanuman langurs (*Presbytis entellus*). *Int J Primatol* 13:245-285
- Nowell K, Jackson P (1996) Wild Cats: Status survey and conservation action plan. IUCN/SSC Cat Specialist Group, Cambridge
- Oates (1987) Food distribution and foraging behavior. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of

Chicago Press, Chicago, pp 197-209

Ohsawa H (1979) Herd dynamics. In: Contributions to Primatology, Vol 16: Ecological and sociological studies of gelada baboons. Kawai M (eds) Basel: S Karger, pp 47-80

Olupot W, Chapman CA, Brown CH, Waser PM (1994) Mangabey (*Cercocebus albigena*) population density, group size, and ranging: A twenty year comparison. Am J Primatol 32:197-205

Onuma M (2002) Daily ranging patterns of the proboscis monkey, *Nasalis larvatus*, in coastal areas of Sarawak, Malaysia. Mammal study 27:141-144

Pielou EC (1966) Shannon's formula as a measure of specific diversity: Its use and misuses. Am Nat 104:463-465

Pinto LP and Setz EZF (2004) Diet of *Alouatta belzebul discolor* in an amazonian rain forest of northern Mato Grosso State, Brazil. Int J Primatol 25:1197-1211

Raemaekers J (1980) Causes of variation between months in the distance traveled daily by gibbons. Folia Primatol 34:46-60.

Ranglack GS and Yeager CP (1986) Survey of intestinal parasites found in proboscis monkeys (*Nsalis larvatus*) and long-tailed macaques (*Macaca fascicularis*). Primate Reports 14:249

Salter RE, Mackenzie NA (1985) Conservation status of the proboscis monkey in Sarawak. Biological Conservation 33: 119-132

Salter RE, Mackenzie NA, Aken KM, Chai PPK (1985) Habitat use, ranging behaviour, and food habits of the proboscis monkey, *Nasalis larvatus* (van Wurmb), in Sarawak. Primates 26:436-451

- van Schaik CP, van Hooff J (1983) On the ultimate causes of primate social systems. *Behaviour* 85:91-117
- Schultz AH (1942) Growth and development of the proboscis monkey. *Bull Mus Comp Zool (Harvard)* 89:279-314
- Sha JCM (2006) Distribution, abundance and conservation of proboscis monkey (*Nasalis larvatus*) in Sabah, Malaysia. Master Thesis. Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah
- Stanford CB (1991) The capped langur in Bangladesh: Behavioral ecology and reproductive tactics. Karger, New York
- Struhsaker TT, Leland L (1987) Colobines: Infanticide by adult males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 83-97
- Terborgh J (1983) *Five New World Primates: A study in Comparative Ecology*. Princeton University Press, Princeton, New Jersey
- Waterman PG (1984) Food acquisition and processing as a function of plant chemistry. In: Chivers, DJ, Wood BA, Bilsborough A (eds), *Food Acquisition and Processing in Primates*, Plenum Press, New York, pp 177-211
- Yeager CP (1984) The proboscis monkey of Borneo. *The Brookfield Bison* 1:18
- Yeager CP (1989) Feeding ecology of the proboscis monkey (*Nasalis larvatus*). *Int J Primatol* 10:497-530
- Yeager CP (1991a) Possible antipredator behavior associated with river crossings by proboscis monkeys (*Nasalis larvatus*). *Am J Primatol* 24: 61-66
- Yeager CP (1991b) Proboscis monkey (*Nasalis larvatus*) social organization: intergroup

patterns of association. *Am J Primatol* 23:73-86

Yeager CP (1992) Proboscis monkey (*Nasalis larvatus*) social organization: the nature and possible functions of intergroup patterns of association. *Am J Primatol* 26:133-137

Yeager CP (1993) Ecological constraints on intergroup associations in the proboscis monkey (*Nasalis larvatus*). *Tropical Biodiversity* 1:89-100

Yeager CP (1995) Does Intraspecific variation in social systems explain reported differences in the social structure of the proboscis monkey (*Nasalis larvatus*)? *Primates* 36:575-582

Yeager, C. P. and Blondal, T. K. 1992. Conservation status of the proboscis monkeys (*Nasalis larvatus*) at Tanjung Puting National Park, Kalimantan Tengah, Indonesia
In. Ismail et al. (eds) *Forest biology and conservation in Borneo*. Center for Borneo Studies, Publication No. 2

Table 1 Age / sex categories used in this study (Bennett and Sebastian, 1988 were based)

Category	Age estimation (year)	Criteria
Adult male (AM)	6 -	Male of full body size with fully developed nose and well-developed fat layer on waist
Adult female (AF)	6 -	Female of full body size. Compared to the adult male, she has a smaller nose. Compared to the subadult female, she has a elongated nipples.
Subadult male (SAM)	4 - 6	Male more than 3 / 4 full body size but without fully developed nose and / or mane across back.
Subadult female (SAF)	4 - 6	Female more than 3 / 4 but not yet fully adult body size.
Juvenile (J)	2 - 4	Monkey with adult coloured face and brown fur coat, but not yet 3 / 4 full adult size.
Infant (I)	0 - 2	Monkey with dark brown or black skin on face.

Table 2 Composition of one-male, all-male and mixed groups in each month. Each census was conducted in an area of 6 km along the tributary Menanggul River.

	May/05	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan/06	Feb	Mar	Apr	May
No. of censuses	7	8	6	12	9	12	11	10	13	22	10	10	8
No. of groups per census	5-10	3-10	2-11	3-15	2-11	2-13	3-8	2-7	2-11	0-5	0-10	2-11	3-11
Group size	3-25	3-24	3-20	3-21	3-22	3-29	3-28	3-24	2-29	2-24	3-27	4-31	4-27
Mean \pm SD	12.1 \pm 2.0	10.8 \pm 2.2	11.6 \pm 3.1	11.8 \pm 3.8	10.1 \pm 3.3	13.0 \pm 2.8	13.0 \pm 1.7	12.3 \pm 1.6	13.6 \pm 3.2	12.1 \pm 1.5	12.0 \pm 3.7	15.8 \pm 2.7	15.3 \pm 2.4
One-male group	AM	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	AF	5.4	5.1	5.0	5.4	4.6	5.3	5.3	5.3	4.5	4.6	5.9	5.7
	SAF	1.1	0.6	0.2	0.2	0.5	0.4	0.2	0.1	0.2	0.4	0	0.7
	J	2.5	2.2	2.4	2.0	2.0	3.2	2.7	3.4	3.5	3.0	4.1	4.1
	I	2.0	2.5	3.0	3.2	2.0	3.2	3.2	3.8	3.0	3.0	4.7	3.8
No. of groups per census	-	-	-	-	0-1	0-1	0-2	0-6	0-4	0-5	0-2	0-3	0-3
Group size	-	-	-	-	12-13	11-13	5-15	6-11	2-11	5-14	3-10	4-11	2-18
Mean \pm SD	-	-	-	-	12.5 \pm 0.4	12.0 \pm 0.4	8.5 \pm 0.8	8.4 \pm 0.5	6.8 \pm 1.1	9.8 \pm 0.5	6.6 \pm 0.8	7.8 \pm 0.9	10.1 \pm 0.9
All-male group	AM	-	-	-	3.0	2.5	1.7	2.4	1.5	2.1	2.0	1.8	1.6
	SAM	-	-	-	6.5	4.5	1.8	2.4	1.8	3.0	2.5	2.6	3.6
	J	-	-	-	2.0	5.0	3.5	3.6	3.5	4.6	2.1	3.4	4.9
	I	-	-	-	1.0	0	1.5	0	0	0	0	0	0
No. of groups per census	0-1	0-1	-	0-1	-	0-1	-	-	0-2	0-2	0-1	0-1	0-1
Group size	13-15	21-25	-	12-15	-	7-15	-	-	6-17	6-24	-	-	-
Mean \pm SD	14.0 \pm 1.4	22.7 \pm 2.1	-	13.5 \pm 2.1	-	11.7 \pm 4.2	-	-	11.7 \pm 5.5	15.0 \pm 12.7	10.0	11.0	9.0
Mixed-group	AM	3.0	2.7	-	2.0	2.3	-	-	1.3	1.0	3.0	2.0	4.0
	AF	6.0	11.0	-	7.5	5.0	-	-	2.3	2.5	1.0	1.0	2.0
	SA	2.5	1.7	-	0	0	-	-	0.7	3.0	3.0	4.0	2.0
	J	1.0	4.0	-	0.5	1.7	-	-	5.7	7.5	2.0	4.0	0
	I	1.5	3.3	-	3.5	2.7	-	-	1.7	1.0	1.0	0	1.0
No. of individuals per census	65-140	30-144	21-117	41-178	35-107	43-179	34-130	33-101	33-160	0-63	1-141	44-155	73-218

AM, AF, MSA, FSA, J and I: mean number of adult males, adult females, subadults males, subadult females, juveniles and infants, respectively

Table 3 Monthly total hours for observing behaviors of BE-Group adult members.

Month	Total	Adult male	Adult females										
		Bejiita	ChiChi	Bulma	Lunch	Arare	Bigmama	Midori*					
2005													
May	167.9	97.7	35.4	24.4	0	10.3	0	0	-				
June	279.6	186.3	9.8	23.4	12.0	10.5	37.7	-					
July	270.1	171.2	28.1	24.7	33.8	12.4	0	-					
August	266.0	146.0	106.6	0	11.8	1.6	0	-					
September	216.6	146.2	58.7	0	0	11.7	0	-					
October	331.9	179.5	106.9	21.0	0.8	11.7	12.0	-					
November	289.6	146.6	60.5	11.6	12.0	23.6	35.4	-					
December	365.3	180.9	82.7	35.0	30.8	24.0	12.0	-					
2006													
January	305.8	155.6	66.3	28.1	31.7	12.0	12.1	-					
February	69.2	35.0	0	0	0	34.2	0	-					
March	282.9	160.9	37.0	23.9	36.4	24.7	0	0					
April	312.6	178.3	42.3	0	12.2	32.1	23.6	24.0					
May	348.7	183.7	47.6	36.1	11.7	35.5	9.9	24.2					
Total	3506.3	1967.8	681.7	228.1	193.2	244.3	142.8	48.3					

* transferred into the group in March 2006

Table 4 Percentages of activities in each adult of BE-Group, Others: grooming and copulation. Observation was conducted from May 2005 to May 2006.

	Resting	Feeding	Moving	Others
Bejita	75.9	20.4	3.6	0.1
SD	8.9	8.7	1.6	0.3
ChiChi	78.0	17.9	3.0	1.1
SD	8.2	7.4	1.5	2.2
Bulma	78.4	17.7	3.2	0.7
SD	10.3	8.6	2.0	2.2
Lunch	74.5	20.5	3.5	1.5
SD	11.1	9.3	1.5	2.4
Arare	76.1	19.4	3.4	1.1
SD	10.6	10.5	1.4	1.2
Bigmama	79.6	16.4	3.4	0.6
SD	6.7	6.3	1.1	0.9
Midori	73.9	21.0	3.2	2.0
SD	5.8	7.2	1.1	0.7
Total	76.4	19.5	3.5	0.5

Table 5 Floral makeup along 16 trails shown in Figure 1. The total distance of the trails was 7.15 km and the vegetation survey was conducted for trees (> 10 cm in DBH) and vines (> 5 cm in diameter) on the trail or within 1 m from the edge of trail (i. e. survey area = 2.15 ha).

Family	Species	Life form	N	Density		Basal area (cm ²)		Rank	
				/ ha	Rank	/ tree or vine	/ ha	Tree	Vine
ANACARDIACEAE	<i>Androtium astylum</i>	Tree	1	0.5	128	104.9	48.9	135	
	<i>Buchanania arborescens</i>	Tree	10	4.7	52	736.1	3431.7	22	
	<i>Dracontomelon dao</i>	Tree	15	7.0	39	502.1	3511.4	20	
	<i>Koordersiodendron pinnatum</i>	Tree	2	0.9	105	770.5	718.4	61	
	<i>Mangifera parvifolia</i>	Tree	3	1.4	87	911.3	1274.6	48	
	<i>Melanochyla auriculata</i>	Tree	2	0.9	106	406.2	378.7	76	
ANNONACEAE	<i>Artabotrys suaveolens</i>	Vine	26	12.1	24	50.7	614.4		6
	<i>Cananga odorata</i>	Tree	4	1.9	79	718.1	1339.2	47	
	<i>Polyalthia sumatrana</i>	Tree	1	0.5	130	191.2	89.1	118	
	<i>P. sp. 1</i>	Tree	1	0.5	129	131.2	61.2	129	
	<i>Uvaria lobbiana</i>	Vine	1	0.5	131	25.8	12.0		38
	<i>U. sp. 1</i>	Vine	1	0.5	132	27.0	12.6		35
APOCYNACEAE	<i>Parameria polyneura</i>	Vine	1	0.5	133	24.1	11.2		40
	<i>Tabernaemontana macrocarpa</i>	Tree	1	0.5	134	575.2	268.2	90	
	<i>Urceola sp. 1</i>	Vine	2	0.9	107	40.6	37.9		25
	<i>Willughbeia angustifolia</i>	Vine	1	0.5	135	27.0	12.6		36
AQUIFOLIACEAE	<i>Ilex cymosa</i>	Tree	28	13.1	19	486.6	6352.1	12	
BOMBACACEAE	<i>Durio kutejensis</i>	Tree	1	0.5	136	140.4	65.5	125	
BURSERACEAE	<i>Canarium decumanum</i>	Tree	1	0.5	137	102.0	47.6	137	
	<i>C. denticulatum</i>	Tree	2	0.9	108	107.0	99.8	115	
CELASTRACEAE	<i>Lophopetalum multinervium</i>	Tree	2	0.9	109	794.5	740.8	60	
CHRYSOBALANACEAE	<i>Kostermanthus heteropetalus</i>	Tree	1	0.5	138	3316.6	1546.2	42	
	<i>Maranthes corymbosa</i>	Tree	3	1.4	88	198.7	277.9	88	
	<i>Parinari oblongifolia</i>	Tree	3	1.4	89	2237.7	3129.7	23	
CLUSIACEAE	<i>Calophyllum blancoi</i>	Tree	1	0.5	139	250.6	116.8	112	
	<i>C. pisiferum</i>	Tree	1	0.5	140	556.4	259.4	92	
	<i>Cratoxylum cochinchinense</i>	Tree	8	3.7	60	434.0	1618.5	39	
	<i>C. formosum</i>	Tree	3	1.4	90	619.7	866.7	56	
	<i>Garcinia brevipes</i>	Tree	1	0.5	141	103.2	48.1	136	
	<i>G. parvifolia</i>	Tree	23	10.7	26	144.2	1546.3	41	
	<i>G. sp. 1</i>	Tree	1	0.5	142	353.1	164.6	109	
	<i>Kayea oblongifolia</i>	Tree	1	0.5	143	194.3	90.6	117	
	<i>Mesua elmeri</i>	Tree	23	10.7	27	473.3	5074.5	15	
	<i>M. macrantha</i>	Tree	1	0.5	144	392.4	182.9	106	
	COMBRETACEAE	<i>Combretum acuminatum</i>	Vine	5	2.3	73	25.8	60.2	
<i>Terminalia citrina</i>		Tree	2	0.9	110	194.9	181.7	107	
CONNARACEAE	<i>Agelaea borneensis</i>	Vine	1	0.5	145	26.4	12.3		37
	<i>A. trinervis</i>	Vine	1	0.5	146	46.2	21.6		32
	<i>Connarus grandis</i>	Vine	6	2.8	65	35.1	98.3		18
	<i>Rourea mimosoides</i>	Vine	1	0.5	147	58.0	27.1		29
	<i>R. minor</i>	Vine	11	5.1	49	97.2	498.4		11
CONVOLVULACEAE	<i>Erycibe grandifolia</i>	Vine	1	0.5	148	38.5	18.0		33
DILLENACEAE	<i>Dillenia excelsa</i>	Tree	98	45.7	4	171.2	7822.1	9	
	<i>Tetracera scandens</i>	Vine	3	1.4	91	31.1	43.4		24
DIPTEROCARPACEAE	<i>Dipterocarpus validus</i>	Tree	14	6.5	42	904.6	5904.5	13	
	<i>Parashorea malaanonan</i>	Tree	2	0.9	111	448.8	418.4	75	
	<i>Vatica rassak</i>	Tree	52	24.2	10	338.0	8194.4	8	
	<i>V. umbonata</i>	Tree	2	0.9	112	308.5	287.7	85	
	<i>V. venulosa</i>	Tree	11	5.1	50	462.9	2373.8	30	
EBENACEAE	<i>Diospyros curranii</i>	Tree	23	10.7	28	264.3	2833.9	27	
	<i>D. elliptifolia</i>	Tree	21	9.8	29	240.8	2357.4	31	
	<i>D. euphlebia</i>	Tree	3	1.4	92	135.0	188.9	105	
	<i>D. macrophylla</i>	Tree	1	0.5	149	407.0	189.8	104	
	<i>D. wallichii</i>	Tree	6	2.8	66	243.2	680.2	66	
	<i>D. sp. 1</i>	Tree	6	2.8	67	182.7	511.0	74	
	<i>D. sp. 2</i>	Tree	6	2.8	68	486.8	1361.7	46	
	<i>D. sp. 3</i>	Tree	5	2.3	74	41.4	96.5	116	
ELAEOCARPACEAE	<i>Elaeocarpus macrocarpus</i>	Tree	1	0.5	150	539.3	251.4	95	
	<i>E. nitidus</i>	Tree	15	7.0	40	325.9	2279.4	32	
	<i>E. stipularis</i>	Tree	6	2.8	69	328.2	917.9	55	

Table (Continued 1)

Family	Species	Life form	N	Density		Basal area (cm ²)		Rank	
				/ ha	Rank	/ tree or vine	/ ha	Tree	Vine
ERYTHROXYLACEAE	<i>Erythroxylum cuneatum</i>	Tree	2	0.9	113	251.3	234.3	98	
EUPHORBIACEAE	<i>Antidesma thwaitesianum</i>	Tree	33	15.4	14	423.6	6517.7	11	
	<i>Aporosa acuminatissima</i>	Tree	1	0.5	151	175.1	81.6	120	
	<i>A. nigricans</i>	Tree	4	1.9	80	198.5	370.3	79	
	<i>Baccaurea bracteata</i>	Tree	3	1.4	93	240.6	336.5	82	
	<i>B. stipulata</i>	Tree	18	8.4	34	120.3	1009.1	53	
	<i>Bridelia penangiana</i>	Tree	3	1.4	94	167.2	233.8	99	
	<i>B. stipularis</i>	Vine	30	14.0	18	53.3	744.9		4
	<i>Cleistanthus myrianthus</i>	Tree	19	8.9	33	313.6	2778.0	28	
	<i>Croton caudatus</i>	Vine	46	21.4	11	34.2	732.7		5
	<i>C. oblongus</i>	Tree	82	38.2	5	182.3	6969.5	10	
	<i>Drypetes castilloi</i>	Tree	15	7.0	41	160.8	1124.7	52	
	<i>D. sp. 1</i>	Tree	1	0.5	152	176.6	82.3	119	
	<i>Excoecaria indica</i>	Tree	111	51.7	3	1454.3	75257.3	1	
	<i>Glochidion macrostigma</i>	Tree	2	0.9	114	59.3	55.3	131	
	<i>G. obscurum</i>	Tree	20	9.3	30	164.4	1532.8	43	
	<i>G. sp. 1</i>	Tree	2	0.9	115	187.7	175.0	108	
	<i>Macaranga conifera</i>	Tree	5	2.3	75	303.5	707.4	62	
	<i>Mallotus floribundus</i>	Tree	1	0.5	153	47.4	22.1	139	
	<i>M. muticus</i>	Tree	149	69.5	1	642.4	44622.8	2	
	<i>M. penangensis</i>	Tree	18	8.4	35	181.9	1526.8	44	
	<i>Margaritaria indica</i>	Tree	5	2.3	76	346.0	806.5	57	
	<i>Paracroton pendulus</i>	Tree	8	3.7	61	182.1	679.1	67	
FLACOURTIACEAE	<i>Hydnocarpus polypetalus</i>	Tree	4	1.9	81	176.3	328.7	83	
	<i>H. sumatrana</i>	Tree	36	16.8	13	316.3	5308.4	14	
	<i>H. woodii</i>	Tree	1	0.5	154	139.8	65.2	126	
	<i>Xylosma sumatrana</i>	Tree	67	31.2	7	317.4	9913.2	6	
GNETACEAE	<i>Gnetum gnemonoides</i>	Vine	4	1.9	82	58.2	108.5		17
LAMIACEAE	<i>Teijsmanniodendron bogoriense</i>	Tree	10	4.7	53	392.4	1829.5	36	
	<i>Vitex pinnata</i>	Tree	55	25.6	9	659.9	16919.6	5	
LAURACEAE	<i>Cinnamomum sp. 1</i>	Tree	1	0.5	155	160.5	74.8	121	
	<i>Cryptocarya sp. 1</i>	Tree	5	2.3	77	127.2	296.5	84	
	<i>C. sp. 2</i>	Tree	1	0.5	156	123.0	57.3	130	
	<i>Dehaasia cuneata</i>	Tree	9	4.2	57	378.8	1589.4	40	
	<i>Endiandra sp. 1</i>	Tree	12	5.6	45	248.2	1388.4	45	
	<i>E. sp. 2</i>	Tree	8	3.7	62	327.6	1221.9	50	
	<i>Litsea sp. 1</i>	Tree	1	0.5	157	541.9	252.6	94	
	<i>L. sp. 2</i>	Tree	1	0.5	158	233.9	109.0	114	
	<i>Nothaphoebe sp. 1</i>	Tree	2	0.9	116	687.5	641.0	68	
LECYTHIDACEAE	<i>Barringtonia macrostachya</i>	Tree	32	14.9	16	180.4	2690.8	29	
	<i>Planchonia valida</i>	Tree	1	0.5	159	3846.5	1793.2	37	
LEGUMINOSAE	<i>Acacia borneensis</i>	Vine	10	4.7	54	30.6	142.6		16
	<i>Albizia corniculata</i>	Vine	28	13.1	20	63.1	824.2		3
	<i>Bauhinia diptera</i>	Vine	26	12.1	25	47.4	574.1		7
	<i>Cassia indica</i>	Tree	3	1.4	95	80.6	112.8	113	
	<i>Crudia ornata</i>	Tree	1	0.5	160	144.5	67.4	123	
	<i>C. reticulata</i>	Tree	27	12.6	22	278.5	3505.8	21	
	<i>Cynometra ramiflora</i>	Tree	3	1.4	96	177.8	248.6	96	
	<i>Dalbergia parvifolia</i>	Vine	38	17.7	12	30.6	542.0		8
	<i>Derris elegans</i>	Vine	2	0.9	117	27.9	26.0		31
	<i>D. sp. 1</i>	Vine	5	2.3	78	31.9	74.2		20
	<i>D. sp. 2</i>	Vine	1	0.5	161	58.0	27.1		30
	<i>Dialium indum</i>	Tree	1	0.5	162	4582.0	2136.1	33	
	<i>Entada rheedei</i>	Vine	32	14.9	17	75.3	1123.9		2
	<i>Koompassia excelsa</i>	Tree	1	0.5	163	611.0	284.8	86	
	<i>Millettia nieuwenhuisii</i>	Vine	20	9.3	31	57.6	537.0		9
	<i>M. sp. 1</i>	Vine	4	1.9	83	94.2	175.6		14
	<i>M. sp. 2</i>	Vine	2	0.9	118	15.4	14.4		34
	<i>Ormosia sumatrana</i>	Tree	2	0.9	119	298.1	278.0	87	
	<i>Pongamia pinnata</i>	Tree	11	5.1	51	573.8	2942.5	26	
	<i>Sindora leiocarpa</i>	Tree	2	0.9	120	243.9	227.4	100	
	<i>Spatholobus macropterus</i>	Vine	18	8.4	36	60.4	506.9		10
LOGANIACEAE	<i>Strychnos ignatii</i>	Vine	2	0.9	121	39.0	36.3		27
	<i>S. minor</i>	Vine	3	1.4	97	45.5	63.6		21
LOPHOPYXIDACEAE	<i>Lophopyxis maingayi</i>	Vine	113	52.7	2	47.3	2491.8		1
LYTHRACEAE	<i>Lagerstroemia speciosa</i>	Tree	6	2.8	70	227.4	636.0	69	

Table (Continued 2)

Family	Species	Life form	N	Density		Basal area (cm ²)		Rank		
				/ ha	Rank	/ tree or vine	/ ha	Tree	Vine	
MELASTOMACEAE	<i>Memecylon edule</i>	Tree	1	0.5	164	116.8	54.4	132		
	<i>M. paniculatum</i>	Tree	6	2.8	71	133.6	373.7	78		
	<i>Pternandra galeata</i>	Tree	65	30.3	8	1379.0	41789.1	3		
MELIACEAE	<i>Aphanamixis sp. 1</i>	Tree	1	0.5	165	106.7	49.7	134		
MENISPERMACEAE	<i>Haematocarpus validus</i>	Vine	1	0.5	166	25.8	12.0		39	
MORACEAE	<i>Artocarpus kemando</i>	Tree	2	0.9	122	238.4	222.3	102		
	<i>Ficus benjamina</i>	Tree	1	0.5	167	1256.0	585.5	71		
	<i>F. binnendijkii</i>	Tree	14	6.5	43	665.3	4342.5	16		
	<i>F. cf. lanata Bl var foveolata</i>	Vine	2	0.9	123	39.8	37.1		26	
	<i>F. crassiramea</i>	Tree	4	1.9	84	2129.5	3971.1	19		
	<i>F. globosa</i>	Vine	1	0.5	168	98.4	45.9		23	
	<i>F. variegata</i>	Tree	1	0.5	169	803.8	374.8	77		
MYRISTICACEAE	<i>Knema laurina</i>	Tree	4	1.9	85	115.6	215.6	103		
	<i>Myristica sp. 1</i>	Tree	2	0.9	124	743.3	693.0	65		
	<i>M. sp. 2</i>	Tree	8	3.7	63	256.0	954.6	54		
MYRSINACEAE	<i>Ardisia sp. 1</i>	Tree	1	0.5	170	133.8	62.4	128		
	<i>Embelia philippinensis</i>	Vine	2	0.9	125	35.9	33.4		28	
MYRTACEAE	<i>Eugenia litseaefolia</i>	Tree	16	7.5	38	255.1	1902.8	35		
	<i>E. sandakanensis</i>	Tree	3	1.4	98	197.1	275.6	89		
	<i>E. sp. 1</i>	Tree	3	1.4	99	94.5	132.2	111		
	<i>E. sp. 2</i>	Tree	33	15.4	15	544.9	8383.6	7		
	<i>E. sp. 3</i>	Tree	28	13.1	21	317.9	4149.6	18		
	<i>E. sp. 4</i>	Tree	1	0.5	171	754.4	351.7	81		
	<i>E. sp. 5</i>	Tree	1	0.5	172	99.8	46.5	138		
	<i>Syzygium fastigiatum</i>	Tree	12	5.6	46	133.8	748.3	59		
OLEACEAE	<i>Chionanthus pluriflorus</i>	Tree	2	0.9	126	623.4	581.3	72		
POLYGALACEAE	<i>Xanthophyllum flavescens</i>	Tree	12	5.6	47	308.4	1725.1	38		
PROTEACEAE	<i>Helicia robusta</i>	Tree	3	1.4	100	188.8	264.0	91		
RHAMNACEAE	<i>Ventilago dichotoma</i>	Vine	12	5.6	48	37.6	210.3		13	
	<i>Ziziphus borneensis</i>	Vine	3	1.4	101	56.6	79.2		19	
RHIZOPHORACEAE	<i>Carallia brachiata</i>	Tree	13	6.1	44	515.3	3122.9	25		
RUBIACEAE	<i>Diplospora sp. 1</i>	Tree	1	0.5	173	159.1	74.2	122		
	<i>Gardenia tubifera</i>	Tree	3	1.4	102	184.3	257.8	93		
	<i>Ixora elliptica</i>	Tree	2	0.9	127	150.9	140.7	110		
	<i>Nauclea orientalis</i>	Tree	3	1.4	103	496.8	694.8	64		
	<i>N. subdita</i>	Tree	77	35.9	6	490.4	17602.4	4		
	<i>Neolamarckia cadamba</i>	Tree	7	3.3	64	373.8	1219.9	51		
	<i>Neonauclea excelsa</i>	Tree	4	1.9	86	277.5	517.5	73		
	<i>Pleiocarpidia sandahanica</i>	Tree	18	8.4	37	146.7	1231.5	49		
	<i>Uncaria callophylla</i>	Vine	10	4.7	55	33.4	155.9		15	
	<i>U. ferrea</i>	Vine	20	9.3	32	30.4	283.8		12	
	RUTACEAE	<i>Clausena excavata</i>	Tree	3	1.4	104	171.0	239.2	97	
	SAPINDACEAE	<i>Dimocarpus longan</i>	Tree	1	0.5	174	756.9	352.9	80	
<i>Lepisanthes amoena</i>		Tree	1	0.5	175	137.8	64.2	127		
<i>Mischocarpus sundaicus</i>		Tree	1	0.5	176	112.6	52.5	133		
<i>Nephelium uncinatum</i>		Tree	1	0.5	177	478.2	222.9	101		
<i>Pometia sp. 1</i>		Tree	1	0.5	178	142.5	66.4	124		
SAPOTACEAE	<i>Madhuca dubardii</i>	Tree	9	4.2	58	178.8	750.3	58		
	<i>Payena microphylla</i>	Tree	1	0.5	179	1355.9	632.1	70		
STERCULIACEAE	<i>Pterospermum macrocarpum</i>	Tree	10	4.7	56	903.6	4212.4	17		
SYMPLOCACEAE	<i>Symplocos celastriifolia</i>	Tree	6	2.8	72	248.5	695.0	63		
TILIACEAE	<i>Colona serratifolia</i>	Tree	9	4.2	59	481.4	2019.9	34		
	<i>Grewia acuminata</i>	Vine	1	0.5	180	23.0	10.7		41	
	<i>Microcos crassifolia</i>	Tree	27	12.6	23	248.3	3125.5	24		

Table 6 Food items and parts of each item consumed by focal members of BE-Group from May 2005 to May 2006.

Family	Species	2005 May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	2006 Jan	Feb	Mar	Apr	May
ANACARDIACEAE	<i>Androtium astylum</i>	Lv Fr						Lv						
	<i>Buchanania arborescens</i>		Lv				Lv							Lv
	<i>Dracontomelon dao</i>	Lv						Fl	Lv			Lv		
	<i>Mangifera griffithii</i>								Lv	Lv				
	<i>Melanochyla auriculata</i>								Lv	Lv		Lv		
	<i>M. caesia</i>										Lv			Lv
	<i>Pegia sarmentosa</i>								Lv	Lv				
ANNONACEAE	<i>Alphonsea javanica</i>						Lv							
	<i>Artabotrys suaveolens</i>		Lv					Fl	Lv	Lv				
	<i>Uvaria lobbiana</i>		Lv						Lv			Lv		
APOCYNACEAE	<i>Chilocarpus vernicosus</i>		Lv											
	<i>C. sp. 1</i>							Lv		Lv				
	<i>Ichnocarpus frutescens</i>											Lv		
	<i>Parameria polyneura</i>	Lv	Lv				Lv	Lv	Lv			Lv	Lv	
	<i>Urceola sp. 1</i>											Fl	Lv Fl	Lv
	<i>Willughbeia angustifolia</i>		Lv	Lv			Lv	Lv						
	<i>Willughbeia angustifolia</i>		Lv			Fl		Fr		Lv		Lv		
AQUIFOLIACEAE	<i>Ilex cymosa</i>		Lv			Fl				Lv		Lv		
ARACEAE	<i>Pothos sp. 1</i>													Lv
BLECHNACEAE	<i>Stenochlaena palustris</i>								Lv	Lv		Lv	Lv	
BOMBACACEAE	<i>Durio grandiflorus</i>												Lv	
BURSERACEAE	<i>Canarium denticulatum</i>			Lv			Lv		Lv					
	<i>C. odontophyllum</i>						Lv							
	<i>C. sp. 1</i>								Lv					
	<i>C. sp. 2</i>						Lv			Lv				
	<i>C. sp. 3</i>												Lv	
CECROPIACEAE	<i>Poikilospermum suaveolens</i>					Lv								
CHRYSOBALANACEAE	<i>Atuna cordata</i>	Lv								Lv	Lv	Lv		Lv
	<i>Licania splendens</i>												Lv	
	<i>Maranthes corymbosa</i>			Lv	Lv	Lv	Lv		Lv			Lv		
	<i>Parinari oblongifolia</i>			Lv									Lv	
CLUSIACEAE	<i>Cratoxylum formosum</i>		Lv			Lv	Lv	Lv	Lv	Lv	Lv	Lv Fl	Lv	
	<i>C. sumatranum</i>						Lv							
	<i>Garcinia brevipes</i>											Lv		
	<i>G. parvifolia</i>						Lv	Fr						
	<i>G. rostrata</i>							Lv Fr	Fr	Fr				Lv
	<i>Kayea oblongifolia</i>					Lv								
	<i>Mesua elmeri</i>						Lv			Lv	Lv	Lv	Lv	
	<i>M. macrantha</i>												Lv	
COMBRETACEAE	<i>Combretum acuminatum</i>	Lv	Lv					Fr				Lv		
	<i>Terminalia citrina</i>	Lv												
CONNARACEAE	<i>Agelaea borneensis</i>				Lv							Lv	Lv	
	<i>A. trinervis</i>		Lv	Lv				Lv	Lv					
	<i>Connarus grandis</i>													Lv
	<i>Rourea mimosoides</i>							Lv				Lv		
	<i>R. minor</i>					Fr		Lv				Lv		Lv
	<i>R. sp. 1</i>	Lv												
CONVOLVULACEAE	<i>Erycibe grandifolia</i>						Lv							
	<i>Merremia borneensis</i>								Lv					

Lv: leaves; Fr: fruits; Fl: flowers; Cx: calyx; Ba: bark; Tn: termite nest

Table (Continued 1)

Family	Species	2005 May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	2006 Jan	Feb	Mar	Apr	May
CTENOLOPHONACEAE	<i>Ctenolophon parvifolius</i>						Lv							
CUCURBITACEAE	<i>Zanonia indica</i>		Lv	Lv	Lv					Lv				
DILLENACEAE	<i>Dillenia excelsa</i>	Lv Fl	Fl	Fl	Fl	Fl	Fl Fr	Fl Fr	Lv Fl				Fl	
	<i>Tetracera scandens</i>		Lv Fr	Fr	Fr			Fr	Lv	Fr				Lv
DIOSCOREACEAE	<i>Dioscorea laurifolia</i>						Lv		Lv					
DIPTEROCARPACEAE	<i>Shorea leprosula</i>		Lv											
	<i>Vatica rassak</i>			Lv	Lv	Lv Fl			Lv	Lv	Lv		Lv	Lv
	<i>V. venulosa</i>		Lv	Lv Fl	Lv Fl		Lv							
EBENACEAE	<i>Diospyros curranii</i>						Lv	Lv						
	<i>D. sp. 4</i>			Lv										
	<i>D. sp. 5</i>		Lv											
ELAEOCARPACEAE	<i>Elaeocarpus nitidus</i>	Lv	Lv	Lv	Lv			Lv	Lv	Lv Fr	Lv	Lv	Lv	Lv
	<i>E. stipularis</i>								Lv	Lv				
EUPHORBIACEAE	<i>Antidesma thwaitesianum</i>	Lv	Lv	Lv Fl			Lv	Fr	Lv Fr				Lv Fl	Fl
	<i>Aporosa acuminatissima</i>			Lv										
	<i>Baccaurea stipulata</i>	Lv	Lv				Lv	Lv	Lv	Lv				Lv
	<i>Bridelia penangiana</i>				Lv							Lv		
	<i>B. stipularis</i>		Lv	Lv	Lv	Lv	Lv Fl	Lv Fr Fl	Lv Fr	Lv	Lv	Lv Fr	Lv	Lv
	<i>Cleistanthus myrianthus</i>		Lv		Lv	Lv	Lv		Lv	Lv	Lv	Lv	Lv	Lv
	<i>Croton caudatus</i>		Lv				Lv							
	<i>C. oblongus</i>	Lv	Lv										Lv	
	<i>Drypetes castilloi</i>				Lv				Lv	Lv		Lv		
EUPHORBIACEAE	<i>Excoecaria indica</i>	Lv	Lv		Lv		Lv							Lv
	<i>Macaranga conifera</i>								Lv					Lv
	<i>M. depressa</i>								Lv			Lv		
	<i>Mallotus floribundus</i>		Fr				Lv						Lv	Lv
	<i>M. muticus</i>	Lv	Lv Fr Fl	Lv Fr	Lv Fr	Lv	Lv	Lv Fl	Lv Fl	Lv	Lv	Lv	Lv Fl	Lv Fl
	<i>M. penangensis</i>	Lv	Lv	Lv Fr										
	<i>Margaritaria indica</i>		Lv	Lv Fr	Lv Fr		Lv	Lv				Lv Fl	Lv	Lv Fr
	<i>Paracroton pendulus</i>											Lv		
FLACOURTIACEAE	<i>Hydnocarpus sumatrana</i>	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv		Lv	Lv
	<i>Xylosma sumatrana</i>		Lv				Lv		Lv Fl	Lv		Lv		
GNETACEAE	<i>Gnetum gnemonoides</i>	Lv					Lv		Lv					Lv
LAMIACEAE	<i>Teijsmanniodendron bogoriense</i>						Lv Fr	Lv	Lv Fl					
	<i>Vitex pinnata</i>		Lv	Lv	Lv	Lv	Lv	Lv Fl	Lv					Lv
LAURACEAE	<i>Alseodaphne insignis</i>						Fr	Lv Fr Cx	Lv Fr Cx	Fr			Fr Cx	
	<i>Cinnamomum sp. 1</i>								Lv				Lv	
	<i>Dehaasia cuneata</i>		Lv	Lv Fr	Fr	Lv Fr	Lv		Lv Fl	Lv Fl	Lv	Lv		
	<i>Endiandra sp. 1</i>						Lv		Lv					
	<i>E. sp. 2</i>									Lv				
	<i>Litsea sp. 2</i>						Lv							
	<i>L. sp. 3</i>		Lv											
	<i>Nothaphoebe sp. 1</i>						Lv					Lv		
LECYTHIDACEAE	<i>Barringtonia macrostachya</i>			Lv									Lv	
	<i>Planchonia valida</i>									Lv				
LEGUMINOSAE	<i>Acacia borneensis</i>				Lv		Lv		Lv	Lv	Lv	Lv	Lv	
	<i>Airyantha borneensis</i>	Lv			Lv	Lv	Lv							
	<i>Albizia corniculata</i>	Lv	Lv	Lv Fr	Lv	Lv	Lv	Lv	Lv		Lv	Lv	Lv	Lv

Lv: leaves; Fr: fruits; Fl: flowers; Cx: calyx; Ba: bark; Tn: termite nest

Table (Continued 2)

Family	Species	2005 May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	2006 Jan	Feb	Mar	Apr	May
LEGUMINOSAE	<i>A. dolichadena</i>						Lv		Lv				Lv	Lv
	<i>Bauhinia diptera</i>		Lv Fr	Lv	Lv		Lv	Lv	Lv	Lv			Lv	Lv
	<i>Caesalpinia crista</i>								Lv					
	<i>Crudia ornata</i>							Lv Fr						
	<i>C. reticulata</i>		Lv	Lv				Lv Fr	Fr	Lv				
	<i>Cynometra ramiflora</i>			Lv	Lv	Lv Fr	Lv		Lv Fr	Lv	Lv		Lv	Lv
	<i>Dalbergia parvifolia</i>	Lv	Lv	Lv	Lv Fr	Lv		Lv	Lv	Lv			Lv	Lv
	<i>Derris elegans</i>		Lv		Lv		Lv		Lv				Lv	
	<i>D. sp. 1</i>		Lv			Lv	Lv	Lv		Lv				Lv
	<i>D. sp. 2</i>	Lv	Lv					Lv						
	<i>D. sp. 3</i>									Lv				
	<i>D. sp. 4</i>									Lv				
	<i>Dialium indum</i>								Lv					
	<i>Entada rheedei</i>	Lv	Lv	Lv	Lv		Lv	Lv	Lv	Lv				
	<i>Millettia nieuwenhuisii</i>		Lv		Fr		Lv			Lv				
	<i>Ormosia sumatrana</i>	Lv				Lv			Lv					Lv
	<i>Pongamia pinnata</i>	Lv		Lv	Lv	Lv		Lv	Lv				Lv	Lv
	<i>Sindora leiocarpa</i>		Lv					Fr	Lv				Fl	
	<i>Spatholobus macropterus</i>	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv
LEGUMINOSAE 1								Fr						
LOGANIACEAE	<i>Strychnos minor</i>				Fr	Lv Fr	Lv							
LOPHOPYXIDACEAE	<i>Lophopyxis maingayi</i>	Lv	Lv Fr	Lv Fr	Lv Fr	Lv Fr	Lv Fr	Lv	Lv	Lv	Lv	Lv	Lv	Lv
LORANTHACEAE	<i>Dendrophthoe longituba</i>						Lv	Fl						
	<i>Macrosolen sp. 1</i>												Lv Fl	
LYTHRACEAE	<i>Lagerstroemia speciosa</i>						Lv						Lv	Lv
	<i>L. sp. 1</i>		Fl	Fl									Fl	
MELASTOMATAACEAE	<i>Memecylon paniculatum</i>		Lv			Lv	Lv							Lv
	<i>Pternandra galeata</i>	Lv	Lv		Fr		Lv	Lv	Lv				Lv	Fr
MELIACEAE	<i>Dysoxylum sp. 1</i>								Lv					
	<i>Walsura pinnata</i>						Lv							
MENISPERMACEAE	<i>Haematocarpus validus</i>							Lv						
MORACEAE	<i>Artocarpus sp. 1</i>				Lv Fr	Fr	Lv		Lv					
	<i>A. sp. 2</i>	Lv												
	<i>Ficus annulata</i>				Fr				Fr	Lv Fr		Fr		
	<i>F. benjamina</i>		Lv							Lv		Lv		
	<i>F. binnendijkii</i>	Lv	Lv	Lv Fr	Lv	Lv	Lv Fr	Lv Fr	Lv Fr	Lv Fr	Lv Fr	Lv Fr	Lv Fr	Lv Fr
	<i>F. crassiramea</i>	Lv	Lv	Lv	Lv	Lv	Lv						Lv	
	<i>F. depressa</i>		Lv											
	<i>F. forstenii var. villosa</i>				Lv		Lv			Lv		Fr		
	<i>F. globosa</i>	Lv				Lv Fr		Lv Fr	Fr	Fr		Fr		Fr
	<i>F. cf. lanata var. foveolata</i>						Lv	Lv	Lv			Fr	Lv Fr	
	<i>F. pellucidopunctata</i>			Fr										
	<i>F. racemosa var. elongata</i>			Lv										
	<i>F. sundaica var. beccarianum</i>				Lv Fr	Lv	Lv	Fr	Lv	Lv Fr		Lv		Lv
	<i>F. sundaica var. impressicostata</i>		Lv											
MORACEAE	<i>F. virens var. glabella</i>		Lv				Lv Fr		Lv			Fr		
	<i>F. sp. 1</i>	Lv					Lv	Lv		Lv Fr			Fr	Lv
	<i>F. sp. 2</i>		Lv							Lv				
	<i>F. sp. 3</i>								Lv					
	<i>F. sp. 4</i>					Lv								

Lv: leaves; Fr: fruits; Fl: flowers; Cx: calyx; Ba: bark; Tn: termite nest

Table (Continued 3)

Family	Species	2005 May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	2006 Jan	Feb	Mar	Apr	May
MORACEAE	<i>Ficus</i> sp. 5		Lv											
	<i>F.</i> sp. 6								Lv					
	<i>F.</i> sp. 7													Lv
	<i>F.</i> sp. 8	Lv												
	<i>F.</i> spp.	Lv	Lv											
MYRISTICACEAE	<i>Knema laurina</i>							Lv						
	<i>Myristica</i> sp. 1	Lv												
	<i>M.</i> sp. 2								Lv	Lv				
MYRTACEAE	<i>Eugenia litseaefolia</i>	Lv Fr	Lv			Lv		Lv						Fr
	<i>E.</i> sp. 2		Fr			Ba	Lv Ba	Ba	Lv	Ba		Lv Ba	Lv	
	<i>E.</i> sp. 4		Lv		Lv			Lv						
	<i>E.</i> sp. 6							Lv						
	<i>E.</i> sp. 7									Lv				
	<i>E.</i> sp. 8	Lv			Lv				Lv Fr					
	<i>E.</i> sp. 9												Lv	Fr
	<i>E.</i> spp.		Lv	Lv	Lv		Lv	Lv		Lv		Lv		
	<i>Syzygium fastigiatum</i>		Fl	Fr Fl	Fr					Lv				
OPILIACEAE	<i>Champereia manillana</i>			Lv										
OXALIDACEAE	<i>Dapania grandifolia</i>		Lv											
PASSIFLORACEAE	<i>Passiflora foetida</i>								Lv					
POLYGALACEAE	<i>Xanthophyllum flavescens</i>					Lv		Lv				Lv	Lv	Lv
	<i>X. neglectum</i>											Lv	Lv	
PROTEACEAE	<i>Helicia robusta</i>													Fl
RHAMNACEAE	<i>Ventilago dichotoma</i>		Lv		Lv	Lv	Lv	Lv	Lv			Lv	Lv	Lv
	<i>Ziziphus borneensis</i>							Lv Fr	Fr					
	<i>Z. havilandii</i>		Lv				Lv		Lv	Lv		Lv	Lv	Lv
RHIZOPHORACEAE	<i>Carallia brachiata</i>	Lv		Lv		Lv	Lv	Lv Fr Fl	Lv Fl	Lv Fl	Lv	Lv Fr	Lv Fl	Lv
RUBIACEAE	<i>Gardenia tubifera</i>							Lv	Lv	Lv		Lv	Lv	Lv
	<i>Nauclea orientalis</i>			Fl				Fr	Fr					
	<i>N. subdita</i>	Lv	Lv Fl	Lv Fl			Fr	Lv Fr Fl	Fr	Lv Fr Fl	Fr	Lv	Fr	
	<i>Neolamarckia cadamba</i>								Lv					
	<i>Neonauclea excelsa</i>									Lv		Lv	Lv	Lv
	<i>Pleiocarpidia sandahanica</i>							Lv	Lv					
SANTALACEAE	<i>Scleropyrum wallichianum</i>								Lv					
SAPINDACEAE	<i>Dimocarpus longan</i>								Lv				Lv	
SAPOTACEAE	<i>Madhuca dubardii</i>						Lv		Lv			Lv		
	<i>Palaquium stenophyllum</i>						Lv							
STERCULIACEAE	<i>Heritiera elata</i>			Lv									Lv	
	<i>Pterospermum macrocarpum</i>	Fl	Lv	Fl	Fl		Lv	Lv	Lv	Lv	Lv	Lv	Lv	Fl
SYMPLOCACEAE	<i>Symplocos celastrifolia</i>											Lv	Fl	Fl
THEACEAE	<i>Camellia lanceolata</i>	Lv						Lv						
TILIACEAE	<i>Grewia acuminata</i>						Lv							
	<i>Microcos crassifolia</i>									Lv			Lv	Lv
VITACEAE	<i>Cayratia trifolia</i>		Lv		Lv	Lv			Lv	Lv		Lv Fl	Lv	
Termite nest	<i>Microcerotermes distans</i>	Tn	Tn	Tn	Tn			Tn	Tn	Tn		Tn	Tn	Tn
Unknown (T or V)		Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv
Unknown (T)		Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv
Unknown (V)		Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv	Lv

Lv: leaves; Fr: fruits; Fl: flowers; Cx: calyx; Ba: bark; Tn: termite nest

Table 7 Time allocation to fruits, young leaves, flowers, mature leaves and others in each adult of BE-Group. Observation was conducted from May 2005 to May 2006.

	Fruits	Young leaves	Flowers	Mature leaves	Others
Bejita	21.3	71.4	6.8	0.04	0.4
SD	23.0	26.4	11.7	0.2	1.9
ChiChi	26.1	67.3	6.2	0	0.4
SD	28.1	28.6	10.4	0	1.8
Bulma	21.3	73.3	5.4	0	0
SD	24.9	27.3	11.0	0	0
Lunch	33.2	61.4	4.6	0	0.8
SD	34.9	36.4	13.8	0	2.7
Arare	26.8	67.4	4.9	0	0.8
SD	29.8	29.6	7.7	0	3.2
Bigmama	23.5	61.1	15.4	0	0
SD	26.6	31.6	21.6	0	0
Midori	30.4	60.1	9.6	0	0
SD	30.3	32.6	11.1	0	0
Total	25.9	65.9	7.7	0.03	0.5

Table 8 Dominant tree or vine species with many fruits and flowers which were not consumed by proboscis monkeys at all, with results of facultative observation of orangutan and long-tailed macaque consuming fruits of some species.

Species	Life form	N	Proboscis monkey		Orangutan		Long-tailed macaque	
			Fruit	Flower	Fruit	Flower	Fruit	Flower
<i>Lophopyxis maingayi</i>	Vine	113		x				
<i>Excoecaria indica</i>	Tree	111	x	x				Fruit*
<i>Croton oblongus</i>	Tree	82	x	x				
<i>Xylosma sumatrana</i>	Tree	67	x					
<i>Pternandra galeata</i>	Tree	65		x				
<i>Vitex pinnata.</i>	Tree	55	x					Fruit
<i>Vatica rassak</i>	Tree	52	x					
<i>Croton caudatus</i>	Vine	46	x	x				
<i>Entada rheedei</i>	Vine	32	x	x				Fruit
<i>Microcos crassifolia</i>	Tree	27	x	x				Fruit
<i>Artabotrys suaveolens</i>	Vine	26	x					
<i>Glochidion obscurum</i>	Tree	20	x	x				
<i>Uncaria ferrea</i>	Vine	20	x	x				
<i>Baccaurea stipulata</i>	Tree	18	x	x				
<i>Pleiocarpidia sandahanica</i>	Tree	18	x	x				
<i>Dracontomelon dao</i>	Tree	15	x					Fruit

* Long-tailed macaques did not consume fresh fruits on the trees, though they were once observed taking some old and dry fruits floating in the river

Table 9 Comparison between time spent for feeding on each species and time expected from availability estimated from vegetation survey. The availability was calculated using the following formula. Availability = $B_k \cdot (n_{ki} / N_k) / 12$ where N_k is the total number of plants, n_{ki} is the number of tree or vine plants with fruits, flowers or young leaves in month i and B_k is total basal area per hectare in the species k . For N_k and B_k , cf. Table 3. PO, NG and NU: positive, negative and neutral preference of proboscis monkeys, respectively.

Fruits

Tree

Species	Availability	Observed Time (min.)	Expected Time (min.)	Preference
<i>Androtium astylum</i>	0	19.6	0	
<i>Ilex cymosa</i>	227	66.6	55.3	
<i>Garcinia parvifolia</i>	207	13.0	50.6	
<i>Dillenia excelsa</i>	718	7.6	175.2	
<i>Elaeocarpus nitidus</i>	165	6.2	40.2	
<i>Antidesma thwaitesianum</i>	1383	12.0	337.2	NG
<i>Mallotus floribundus</i>	0	1.0	0	
<i>M muticus</i>	2845	2059.5	694.0	PO
<i>M penangensis</i>	113	0.7	27.6	
<i>Margaritaria indica</i>	134	48.7	32.8	
<i>Teijsmanniodendron bogoriense</i>	76	15.8	18.6	
<i>Dehaasia cuneata</i>	74	284.4	17.9	PO
<i>Crudia ornata</i>	0	44.9	0	
<i>C reticulata</i>	43	574.9	10.6	PO
<i>Cynometra ramiflora</i>	7	58.1	1.7	
<i>Sindora leiocarpa</i>	0	20.9	0	
<i>Pternandra galeata</i>	10608	8.4	2587.7	NG
<i>Ficus binnendijkii</i>	284	1162.0	69.4	PO
<i>Eugenia litseaefolia</i>	10	1152.9	2.4	PO
<i>E sp. 2</i>	212	212.3	51.6	PO
<i>Syzygium fastigiatum</i>	26	59.6	6.3	
<i>Carallia brachiata</i>	300	62.3	73.2	
<i>Nauclea orientalis</i>	58	29.7	14.1	
<i>N subdita</i>	8134	330.0	1984.3	NG

G-test: $G = 31307$ and $p < 0.0001$

Vine

Species	Availability	Observed Time (min.)	Expected Time (min.)	Preference
<i>Bridelia stipularis</i>	238	180.8	849.7	NG
<i>Combretum acuminatum</i>	1	31.4	3.6	
<i>Rourea minor</i>	8	54.0	27.0	
<i>Tetracera scandens</i>	4	305.0	12.9	PO
<i>Albizia corniculata</i>	128	4.5	455.4	NG
<i>Bauhinia diptera</i>	0	4.8	0	
<i>Dalbergia parvifolia</i>	31	8.0	110.3	
<i>Millettia nieuwenhuisii</i>	18	0.3	63.9	
<i>Strychnos minor</i>	2	38.8	6.3	
<i>Lophopyxis maingayi</i>	340	1612.3	1213.8	NU
<i>Ficus cf. lanata Bl var foveolata</i>	3	20.1	11.0	
<i>F globosa</i>	15	388.3	54.6	PO
<i>Ziziphus borneensis</i>	15	215.4	55.0	PO

G-test: $G = 4686$ and $p < 0.0001$

(Continued 1)

Flowers

Tree

Species	Availability	Observed Time (min.)	Expected Time (min.)	Preference
<i>Dracontomelon dao</i>	98	14.3	10.6	
<i>Ilex cymosa</i>	1361	18.1	148.0	
<i>Cratoxylum formosum</i>	24	26.2	2.6	
<i>Dillenia excelsa</i>	2774	405.6	301.6	NU
<i>Vatica rassak</i>	341	59.4	37.1	
<i>V venulosa</i>	0	31.0	0	
<i>Antidesma thwaitesianum</i>	1185	329.1	128.9	PO
<i>Mallotus muticus</i>	4617	399.1	502.0	NU
<i>Margaritaria indica</i>	27	182.4	2.9	PO
<i>Xylosma sumatrana</i>	2071	7.2	225.2	NG
<i>Teijsmanniodendron bogoriense</i>	122	17.0	13.3	
<i>Vitex pinnata</i>	6358	2.2	691.3	NG
<i>Dehaasia cuneata</i>	162	93.1	17.6	
<i>Sindora leiocarpa</i>	0	10.8	0	
<i>Syzygium fastigiatum</i>	73	32.7	7.9	
<i>Helicia robusta</i>	66	1.3	7.2	
<i>Carallia brachiata</i>	1942	240.7	211.1	NU
<i>Nauclea orientalis</i>	39	73.1	4.2	
<i>N subdita</i>	3277	246.2	356.3	NU
<i>Pterospermum macrocarpum</i>	211	456.4	22.9	PO
<i>Symplocos celastrifolia</i>	68	52.6	7.3	

G-test: G = 5860 and p < 0.0001

Vine

Species	Availability	Observed Time (min.)	Expected Time (min.)	Preference
<i>Artabotrys suaveolens</i>	71	33.9	80.1	
<i>Urceola</i> sp. 1	3	297.1	3.6	PO
<i>Bridelia stipularis</i>	257	42.8	290.0	NG

G-test: G = 2405 and p < 0.0001

(Continued 2)
 Young leaves
 Tree

Species	Availability	Observed Time (min.)	Expected Time (min.)	Preference
<i>Androtium astylum</i>	49	11.2	2.4	
<i>Buchanania arborescens</i>	3317	27.3	160.1	
<i>Dracontomelon dao</i>	3375	33.7	162.9	
<i>Melanochyla auriculata</i>	331	90.0	16.0	
<i>Ilex cymosa</i>	6163	24.2	297.5	NG
<i>Canarium denticulatum</i>	83	10.5	4.0	
<i>Maranthes corymbosa</i>	278	448.3	13.4	PO
<i>Parinari oblongifolia</i>	2782	16.0	134.3	
<i>Cratoxylum formosum</i>	746	276.2	36.0	PO
<i>Garcinia brevipes</i>	40	4.4	1.9	
<i>G parvifolia</i>	1473	13.8	71.1	
<i>Kayea oblongifolia</i>	75	5.0	3.6	
<i>Mesua elmeri</i>	4100	488.6	197.9	PO
<i>M macrantha</i>	168	11.6	8.1	
<i>Terminalia citrina</i>	129	8.7	6.2	
<i>Dillenia excelsa</i>	7589	49.5	366.3	NG
<i>Vatica rassak</i>	6763	110.4	326.5	NG
<i>V venulosa</i>	2140	75.4	103.3	
<i>Diospyros curranii</i>	2208	9.8	106.6	
<i>Elaeocarpus nitidus</i>	2165	720.6	104.5	PO
<i>E stipularis</i>	841	61.6	40.6	
<i>Excoecaria indica</i>	74353	92.5	3589.1	NG
<i>Antidesma thwaitesianum</i>	5744	70.6	277.3	NG
<i>Aporosa acuminatissima</i>	143	5.7	6.9	
<i>Baccaurea stipulata</i>	953	138.8	46.0	
<i>Bridelia penangiana</i>	227	301.0	11.0	PO
<i>Cleistanthus myrianthus</i>	2681	223.5	129.4	NU
<i>Croton oblongus</i>	6807	41.6	328.6	NG
<i>Drypetes castilloi</i>	1043	232.6	50.4	PO
<i>Macaranga conifera</i>	707	10.7	34.1	
<i>Mallotus floribundus</i>	22	79.1	1.1	
<i>M muticus</i>	38883	2687.1	1876.9	NU
<i>M penangensis</i>	1435	13.3	69.3	
<i>Margaritaria indica</i>	780	558.3	37.6	PO
<i>Paracroton pendulus</i>	651	1.0	31.4	
<i>Hydnocarpus sumatrana</i>	4706	316.0	227.2	NU
<i>Xylosma sumatrana</i>	9654	82.5	466.0	NG
<i>Teijsmanniodendron bogoriense</i>	1723	5.6	83.2	
<i>Vitex pinnata</i>	16586	109.5	800.6	NG
<i>Cinnamomum sp. 1</i>	25	6.5	1.2	
<i>Dehaasia cuneata</i>	1516	222.3	73.2	PO
<i>Endiandra sp. 1</i>	1331	9.0	64.2	
<i>E sp. 2</i>	1196	19.9	57.8	
<i>Litsea sp. 2</i>	109	5.1	5.3	
<i>Nothaphoebe sp. 1</i>	561	2.4	27.1	
<i>Barringtonia macrostachya</i>	2600	15.6	125.5	
<i>Planchonia valida</i>	1793	2.0	86.6	
<i>Crudia ornata</i>	39	6.1	1.9	
<i>C reticulata</i>	2348	78.9	113.3	
<i>Cynometra ramiflora</i>	221	1697.2	10.7	PO
<i>Dialium indum</i>	1780	12.4	85.9	
<i>Ormosia sumatrana</i>	232	217.2	11.2	PO

(Continued 3)

Tree

Species	Availability	Observed Time (min.)	Expected Time (min.)	Preference
<i>Pongamia pinnata</i>	2251	206.5	108.7	NU
<i>Sindora leiocarpa</i>	218	9.3	10.5	
<i>Lagerstroemia speciosa</i>	442	15.1	21.3	
<i>Memecylon paniculatum</i>	358	32.1	17.3	
<i>Pternandra galeata</i>	39860	78.7	1924.1	NG
<i>Ficus benjamina</i>	586	387.8	28.3	PO
<i>F binnendijkii</i>	3464	1931.3	167.2	PO
<i>F crassiramea</i>	1737	141.6	83.9	
<i>Knema laurina</i>	193	7.6	9.3	
<i>Myristica sp. 1</i>	924	0.2	44.6	
<i>M sp. 2</i>	1004	18.2	48.5	
<i>Eugenia litseaefolia</i>	1596	35.3	77.0	
<i>E sp. 2</i>	8807	40.4	425.1	NG
<i>E sp. 5</i>	352	24.2	17.0	
<i>Syzygium fastigiatum</i>	733	20.9	35.4	
<i>Xanthophyllum flavescens</i>	1605	60.0	77.5	
<i>Carallia brachiata</i>	3063	2258.1	147.8	PO
<i>Gardenia tubifera</i>	222	65.8	10.7	
<i>Nauclea subdita</i>	16459	64.1	794.5	NG
<i>Neolamarckia cadamba</i>	1191	14.2	57.5	
<i>Neonauclea excelsa</i>	517	21.5	25.0	
<i>Pleiocarpidia sandahanica</i>	1083	13.4	52.3	
<i>Dimocarpus longan</i>	323	33.1	15.6	
<i>Madhuca dubardii</i>	625	7.2	30.2	
<i>Pterospermum macrocarpum</i>	3230	158.1	155.9	
<i>Symplocos celastrifolia</i>	647	1.7	31.2	
<i>Microcos crassifolia</i>	2894	42.5	139.7	

G-test: G = 56541 and p < 0.0001

(Continued 4)

Vine

Species	Availability	Observed Time (min.)	Expected Time (min.)	Preference
<i>Artabotrys suaveolens</i>	815	27.3	498.7	NG
<i>Uvaria lobbiana</i>	17	2.2	10.1	
<i>Parameria polyneura</i>	17	279.6	10.3	PO
<i>Urceola sp. 1</i>	57	50.7	34.8	
<i>Willughbeia angustifolia</i>	19	81.6	11.5	
<i>Combretum acuminatum</i>	83	61.5	50.7	
<i>Agelaea borneensis</i>	18	22.8	11.3	
<i>A trinervis</i>	30	30.2	18.1	
<i>Connarus grandis</i>	143	1.6	87.7	
<i>Rourea mimosoides</i>	30	62.5	18.6	
<i>R minor</i>	668	59.7	408.8	NG
<i>Erycibe grandifolia</i>	27	3.2	16.5	
<i>Tetracera scandens</i>	62	49.7	37.6	
<i>Bridelia stipularis</i>	1083	301.0	662.6	NU
<i>Croton caudatus</i>	986	20.3	602.8	NG
<i>Gnetum gnemonoides</i>	125	12.8	76.8	
<i>Acacia borneensis</i>	214	663.0	130.8	PO
<i>Albizia corniculata</i>	1155	258.6	706.7	NG
<i>Bauhinia diptera</i>	707	1081.3	432.2	PO
<i>Dalbergia parvifolia</i>	713	1514.4	436.2	PO
<i>Derris elegans</i>	39	89.9	23.8	
<i>D sp. 1</i>	97	65.6	59.0	
<i>Derris sp. 2</i>	37	89.2	22.8	
<i>Entada rheedei</i>	1532	245.6	937.2	NG
<i>Millettia nieuwenhuisii</i>	711	21.2	435.2	NG
<i>Spatholobus macropterus</i>	739	1372.4	452.2	PO
<i>Strychnos minor</i>	90	26.0	55.1	
<i>Lophopyxis maingayi</i>	3062	1605.4	1873.1	NU
<i>Haematocarpus validus</i>	17	1.2	10.1	
<i>Ficus cf. lanata Bl var foveolata</i>	28	40.1	17.0	
<i>F globosa</i>	264	59.5	161.3	
<i>Ventilago dichotoma</i>	300	320.5	183.6	PO
<i>Ziziphus borneensis</i>	109	42.0	66.6	
<i>Grewia acuminata</i>	15	6.2	9.0	

G-test: G = 11259 and p < 0.0001

Table 10 Parts of each fruit consumed by proboscis monkeys.

Species	Calyx	Flesh	Seed	Season
<i>Androtium astylum</i>				May / 05
<i>Ilex cymosa</i>				Nov
<i>Garcinia parvifolia</i>				Nov
<i>G. rostrata</i>				Nov - Jan
<i>Combretum acuminatum</i>				Nov
<i>Rourea minor</i>				Sep
<i>Dillenia excelsa</i>				Oct - Nov
<i>Tetracera scandens</i>				Jun - Aug, Nov, Jan
<i>Elaeocarpus nitidus</i>				Jan
<i>Antidesma thwaitesianum</i>				Nov - Dec
<i>Bridelia stipularis</i>				Nov - Dec, Mar
<i>Mallotus floribundus</i>				Jun
<i>M. muticus</i>				Jun -Aug
<i>M. penangensis</i>				Jul
<i>Margaritaria indica</i>				Jul - Aug, Mar
<i>Teijsmanniodendron bogoriense</i>				Oct
<i>Alseodaphne insignis</i>				Oct - Jan, Apr
<i>Dehaasia cuneata</i>				Jul - Sep
<i>Albizia corniculata</i>				Jul
<i>Bauhinia diptera</i>				Jun
<i>Crudia ornata</i>				Nov
<i>C. reticulata</i>				Nov - Dec
<i>Cynometra ramiflora</i>				Aug, Dec
<i>Dalbergia parvifolia</i>				Aug
<i>Millettia nieuwenhuisii</i>				Aug
<i>Sindora leiocarpa</i>				Oct
LEGUMINOSAE 1				Nov
<i>Strychnos minor</i>				Aug -Sep
<i>Lophopyxis maingayi</i>				Jun - Oct
<i>Pternandra galeata</i>				Aug, Apr
<i>Artocarpus</i> sp. 1				Apr -Sep
<i>Ficus annulata</i>				Aug, Dec - Jan, Mar
<i>F. binnendijkii</i>				Jul, Oct - May
<i>F. forstenii</i> var. <i>villosa</i>				Mar
<i>F. globosa</i>				Sep, Nov - Jan, Mar, May / 06
<i>F. cf. lanata</i> var. <i>foveolata</i>				Mar -Apr
<i>F. pellucidopunctata</i>				Jul
<i>F. sundaica</i> var. <i>beccarianum</i>				Aug, Nov, Jan
<i>F. virens</i> var. <i>glabella</i>				Oct, Mar
<i>F. sp. 1</i>				Jan, Apr
<i>Eugenia litseaefolia</i>				May / 05, May / 06
<i>E. sp. 2</i>				Jun
<i>E. sp. 8</i>				Dec
<i>E. sp. 9</i>				May / 06
<i>Syzygium fastigiatum</i>				Jul - Aug
<i>Ziziphus borneensis</i>				Nov - Dec
<i>Carallia brachiata</i>				Nov, Mar
<i>Nauclea orientalis</i>				Nov -Dec
<i>N. subdita</i>				Oct - Feb, Apr

Table 11 Stepwise regression analysis for testing the effect of consumption (A) or availability (B) of flowers, fruits and young leaves on monthly dietary diversity or migration distance.

	coefficient	SE	df	Deviance (%)	$\chi(p)$
(A) On monthly dietary diversity					
Null			11	0.86	
Intercept	3.14	0.12			
Fruit consumption	-3.89	1.92	1	0.25 (29)	0.043
(B) On monthly migration distance					
Null			11	374834	
Intercept	-1678.06	1420.75			
Fruit availability	-2.97	0.84	1	154682 (41)	0.0028
Young leaf availability	1.65	0.86	1	64444 (17)	0.054

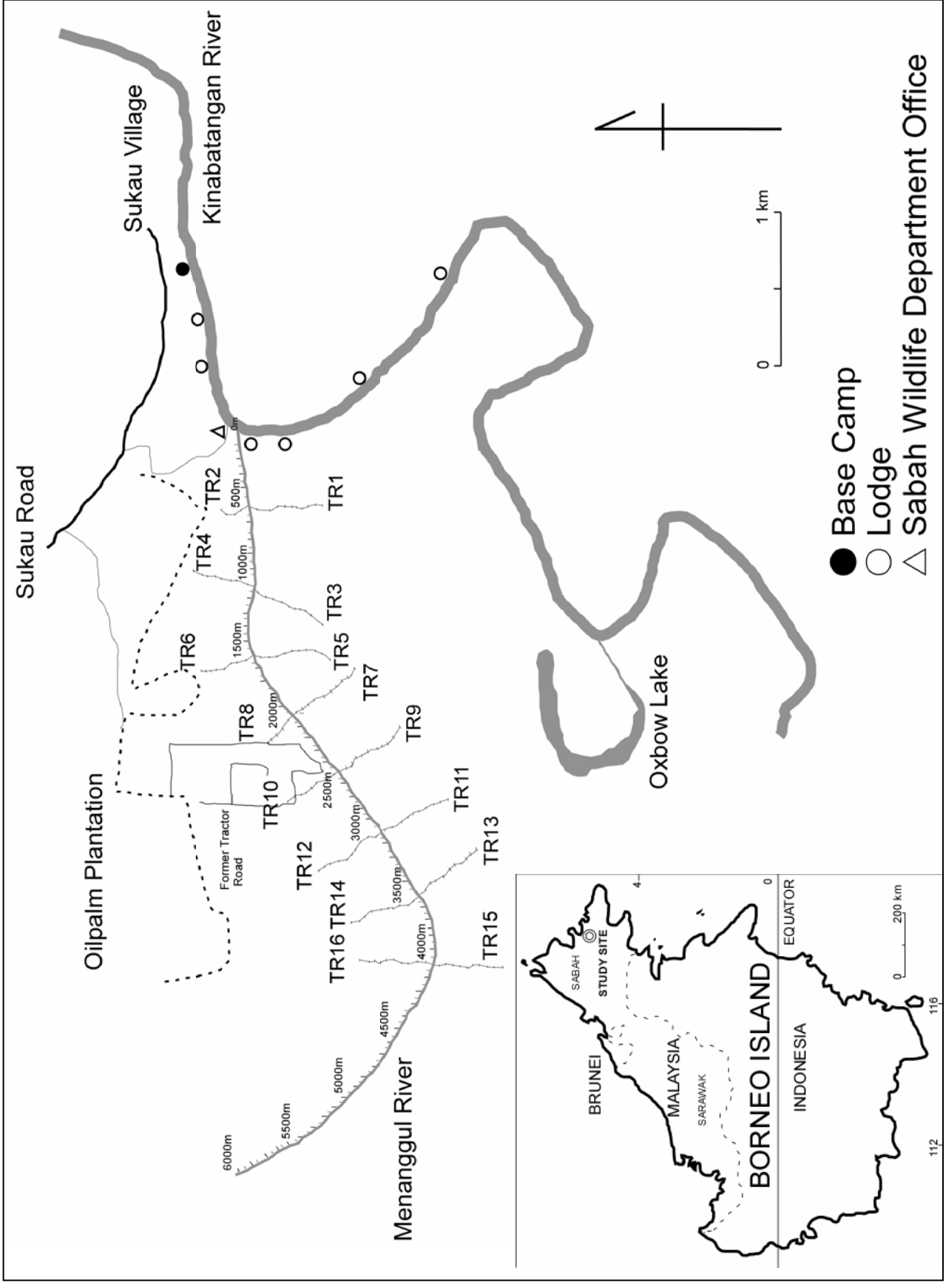


Fig. 1 Study area in Sabah, Malaysia.
TR 1 – 16: Trail code

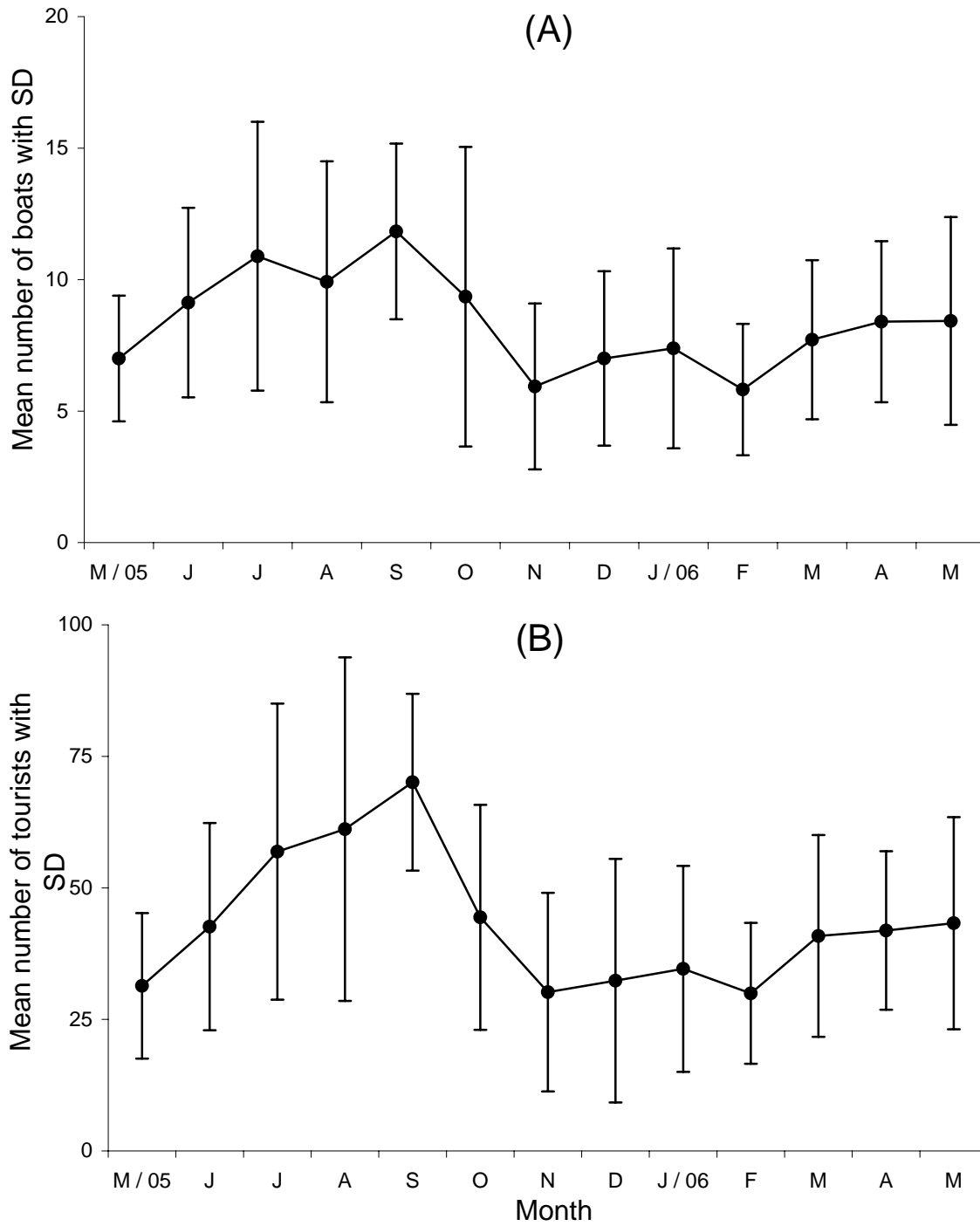


Fig. 2 The monthly mean number of boats (A) and tourists (B) per day in the Menanggul River. Vertical bars indicate standard deviation.

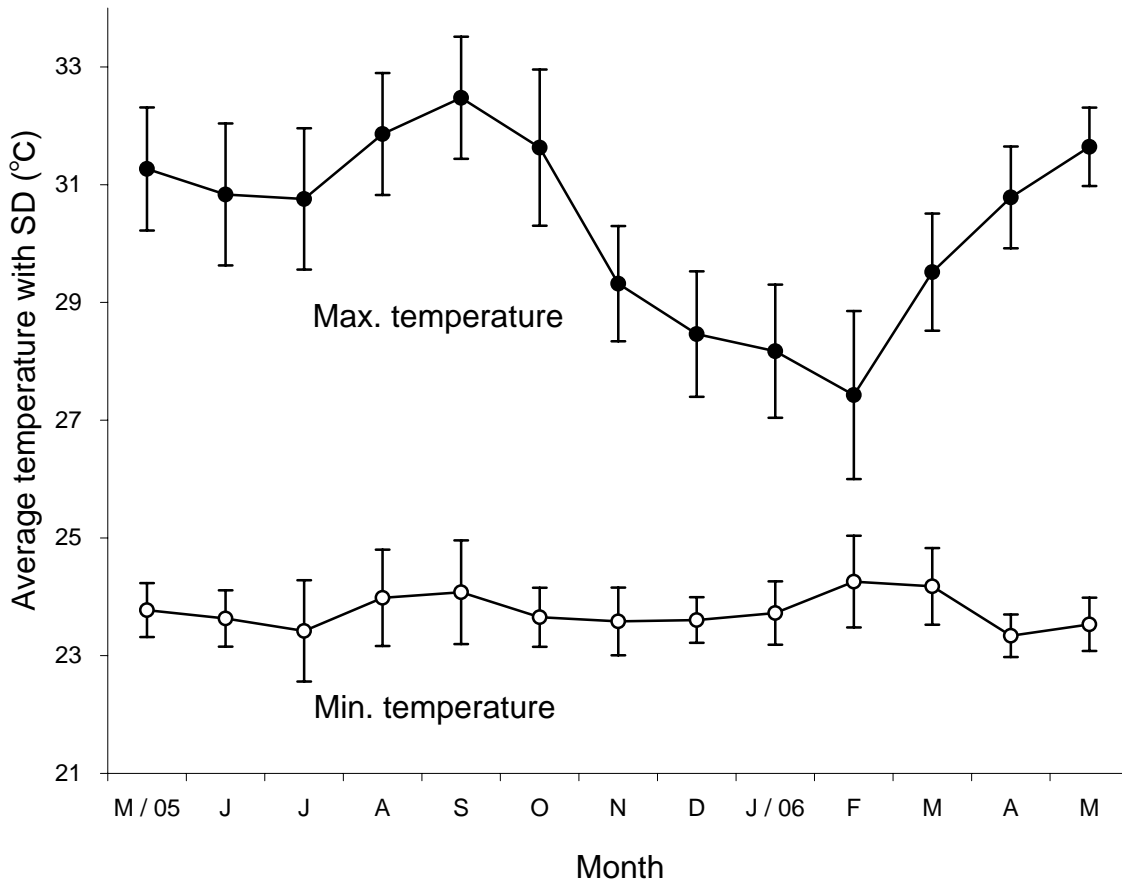


Fig. 3 Monthly averages of minimum and maximum daily temperatures at base camp. Vertical bars indicate standard deviation.

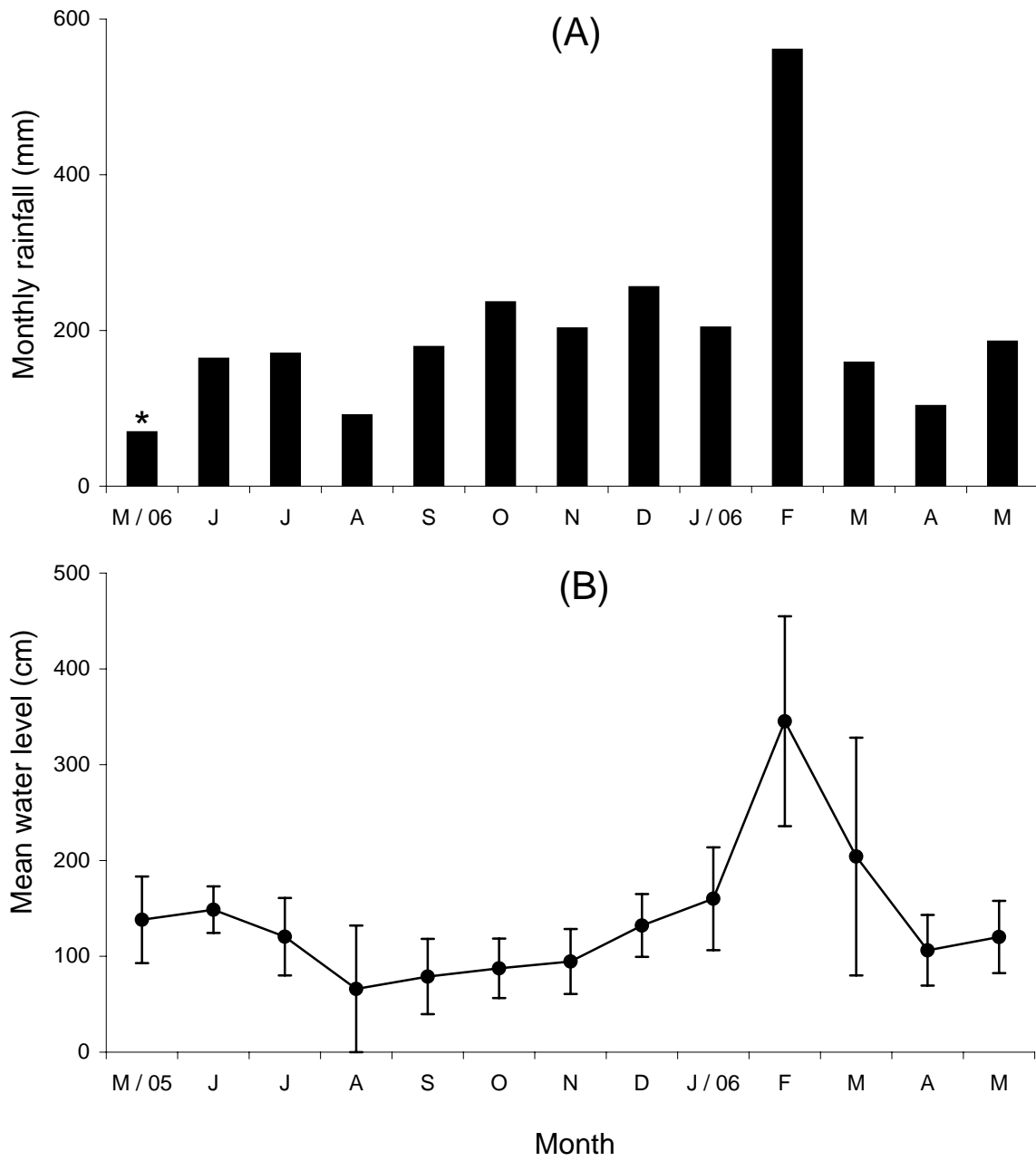


Fig. 4 Monthly rainfall (A) and the average river level with standard deviation in each month (B). * Only 25 days' rainfall data available in May 2005.

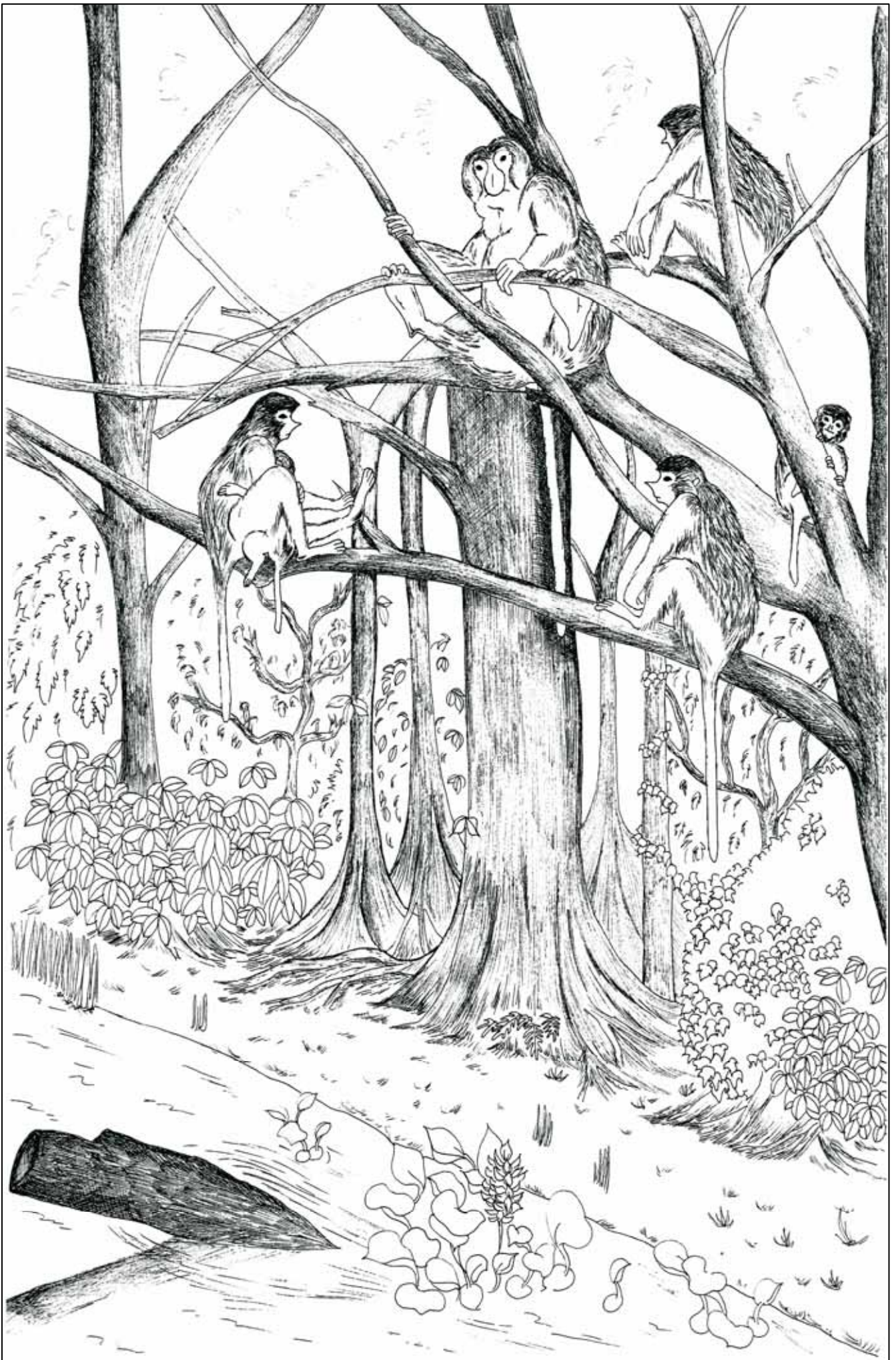


Fig. 5 One-male group at sleeping site

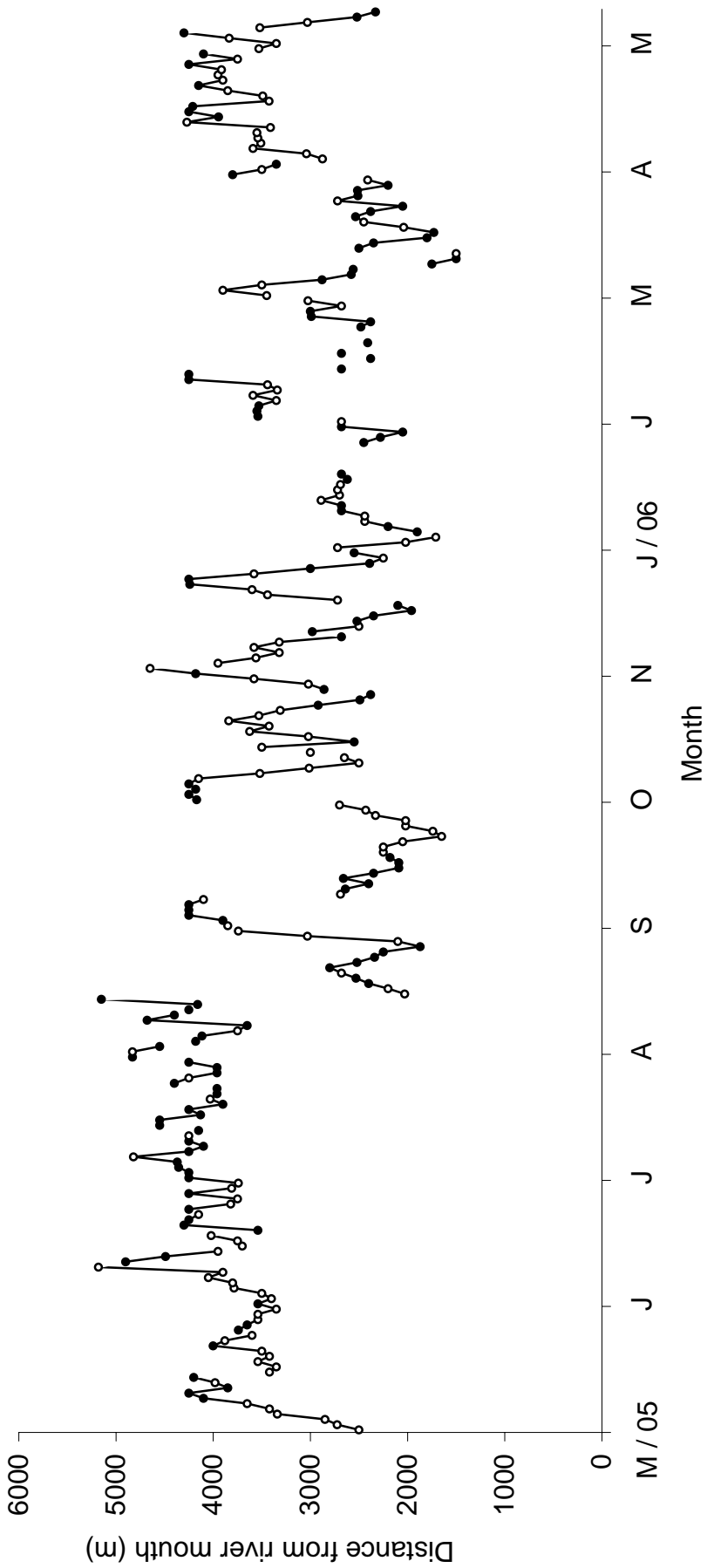


Fig. 6 Temporal trend of sleeping sites of BE-Group. Open and filled circles indicate left and right banks, respectively.

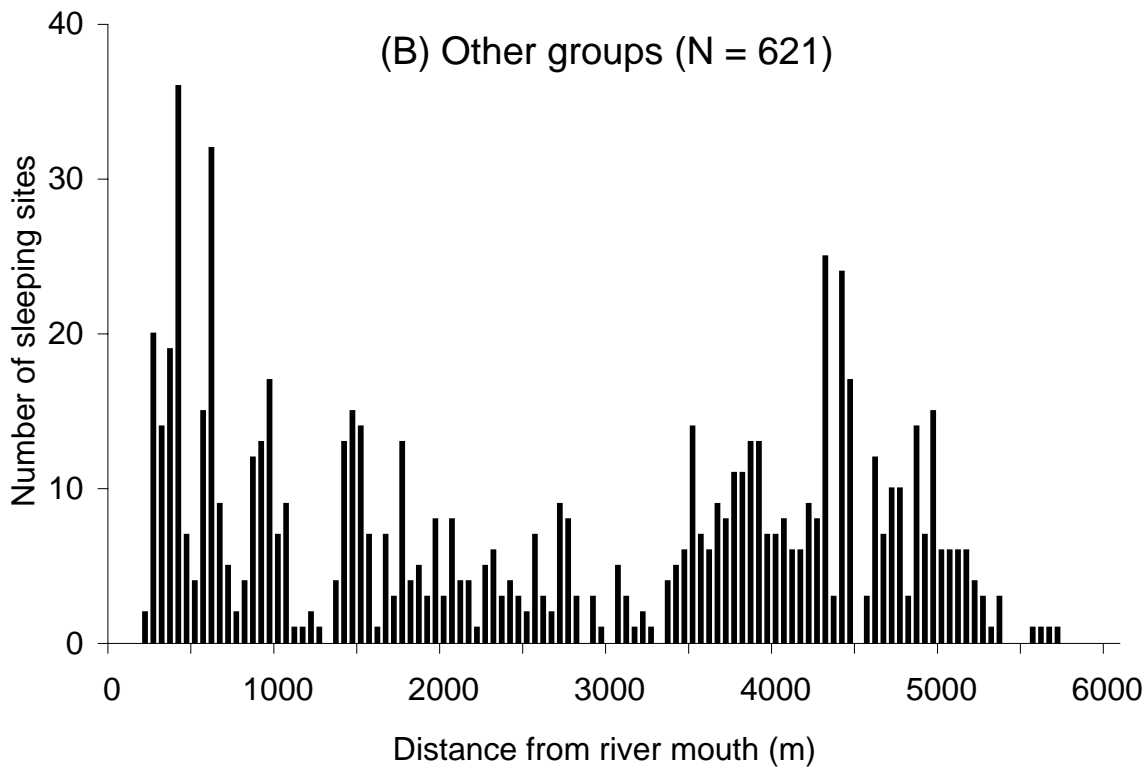
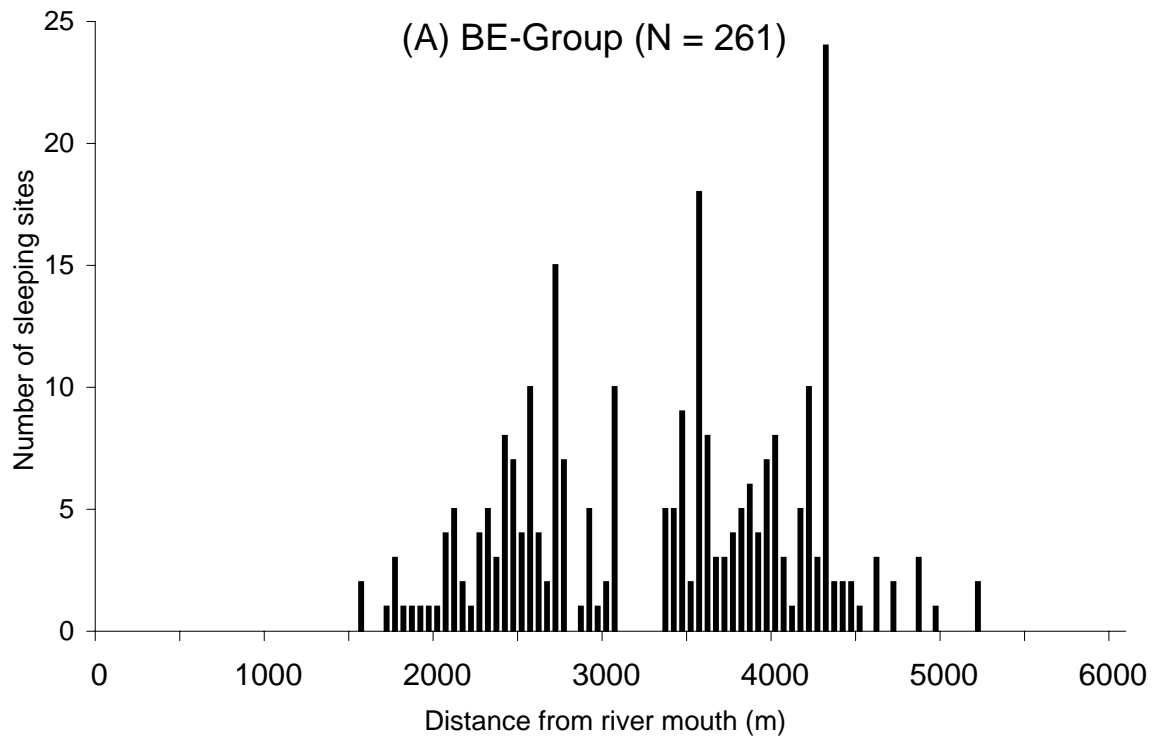


Fig. 7 Distribution of sleeping sites of BE-Group (A) and other groups (B) along riversides of the Menanggul River from May 2005 to May 2006.

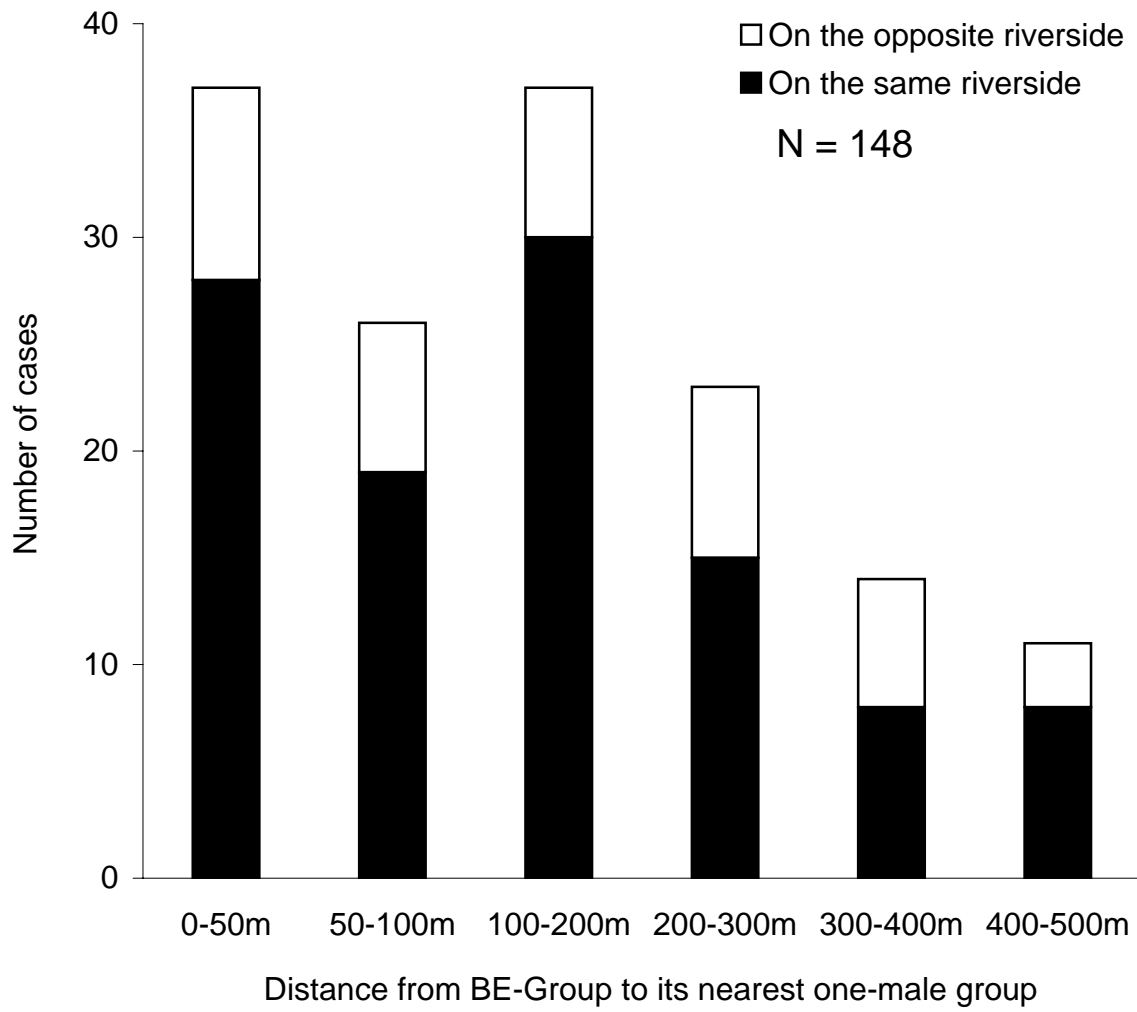


Fig. 8 Frequency distribution of distances between BE-Group and its nearest one-male group.

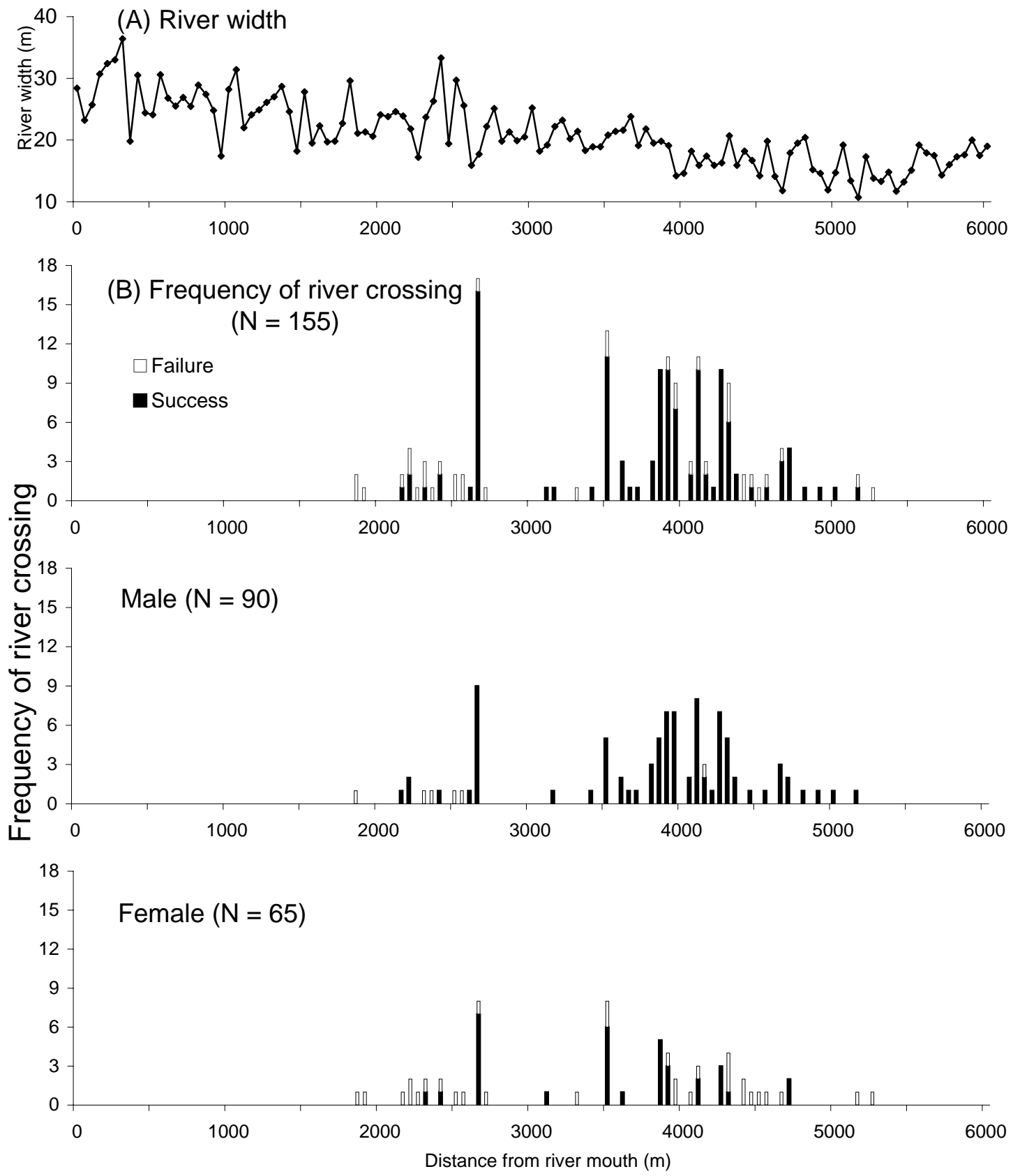


Fig. 9 River width (A) and frequency of river crossing at each point of river (B). In B, top: data for male and female were pooled; middle: data for male; bottom: data for females.

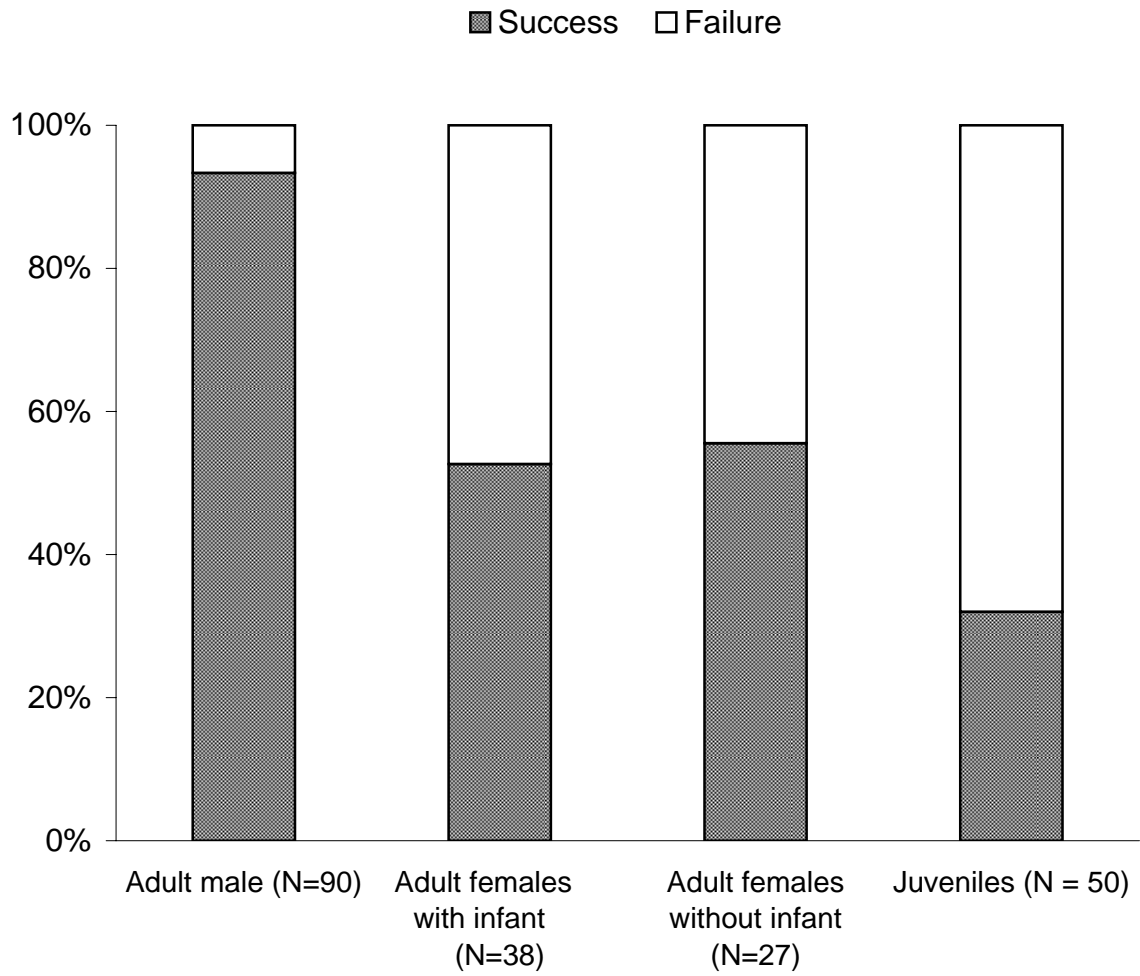


Fig. 10 Comparison of success ratio in river crossing among adult male, adult females with infant or without infant and juveniles. Data for juveniles were facultatively taken when focal monkeys were followed.



Fig. 11 Infant (A) and juvenile (B) attacked by clouded leopards which suddenly bit neck of the victims.

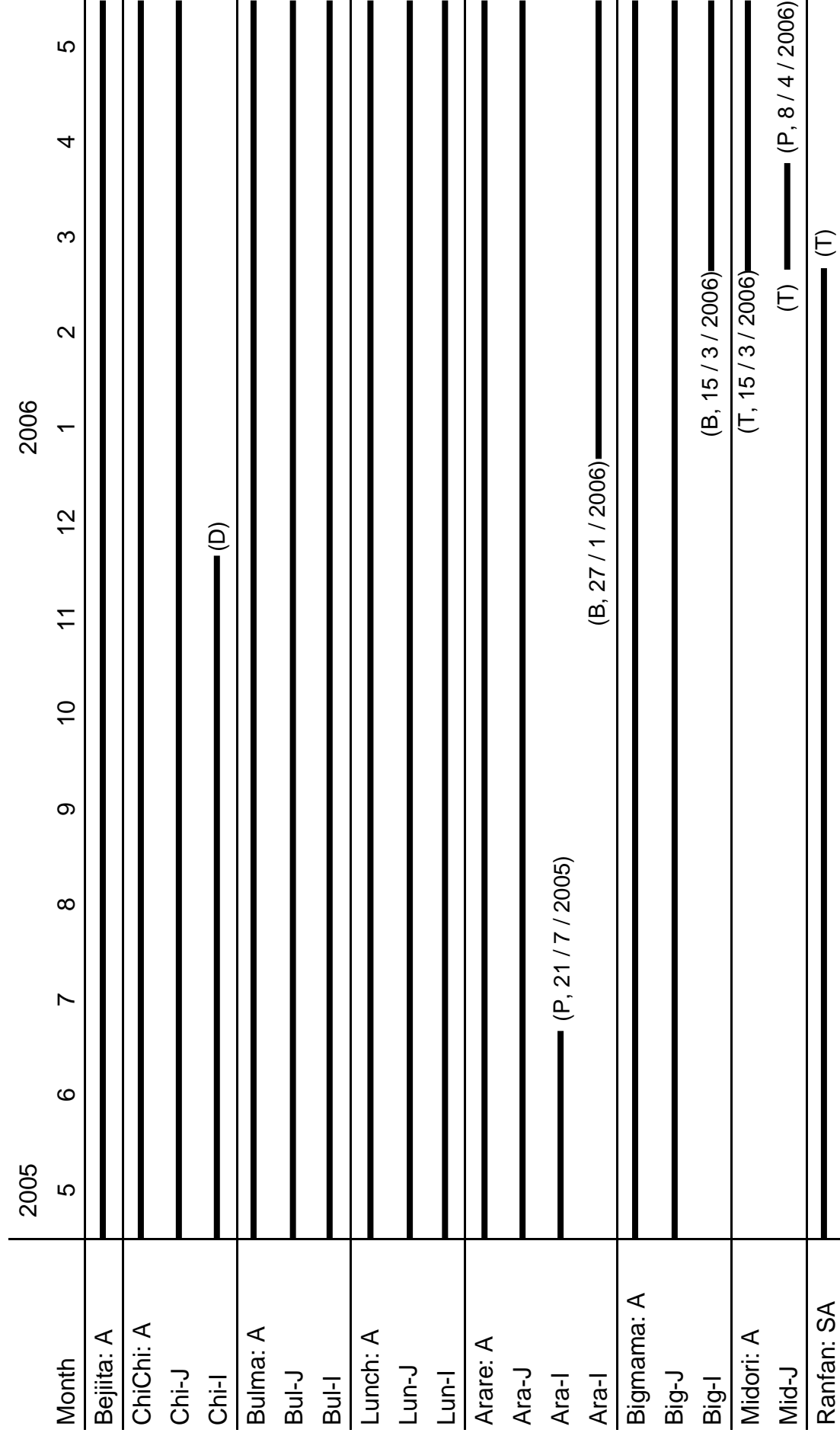


Fig. 12 Composition of BE-Group from May 2005 to May 2006. Dates of birth or transfer are shown only when the event was not observed on the previous day. A: adult; SA: subadult; J: juvenile; I: infant B: birth; T: transfer; P: predation; D: disappear

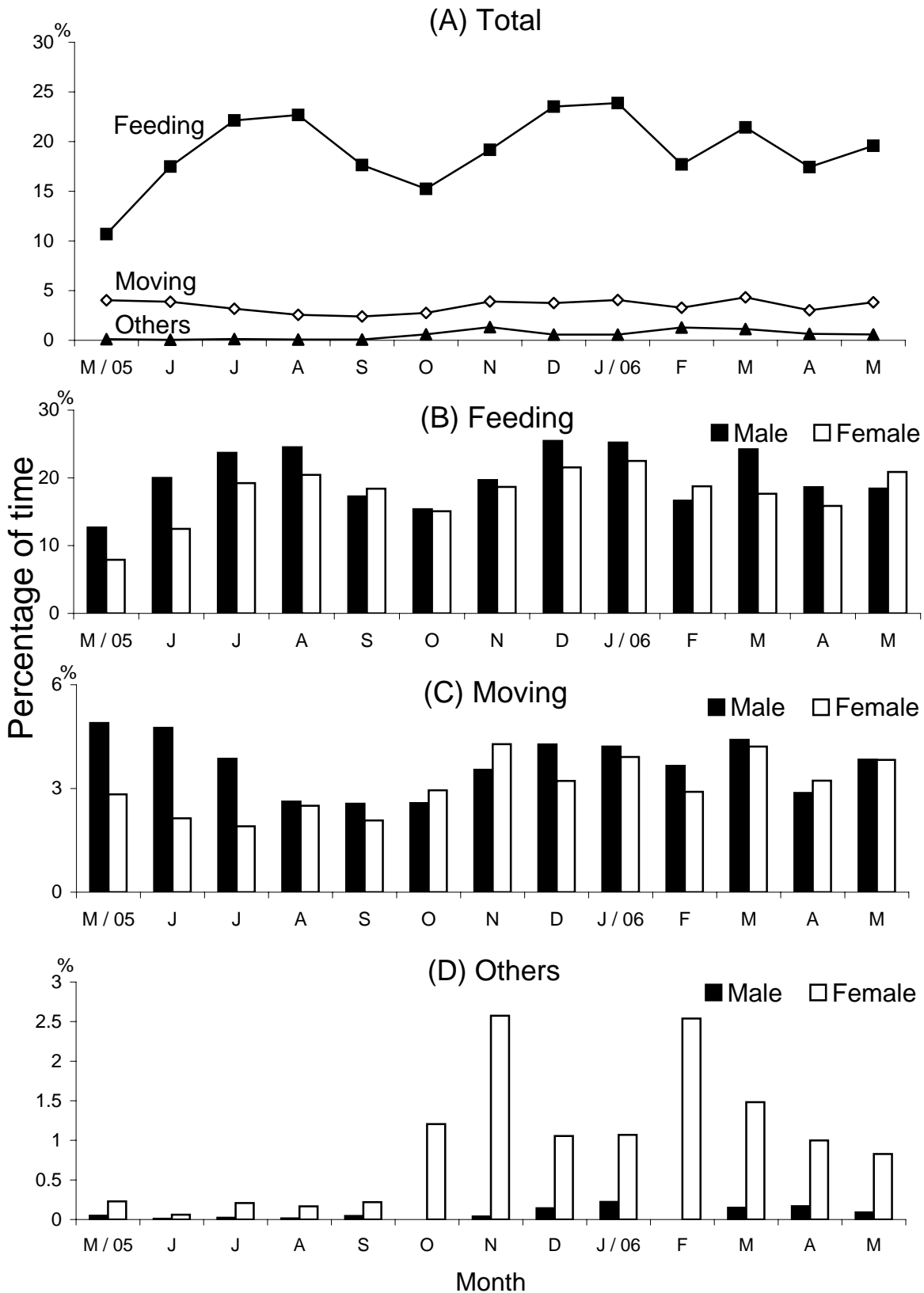


Fig. 13 Seasonal fluctuation of time allocation to three activities, i. e. feeding, moving and others (grooming and copulation). A: Data for adult male and females are pooled. B-D : Data for male and females are separately shown.

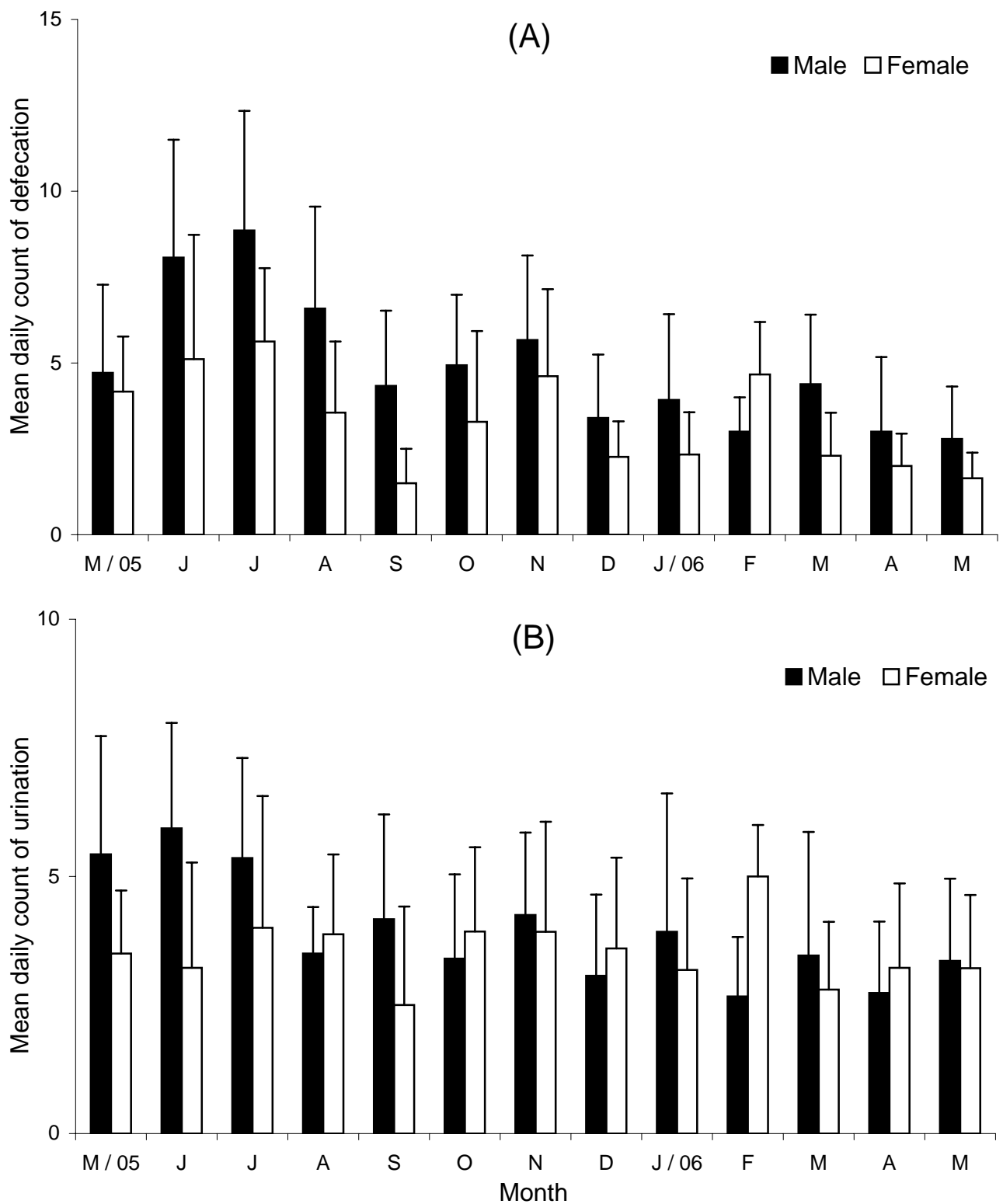


Fig. 14 Mean daily count of (A) defecation and (B) urination with standard deviation in each month.

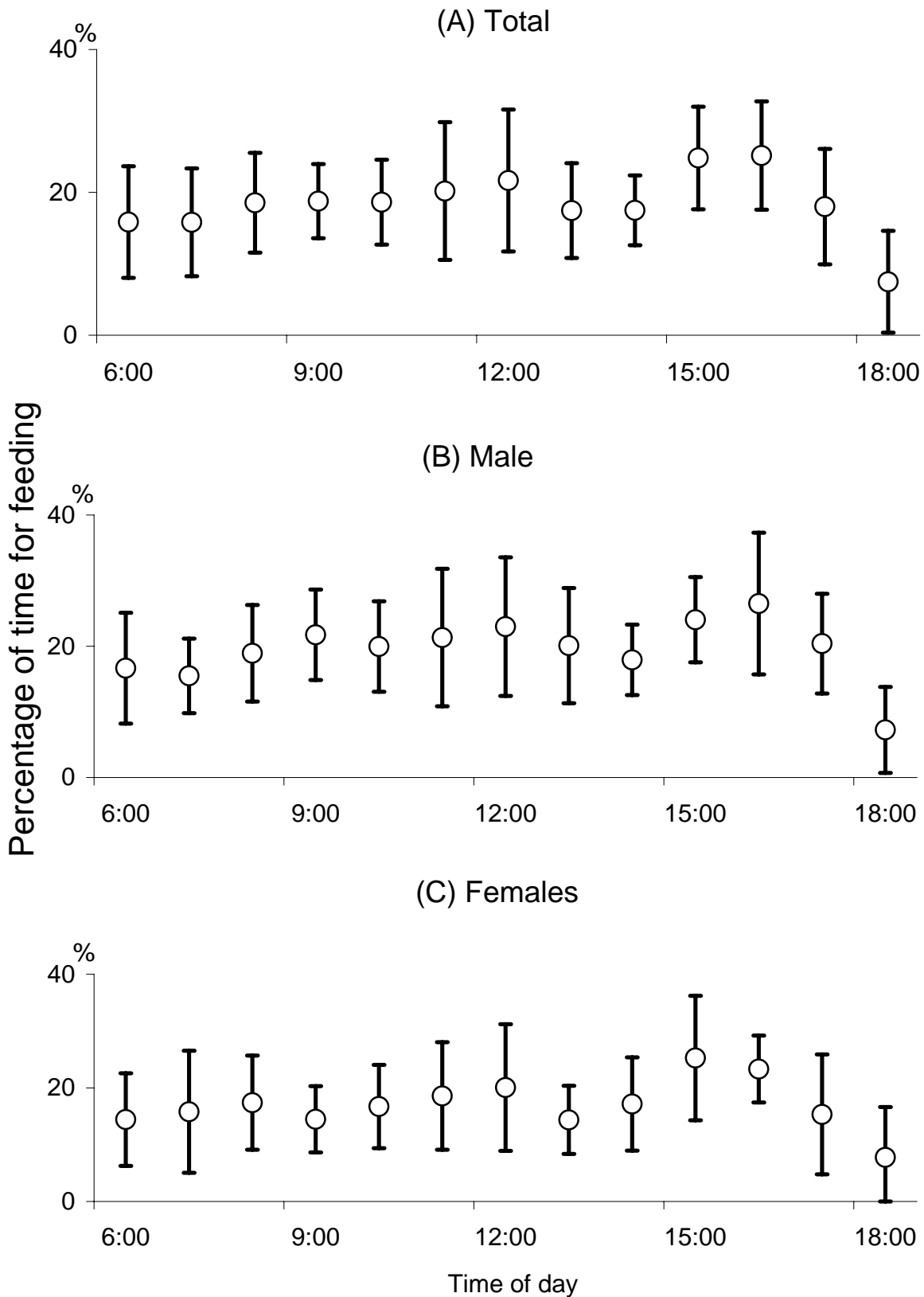


Fig. 15 Daily feeding rhythm of all focal members (A), adult male (B) and adult females (C). At intervals of one hour, monthly time allocation to feeding was calculated in percentage and mean with SD (n: 13 months) is shown for each hour.

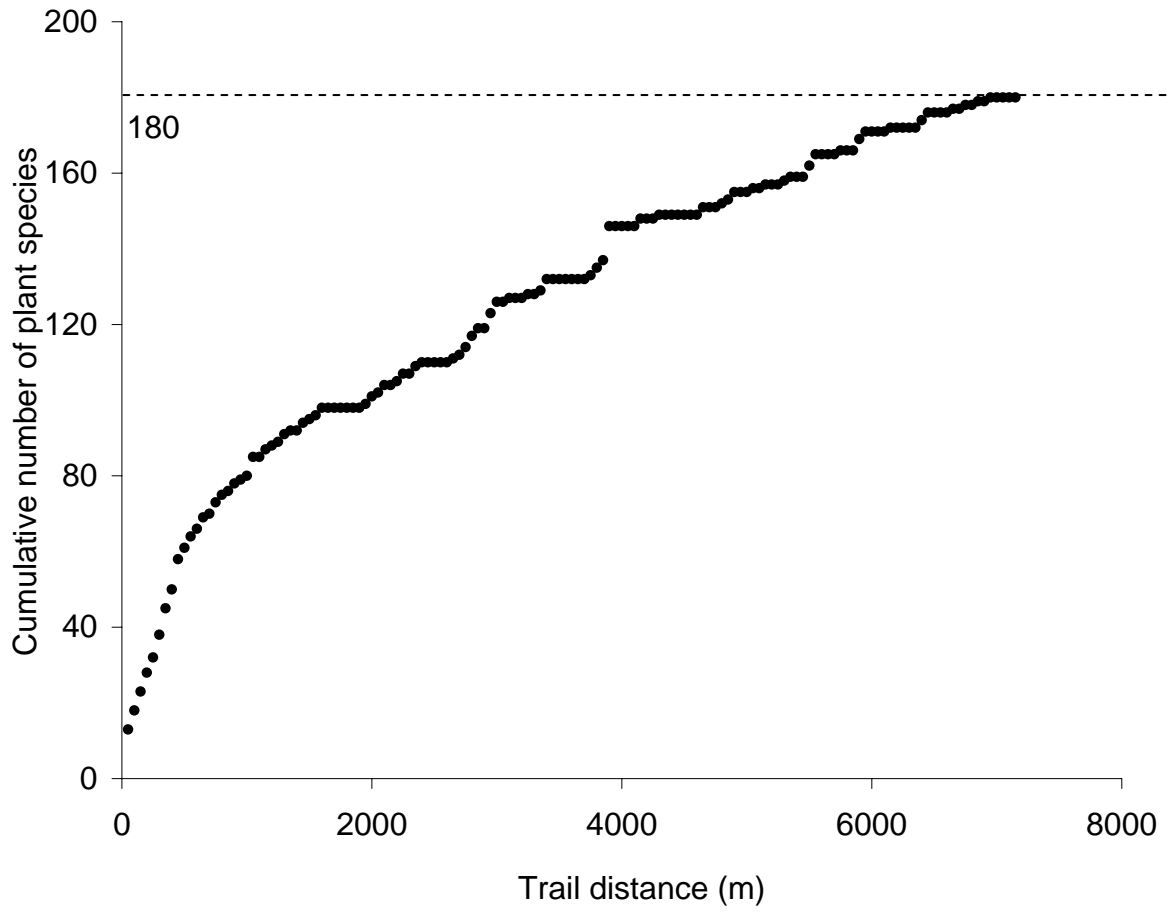


Fig. 16 Cumulative number of plant species found along trails from TR 1 to TR 16.

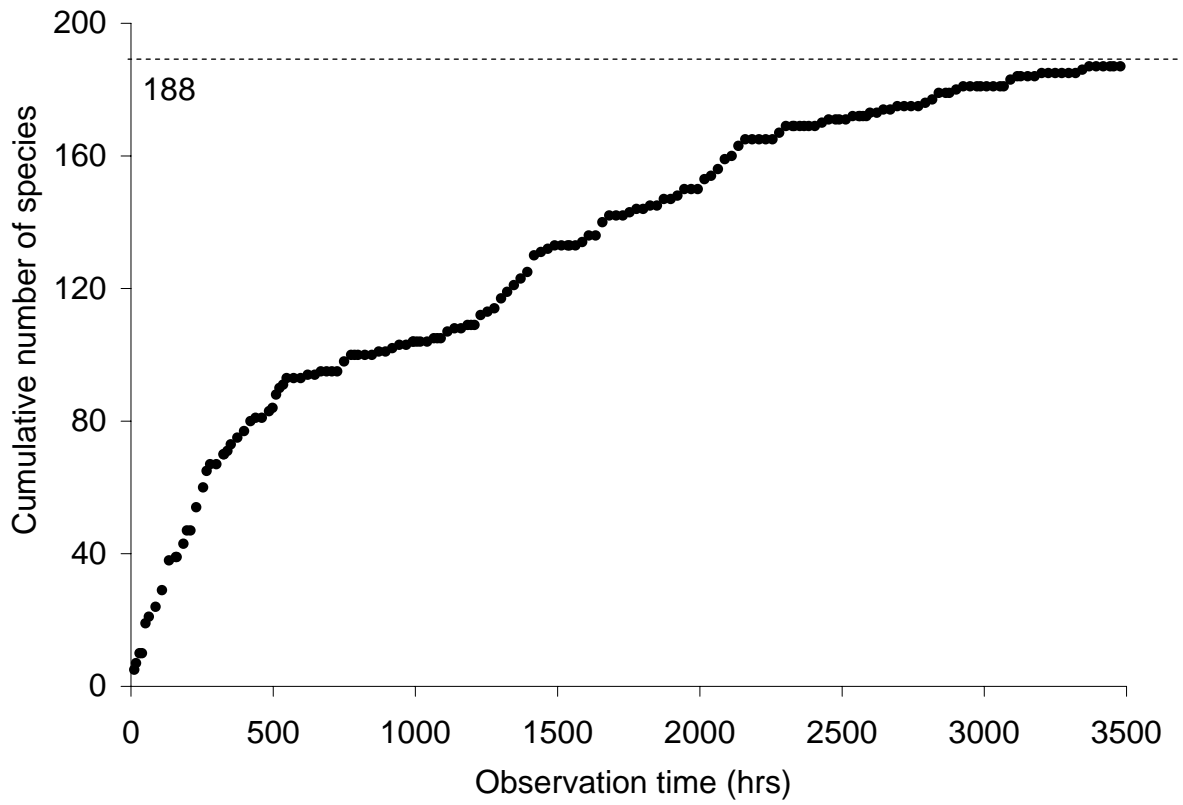


Fig. 17 Cumulative number of plant species consumed by proboscis monkeys from May 2005 to May 2006.

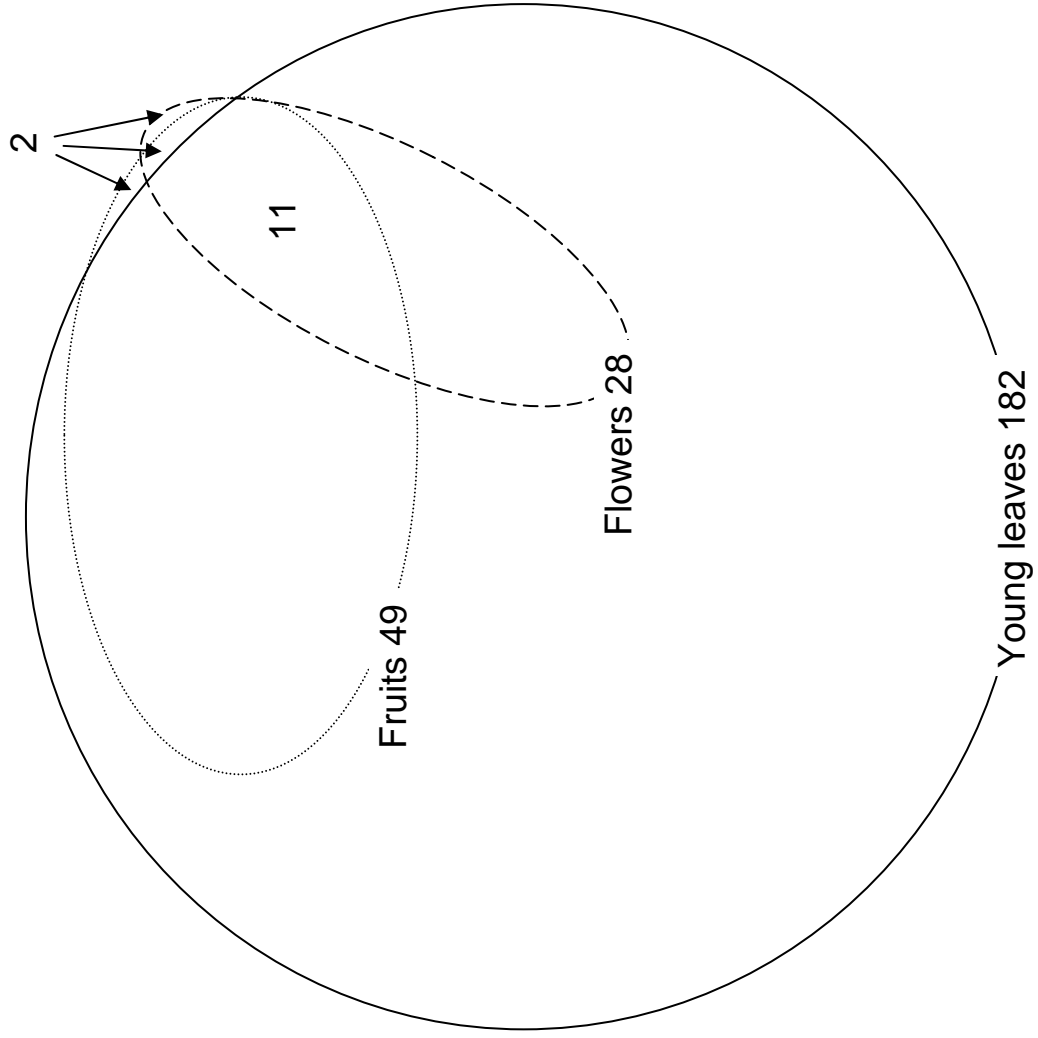


Fig. 18 Number of plant species providing young leaves, fruits and / or flowers.

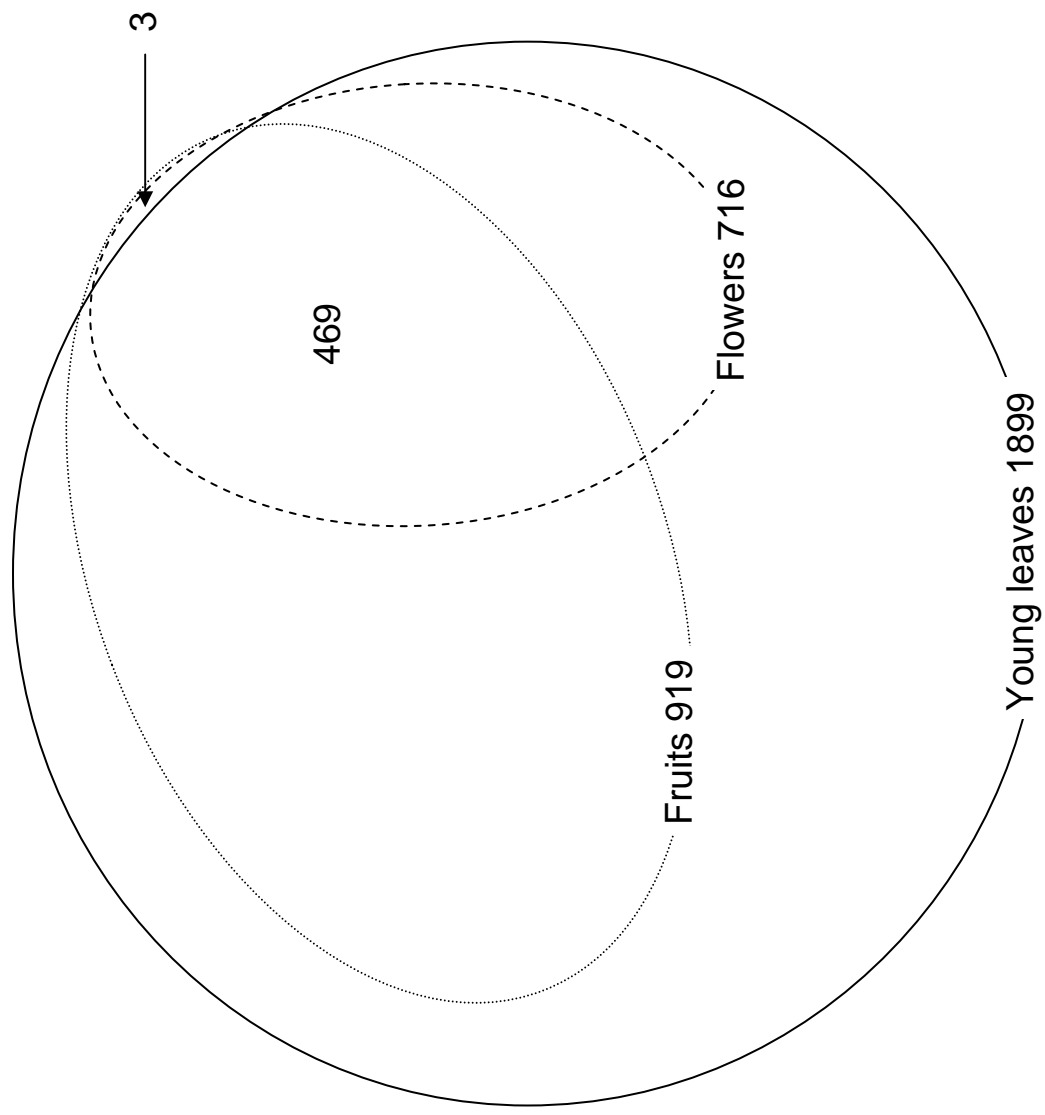


Fig. 19 Numbers of along-trail trees and vines of plant species which were confirmed to be consumed young leaves, fruits or flowers by focal adults (see Tables 3 and 4).

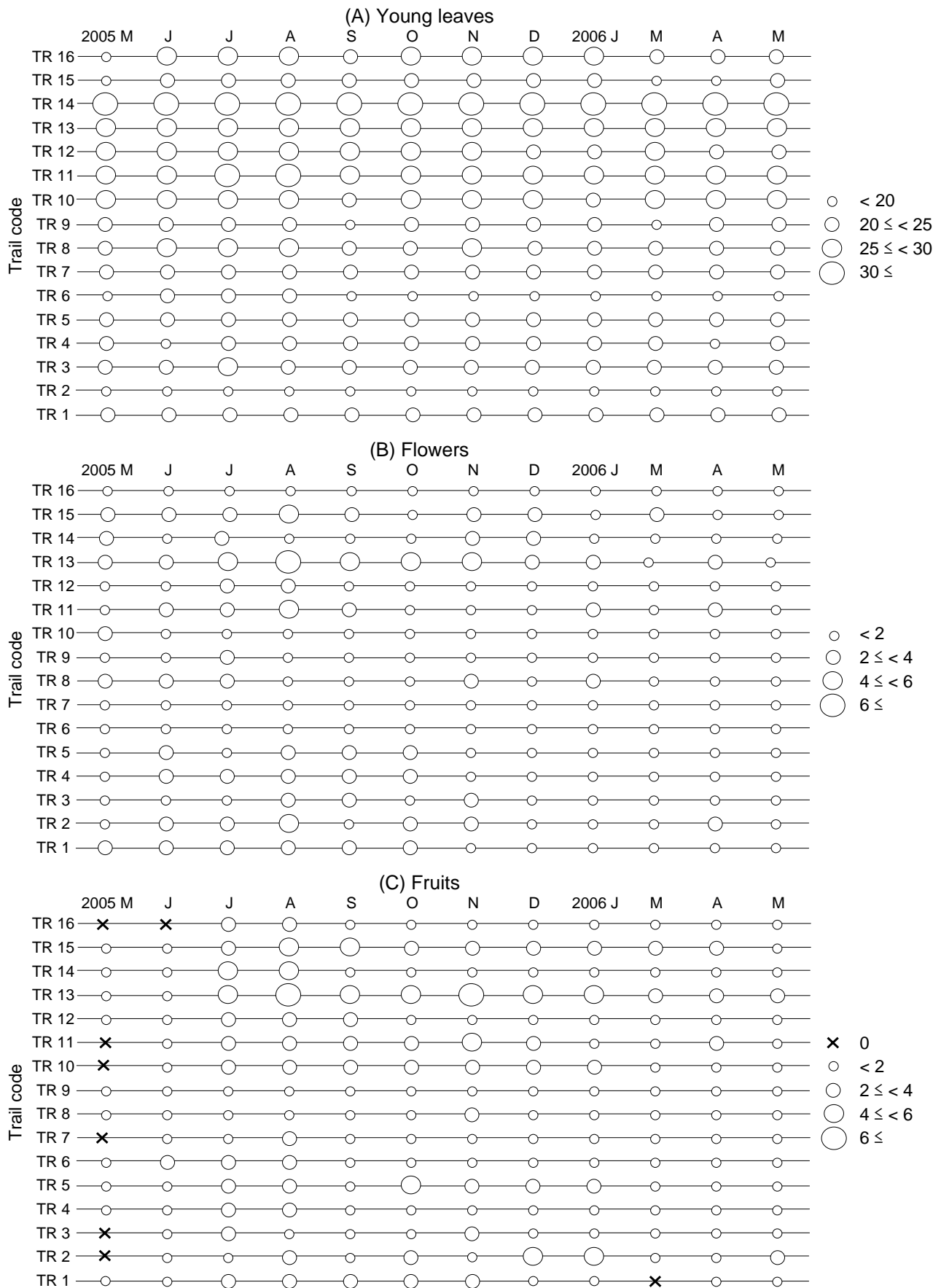


Fig. 20 Spatiotemporal distribution of availability of young leaves, flowers and fruits. Size of each circle indicates the number of plants with young leaves, flowers or fruits. Odd and even numbers of trail mean the southern and northern sides of Menanggul River, respectively. Since some trails are shorter than the others, number of plants per 100 m is adopted.

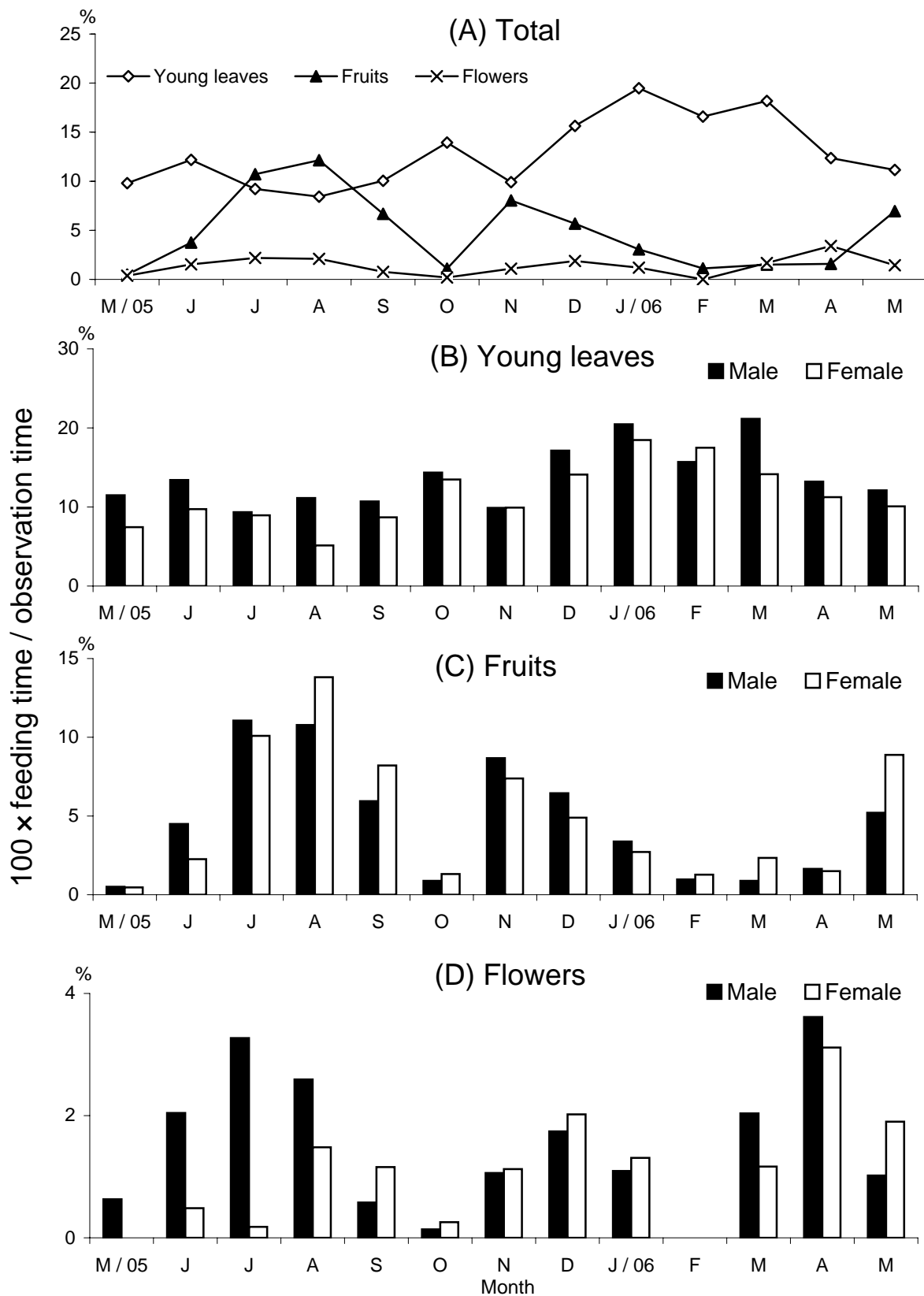


Fig. 21 Seasonal fluctuation of time allocation to three food items, i. e. young leaves, fruits and flowers. A: total of adult male and females. B-D represent the differences between male and females. In t-test, the sexual difference was not statistica

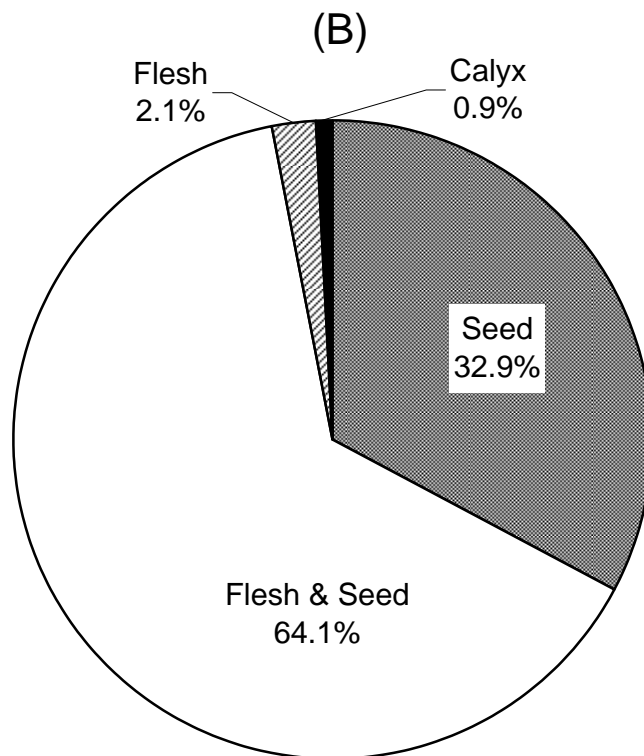
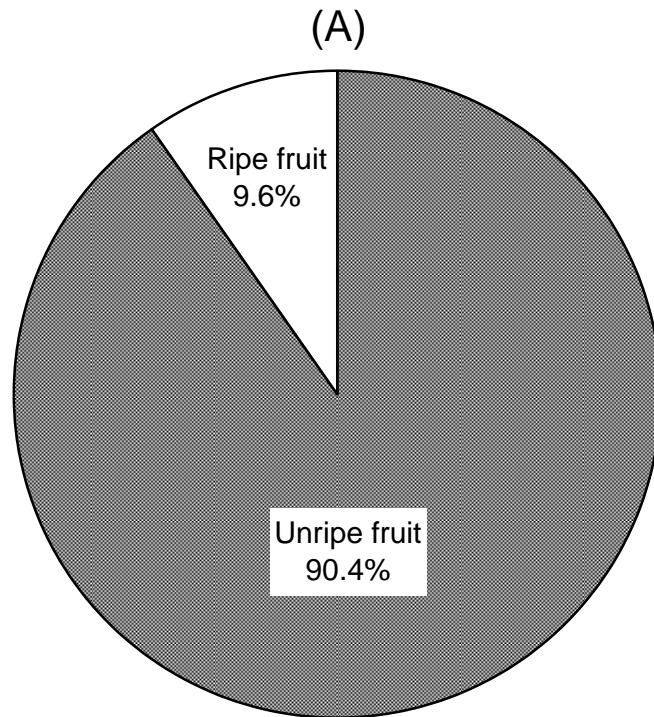


Fig. 22 Time allocation to consumption of ripe or unripe fruits (A) and to four fruit parts, i. e. seed only, flesh & seed, flesh only, calyx (B).



(A) Unripe stage 1



(B) Unripe stage 2



(C) Unripe stage 3



(D) Ripe stage

Fig. 23 Ripening of *Alseodaphne insignis* fruit. A: fruit is still small and hard; B: fruit grows, but still hard; C: the fruit size nearly reaches maximum, but still unripe fruit; D: ripe fruit. Proboscis monkeys eat only calyx at unripe stage 1, occasionally only calyx and frequently both the calyx and flesh at stage 2, and only seed at stage 3 and ripe stage.

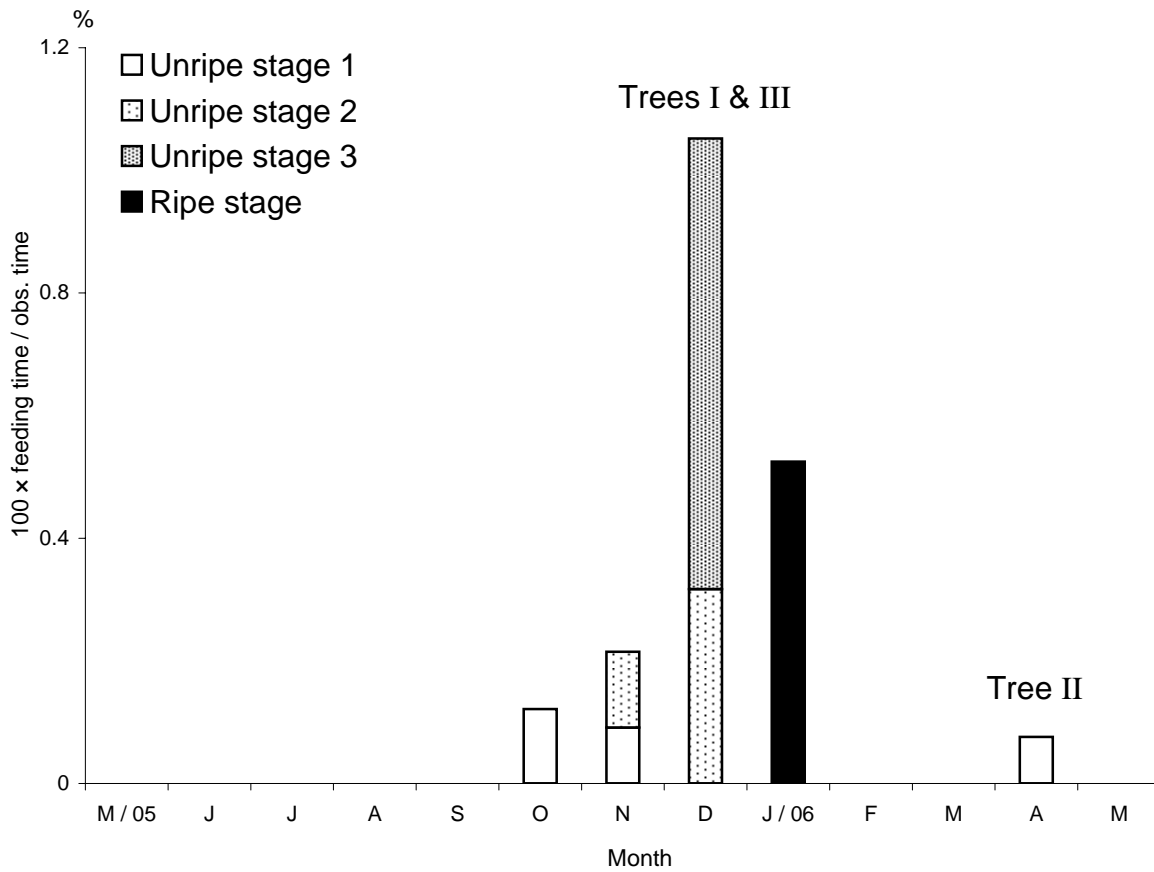


Fig. 24 Monthly trends of time allocation to the consumption of *Alseodaphne insignis* fruits. On trees I and III, the fruits grew from unripe stage in October to ripe stage in January and proboscis monkeys consumed only calyxes in October, calyxes and flesh in November, calyxes, flesh and seeds in December and only seeds in January.

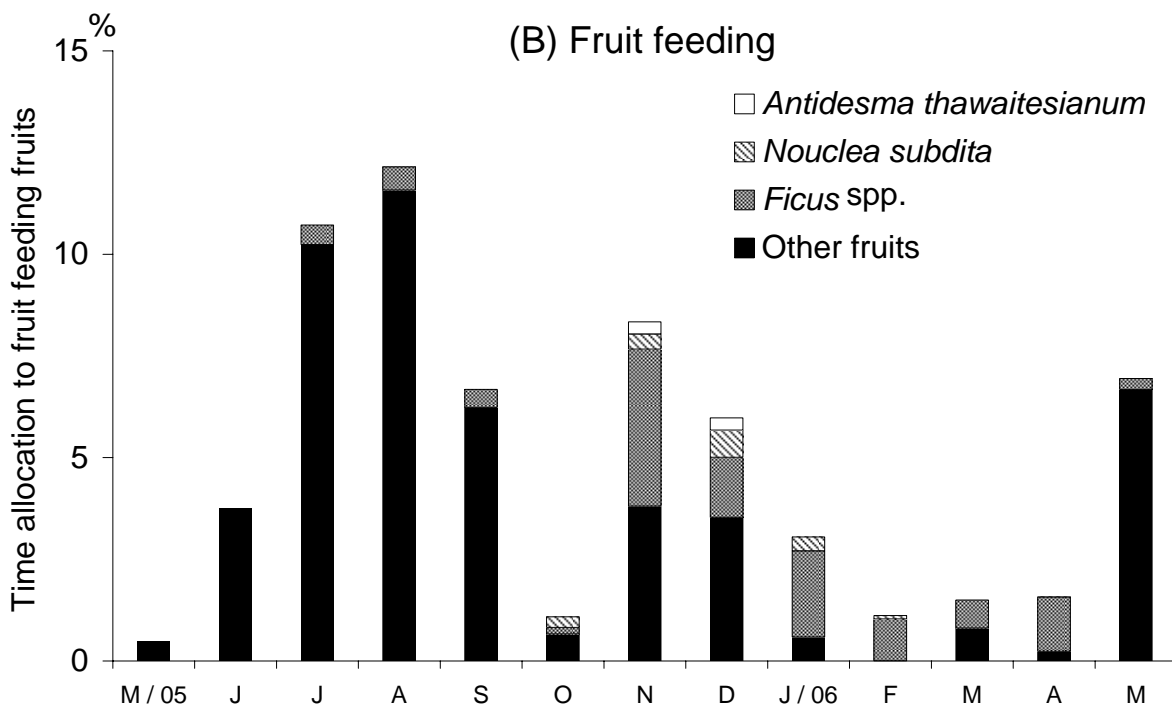
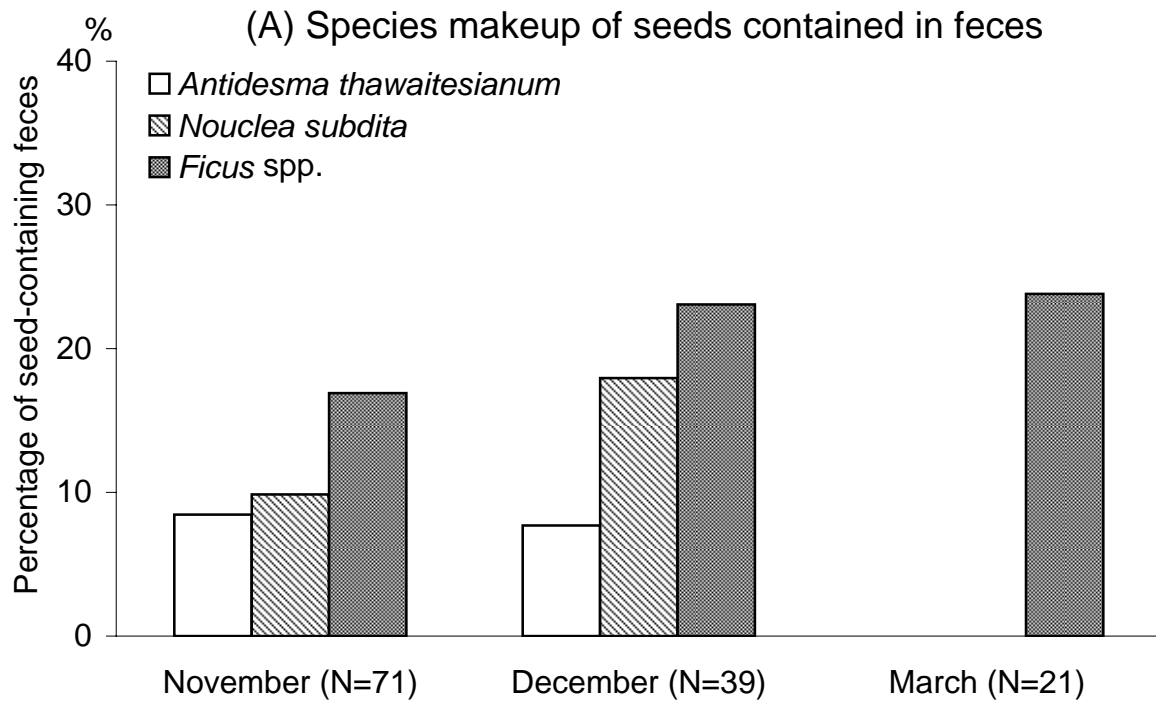


Fig. 25 Species makeup of seeds contained in feces (A) and seasonal trends of time allocation to fruit feeding (B). Whereas a total of 400 feces were examined during 13 months, fruit seeds of only three species were found in 43 feces examined in November, December and March.

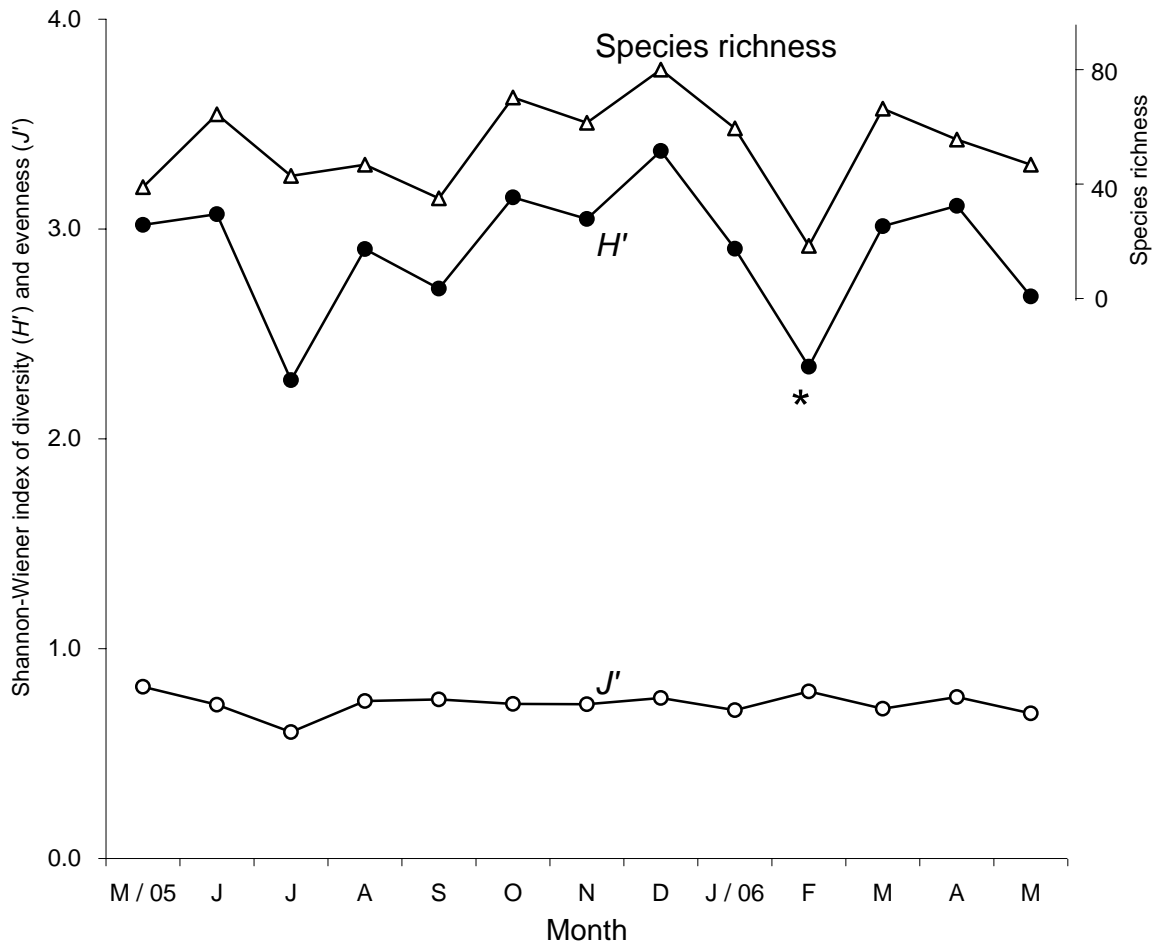


Fig. 26 Seasonal trends of food menu diversity (H'), evenness (J') and species richness (number of species). Shannon-Wiener's diversity and evenness indices were calculated from data shown in Appendix I. Stepwise regression detected a significantly negative correlation between the seasonal fluctuations of fruits consumption and food menu diversity (H') ($p = 0.043$ see Table 8). * Only 3 days' data available for February 2006.



(A)



(B)

Fig. 27 A papery bark tree of *Eugenia* sp. 2 (A) and a nest of *Microcerotermes distans* (B).

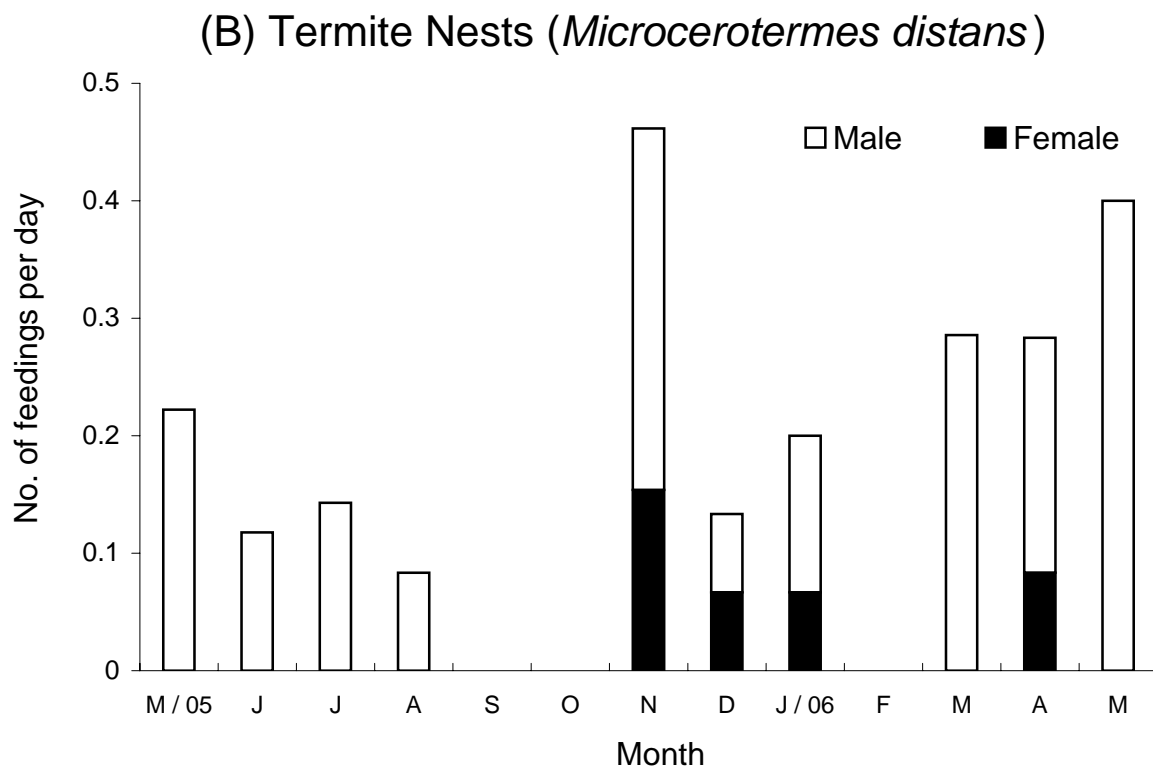
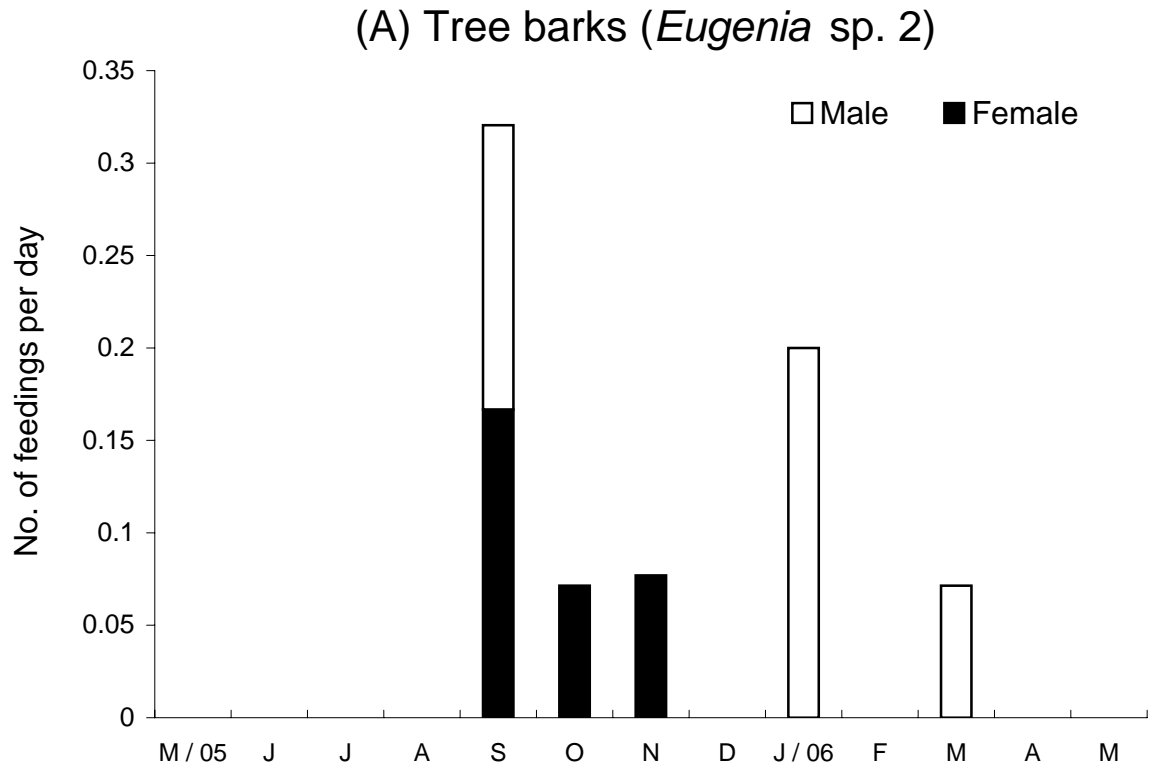


Fig. 28 Seasonal fluctuation of feeding on *Eugenia* sp. 2 barks (A) and *Microcerotermes distans* nest (B).

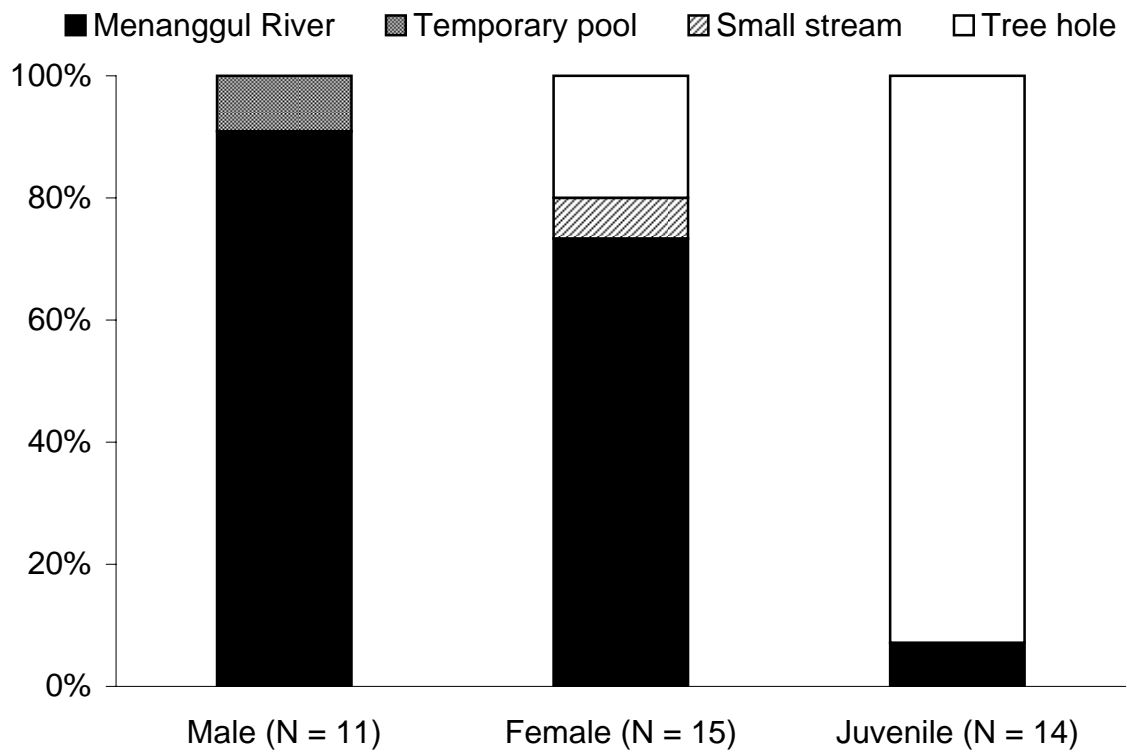


Fig. 29 Comparison of water sources among male, female and juvenile.

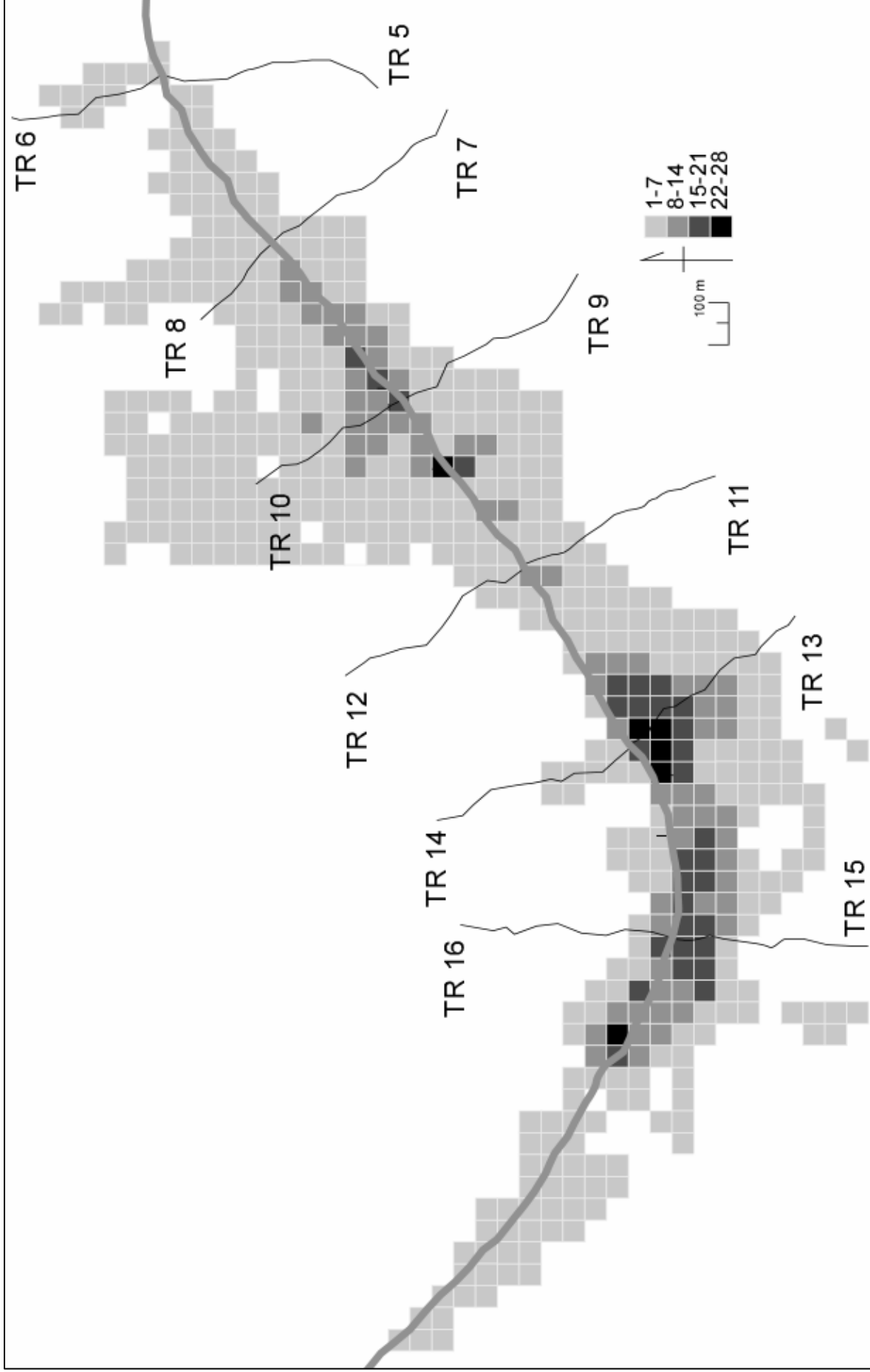


Fig. 30 50 m x 50 m grids used by BE-Group during study period. Gradation of shade indicates the total number of usages.

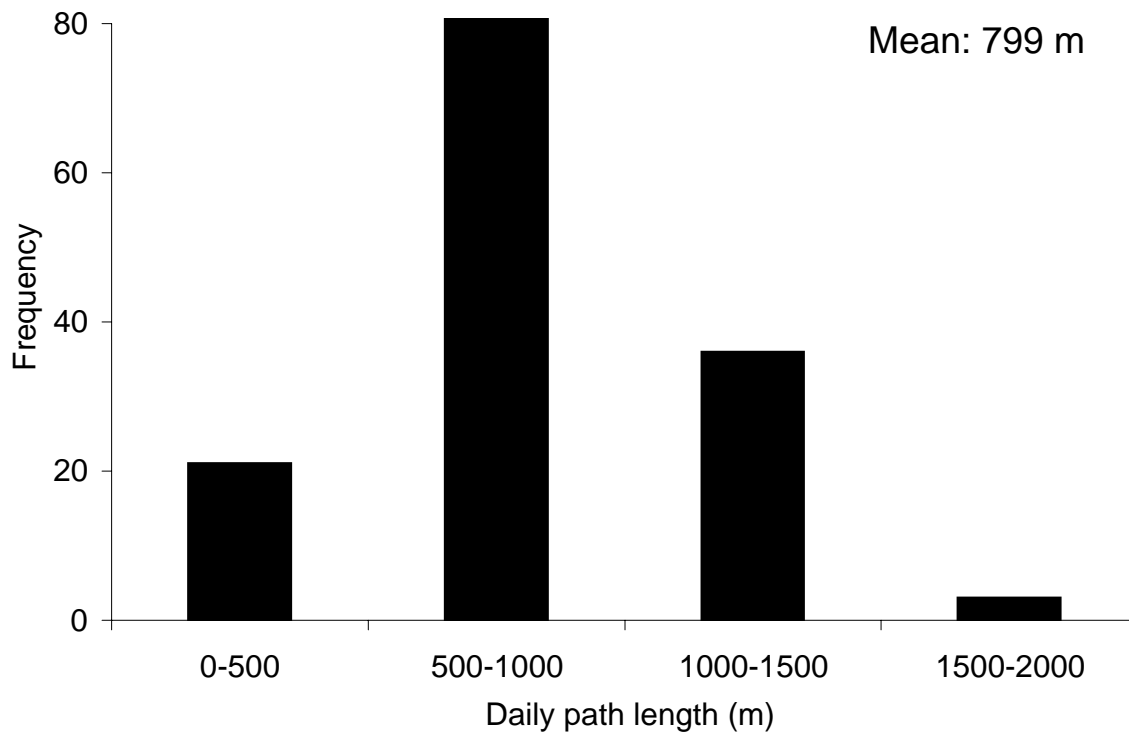


Fig. 31 Frequency distribution of daily path length (N=161 days). Only days when the full-day following of BE-Group was successful were used for this analysis.

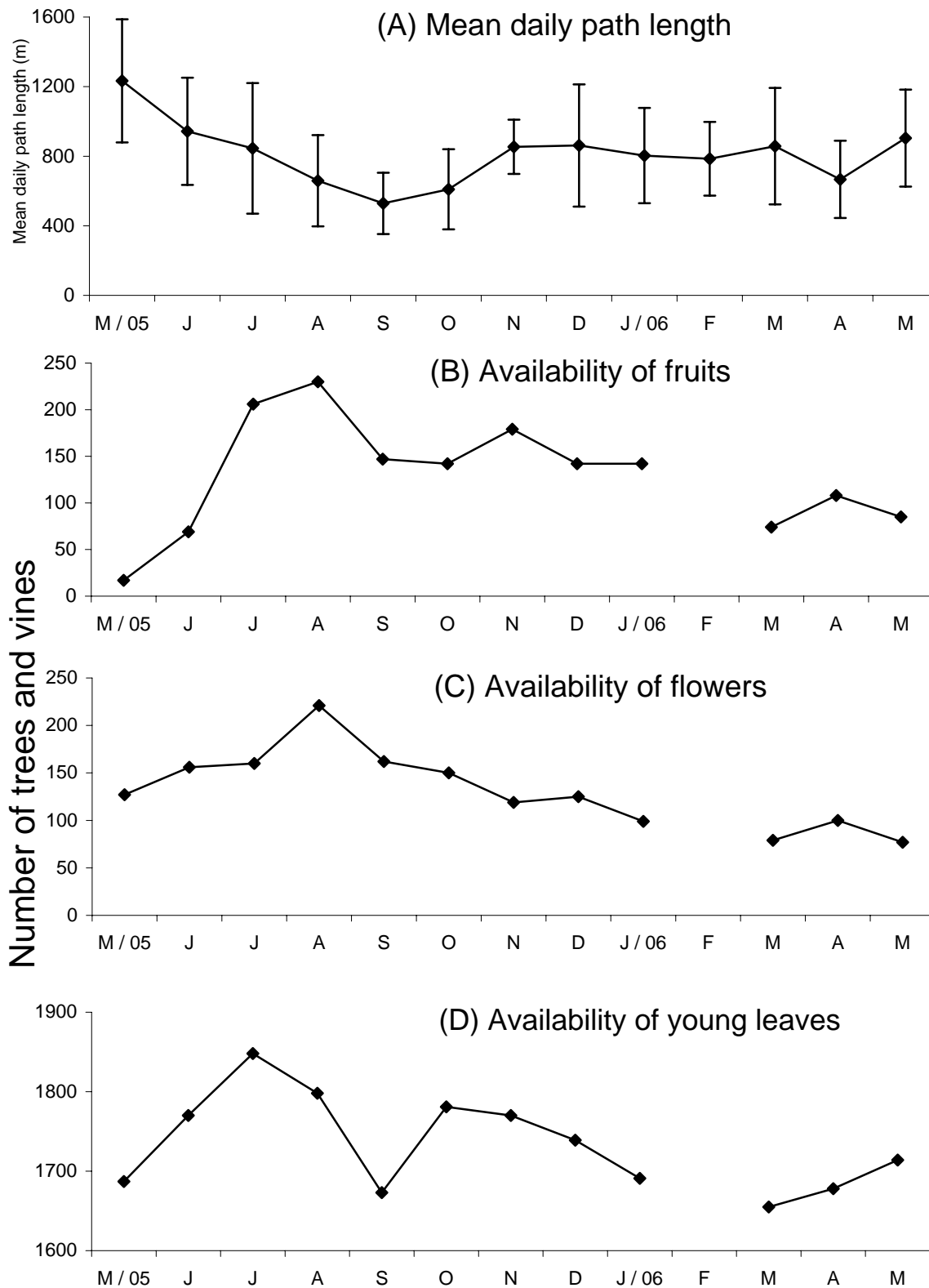


Fig. 32 Seasonal fluctuation of mean daily path length with SD (A) and availabilities of fruits (B), flowers (C) and young leaves (D). Stepwise test detected that grid usage was negatively correlated with availability of fruits ($p = 0.0028$ see Table 8), but not of flowers and young leaves.

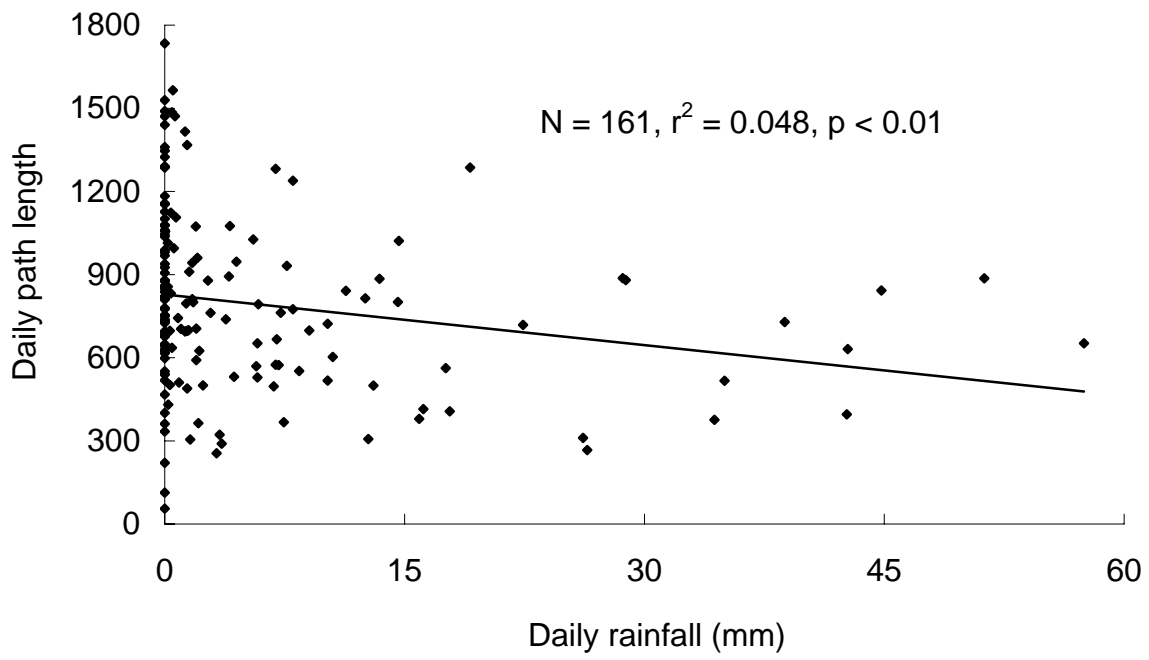


Fig. 33 Correlation between daily path length (m) and daily rainfall (mm). r^2 : Spearman's rank correlation.

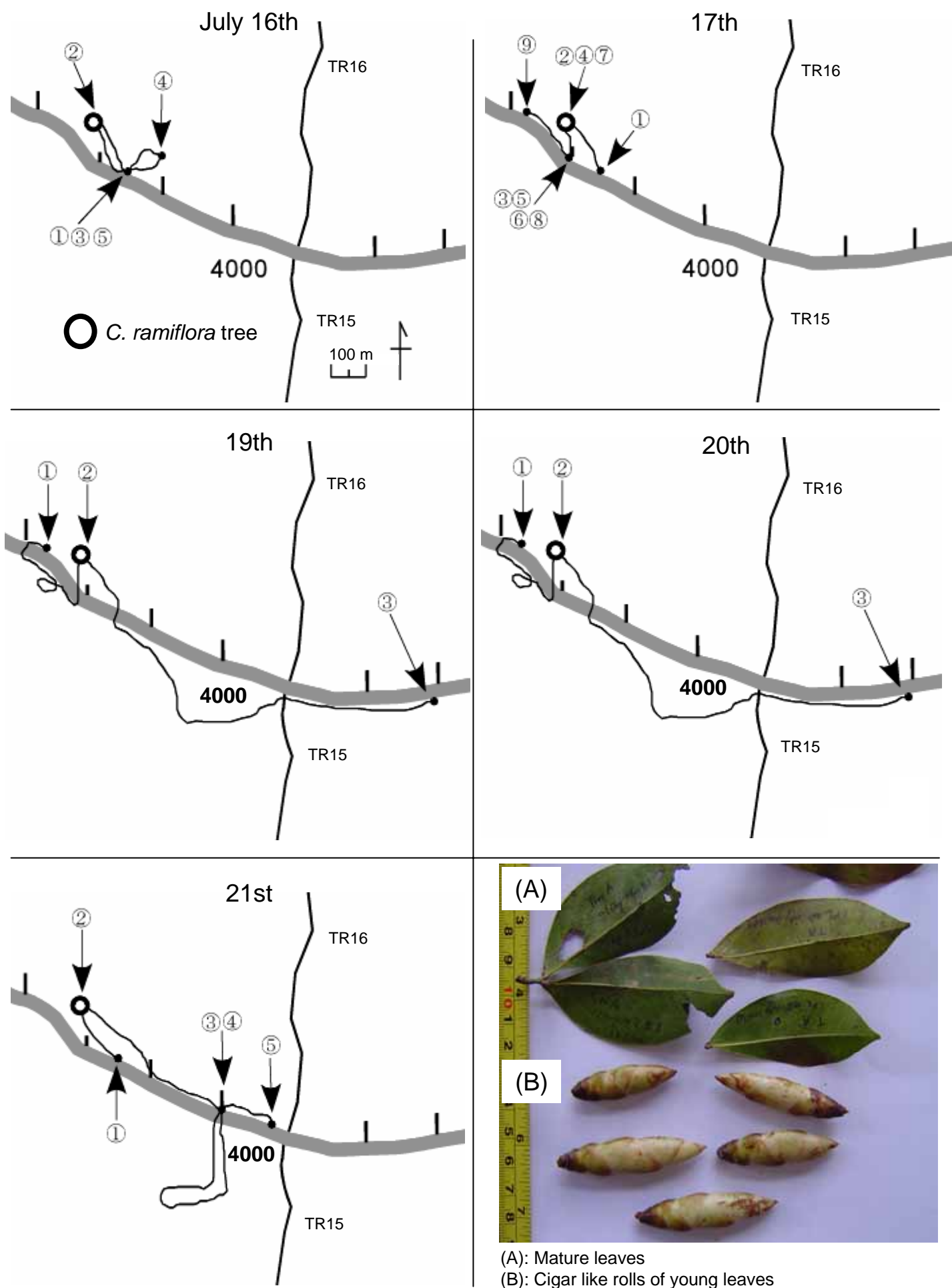


Fig. 34 Behavioral core tree species *C. ramiflora* with cigar like rolls of young leaves. BE-Group was frequently attracted to a large *C. ramiflora* tree when it had many cigar like rolls of young leaves.

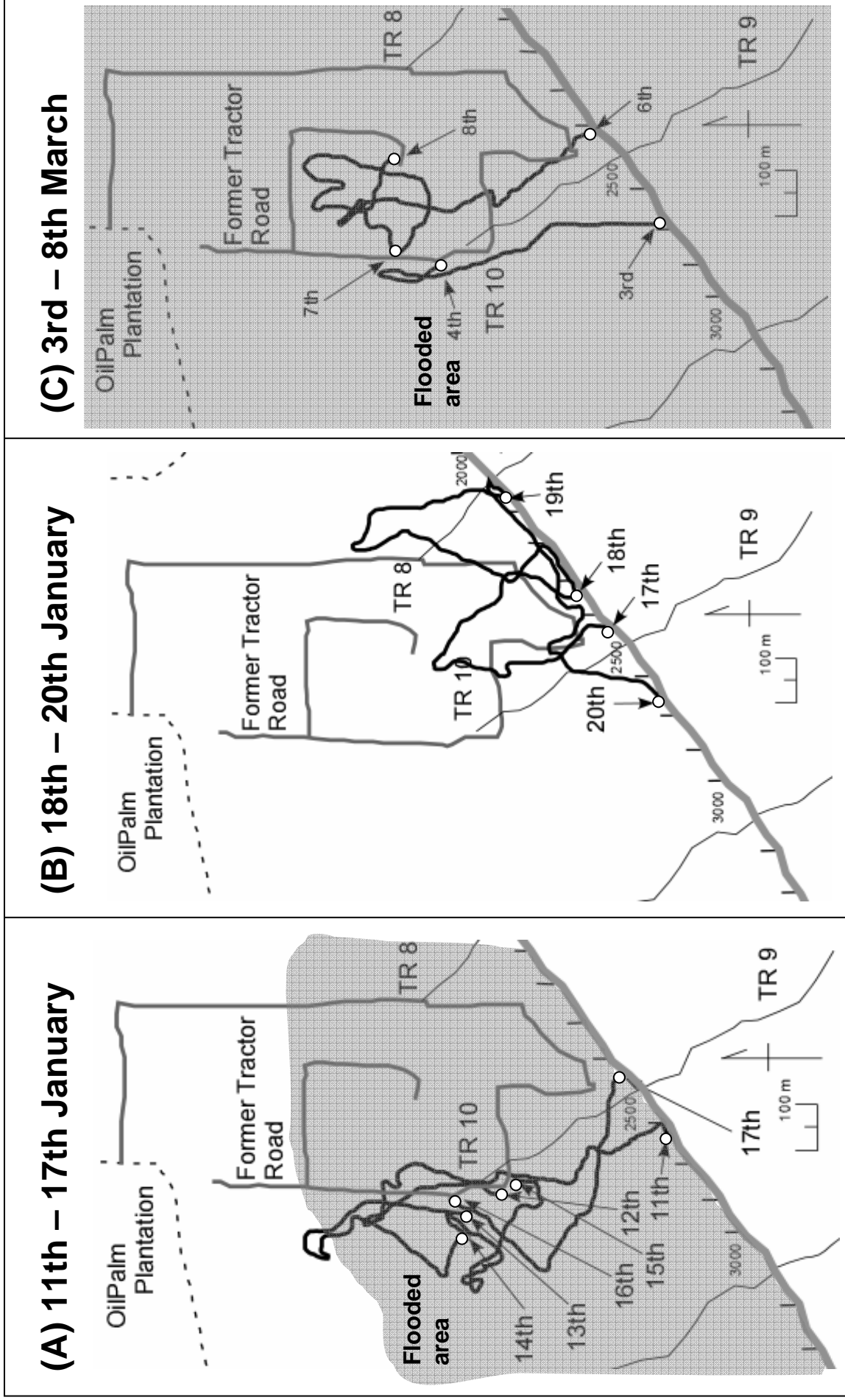


Fig. 35 Comparison of sleeping-site distribution between flooded and non-flooded days. Open circles are sleeping sites. On flooded days, sleeping sites were frequently located in the forest (A and C) whereas BE-Group always returned to river bank on non-flooded days (B).

(A)



(B)



Fig. 36 Former tractor road in dry season (A) and rainy season (B).

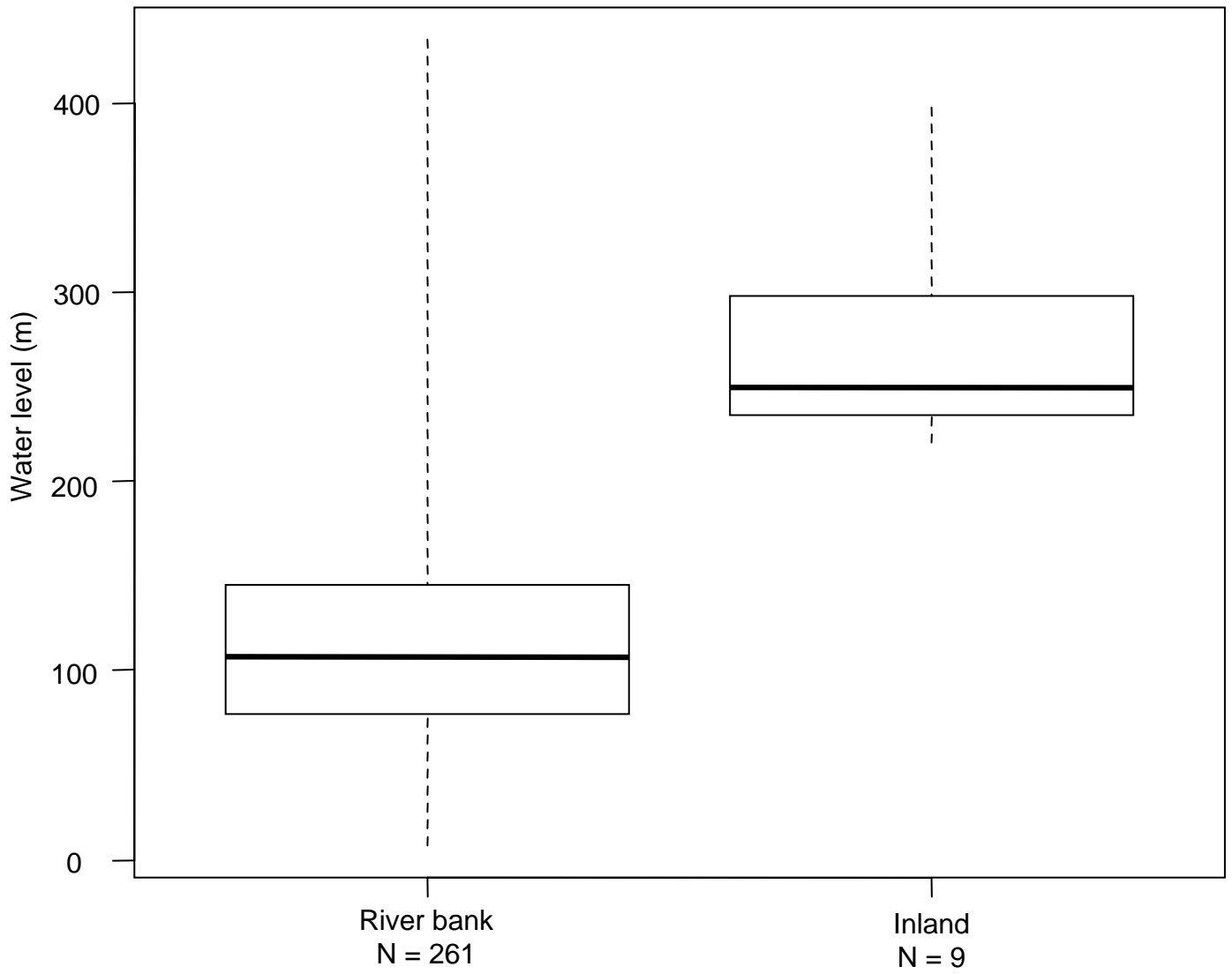


Fig 37 Relation between water level and sleeping sites (river bank or inland). Bold line: median; dotted line: range; box: 25% range from the median to both sides.

Appendix (Continued 1)

FLACOURTIACEAE	<i>Hydnocarpus sumatrana</i>	0.03	0	0.02	0.41	0.26	0.84	0.28	0.94	0.74	0.04	0	1.48	0.22
	<i>Xylosma sumatrana</i>	0	0.16	0	0	0	0.04	0	1.10	0.17	0	0.02	0	0
GNETACEAE	<i>Gnetum gnemonoides</i>	0.05	0	0	0	0	0.03	0	0.06	0	0	0	0	0.08
LAMIACEAE	<i>Teijsmanniodendron bogoriense</i>	0	0	0	0	0	0.28	0	0.36	0	0	0	0	0
	<i>Vitex pinnata</i>	0	0.20	0.23	0.17	0.37	0.08	0.18	0.39	0	0	0	0.26	0
LAURACEAE	<i>Alseodaphne insignis</i>	0	0	0	0	0	0.41	0.62	4.01	1.61	0	0	0.42	0
	<i>Cinnamomum</i> sp. 1	0	0	0	0	0	0	0	0.04	0	0	0	0.07	0
	<i>Dehaasia cuneata</i>	0	0.25	0.78	1.55	2.91	0.24	0	1.32	2.00	0.94	0	0	0
	<i>Endiandra</i> sp. 1	0	0	0	0	0	0.06	0	0.09	0	0	0	0	0
	<i>E.</i> sp. 2	0	0	0	0	0	0	0	0	0.33	0	0	0	0
	<i>Litsea</i> sp. 2	0	0	0	0	0	0.09	0	0	0	0	0	0	0
	<i>L.</i> sp. 3	0	0.19	0	0	0	0	0	0	0	0	0	0	0
	<i>Nothaphoebe</i> sp. 1	0	0	0	0	0	0	0	0	0	0	0.03	0	0
LECYTHIDACEAE	<i>Barringtonia macrostachya</i>	0	0	0	0	0	0	0	0	0	0	0.25	0	0
	<i>Planchonia valida</i>	0	0	0	0	0	0	0	0.03	0	0	0	0	0
LEGUMINOSAE	<i>Acacia borneensis</i>	0	0	0	0.02	0	1.41	0	4.27	3.43	0.79	0.86	0.26	0
	<i>Airyantha borneensis</i>	0.03	0	0	0.04	0	0	0	0	0	0	0	0	0
	<i>Albizia corniculata</i>	0.27	0.31	0.74	0.16	0.12	0.34	0.43	0.11	0	0.06	0.60	0.32	0.91
	<i>A. dolichadena</i>	0	0	0	0	0	0.50	0	0.06	0	0	0.09	0.07	0
	<i>Bauhinia diptera</i>	0	1.40	0.03	0.18	0	1.36	0.03	0.36	0.21	0	5.07	7.61	1.87
	<i>Caesalpinia crista</i>	0	0	0	0	0	0	0	0.06	0	0	0	0	0
	<i>Crudia ornata</i>	0	0	0	0	0	0	0.85	0	0	0	0	0	0
	<i>C. reticulata</i>	0	0.23	0.23	0	0	0	2.83	7.14	0.47	0	0	0	0
	<i>Cynometra ramiflora</i>	0	0	10.44	1.52	2.17	0	0	10.74	0.37	0.52	0	0.44	3.02
	<i>Dalbergia parvifolia</i>	1.83	1.46	0.60	1.27	2.05	0	1.80	0.90	0.54	0	5.44	0.06	9.57
	<i>Derris elegans</i>	0	0.36	0	0.37	0	0.19	0	0.33	0	0	0.25	0	0
	<i>D.</i> sp. 1	0	0.25	0	0	0.05	0.22	0.10	0	0	0	0	0	0.46
	<i>D.</i> sp. 2	0.70	0.76	0	0	0	0	0	0	0	0	0	0	0
	<i>D.</i> sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>D.</i> sp. 4	0	0	0	0	0	0	0	0	0.39	0	0	0	0
	<i>Dialium indum</i>	0	0	0	0	0	0	0	0.21	0	0	0	0	0
	<i>Entada rheedei</i>	0.04	0.65	0.03	0.18	0	1.45	0.18	1.43	0.09	0	0	0	0.03
	<i>Millettia nieuwenhuisii</i>	0	0.12	0	0	0	0.07	0	0	0.15	0	0	0	0
	<i>Ormosia sumatrana</i>	0.35	0	0	0	0.67	0	0	2.24	0	0	0	0.35	0
	<i>Pongamia pinnata</i>	0.09	0	0.31	0.27	0.20	0	0.10	0	0	0	0.08	0.12	2.26
	<i>Sindora leiocarpa</i>	0	0.07	0	0	0	0.35	0.09	0	0	0	0.18	0	0
	<i>Spatholobus macropterus</i>	0.14	2.65	1.95	2.94	3.06	6.43	1.02	0	0	0.22	0.10	1.08	3.24
LEGUMINOSAE 1		0	0	0	0	0	0	0.29	0	0	0	0	0	0
LOGANIACEAE	<i>Strychnos minor</i>	0	0	0	0.33	0.74	0	0	0	0	0	0	0	0
LOPHOPYXIDACEAE	<i>Lophopyxis maingayi</i>	0.17	2.95	3.76	13.81	10.24	6.10	1.47	1.12	0.41	1.36	1.37	5.38	5.51
LORANTHACEAE	<i>Dendrophthoe longituba</i>	0	0	0	0	0	0.08	0.06	0	0	0	0	0	0
	<i>Macrosolen</i> sp. 1	0	0	0	0	0	0	0	0	0	0	0.45	0	0
LYTHRACEAE	<i>Lagerstroemia speciosa</i>	0	0	0	0	0	0.18	0	0	0	0	0.04	0	0.03
	<i>L.</i> sp. 1	0	0.06	0.10	0	0	0	0	0	0	0	0.14	0	0
MELASTOMATACEAE	<i>Memecylon paniculatum</i>	0	0.17	0	0	0.06	0.11	0	0	0	0	0	0.20	0
	<i>Pternandra galeata</i>	0.03	0.33	0	0.03	0	0.11	0.56	0.27	0	0	0	0.11	0
MELIACEAE	<i>Dysoxylum</i> sp. 1	0	0	0	0	0	0	0	0.41	0	0	0	0	0
	<i>Walsura pinnata</i>	0	0	0	0	0	0.68	0	0	0	0	0	0	0
MENISPERMACEAE	<i>Haematocarpus validus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
MORACEAE	<i>Artocarpus</i> sp. 1	0	0	0	3.44	0.58	0.08	0	0.66	0	0	0	0	0
	<i>A.</i> sp. 2	0.15	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Ficus annulata</i>	0	0	0	0.77	0	0	0	0.38	0.22	0	0	0	0
	<i>F. benjamina</i>	0	1.23	0	0	0	0	0	0	1.43	0	3.80	0	0
	<i>F. binnendijkii</i>	1.48	2.01	1.66	2.45	5.26	6.45	9.24	6.98	7.91	1.34	1.35	3.13	2.29
	<i>F. cf. lanata</i> var. <i>foveolata</i>	0	0	0	0	0	0.16	0.17	0	0	0	0.04	0.62	0
	<i>F. crassiramea</i>	0.85	0.59	0.16	0.28	0.27	0.20	0	0	0	0	0	0	0
	<i>F. depressa</i>	0	0.03	0	0	0	0	0	0	0	0	0	0	0
	<i>F. forstenii</i> var. <i>villosa</i>	0	0	0	0.40	0	0.71	0	0	0.36	0	0.27	0	0
	<i>F. globosa</i>	0.61	0	0	0	1.05	0	3.90	0.14	1.02	0	0.52	0	0.23
	<i>F. pellucidopunctata</i>	0	0	0.31	0	0	0	0	0	0	0	0	0	0
	<i>F. racemosa</i> var. <i>elongata</i>	0	0	0.03	0	0	0	0	0	0	0	0	0	0
	<i>F. sundaica</i> var. <i>beccarianum</i>	0	0	0	1.00	0.79	1.46	0.06	0.76	1.53	0	0.48	0	0.55
	<i>F. sundaica</i> var. <i>impressicostata</i>	0	0.33	0	0	0	0	0	0	0	0	0	0	0
	<i>F. virens</i> var. <i>glabella</i>	0	0.03	0	0	0	0.57	0	0.03	0	0	0.13	0	0
	<i>F.</i> sp. 1	0.37	0	0	0	0	0.19	0.05	0	4.05	0	0	0.83	0.42
	<i>F.</i> sp. 2	0	0.23	0	0	0	0	0	0	2.80	0	0	0	0
	<i>F.</i> sp. 3	0	0	0	0	0	0	0	0.07	0	0	0	0	0
	<i>F.</i> sp. 4	0	0	0	0	0.81	0	0	0	0	0	0	0	0
	<i>F.</i> sp. 5	0	0.03	0	0	0	0	0	0	0	0	0	0	0
	<i>F.</i> sp. 6	0	0	0	0	0	0	0	0.33	0	0	0	0	0
	<i>F.</i> sp. 7	0	0	0	0	0	0	0	0	0	0	0	0	1.24
	<i>F.</i> sp. 8	0.14	0	0	0	0	0	0	0	0	0	0	0	0
MYRISTICACEAE	<i>Knema laurina</i>	0	0	0	0	0	0	0.13	0	0	0	0	0	0
	<i>Myristica</i> sp. 1	0.004	0	0	0	0	0	0	0	0	0	0	0	0
	<i>M.</i> sp. 2	0	0	0	0	0	0	0	0.13	0.18	0	0	0	0
MYRTACEAE	<i>Eugenia litseaefolia</i>	0.73	0.05	0	0	0.19	0	0.11	0	0	0	0	0	18.72
	<i>E.</i> sp. 2	0	3.54	0	0	0.31	0.09	0.05	0.06	0.31	0	0.27	0.50	0
	<i>E.</i> sp. 4	0	0.02	0	0.15	0	0	0.23	0	0	0	0	0	0
	<i>E.</i> sp. 6	0	0	0	0	0	0	0.46	0	0	0	0	0	0
	<i>E.</i> sp. 7	0	0	0	0	0	0	0	0	0.03	0	0	0	0
	<i>E.</i> sp. 8	0.10	0	0	0.86	0	0	0	0.70	0	0	0	0	0
	<i>E.</i> sp. 9	0	0	0	0	0	0	0	0	0	0	0	0.12	4.04
	<i>Syzygium fastigiatum</i>	0	0.11	0.67	0.75	0	0	0	0	0.35	0	0	0	0

Appendix (Continued 2)

OPILIAEAE	<i>Champereia manillana</i>	0	0	0.12	0	0	0	0	0	0	0	0	0	0
OXALIDACEAE	<i>Dapania grandifolia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0.16
PASSIFLORACEAE	<i>Passiflora foetida</i>	0	0	0	0	0	0	0	0.05	0	0	0	0	0
POLYGALACEAE	<i>Xanthophyllum flavescens</i>	0	0	0	0	0.29	0	0.23	0	0	0	0.20	0.12	0.15
	<i>X. neglectum</i>	0	0	0	0	0	0	0	0	0	0	0.18	0.70	0
PROTEACEAE	<i>Helicia robusta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
RHAMNACEAE	<i>Ventilago dichotoma</i>	0	0.85	0	0.92	0.13	1.44	0.06	0.03	0	0	0.63	0.34	0.93
	<i>Ziziphus borneensis</i>	0	0	0	0	0	0	3.28	1.01	0	0	0	0	0
	<i>Z. havilandii</i>	0	0.33	0	0	0	0.08	0	0.42	0.52	0	0.24	0.30	0
RHIZOPHORACEAE	<i>Carallia brachiata</i>	1.12	0	0.63	0	0.08	0.52	9.54	4.49	19.09	1.10	3.37	2.62	0.11
RUBIACEAE	<i>Gardenia tubifera</i>	0	0	0	0	0	0	0.13	0.48	0.03	0	0.05	0.04	0.37
	<i>Nauclea orientalis</i>	0	0	1.22	0	0	0	0.06	0.44	0	0	0	0	0
	<i>N. subdita</i>	0.19	2.62	0.99	0	0	0.90	1.98	2.40	1.48	0.06	0.04	0	0
	<i>Neolamarckia cadamba</i>	0	0	0	0	0	0	0	0.24	0	0	0	0	0
	<i>Neonauclea excelsa</i>	0	0	0	0	0	0	0	0	0.11	0	0	0.22	0
	<i>Pleiocarpidia sandahanica</i>	0	0	0	0	0	0	0.07	0.16	0	0	0	0	0
SANTALACEAE	<i>Scleropyrum wallichianum</i>	0	0	0	0	0	0	0	0.23	0	0	0	0	0
SAPINDACEAE	<i>Dimocarpus longan</i>	0	0	0	0	0	0	0	0.24	0	0	0	0.31	0
SAPOTACEAE	<i>Palaquium stenophyllum</i>	0	0	0	0	0	0.08	0	0	0	0	0	0	0
	<i>Madhuca dubardii</i>	0	0	0	0	0	0	0	0.07	0	0	0.04	0	0
STERCULIACEAE	<i>Heritiera elata</i>	0	0	0.14	0	0	0	0	0	0	0	0.04	0	0
	<i>Pterospermum macrocarpum</i>	0.54	0.23	0.26	3.74	0	0.10	0.05	0.87	0	0.09	0.79	0.49	3.07
SYMPLOCACEAE	<i>Symplocos celastrifolia</i>	0	0	0	0	0	0	0	0	0	0	0.03	0.68	0.20
THEACEAE	<i>Camellia lanceolata</i>	0.14	0	0	0	0	0	0	0	0	0	0	0	0
TILIACEAE	<i>Grewia acuminata</i>	0	0	0	0	0	0.10	0	0	0	0	0	0	0
	<i>Microcos crassifolia</i>	0	0	0	0	0	0	0	0	0.25	0	0	0.39	0.07
VITACEAE	<i>Cayratia trifolia</i>	0	0.04	0	0.61	0.55	0	0	0.12	0.12	0	0.47	0.32	0
	Total feeding hrs	15.7	45.4	54.6	58.3	37.9	49.4	54.9	82.9	72.6	12.3	59.5	53.9	67.8
	Total observation hrs	167.9	279.6	264.1	266.0	216.6	339.7	289.6	358.7	305.8	69.2	280.2	312.6	348.7
	Shannon-Wiener Index (<i>H'</i>)	3.02	3.07	2.28	2.90	2.72	3.15	3.05	3.37	2.91	2.34	3.01	3.11	2.68
	Evenness (<i>J'</i>)	0.82	0.73	0.60	0.75	0.76	0.74	0.74	0.77	0.71	0.80	0.71	0.77	0.69