

Frugivory in sun bears (*Helarctos malayanus*) is linked to El Niño-related fluctuations in fruiting phenology, East Kalimantan, Indonesia

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Sun bear (*Helarctos malayanus*) frugivory and fruiting phenology was investigated in a lowland dipterocarp forest in East Kalimantan, Indonesia. Two mast fruiting events, both coinciding with El Niño/Southern Oscillation events, occurred 4 years apart, resulting in large fluctuations in fruit availability. Sun bear fruit availability decreased from 13 trees ha⁻¹ fruiting month⁻¹ during the mast fruiting to 1.6 trees ha⁻¹ fruiting month⁻¹ during the intermast period. Almost 100% of sun bear diet consisted of fruit during mast fruiting period, whereas sun bear diet was predominantly insectivorous during intermast periods. The majority of sun bear fruit trees displayed 'mast-fruiting' and 'supra-annual' fruiting patterns, indicating sporadic productivity. Sun bears fed on 115 fruit species covering 54 genera and 30 families, with *Ficus* (Moraceae) being the main fallback fruit. The families Moraceae, Burseraceae, and Myrtaceae contributed more than 50% to the sun bear fruit diet. Sun bear fruit feeding observations were unevenly distributed over forest types with more observations in high-dry forest type despite fewer fruiting events, possibly due to a side-effect of high insect abundance that causes bears to use these areas more intensively. The possible evolutionary pathways of sun bears in relation to the Sundaic environment are discussed. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, 89, 489–508.

ADDITIONAL KEYWORDS: Borneo – community fruiting – ENSO – fruiting synchrony – lowland dipterocarp forest – mast fruiting – Ursidae.

INTRODUCTION

Irregular community flowering and fruiting have been recorded throughout south-east Asian forests (Wood, 1956; Medway, 1972; Appanah, 1985; Ashton, Givnish & Appanah, 1988; Sakai, 2002). The canopy and emergent trees of these forests are dominated by trees of the Dipterocarpaceae, distinguished by a unique reproductive pattern (Medway, 1972; Appanah, 1985; Curran *et al.*, 1999), causing them to flower and fruit at intervals of 2–10 years with little or no reproductive activity inbetween (Medway, 1972; Ashton *et al.*, 1988; Curran & Leighton, 2000). A large proportion of

individual trees, covering varied taxonomic groups (Appanah, 1985; Sakai *et al.*, 1999) and flowering syndromes (Momose *et al.*, 1998), flower and fruit synchronously with these dipterocarps. The size of the area taking part in such a general flowering/mast fruiting event and intensity can vary substantially, from a river valley to the whole of Peninsular Malaysia (Ashton *et al.*, 1988; Yasuda *et al.*, 1999).

The mechanism that triggers these synchronized flowering events is unclear, although a drop in nighttime temperature (≥ 2 °C for three or more consecutive days), some 2 months before the onset of flowering, has received substantial support (Ashton *et al.*, 1988; Yasuda *et al.*, 1999; but see also Corlett & Frankie, 1998). In Borneo, temperature drops associated with

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the El Niño/Southern Oscillation (ENSO) phenomenon have preceded mast events (Ashton *et al.*, 1988), although Yasuda *et al.* (1999) reported a night-time temperature drop preceding a mast fruiting event during a La Niña episode in Peninsular Malaysia. The influence of ENSO on mast fruiting varies throughout south-east Asia (Wich & van Schaik, 2000), but is reportedly strongest on the eastern sides of the Malaysian land masses, especially in East Kalimantan (Ashton *et al.*, 1988).

Mast fruiting events provide an overabundance of fruit for a short period of time and are often followed by periods of low fruit production, probably due to exhaustion of energy reserves (van Schaik, 1986; Sork, 1993). The temporal and spatial patchiness and high variability in fruit production in south-east Asia cause these forests to have a much lower overall productivity than tropical forests in Africa and South America (Appanah, 1985). Janzen (1974) hypothesized that prolonged fruit scarcity in these dipterocarp forests limits populations of granivores and frugivores during nonmast years. These primary consumers have adapted in a variety of ways to the lack of fruit. Many mammals show a dietary switch and resort to feeding on items of lower nutritional value (Leighton & Leighton, 1983; Peres, 1994; Knott, 1998), materials with increased handling time (e.g. palm-nuts; Strushaker & Leyland, 1977), plants that contain chemical deterrents (Foster, 1977), or diffusely scattered resources that increase foraging time (Terborgh, 1983). The synchronized timing of reproduction in relation to periods of fruit abundance (Fogden, 1972; van Schaik & van Noordwijk, 1985; Goldizen *et al.*, 1988), changes in range use (Joshi, Garshelis & Wang, 1995), and migration (Caldecott, 1988; Curran & Leighton, 2000) have also been recorded for certain mammal species.

Only rarely has food scarcity between mast events been so severe that it leads to documented famine and starvation. Curran & Leighton (2000) observed emaciated and starving bearded pigs at their study site in West Kalimantan during intermast periods and Knott (1998) found that orangutans suffered negative energy budgets during the lean fruit period after a mast at the same study site.

A variety of plant species that produce edible parts during periods of low fruit availability have been labelled fallback resources (Conklin-Brittain *et al.*, 1998). Fallback resources are critical for metabolic maintenance when preferred foods are unavailable (Leighton & Leighton, 1983; Terborgh, 1986) and their abundance potentially sets the carrying capacity for primary consumers (van Schaik, Terborgh & Wright, 1993). The magnitude and duration of the period of fruit scarcity, the availability of fallback foods, and the physiological and behavioural flexibilities of animal species all play an important role in determining how

successfully animals adapt to lean periods. Figs have been reported to be the main fallback food item during fruit lows for many frugivorous species in East Kalimantan (Leighton, 1993), as well in Neotropical sites (Terborgh, 1986).

The sun bear (*Helarctos malayanus*), one of the largest mammals of the Bornean rainforest, has mainly been described as a frugivore, augmenting its diet with a variety of insects, small mammals, and honey (Lekagul & McNeely, 1977; Kunkun, 1985; Wong, Sevheen & Ambu, 2002). They are effective dispersers of the seeds of several plant species (McConkey & Galletti, 1999; G. M. Fredriksson, unpubl. data). In the present study, the sun bear was chosen as a model large frugivore faced with annual and supra-annual variations in fruit availability in East Kalimantan, where the effects of ENSO on mast fruiting events are strong (Ashton *et al.*, 1988; Wich & van Schaik, 2000). The study was carried out at the eastern-most limit of the sun bear distribution range, which covers most of tropical mainland south-east Asia, from the Eastern tip of India, through Myanmar, Laos, Thailand, Cambodia, Vietnam, and Malaysia to the islands of Sumatra and Borneo (Sevheen, 1999).

The aims of this study were: (1) to study the extent of frugivory in sun bear diet; (2) to investigate the temporal variations in fruit availability in East Kalimantan; (3) to investigate fruiting patterns of fruit species important in the diet of the sun bear and distribution of these over topographical types; and (4) to determine which fruit taxa are important as fallback resources for sun bears during intermast periods.

MATERIAL AND METHODS

STUDY SITE AND CLIMATE DATA

The study was carried out in a lowland dipterocarp forest, the Sungai Wain Protection Forest, East Kalimantan, Indonesian Borneo (1°05'S, 116°49'E) (Fig. 1). The reserve covers a watercatchment area of ~10 000 ha. Approximately 50% of the reserve was affected by forest fires in March to April 1998 (Fredriksson, 2002), during one of the most severe ENSO-related droughts ever recorded (McPhaden, 1999), leaving an unburned central core of some 4000 ha of primary forest. Data for the study were collected in the unburned primary forest. The topography of the reserve consists of gentle to sometimes steep hills, and is intersected by many small rivers. Elevations range from 30–150 m a.s.l. The most common families [diameter at breast height (d.b.h.) > 10 cm], are Euphorbiaceae, Dipterocarpaceae, Sapotaceae, and Myrtaceae. The relative dominance of Dipterocarpaceae increases substantially in larger size classes. Together, the 25 most common species form 40% of total stem

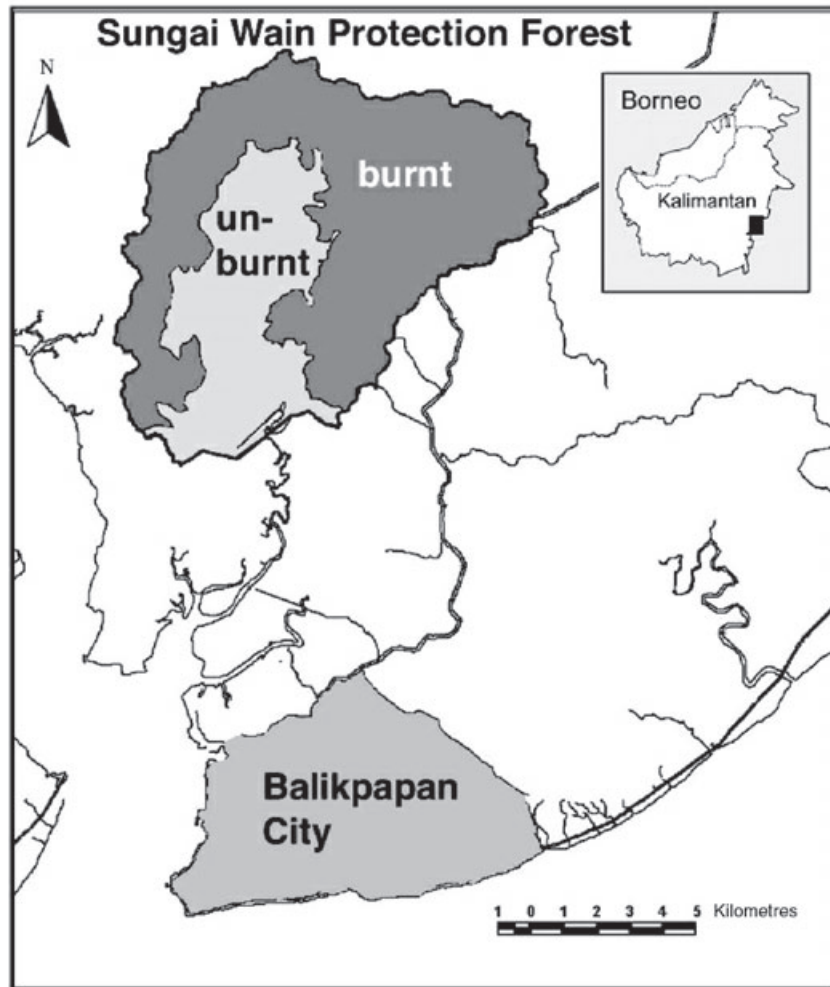


Figure 1. Map of the Sungai Wain study site in East Kalimantan, showing the unburnt forest core where data were collected.

density (van Nieuwstadt, 2002). Palmae (also called Family Arecaceae) are common in the subcanopy and understory, and Zingiberaceae, Marantaceae, Araceae, and Pandanaceae are widespread in the understory.

Daily rainfall, minimum-maximum temperature and humidity data were collected between January 1998 and October 2002, at ground level in the primary forest. Rainfall patterns were calculated on a yearly basis, using Mohr's Index (Whitmore, 1985). At the start of the study, rainfall was below average due to the ENSO event that was in progress (van Nieuwstadt, 2002). Although rainfall patterns in the region are not consistent on an annual basis, a distinction could be made between a 'wet' season (November to April) and a 'dry' season (May to October) (t -test, $t = 4.96$, $d.f. = 6$, $P = 0.002$). Out of 58 months that rainfall data were collected, 12 months had rainfall below 100 mm, classified as dry months (Walsh & Newbery, 1999). Nine of these occurred between May

to September, the remaining three dry months were during the (1998) ENSO (January to March 1998). Rainfall type falls within the category of 'slightly seasonal' according to Mohr's index, with average annual rainfall 2968 ± 510 mm year⁻¹. Temperature remained stable throughout the study period with average maximum of 29.7 ± 0.7 °C and minimum 23.2 ± 0.4 °C, with an annual average of 26.5 ± 0.2 °C, equal to the average temperature of 26.5 °C reported for the region historically (Berlage, 1949).

CLASSIFICATION OF TOPOGRAPHICAL TYPES

Five topographical types were discerned: swamp, alluvial, slope, high-flat, and ridge (Fredriksson & Nijman, 2004). Swamp type was assigned to areas that showed signs of regular inundation (pneumatophore roots) or were permanently inundated, and had a high density of rattans, small trees and saplings, and a

large numbers of climbers. This classification of swamp forest refers to swampy patches within the drier forest matrix and has no relation to large areas of peat or fresh-water swamp forest (e.g. as found in south-central Borneo). Alluvial type was allocated to flat, non-inundated areas close to rivers characterized by large trees. High-flat type was assigned to flat areas at higher elevated sites away from rivers, usually with large trees. Slope type was assigned when an area had a relatively steep inclination ($> 12^\circ$). Ridge type was allocated to narrow hill tops with steep sides, or crests of longer hill chains. The relative availability of these forest types was determined by means of transects (total length 18.5 km) laid out in an east–west and north–south direction where the topographical type was recorded every 25 m. Slope topographical type covered $45.3 \pm 9.1\%$ of the study area, followed by high-flat ($24.8 \pm 9.3\%$), alluvial ($17.3 \pm 4.0\%$), ridge ($6.7 \pm 2.7\%$), and swamp ($5.9 \pm 4.6\%$).

FRUITING PHENOLOGY DATA COLLECTION

Two phenology data sets were collected during this study, using the same methodology. Phenology studies commenced in January 1998 and continued until July 2002. Data were collected in all but two of 55 months (March 1998 and February 2002).

Phenology plots

Ten 0.1-ha phenology plots (100×10 m), were established with two plots located in each of the five topographical types. All trees ≥ 10 cm d.b.h. were measured, labelled, and identified by botanists from the Wanariset Herbarium. The total number of live trees in the 1-ha of plots at the start of the study was 549 individuals, covering 186 species. Every month at around the same date (third week), all trees in these plots were observed with 10×40 Leica binoculars. The relative abundance of flowers, young and mature fruits, and young and old leaves, in relation to size of the crown, was estimated, although only the presence/absence of fruit is considered for analysis in the present study.

Specific sun bear fruit trees

The second data set contained 104 trees of 11 species (≥ 10 cm d.b.h.) known or thought to be important in the diet of the sun bear. The species of trees in this sample were based on primary fruits found in sun bear scats and trees frequently covered with sun bear claw marks (signs of bears climbing the trees), as well as information from local people. Individual trees of these species were encountered by chance in the forest, measured, labelled, and reobserved on a monthly basis. The following taxa were included: *Monocarpia kalimantanensis* ($N = 10$) (Annonaceae), *Durio dulcis*

($N = 10$), *Durio oxleyanus* ($N = 10$), *Durio zibethinus* ($N = 2$) (Bombacaceae), *Dacryodes rugosa* ($N = 11$), *Dacryodes rostrata* ($N = 10$), *Santiria* spp. ($N = 10$) (Burseraceae), *Ficus* spp. ($N = 11$), *Artocarpus integer* ($N = 10$) (Moraceae), *Ochanostachys amentaceae* ($N = 10$) (Olacaceae), and *Tetramerista glabra* ($N = 10$) (Tetrameristaceae). Three of the 11 taxa were added later during the study period, when it was found that bears fed substantially on them (*Monocarpia*, June 1999; *Ficus* spp., June 1999; *Santiria* spp., June 2000).

FRUGIVORY IN SUN BEARS

The study on the extent of frugivory in sun bears was based on faecal samples and direct feeding observations. Faeces were systematically collected between October 1997 and July 2002 from both wild and reintroduced bears, with sun bear scats being clearly identifiable due to their scent, texture, and size. Collection occurred along transects and trails that intersected the home ranges of three wild radiocollared female sun bears, monitored between 1999 and 2001, and at specific sites where these bears were located by triangulation. In addition, randomly located scats from unmarked wild bears were collected throughout the forest whenever encountered. Scats from three captive-reared bears that were radiocollared and gradually reintroduced into the forest were also collected. Scats from these bears were included only after they had been acclimated to living in the forest for at least 6 months.

All faecal samples were weighed and washed through a 0.2-mm mesh-sized sieve and dried in the sun. Identification of seeds, and seedlings after germination trials, was carried out by the Wanariset Herbarium. Scat contents were sorted into a five main categories: (1) fruit (whole or broken seed counts); (2) flowers; (3) insects; (4) pith (meristem) and (5) debris (termite nest remains; wood; resin). A visual estimate was made of the relative volume of each category. To calculate the frequency of occurrence of fruit in scats for each month, the running mean was calculated for three consecutive months. This was performed because fruit scats collected in a given month could be up to several weeks old when collected, representing fruits eaten that month or the month before. Second, faecal data collected late in the month might be more comparative with the fruit situation for the following month because phenology data were collected towards the end of each month. Faecal samples were collected in all but five out of 57 months of scat collection.

Direct feeding observations were obtained on a regular basis from reintroduced bears as well as *ad libitum* from wild sun bears. Reintroduced bears were habituated for visual observations and twice a week observations of each bear were carried out. Data col-

lection from observations was continuous, and time of initiation and termination of each activity recorded. On average, bears were observed 7.0 ± 1.5 h during observation days ($N = 711$), comprising approximately 50% of their active hours in a day (G. M. Fredriksson, unpubl. data). During foraging observations, the total time spent handling a food source (e.g. foraging in or around a fruiting tree, or handling a termite nest), as well as the actual time spent feeding on that food source (i.e. how much time spent actually swallowing food), and which part of a food item was eaten (e.g. pulp, seeds, exocarp), were recorded. With larger food items (e.g. large fruits), the exact number of items consumed was recorded. Samples were collected of all food items for subsequent identification. Data from the initial 6–8 months of observations were not used in the data analyses because, during this time, released bears still received supplementary foods. The period of direct observations used for analysis spanned 31 months, from October 1998 to April 2001.

CLASSIFICATION OF FRUITING TYPES AND SPATIAL DISTRIBUTION OF SUN BEAR FRUIT SPECIES

The flowering and fruiting patterns of all trees combined, and separate species/genera, were classified according to timing and frequency of flowering and fruiting events. The 'mast fruiting' period was defined as the period where fruit production was 1.96 standard deviations above the mean, following the definition for mast fruiting proposed by Wich & van Schaik (2000). When all fruiting events of a species occurred during this mast fruiting period, the species was categorized as a 'mast-species'. When the fruiting frequency was greater than one per year, the species would be categorized as 'subannual'; when it fruited once a year, it was classified as 'annual'; and when fruiting occurred less than once a year, but not during mast fruiting periods, it was classified as 'supra-annual' (*sensu* Sakai *et al.*, 1999). When a species included individuals of more than one fruiting type, the fruiting type of the majority of individuals was considered as the fruiting type for this species.

The term 'fruiting event' is used to describe a tree with fruit during one monthly observation period or several consecutive observation periods. The term 'sun bear food tree' refers to trees from species that were found to occur in the diet of the sun bear. The distribution of sun bear fruit species among topographical types was determined by classifying all trees (≥ 10 cm d.b.h.) from the ten 0.1-ha phenology plots into sun bear food and nonfood species, and calculating the percentage of sun bear food trees for each topographical type.

DATA ANALYSIS

Two analyses were performed to evaluate the temporal pattern of fruiting events. First, an index of aggregation, Morisita's index, I_d (Morisita, 1962), independent of sample size, was calculated based on temporal distribution of fruiting events for 17 3-month periods (*sensu* Sakai *et al.*, 1999) from January 1998 to July 2002. I_d is near 1 in distributions that are essentially Poisson, > 1 in clumped distributions, and < 1 in cases of regular or seasonal reproduction (Morisita, 1962; Krebs, 1999). Second, a χ^2 test for goodness of fit was performed to examine whether the observed distribution of fruiting events significantly deviated from random distribution. This test was performed assuming that fruiting events occurred at random throughout the 17 3-month periods (when sample size of fruiting events was ≥ 70) or eight 6-month periods (when sample size of fruiting events was between 35 and 69) because the expected number of fruiting events in a unit period (3 or 6 months) must be five or more (Sokal & Rohlf, 1981). These two analyses were conducted on separate genera important in the diet of the sun bear, as well as for all trees monitored for their monthly phenology combined.

To test for differences in number of trees fruiting between periods, the study period was divided into four periods of 12 months starting in May 1998, after the first mast-fruiting event. Kruskal–Wallis one-way analyses of variance and χ^2 tests were applied to test for differences between periods and habitat types, with $P < 0.05$ being considered statistically significant. When multiple comparisons between treatments were conducted (Siegel & Castellan, 1988), Bonferroni techniques were applied to limit overall experimental error (Sokal & Rohlf, 1981). All values reported are the mean ± 1 standard deviation (SD) and statistical analyses were performed with Sigma Stat 1.0.

RESULTS

TEMPORAL VARIATION IN FRUITING PHENOLOGY

The mean percentage of all trees fruiting in the ten 0.1-ha plots over the 53 months (January 1998 to July 2002) was $2.4 \pm 3.4\%$; masting was thus defined as $> 9.1\%$ of trees fruiting [$2.4 + (1.96 \times 3.4)$]. Two distinct mast-fruiting peaks lasting 2 months each were discerned, with the first in progress at the start of data collection in January to February 1998, and a second peak almost 4 years later, during November to December 2001 (Fig. 2). Both masting events took place during ENSO episodes (NOAA-CIRES, 2003).

During the first masting event, 15.7% of trees (86 of 549) fruited and, during the second, 10.3% of trees (49 of 474) carried fruit. During the intermast period,

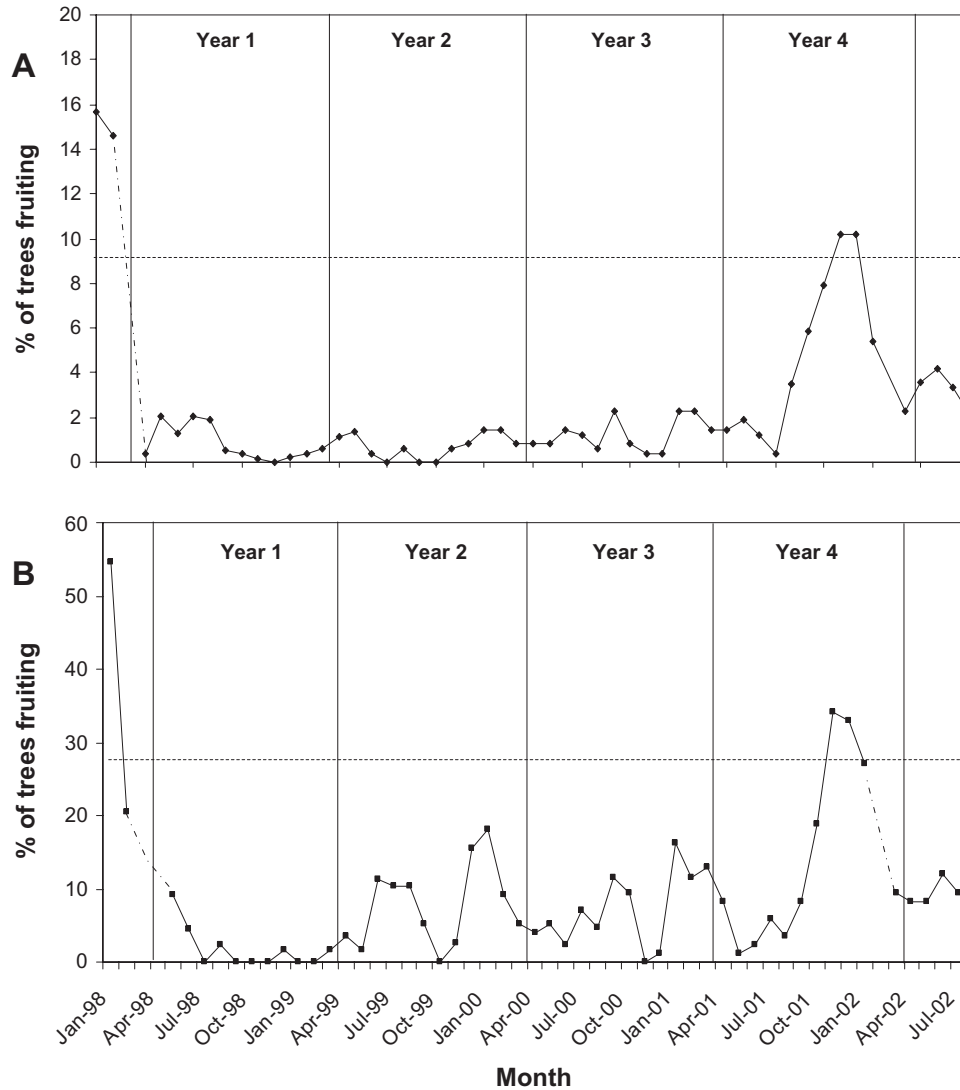


Figure 2. A, temporal changes in fruiting phenology of trees (≥ 10 cm d.b.h., $N = 549$) from 10 0.1-ha plots, showing two mast fruiting events. B, fruiting phenology of selected sun bear fruit trees ($N = 104$, data set II), mast and nonmast species combined. The horizontal line indicates the threshold above which masting is defined to occur.

fruit production averaged $1.6 \pm 0.6\%$ trees ha^{-1} fruiting month^{-1} . Fruit production differed significantly between years (years 1–4 in Fig. 2A), following the 1998 masting event (Kruskal–Wallis, $H = 18.1$ d.f. = 3, $P < 0.001$). Fruit production was significantly lower in the first 2 years (April 1998 to March 2000) than in the fourth year (April 2001 to March 2002) (Dunn–Šidák, $Q > 3.6$, $P < 0.05$ for both years).

In the ten 0.1-ha plots, 26.2% of trees (144 of 549) were species encountered in the diet of sun bears, although only 37% (53 of 144) of these trees were reproductively active during the study, representing 9.7% of all trees (≥ 10 cm d.b.h.) found in 1 ha. From these 53 reproductively active sun bear fruit trees, 128

fruiting events were recorded over 53 months of monitoring, with 52 events (40.6%) during the two masting events (4 months). During mast fruiting months, 13.0 ± 2.2 sun bear fruit trees ha^{-1} month^{-1} fruited whereas, during the intermast interval, only 1.6 ± 1.8 sun bear fruit trees ha^{-1} month^{-1} produced fruit. In the first 2 years after the 1998 masting event, fruiting by sun bear tree species was very low with only 0.6 ± 0.8 trees ha^{-1} fruiting month^{-1} . In the third year fruiting increased to 2.5 ± 2.1 trees ha^{-1} fruiting month^{-1} .

Fruiting by selected sun bear fruit trees (second phenology data set) also differed significantly over years (Kruskal–Wallis, $H = 14.8$, d.f. = 3, $P = 0.002$),

with 3 years after the 1998 masting event having lower fruit production than the fourth year (Dunn-Šidák, $Q > 2.8$, $P < 0.05$ for all years) (years 1–4 in Fig. 2B). Fruit production was almost absent in the first year following the 1998 mast fruiting event. Mean percentage of sun bear trees fruiting, over the 53 months was $8.9 \pm 10.2\%$; hence, mast-fruiting for these was defined as when $> 29\%$ of trees under observation were fruiting. Two distinct mast-fruiting peaks for these selected sun bear trees coincided with the two mast fruiting events among all trees (Fig. 2).

Three times during the study period did temperature drop below the 'critical' value of $21\text{ }^\circ\text{C}$, proposed as the low night-time temperature threshold triggering the onset of general flowering (Ashton *et al.*, 1988). Each of these minima lasted only one night and lowest temperature recorded was $20.7\text{ }^\circ\text{C}$ (July 2002). These minor drops in temperature did not correlate to a subsequent onset of general-flowering. The temperature drop in July 2002 occurred when a smaller general flowering event was already well under way.

FRUITING PATTERNS AND TYPES

In total, 639 fruiting events were recorded from all trees ($N = 549$) in the ten 0.1-ha plots (Table 1). More than half of these fruiting events (330 of 639; 51.6%) were concentrated during the mast-fruiting periods. Fruiting events were significantly clustered over 3-month periods (Table 1) ($I_d = 2.52$, $\chi^2 = 946.9$, d.f. = 16, $P < 0.001$). A high proportion of trees (61.4%) were never observed to fruit during the study period (Table 1). The most common fruiting type in the plots was mast-fruiting (16.4% of trees), followed by supra-annual fruiting pattern (14.4% of trees). Only 2% of trees displayed an annual fruiting pattern and 5.8% of individuals a subannual pattern.

Among 104 sun bear trees that we monitored, 378 fruiting events were recorded. These were also found to be clustered over 3-month periods ($I_d = 1.77$, $\chi^2 = 363.6$, d.f. = 16, $P < 0.001$). Several species/genera displayed highly clumped fruiting patterns (*Durio* spp., *A. integer*, *Dacryodes* spp., *O. amentaceae*) (Table 1). Intermediate fruiting patterns were observed for *T. glabra* and *Santiria* spp. The former species had significantly lower number of trees fruiting though in the first 18 months after the 1998 masting and ENSO event than in the subsequent 18 months (Mann–Whitney U -rank sum test: mean rank 1 = 14.3, mean rank 2 = 22.7, $N = 36$, $Z = -2.614$, $P = 0.017$).

The lowest index of aggregation (most random fruiting) was found in *Ficus* spp. *Monocarpia kalimantanensis* had the second lowest index of aggregation, but fruiting was not randomly distributed ($I_d = 1.07$, $\chi^2 = 19.72$, d.f. = 11, $P < 0.05$) (Table 1). Mean d.b.h.

of selected sun bear fruit trees was larger (44.7 ± 21.1 cm) than the mean d.b.h. of all monitored trees in the 0.1-ha plots (21.1 ± 14.3 cm) (Mann–Whitney U -rank sum test: mean rank 1 = 501, mean rank 2 = 285, $N = 617$, $Z = 9.4$, $P < 0.001$). However, 31.7% of these selected sun bear fruit trees were never observed fruiting. Based on the majority of observations, taxa were divided into those only found fruiting during masting events (mast species: *Durio* spp., *A. integer*, *Dacryodes* spp., and *O. amentaceae*) and those that also fruit during intermast periods (non-mast species: *Ficus* spp., *Santiria* spp., *T. glabra*, and *M. kalimantanensis*) (Table 1).

FAECAL ANALYSES

A total of 1209 sun bear scats were collected (77 between October 1997 to April 1998, 280 in the first year after the 1998 mast (May 1998 to April 1999), 305 in second year, 391 in the third year, 137 in the fourth year, and 19 in May to June 2002). Fruit remains were encountered in 58.5% of faecal samples (706 of 1209), and in 46 of 52 months (88.5%) that scats were collected. Insect remains (primarily termites) were encountered in 75.4% of scats (911 out of 1209). Among all 706 fruit scats, most (74.2%) contained remains of one fruit species, 20.8% contained two species, 4.2% contained three, and 0.7% contained four species of fruit. Of 706 scats collected with fruit remains, 40.4% (238) contained 100% fruit.

Remains of 83 distinct fruit species belonging to 39 genera in 23 different families were identified in sun bear scats. The most common genera encountered in scats were *Ficus* spp. (23.2% of scats), *Dacryodes* spp. (12.5% of scats; *D. rugosa* and *D. rostrata* combined), *Syzigium* spp. (12.3% of scats) and *Santiria* spp. (11.2% of scats) (Appendix 1). Bears primarily fed on fruits from trees (60% of identified species) with remaining fruit species being primarily from monocots (Appendix 2). Only four species of liana were positively identified to be consumed by sun bears and liana fruit resources made up $< 1\%$ of fruit scats.

Moraceae was the most species rich family occurring in the diet of sun bears, with 14 species, followed by Palmae which featured with ten species (Appendix 2). The family Euphorbiaceae, which dominated in the phenology plots (21.4% of stems ≥ 10 cm d.b.h.), featured with only four species in the diet, three of which were *Baccaurea* spp. (Appendix 2). The 11 selected sun bear fruit tree taxa monitored for their phenology were encountered in 66.1% of fruit scats, indicating their importance in the fruit diet of sun bears.

Frequency of occurrence of fruit in scats differed between years (Fig. 3) (Kruskal–Wallis $H = 23.0$, d.f. = 3, $P < 0.001$). The first year after the 1998 mast had significantly lower occurrence of fruit than the

Table 1. Morisita index and fruiting patterns for the 1-ha phenology plots (≥ 10 cm d.b.h.) and for main sun bear fruit genera/species

	<i>N</i> (months)	<i>N</i> (trees)	<i>N</i> (fruiting events)	Morisita index (I_d)	χ^2	Fruiting pattern								
						Nonfruiting	Mast-fruiting	Supra-annual	Annual	Sub-annual				
Phenology plots														
All trees combined	53	549	639	2.52	***	61.4†	16.4	14.4	2	5.8				
Bear food species	53	144	128	2.35	***	63.1	13.2	18.8	0.7	4.2				
Non-bear food species	53	405	511	2.55	***	60.8	17.5	12.8	2.5	6.4				
Selected sun bear fruit trees	52	102	378	1.77	***	31.7	34.6	10.6	2.9	20.2				
Artocarpus integer	52	10	44	5.69	***	–	10‡	–	–	–				
<i>Dacryodes rostrata</i> and <i>Dacryodes rugosa</i>	52	21	44	6.72	***	11	9	1	–	–				
<i>Durio dulcis</i> and <i>Durio</i> <i>oxleyanus</i>	52	22	32	4.69	–	10	12	–	–	–				
<i>Ficus</i> spp.	38	11	29	0.99	–	2	–	3	2	4				
<i>Monocarpia kalimantanensis</i>	37	10	118	1.07	*	1	–	1	–	8				
<i>Ochanostachys amentaceae</i>	53	10	9	5.19	–	4	5	1	–	–				
<i>Santiria</i> spp.	25	10	8	2.32	–	5	–	4	–	1				
<i>Tetramerista glabra</i>	52	10	94	2.06	***	–	–	1	1	8				

–, too small a sample size. †percent of trees; ‡no of trees.

* $P = 0.05$; *** $P < 0.001$.

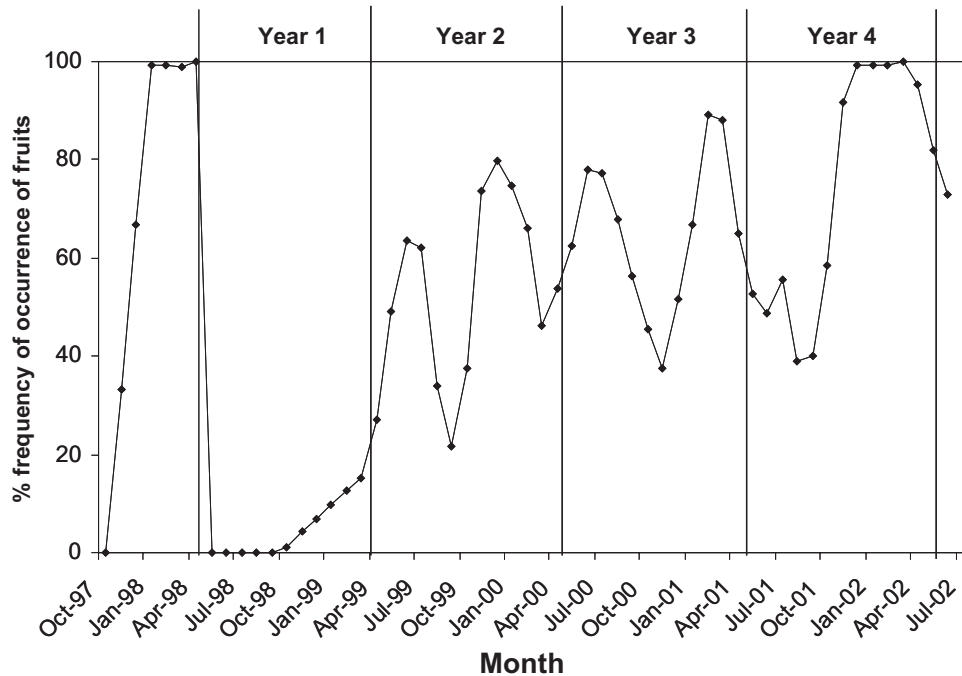


Figure 3. Frequency of occurrence of fruit in scats ($N = 706$ out of 1209) based on running mean of three consecutive months.

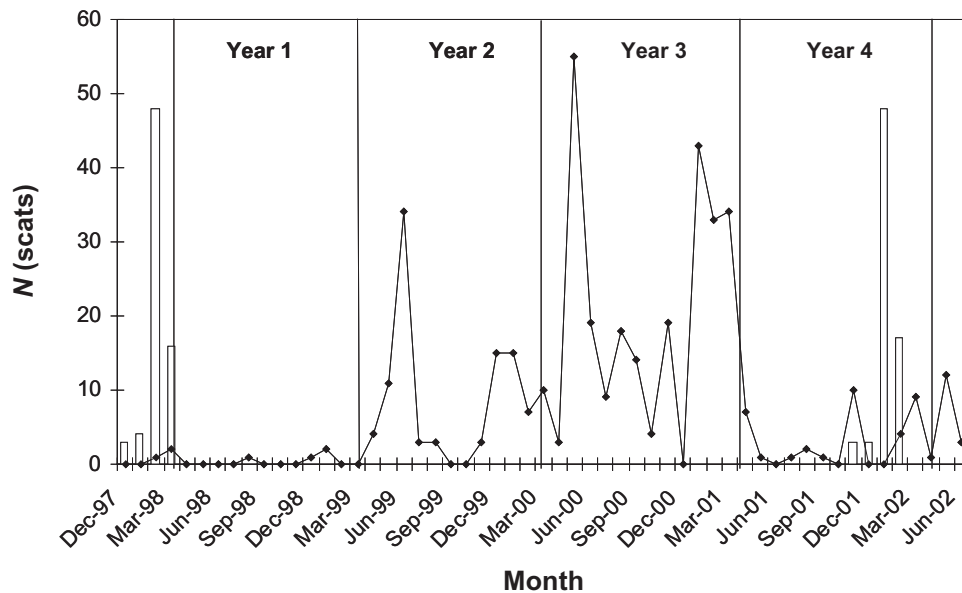


Figure 4. Faecal samples containing fruit remains divided into mast and nonmast species (706 of 1206 scats collected). Bars indicate scats containing mast fruit species, lines indicate scats containing nonmast fruit species. Most scats collected in the first year contained insect matter.

three subsequent years (Dunn-Šidák, $Q > 3.1$, $P < 0.05$ for all years). Sun bears appeared to be almost entirely frugivorous during the two mast-fruiting events (fruits found in 73 of 74 scats and 83 of 85 scats, respectively). Sun bears primarily fed on mast fruit species during

the short period when they were available (Fig. 4), ignoring the 'nonmast' species, although these also had higher fruiting activity during the masting events, possibly indicating a preference for the mast species. By contrast, fruits were nearly absent in the diet of sun

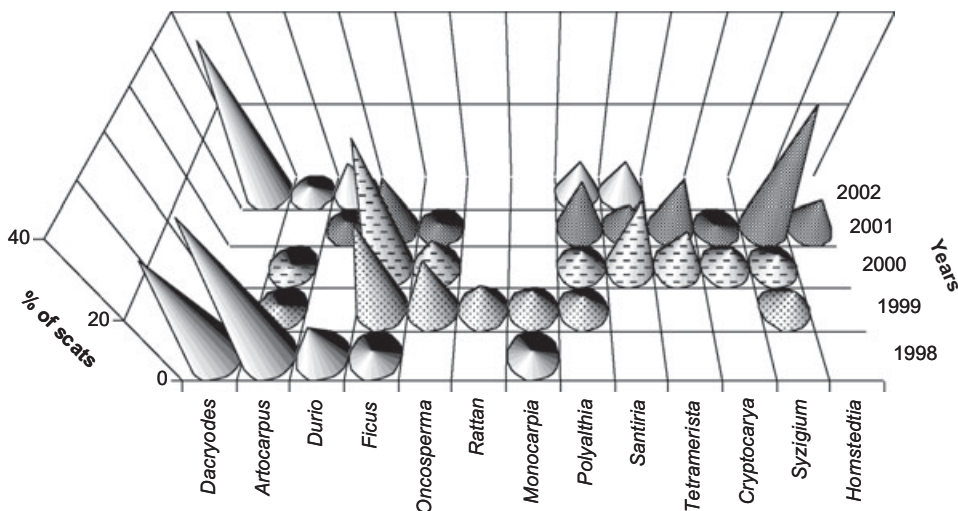


Figure 5. Annual fluctuations in contribution of main plant genera to the sun bear diet. The category 'rattan' covers several genera.

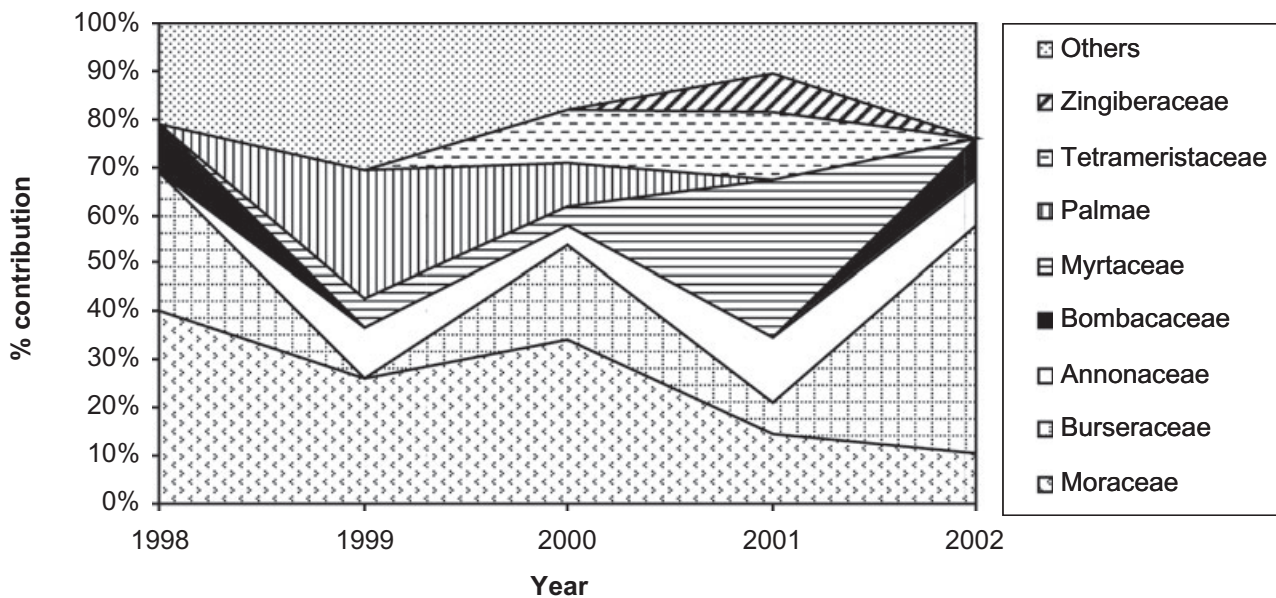


Figure 6. Annual changes in contribution of plant families to the sun bear diet.

bears for a period of 12 months following the 1998 masting event (Fig. 4). All sun bear scats collected during this first post ENSO/mast period primarily contained insect remains.

TEMPORAL VARIATION IN USE OF FRUIT RESOURCES

Based on faecal samples collected between October 1997–July 2002, the family Moraceae dominated the fruit diet of sun bears (26% of fruit scats), followed by Burseraceae (19%), Myrtaceae (9%), Annonaceae (8%), Palmae (8%), Tetrameristaceae (6%), and Bom-

bacaceae (3%). The importance of various fruit families, genera, and species varied substantially over seasons and years (Figs 5, 6). In the first year, incorporating the first mast-fruited event, the main plant genera in the diet were Artocarpus (Moraceae), Dacryodes (Burseraceae), and Durio (Bombacaceae). Sun bears consumed copious amounts of these, mostly large seeded (up to 45 mm), fruits. For example, a single scat could contain > 400 *D. rugosa* seeds (seed length 15 mm; maximum scat weight 400 g).

In the second year, with the lowest overall fruit availability, *Ficus* (Moraceae) was the dominant

genus. Figs were the most frequently occurring fruit genus encountered in scats throughout the study period (164 of 706 fruit scats), and also occurred in 58.7% of months that scats were collected. However, the occurrence of scats containing fig remains was clumped temporally ($I_d = 1.96$, $\chi^2 = 170.7$, d.f. = 14, $P < 0.001$). After the 1997–98 ENSO, figs hardly featured in faecal samples for a period of 12 months. No correlation was found between number of fruiting fig trees and number of scats encountered each month with fig remains (Spearman rank correlation: $R^2 = 0.22$, $P = 0.193$, $N = 37$).

A number of taxa from the Palmae family also featured in the diet during these periods with extreme fruit lows (i.e. *Oncosperma horridum*, *Borassodendron borneensis*, *Polydarpus* sp., the rattans *Calamus* spp., *Daemonorops* spp., *Korthalsia* spp.). Fruits of *O. horridum*, clusters of small hard drupes, were encountered in 49 scats.

Certain species in the family Annonaceae were also found to be important for sun bears during the inter-mast period. Two unidentified species of *Polyalthia* with large (up to 55 mm) fatty fruits were frequently encountered in scats (51 of 706) in the third year of the study, whereas *Polyalthia sumatrana*, which reaches high densities in the forest, was not encountered in scats at all. Fruits of *M. kalimantanensis*, though available throughout most of the study period, were only consumed during the fruit low period.

In the third year *Ficus* spp., *Santiria* spp., and *T. glabra* dominated the fruit diet. In the fourth year, *Syzigium* spp. dominated the fruit diet and to a lesser extent figs. The ginger *Hornstedtia* cf. *reticulata* (Zingiberaceae) also appeared in scats. In the fifth year *Dacryodes* spp. and *Durio* spp. were again consumed copiously during the masting event, followed by *Santiria* spp. (post masting event) (Fig. 5).

DIRECT FEEDING OBSERVATIONS

From direct observations ($N = 4977$ h) sun bears were found to feed on fruits for $10.3 \pm 4.3\%$ of their feeding time ($N = 3$ bears), although the observation period did not include the mast fruiting events. Remaining feeding time was primarily spent on insect matter (termites, ants, beetle larvae, cockroaches, stingless bees), as well as small quantities of flowers and vegetative matter. Although relatively little time was spent feeding on fruits, sun bears were still observed to feed on fruits on $43.3 \pm 6.0\%$ of days that observation were carried out ($N = 711$ days).

We directly observed 568 fruit feeding events during which bears fed on at least 58 different fruit species of 30 genera and 20 families (Appendix 2). Plants of 62 fruit-feeding events remained unidentified. Sun bears mainly fed on fruits that had dropped to the forest

floor, and trees were only climbed in 25.4% of fruit-feeding events (144 of 568). Average diameter of trees climbed by sun bears for fruit feeding was 33.6 cm d.b.h. (range 5–150 cm). The three main genera observed to be fed upon during direct observations almost make up 50% of fruit feeding time (Appendix 1).

Several fruit species which rank high in occurrence from scats, especially mast fruiting species, were not observed to be fed upon during direct observations (Appendix 1) because the observation period did not cover the masting events. The genus *Litsea* (Lauraceae) ranks fourth in frequency during direct observations but was rarely found in scats. This is probably due to the fact that seeds from these fruits are soft and were probably destroyed during feeding, with few remains of *Litsea* spp. identified in scats. Fruits of the palm *B. borneensis* were relatively frequently observed to be fed upon by the bears (ranking ninth), although this primarily constituted of chewing on the fibres which surround the extremely hard endocarp. In scats, fibres would occasionally be encountered which, in most cases, remained unidentified. The total number of different fruit species fed upon by sun bears, from both scats and observations combined, was at least 115, belonging to 54 genera in 30 families (Appendix 2).

FRUIT RESOURCES IN RELATION TO TOPOGRAPHICAL TYPES

Fruit feeding observations were found unevenly distributed over topographical types when looking at their relative availability ($\chi^2 = 476.6$, d.f. = 4, $P < 0.001$). More fruit-feeding was observed in swamp ($\chi^2 = 429.5$, d.f. = 1, $P < 0.001$) compared to the other topographical types combined, and significantly less fruit feeding observations in slope habitat ($\chi^2 = 106.1$, d.f. = 1, $P < 0.001$) than expected. Actual fruiting events by sun bear fruit trees, derived from the ten 0.1-ha phenology plots, were also found unequally distributed among topographical types ($\chi^2 = 35.1$, d.f. = 4, $P < 0.001$), with more fruiting events in swamp ($\chi^2 = 13.1$, d.f. = 1, $P < 0.001$) and ridge topographical type ($\chi^2 = 11.6$, d.f. = 1, $P < 0.001$) compared to all other topographical types combined, and less fruiting events in high-flat topographical type ($\chi^2 = 10.4$, d.f. = 1, $P < 0.01$) than expected (Table 2).

The distribution of fruit feeding observations in relation to actual fruiting events (fruit production) in the different topographical types was also unequally distributed ($\chi^2 = 417.9$, d.f. = 4, $P < 0.001$). Despite a high number of fruiting events, ridge topographical type was significantly less used ($\chi^2 = 206.9$, d.f. = 1, $P < 0.001$) compared to all other topographical types combined. More fruit feeding observations where

Table 2. Chi-square test results of the distribution of sun bear fruit feeding observations and fruiting events of sun bear fruit trees in relation to availability of topographical types

Topographical types	Availability topographical types (% \pm SD)	Sun bear fruit trees [†] (no. of fruit trees)	Fruiting events sun bear fruit trees [‡]		Fruit feeding observations [§]		
			No. of fruiting events	χ^2	No. of obs	χ^2 (FFO vs. FE)	χ^2 (FFO vs. ATT)
Swamp	5.9 \pm 4.6	40	42	** >	150	* >	* <
Alluvial	17.3 \pm 4.0	39	21		125		* >
High-flat	24.8 \pm 9.3	14	11	* <	136		** >
Slope	45.3 \pm 9.1	28	13		135	* <	** >
Ridge	6.7 \pm 2.7	23	41	** >	22		** <
Total		144	128		568		

^aNumber of sun bear fruit trees in ten 0.1-ha phenology plots (0.2 ha per topographical type); ^bnumber of fruiting events from sun bear trees in phenology plots between January 1998 to July 2002; ^cnumber of fruit feeding observations during 711 days of observations.

FFO, fruit feeding observations; ATT, availability of topographical types; FE, fruiting events; >, more than expected; <, less than expected.

* $P < 0.01$; ** $P < 0.001$.

observed in high-flat ($\chi^2 = 170.4$, d.f. = 1, $P < 0.001$) and slope habitat ($\chi^2 = 115.3$, d.f. = 1, $P < 0.001$) than expected from the number of actual fruiting events (Table 2).

DISCUSSION

Fruiting phenology in Sungai Wain was highly aseasonal and fluctuated largely between years. The majority of reproductive fruit trees used by sun bears displayed a supra-annual or mast fruiting pattern, indicating that fruit production by species occurring in the diet of the sun bear is irregular and consists of a short boom and prolonged bust situation. Two mast fruiting events that occurred during the 53 months of observations were spaced 4 years apart, falling well in the ~2–10-year interval that has been reported for other sites in South-east Asia (Medway, 1972; Appanah, 1985; Ashton *et al.*, 1988; Curran & Leighton, 2000; Wich & van Schaik, 2000; Sakai, 2002; Marshall, 2004). During the two masting events 15.7% and 10.3% of trees, respectively, produced fruits. This coincides with the figure reported by Sakai *et al.* (1999) for 'general flowering' when > 10% of individuals under observation were flowering in Sarawak (Malaysian Borneo).

A combination of exhausted energy reserves from mast fruiting species, and possibly disrupted fruiting patterns of intermast fruit resources, resulted in a prolonged period of fruit scarcity. Fruit production slowly built up over 4 years to the second masting event. Both masting events took place during ENSO episodes (NOAA-CIRES, 2003). The strong influence

of ENSO events in East Kalimantan can also be witnessed from prolonged droughts and associated forest fires that repeatedly affect the region (Leighton & Wirawan, 1986; Hoffmann, Hinrichs & Siegert, 1999; Siegert *et al.*, 2001). No temperature drop, proposed as a potential trigger for general flowering (Ashton *et al.*, 1988; Yasuda *et al.*, 1999), was observed in the ~2 months preceding general flowering in 2001, indicating that other factors probably play a role in the onset of mass-flowering (Corlett & LaFrankie, 1998).

Over the ~5-year study period, sun bears were found to feed on a large variety of fruits (115 species). Although 60% of scats collected contained fruit remains, sun bears were found to spend only 10% of their feeding time on fruits during direct observations. The remainder of feeding time was spent on invertebrates. This discrepancy could be due to two factors. First, decay rates of scats containing primarily insect remains are much quicker than those containing fruit remains. Insect scats disappear within 24 h due to dung beetle activity, whereas fruit scats remain visible up to 3 weeks (G. M. Fredriksson unpubl. data). This indicates that studying the diet of sun bears based on faecal analysis alone could strongly bias the results towards frugivory. On the other hand, most fruits are large compared to insects and during a short fruit foraging session large quantities of fruits can be consumed, the remains of which can be expelled in several scats.

During mast fruiting events, sun bears were found to be almost purely frugivorous. Mast fruiting species fed upon by sun bears produce succulent fleshy fruits and are probably important in the ecology of sun bears

for building up energy reserves or restoring lost energy reserves for the prolonged intermast periods when few fruit resources are available. The main sun bear mast fruit genera (*Durio* spp., *Dacryodes* spp., and *Artocarpus* spp.) have high energy, protein, fat, and potassium values (Voon & Kueh, 1999). The ability to store large amounts of energy as fat to survive periods of food shortages is well developed in bear species living in temperate regions, where bears hibernate during winter. Orangutans, which occur sympatrically with sun bears throughout much of the lowland forests in Sumatra and Borneo, have substantial dietary overlap with sun bears (Galdikas, 1988; Leighton, 1993; Knott, 1998; G. M. Fredriksson, unpubl. data), at least on Borneo. Orangutans in West Kalimantan were found to gorge themselves during a masting event on nondipterocarp fruits and consumed two- to three-fold the amount of calories needed for daily energy requirements, putting on fat reserves (Knott, 1998). Subsequently, during the intermast period, orangutans were living off these stored reserves and losing weight (Knott, 1998). Sun bears in East Borneo appear to be seriously affected by prolonged fruit scarcity with potentially elevated mortality due to predation (Fredriksson, 2005) or starvation (G. M. Fredriksson, unpubl. data; Wong *et al.*, 2005). Most of the mast species consumed by sun bears and orangutans are higher in caloric content than non-mast fruits (Leighton, 1993; Knott, 1998; Voon & Kueh, 1999; G.M. Fredriksson, unpubl. data). This might explain why intermast species were not consumed by bears during the mast period, even though many of these also produced larger crops during general masts.

Densities of large strangling figs in Sungai Wain are low, but small hemi-epiphytic figs, producing minor fruit crops, are relatively abundant (G. M. Fredriksson unpubl. data). Despite the scarcity of large stranglers, figs were the most commonly consumed fruit genus by sun bears during the prolonged intermast period, witnessed both from scats and direct observations. Although figs are low in overall energy value compared to many of the mast fruit species, they contain high protein and calcium values (O'Brien *et al.*, 1998; Voon & Kueh, 1999). Figs also displayed the most random fruiting pattern and were the most frequently available fruit genus. Probably due to the combination of these factors, figs appear to be one of the main fallback fruit resources for sun bears, as for a variety of other wildlife in the South-east Asia (Leighton & Leighton, 1983; van Schaik, 1996; Sugardjito & te Boekhorst, van Hooff Jaram, 1987; Kinnaird, O'Brien & Suryadi, 1999). Figs are also encountered in the diet of several other bear species inhabiting (sub)tropical regions (e.g. sloth bear *Melursus ursinus*, Joshi, Garshelis & Smith, 1997; Asiatic black bear *Ursus thi-*

betanus, Hwang, Garshelis & Wang, 2002; spectacled bear *Tremarctos ornatus*, Peyton, 1980).

In the first year after the strong ENSO, few scats with fig remains were encountered even though fruiting by all other intermast species was negligible. An increase in fig consumption was only observed after May 1999 (13 months after the ENSO event). Monitoring of fig phenology commenced in June 1999, after which fig fruits appeared available on a continuous basis. Harrison (2001) reported that flower and fruit production of dioecious figs decreased or even ceased after the 1997–98 ENSO drought in Sarawak (Malaysian Borneo). Under normal conditions, figs produce fruits all year round to maintain species-specific pollinator relationships with fig wasps which have a short live span (Harrison, 2001; Shanahan *et al.*, 2001). Fig wasps became locally extinct after the ENSO event and, for some fig species, took more than 2 years to recover (Harrison, 2001). Although monoecious figs in Sarawak did not suffer extinction of pollinators, Harrison (2001) found that pollination rates were lower after the ENSO drought for some of these (e.g. *Ficus benjamina*). It is therefore possible that sun bears hardly consumed figs in the first year after the ENSO event because simply fewer fig fruits were available.

Fruit production of *T. glabra*, another important intermast fruit resource, also appeared disrupted after the (1998) ENSO event. This species normally produces fruit all year round (Soerianegara & Lemmens, 1993) but, after the 1998 mast, *T. glabra* only became available again in early 2000. Although *T. glabra* featured in only 8% of fruit scats, most large trees of this species in Sungai Wain are covered with multiple-age claw marks, indicating frequent and repeated usage by sun bears. *Tetramerista glabra* has been identified as an important fruit species during lean periods for orangutans (Singleton & van Schaik, 2001) and bearded pigs (Curran & Leighton, 2000).

During the initial period post-ENSO, when fruits like *Ficus* and *T. glabra* were virtually absent, various fruits from the Palmae family featured in the bear diet. Although few palms were included in the monthly phenology, our general observations suggested that many species in the palm family displayed a continuous fruiting pattern. Many fruits in the Palmae family are rich in oils and carbohydrates and have been found to be important food for primates in South-east Asia during food lean periods (Lucas & Corlett, 1991). Fruits of the ginger *H. cf. reticulata* started appearing in the diet after 2001. Densities of this ginger species increased substantially in later stages of the study (G. M. Fredriksson, pers. obs.), probably due to increased light conditions at the forest floor level, following elevated mortality of large trees after the 1998 ENSO drought (van Nieuwstadt, 2002).

Acorns (*Lithocarpus* spp. and *Quercus* spp. Fam. Fagaceae), popular in the diet of several other bear species (Asiatic black bear: Huygens & Hayashi, 2001; Hwang *et al.*, 2003; American black bear *Ursus americanus*, Inman & Pelton, 2002) were rarely encountered in the diet of sun bears at this lowland site, despite a relatively high density of these genera. On the other hand, half of the scats collected in the mountainous interior of Borneo during other surveys, contained acorn remains (G. M. Fredriksson, unpubl. data), in accordance with the statement by Davies & Payne (1982: 91) noting that sun bears 'feed on large quantities of the hard seeds of the Fagaceae family'. It is possible that sun bears living at higher elevations feed more on oaks because densities of species with succulent fruits decrease rapidly at higher altitudes (Djojosedharmo & van Schaik, 1992), whereas Fagaceae increase in density (Pendry & Proctor, 1997).

Interestingly, sun bears were found feeding more on fruits in high-flat forest type, compared to other topographical types, despite lower fruit production. This could be due to sun bears using this forest type more intensively because insect food resources reach higher densities in this drier forest type (G. M. Fredriksson unpubl. data). Sun bears focus on the more stable invertebrate food resource during the intermast period, opportunistically feeding on fruits encountered when foraging for insects, making the overall foraging strategy more efficient. Conversely, sun bears spent less time feeding on fruit resources in ridge topographical types despite the fact that fruit productivity was higher than expected. Ridge tops are disproportionately used by humans for travel through the forest. In Sumatra, Griffiths & van Schaik (1993) found that sun bears switched to a more nocturnal activity pattern in areas of high human usage and, although at this study site, sun bears remained diurnal (G. M. Fredriksson unpubl. data), it is possible they spatially avoided this topographical type due to higher levels of human passage.

Overall at this lowland study site, three plant families [Moraceae (26%), Burseraceae (19%), and Myrtaceae (9%)] made up more than 50% of the sun bear fruit diet throughout the study period. The density and distribution of these genera could be a contributing factor to regional differences in sun bear densities, and conservation of fruit trees from these genera should be incorporated in forest management practices because they contribute disproportionately to the diet of sun bears.

To obtain a comprehensive picture concerning which fruit resources are important in the diet of sun bears, it is essential to carry out long-term observations, taking into account the multiyear phenological cycles observed in Sundaic forests. The proportional representation of various food items depended heavily on

the overall phenological status of the forest during the sampling period. During the initial stages of the present study, it appeared that sun bears were pure frugivores, although sun bears would have appeared primarily insectivorous if the study had commenced several months later.

From the present analysis, a picture emerges of the general feeding ecology of sun bears. They are adaptable and easily switch to more nutritious resources whenever these become available, whereas they appear to be able to effectively store fat and thus survive during periods of low food availability. Sun bears share these traits with other large frugivores and omnivores in island south-east Asia, such as the orangutan (Leighton & Leighton, 1983; Knott, 1998) and bearded pig (Caldecott, 1988). We speculate that these species have evolved these traits in response to the specific ecological challenges posed by an environment dominated by supra-annual periods of low food availability interspersed by brief periods of glut. To test this idea, it is interesting to compare the evolution of sun bears with its nearest relatives in mainland south-east Asia, where such intra-annual cycles are less dominant.

The taxonomic classifications and phylogenetic relationships within the Ursidae remain subject to controversies. The main problem being that the family Ursidae represents a typical example of rapid evolutionary radiation and recent speciation events, dating back to mid-Miocene, approximately 6–8 Mya (Kurtén, 1968; Goldman, Giri & O'Brien, 1989; Talbot & Shields, 1996; Waits *et al.*, 1999; Yu *et al.*, 2004). Previous phylogenetic studies placed the sun bear as a sister taxon to the youngest diverging clade, containing brown bears and polar bears (Talbot & Shields, 1996; Waits *et al.*, 1999). A more recent analysis, based on nuclear DNA (Yu *et al.*, 2004) and morphology (Sacco & van Valkenburgh, 2004) provides strong support for the sun and sloth bear being sister taxa. This appears to be more reasonable from a morphological standpoint, with the sloth bear and sun bear being Asian subtropical or tropical species and markedly distinguished from other bears, including the sympatric Asiatic black bear, by their morphological and behavioural specializations that are likely due to recent adaptive change (Hall, 1981; Nowak & Paradiso, 1983; Goldman *et al.*, 1989).

The sun bear, which is the only bear species living in island south-east Asia, probably diverged between 4 and 2.5 Mya from the other species of south-east Asia (Talbot & Shields, 1996; Waits *et al.*, 1999). It remains unclear what caused the rapid split between these species, although Meijaard (2003, 2004b) hypothesized a vicariance model in which the ancestral sun bear became isolated in what is now Sundaland. By that time, the rising Himalayas had resulted in

increasing dry Asian climates and stronger monsoonal patterns, causing a change in the vegetation of this region (Morley, 2000). It is possible that, by the time sun bears evolved in Sundaland, they did so in an environment more and more affected by supra-annual fruiting patterns. Did these environmental conditions shape the present-day ecology of Bornean sun bears?

The closest relative of the sun bear, the sloth bear (Yu *et al.*, 2004), currently ranges from Nepal south through India and Sri Lanka and is the ursid species most specifically adapted to feeding on insects (Laurie & Seidensticker, 1977; Joshi *et al.*, 1997). Laurie & Seidensticker (1977) speculated that the sloth bear was able to enter the myrmecophagous niche because competitors that feed on insects are allopatric in the sloth bear habitat.

It might not have been an option for the sun bear to evolve into the insectivorous niche due to a number of sympatrically occurring myrmecophages (pangolins: *Manis* spp.), nor to evolve into a more carnivorous niche due to the presence of several more efficient feline competitors, and a relatively low prey biomass in south-east Asia (Meijaard, 2004a). Hence, the sun bear appears to have evolved more in the direction of primates; being agile in trees and able to access a variety of fruit resources when available, but also feeding substantially on insects, which are the most stable food resource in tropical forests (Kikkawa & Dwyer, 1992). The sun bear has evolved a combination of morphological adaptations that are able to exploit these two main food resources in the tropical rainforest. Some of these are useful for tree climbing, such as small body size (weight between 27 and 65 kg; Lekagul & McNeely, 1977), extremely long claws, naked soles, flattened chest, and strongly inward curving feet (Pocock, 1941). Several physical features are indicative of insect feeding, such as the longest tongue among the ursids, mobile lips, a nearly naked snout, huge canines (practical for opening hardwood in search for insects), and exceptionally large paws comparative to body size that are useful for digging up termites and ants, as well as breaking into logs. They are thus well adapted to use a wide variety of resources in different feeding strata. Additionally, the Bornean sun bear is significantly smaller than the Sumatran or Malaysian/mainland sun bear (Meijaard, 2004b), and this is possibly another adaptation linked to evolution in the most nutrient poor part of Sundaland (MacKinnon *et al.*, 1996). All of these factors combined make the evolution of sun bears in the typical Sundaic environment a likely scenario.

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APPENDIX 1

Main sun bear fruit taxa from faecal analyses ($N = 1209$, October 1997 to June 2002) and direct observations ($N = 4977$ h, October 1998 to April 2001).

Faecal analyses	Family	%	Feeding observations	Family	%
<i>Ficus</i> spp.	Moraceae	23.2	<i>Ficus</i> spp.	Moraceae	17.6
<i>Syzygium</i> spp.	Myrtaceae	11.8	<i>Syzygium</i> spp.	Myrtaceae	17.3
<i>Santiria</i> spp.	Burseraceae	11.2	<i>Santiria</i> spp.	Burseraceae	14.2
<i>Dacryodes rugosa</i> *	Burseraceae	10.3	<i>Litsea</i> sp.	Lauraceae	6.4
<i>Tetramerista glabra</i>	Tetrameristaceae	8.1	<i>Rattan</i> spp.	Palmae	6.4
<i>Polyalthia</i> spp.	Annonaceae	7.4	<i>Monocarpia kalimantanensis</i>	Annonaceae	5.8
<i>Oncosperma horridum</i>	Palmae	6.9	<i>Oncosperma horridum</i>	Palmae	5.5
<i>Artocarpus integer</i> *	Moraceae	5.8	<i>Tetramerista glabra</i>	Tetrameristaceae	4.0
<i>Cryptocarya</i> sp.	Lauraceae	2.3	<i>Borassodendron borneensis</i>	Palmae	2.8
<i>Hornstedtia cf reticulata</i>	Zingiberaceae	2.3	<i>Polydarpus</i> sp.	Palmae	2.6
<i>Monocarpia kalimantanensis</i>	Annonaceae	2.3	<i>Diospyros</i> spp.	Ebenaceae	1.2
<i>Dacryodes rostrata</i> *	Burseraceae	2.1	<i>Cryptocarya</i> sp.	Lauraceae	1.0
<i>Artocarpus anisophyllus</i> *	Moraceae	2.0	<i>Garcinia</i> spp.	Guttiferae	0.9
<i>Durio dulcis</i> *	Bombacaceae	1.8	<i>Polyalthia</i> spp.	Annonaceae	0.8
<i>Durio oxleyanus</i> *	Bombacaceae	1.8	<i>Knema</i> sp.	Myristicaceae	0.8
<i>Rattan</i> spp.	Palmae	1.7	<i>Mangifera</i> spp.	Anacardiaceae	0.8
<i>Baccaurea</i> spp.	Euphorbiaceae	1.6	<i>Baccaurea</i> spp.	Euphorbiaceae	0.8
<i>Artocarpus nitidus</i>	Moraceae	1.4	<i>Lithocarpus gracilis</i>	Fagaceae	0.7
<i>Garcinia</i> spp.	Guttiferae	1.4	<i>Aglaiia</i> sp.	Meliaceae	0.6
<i>Mangifera</i> spp.	Anacardiaceae	1.3	<i>Barringtonia</i> sp.	Euphorbiaceae	0.4

*Mast-fruiting species; percentages indicate percentage of faecal samples containing a particular taxon, or percentage of fruit feeding time spent on a taxon; 'Rattan' incorporates several genera.

APPENDIX 2

Overall list of plant species occurring in the diet of the sun bear (faecal analyses and observations) in Sungai Wain between October 1997 to July 2002

Species	Family	Scat/observation*	Part eaten	Growth form
<i>Aglaiia</i> sp.	Meliaceae	S	fr	Tree
<i>Alangium ridley</i>	Alangiaceae	S	fr	Tree
<i>Annonaceae</i> sp. 1	Annonaceae	S/O	fr	Liana
<i>Annonaceae</i> sp. 2	Annonaceae	S/O	fr	Liana
<i>Artocarpus anisophyllus</i>	Moraceae	S/O	fr	Tree
<i>Artocarpus dadah</i>	Moraceae	S/O	fr	Tree
<i>Artocarpus integer</i>	Moraceae	S/O	fr	Tree
<i>Artocarpus nitidus</i>	Moraceae	S/O	fr	Tree
<i>Artocarpus</i> sp. 1	Moraceae	O	fr	Tree
<i>Artocarpus</i> sp. 2	Moraceae	O	fr	Tree
<i>Baccaurea bracteata</i>	Euphorbiaceae	S/O	fr	Tree

APPENDIX 2 *Continued*

Species	Family	Scat/observation*	Part eaten	Growth form
<i>Baccaurea macrocapra</i>	Euphorbiaceae	S/O	fr	Tree
<i>Baccaurea</i> sp. 1	Euphorbiaceae	S	fr	Small tree
<i>Barringtonia</i> sp. 1	Lecythidaceae	O	flo	Small tree
<i>Borassodendron borneensis</i>	Palmae	S/O	fr, flo	Big palm
<i>Calamus</i> sp. 1	Palmae	S/O	fr	Rattan palm
<i>Calamus</i> sp. 2	Palmae	S/O	fr	Rattan palm
<i>Crypteronia</i> sp.	Crypteroniaceae	S/O	fr	Tree
<i>Cryptocarya</i> sp.	Lauraceae	S/O	fr	Tree
<i>Dacryodes rostrata</i>	Burseraceae	S/O	fr	Tree
<i>Dacryodes rugosa</i>	Burseraceae	S/O	fr	Tree
<i>Daemonorops</i> sp. 1	Palmae	S/O	fr	Rattan palm
<i>Dehaasia</i> sp.	Lauraceae	S/O	fr	Tree
<i>Dialium indum</i>	Caesalpiniaceae	S/O	fr	Tree
<i>Diospyros</i> sp. 1	Ebenaceae	S/O	fr	Tree
<i>Diospyros</i> sp. 2	Ebenaceae	S/O	fr	Tree
<i>Diospyros</i> sp. 3	Ebenaceae	S/O	fr	Tree
<i>Durio dulcis</i>	Bombacaceae	S	fr	Tree
<i>Durio graveolens</i>	Bombacaceae	S	fr	Tree
<i>Durio lanceolata</i>	Bombacaceae	S/O	fr	Tree
<i>Durio oxleyanus</i>	Bombacaceae	S/O	fr	Tree
<i>Dysoxylum</i> sp.	Meliaceae	S	fr	Tree
<i>Eugenia polyanthe</i>	Myrtaceae	S/O	fr	Small tree
<i>Ficus benjamina</i>	Moraceae	S/O	fr	Strangler
<i>Ficus lowii</i>	Moraceae	O	fr	Small tree
<i>Ficus</i> sp. 1	Moraceae	O	fr	Strangler
<i>Ficus</i> sp. 2	Moraceae	S/O	fr	Strangler
<i>Ficus</i> sp. 3	Moraceae	O	fr	Strangler
<i>Ficus</i> sp. 4	Moraceae	O	fr	Strangler
<i>Ficus</i> sp. 5	Moraceae	O	fr	Strangler
<i>Ficus</i> sp. 6	Moraceae	O	fr	Tree
<i>Garcinia mangostana</i>	Guttiferae	S/O	fr	Tree
<i>Garcinia parvifolia</i>	Guttiferae	S/O	fr	Tree
<i>Garcinia</i> sp. 1	Guttiferae	S/O	fr	Tree
<i>Glochidion</i> sp.	Euphorbiaceae	S	fr	Tree
<i>Hornstedtia</i> cf <i>reticulata</i>	Zingiberaceae	S	fr	Undergrowth
<i>Horsfieldia</i> sp.	Myristicaceae	S/O	fr	Tree
<i>Ilex</i> sp.	Aquifoliaceae	S	fr	Tree
<i>Knema laterica</i>	Myristicaceae	S/O	fr	Tree
<i>Knema</i> sp. 1	Myristicaceae	S/O	fr	Tree
<i>Korthalsia</i> sp. 1	Palmae	S/O	fr	Rattan palm
<i>Korthalsia</i> sp. 2	Palmae	S/O	fr	Rattan palm
<i>Lansium domesticum</i>	Meliaceae	S	fr	Tree
<i>Licuala spinosa</i>	Palmae	O	fr, lb, flo	Undergrowth
<i>Lithocarpus gracilis</i>	Fagaceae	S/O	fr	Tree
<i>Lithocarpus</i> sp. 1	Fagaceae	S/O	fr	Tree
<i>Litsea angulata</i>	Lauraceae	S/O	fr	Tree
<i>Litsea</i> sp. 1	Lauraceae	S/O	fr	Tree
<i>Litsea</i> sp. 2	Lauraceae	S/O	fr	Tree
<i>Madhuca kingiana</i>	Sapotaceae	S/O	flo	Tree
<i>Magnoliaceae</i> sp. 1	Magnoliaceae	O	fr	Tree
<i>Magnoliaceae</i> sp. 2	Magnoliaceae	O	fr	Tree
<i>Mangifera caesia</i>	Anacardiaceae	O	fr	Tree
<i>Mangifera foetida</i>	Anacardiaceae	O	fr	Tree
<i>Mangifera</i> sp. 1	Anacardiaceae	O	fr	Tree

APPENDIX 2 *Continued*

Species	Family	Scat/observation*	Part eaten	Growth form
<i>Mangifera torquenda</i>	Anacardiaceae	O	fr	Tree
<i>Marantaceae</i> sp.	Marantaceae	O	lb, flo	Undergrowth
<i>Microcos</i> sp.	Tiliaceae	S/O	fr	Tree
<i>Monocarpia kalimantanensis</i>	Annonaceae	S/O	fr	Tree
<i>Nephelium</i> sp.	Sapindaceae	S/O	fr	Tree
<i>Oncosperma horridum</i>	Palmae	S/O	fr, flo	Palm
<i>Palaquium</i> sp.	Sapotaceae	S/O	fr	Tree
<i>Pandanus</i> sp. 1	Pandanaceae	O	lb, fr	Undergrowth
<i>Pinanga</i> sp.	Palmae	O	lb, fr	Small palm
<i>Polyalthia</i> sp. 1	Annonaceae	S/O	fr	Tree
<i>Polyalthia</i> sp. 2	Annonaceae	S/O	fr	Tree
<i>Polydocarpus</i> sp.	Palmae	S/O	fr	Palm
<i>Pternandra</i> sp.	Melastomataceae	S/O	fr	Small tree
<i>Quercus argentata</i>	Fagaceae	S/O	fr	Tree
<i>Quercus</i> sp. 1	Fagaceae	S/O	fr	Tree
<i>Santiria oblongifolia</i>	Burseraceae	S/O	fr	Tree
<i>Santiria tomentosa</i>	Burseraceae	S/O	fr	Tree
<i>Sida</i> sp.	Malvaceae	S	fr	Shrub
<i>Syzigium tawahense</i>	Myrtaceae	O	fr	Tree
<i>Syzigium</i> sp. 1	Myrtaceae	S/O	fr	Tree
<i>Syzigium</i> sp. 2	Myrtaceae	S/O	fr	Tree
<i>Syzigium</i> sp. 3	Myrtaceae	S/O	fr	Tree
<i>Tetramerista glabra</i>	Tetrameristaceae	S/O	fr	Tree
<i>Uvariastrum</i> sp.	Annonaceae	S/O	fr	Liana
<i>Walsura</i> sp. 1	Meliaceae	S/O	fr	Tree
<i>Willughbeia angustifolia</i>	Apocynaceae	S/O	fr	Liana
<i>Xerospermum norhonianum</i>	Sapindaceae	S/O	fr	Tree
<i>Xerospermum</i> sp. 1	Sapindaceae	S/O	fr	Tree
Unidentified	(22 different species)	S/O	fr	

Total species = 115. Total genera = 54. Total families = 30.

*S, encountered in scats; O, direct feeding observation; S/O, encountered both in the diet from scats and observations; fr, fruit; flo, flower; lb, leafbase/pith.