CHAPTER IV

THE EFFECTS OF FAMINE ON MALAYAN SUN BEARS AND BEARDED PIGS IN LOWLAND TROPICAL FOREST OF SABAH, MALAYSIAN BORNEO

ABSTRACT

We observed a period of famine in the lowland tropical rainforest of Sabah, Malaysia from August 1999 to October 2000. All six Malayan sun bears that were captured and radio-collared were in poor physical condition, and two were later found dead. The physical condition of bearded pigs that were captured, observed, or photographed by camera traps also revealed that the pigs were in various stages of emaciation and starvation. We surmise that the famine resulted from prolonged scarcity of mass fruiting in the study area. The phenomena of emaciated animals and fruit scarcity have also been reported from other areas of Borneo. Lowland tropical rainforest trees of Borneo display supra-annual synchronized mass fruiting. We believe that the starvation we observed and the generally low density of large animals in Borneo forests is a consequence of a history of prolonged food scarcity during non-mass fruiting years.

INTRODUCTION

The Malayan sun bear (*Helarctos malayanus*) is the smallest of the eight living bear species. Adults are about 120 to 150 cm long and weigh 27 to 65 kg (Stirling 1993). They were originally found in the dense forest of Bangladesh, Myanmar, Thailand, Laos, Kampuchea, Vietnam, Southern China, Peninsular Malaysia, and the islands of Sumatra and Borneo (Stirling 1993). They remain the least known bear species in the world and one of the most neglected large mammal species in Southeast Asia (Servheen 1999). Even basic biological facts such as food habits, home range size, and reproductive biology are poorly known. The diet of Malayan sun bears includes beetles, beetle larvae, termites, bees' nests and wild fruits (Wong et al. in press). Davies and Payne (1982) report that sun bears are found throughout dipterocarp and lower montane forests of Sabah, Malaysia from 0 to 1350 m in elevation, but are common nowhere.

In contrast to sun bears, the bearded pig (*Sus barbatus*) is still widespread throughout Borneo but is declining (Caldecott et al. 1993). Adults are 120 cm to 152 cm long and usually weigh 57-83 kg, or up to 120 kg or more when in good condition (Payne et al. 1985). Although they occur in Peninsula Malaysia, Sumatra, Borneo, Palawan and neighboring islands, and in the Philippines (Payne et al. 1985), the species is rare except in Borneo (Caldecott et al. 1993). Bearded pigs are known to migrate over considerable distances in Sarawak and East Kalimantan to follow the harvest of illipe nuts (*Shorea* spp.) (Caldecott and Caldecott 1985; Caldecott 1988). The diet of bearded pigs includes fallen fruits and seeds, roots, herbs and other plant material, earthworms and other small animals (Payne et al. 1985). Bearded pigs are considered to be potential ecosystem "engineers," playing important roles as seed dispersers, seed predators, and agents of physical disturbance (Ickes and DeWalt 1999; Curran and Leighton 2000).

Malayan sun bears and bearded pigs are sympatric in the tropical rainforests of Borneo; these forests are well recognized as one of the most diverse ecosystems on earth. For instance, P. Ashton found 700 species of trees in 10 selected 1-ha plots in Borneo (in Wilson 1988), and Proctor et al. (1983) reported the above ground biomass from 1-ha plot of tropical forest in Mulu, Sarawak reached more than 500,000 kg/ha. This high biodiversity and biomass results from a stable climate, with high solar radiation, temperature, rainfall, and humidity (Huston 1994; Richards 1996). Unlike temperate and artic regions with distinct growing seasons for plants, the rainforests of Borneo lack distinct seasonality and thus give a general superficial impression of constant food abundance and even surplus for wildlife communities that live in the forest. However, many tropical rainforests experience seasonally variable fruit production that influences mammalian frugivore and granivore communities dependent on such forests. These influences range from reduction in numbers and population size (Kaufmann 1962; Milton 1982; Milton 1990; Wright et al. 1999), changes in home range size (Judas and Henry 1999), seasonal movement and nomadic behavior (Kiltie and Terborgh 1983; Caldecott and Caldecott 1985; Caldecott 1988; Bodmer 1990), and to extreme cases, mass starvation, extreme famine, and even mass mortality (Kaufmann 1962; Foster 1982; Milton 1982; Wright et al. 1999).

In this paper, we report on a famine period in a lowland tropical rainforest of Borneo where we observed emaciated and dying Malayan sun bears and bearded pigs during a three-year field study on the biology and ecology of the Malayan sun bear. Information on bearded pigs was collected as peripheral data during this sun bear project.

STUDY AREA

This study was conducted between May 1998 and December 2000 at the Ulu Segama Forest Reserve situated on the eastern side of the Malaysian state of Sabah, island of Borneo (Figure 1) ($4^0$57’40”N $117^0$48’00E, 100-1200 m elevation). The reserve encompasses both forests that were selectively logged by the Sabah Foundation on a 100-year timber license, and primary forest including the 43,800 ha Danum Valley Conservation Area (Marsh and Greer 1992). The area has been used as a research site since 1985 to study the ecology of tropical forest flora and fauna and the effects of logging on various ecosystem components (Marsh and Greer 1992). Lowland, evergreen dipterocarp forest comprises about 91% of the conservation area; the remaining area is lower montane forest (Marsh and Greer 1992). Lower montane forest extends from 750 to 1500 m and differs from lowland rainforest in that it has a lower canopy with fewer, smaller emergent trees (Whitmore 1984). Approximately 88% of the total volume of large trees in the conservation area are dipterocarps (Marsh and Greer 1992).

The Danum Valley Conservation Area is surrounded by approximately one million hectares of selectively logged forest. Logging follows the Monocyclic Unit System (Poore 1989) with a 60-year rotation. It involves harvesting all healthy, commercially valuable tree species with a diameter at breast height (dbh) > 60 cm occurring on slope of < 20^o (Marsh 1995). Both conventional tractor logging and overhead cable techniques are used on moderate terrain and steeper slopes. Studies on the impacts of this logging method show that a harvesting of 3-7% of the trees with > 60 cm dbh (translates to 8-18 trees ha^{-1}) destroys over 50% of the trees > 30 cm dbh by logging and road building processes (Wilson and Wilson 1975; Johns 1985, 1988, 1992). Timber extraction rates in the Ulu Segama Forest Reserve are typically high, averaging 118 m^3ha^{-1} over the period 1970-90, with a range of 73-166 m^3ha^{-1} between different logging areas (Marsh and Greer 1992) (this compares to the extraction level of 8.4 and 13.5 m^3ha^{-1} in Neotropical and African rainforests: Yeom 1984). This number represents the removal of about 8 trees ha^{-1} during the logging operation: less than the average extraction rate of 12-15 trees ha^{-1} typical in the rest of Malaysia (Marsh 1995). Compared with other selectively logged forests in Sabah and Malaysia, some parts of the logged forests in the study area can be considered as “good quality” forest, due to relatively lower extraction rates and less human disturbance (such as illegal logging).

When logging is complete in an area, a mosaic of vegetation types remaining, from relatively undisturbed forest, through forested area dominated by pioneer trees, such as *Macaranga, Octomeles, Neolamarkia* and *Duabanga*, to more open area of grasses, ferns, vines, and climbing bamboo (*Dinochloa* spp.), and finally to exposed and compacted mineral soil with little or no vegetation (Willott 2000). These successional forest mosaics have a tendency to increase total biodiversity. In a 1 ha study on floristic composition and forest structure of both primary and logged forest in the study area, Ahmad (2001) found a higher species richness at the family, genus, and species level in a 10-year old logged forest than in primary forest. Another similar floristic composition of 4 ha of primary and 10-year old logged forest in the study area revealed higher species richness in primary sites than logged forest sites (291 for primary forest and 274 for logged forest) (Hussin 1994). In general, primary forests are characterized by a taller (45 m compared to 15 m), more well-developed, and less open upper canopy (5.3% compared to 10.7%) than logged forest (Ahmad 2001; Willott 2000). Logged forests, on the other hand, are usually covered by dominant species of certain trees like *Macaranga* and *Mallotus* with abundant vine covers, climbers, and herbs, notably *Melastomata*, *Piper*, and many ginger species (Ahmad 2001). Hussin (1994) reported that the total fruiting frequency of all trees in primary forest was significantly higher than in logged forest. During a mass fruiting in the study area in September 1990, fruit production was clearly higher in the primary forest than in the logged forest (Hussin 1994).

Fig trees are not a synchronous mass fruiting species and can fruit at any time during the year. There are more fig trees in primary forests than logged forests in Ulu Segama Forest Reserve (3 individuals/ha in primary forest compared to 1.75 individuals/ha in logged forest) (Hussin 1994) and Sungai Tekan Forest Concession, West Malaysia (Johns 1983). Figs are an important food source of Malayan sun bear and bearded pigs (Wong et al. in press).

The climate of Ulu Segama Forest Reserve is weakly influenced by two monsoons (Marsh and Greer 1992), but influenced by the El Nino Southern Oscillation (ENSO) events that were recorded during 1986-87, 1991-92, and 1997-98. Annual rainfall and monthly rainfall at Danum Valley Field Center (DVFC) (located within Ulu

Segama Forest Reserve and the center of the field effort) is, on average 2700 mm and 230 mm, respectively (unpubl. station records 1986-2000 by Royal Society SE Asia Rainforest Research Program: Hydrology Project [University of Manchester, University of Wales Swansea, University of Lancaster, University Malaysia Sabah]), with the wettest period between October and January and the dry period between July and September. Figure 2, Figure 3 and Figure 4 shows total monthly rainfall from 1997 to 2000, total monthly rainfall from 1986-2001, and annual rainfall from 1986 to 2000, respectively. Mean daily temperature at the field center during 1999-2000 was 26.7^{o} C. Soils in the reserve include ultisols, inceptisols and alfisols (Newbery *et al*. 1992; Marsh and Greer 1992).

The study area was concentrated in approximately 150 km^2 of approximately 60% logged and 40% unlogged forest adjacent to the DVFC (Figure 5). Primary unlogged forest could be found in the 48,000 ha conservation area and the water catchment area of the field center. Logged forest consisted of different logging coupes or cutting units, from which timber was extracted between 1981 and 1991. The elevation in the study area ranged between 150 m and 600 m.

METHODS

The study was divided into two phases. Phase I was conducted from June to August 1998, and Phase II from January 1999 to December 2000. Phase I involved a preliminary survey of sun bear presence in both logged and unlogged forests, and a search for baits attractive to bears. The techniques in Phase I were necessary for the completion of Phase II. Phase II involved collecting information on the basic biology of sun bears through the capture and radio-tracking of animals in the forests.

Animal Capture

Techniques of animals capture and use of automatic cameras can be found in Wong et al. (in press). We used an aluminum culvert trap (Teton Welding and Machine, Choteau, Montana, U.S.A.) and three locally made 55-gal. barrel traps to capture sun bears. Trapping operations started on February 24, 1999 and ended on December 11, 2000. Each trap was equipped with a radio-transmitter that would begin transmitting signals once the trap's door was closed. Signals from the traps' transmitters were monitored several times each day. We checked the traps immediately after receiving these signals to minimize the holding time of captured animals in the traps. A variety of baits were used for trapping, but chicken entrails proven to be the most effective. Captured bears were immobilized with Zoletil (tiletamine HCL/ zolazepam HCL) (4 mg/kg of estimated body mass) (Virbac Laboratories, Carros, France) delivered with a jab stick. Each bear was fitted with a MOD-400 radio-collar transmitter (Telonics, Inc., Mesa, Arizona, U.S.A.), operating in the 150-151 MHz frequency range. Each collar weighed about 300 g, less than 2% of the bear's body mass, and were designed for 18 months of battery life. Animal handling procedures followed the approved University of Montana animal welfare protocol. Captured bearded pigs were not handled because they were a non-target species; bearded pigs were released immediately.

We located radioed bears using standard methods of ground-based triangulation (White and Garrott 1990) with a TR-4 receiver (Telonics, Inc., Mesa, Arizona, U.S.A.) and a hand held RA-14K directional antenna (Telonics, Inc., Mesa, Arizona, U.S.A.). Each location was taken from at least 2 different locations at approximately 90 degree angles from the bear's position within 30 minutes, or simultaneously taken by 2 people in 2-way radio contact. Bear locations were visited within 2-4 hours after coordinates were taken. Bears were also tracked on foot when possible at a distance so as to not disturb the bear; we examine activity sites soon after the bear left. At each radiolocation site, we looked for any feeding evidence, such as bear scats, feeding sites, and claw marks on trees. Thirty-two bear encounters in the forest within 300 m of the triangulated locations of radioed bears reinforced our confidence in accuracy. Sightings were also valuable opportunities to observe physical conditions of radioed bears. Another opportunity to examine the condition of radioed bears was when animals were recaptured. Except on one occasion, recaptured bears were released immediately on site without handling.

Camera trapping

Camera trapping is an effective tool to document not only the presence of animals (Bull et al. 1992; Gysel et al. 1956; Kucera and Barrett 1993), but also their behavioral ecology (Savidge and Seibert 1988; Picman and Schriml 1994), and activity periods (Dodge and Snyder 1960; Carthew and Slater 1991; Pei 1995), as well as for population estimates (Mace et al. 1994). Camera trapping is also an ideal system to collect information on elusive species in dense forest, such as Malayan sun bears (Griffiths and van Schaik 1993a & b; van Schaik and Griffiths 1996; Mudappa 1998; Karanth 1999; Franklin et al. 1999). In our study, camera trapping also served as an effective tool to monitor the physical condition of bears and pigs as the physical condition of individual animals can be clearly revealed from the photographs taken. We used ten camera traps from June to August 1998, and May 1999 to December 2000. Each camera unit consisted of a fully automatic (auto focus/advance/flash), weather-proof, point-and-shoot 35-mm Pentax 606 camera combined with a passive infrared motion and heat sensor designed specifically for detecting animals in the wild (Wildlife Research Laboratory, Department of Wildlife Conservation, National Pingtung University of Science and Technology, Taiwan R. O. C.). Sites for cameras were carefully chosen near areas of potential wildlife use, such as animal trails, water pools, mud wallows, and trap sites. A variety of baits such as chicken entrails, meat scraps, fishes, fruit, liver-oil, fruit extracts, honey, air refresher, etc. were used at most camera stations to attract animals to the camera stations.

We visually rated photographed bears and pigs subjectively into five different categories of physical condition. These categories ranged from very poor, poor, fair, good, and very good, based on the physical appearances of the animals. Physical appearances such as fur color, relative size of neck, body fat and muscle appearance, protruding zygomatic arch, scapulae, vertebral columns, ribs, and hipbones, were considered (Table 1).

Forest fruit production

Long-term monitoring of tree productivity is very important and basic to the understanding of ecosystem function, and especially the relationship between producers and consumers (Ahmad 2001). Because we have little information on the exact species of fruit consumed by bears or pigs, the monitoring of fruit production of these specific food trees would be impossible. Nevertheless, we documented monthly production of fruits of non-dipterocarp trees in both primary forest and logged forest to understand the periods when wild fruits are available for the consumption by such as bears and pigs. We assumed that the fruit trees that the bears and pigs feed on would have similar fruiting patterns to the trees monitored. Ahmad (2001) in the study area and monitored the leafing, flowering, and fruiting activities of trees $\geq$ 10 cm dbh monthly from August 1997- May 1999 in primary and logged tropical rainforest. We continued monitoring the same trees for another 19 months from June 1999 to December 2000 after N. Ahmad had finished her study. The botanical plots were placed in primary forest 1 km south of DVFC, and the other about 1.5 km northeast of DVFC that was selectively logged in 1989. Each botanical plot consisted of five tree transects, each measuring 20 x 100 m, that were placed systematically along two km of trails in each forest type for tree inventory. Each tree transect was further divided into five sub-plots of 20 x 20 m. The total area sampled was 1 ha in each forest type (Ahmad 2001). Trees with $\geq$ 10 cm dbh inside the sub-plots were tagged, numbered, and identified species by qualified botanists from Forest Research Center, Sabah Forestry Department (Ahmad 2001).

RESULTS

A total of six bears (5 male, 1 female), and six bearded pigs (4 male, 2 female) were captured in 2,372 trap nights. Trapping success was extremely low (1 bear/ 396 trap nights, and 1 pig/ 396 trap nights) probably due to the wariness of bears and pigs entering traps, and also the low density of sun bears in the study area (Chapter 3). Table 2 and Table 3 lists the physical parameters for all captured bears and pigs.

Emaciated sun bears

We first noticed emaciated animals when Bear #124 was recaptured on August 3, 1999. We sedated and handled Bear #124 to check on his gun shot wounds, which were discovered during his first capture in July 10, 1999. Bear #124 lost 2 kg within 3 weeks and looked slightly emaciated. Two days later, we observed Bear #125 at close range, and noticed he also looked emaciated. We then suspected that the radio-collar might pose an adverse effect on the bears. However, the poor condition of bears became more obvious when Bear #123, an old male bear, was captured in primary forest on August 7, 1999. Although fully grown, Bear #123 weighted only 34 kg, and lacked the fit and muscular look of Bear #125 and Bear #124 captured earlier (Table 2). Bear #123 appeared skinny, with protruding hipbones, and he showed characters of malnutrition and old age. His fur was dried, slightly sparse, with many white hairs and loose skin. Bear #123 was found dead a month later inside a hollow tree trunk. The straight-line distance between the capture site and the location of the tree where Bear #123 found dead was 8 km. The causes of death of Bear #123 could be a combination of old age, starvation and to a lesser extent, stress from handling.

On October 7, 1999, we observed Bear #125 in extremely poor condition in a tree cavity. He was surprisingly shy, and allowed us to within a meter without showing any aggression. Besides having sparse hair, his protruding zygomatic arch, scapulae, ribs, vertebrae, hipbones and his loose skin clearly indicated his extreme malnutrition. Two days later, we found him in another tree cavity exhibiting similar behavior and condition. We suspected that Bear #125 was wounded by a poacher, just like Bear #124, as he had several silvery white spots that resembled shotgun pellet wounds scattered on his body. A decision was made to handle Bear #125 on October 11. What we thought to be shotgun pellet wounds turned out to be large, engorged female ticks. Bear #125 lost approximately 32% of his body weight since his first capture on June 22, 1999, and weighted only 30 kg (Figure 6). He was found dead the next day where we had left him to recover from sedation. His carcass was sent to Sabah Wildlife Department for necropsy to determine the causes of death. We found an infection on his mouth and a hemorrhage on his left ribs caused from severe impacts. Bear #125 could have been injured by other large animals, possibly pigs or bears. We concluded that Bear #125 died from a combination of malnutrition, old age, injured, mouth infections and probably stress from handling. A special report was submitted to the Danum Valley Management Committee to further discuss the death of Bear #125 and Bear #123 (Wong 2000).

Another emaciated sub-adult male bear (Bear #122) was captured on May 4, 2000. Although Bear #122 weighed 30 kg, his physical condition was not as poor as Bear #125 when he died. This was due to his smaller size and younger age. Bear #122 had dense black fur on his body with the exception of the belly. His physical condition was closely monitored for the next seven months from 21 sightings and 28 photographs after his first capture. His physical condition deteriorated gradually and was very poor in late August and September. Figure 7 taken on July 28, 2000 shows Bear #122 in “very poor” condition. Another four photographs taken a month later showed that the condition of Bear #122 became even worse. Bear #122 was recaptured for the first time on July 4 and later learned to exploit the bait (chicken entrails) in traps and became a “trap happy” bear, seeking the bait in traps repeatedly. Between August 19 and October 3, 2000, he was recaptured seven times. Each time he was recaptured, Bear #122 had consumed all available baits and sat quietly inside the trap until we released him. We suspect that this “trap happy” behavior was probably caused by his desperate need for food. In October, the home range of Bear #122 expanded south and incorporated a garbage dumpsite where garbage from the DVFC and the FACE nursery was disposed. He utilized the garbage and remained in the vicinity of the dumpsite until June 2001. His physical condition improved as indicated by another photograph of Bear #122 taken on October 29, 2000, at the dumpsite. Bear #122 looked healthier, having sleek black fur and a muscular body.

The only female bear in our study, captured on September 24, 2000, Bear #121, also showed signs of severe starvation, weighing only 20 kg as an adult. For comparison, three captive female Malayan sun bears kept in Sepilok Orangutan Rehabilitation Center weighed 33-40 kg (S.K.K.S. Nathan, Veterinarian, Sepilok Orangutan Rehabilitation Center, Sabah Wildlife Department, Sabah, Malaysia, personal communication 2000). Two wild, adult female sun bears captured in Sungai Wain Forest Reserve, East Kalimantan, Indonesia, by G. Frederiksson in mid 1999, which Frederiksson considered as “very skinny,” weighed 23 kg and 25 kg (G. Frederiksson, Tropenbos-Kalimantan, Indonesia, personal communication, 1999). Ten photographs of Bear #121 taken in late July before she was first captured also indicated her malnutrition.

Forty-two photographs of Bear #120 (adult male) were taken between early August and late September. These photos revealed his malnourished appearance before his capture on October 11, 2000. His emaciated body, sparse hair, and loose skin or what we described as a "wrinkled skin" condition, were an indication of starvation and malnutrition (Figure 8). Interestingly, the physical condition of Bear #120 improved significantly by the time he was captured on October 11, 2000. Although lacking body fat, his physical appearance was much more muscular and he was covered with sleek black fur. Another four photographs of Bear #120 taken in November also indicated similar good physical condition. On November 5, 2000, we observed at close range a full-grown, unmarked bear climbing down from a fruiting fig tree. This bear looked slim but healthy by having sleek black fur. Another two photographs taken at the same location on November 13 showed a healthy looking bear climbing down from the same fig tree (Figure 9). In summary, we observed emaciated sun bears from August 1999 to October 2000. However, we found two exceptions unmarked bears, photographed between March and May 2000 at the northeast and southeast corner of our study area, who appeared to be in somewhat better condition (Table 4).

Emaciated bearded pigs

Except for a fat bearded pig captured in a snare in early March 2000, all of the other 5 pigs captured in either culvert traps or barrel traps between February and July 2000 were in various stages of starvation. An adult pig captured in primary forest on April 27, 2000 was extremely skinny with most bones visible and little body muscle remaining (Figure 10). Another bearded pig in similar poor physical condition was captured in early June 2000 in logged forest. The other two smaller sized, female pigs captured on July 2000 also showed signs of starvation (Table 2). Although new tracks of pigs were encountered almost daily near traps, and photographs of pigs were often taken near trap sites, we rarely captured pigs. As a result, those pigs that were captured in traps were likely in desperate need of food. Starvation likely contributed to the capture of the most desperate animals.

However, evidence of starving pigs did not come only from captures. Further evidence of famine in the forest came from the emaciated bearded pigs that were sighted in the vicinity of DVFC, along logging roads, and in the forest. At least eight different emaciated bearded pigs were recorded foraging in garbage bins and kitchen waste at the vicinity of DVFC from January to September 2000. Several habituated, resident bearded pigs that stayed near DVFC often charged these new, non-resident pigs. It was unusual for those emaciated pigs to show up around DVFC because of the presence of resident, habituated pigs. These resident pigs showed strong territorial behavior even among themselves and some dominant boars would not tolerate their subordinates to use their favorite feeding sites (S.T. Wong, personal observation). The first extremely emaciated pig sighted during the entire study period was in January 2000. This sub-adult pig was found dead near DVFC a week after we took its photograph (Figure 11). On March 2000, a rotten carcass of a bearded pig was found beside a forest trail about 1 km west of DVFC. We suspected that the pig died from starvation, although the actual cause of death was unknown. Several anecdotal sightings of emaciated pigs by the field crews and staff from DVFC in 2000 provided additional evidence of this famine period. Several DVFC staff who sighted these pigs stated that they had never seen such extremely skinny animals, despite being in DVFC for more than 10 years.

During the entire study period, camera traps took 142 photographs of bearded pigs. After eliminating photographs taken continuously of the same pig, a total of 90 photographs were used to assess monthly physical condition of bearded pigs for 10 months from July 1998 to August 2000 (Figure 12). The missing data on Figure 12 resulted because: a) no cameras were set up between September 1998 and March

1999, and b) no photographs of pigs were taken from March - June, October -November 1999, January - March, and June 2000. The results showed that the majority of the bearded pigs with “good” physical condition were photographed before September 1999, and individual pigs with “poor” or “very poor” physical condition were mainly photographed after March 2000 (Figure 13). However, we did find a few exceptions. A pig with “very good” physical condition was photographed in April 2000, and two pigs with “poor” physical condition were photographed in August 1998.

Forest Fruit production

Ahmad (2001) sampled 904 trees greater than 10 cm dbh in two 1-ha plots, one in primary forest and one in logged forest. Tree density was 465 stems ha^{-1} for primary forest and 439 stems for logged forest. The inventory of trees revealed a total of 185 species, which belonged to 111 genera and 46 plant families. A total of 715 non-dipterocarp trees were monitored for monthly fruit production, of which 392 trees (92 species) were in primary forest, and 323 trees (116 species) were in logged forest (Ahmad 2001).

We combined the 19 months of forest fruit production data collected in our study with the 22 months of data collected by Ahmad (2001) to investigate fruiting patterns. In general, the 41 months of data collection revealed very low fruit production, with an average of 2 trees and 3 trees fruiting each month in primary forest and logged forest respectively (Figure 14 and Figure 15). Only one distinct fruiting peak was recorded on September and October 1998, with 28 (3.92%) and 14 (1.96%) trees fruiting in logged and primary forests, respectively. Fruiting trees in primary forest and logged forest seem evenly distributed, although the total number of fruiting trees in logged forest was slightly greater than in primary forest. Ahmad (2001) found that the flowering pattern in the primary forest differed significantly than that of logged forest (Kolmogorov-Smirnov, Z=

2.1106, $p<0.05$), while fruiting patterns did not (Kolmogorov-Smirnov, Z= 0.9045, $p>0.05$).

DISCUSSION

Physical condition of Malayan sun bears and bearded pigs is strongly influenced by the availability of both plant and animal foods in the forest. Unfortunately, limited information is available on the proportion of these two kinds of food in the diet of bears and pigs. We also lack information on the temporal scale of relative abundance of animal food items during the study period. Therefore, the influence of specific animal food items on the physical condition of bears and pigs was not accounted for in this study.

Two assumptions were made when we evaluated the relationship of fruit productivity to the physical condition of animals. First, we assumed that the majority of sun bear and bearded pig diets consisted of fruits when available. Frederiksson (2001) and Kusters (2001) reported that sun bears and bearded pigs feed on more than 50 and 83 plant species respectively. These fruits range from lipid-rich nuts and drupe (e.g., Fagaceae, Euphorbiaceae), sugar-rich pulp fruits (e.g., Ebenaceae, Sapindaceae), to low nutrient figs (Moraceae). Second, we assumed that the abundance of animal food items, such as termites, beetles, beetle larvae, and earthworms, remained relatively constant during the study period at low density. Burghouts et al. (1992) reported termite densities were much lower in the study area (ca. 100 m^{-2}) than in other rainforests in Asia and Africa (> 1000 m^{-2}). The low termite density may be related to the low organic matter content of the soil in the Ulu Segama Forest Reserve (Burghouts et al. 1992).

The lowland tropical rainforest trees of Borneo and western Malesia (Sumatra and Peninsula Malaysia) display a synchronized mass flowering event followed by a mass fruiting event (MacKinnon et al. 1996). This synchrony can be related to decreases in rainfall and prolonged periods of drought (Woods 1956; Janzen 1974; Appanah 1985;

Aston et al. 1988). At irregular intervals of two to ten years, most species of dipterocarp, together with members of the Burseraceae, Fagaceae, Myristicaceae, Polygalaceae, and Sapotaceae, fruit almost simultaneously (MacKinnon et al. 1996). Over a period of few weeks or months, nearly all dipterocarps, and up to 88% of all canopy species, can flower after a long period of no reproductive activity (Appanah 1981, 1985). Such mass fruiting is behaviorally very similar to the supra-annual sexual phenology displayed by many North American and European canopy-member trees, such as *Abies, Carya, Fagus, Pinus, Quercus* and *Tsuga* (Janzen 1974). This synchrony is not absolute however. Due to the high temperature and rainfall throughout the year within lowland rainforests in Borneo, some trees are flowering, fruiting, and leafing at any time of the year (MacKinnon et al. 1996).

Since 1985, three mass fruiting events have occurred in the study area in the Ulu Segama Forest Reserve in 1986, 1990, and 1996. Minor fruiting peaks were also recorded in the study area outside these mass fruiting events. Ahmad (2001) recorded one minor fruiting pick in September-October 1998, where 1.2% and 2.8% of trees fruited in primary and logged forests respectively. During 18 months of phenological study in the same forests, Hussin (1994) recorded a mass fruiting even in September 1990 and a minor fruiting event between July and August 1991 in the study area. He recorded 10.4% and 7.4% of trees fruited in primary and logged forest respectively in the 1990 fruiting event. However, during the minor fruiting event in August 1991, the percentage of fruiting trees in primary forest (5.7%) was slightly lower than that in logged forest (6.0%). In general, fruit production in the study area from August 1997 to December 2000 was comparatively low during non-mass fruiting years. A similar trend was also reported by Heydon (1994) in his studies on the ecology of fruigivorous ungulates in the study area.

Ahmad (2001) found minimum temperature was significantly and negatively related to the number of overstory trees that fruited in both primary and logged forest. According to her, minimum temperature during the dry spell before the onset of rain may have influenced how many trees fruited. Low minimum temperatures (LMT) were also reported to correspond to mass-flowering events that occurred roughly two months later in western Peninsula Malaysia in 1976, 1981, 1982, and 1985 (Aston et al. 1988). An analysis of meteorological records suggests that the induction is caused by a drop of roughly 2^{o} C or more in minimum nighttime temperature (< 20^{o} C) for three or more nights (Aston et al. 1988). T. Inoue (in Wright et al. 1999) reported that the LMT cued the development of reproductive buds during El Nino Southern Oscillation (ENSO) event in Sarawak in 1997-98. Similar mass fruiting tree response to low temperatures has also being documented in the moist evergreen forests in Uganda (Chapman et al. 1999) and Gabon (Tutin and Fernandez 1993).

On the other hand, other studies have related flowering and fruiting in Peninsula Malaysia and Borneo with a sharp increase in sunshine (Wycherley 1973; Ng 1977) and/or a dry period (a period of several rainless weeks), especially during ENSO events (Wood 1956; Ashton 1969; Medway 1972; Ng 1977, Appanah 1985; Curran et al. 1999; Curran and Leighton 2000). The major fruiting periods recorded by Hussin (1994) and Ahman (2001) occurred between August and October. These periods coincided with wet months and an extremely dry month (monthly rainfall = 11.3 to 24.4 mm, compared to mean monthly rainfall= 230 mm) five months before the fruiting peak. These fruiting patterns were similar with other studies reported by Medway (1972), Bennett (1983), and Johns (1983b), who demonstrated that the patterns of flowering and fruiting were affected by wet and dry seasons. In addition, Putz (1979) found no strong seasonality during his four year phenological study of lowland rainforest trees in Peninsula Malaysia, but he did find that more species of trees tended to flower and later bear fruits after dry spells regardless of whatever time of the year these occurred. In more seasonal forests, most flowering tends to occur at the end of the dry season (Mabberley 1983).

The influence of rainfall on fruiting in tropical rainforest was best documented on Barro Colorado Island, Panama. Foster (1982) and Wright et al. (1999) recorded four episodes of extreme famine, and ten episodes of mild famine in tropical rainforest of Barro Colorado Island, in a 51-year period. All of these famine episodes were associated with anomalously heavy rains in the later part of the dry season. These famine events resulted in a mass starvation of the vertebrate consumers. These terrestrial and arboreal mammals foraged longer, fed on novel foods, were emaciated, and died in unusual numbers.

The famine events on Barro Colorado Island were very similar to those observed in our study. Immediately after the ENSO (negative Southern Oscillation Index [SOI]) event in 1997-98 that caused a record low annual rainfall, the onset of La Nina (positive SOI) brought high precipitation to the study area (Figure 2). In fact, 1999 and 2000 marked the record high annual rainfall in 16 years of meteorological data at DVFC since 1986. Monthly rainfalls for 22 months from September 1998 to June 2000 all exceeded the mean monthly rainfall, with the exception of November 1998, and September to November 1999. It is likely that this heavy rainfall caused the "wet" dry-season and further disrupted the fruiting peak that should have occurred in August – October of 1999 and 2000. This situation was similar to Foster (1982) hypothesized that dry-season rains prevent many tree species from attaining the threshold levels of drought required to initiate flowering and then fruiting.

Wright and van Schaik (1994) reported that light-limited trees produce new leaves and flowers during the season of maximum irradiation. They found correlations between plant performance and irradiance suggesting that light limits many tropical forest trees, even in the canopy. Thus, above average radiation may stimulate fruit production during El Nino events (Wright et al. 1999). In contrast, during the La Nina events in the year following the ENSO, rainy weather and heavy clouds may reduce fruit production in tropical forest. This theory was supported by photosynthetic measurements suggesting that light limits many tropical trees (Wright and van Schaik 1994). Low photosynthetic photon flux densities (PPFD) associated with cloudy conditions frequently limited wet-season photosynthesis by the canopy emergent *Ceiba pentandra* in central Panama (G. Zotz and K. Winter in Weight and van Schaik 1994). Thus, the low rainfall in April 1990, March 1991(Hussin 1994), April 1998 (Ahmad 2001), and June 2001 in the study area may have cued the fruiting peak five months later on September 1990, August 1991, September 1998, and November 2001 respectively. Nevertheless, long-term meteorological records and phenological data are needed to fully evaluate the relationship between climatic factors and the variation in fruit production in the study area.

Apart from the examples from Barro Colorado Island, Van Schaik et al. (1993) reported that evidence of animal starvation in more humid tropical forests is lacking. They found no evidence of mass mortality in tropical forests, such as Cashu, Peru, and Ketambe, Sumatra, despite long-term observations. This may be due to the impact of large forest carnivores such as jaguars (*Panthera onca*), and pumas (*Puma concolor*) in the Neotropics, and leopards (*Panthera pardus*) and tigers (*Panthera tigris*) in old-world tropics keeping their prey species, the primary consumers, at low population levels. In contrast, both Barro Colorado Island and Borneo, including the study area, lack large predators that could effectively keep the population density of primary consumers at low levels. The two large predators that are known to prey on sun bears and bearded pigs are the reticulated python (*Python reticulatus*) (G. Frederiksson, Tropenbos-Kalimantan, Balikpapan, Indonesia, personal communication, 2000) and clouded leopard (*Neofelis nebulosa*) (Payne et al. 1985). Full-grown reticulated pythons (7 – 10 m in length) that are capable of preying on sun bears and pigs are extremely rare throughout Borneo. The clouded leopard is actually a medium-sized cat weighing 12-23 kg (Nowak 1991) and is only capable of preying on juvenile pigs or piglets, primates, and medium to small-sized forest ungulates. Thus, in the study area there is no regulation of primary fruit consumer density by large predators. It may be that, in lieu of predation, starvation may be the most important regulatory factor on the population density of primary consumers in the Borneo tropical ecosystem. The principal cause of starvation for consumers appears to be mass fruiting failures.

Similar observation of emaciated Malayan sun bears and bearded pigs have been reported by G. Frederiksson (Tropenbos-Kalimantan, Balikpapan, Indonesia, personal communication, 2000), Curran and Leighton (2000), and J. Payne (in litt., 22 Jul 2000). Two female adult sun bears captured by G.Frederiksson on July 1999 in Sungai Wain Forest Reserve, East Kalimantan, were in various stages of starvation weighing 23 and 25 kg. One of these bears was found dead on September 1999 in extremely poor physical condition, and the skeletons of the other found later in the year. Although the cause of death for the latter bear was difficult to determine, it was believed that this bear too suffered from starvation. Curran and Leighton (2000) reported numerous emaciated pigs ranged throughout their study area in Gunung Palung National Park, West Kalimantan, in early 1990, and many became destructive pests of their research camp. They also witnessed numerous battles among these emaciated pigs over food sources, and surviving adults had many tusk-shaped scars and wounds (Current and Leighton 2000). At least six large, adult pigs were found dead and many other large adult boars starved at their study site approximately three years after the last mass fruiting in 1987 and before the onset of the next mass fruiting in 1991 (Current and Leighton 2000). They believed, from these observations, that the length of the mass fruiting cycle seems sufficient to depress the populations of bearded pigs in this forest

(Curran and Leighton 2000). Coincidently, emaciated bears and pigs in our study area also occurred three to four years after the last mass fruiting in 1996 and a year before the onset of the 2001 mass fruiting.

Looking at historic information, J. Payne (pers commun.) reported that he often saw “quite thin” pigs many times that he believed were suffering from starvation during periods with low food availability. He also found a dead pig on a logging road near our study area that he thought had died of starvation. He also shows an illustration of this juvenile bearded pig during a period of low food abundance. (Payne et al. 1985, p 137)

It seems clear that the periods between mass fruiting years are periods of low food abundance for frugivores and omnivores in lowland tropical forests of Borneo. It seems possible that these periods of scarcity would be intensified and result in famine for frugivores and omnivores during any prolonged wet season that might disrupt a “minor” fruiting period.

During intervals between mass fruiting, it seems likely that Malayan sun bears survive by feeding on invertebrates, such as termites, beetles, beetles larvae, and asynchronously fruiting species, such as *Ficus* spp., *Eugenia* spp., *Lithocarpus* spp., and some vertebrates (Wong et al. in press). Bearded pigs may survive during these periods by feeding on a wide range of asynchronously fruiting species, such as *Lithocarpus* spp. and *Quercus* spp. in the montane zone, and *Tetramerista glabra* and *Palaquium leicarpum* in peat swamps, and by scavenging the forest floor for palm meristems and earthworms (Curran and Leighton 2000).

Bearded pigs in Sarawak and East Kalimantan are known for their irregular mass migratory behavior that seems to follow crops of illipe nuts (*tengkawang*) (*Shorea* spp.) (Caldecott and Caldecott 1985; Pfeffer and Caldecott 1986). In Sabah, there are no signs of such long-distance migration behavior by pigs, even in the early 1980’s when bearded pigs were common year-round in the study area and when forests were more contiguous in the lowlands and less fragmented by logging (J. Payne, in litt., 22 Jul 2000). For resident bearded pigs in the study area, the length of time between mass fruiting intervals may prevent many juveniles from reaching maturity and may increase mortality of old and weak individuals (Curran and Leighton 2000). Similarly for sun bears, the length of time between mass fruiting intervals likely contributes to increased mortality and lower densities, particularly for older, weaker, injured, and sick individuals.

Janzen (1974) suggests that in habitat with a climate favorable to animals, yet with low productivity due to bad soils, strong anti-herbivore plant defenses have evolved with leaves containing exceptionally high concentrations of defensive chemicals. This leads to low animal densities, enabling mass fruiting to work through satiation of the lowered number of seed predators in Malesian dipterocarp forest (Janzen 1974). This reduction in seed predator density serves to enhance seed and seedling survival when a mass fruiting occurs. Thus, long periods without fruit production are an indirect cause of low frugivore and omnivore numbers. This hypothesis remains generally untested due to few long-term studies necessary to evaluate the population fluctuation of frugivores and other mammals in the tropics (Wright et al. 1999).

General low wildlife population densities in tropical forests of Borneo were reported by Inger (1980), when he compared densities of floor-dwelling amphibians and reptiles in various sites in Southeast Asia and Central America. He related the low densities of floor-dwelling amphibians and reptiles in Borneo and Peninsular Malaysia to two distinctive features found in these forests: 1) high proportions of tree species in these forests are members from one single tree family, Dipterocarpaceae; and 2) dipterocarps are noted for their synchronized mass fruiting behavior, with intervals between fruiting from two to ten years (Woods 1956; Janzen 1974; Appanah 1985; Aston et al. 1988). Inger (1980) suspected that mass fruiting should result in lower abundance of arthropod primary consumers during non-mass fruiting years. This consequently reduces the total biomass of insect populations, with consequent reductions in numbers of insectivore secondary consumers, such as amphibians and reptiles (Scott 1976; Inger 1980). Other vertebrates, both frugivorous and insectivorous, should also be reduced as well (Inger 1980).

Fleming (1979) demonstrated a higher proportion of fruit, nectar, and plant feeders in Panama than Peninsula Malaysia, when trying to compare the trophic structure of tropical bats and non-volant mammals between these two regions. Karr (1972) and M. Wong (in Appanah 1985) also found the density of birds in Indo-Malaysian forests are significantly lower than those in African and Neotropical forests where mass fruiting does not occur. Our observations on emaciated bears and pigs in this study during a period of no mass fruiting provide additional evidence to support this hypothesis.

Inger (1980) suggested that low animal densities in Indo-Malayan rainforests are a consequence rather than the cause of mass fruiting. This is contrary to Janzen's (1974) suggestion that mass fruiting evolved in Indo-Malaya rainforests because of the low animal densities found here. Janzen (1974) suggested that satiation of seed predators during mass fruiting works successfully in dipterocarp forests only because there are fewer animals present resulting in lower levels of seed predation. Janzen (1974) assumed that mass fruiting was a mechanism of escape from seed predators that could not evolve successfully with high numbers of frugivores and omnivores. A unique feature of Malesian forests is the dominance by a single tree family with consequent fruiting synchrony. Such forest dominance by a single tree family is not found in other forests where mass fruiting does not occur, such as Africa or the Neotropics. Mass fruiting is only found in three tropical forest areas: Borneo, Sumatra, and Peninsular Malaysia. The synchrony of mass fruiting appears to be most pronounced in Borneo. This may explain why no large carnivores are able to exist in Borneo given the low prey densities there. This is in contrast to Sumatra and Peninsular Malaysia where large predators are able to exist. More long-term ecological studies are necessary to fully understand the ecological interactions between mass fruiting and animal communities in this region.

Regardless of whether low animal density is a consequence or cause of mass fruiting, the trophic interactions that determine distributions and abundances of organisms in the lowland tropical rainforest of Borneo are primarily controlled by resource availability at the bottom of the food chain. According to this bottom-up view, organisms on each trophic level are food limited (Power 1992). It is very likely that the low density of frugivores and omnivores such as the Malayan sun bears and bearded pigs in the study area and in other dipterocarp forests in Borneo is related to prolonged food scarcity and resulting starvation during non-mass fruiting years. Heydon (1994), and Heydon and Bulloh (1996), reported a significant increase of grazers and browsers such as sambar deers (*Cervus unicolor*) and common muntjacs (*Muntiacus muntjac*) in logged forests in the study area due to the sudden increase of foliage in these disturbed sites. Based on these findings, we surmise that the densities of grazers and browsers tend to be low in primary forests that once carpeted the entire island of Borneo. This is because these primary forests have limited openings and few disturbed sites that favor the growth of plants browsed by herbivores. The absence of large carnivores in Borneo is a consequence of this low density of frugivores, omnivores, and herbivores that, in turn, is related to the ecological effects of mass fruiting cycles and the structure of the forest itself.

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Table 1. Criteria of appearance that were used to rate the physical conditions of Malayan sun bears and bearded pigs in Ulu Segama Forest Reserve, Sabah, Malaysia.

Category	Fur condition	Neck size	Body fat and muscle	Scapulae, vertebral columns, ribs, hipbones
Very good	Sleek, dense	Think	Fat, muscular	Not visible
Good	Sleek, dense	Thick	Little fat, muscular	Not visible
Fair	Dense	Medium	Lack fat, muscular	Slightly visible
Poor	Dull	Narrow	Lack fat, slim	Visible ribs, less protruding bones
Very poor	Dull, spare	Narrow	Lack fat, little muscle remained	Protruding

Table 2. Physical parameters and capture information for radio-collared Malayan sun bears in Ulu Segama Forest Reserve, Sabah, Malaysia.

ID #	Sex	Capture Date	Date Last Monitored	Age Class	Body Condition	Wt (kg)	TL (cm)	SL (cm)
125	M	22 June 99	12 Oct 99	Old	Fair	44	121	20
124	M	10 Jul 99	20 Sep 99	Old	Fair	40	124	24
123	M	7 Aug 99	10 Sep 99	Old	Poor	34	124	20
122	M	4 May 00	25 Jul 01	Sub-Ad	Poor	30	117	
121	F	24 Sep 00	25 Sep 00	Adult	Very poor	20	110	20
120	M	11 Oct 00	11 Jun 01	Adult	Fair	40	123	21

Age – Based on tooth wear, tooth color, body size, and overall condition
Body condition – Based on fat level, fur condition, and general appearance. Divided into 5 categories: range from “very poor”, “poor”, “fair”, “good” and “very good”.
Wt – Body weight, during first captured
TL – Total body length.
SL – shank length

Table 3. Capture information of bearded pigs in Ulu Segama Forest Reserve, Sabah, Malaysia.

Sex	Capture Date	Age Class	Body Condition	Estimated weight*
M	8 Mar 99	Adult	Very good	150 kg
M	1 Feb 00	Sub- adult	Poor	20 kg
M	27 Apr 00	Adult	Very poor	35 kg
M	9 Jun 00	Adult	Very poor	35 kg
F	7 Jul 00	Sub-adult	Poor	15 kg
F	25 Jul 00	Juvenile	Poor	10 kg

Age – Based on body size, and overall condition
Body condition – Based on body fat level, and general appearance. Divided into 5 categories: range from "very poor", "poor", "fair", "good" and "very good".
*weight were estimated visually while the pigs were in the traps.

Table 4. Physical appearance of Malayan sun bears determined from photographs taken by camera traps at Ulu Segama Forest Reserve, Sabah, Malaysia (n=198).

Bear ID	N	Location	Chronological description of physical condition
124	56	Coupe 88	July 99: “fair”; Aug 99: “poor”
122	28	Coupe 88	May 00: “poor”; Jul- Aug 00: “very poor”; late October 00: “fair”
121	10	Coupe 89	July 00: “poor”
120	53	Coupe 89	Aug-Sep 00: “poor”; Nov 00: “fair”
Unmarked "A"	44	Coupe 83	Mar-May 00: “fair”
Unmarked "B"	2	Coupe 88	May 00: “fair”
Unmarked "C"	2	Coupe 89	Nov 00: “fair”
Unmarked "D"	2	Coupe 89	Jul 00: “poor”
Unmarked "E"	1	Coupe 89	Aug 00: “poor”

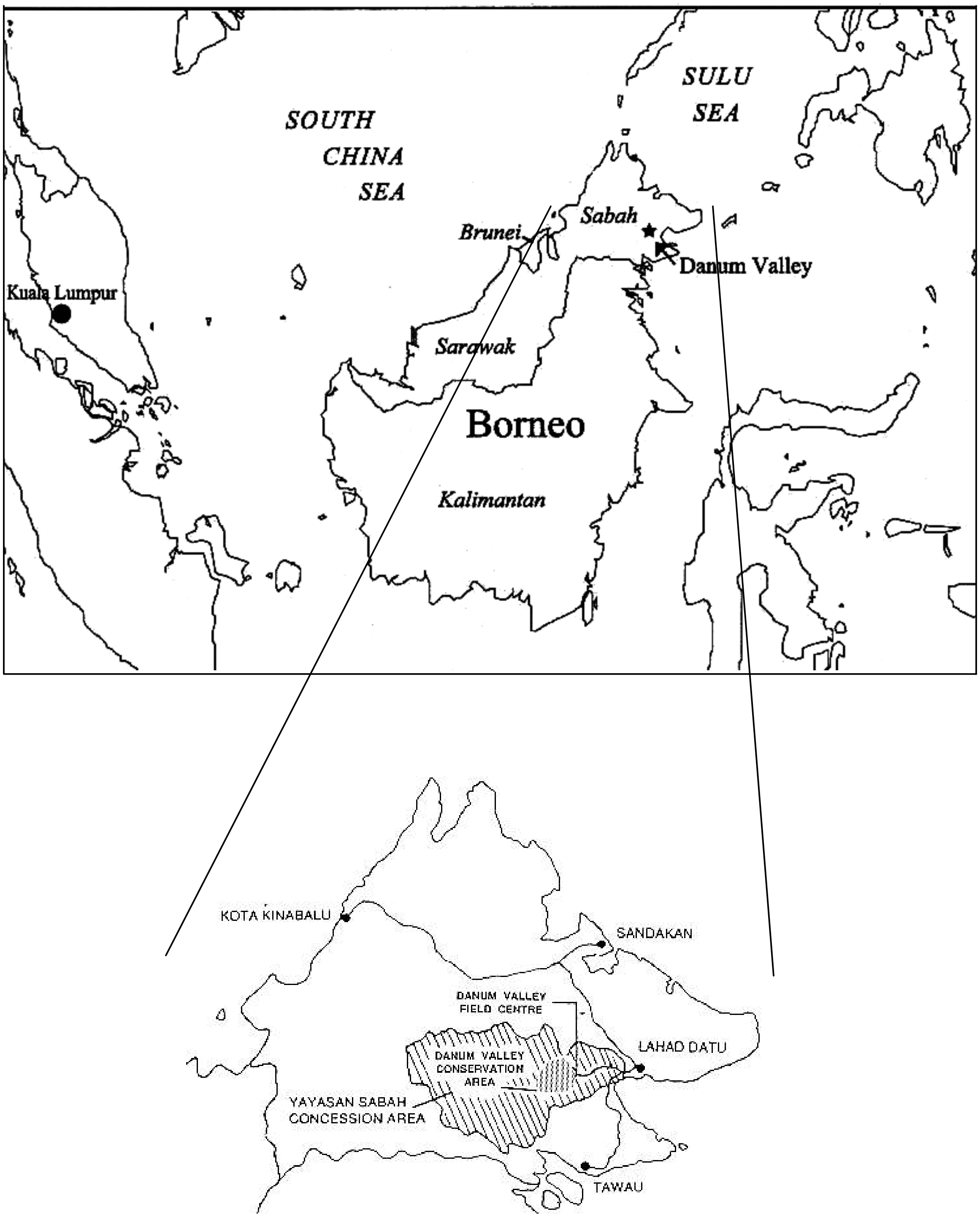

Figure 1. The location of the study area, based at Danum Valley Field Center at the state of Sabah, Northern Borneo.

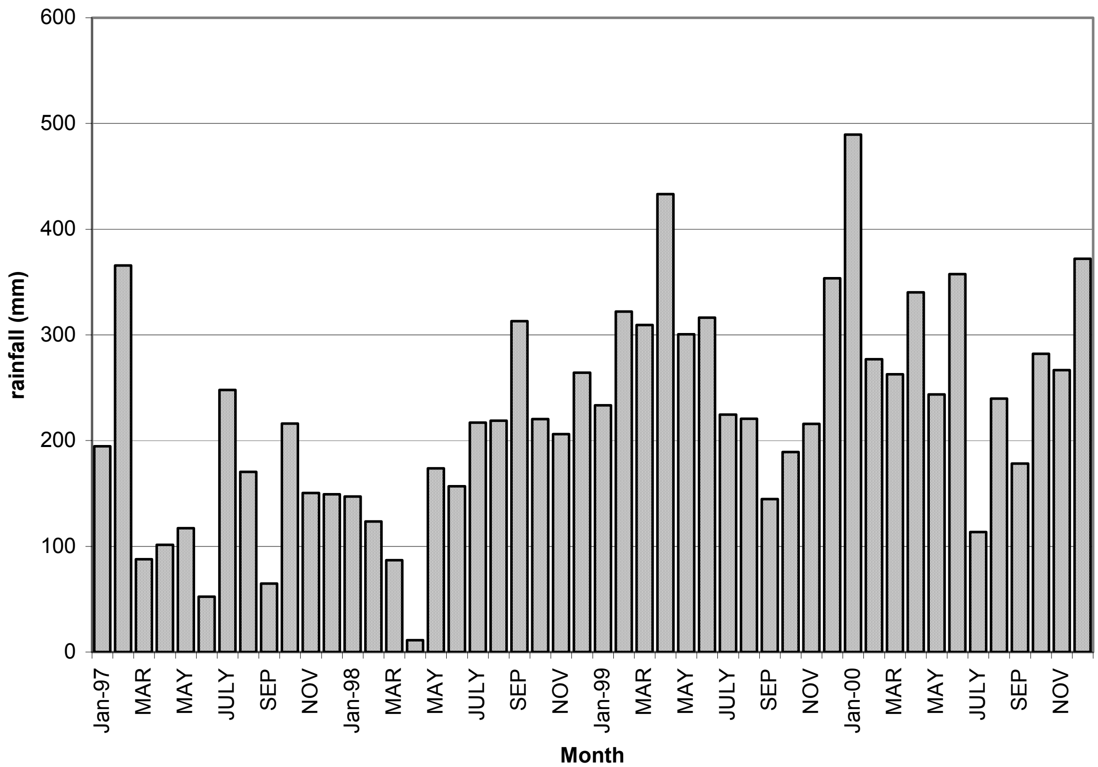

Figure 2. Monthly rainfall at Danum Valley Field Center, Ulu Segama Forest Reserve, Sabah, Malaysia, 1997-2000. Note the low rainfall during the 97-98 El Nino year in contrast to the high rainfall during 99-00 La Nina year.

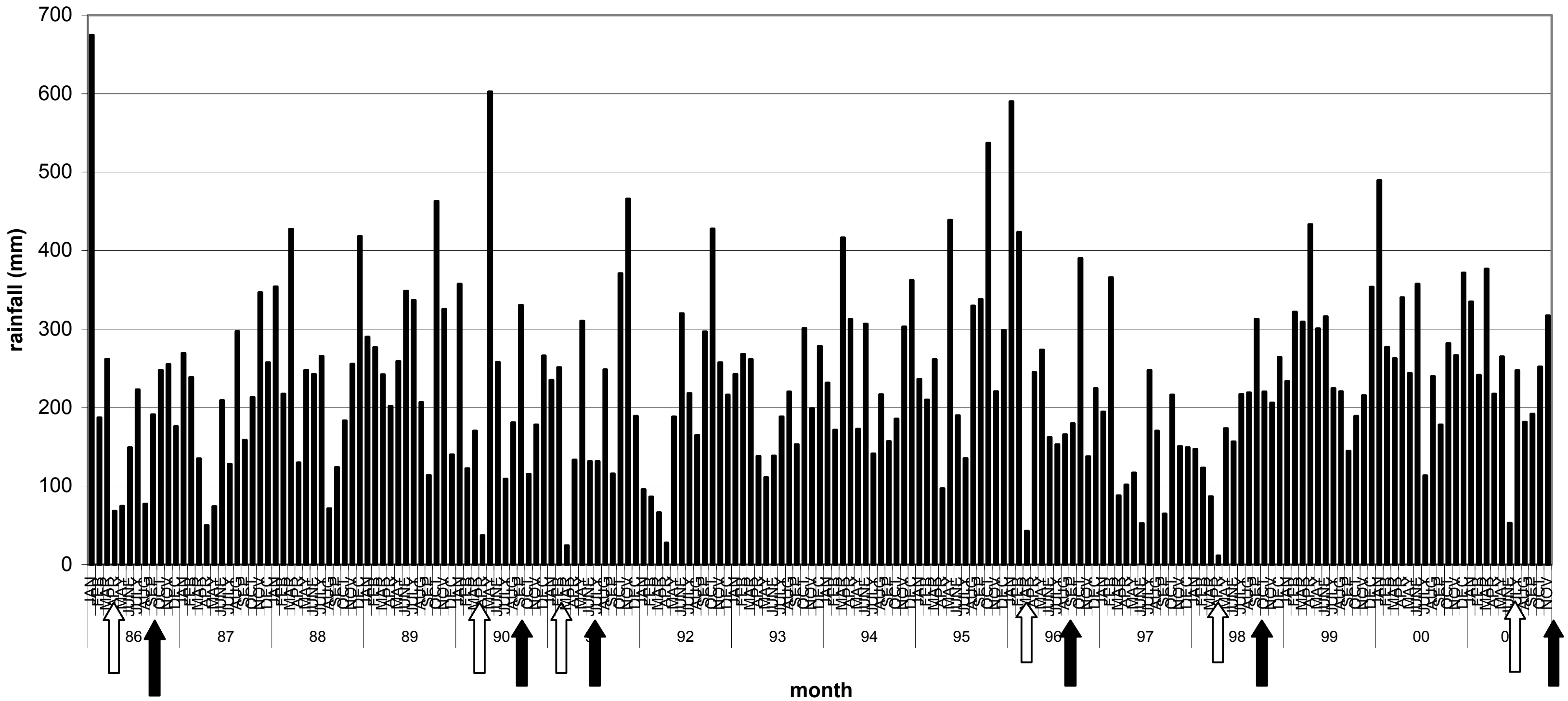

Figure 3. Monthly rainfall at Danum Valley Field Center, Ulu Segama Forest Reserve, Sabah, Malaysia, 1986-2000. Note the low rainfall (⇨) on April 1986, April 1990, March 1991, March 1996, April 1998, and June 2001 may correlated to the fruiting seasons (➡) five months after these low rain months, in which 1986, 1990, and 1996 fruiting seasons were mass fruiting. No phenological information available between 1986-90, and 1993-95.

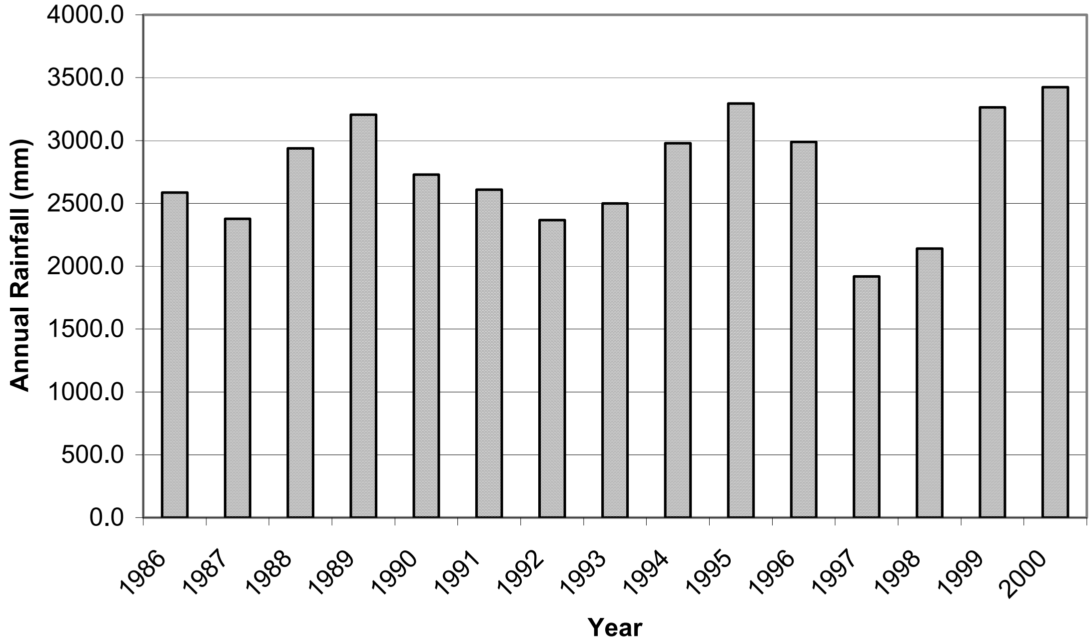

Figure 4. Annual rainfall at Danum Valley Field Center, Ulu Segama Forest Reserve, Sabah, Malaysia, 1986-2000. Note the low rainfall during the 97-98 El Nino years in contrast to the high rainfall during 99-00 La Nina years.

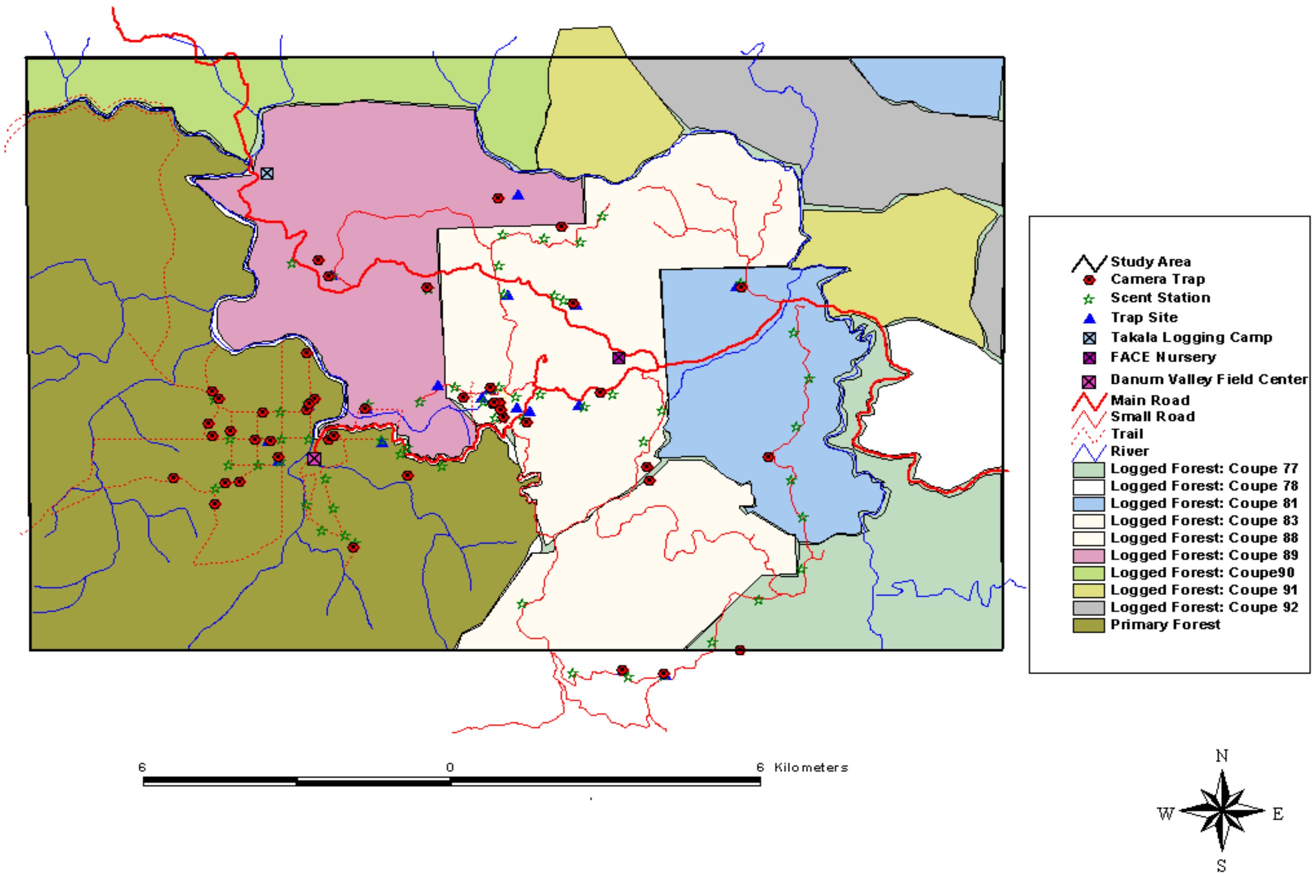

Figure 5. The study area covered approximately 150 km^2 of both logged and primary forest adjacent to the Danum Valley Field Center.

Figure 6. Bear #125 on October 11, 1999. The sparse hairs, protruding zygomatic arch, scapulae, ribs, vertebrae, and hipbones clearly indicated his extreme malnutrition. He lost approximately 32% of his body weight since his first captured by weighing only 30 kg.

Figure 7. Bear #122 photographed on July 28, 2000, revealed his “very poor” physical condition.

Figure 8. Bear #120 photographed on 23 August 2000 revealed his malnourished appearance before his captured on October 11, 2000. He has an emaciated body, sparse hairs, and loose skin that resulted in “wrinkle skin,” which were indications of starvation and malnutrition.

Figure 9. A healthy looking unmarked bear climbing down from a fruiting fig tree on November 13, 2000.

Figure 10. An adult pig captured in primary forest on April 27, 2000 was extremely skinny with most bones visible under its skin and little body muscle remained. The pig was capable of fleeing after we pushed him out of the trap.

Figure 11. The first extremely emaciated pig sighted on January 2000, at Danum Valley Field Center. This sub-adult pig was seen charged by resident pigs and found dead near our quarters a week later.

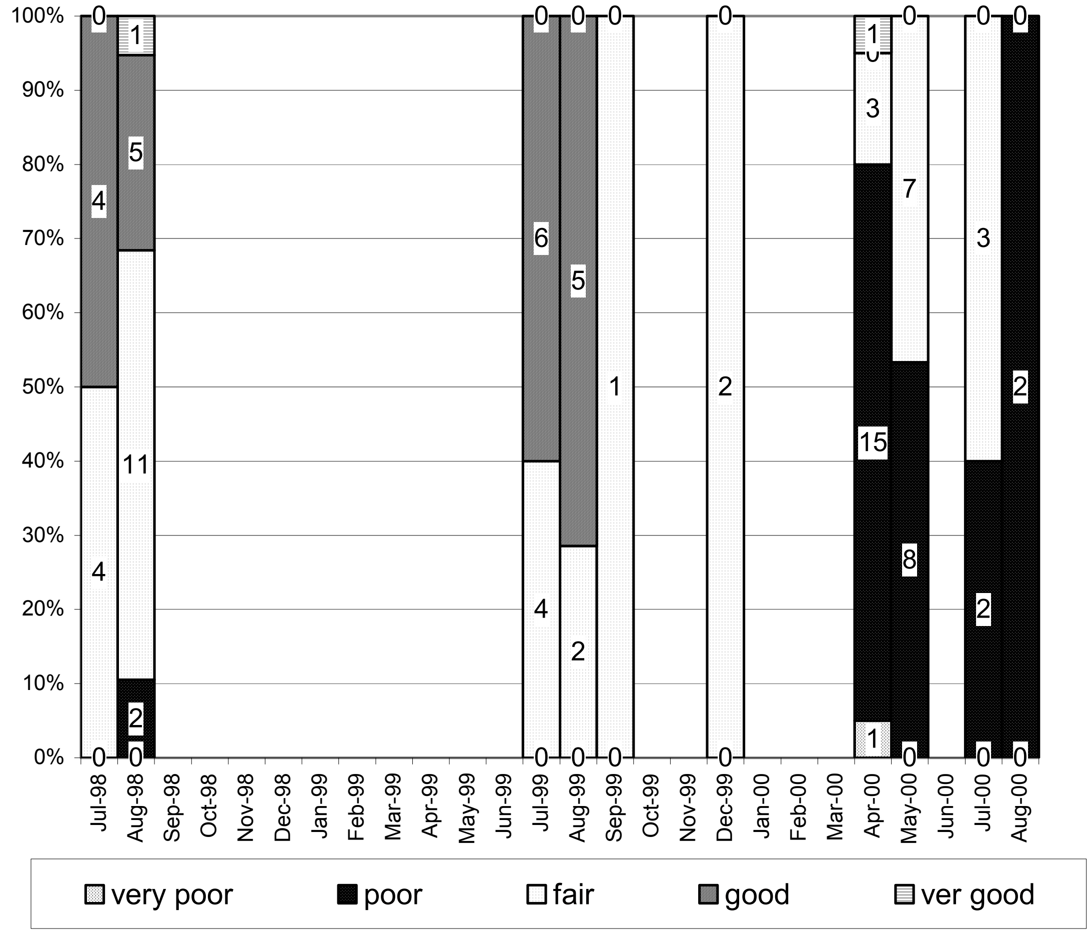

Figure 12. Physical condition of bearded pigs photographed in Ulu Segama Forest Reserve, Sabah, Malaysia (n=90). Numbers in bars indicate the number of photographs taken. The missing data resulted because no camera trap was set between September 1998 and June 1999, and no photographs of pigs were taken on October -November 1999, January - March, and June 2000.

Figure 13. Example of emaciated pig photographed on 6 April 2000 with camera trap in the study.

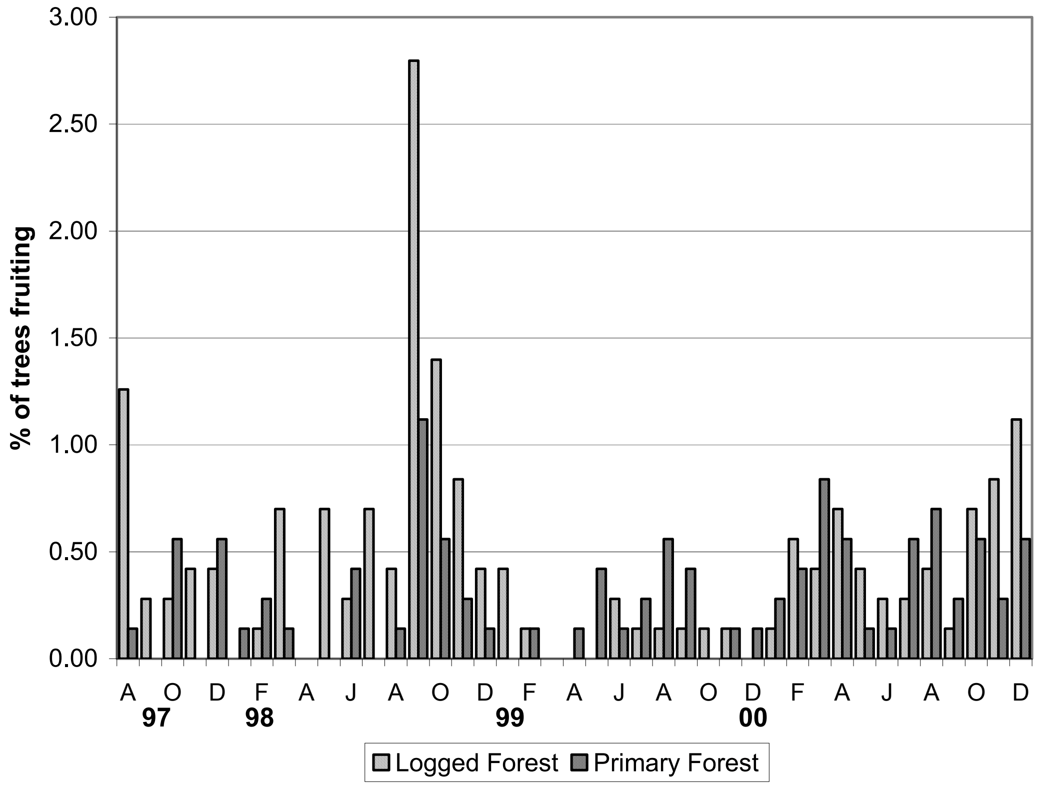

Figure 14. Fruiting frequency of trees in primary forest and logged forest from August 1997 to December 2000 at Ulu Segama Forest Reserve, Sabah, Malaysia (n=715).

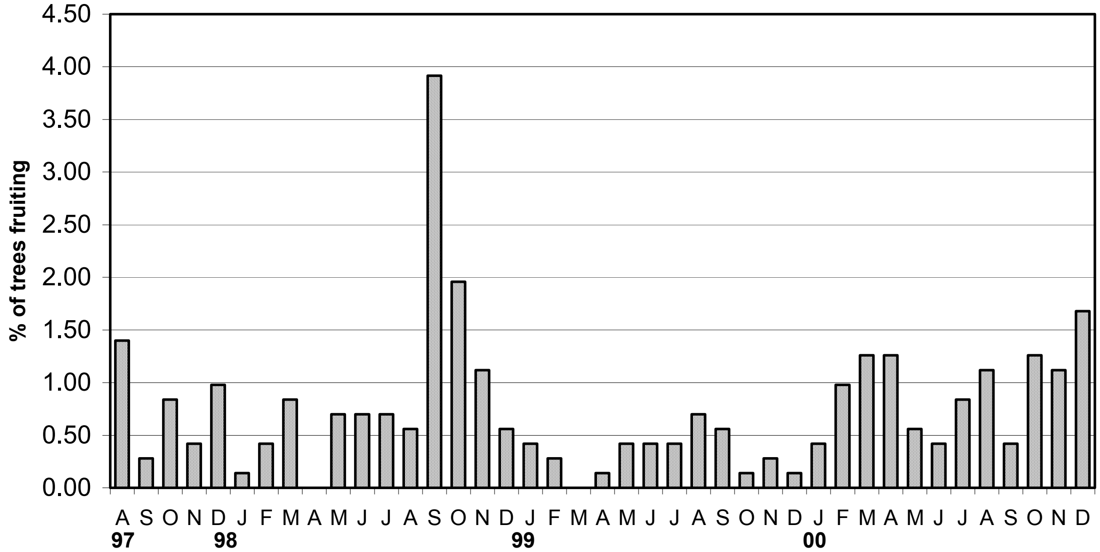

Figure 15. Percentage of total fruiting trees August 1997 to December 2000 at Ulu Segama Forest Reserve, Sabah, Malaysia (n=715).