

The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans

Are Sumatran forests better orangutan habitat than Bornean forests?†

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† Sadly John Proctor died in 2006 during the preparation of this manuscript. We take this opportunity to acknowledge his valuable contributions to tropical ecology and conservation, especially on Borneo, but also in a number of other sites around the globe.

7.1 Introduction

The chapters in this volume provide evidence that the socio-ecology of Sumatran orangutans (*Pongo abelii*) and Bornean orangutans (*Pongo pygmaeus*) differs substantially, but the extent to which these differences reflect species or subspecies (i.e., genetic) differences as opposed to ecological (i.e., habitat quality) differences is largely unknown. It is generally assumed that plant productivity is higher in Sumatran forests than in Bornean forests because Sumatra's younger, predominantly volcanic soils are more fertile than the soils found on Borneo (MacKinnon *et al.* 1996; Rijksen and Meijaard 1999). It is also assumed that Sumatran forests are of higher quality for orangutans than Bornean forests, and that this is both the proximate and ultimate cause of many of the differences between the two orangutan species (Delgado and van Schaik 2000; van Schaik 2004). To date few attempts to directly test these assumptions have been made (Wich *et al.* in review).

Comparisons of several attributes of Sumatran and Bornean orangutan population ecology, reproduction, and life history suggest that the availability of foods is greater, and perhaps more stable, on Sumatra than on Borneo. First, orangutan population density in similar habitats is consistently reported to be higher on Sumatra than Borneo (Rijksen and Meijaard 1999; Chapter 6 this volume). Second, the altitudinal limit at which orangutans are regularly found is higher in Sumatra (1000 m) than Borneo (500 m), suggesting that food availability may differ between the two islands at similar altitudes (Djojosedharmo and van Schaik 1992; Rijksen and Meijaard 1999). Third, field studies have shown that individuals in a population of Bornean orangutans occasionally experienced relatively extreme periods of negative energy balance (Knott 1998a) while those in a population of Sumatran orangutans did not (Wich *et al.* 2006a). Fourth, conception rates of female orangutans appear to be highly dependent on fruit availability on Borneo (Knott 1998a), but not on Sumatra (Wich *et al.* 2006b). Fifth, the amount of fruit in the diet is much less temporally variable for Sumatran orangutans than for Bornean orangutans (Wich *et al.* 2006a), and, in contrast to Borneo (Knott 1998a), the

amount of fruit in orangutan diets on Sumatra is largely unrelated to overall fruit abundance (Wich *et al.* 2006a). Sixth, differences in the structural features of their mandibles indicate that Bornean orangutans rely more heavily on bark and relatively tough fallback foods than do Sumatran orangutans (Taylor 2006a and Chapter 2 this volume). Finally, some life history variables suggest that Sumatran orangutans have 'slower' life histories than their Bornean counterparts (Wich *et al.* 2004b, Chapter 5 this volume), suggesting that over their evolutionary history Bornean orangutans experienced higher extrinsic mortality, perhaps due to periodic periods of fruit scarcity.

These and other strands of evidence have provided indirect support for the hypothesis that Sumatran forests provide better orangutan habitat than Bornean forests. In this chapter we explore this issue more directly by examining general patterns of plant productivity between the two islands, comparing indices of orangutan food availability between sites on the two islands, and considering how habitat quality limits orangutan population density.

7.2 Hypotheses and methodological considerations

7.2.1 General patterns of productivity

As noted above, it is generally assumed that the younger, volcanic soils found on much of Sumatra support higher levels of plant productivity than the older, more weathered soils found on most of Borneo. In a recent paper, we used a simple measure (the percentage of trees per month that carry fruit) to compare forest fruit production between Sumatra and Borneo (Wich *et al.* in review). Here we briefly review this general analysis and consider additional axes along which productivity might be compared between islands, sites, and habitats by testing the following hypotheses:

Hypothesis 1: Mean fruit availability is higher on Sumatra than Borneo

Because patterns of fruit availability differ dramatically between forest types (Marshall and Leighton 2006; Cannon *et al.* 2007a, b), we tested

this hypothesis separately for peat swamp, riverine, and dryland forests. We compared the overall average percentage of stems >15 cm diameter at breast height (dbh) fruiting per month.

Hypothesis 2: Period-specific food availability is higher on Sumatra than Borneo

Fruit production by most South East Asian trees is highly variable between years (van Schaik 1986; Curran and Leighton 2000; Wich and van Schaik 2000, Fredriksson *et al.* 2006, Sakai *et al.* 2006; Brearley *et al.* 2007; Cannon *et al.* 2007a, b). As many tree taxa fruit in synchrony both during mast fruit events and non-mast fruit peaks, distinct community peaks and troughs in fruit availability are readily identifiable (Marshall 2004). As our site phenological samples included different proportions of these peaks and troughs in fruit production, our comparisons of mean overall fruit availability (H1) may obscure differences in fruit abundance between the two islands. To test this hypothesis we used operational definitions to characterize each month at each site as a high fruit period, medium fruit period, or low fruit period. We then compared fruit availability during these periods between Sumatran and Bornean sites. We conducted separate comparisons for different tree size classes: 15–29.9, 30–44.9, 45–59.9, 60–74.9, 75–89.9, ≥ 90 cm dbh.

Hypothesis 3: Periods of high fruit abundance are more common in Sumatran forests than Bornean forests

Differences in mean levels of fruit availability between the two islands in different periods and tree size classes may not fully encapsulate differences in fruit abundance. For example, in theory, although Sumatran sites may have more fruit available during any given period than Bornean sites, if high fruit periods were more common on Borneo than Sumatra, then this may reduce the overall disparity between sites on the two islands. We compared the percentage of months at each site in which a given percentage of trees were fruiting using three arbitrarily chosen cutoffs: >15%, 20%, and 25% of stems fruiting per month, and examined the hypothesis separately in different tree size classes.

Hypothesis 4: Mast fruit events are more common in Sumatran forests than Bornean forests

Many plants in South East Asian forests characteristically exhibit masting behavior, fruiting in synchrony after several years of reproductive inactivity (Medway 1972; Appanah 1981; Ashton *et al.* 1988, Wich and van Schaik 2000; Cannon *et al.* 2007a). Masts are periods of tremendous food abundance and high caloric intake for vertebrate frugivores (Leighton and Leighton 1983; Curran and Leighton 2000; Marshall and Leighton 2006), during which these animals may be more likely to reproduce (van Schaik and van Noordwijk 1985a; Knott 1998a). Here we hypothesized that mast fruit events are more common in Sumatran forests than Bornean forests.

Hypothesis 5: Periods of low fruit abundance are more common in Bornean forests than Sumatran forests

Periods of low plant productivity (and therefore low food availability) are likely to be disproportionately important in setting carrying capacity for some tropical forest vertebrates (Cant 1980; Marshall and Leighton 2006). Here we hypothesized that these 'ecological crunch' periods are more common in Bornean forests than Sumatran forests. We used two definitions of periods of low food abundance: periods with <10% and <5% of stems fruiting, and examined the hypothesis separately in different tree size classes.

Hypothesis 6: Periods of low fruit abundance are longer in Bornean forests than Sumatran forests

In a follow-up to H5, we hypothesized that periods of low food abundance are of longer duration in Bornean forests than Sumatran forests. Our specific prediction was that the maximum recorded duration of low fruit periods would be longer at Bornean sites than Sumatran sites. We tested this hypothesis in each tree size class using the two definitions used for H5 (<10% and <5% of stems fruiting) and also examined a more extreme case: <1 % of stems fruiting.

Hypothesis 7: Trees in Sumatra fruit for longer periods than do trees in Borneo.

We hypothesized that on average, trees in Sumatra spend a greater percentage of the time in a

reproductively active state than do trees on Borneo. We examined each tree size class separately.

We recognize that these hypotheses are not mutually exclusive, nor do they all constitute independent measures. However, because they address variation in food availability in a number of ways, they complement each other in an attempt to examine the overarching question of whether Sumatran forests are better quality habitat for orangutans than Bornean forests.

7.2.2 Availability of orangutan foods

Our initial set of hypotheses addressed the basic question of whether Sumatran forests are, in general, more productive than Bornean forests, but we are most interested in knowing whether there are differences in orangutan food availability between the two islands. Unfortunately, at present we lack robust methods to assess the total abundance of orangutan foods in a way that is strictly comparable across sites and between islands. Simple phenological (e.g., percent orangutan food trees with fruit per month per unit area) or floristic (e.g., density or basal area of orangutan food trees) measures are hard to compare between sites because we do not have a systematic way to assess what 'orangutan food' is across sites. Use of site-specific feeding lists is problematic for at least two reasons. First, studies of longer duration accumulate longer food lists (see Chapter 9), so even if two forests were identical in their floristic composition, longer-term sites would assess their forests as having more orangutan food, based on their more complete feeding lists. Explicitly controlling for study duration (as Russon *et al.* have done in Chapter 9) and relative representation of months of high and low fruit availability between sites could reduce the impact of this sort of bias.

A second, less tractable, problem relates to the fact that orangutans are highly selective feeders that live in highly diverse rainforests with many hundreds of potential food items. Orangutans select fruit crops based on a number of criteria, including pulp weight per fruit and crop size (Leighton 1993), and ignore foods of lower preference rank (i.e., use/availability *sensu* Leighton 1993) when more preferred items are available. Thus, a plant item may

be available at two sites, but not recorded as food at one site because orangutans at that site may never (or very rarely) have to move far enough down their preference ranking to eat it. A simple hypothetical comparison illustrates this point. Assume that orangutan foods A, B, C, D, and E are arranged in decreasing order based on an objective measure of profitability. Further assume that all five items are present in the Sumatran flora and only items C, D, and E are found on Borneo, and that sampling effort is identical at two orangutan study sites, one located on each island. Orangutans at the Sumatran site consume items A, B, C and orangutans at the Bornean site consume items C, D, and E. Comparison of food availability between the two sites based on food lists would measure food availability on Sumatra as the sum of the density of plants A, B, and C and food availability on Borneo as the density of plants C, D, and E. Such a comparison would underestimate the true availability of potential orangutan food on Sumatra (sum of density of A, B, C, D, and E). This bias may be particularly misleading because low preference, low-quality items (e.g., D and E) are likely to be more common in the environment than higher quality items (Marshall and Wrangham 2007). For example, Sumatran orangutans rarely eat inner bark while Bornean orangutans habitually do during periods of low food availability (Knott 1998a; Wich *et al.* 2006a). Although orangutans are selective in the species from which they eat inner bark, it is an abundant resource. Therefore comparisons of food availability between the two islands that included inner bark as food on Borneo but not on Sumatra would be misleading.

Complete avoidance of this sort of bias would require far more detailed long-term feeding data, floristic inventories, and site-specific preference analyses than are currently available. However, this need not prohibit us from testing preliminary hypotheses about orangutan food availability between sites. Based on long-term data from a number of sites we can identify high preference (i.e., items used disproportionately often relative to abundance) that are important components of the diets of orangutans on both islands, that is the 'C' items listed in the hypothetical example (e.g., *Tetramerista glabra*, *Neesia* spp.). For these taxa we test two basic hypotheses (H8 and H9).

Hypothesis 8: Fruits of relatively high preference that are eaten at sites on both islands are more abundant on Sumatra than on Borneo

For this simple comparison we compare the stem densities of the following taxa in swamp forests: *Tetramerista glabra* (Tetrameristaceae), *Sandoricum beccarianam* (Meliaceae), and *Neesia* spp. (*N. cf. malayana* in Sumatra, *N. altissima* in Borneo, Malvaceae), and the following taxa in dryland forests: *Artocarpus elasticus* (Moraceae), *Dracontomelon dao* (Anacardiaceae), and the two *Neesia* spp. We also compared the stem densities of the following common food genera between dryland forest sites: *Aglaiia* (Meliaceae), *Artocarpus*, *Blumeodendron* (Euphorbiaceae), *Castanopsis* (Fagaceae), *Garcinia* (Clusiaceae), *Litsea* (Lauraceae), *Lithocarpus* (Fagaceae), and *Nephelium* (Sapindaceae). All plant names follow The Angiosperm Phylogeny Group II (2003).

Hypothesis 9: Orangutan food trees are more productive on Sumatra than Borneo

We predicted that orangutan fruit tree taxa found on both Sumatra and Borneo would be more productive (measured in number of fruiting events per year) on Sumatra than Borneo. Due to limited sample sizes and different levels of taxonomic identification at different sites, we conducted our analysis at the level of genera for the following taxa: *Aglaiia*, *Blumeodendron*, *Castanopsis*, *Garcinia*, *Litsea*, *Lithocarpus*, *Nephelium*, and *Tetramerista*. We also lumped similar genera in Myristicaceae (e.g., *Knema*, *Myristica*, *Horsfieldia*) for comparison between islands within this family.

Hypothesis 10: Stem densities of dipterocarp trees are higher on Borneo than Sumatra

One of the characteristic features of Malesian tropical forests is the presence of large, canopy trees in the Dipterocarpaceae (Whitmore 1985; Curran *et al.* 1999). Most taxa in this family exhibit supra-annual mast fruiting events separated by extended periods of reproductive inactivity (Ashton *et al.* 1988; Curran and Leighton 2000; Curran and Webb 2000; Brearley *et al.* 2007; Cannon *et al.* 2007a). Many other taxa join these mast fruiting events (van Schaik 1986; Marshall 2004; Cannon *et al.* 2007a,b) and inter-mast periods are times of food

scarcity for vertebrate frugivores (van Schaik and van Noordwijk 1985a; Knott 1998a; Marshall and Leighton 2006). Forests with a higher proportion of masting taxa would be expected to exhibit more extreme temporal variation in fruit availability, which might make such forests less hospitable for frugivorous vertebrates. Although many other tree taxa also mast, the proportion of trees in a forest that are dipterocarps may be a reasonable proxy for the severity with which masts affect orangutans, because when a larger proportion of plant biomass and productivity is sequestered in the rarely fruiting dipterocarp trees, there are fewer nutrients available for trees which more regularly produce important orangutan fruits. Here we predict that the stem density of dipterocarps is higher in sites on Borneo than Sumatra.

Hypothesis 11: The densities of large figs are higher on Sumatra than Borneo

Like many other vertebrate frugivores (Leighton and Leighton 1983; Terborgh 1986; O'Brien *et al.* 1998; Marshall and Leighton 2006), orangutans heavily utilize figs during periods when preferred fruits are scarce (Leighton 1993; Knott 1999a; Wich *et al.* 2006a). It has been hypothesized that the larger party sizes and higher population density of orangutans reported on Sumatra relative to Borneo are at least partly the result of the higher density of large strangler figs found there (Delgado and van Schaik 2000). Yet to our knowledge no quantitative comparison of fig densities has previously been presented. Comparisons of fig densities among sites is not as straightforward as comparisons of tree taxa because the figs that are most important for orangutans are large, hemiepiphytic figs whose diameters are not easy to measure in a standardized way. In addition, different studies have measured fig density in different ways: some have recorded the diameter of the largest fig root of individuals located in plots (e.g., Marshall 2004), others have used line-transect sampling methods to assess the density of large, free-standing stranglers (i.e., 'those that had fully encompassed their host and had a full crown at the tree's canopy level'; Wich *et al.* 2004a, p. 179). Despite these limitations, we use currently available estimates to test the prediction that fig density is higher on Sumatra than Borneo.

7.2.3 Effects of habitat quality on orangutan populations

In our title we posed the central question of this chapter: are Sumatran forests better orangutan habitat than Bornean forests? Stated another way: do Sumatran forests have higher orangutan carrying capacities than Bornean forests? In the preceding sections we described how we attempted to address this question by examining general patterns of fruit production (7.2.1) and the availability of orangutan foods (7.2.2) on both islands. In this section we consider a closely related question: what determines habitat quality for orangutans? Understanding the ecological factors that limit primate populations is a fundamental goal of the study of primate ecology. Yet even if we set aside other potential limiting factors, such as disease or predation, and focus on the role of food, we still have a limited theoretical and empirical understanding of how resources set carrying capacity for primate populations (Marshall and Leighton 2006), particularly long-lived species such as orangutans. Full consideration of this question is beyond the scope of this chapter. Here we simply examine the following five basic hypotheses about ecological correlates of orangutan population density:

Hypothesis 12: Orangutan population densities are positively correlated with mean fruit availability

Most primatologists assume that food availability is the key variable limiting the population density of most primates, and some studies have reported strong correlations between simple measures of food availability and primate population density (e.g., Mather 1992; Chapman and Chapman 1999). Therefore we first test the hypothesis that orangutan population density is positively correlated with mean fruit abundance.

Hypothesis 13: Orangutan population densities are positively correlated with fruit availability during high fruit periods (HFP)

On Borneo, orangutan reproduction has been shown to be closely tied to periods of resource abundance (Knott 1998a). While this result was not replicated at a Sumatran site (Wich *et al.* 2006a), it is

plausible to hypothesize that sites with more food available during fruit peaks might permit a higher proportion of females to attain a positive energy balance and therefore reproduce. If these sites consistently exhibit greater fruit availability during HFP, they may sustain higher population densities. Here we test the resulting prediction, that orangutan population density is positively correlated with fruit availability during HFP.

Hypothesis 14: Orangutan population densities are positively correlated with fruit availability during low fruit periods (LFP)

Classic ecological theory predicts that periods of food shortage set the population size of most organisms that are limited by resources. This is especially true for species whose populations grow at relatively slow rates (e.g., primates), since they are unable to closely track temporal fluctuations in food availability (Wiens 1977). For such species, food may be superabundant most of the time, and populations can go for many months (or years) without experiencing any resource limitation (Cant 1980). However occasional periods of food scarcity may cause an increase in levels of mortality (Wiens 1977; Foster 1974 in Cant 1980), resulting in bottlenecks that ultimately limit population size (Milton 1982; Davies 1994). Under this scenario population size will be positively correlated with food abundance during periods of resource scarcity

Hypothesis 15: Orangutan population density is positively correlated with the availability of figs
Primatologists use the term 'fallback foods' to denote resources of relatively low preference whose use is inversely correlated with the availability of preferred foods (Conklin-Brittain *et al.* 1998; Marshall and Wrangham 2007). Although they may be eaten during other periods, fallback foods are most important during periods of low food availability (Marshall and Wrangham 2007). Thus, following the logic outlined above (Hypothesis 14), the availability of fallback foods is thought to limit primate population density. Figs are important fallback foods for orangutans (Sugardjito 1986; Leighton 1993; Knott 1999a; Wich *et al.* 2006a; Marshall *et al.* in review). Initial tests suggest that figs are extremely important in setting the carrying

capacity on Borneo for gibbons (Marshall and Leighton 2006) and Western Bornean orangutans (Marshall *et al.* in review), but not for leaf monkeys (Marshall 2004) or Eastern Bornean orangutans (Marshall *et al.* 2006, 2007). On Sumatra, orangutan population density in dryland forests has been shown to be correlated with the availability of large strangler figs (Wich *et al.* 2004a). Here we use our comparative data set to test the prediction that orangutan density is positively correlated with the stem density of figs.

Hypothesis 16: Orangutan population density is inversely correlated with dipterocarp density. As described above (Hypothesis 10), forests with higher stem densities of dipterocarp trees may be less hospitable for orangutans for at least two reasons. First, forests in which a high proportion of stems are masting dipterocarps are likely to exhibit extreme temporal fluctuations in food availability. Second, as rainforest trees are subject to intense competition for light and nutrients, forests with high dipterocarp density will necessarily have a lower stem density of important orangutan fruit trees. At Gunung Palung, long-term orangutan densities across six forest types are strongly negatively correlated with the total basal area of Dipterocarpaceae trees ($r^2 = 0.79$, $p = 0.018$; Marshall and Leighton unpublished data). Here we test the prediction that orangutan population density is negatively correlated with the stem density of dipterocarp trees.

7.3 Study sites

We gathered data on orangutan density, phenology, and floristic composition from three Sumatran sites and nine Bornean sites (see Box 7.1). At one of the Sumatran sites (Sekundur) we gathered data separately in both logged and unlogged forests. Of the Bornean sites, three had experienced selective logging (Tuanan, Sabangau, and Kinabatangan), while the other six sites were unlogged. All sites are located in Indonesia, with the exception of Kinabatangan and Danum Valley, which are located in the Malaysian state of Sabah. Due to differences in sampling methodology and data availability, not all sites were included in all comparisons. Box 7.1 we provide brief descriptions of our study sites,

list the acronym by which they will be referred throughout the paper, and provide references for key papers providing additional descriptions of the sites. At each site trained observers scored all stems with diameters at breast height (dbh) >15 cm in phenology plots for presence/absence of fruit each month. Monitored stems were not located in plots at Barito Ulu (see Box 7.1).

7.4 Are Sumatran forests more productive than Bornean forests?

Although various measures of forest productivity are commonly used (e.g., rates of biomass accumulation, litterfall), for this analysis we focused on the measure that is likely to be most relevant for a large frugivorous vertebrate, namely the percentage of stems carrying fruit per month. Analysing multiple data sets of different durations and sampling intensities presented a number of computational problems that had to be overcome before we could analyse our data sets in an unbiased way. In Box 7.2 we provide a brief overview of methods, and refer readers to Wich *et al.* (in review) for further details on the analysis.

We first tested the basic hypothesis that mean overall habitat-specific fruit availability was higher on Sumatra than Borneo (Hypothesis 1). In riverine forests, sites differed in their overall fruit availability ($F_{2,160} = 31.3$, $p < 0.001$) and post hoc tests revealed that the Sumatran site (SB-RF) had a higher percentage of stems fruiting per month than did either of the two Bornean sites (GP-RF, KUT-RF; $p < 0.001$). Peat-swamp forest comparisons showed the same patterns: overall fruit availability differed between sites ($F_{2,181} = 270.3$, $p < 0.001$) and the Sumatra site (SB-PS) had a mean higher percentage of stems fruiting per month than did either of the two Bornean sites (GP-PS, TP; $p < 0.001$). There was also significant variation in fruit availability between the dryland sites ($F_{2,707} = 58.2$, $p < 0.001$). One Sumatran site (KET-LS) had significantly higher mean fruit availability than any other site ($p < 0.001$). The other two unlogged dryland Sumatran sites (SB-DF, SEK-P) were not more productive than the Bornean sites. These results indicate strong support of Hypothesis 1 for peat and riverine forests, and mixed support in dryland forests.

Box 7.1 Site descriptions

Sumatran sites

Ketambe (KET, 3°1'N, 97°39'E) is located in the upper Alas valley in Gunung Leuser National Park, Leuser Ecosystem. This study area mainly consists of primary dryland rain forest and has been described in detail by Rijkssen (1978), van Schaik and Mirmanto (1985) and Wich and van Schaik (2000). Stems ($n = 600$) were monitored for 153 months between September 1988 and May 2001.

Sekundur (SEK, 3°1'N, 98°02'E) is located in the east of Gunung Leuser National Park, Leuser Ecosystem (Knop *et al.* 2004). Sekundur encompasses diverse lowland dipterocarp forests and rich alluvial forest (de Wilde and Duyfjes 1996). We included separate data sets from logged (SEK-L) and primary (i.e., unlogged, SEK-P). Stems ($n_L = 234$, $n_P = 246$) were monitored for 12 months in both logged and unlogged forests between June 2000 and May 2001.

Suaq Balimbing (SB, 3°04'N, 97°26'E) is located in the western coastal plain of the Leuser Ecosystem, and consists of a variety of floodplain and hill forest habitats (Wich and van Schaik 2000). We included samples from peat swamp (SB-PS), dry hill forest (SB-DF), and riverine forest (SB-RF). Stems ($n_{PS} = 424$, $n_{DF} = 309$, $n_{RF} = 183$) were monitored for 66 months (67 month in SB-DF) between February 1994 and August 1999.

Bornean sites

Barito Ulu (BU, 114°E, 0°06'S) is located in Central Kalimantan. The research area covers 430 ha and contains a diverse mosaic of forest types. These include several types of tropical lowland rain forest (Brearley *et al.* 2004, 2007). The phenology of an unbiased sample of stems were monitored in dry lowland forest. These stems were not located in botanical plots but were represented in the sample in proportion to their stem abundance in plots. Stems ($n = 134$) were monitored for 124 months between November 1990 and June 2000.

Gunung Palung (GP, 1°S, 110°7'E) is located in Gunung Palung National Park, West Kalimantan. Data were collected in several distinct forest types at the Cabang Panti Research Station: peat swamp (GP-PS, 5–10 m above sea level [asl]), riverine forest (GP-RF, freshwater swamp; 5–10 m asl), and three types of dryland forest (GP-AB, GP-LS, and GP-LG: alluvial bench, lowland sandstone, and lowland granite; 5–400 m asl). General descriptions and detailed data on the plant composition of each habitat are provided in Webb (1997), Cannon and Leighton (2004), Marshall (2004), and Cannon *et al.*

(2007a, b). Stems ($n_{PS} = 779$, $n_{RF} = 890$, $n_{AB} = 718$, $n_{LS} = 1139$, $n_{LG} = 934$) were monitored for 79 months between January 1986 and September 1991.

Kutai (KUT, 0°4'N, 117°16'E) is located in Kutai National Park in East Kalimantan. Data were collected at the Mentoko Research Site in riverine forest (KUT-RF), alluvial forest (KUT-AB), and dry lowland forest on well-drained sandstone/mudstone derived soils (KUT-LS; Leighton and Leighton 1983; Leighton 1993). Stems ($n_{RF} = 103$, $n_{AB} = 221$, $n_{LS} = 1352$) were monitored for 23 months between October 1977 and August 1979.

Sungai Wain (SW, 1°5'S, 116°49'E) is located in the Sungai Wain Protected Forest, East Kalimantan and consists of lowland dipterocarp forest. The topography of the reserve consists of gentle to sometimes steep hills, and is intersected by many small rivers (Fredriksson *et al.* 2006). Stems ($n = 315$) were monitored for 55 months between January 1998 and July 2002.

Tanjung Puting (TP, 2°46'S; 111°52'E) is located in Tanjung Puting National Park, Central Kalimantan. Data were collected at Natai Lengkuas Station in peat samps that were periodically flooded with freshwater (Yeager 1989). Stems ($n = 891$) were monitored for 40 months between April 1993 and June 1996.

Tuanan (TUA, 2°09'S; 114°26'E) is located in the Mawas Reserve, Central Kalimantan. The site consists of peat swamp on shallow peat (≤ 2 m deep). The site is disturbed, having been subject to selective commercial logging in the early 1990s, followed by opportunistic logging until the end of 2002 (van Schaik *et al.* 2005a). Stems ($n = 1433$) were monitored for 24 months between April 2003 and March 2005.

Sabangau (SAB, 2°19'S; 114°00'E) is located in Central Kalimantan within the Natural Laboratory for the Study of Peat-swamp Forest. The habitat type is mixed peat-swamp forest with a peat depth of 1–4 m (Page *et al.* 1999). The study area was selectively logged from 1991–1997, followed by illegal logging until March 2004. Stems ($n = 404$) were monitored for 25 months between September 2003 and September 2005.

Danum Valley (DV, 4°8'N, 117°8'E) is located in Sabah. Botanical plots in two primary lowland dipterocarp forest locations, separated by 14 km, were monitored for fruit availability. Stems ($n = 427$) in one plot were monitored for 14 months between December 1992 and January 1994 and stems ($n = 173$) in the other plots were monitored for 17 months between June 1992 and October 1993.

continues

Box 7.1 continued

Kinabatangan (KIN, 118°8'E, 5°32'N) is located in Sabah along the Kinabatangan River. A large portion of the study area is flat and low (10–20 m asl), with the remainder covered in low mudstone hill peaks of ~50 m asl. Most of the area is poorly drained and subject to periodic flooding. Sampling at this site was not

conducted in an unbiased way as trees were not sampled in proportion to their abundance (i.e., not in plots). Therefore we did not include this site in comparisons except for comparisons of phenology of specific food taxa. Stems were monitored for 44 months between January 2001 and December 2004.

Box 7.2 Analytical methods

We utilized only unbiased samples of tree phenology in which tree stems were present in the sample in direct proportion to their density in the forest (i.e., in plots, or in one case, using the point quarter method). We analyzed different tree size classes, periods, and forest types separately, as we expected phenological patterns to covary with all three variables. Lianas were excluded from the analysis as they were unfortunately not sampled at most sites. We restricted this analysis to unlogged sites. Mean sampling duration was 55 months (range 12–153). We calculated the percent of stems with fruit (of any maturation state) per month, by site, habitat, and tree size class. We

log transformed and standardized the monthly percent scores (i.e., converted them to z-scores), and used objective criteria to assign months as periods of high ($Z > 1$), low ($Z < -1$), or medium ($-1 \leq Z \leq 1$) fruit availability. We then compared fruit abundance among sites within each of these periods, as site samples differed in the proportion of total sample months that were in periods of high and low fruit availability. Minimum sample sizes were required to include a site in a particular fruit period analysis (≥ 3 months) and tree size class (≥ 10 stems per size class). We used one-way ANOVA tests to compare distributions and Tukey HSD post-hoc tests to compare pairs of sites.

Our second hypothesis (Hypothesis 2) entailed a more refined comparison of fruit availability between the two islands based on period and tree size class. In riverine forests, sample sizes limited our comparisons to three tree size classes (15–29.9, 30–44.9, 45–59.9 cm dbh). Fruit production differed in each size class and period. Post-hoc tests revealed that the Sumatran site (SB-RF) had the highest fruit availability in the 15–29.9 (all Tukey post-hoc tests $p < 0.01$) and 30–44.9 (all Tukey post-hoc tests $p < 0.001$) cm dbh classes during all periods except during high fruit periods in the 15–29.9 cm dbh size class, when there were no differences between sites. Peat forest comparisons revealed similar patterns: fruit availability varied significantly in each period and size class, and in all periods but one (low fruit periods in the 15–29.9 cm dbh class) the Sumatran site exhibited a significantly higher percentage of stems fruiting than either of the two

Bornean sites (Tukey post-hoc tests, all $p < 0.001$). Sample sizes were insufficient to compare peat forest fruit production in the two largest size classes (i.e., 75–89.9, ≥ 90 cm dbh). The comparisons of dryland forests demonstrated that KET (Sumatra) was the most productive site in all periods and tree size classes (all Tukey post-hoc tests $p < 0.001$) and that the other two dryland Sumatran sites were not consistently more productive than Bornean sites. However the largest tree size class (≥ 90 cm dbh) at SB-DF (also Sumatran) was the next most productive site after KET, significantly more than the Bornean sites. Details and statistics for all comparisons are provided in Wich *et al.* (in review).

The tests of Hypotheses 1 and 2 provided general support for the idea that Sumatran forests are more productive than Bornean forests. This pattern was overwhelmingly true in both peat and riverine forests, but less evident in dryland forests. This

may be due to a lack of nutrient inputs from large mountains in Suaq hills and particularly Sekundur (Wich *et al.* in review). Interestingly, although the dryland forest exceptions to the general patterns were not consistently found in any particular period, they were only manifest in the small tree size classes. At larger size classes the higher fruit availability in Sumatra was magnified. This is of particular relevance to orangutans, who preferentially feed in large trees (Leighton 1993). This suggests that not only are Sumatran forests more productive than Bornean forests in general, this pattern is especially pronounced in the type of productivity of most importance to orangutans.

Hypothesis 3 examined whether, for a given habitat and tree size class, a greater percentage of months were periods of high fruit availability in Sumatra than in Borneo. We confined this analysis to sites from which we had at least 2 years of data, as sites with relatively short sampling durations were more susceptible to sampling error, leading to spurious results. We examined this prediction for all tree size classes in each habitat type, and used three operational definitions for periods of high fruit availability: months with >15%, >20%, and >25% of stems fruiting. We tested these hypotheses by calculating one-way χ^2 statistics within each tree size class and habitat type. In the cases for which there were a sufficient number of stems in a size class to test our hypotheses (i.e., $n \geq 10$), the majority of our comparisons showed that a significantly higher percentage of months in the samples from the Sumatran sites were high fruit availability months than in samples from the Bornean sites ($\chi^2 \geq 3.84$, $p < 0.05$; see Table 7.1). There were no comparisons in which Bornean sites had a significantly higher percentage of months with high fruit availability than Sumatran sites.

Next we tested Hypothesis 4, that mast fruit events are more common on Sumatra than Borneo. As mast fruit events are rare and comparing mast frequency between the sites presented in this paper would be susceptible to sampling error as mean sampling duration was <5 years, we used published data on masting frequency for Bornean and Sumatran sites provided in Wich and van Schaik (2000). In this limited sample there was no difference in mast frequency between the Sumatran sites

($n = 2$, mean 0.25 masts per year) and Bornean sites ($n = 4$, mean 0.24 masts/year; $\chi^2 = 0.05$, $p = 0.81$).

Our fifth hypothesis postulated that periods of low fruit availability are more common on Borneo than Sumatra. As with Hypothesis 3, we excluded sites for which we had less than 2 years of data. In riverine forests (SB-RF, GP-RF) using both definitions of low fruit periods (<5% and <10% of stems fruiting per month), in all dbh classes the Sumatran sites had a smaller percentage of months in low fruit periods than Bornean sites (both definitions: Mann-Whitney $\chi^2 = 3.86$, $df = 1$, $p = 0.045$; Fig. 7.1a, b). The same pattern held for peat sites (SB-PS, GP-PS, TP-PS), in all dbh classes and for both definitions of low fruit periods Sumatran sites had a smaller percentage of months in low fruit periods (<5% stems fruiting: Mann-Whitney $\chi^2 = 6.15$, $df = 1$, $p = 0.01$; <10% stems fruiting: Mann-Whitney $\chi^2 = 5.17$, $df = 1$, $p = 0.02$; Fig. 7.1c, d). Results for dryland forests (SW-DF, BU, GP-AB, GP-LS, GP-LG, KET-DF, SB-DF) were similar; in all dbh classes and for both definitions of low fruit periods, Sumatran sites had a smaller percentage of months in low fruit periods (<5% stems fruiting: Mann-Whitney $\chi^2 = 9.86$, $df = 1$, $p = 0.002$; <10% stems fruiting: Mann-Whitney $\chi^2 = 13.7$, $df = 1$, $p = 0.0002$; Fig. 7.1e, f).

Hypothesis 6 postulated that periods of low food availability would be of longer duration in Bornean forests than Sumatran forests. As sites for which data were collected over longer periods are more likely to include longer periods of low food availability (i.e., they are censored observations), prior to testing these hypothesis we examined the effect of study duration on the maximum number of consecutive low fruit months. To do this we assumed each tree size class at each site was an independent datum, and regressed the maximum number of consecutive low fruit period months against the study duration in each forest type. In none of the three forest types was maximum low fruit period duration (using any of the three definitions) significantly correlated with study duration. We therefore conducted all comparisons using data from all sites without controlling for sample duration. In riverine forests, while there were no significant differences between Bornean and Sumatran sites, all comparisons suggested a trend toward shorter low fruit periods in Sumatran sites: LFP = <1 %

Table 7.1 The percentage of months sampled that were periods of high fruit availability at sites on Sumatra (SUM) and Borneo (BOR) in three forest types

Island	Site	15–29.9 cm dbh			45–59.9 cm dbh			75–89.9 cm dbh		
		% month >15%	% month >20%	% month >25%	% month >15%	% month >20%	% month >25%	% month >15%	% month >20%	% month >25%
Peat forest										
SUM	SB-PS	0.0	0.0	0.0	95.4	90.8	56.9	NA	NA	NA
BOR	GP-PS	0.0	0.0	0.0	6.3	2.5	0.0	22.8	7.6	7.6
BOR	TP-PS	0.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0
		NS	NS	NS	****	****	****	NA	NA	NA
Riverine forest										
										NS
SUM	SB-RF	16.4	1.6	0.0	41.0	18.0	3.3	NA	NA	NA
BOR	GP-RF	2.5	0.0	0.0	7.6	3.8	1.3	9.2	6.6	6.6
		****	*	NS	****	***	NS	NA	NA	NA
Dry forest										
SUM	KET-DF	18.3	6.5	1.3	75.2	62.1	44.4	90.8	89.5	82.4
SUM	SB-DF	3.0	0.0	0.0	1.5	0.0	0.0	21.2	18.2	18.2
BOR	SW-DF	0.0	0.0	0.0	7.5	5.7	1.9	NA	NA	NA
BOR	BU	0.0	0.0	0.0	0.0	0.0	0.0	NA	NA	NA
BOR	GP-AB	2.5	0.0	0.0	11.4	7.6	7.6	17.7	13.9	12.7
BOR	GP-LS	1.3	0.0	0.0	11.4	3.8	2.5	16.5	11.4	10.1
BOR	GP-LG	0.0	0.0	0.0	7.6	7.6	3.8	8.9	8.9	7.6
		**	*	*	NS	NS	NS	*	*	*

The table shows the comparisons using three definitions of high fruit periods: months with greater than 15, 20, and 25% of stems fruiting. Regardless of the definition used, in the three forest types and most tree size classes the Sumatran sites had a higher percentage of months that were high fruit periods. Only three tree size classes are included here: 15–29.9 cm dbh, 45–59.9 cm dbh, and 75–89.9 cm dbh; patterns in other tree size classes were comparable. Beneath each column is the result of the one-way χ^2 test of the hypothesis that Sumatran sites had a higher percent of high fruit periods than Bornean sites; na = not applicable (limited sample size), NS, $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.0025$, **** $p < 0.0005$.

stems fruiting (Mann–Whitney $\chi^2 = 1.51$, DF = 1, $p = 0.22$), LFP = <5 % stems fruiting (Mann–Whitney $\chi^2 = 2.15$, df = 1, $p = 0.14$), or LFP = <10 % stems fruiting (Mann–Whitney $\chi^2 = 3.40$, df = 1, $p = 0.07$). Peat forest comparisons using all three definitions showed that Sumatran samples tended to have low fruit periods of shorter maximum duration: LFP = <1 % stems fruiting (Mann–Whitney $\chi^2 = 4.29$, df = 1, $p = 0.04$), LFP = <5 % stems fruiting (Mann–Whitney $\chi^2 = 4.24$, df = 1, $p = 0.04$), or LFP = <10 % stems fruiting (Mann–Whitney $\chi^2 = 3.20$, df = 1, $p = 0.07$). Finally, our comparisons of the duration of low fruit periods in dryland forests showed that Sumatran forests had significantly shorter low fruit periods when they were defined as months <5% stems fruiting (Mann–Whitney $\chi^2 = 4.61$, df = 1, $p = 0.03$) or <10% of stems fruiting

(Mann–Whitney $\chi^2 = 5.04$, df = 1, $p = 0.03$). There were no significant differences between sites on the two islands using the <1 % definition in dryland forests when all tree size classes were considered together (Mann–Whitney $\chi^2 = 0.22$, df = 1, $p = 0.64$). Although sample sizes precluded separate formal tests within every tree size class and forest type, in the majority of comparisons in peat (9/10), riverine (11/12), and dryland (11/16) forests the Sumatran sites had shorter maximum durations of low fruit periods regardless of definition. As with Hypotheses 1 and 2, these patterns were more pronounced in large tree size classes (>45 cm dbh), where all Sumatran sites had shorter durations of low fruit periods than Bornean sites.

Our final hypothesis in this section (Hypothesis 7) examined whether trees in Sumatran forests spend

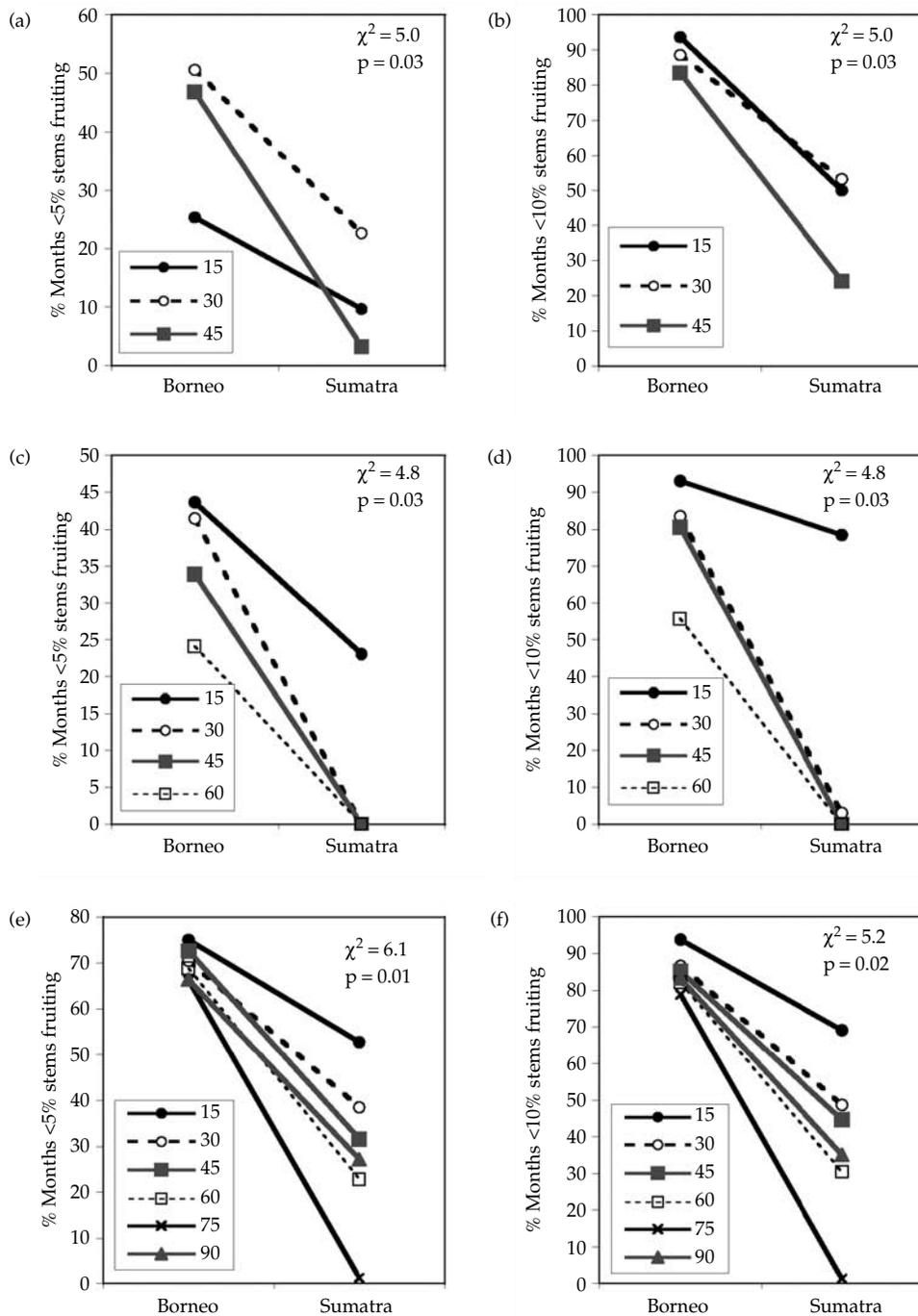


Figure 7.1 Frequency of low fruit periods in Bornean and Sumatran forests in different tree size classes. Graphs compare the percentage of months with less than 5% (a, c, e) and 10% (b, d, f) of stems fruiting. Graphs a and b compare the mean values of the percent of stems fruiting in a dbh class from all riverine forest sites. Graphs c and d compare the mean values of the percentage of stems fruiting in a dbh class from all peat forest sites. Graphs e and f compare the mean values of the percent of stems fruiting in a dbh class from all dryland forest sites. Tree size classes are denoted by '15' = 15–29.9 cm dbh, '30' = 30–44.9 cm dbh, etc. Note that differences are more pronounced in larger tree size classes. P values and χ^2 approximations for Mann–Whitney tests of each comparison are given in the top right-hand corner of each box; $df = 1$ for all comparisons.

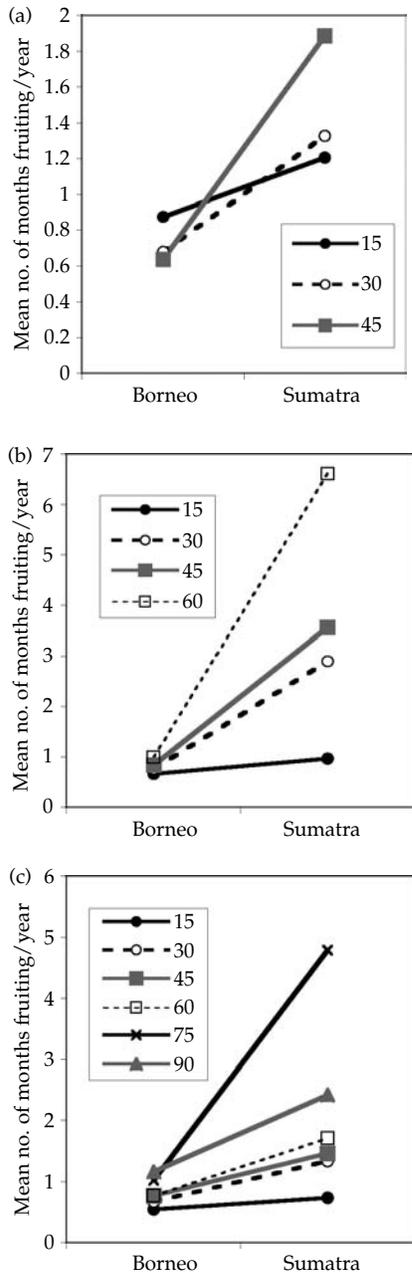


Figure 7.2 Mean number of months with fruit per year for trees at Bornean and Sumatran sites. The figure shows that in trees in riverine (a, Mann–Whitney $\chi^2 = 7.52$, $p = 0.006$), peat (b, Mann–Whitney $\chi^2 = 7.52$, $p = 0.006$), and dryland (c, Mann–Whitney $\chi^2 = 5.39$, $p = 0.02$) forests on Sumatra fruited for a greater number of months per year than in forests on Borneo. Comparisons are presented separately for tree size classes, following the legend in Figure 7.4. Note that differences between islands are more pronounced in larger tree size classes.

a larger percentage of time bearing fruit than do trees in Bornean forests. The hypothesis was supported for all tree size classes in riverine, peat, and dryland forests (Fig. 7.2a, b and c respectively). In many cases differences between the islands were quite pronounced; Bornean trees tended to fruit less than 1 month per year, whereas Sumatran trees typically fruited for two or three times as long, sometimes much more.

In sum, the results of these hypothesis tests indicate that, compared to Bornean forests, Sumatran forests have a higher percentage of stems bearing fruit overall (Hypothesis 1), have higher fruit availability during periods of low, medium, and high fruit availability (Hypothesis 2), are more often in periods of high fruit availability (Hypothesis 3, but not masts Hypothesis 4), and experience periods of low food abundance less often (Hypothesis 5) that tend to last for shorter durations (Hypothesis 6). Trees in Sumatran forests spend a larger percentage of the time bearing fruit than do trees in Bornean forests (Hypothesis 7). Taken together, these tests provide considerable support for the general hypothesis that Sumatran forests are generally more productive than Bornean forests. In the next section we examine this hypothesis by comparing indices of orangutan food availability between sites on the two islands.

7.5 Are Sumatran forests better orangutan habitat than Bornean forests?

As discussed in Section 7.2.2, while our comparisons of overall productivity are indicative of differences in fruit availability between the two islands, they may not reflect differences in the quality of forests for orangutans. In theory, the strong differences in fruit production reported above may be largely driven by plant taxa that are not consumed by orangutans. In order to determine whether Sumatran forests are better orangutan habitat than Bornean forests, in this section we examine differences in the stem densities of orangutan food trees (Hypothesis 8) and examine whether orangutan food trees are more productive on Sumatra than Borneo (Hypothesis 9). We also compare the stem densities of dipterocarp trees on Borneo and

Sumatra (Hypothesis 10), and consider the availability of figs on the two islands (Hypothesis 11).

Hypothesis 8 predicted that fruits of relatively high preference eaten on both islands are more abundant on Sumatra than Borneo. First, we compared the stem densities of *Tetramerista glabra*, *Sandoricum beccarianum*, and *Neesia* spp. in swamp forests. We include two Bornean peat swamp sites (GP-PS, TP-PS) in this comparison as data from the riverine and peat-swamp forests at the Sumatran site (SB) could not be separated. Stem densities from swamp forests at Suaq are means of all swamp plots estimated from Figure 13 in Singleton and van Schaik (2001), for all other sites we used precise values from plots. For all three taxa, the Sumatran site had an order of magnitude higher stem densities (Fig. 7.3a). Our comparisons of *Artocarpus elasticus*, *Dracontomelon dao*, and *Neesia* spp. in dry forests showed similarly higher densities at the Sumatran site (KET; Fig. 7.3b). Finally, stem densities of the common food genera *Aglaiia*, *Artocarpus*, *Blumeodendron*, *Castanopsis*, *Garcinia*, *Lithocarpus*, and *Nephelium* in dryland forest sites were highest at the Sumatran site (KET) in all comparisons (Fig. 7.3c). Formal statistical tests within each plant taxon were precluded as we only had data from one study site in Sumatra for the swamp and dry forest comparisons. However, for all 13 taxa comparisons the Sumatran site had the highest stem densities of all sites. Pairwise comparison of the average for all Bornean sites against the Sumatran site for each taxon showed that the Sumatran site had significantly higher stem densities of our selected food trees (t -ratio = 3.26, df = 12, p = 0.007).

Our ninth hypothesis examined whether particular tree taxa were more productive on Sumatra than on Borneo. In order to increase the sample sizes for our comparisons, we included logged Bornean sites in our comparison (i.e., KIN, TUA, SAB). Sample sizes and limited botanical identification precluded data from the logged Sumatran site (SEK-L). In our test we were limited to nine taxa (listed in Table 7.2) for which we had sufficient sample sizes to make meaningful comparisons. For each stem in these taxa, we counted the number of distinct fruiting events (identified by a stem going through a full cycle from flower buds to ripe fruits followed by at least one month of reproductive

inactivity) and divided this by the number of years over which data were collected. As noted above, in order to maximize sample sizes, comparisons were made using all stems (logged and unlogged, lumped forest types) unless there was a significant difference between logged and unlogged forests. In those instances (*Garcinia* and *Litsea*, where fruiting frequency was higher in logged forest, Table 7.2), we compared the value from unlogged Bornean forests with (unlogged) Sumatran forests.

In cases where a sample included two habitat types (n = 5; e.g., *Aglaiia* in dry forests and swamps) we also reran analyses to ensure that inclusion of different forest types had not skewed results. For some trees within Borneo, fruiting frequency was higher in one forest type than another, but no consistent patterns were detected between forest types and these differences did not affect inter-island comparisons.

The results of our test of Hypothesis 9 were mixed (Table 7.2). Fruiting frequency was significantly higher at Sumatra sites for some taxa (*Aglaiia*, *Garcinia*, *Lithocarpus*, *Nephelium*, and Myristicaceae) but not others (*Blumeodendron*, *Castanopsis*, *Litsea*, *Tetramerista*). There are no obvious differences between the two groups of taxa: both contain large and small trees, masting and non-masting species, and species that fruit for relatively long and short durations. There was no taxon for which fruiting frequency was higher on Borneo than Sumatra.

We also predicted that the stem density of dipterocarp trees was higher on Borneo than on Sumatra (Hypothesis 10). As with Hypothesis 8, the fact that we only had plot data from a single Sumatran site (KET) precluded a formal test of this hypothesis. However, the differences between sites are striking. Dipterocarp stem densities at Ketambe (Sumatra) were 4.48 stems/ha; while mean stem densities on Borneo were 20.6 stems/ha for swamp forests (GP-FS, GP-PS, and TP-PS, standard deviation [sd] = 8.13) and 68.2 stems/ha in dryland forests. There was substantial variation in dipterocarp density among the Bornean dryland sites (sd = 50.2), with the lowest densities predictably found in the logged site (KIN = 25.7 stems/ha, dipterocarps are prized timber species), intermediate densities at Gunung Palung (GP-AB = 40.2 stems/ha, GP-LS = 45.8 stems/ha, GP-LG = 67.2 stems/ha), and the

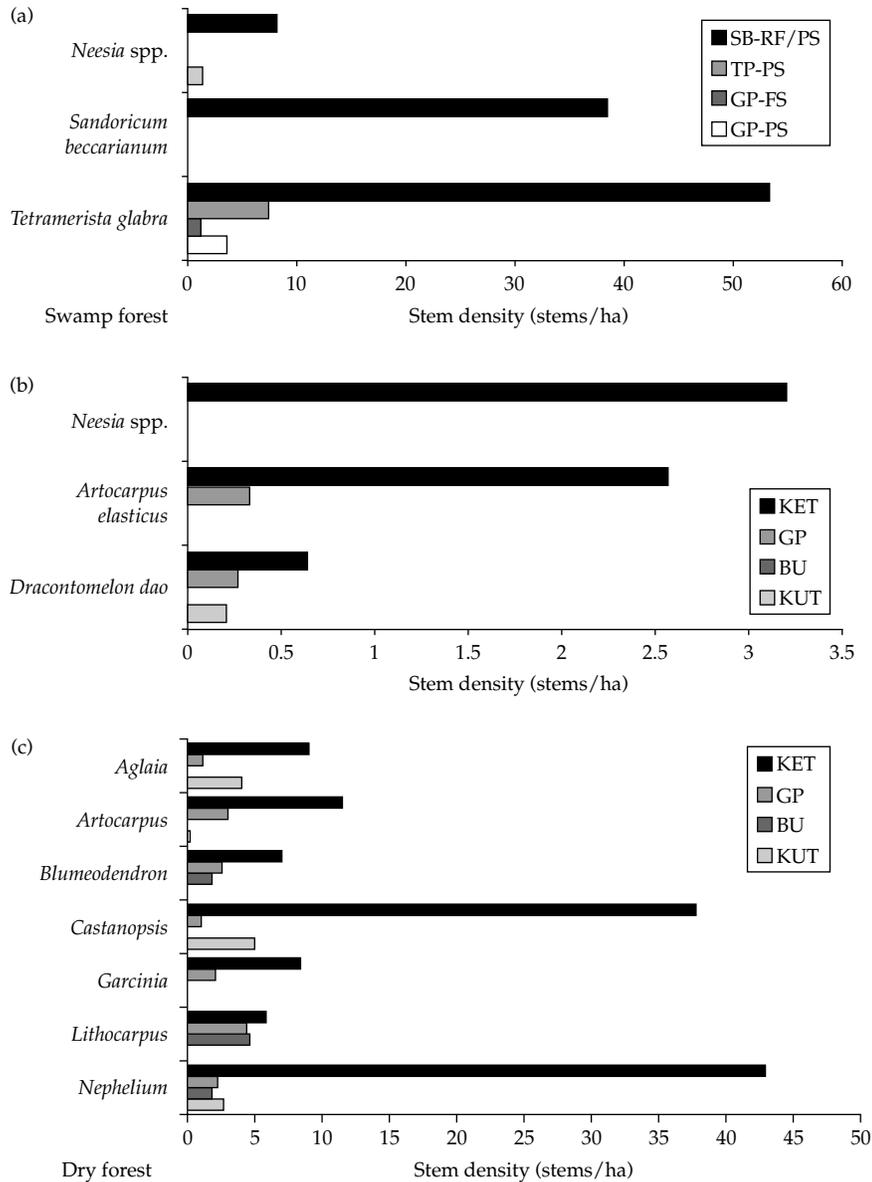


Figure 7.3 Stem density (stems per ha) of commonly eaten orangutan food species in (a) swamp forests and (b) dry forests; and (c) food genera in dry forests. Sumatran sites are indicated with black bars, other sites are on Borneo. For all comparisons the Sumatran site has the highest stem density. Data from Gunung Palung (GP) are the average of plots in the alluvial bench, lowlands sandstone, and lowland granite habitats and Kutai (KUT) data are the average of sandstone and alluvial forest. Note scales on x-axes differ.

highest densities at Barito Ulu (155.2 stems/ha). Although a larger sample will be required before generalizations can be made, these data suggest that dipterocarp densities may be substantially higher on Borneo than on Sumatra. If so, as dipterocarps

comprise a substantial proportion of biomass in Bornean forests, there is less space and are fewer nutrients available for non-dipterocarp trees which may fruit at more regular intervals and/or produce fruits that are more highly prized by orangutans.

Table 7.2 Fruiting frequency of select tree taxa on Borneo and Sumatra

Taxon	Borneo			Sumatra	Sumatra >Borneo
	Unlogged	Logged	Logged >Unlogged	Unlogged	
Aglaia	0.29 (83)	0.18 (11)	No	0.49 (48)	$\chi^2 = 7.75, p = 0.005$
Blumeodendron	0.27 (24)	0.36 (4)	No	0.37 (8)	No
Castanopsis	0.36 (14)	(0)	Not applicable	0.49 (22)	No
Garcinia	0.26 (154)	0.69 (50)	Yes, $z = 4.01 p < 0.0001$	0.94 (7)	$\chi^2 = 13.5, p = 0.0002$
Lithocarpus	0.33 (102)	0.58 (7)	Trend, $z = 1.71 p < 0.08$	0.57 (20)	$\chi^2 = 5.01, p = 0.025$
Litsea	0.25 (54)	0.53 (24)	Yes, $z = 2.75 p < 0.006$	0.47 (14)	No
Nephelium	0.23 (21)	(0)	Not applicable	0.46 (8)	$\chi^2 = 4.04, p = 0.04$
Tetramerista	0.60 (36)	(0)	Not applicable	0.68 (15)	No
Myristicaceae	0.33 (246)	0.33 (52)	No	0.59 (43)	$\chi^2 = 15.6, p < 0.0001$

Cells indicate the mean number of fruit events per year; sample sizes (number of stems) are provided in parentheses. Data are provided from logged and unlogged sites in Borneo. The column entitled 'Logged >Unlogged' shows the results of a two-tailed Mann–Whitney test for differences in fruiting frequency between logged and unlogged sites on Borneo. There were no instances where a taxon at unlogged sites had significantly higher fruiting frequency than at logged sites. The column entitled 'Sumatra>Borneo' shows the results of a two-tailed Mann–Whitney test for differences in fruiting frequency between sites on Borneo and Sumatra. See text for details.

Our final prediction was that fig densities are higher on Sumatra than on Borneo (Hypothesis 11). To increase our sample size for Sumatra we used data on fig densities from four unlogged Sumatran lowland sites: KET, SEK-P, Mamas, and Samarkilang (data from Wich *et al.* 2004a). We used fig densities from the following dryland sites on Borneo: three habitats at GP (Marshall 2004), KUT (Leighton 1993), and KIN (Ancrenaz *et al.* 2004a). Although three of the Sumatran sites (KET, Mamas, and Samarkilang) had far higher stem densities of figs than any of the Bornean sites, overall there was no significant difference in fig stem densities between islands. Differences in data collection methods used at these sites probably serve to reduce the differences between the islands, perhaps obscuring a significant difference. Data from Sumatra indicated the abundance of only large, free-standing strangler figs, while data from Borneo included many smaller figs. A comparison that included more directly comparable measures will be required to test this hypothesis more precisely.

7.6 Ecological correlates of orangutan density

We tested five simple hypotheses about the relationship between orangutan population den-

sity and various ecological measures of habitat productivity, food availability, and seasonality. We tested each hypothesis in two ways using orangutan density estimates from sites for which we had phenology data. First, we used density estimates derived from direct observations of orangutans on line transects (N = 13 locations, Sumatra: KET, SB-DF, SB-PS, SEK-P, SEK-L; Borneo: BU, GP-PS, GP-FS, GP-AB, GP-LS, GP-LG, KUT-AB, TP). Second, we used density estimates derived from nest surveys (N = 12, Sumatra: KET, SB-DF, SB-PS, SEK-P; Borneo: DV, BU, GP-PS, GP-LS, GP-LG, TP, SAB, TUA), using standardized nest density estimates presented in Husson *et al.* (Chapter 6 this volume). We conducted Ordinary Least Squares (OLS) regressions with orangutan population density as the dependent variable. We log + 1 transformed all values due to non-normality, with the exception of density estimates from direct sightings, which were normally distributed and did not require transformation. In general, hypothesis tests using density estimates from direct sightings and from nest surveys produced similar results, although relationships incorporating density from direct sightings were cleaner and more significant. This makes sense as orangutans range widely to track temporal and spatial variation in fruit availability (Singleton and van Schaik 2001; Buij *et al.* 2002), so

point estimates of orangutan population density based on nest transects are likely to be less well correlated with long-term carrying capacities than are estimates based on direct observations, which are generally gathered over substantially longer periods. In the interest of space we present results from direct surveys only—but in all cases hypothesis tests using nest density estimates yielded qualitatively similar patterns.

Some of the hypotheses that we tested were not mutually exclusive. Furthermore, we did not have data from a sufficient number of sites to conduct the full set of multivariate analyses required to examine the relative importance of the proposed ecological factors limiting orangutan population density. Therefore, the following hypothesis tests should be considered preliminary.

Our first hypothesis of this section (Hypothesis 12) postulated that orangutan density would be positively correlated with mean fruit availability. This hypothesis was strongly supported ($N = 13$, $r^2 = 0.76$, $p = 0.0001$). As a follow-up to this hypothesis, we examined whether population density was positively correlated with fruit abundance during HFP (H13) or LFP (H14). The relationship was strong for LFP ($n = 13$, $r^2 = 0.75$, $p = 0.0001$; Fig. 7.4a) and weak for HFP ($n = 13$, $r^2 = 0.23$, $p = 0.09$). In a multiple regression incorporating measures of availability during LFP and HFP, only LFP was significant ($n = 13$, whole model $r^2 = 0.75$, $p = 0.001$; LFP: $b = 2.78$, $t = 4.52$, $p = 0.001$; HFP: $b = 0.01$, $t = 0.57$, $p = 0.98$). We therefore found strong support of Hypothesis 14 but rejected Hypothesis 13.

We also hypothesized that orangutan population density is positively correlated with the stem density of figs (Hypothesis 15). For this comparison we used only sites for which we had orangutan density estimates based on direct sightings and quantitative estimates of *Ficus* stem density. This included two Sumatran sites (KET, SEK-P) and eight Bornean sites (GP-PS, GP-FS, GP-AB, GP-LS, GP-LG, TP, KIN, KUT). When all sites were included there appeared to be a strong relationship ($n = 10$, $r^2 = 0.60$, $p = 0.008$), however this was entirely due to the inclusion of KET, a highly influential outlier. When KET was removed, the relationship between fig density and orangutan density completely dissolved ($n = 9$, $r^2 = 0.004$, $p = 0.87$). Our data therefore

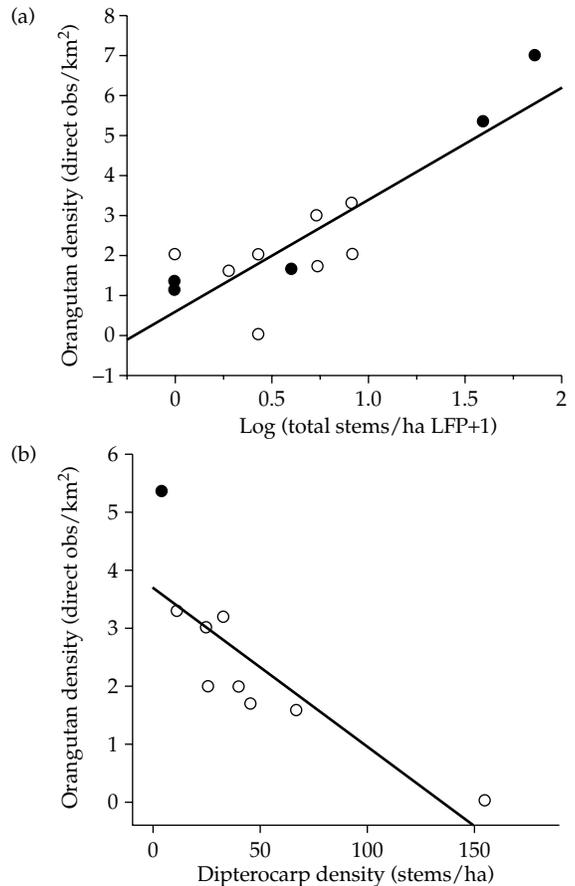


Figure 7.4 Ecological correlates of orangutan population density. (a) Orangutan density is positively correlated with fruit availability during LFP (stems/ha: $n = 13$, $r^2 = 0.75$, $p = 0.0001$) and (b) negatively correlated with the stem density of dipterocarps ($n = 9$, $r^2 = 0.66$, $p = 0.008$). Black circles indicate Sumatran sites, open circles indicate Bornean sites.

do not support the hypothesis that orangutan population density is limited by the stem density of figs.

Our final hypothesis was that orangutan population density is inversely correlated with the stem density of trees in the family Dipterocarpaceae (Hypothesis 16). For this analysis we used only sites for which we had orangutan density estimates based on direct sightings and plot data from which we could calculate the stem density of dipterocarp trees. This included one Sumatran site (KET) and eight Bornean sites (GP-PS, GP-FS, GP-AB, GP-LS,

GP-LG, TP, KIN, BU). We found strong support for this hypothesis, orangutan density was significantly negatively correlated with the stem density of dipterocarp trees ($n = 9$, $r^2 = 0.68$, $p = 0.005$; Fig. 7.4b). This relationship held when the extreme outlier BU was removed ($n = 8$, $r^2 = 0.66$, $p = 0.01$), when the lone Sumatran site was removed ($n = 8$, $r^2 = 0.81$, $p = 0.002$), or when both were removed ($n = 7$, $r^2 = 0.59$, $p = 0.04$).

7.7 Discussion

7.7.1 Comparisons of phenology and floristics

In this chapter we have presented the first broad, quantitative comparison of orangutan habitat quality between Sumatra and Borneo. Our phenological results provide general support for the hypothesis that Sumatran forests are more productive than Bornean forests. For example, the Sumatran sites had a higher percentage of stems in fruit on average and during any given period than did Bornean sites, experienced more frequent high fruit periods than did Bornean sites, and experienced periods of fruit shortage that were rarer, and perhaps also of shorter duration, than did Bornean sites. Our preliminary floristic results indicated that Sumatran forests generally comprise better orangutan habitat than do Bornean forests. For example, compared to the Bornean sites, the Sumatran sites had higher stems densities of figs and some key orangutan food trees, and lower densities of dipterocarp trees. In addition, comparisons of fruiting phenology of key orangutan food trees suggest that some (but not all) genera were more productive on Sumatra than Borneo. Overall, the supposition that Sumatran forests provide a more favorable environment for orangutans than Bornean forests was well supported.

The analysis of data from 12 independent research sites both provided unusual opportunities and imposed serious limitations. The benefits are clear; we were able to conduct a broad comparison of an important ecological hypothesis that would have been impossible using data from only one or two sites. Here we discuss some of the limitations, most of which stem from the fact that this cross-site comparison was a post-hoc exercise. We utilized 12

data sets that were originally collected to address a range of distinct ecological questions. As we compared data sets collected in different locations, at different times, for different durations, and by different people, the possible effects of a number of potential biases require consideration.

The simplest sort of bias that might affect an endeavor such as this is interobserver variation. In theory, if biologists and research assistants working in Sumatran forests were better at finding orangutans or their nests, or systematically biased phenological measures (e.g., by erroneously scoring young leaf buds as immature fruits), then our comparisons would have been compromised. We do not consider this to be a major concern for two reasons. First, we were using simple, replicable indices of fruit presence/absence and nest survey methods that are well established and easily standardized across sites. Second, the work of van Schaik, Wich, and colleagues at Tuanan (Borneo) and Suaq and Ketambe (Sumatra) provide an internal check. The same individuals oversaw data collection (and in some cases gathered data) at locations on both islands, and uncovered the same differences that are apparent in the broader comparisons.

Another type of potential bias was introduced by the fact that data were collected during different periods and for different durations. As phenological patterns are tied to prevailing climatic forces, such as ENSO (Ashton *et al.* 1988; Curran *et al.* 1999; Wich and van Schaik 2000; Cannon *et al.* 2007b), systematic differences between sites on Sumatra and Borneo might have confounded comparisons (e.g., due to global climate change). To test for this, we compared the midpoints of the sampling periods at Sumatran and Bornean sites. There was no systematic bias toward sites on one island being earlier or later ($\text{mean}_{\text{SUM}} = 1997.1$, $\text{mean}_{\text{BOR}} = 1994.5$; $\chi^2 \geq 0.82$, $p = 0.41$). In addition, sampling durations did not differ between sites on the two islands ($\text{mean}_{\text{SUM}} = 77.3$ months, $\text{mean}_{\text{BOR}} = 48.4$ months; $\chi^2 \geq 0.82$, $p = 0.41$). Clearly an ideal comparison would monitor sites over the same periods, however there were no systematic variations in sampling period or duration between sites on the two islands that would obviously bias our results.

Our comparison would also have benefited from including data from a larger number of sites,

particularly on Sumatra. For most comparisons, we were limited to one or two Sumatran sites, which reduces our confidence in the general applicability of our results. This is particularly true of our comparisons of overall fruit production in dryland forests (Hypotheses 1 and 2). In these comparisons, one Sumatran site, Ketambe, was the most productive site, in accordance with our predictions. Yet the other Sumatran dryland forests, at Suaq and Sekundur, were not systematically more productive than Bornean sites. This was not unexpected, as these sites are assumed to have relatively limited nutrient inputs (Wich *et al.* in review). Nevertheless, it raises the question of which site is most representative of Sumatran dryland forests. This will remain an open empirical question until additional data are available for analysis. In addition, small sample sizes limited our statistical power in many analyses.

Finally, we used a relatively coarse measure of fruit productivity to compare sites, namely the percentage of stems with fruit. We used this simple measure as it could be easily extracted from long-term data at each site and directly compared in an unbiased way. However, comparisons of fruit abundance (and ultimately, food availability) between sites could be improved by explicit consideration of crop size and fruit quality (Knott 2005), or better still, fruit trapping.

While some of the potential biases and limitations listed above could not be completely avoided, none of them seem likely to have been the primary cause of the substantial, systematic differences in patterns of phenology and floristics between Sumatra and Borneo that we report. Instead, we interpret our results as evidence in support of the hypothesis that Sumatran forests are better orangutan habitat than Bornean forests. Systematic comparisons of fruit phenology and careful comparisons of floristics at multiple sites on both islands will be required to identify the extent and precise nature of the differences suggested by our results.

7.7.2 Ecological correlates of orangutan population density

Our final set of analyses addressed ecological correlates of orangutan population density. The goal

of these comparisons was to identify which aspects of food availability are most important for limiting orangutan population density. For decades primatologists have sought 'common currencies' that permit direct comparison of food availability or quality among sites (e.g., protein to fiber ratios, pulp weight per patch, food biomass or calories per hectare). This is the ultimate goal, but until sufficient sampling, nutritional analysis, and botanical work are conducted at a range of orangutan sites to permit this comparison, we must rely on relatively simple indices. In addition, as noted above, the question of what limits orangutan population density is an inherently multivariate one, and our sample sizes unfortunately precluded the use of multivariate tests in most comparisons. Nevertheless, our broad sample of phenology and floristics at a range of different sites allows us to uncover several interesting patterns.

Orangutan population density was positively correlated with mean fruit availability across sites. Further analysis indicated that the key element driving this relationship was the availability of food during LFP. This indicates that periodic times of food scarcity (i.e., ecological crunches) are important in setting the carrying capacity for orangutans, as predicted by theory (Cant 1980; Milton 1982; Davies 1994). The implication is that some locations (e.g., Sumatra) or forest types (e.g., peat swamps) sustain higher orangutan population densities because they exhibit less extreme periods of fruit shortage. This suggests that the characteristics of a forest that most directly affect survivorship of females or infants (i.e., the quality and quantity of fallback foods) are more important than characteristics that most directly impact reproduction (i.e., mast frequency, availability of preferred foods) in determining habitat quality for orangutans. This has important implications for orangutan conservation, and for models of orangutan evolution and adaptation.

We did not find support for the hypothesis that orangutan population density is primarily limited by the stem density of figs. Earlier tests of this hypothesis have been mixed, finding support among dryland sites in Sumatra (Wich *et al.* 2004a), but not on Borneo (Marshall *et al.* 2006, 2007, but see Marshall *et al.* in review). At least two explanations

for this inconsistency are possible. The first is that fundamentally different ecological factors limit population density on Borneo and Sumatra. This possibility seems unlikely as the two orangutan species (despite exhibiting differences in many specifics of ecology, social system, and life history) fill fundamentally similar niches and interact with their environments in comparable ways. In addition, although Wich *et al.* (2004a) found that fig density explained variation in Sumatran orangutan density across a range of dryland sites, it did not explain their abundance in Sumatran swamp forests, where figs were largely absent. This suggests a second possibility, that some other ecological factor limits orangutan population density (e.g., food availability during LFP), and that this factor is in turn correlated with fig density in some forest types and locations but not others. Multivariate comparisons that include a larger number of sites and locations will be required to adequately test this hypothesis.

Several primatologists have suggested that the predominance of trees in the Dipterocarpaceae, which normally provide little food for primates, is at least partially responsible for the low primate biomass found in many Malesian forests (Marsh and Wilson 1981; Davies and Payne 1982; Davies 1994). The population density of some South-East Asian primate species has been shown to be negatively correlated with the stem density of dipterocarps, including red leaf monkeys (Davies 1984 in Davies 1994) and long-tailed macaques (Marsh and Wilson 1981). Similarly, we here report a strong negative correlation between orangutan population density and the stem density of dipterocarps. As noted above, this is presumably because orangutans living in forests that are more dominated by dipterocarp trees experience more extreme temporal fluctuations in fruit availability and have fewer non-dipterocarp trees available to them. This relationship may also partly explain why logged forests can often retain substantial densities of orangutans (e.g., Knop *et al.* 2004; Ancrenaz *et al.* 2005; Marshall *et al.* 2006; Meijaard *et al.* 2008). Non-dipterocarp trees and lianas, many of which produce important orangutan foods, may (at least temporarily) flourish in selectively logged forests from which dipterocarps have been removed. This

point emphasizes the potential conservation value of moderately logged forests (Marshall *et al.* 2006; Meijaard and Sheil 2007).

Our results provide support for the hypothesis that Sumatran forests are generally better habitat for orangutans than Bornean forests. This difference in habitat quality is postulated to underpin differences between the morphology, sociality, and life history of Sumatran and Bornean orangutans (Delgado and van Schaik 2000; van Schaik 2004; Wich *et al.* 2004b; Taylor 2006a). A question remains: to what extent do differences between the two orangutan species represent facultative responses to habitat quality, as opposed to deep genetic or temperamental differences between *Pongo abelii* and *P. pygmaeus*? The question is addressed in the final chapter of this volume.

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