

CHAPTER 9.

FAST FOODS OF THE FOREST: THE INFLUENCE OF FIGS ON PRIMATES AND HORNIBILLS ACROSS WALLACE'S LINE

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Abstract

We examine relationships between fruit production and patterns of primate and hornbill densities on Sulawesi and Sumatra, Indonesia. Sumatra lies within the Asian biogeographic realm and has greater biodiversity while Sulawesi lies within Wallacea and has greater endemism. Phenological samples share 51% families, 29% genera but only 7% species. Generally, Sumatran trees are dispersed more often by small birds, bats and squirrels. Sulawesi has more wind-dispersed species. Fruiting is more seasonal on Sulawesi and is related to rainfall while Sumatran fruiting patterns show no relationship with rainfall. Sulawesi has larger trees, larger crops and smaller fruits. Average fruit production is five times higher on Sulawesi. On both islands, figs contribute disproportionately to fruit biomass. Hornbill and primate assemblages are less complex on Sulawesi but biomass of both groups is significantly higher. Hornbills and primates share 41 and 45% of diet species on Sumatra and Sulawesi, respectively. Wide-ranging hornbills on both islands decline in number or leave study areas when fig availability is low. Primates and hornbills (except *Buceros rhinoceros*) do not respond to the availability of other important diet species in the Anacardiaceae, Annonaceae, Meliaceae or Myristicaceae families. Fig availability influences resource defense and grouping patterns of primates and hornbills. We suggest that figs are a keystone guild due to their prime influence on abundance, distribution and behavior of large frugivores in Asia and Wallacea.

Key words: Figs, frugivory, hornbills, Indonesia, primates, Sulawesi, Sumatra

INTRODUCTION

Keystone plants are among the most frequently discussed types of keystone mutualists (Meffe & Carroll, 1994; Peres, 2000; Terborgh, 1986). Keystone plants provide resources such as leaves, flowers, fruits, seeds or even floral nectar or sap to a group of consumers at a level that is much larger than would be expected from their abundance alone (Peres, 2000; Power et al., 1996). Although the definition of keystone species, and therefore keystone plants, has been widely debated (Hulbert,

1997; Power & Mills, 1995; Power et al., 1996), most authors agree that the influence of such species on their communities should be strong and of critical importance to community dynamics. Because of the pivotal roles they play, the loss of keystone plants from a community or ecosystem could have dramatic effects, especially since they should have low ecological redundancy. As conservation biologists, we should be concentrating on identifying potential keystone plants and understanding the degree of complexity, and measuring the strength of interactions provided by such plants. In spite of this, there have been few detailed studies of the population ecology of potential keystone plants and how to recognize them in species-rich plant assemblages (Peres, 2000). Likewise, we know very little about the specific responses of animal communities to the availability of keystone plant resources (Shanahan et al., 2001).

The importance of figs for tropical frugivorous vertebrates, especially birds and primates, has been recognized and figs as a group have been referred to as "keystone species," "keystone mutualists," or a "keystone guild" (Bonaccorso, 1979; Kalko, 1996; Kinnaird et al., 1999; Lambert & Marshall, 1991; Leighton & Leighton, 1983; Terborgh, 1986). Shanahan et al. (2001) show that, conservatively, >10% of the world's birds and >6% of the world's mammals consume figs, making figs the most widely consumed plant genus. The attractiveness of figs for wildlife has been attributed to their asynchronous fruiting patterns, the tendency to produce large crops that ripen synchronously within a tree, the unprotected nature of the fruits and low interannual variation in fruit production (Janzen, 1979). Such fruiting patterns may make figs a reliable food source during times of general fruit scarcity (Foster, 1982; Leighton & Leighton, 1983; Terborgh, 1983; 1986); however, even when other resources are abundant frugivores regularly eat fig fruits (Lambert, 1991; Lambert & Marshall, 1991; Kinnaird et al., 1996, 1999) and in Asia, Wallacea and Australasia, a number of fig specialists have evolved (Shanahan et al., 2001). High concentrations of edible carbohydrates may contribute to the popularity of figs as a food source (Conklin & Wrangham, 1994) even though protein and lipid levels are variable and relatively low (Bronstein & Hoffmann, 1987; Conklin & Wrangham, 1994). Kinnaird et al. (1999), however, found no significant differences in protein and lipid levels for a sample of 20 figs and 35 non-fig fruits from Sulawesi. Additionally, O'Brien et al. (1998) argue that high levels of calcium make figs especially attractive to frugivorous birds and mammals.

Much of the research supporting the importance of figs to wildlife comes from the Neotropics (e.g. Foster, 1982; Kalko et al., 1996; Milton et al., 1982; Terborgh, 1983, 1986). Data from Africa are equivocal and suggest that the keystone role of figs may be context dependent (*sensu* Powers et al. 1996). Guitier-Hion and Michaloud (1989) suggest that figs are unimportant to West African birds and mammals due to their low abundance and low fruit production, while Wrangham et al. (1993) stress the importance of figs to chimpanzees, *Pan troglodytes*, and other frugivores in a Ugandan forest (For more on figs' role in Ugandan forests see Chapman et. al., this volume). In India, Borges (1993) found that fig densities were too low for them to function as keystone species. Several studies from Southeast Asia provide further evidence of the importance of figs to a diverse assemblage of

wildlife including orangutans (Leighton, 1993; Sugardjito et al., 1987), hornbills (Kinnaird et al., 1996; Leighton 1982, Leighton & Leighton 1983) and fruit doves (Lambert 1989). Van Schaik (1996) states that figs may be the single most important wildlife food resource in North Sumatran forests and suggests that wildlife densities may be higher in areas with high densities of large, strangling figs. Similarly, Kinnaird et al. (1999) conclude that the genus *Ficus* is the single most important food resource for Sulawesi's fruit-eating birds and mammals.

Shanahan et al. (2001) argue that research into figs as keystone plant resources must take into account the availability of non-fig fruits versus fig fruits, fig density, fig phenology, and frugivore mobility, and must confirm that figs are suitable for, available to and required by frugivores. Many past studies, although critical in identifying the important role of figs, were short-term, presented data from only one site, and rarely investigated the variability or strength of the interactions between figs and animal guilds, and linkages with other species in the community. Phenological studies, for example, show fig availability at times of community-wide fruit shortage but can only imply that animals will rely on figs during this time. Animal studies on the other hand may show dependence on figs by one or a guild of species, but may not measure the strength of the interaction or if it is context-dependent. Obviously the possible keystone nature of species are best tested experimentally, but such tests are difficult if not impossible in natural systems, and tend to take a long time to show direct and indirect effects (Ernest & Brown, 2001; Power & Mills, 1995).

In this study, we present long-term data on tree fruiting patterns and taxonomic diversity in conjunction with frugivore abundance, feeding ecologies and behavior. Although our study was not experimental, it does allow comparison of communities across two biogeographic regions using similar methods. In particular, we examine the roles of figs in community-wide fruiting patterns and the importance of fruit availability to hornbill and primate assemblages at forest sites on Sumatra and Sulawesi. Specifically, we ask if the contribution to food resource availability by figs at these sites is large relative to their abundance and to the resources produced by the rest of the fruit tree community. We also ask if differences in overall fig availability help explain differences in the capacities of these forests to support their frugivore assemblages, and whether figs influence movement patterns, behavior, and densities in similar ways on these different islands. Finally, by comparing patterns between Asia and Wallacea we may ask if the strength of the interactions vary with fig abundance across spatial and temporal scales and under diverse ecological conditions, or in other words, if the role of figs is context-dependent.

METHODS

Study Sites

Sulawesi – Sulawesi is the third largest island in Indonesia and is the largest and most central island of Wallacea (Figure 1). Wallacea is the remarkable

biogeographical transition zone between Asian and Australasian plants and animals. On Sulawesi, primates of Asian origin co-exist with marsupials of Australasian origin, and Australasian *Casuarina* trees occur sympatrically with Asian Dipterocarps. Due in part to its geologic history, unusual shape and geographic isolation, Sulawesi has a large percentage of endemic birds and mammals. Over 62% of Sulawesi's 127 mammal species are endemic and 27% of the island's 328 bird species are unique, making it one of the most important endemic bird areas in Indonesia (International Council for Bird Preservation 1992).

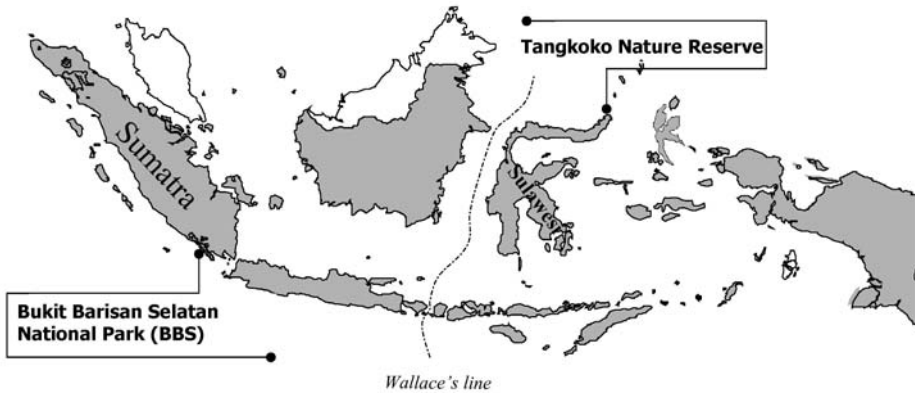


Figure 1. Location of study areas in Indonesia on both sides of Wallace's Line.

The Tangkoko Dua Sudara Nature Reserve (TDS), located on the northernmost tip of Sulawesi ($1^{\circ}34'N$, $125^{\circ}14'E$) is a critically important refuge for Sulawesi's unique bird and mammal fauna (Kinnaird et al., 1996; O'Brien & Kinnaird, 1996; 1997). TDS encompasses approximately 8,900 ha and is isolated from other forests by the sea and by agricultural lands. Forest ranges from sea level to 1,350 m elevation and is broadly classified as lowland tropical rainforest (International Union for Conservation of Nature 1991). Rainfall averages 1,700 mm per year (1992-1994) and is highly seasonal (Figure 2) with occasional droughts associated with the El Niño Southern Oscillation (ENSO; Cahill & Walker, 2000). Volcanoes dominate the reserve: Tangkoko, the recent ash cone, Batu Angus, and the twin peaks of Dua Sudara. Although threatened by agricultural encroachment and severe hunting pressure (O'Brien & Kinnaird, 1996; 2000), TDS supports the largest remaining population of endemic Sulawesi black macaques (*Macaca nigra*). Two hornbill species endemic to Sulawesi occur in TDS, the Sulawesi red-knobbed hornbill (*Aceros cassidix*) and the Tarictic hornbill (*Penelopides exarhatus*). Red-knobbed hornbills at TDS attain some of the highest densities of forest hornbills ever recorded (Kinnaird et al., 1996).

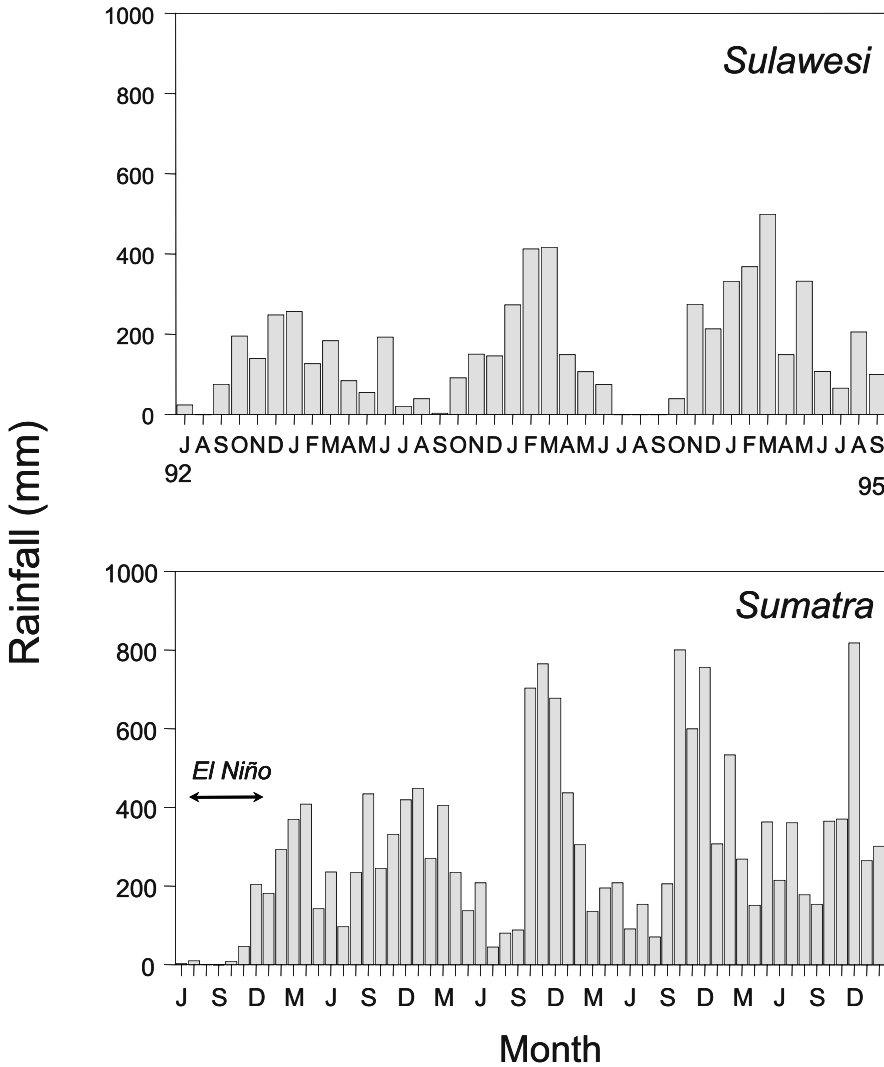


Figure 2. Monthly rainfall (in mm) for TDS and BBS.

We conducted our research from July 1992 through September 1995 within a 440-ha area on the north slope of Tangkoko Volcano. The study area is characterized by a mosaic of habitat types and disturbance regimes including (1) heavily burned areas in which the canopy has been destroyed or severely disturbed (101 ha); (2) 30-year-old regenerating agricultural plots dominated by coconut

(*Cocos nucifera*) and mango (*Mangifera indica*) trees and early successional forest species (25 ha); and (3) lightly disturbed areas with treefall gaps greater than 1 ha in size, or where light fires passed through the understory (271 ha). Forest condition in lightly disturbed areas is highly variable, including broken and closed canopy forest. Closed canopy primary forest accounts for approximately 44 ha and is characterized by large *Palaquium amboinensis*, *Cananga odorata* and *Dracontomelum dao* trees, as well as figs (*Ficus* spp.) and *Livistona rotundifolia* palms. The study area is gridded with trails at 100-m intervals.

Sumatra – Sumatra is Indonesia's second largest island and is characterized by extremely high levels of biodiversity (Whitten et al., 1997). The island's high biodiversity is due, in part, to its size, diversity of habitats, and geologically recent connection to mainland Asia. Sumatran forests are comparable to the forests of Borneo and New Guinea in tree species diversity and contain some unique plant species such as *Rafflesia arnoldii* and *Amorphophallus titanum*, the largest and tallest flowering plants in the world, respectively (Whitten et al., 1997). Sumatra has more mammal species (201) than any other Indonesian island (Payne et al., 1985) and is unusual in supporting populations of most of Asia's large and endangered mammals, including Sumatran tigers (*Panthera tigris sumatrae*), Sumatran rhinoceros (*Dicerorhinus sumatrensis*), elephants (*Elephas maximus*), and Sumatran orang-utans (*Pongo pygmaeus*). Sumatra also has an extremely rich avifauna with an estimated 486 species, but relatively few endemic bird species (21: Whitten et al., 1997).

We conducted research in the Bukit Barisan Selatan National Park (BBS) from July 1997 through February 2002 (Figure 1). BBS is the third largest protected area (3,568 km²) on Sumatra. The park is located in the extreme southwest of the island (4°31' – 5°57'S and 103°34' – 104°43'E) and extends more than 150 km along the Barisan mountain range. BBS contains some of the largest tracts of lowland rainforest remaining on the island and is the major watershed for southwest Sumatra (FAO, 1981). The park's long thin shape gives it more than 700 km of borders adjacent to villages, agriculture and plantation forestry, and poaching and encroachment for logging and agriculture are rife (Kinnaird et al., 2003; O'Brien et al., 2003a). Despite these problems, BBS provides important habitat for a major portion of Sumatra's large charismatic mammals as well as gibbons (*Hylobates agilis* and *Symphalagus syndactylus*: Kinnaird et al., 2003; O'Brien et al., 2003b) and all hornbill species known to occur on the island (O'Brien & Kinnaird, 1996). Annual precipitation ranges from 1,600 mm in dry years to 4,000 mm in wetter years (Figure 2). Although a short dry season generally occurs between June and September, rainfall exceeds 60 mm monthly and the area is considered weakly seasonal (Wright & van Schaik, 1994). Like Sulawesi, Sumatra also experiences periodic ENSO-related droughts (Kinnaird & O'Brien, 1998).

Our study was conducted in WCS/PHKA Way Canguk Research Area, a 900 ha site of lowland forest contiguous with lowland forests of the rest of the park. Intact closed canopy forest covers approximately 492 ha of the study area and is classified into two broad habitat types; the first characterized by tall trees with large diameter-breast-height (DBH) measurements (332 ha) and the second characterized by lower

stature trees with smaller DBHs (160 ha). Disturbed forest covers the remaining 460 ha, is characterized by a more open canopy, a dense understory often dominated by herbaceous plants of the Zingiberaceae family, and generally has experienced ENSO-related fires as recently as 1997. The most recent ENSO fires burned approximately 165 ha of the study area in late September and October 1997 (Kinnaird & O'Brien, 1998). The study area is gridded with trails at 200 m intervals.

Fruit Availability

We established permanent vegetation plots at both study sites to determine densities of fruiting tree species and to monitor fruiting patterns. Plots were larger in size (50 m x 50 m on Sulawesi, 10 m x 50 m on Sumatra) and fewer in number on Sulawesi (22 plots) than Sumatra (100 plots) but represent a similar amount of habitat for the two forests (5.5 ha and 5 ha for Sulawesi and Sumatra, respectively). Plots were placed in stratified random locations along trails throughout the study areas such that there was one plot for every 4-5 ha of forest on Sulawesi and every 8-9 ha of forest on Sumatra. Within plots, we measured, identified and tagged all trees > 10 cm DBH. Because fig trees were underrepresented in the plots at both sites, we established a 2.1 km x 0.02 km transect on Sulawesi and a 7.8 km x 0.1 km transect on Sumatra specifically to monitor fruiting figs.

We visually examined tagged trees for fruit at the beginning of every month. For each fruiting tree, we estimated the total fruit crop using an exponential scale developed by Leighton (1993). We then estimated the percentage of the total crop that was ripe and derived estimates of ripe and unripe fruit crops. Monthly crop production for the entire community was a simple summation; depending on the desired analyses we summed monthly crop production by consumer/disperser type (see below) and by fig and non-fig species separately. We also calculated estimates of monthly fruit biomass by multiplying a species' mean fruit wet weight (Kinnaird & O'Brien, unpublished data) by fruit crops then summing across species. Because we did not have fruit weights for all tree species, we examined the relationship between estimates of fruit biomass and monthly estimates of fruit crop to see if crop could be used as a surrogate for biomass measures of monthly fruit availability. We analysed the relationships by island, using linear regressions (Sokal & Rohlf, 1981) on subsets of non-fig ($N_{\text{Sulawesi}} = 56$, $N_{\text{Sumatra}} = 90$) and fig species ($N_{\text{Sulawesi}} = 21$, $N_{\text{Sumatra}} = 13$) for which we had wet weights. We found significant positive relationships between monthly crop size and fruit biomass for Sulawesi non-fig species ($\ln \text{biomass} = 4.29 + 0.76 \times \ln \text{crop}$; $t = 8.914$, $P < 0.0001$, $N = 24$) and fig species ($\ln \text{fig biomass} = 4.17 + 0.63 \times \ln \text{fig crop}$; $t = 6.14$, $P < 0.0001$, $N = 24$), and a similar, positive relationship for Sumatran non-fig species ($\ln \text{biomass} = 4.78 + 0.76 \times \ln \text{crop}$; $t = 7.63$, $P < 0.0001$, $N = 46$) and fig species ($\ln \text{biomass} = 3.59 + 0.66 \times \ln \text{crop}$; $t = 9.8$, $P < 0.0001$, $N = 46$). We therefore restricted most of our analysis to estimates of fruit crop.

Fruit Classification

In order to examine the effects of spatial and temporal abundance of food resources on particular frugivore densities and population fluctuation, we first classified tree species by frugivore consumers/dispersers. We considered 4 broad fruit classifications: primate, hornbill, wind, and other. The latter category included fruit species consumed by squirrels, bats, and small understory birds. Classifications were made based on our studies of primate and hornbill feeding ecology at both sites (Anggraini et al., 2000; Hadiprakarsa, 2001; Kinnaird, 1998; Kinnaird & O'Brien, 1999; Kinnaird & O'Brien, unpublished data; Kinnaird et al., 1996; Nurcahyo, 2000; O'Brien, 1997; O'Brien & Kinnaird, 1997; Suryadi et al., 1996) and published literature from other sites (Leighton, 1982; Sterck 1995). If a given tree species was consumed by both primates and hornbills, it was classified as a shared resource and monthly estimates of crops were included in fruit crop sums for separate analyses of hornbills and primates. Species classified as 'wind' or 'other' were excluded from the analysis.

Hornbills and Primates

Our study considers the hornbill and diurnal primate communities of northern Sulawesi and southern Sumatra. On Sulawesi, we focused on the island's only two hornbill species, the Sulawesi red-knobbed hornbill (*Aceros cassidix*) and the tarctic hornbill (*Penelopides exarhatus*). Sulawesi contains seven commonly recognized macaque species (Fooden, 1969; Groves, 1980) distributed across the island. Our study concerned the crested black macaque (*Macaca nigra*), which occurs only on the northern peninsula and does not overlap with any of the other macaque species. Southern Sumatra has 9 hornbill species and we concentrated on the five most common species that are known to breed in the study area: rhinoceros (*Buceros rhinoceros*), helmeted (*Rhinoplax vigil*), bushy-crested (*Anorrhinus galeritus*), wreathed (*Rhyticeros undulatus*) and white-crowned (*Berenicornis comatus*) hornbills. Southern Sumatra also has six diurnal primates; we concentrated on the most commonly occurring species, siamangs (*Symphalangus syndactylus*), agile gibbons (*Hylobates agilis*), pig-tail macaques (*Macaca nemistrina*), and banded leaf monkeys (*Presbytis melalophos*).

Density and biomass estimation

We used variable-width line-transect surveys (Burnham et al., 1980; Buckland et al., 1993) to estimate monthly densities of primates and hornbills at both study sites. Surveys were conducted just after completion of phenological sampling and took place between 0600 and 1000 hrs. On Sulawesi, we surveyed red-knobbed hornbills using 10 trails, each 2 km in length with 5 observers simultaneously walking east-west trails 200 m apart (Kinnaird & O'Brien, 1996). A second monthly survey was conducted by a single team on 4 trails, each 4.6 to 5.9 km in length to estimate tarctic hornbill and crested black macaque densities (see O'Brien & Kinnaird,

1996). On Sumatra, three teams of two observers each simultaneously surveyed 12 trails 2.2 kms in length over two mornings followed by 6 trails of 2 kms in length on a third morning. Although Sumatran trails were spaced 200 m apart as on Sulawesi, daily surveys were conducted on alternating trails separated by 400 m. As animals were detected during surveys, we noted the species, number of individuals, detection cue (visual or vocal), location of observer on transect, distance between observer and animal, and compass angle. Compass angle was later converted to angle between observer and animal.

We used DISTANCE software (Laake et al., 1993) to calculate monthly density estimates for the hornbills and crested black macaques on Sulawesi, and for the four most common hornbill species, banded leaf monkeys and pig-tail macaques on Sumatra. Where monthly observations were less than 20, we post-stratified the data and applied a pooled sighting function to monthly data sets. Final models were chosen based on AIC criteria or minimizing the variance due to model selection. Density estimates for territorial gibbons and siamangs were based on complete annual censuses of groups within the Way Canguk study area and range mapping for a subset of these groups.

Biomass estimates for individual hornbill and primate species were calculated as a weighted mean body mass for primate and hornbill species based on published estimates of male, female and juvenile body weights (Kemp, 1995; Rowe, 1996; Smuts et al., 1987), ratio of juveniles to adults and adult sex ratios. We multiplied mean body mass by densities and summed across groups to estimate the biomass of primate and hornbill aggregations for the Sulawesi and Sumatra study sites.

Finally, to test the generality of the relationship between figs and Asian frugivores, we collated density estimates of strangling figs and associated hornbill assemblages using line-transect methods at additional sites on Sulawesi (A. Cahill & J. Walker, unpubl. data), Sumba (Sitompul et al., in press), Seram, and Indonesian Borneo (Kinnaird & O'Brien, unpublished data). We also used published estimates of hornbill and fig density from peninsular Malaysia (Johns, 1983; Whitmore, 1984), Malaysian Borneo (Lambert, 1990; 1991), Indonesian Borneo (Leighton, 1982), and northern Sumatra (Kinnaird et al., 1996; van Schaik, 1996).

Behavior

To assess the degree to which hornbills and primates rely on fruit resources, we conducted studies of the feeding ecology of red-knobbed hornbills (Kinnaird & O'Brien, 1999; Suryadi et al., 1996), tarictic hornbills (O'Brien, 1997), crested black macaques (Kinnaird & O'Brien, 2000; O'Brien & Kinnaird, 1997), four Sumatran hornbill species (Anggraini et al., 2000, Hadiprakarsa & Kinnaird, in press), and siamangs (Nurcahyo 2000, O'Brien et al., 2003b). We also used our unpublished data on Sumatran hornbills delivering food to nests and on siamang diets. Finally, we referred to published literature to estimate the diets of Sumatran macaques, banded leaf monkeys and agile gibbons. Behavioral data on the defense of food resources comes from studies of intergroup interactions and territoriality of crested black macaques (Kinnaird & O'Brien, 1999; 2000), tarictic hornbills (O'Brien,

1997), siamangs (Kinnaird & O'Brien, unpubl. data) and helmeted hornbills (Kinnaird et al., 2003).

RESULTS

Tree Community Composition

Tree community composition differed between the Sumatran and Sulawesi study sites. On Sulawesi, we measured 2021 individuals from 45 families and 88 genera; 163 species were represented including 16 unidentified species. On Sumatra, we measured 2204 individuals from 49 families and 148 genera. Sumatra is far more speciose than Sulawesi, with 304 recognized species and an additional 61 unidentified but distinct species. Over half of the tree families identified (54.8%; Figure 3) occur in both study sites but the two sites share a much lower percentage of genera (29.2%) and species (7.1%). The percentages of unique families were nearly equal for the Sulawesi (21.0%) and Sumatra (24.2%) sites but Sumatra claims a greater percentage of unique genera (51.4%) and species (62.6%) than Sulawesi (19.5 and 30.3%, respectively).

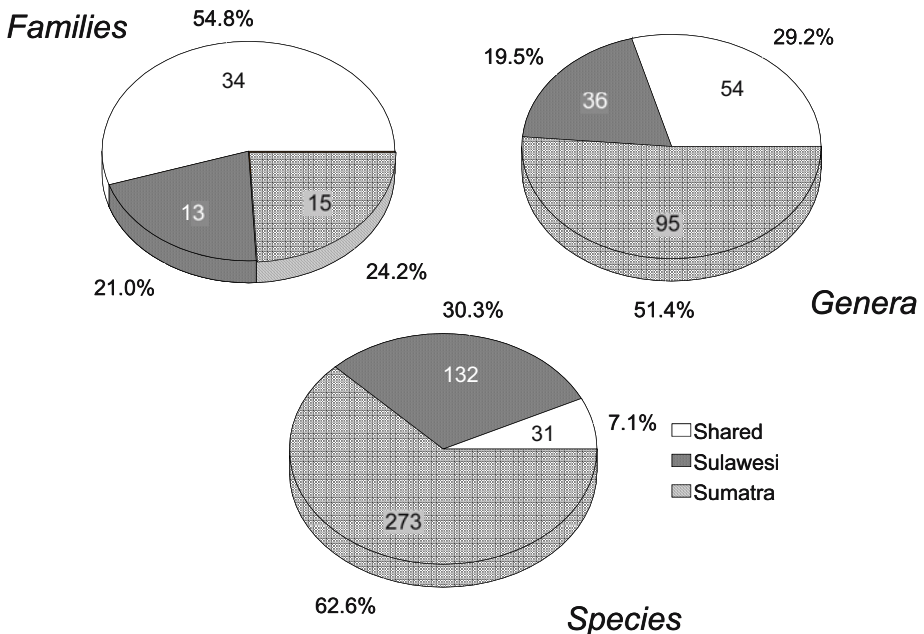


Figure 3. Proportion of tree families, genera and species in samples unique to Sumatra and Sulawesi, and those shared by Sumatra and Sulawesi.

We identified 39 fig species in the TDS study site. Of these, 21 species of figs were identified in plots and transects on Sulawesi for a density of 11.8 figs/ha (115 individuals) in our sample. A second estimate for figs in the study area eaten by hornbills and primates and based on 1.26 km² of transects in the study area is slightly lower at 8.3 figs/ha. In Way Canguk, we identified 32 fig species, including 22 species in the phenological samples, for a density of 1.37/ha (113 individuals). An independent transect survey in Way Canguk gave similar results to the density in the sample.

Fruit Consumers and Dispersers

Primates and hornbills consume the majority of fruit species on Sulawesi (63.9%) and Sumatra (52.6%; Figure 4). Sulawesi is characterized by a greater percentage of wind dispersed species than Sumatra (12.5% vs. 8.27%), while Sumatra has a much larger percentage of fruits consumed by bats, understory birds and squirrels (39.1% vs. 23.6%). Sumatra has a higher diversity of understory fruits compared to Sulawesi. Primates and hornbills show a large degree of overlap in diet species, sharing 45% of all diet species on Sulawesi and 50% on Sumatra. Shared diet species included all *Ficus* species as well as the brightly colored oily drupes of the Lauraceae and Annonaceae families and the dehiscent fruits with lipid rich arils of the Meliaceae and Myristicaceae families. Primates have similar percentages of unique diet species on Sumatra (39.3%) and Sulawesi (39%) while hornbills have a slightly higher percentage of unique diet species on Sulawesi (16.3%) relative to Sumatra (10.6%). Unique primate diet species were of the Euphorbiaceae, Flacourtiaceae, Ebenaceae, Anacardiaceae and Clusiaceae families and were generally dull in color, often hard, and found in the understory or displayed on tree trunks (cauliflorous). Alternatively, the few fruit species unique to hornbills were the larger, dehiscent arillate fruits of the Meliaceae family (i.e. *Chisocheton* spp.), one genera of the Lauraceae (*Litsea* spp.) and fruits of *Canarium* in the family Burseraceae that are protected from primates by urticating hairs.

Fruit and Tree Characteristics

The Sulawesi forest is characterized by having more trees in the larger size classes than that of Sumatra. Frequency distributions of DBH measurements differ significantly between the two sites ($\chi^2=50.99$, $df=9$, $P<0.0001$). Differences are due to greater than expected numbers of trees in the under 20 cm size class in Sumatra, and greater than expected numbers of trees in size classes over 40 cm from Sulawesi (Figure 5). As expected, trees with larger DBH measurements produce larger fruit crops, and crops tend to be larger on Sulawesi than Sumatra ($K-S z_{crop}=2.74$, $P<0.001$). Trees bearing larger crops however, have smaller fruits on both islands ($r_s = -0.30$, $P<0.001$, $N = 178$ species with crop size and fruit weight estimates). Mean fruit weight is significantly heavier on Sumatra than on Sulawesi ($\bar{x}_{Sumatra} = 14.3$ gms, $SE = 2.45$, $N = 139$; $\bar{x}_{Sulawesi} = 6.1$, $SE = 1.6$, $N = 105$;

K-S $z = 1.59$, $P = 0.013$); nearly 20% of the Sumatra fruit samples weigh > 20 gms while only 3.8% of fruits on Sulawesi reach this size (Figure 6). For example, rao (*Dracontomelum dao*) trees produce more, smaller fruits on Sulawesi compared to the fewer, larger fruits produced by these trees on Sumatra. The net effect of the small fruit-large crop relationship is that the distribution of biomass production by the fruit tree communities of Sulawesi and Sumatra is similar on a per species basis. Differences in community-wide fruit biomass should therefore be due to changes in composition of fruit community over time, and changes in the abundance of fruiting trees both by species and for the community overall.

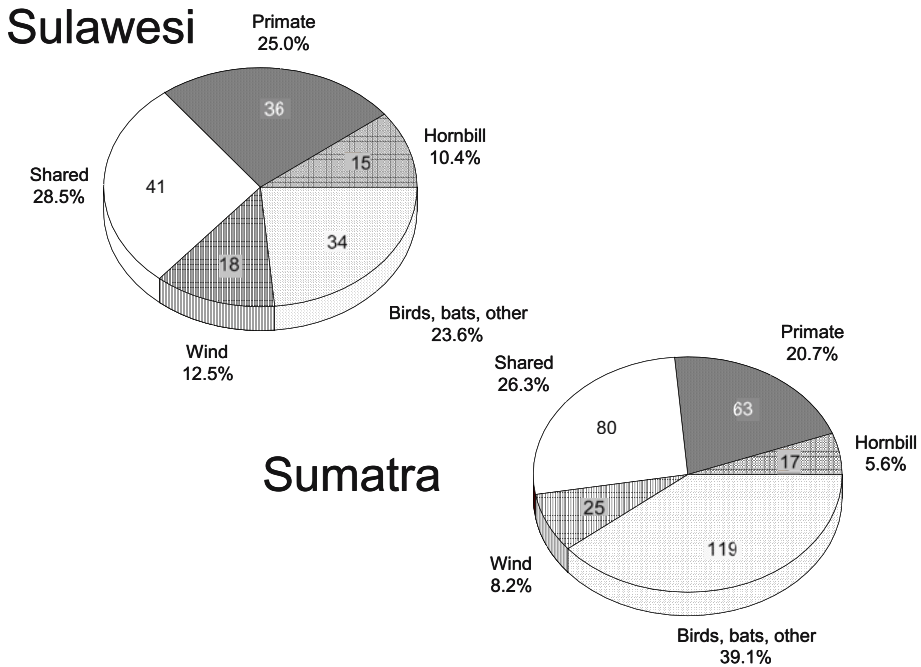


Figure 4. Numbers and percentages of fruit species dispersed by wind and animals on Sulawesi and Sumatra. Shared species are dispersed by hornbills and primates.

Spatio-temporal Patterns of Fruiting

The number of trees in fruit/ha and the total fruit crop produced/ha varied over time at both study sites (Figure 7). Both measures of fruit production were consistently higher for Sulawesi than for Sumatra. More than 40 trees/ha were in fruit during all but 2 months on Sulawesi, while Sumatra had more than 40 trees fruiting/ha during

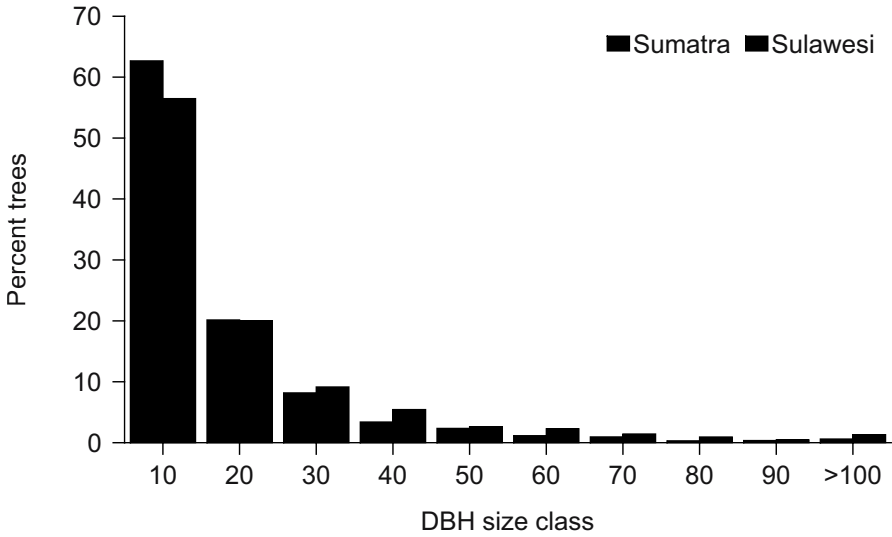


Figure 5. Size distributions of phenology trees (in 10 cm DBH classes) on Sulawesi and Sumatra.

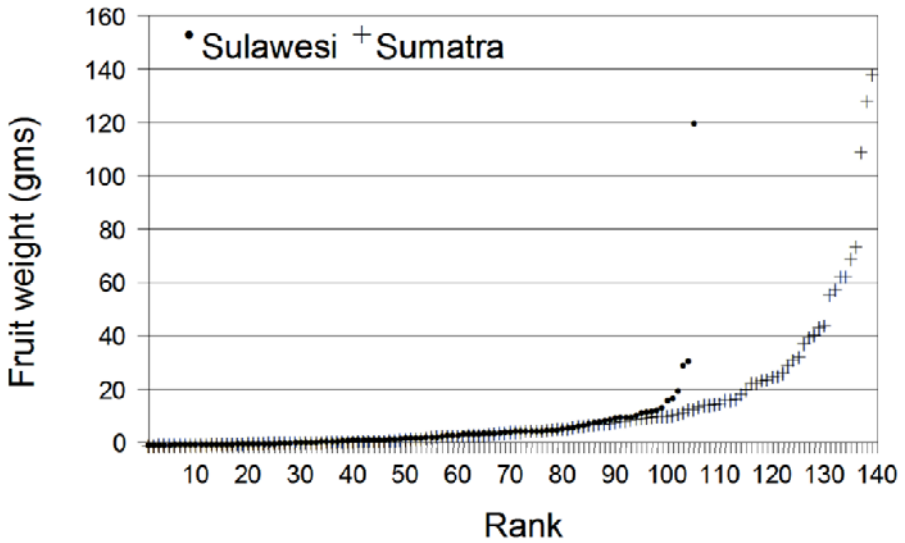


Figure 6. Ranked fruit weights for Sulawesi and Sumatra.

only 4 months. Total crop production varied by orders of magnitude between the two sites; monthly Sulawesi crops measured from hundreds of thousands to millions of fruits while Sumatran crops measured from tens of thousands to hundreds of thousands of fruits (Figure 8). Although figs made up a relatively small percentage of diet trees (hornbill + primate) in fruit at both sites each month, they were available during all months and the contribution of figs to the total monthly fruit crop was large. On average, figs accounted for 2.7% and 3.4% of all fruiting trees/month but contributed more than 64% (maximum 97%) and 50% (maximum 90%) of the total monthly crop production for Sumatra and Sulawesi, respectively.

Mean monthly fruit biomass estimates (kg fruit/ha) calculated from sub-sets of weighed fig and non-fig fruits reflect similar differences in overall fruit availability between the two islands as well as the important contribution of figs. Biomass of non-fig species is, on average, 3.8 times greater (258.4 kg/ha \pm 51.5 vs 51.2 kg/ha \pm 6.4) on Sulawesi than Sumatra. Differences in fig biomass are less dramatic; fig biomass is 1.5 times greater on Sulawesi than Sumatra (32.6 kg/ha \pm 4.8 vs 21.2 kg/ha \pm 1.9). However, figs contribute more to overall mean monthly fruit biomass on Sumatra than Sulawesi (41% and 14.6% of mean monthly fruit biomass, respectively). Estimates of fruit biomass by consumer type (hornbill vs primate) show similar patterns for the two sites. Sulawesi has 4.4 times more primate food per hectare per month (191 \pm 24 kg. vs. 43 \pm 38 kg) and 3 times more hornbill food per hectare per month than Sumatra (55 \pm 7 kg. vs 18 \pm 21 kg). Both island sites have more than twice as much biomass of primate fruits available relative to hornbill fruits.

Fruiting patterns were more seasonal in Sulawesi than Sumatra and were related to rainfall only on Sulawesi. After removing figs from the data sets, monthly crop production on Sulawesi was significantly related to the amount of rain falling one month prior to the fruit sample ($\ln \text{ crop} = 12.42 + 0.0045 \times \text{rain lag1}$; $t=4.36$, $P<0.001$, $N=24$). Fruit crops were not related to rainfall on Sumatra.

Primates of Sulawesi and Sumatra are highly frugivorous with the exception of the banded and silvered leaf monkeys (Table 1). Macaque, siamang and gibbon diets are composed of >60% fruit. Furthermore, macaques, siamangs and gibbons rely heavily on figs for > 40% of the fruit they consume. Only the leaf monkeys, species that specialize on young leaves and unripe seeds, do not consume significant amounts of fruit (Table 1). The fruit portions of macaque, siamang and gibbon diets are highly diverse. For example, crested black macaques eat the fruits of >145 fruit species including 33 species of fig while siamangs eat the fruits of >120 species including 10 species of figs. Although fig species account for only 8-23% of dietary diversity, and only 2.7 to 3.4% of monthly trees in fruit, figs fruits are top diet items for both species in all months, accounting for a major portion of the diet for both species.

For crested black macaques, fruit preference indices based on consumption relative to availability indicate that although figs are highly preferred relative to density (Figure 9; Table 2); densities of individual species are lower than many other food species. Fig preference may be linked to calcium concentrations and associated calcium:phosphorus ratios in figs, the ease of handling, and digestibility.

Black macaques handle figs more rapidly than other fruits. Of the 10 highest fruit ingestion rates (expressed as gms dry matter/min.), 6 are fig species (Kinnaird et al.,1999).

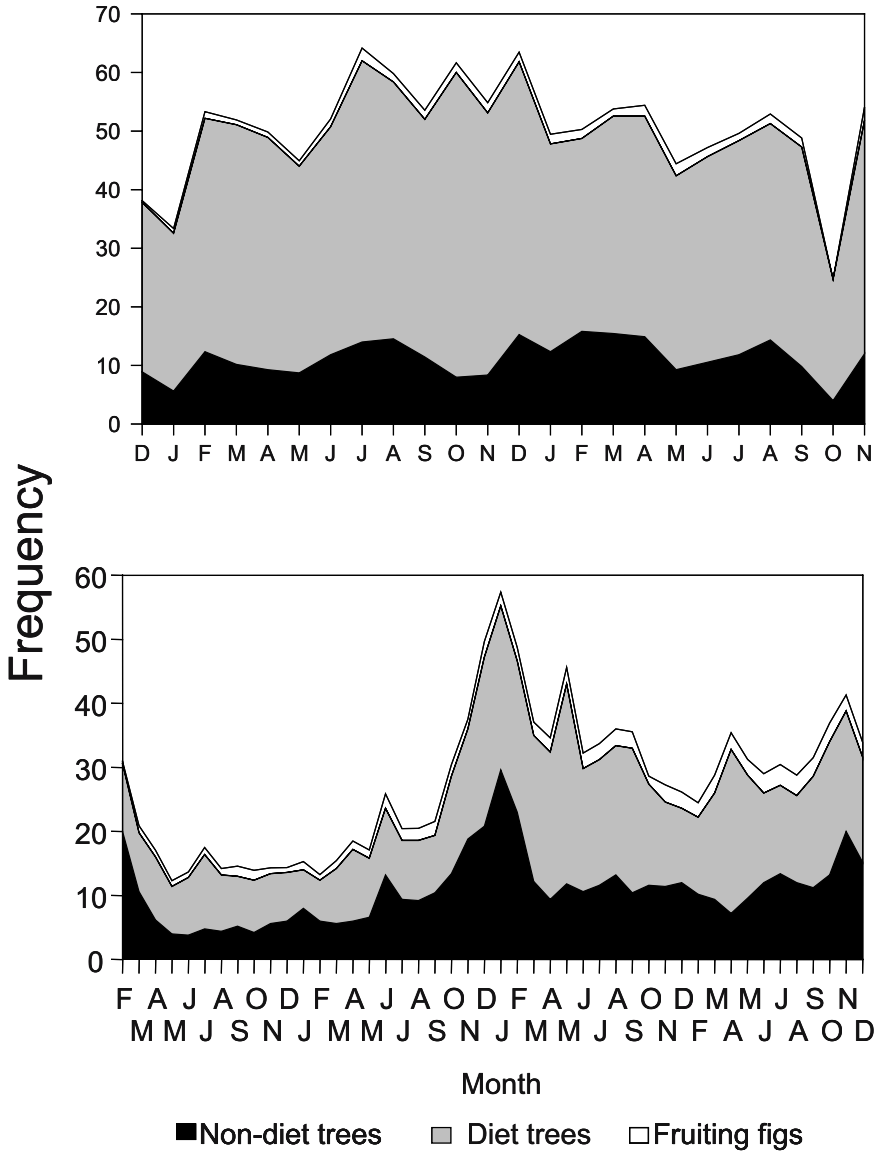


Figure 7. Monthly numbers of fruiting trees for non-diet, diet and fig species.

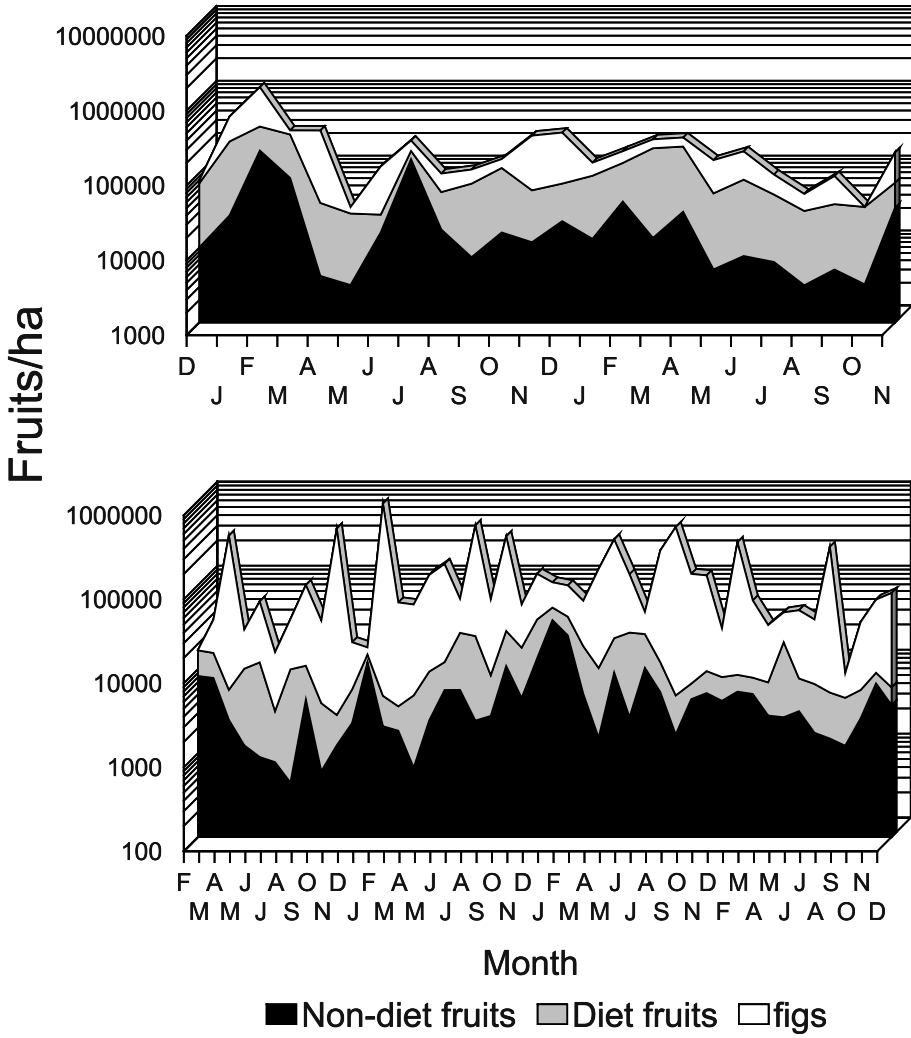


Figure 8. Estimated fruit production for non-diet, diet and fig species.

Table 1. Primate community density, biomass and diet for Sulawesi and Sumatra.

Site	Primate	Territorial	Density (ind/km ²)	Wt. (kg)		Sex ratio Ad:Juv	Biomass (kg/km ²)	% fruit in diet	% fig in fruit diet	
				♀	♂					
Sulawesi	<i>M. nigra</i>	Yes	58	6.6	10.4	3.4	47:53	365.8	68.3	44
	Total							365.8		
Sumatra	<i>H. agilis</i>	Yes	2	5.7	6	1.0	83:17	10.6	65	45
	<i>S. syndactylus</i>	Yes	15.2	10.6	10.9	1.0	66:34	125.0	63	40
	<i>P. melalophus</i>	Yes	23.7	6.6	6.7	>2	50:50	107.1	25	low
	<i>M. nemestrina</i>	No	6.7	7.8	10.4	5.0	50:50	44.5	74	?
	<i>M. fascicularis</i>	No	rare	4.1	5.9	2.5	-		64	40
	<i>T. cristatus</i>	No	rare	8.1	8.6	>2	-		10	rare
	Total							278.2		

Primates vigorously defend figs from conspecifics. Of 182 intergroup encounters between neighboring groups of crested black macaques, 54% were located at fruiting figs. Intergroup encounters escalated into fights with chases, screaming and occasionally grappling and biting as the proportion of figs in the diet increased (Figure 10). Fig consumption accounted for approximately 37% of the variability in proportion of encounters that resulted in fights. Macaques feed for longer periods and in larger foraging groups in figs than in other fruiting plants, and will shift their sleeping trees to monopolize especially fruiting figs. Among siamang groups, intergroup encounters usually involve countercalling between groups at distances less than 100 m. Almost 90% of all siamang intergroup encounters occurred at large fruiting figs.

Is there any other fruit that might elicit a similar response? For primates, rao is an important fruit tree in the family Anacardiaceae. It is a major diet item accounting for 21% of fruit consumed by crested black macaques and 22% of the fruit consumed by siamang. In both study areas, rao are relatively common at 1-2 ind./ha. Still macaques and siamang consume figs twice as often as rao, and neither siamangs nor crested black macaques defend rao.

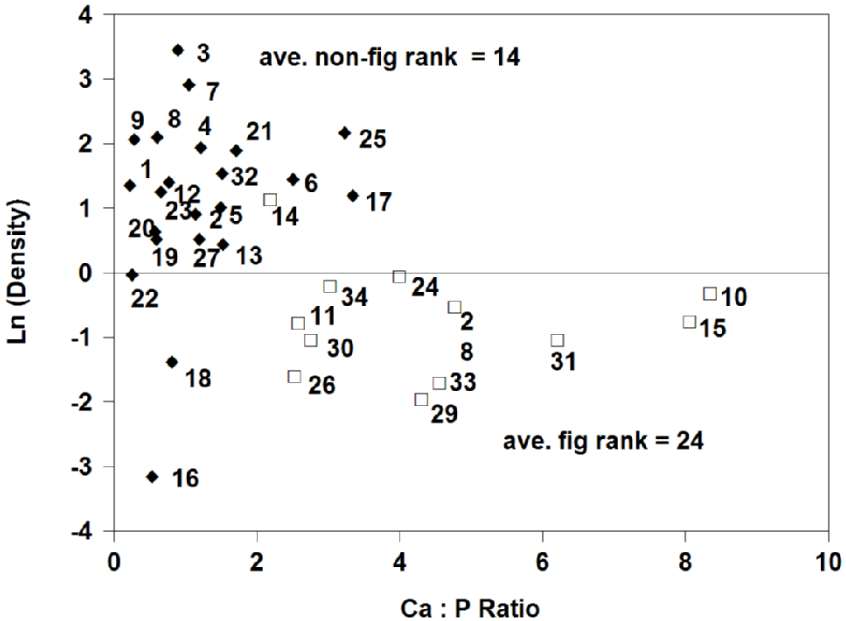


Figure 9. Distribution of fig (open squares) and non-fig (diamonds) fruits by density and Ca:P ratio. Feeding preference ranks of crested black macaques (based on Jacobson's *D*) are given for each fruit species.

Hornbill density and frugivory

As with primates, the hornbill assemblage is more diverse on Sumatra, but overall biomass is much greater on Sulawesi (6 times greater: Table 3). Sulawesi hornbill biomass is dominated by the red-knobbed hornbill with a density greater than all the other hornbills combined.

The hornbills of Sulawesi and Sumatra are more frugivorous than the primates. The diet of every species in our analysis contains > 80% fruit, with the possible exception of white-crowned hornbills (Table 3). Hornbills consume a diversity of fruit species including 56 species on Sulawesi and 74 species on Sumatra. Sulawesi hornbills are more restricted in the families they choose than Sumatra hornbills (Figure 4). Moraceae, Burseraceae, Meliaceae, Myristicaceae, and Annonaceae are the most important families at both sites. The smaller hornbills (≤ 1.5 kg) tend to be territorial, rely more on animal prey and on mid-canopy fruit trees (especially Annonaceae and Meliaceae), and the proportion of figs in their diets is relatively low (18-33% of fruit portion of diet). The larger hornbills (>1.5 kg) are wide-ranging and consume large quantities of figs (73-100% of fruit in diet).

Table 2. Density and rank of density for important diet tree families.

Family	Consumer	Sumatra	Rank	Sulawesi	Rank
Moraceae (Figs)	Both	1.3	10	8.3	6
Anacardiaceae	Primates	6.2	7.5	13.8	4
Annonaceae	Hornbill	44.4	1	29.4	1
Burseraceae	Hornbill	15.2	5	2.5	10
Lauraceae	Hornbill	17.8	4	3.2	8
Clusiaceae	Primates	6.2	7.5	10.5	5
Meliaceae	Hornbill	33	2	5.4	7
Myristicaceae	Hornbill	2.4	9	3.5	9
Ebenaceae	Primates	13.2	6	16.3	3
Euphorbiaceae	Primates	26.2	3	22.0	2

Density fluctuation and fruit resources for non-territorial hornbills

To examine the effect of fruit resources on hornbill movements in and out of the study areas, we restricted our analysis to non-territorial hornbills (*Aceros*, *Rhyticeros*, *Rhinoplax* and *Buceros* species). These genera move over wide areas as determined by variation in monthly estimates and by radio telemetry (red-knobbed hornbills and wreathed hornbills). We compared monthly densities of hornbills to measures of fig and non-fig fruit availability. Non-fig fruits only included known or expected hornbill diet items.

On Sulawesi, red-knobbed hornbill density ranged from 9 to 84 birds/km² during the 24 month study. During 22 months of this study, we also measured fruit supply. The fluctuation in hornbill numbers and distribution of hornbill observations were closely associated with figs, but not with measures of non-fig biomass. Monthly hornbill densities increased significantly with increasing fig biomass ($F=5.43$, $d.f.=3, 18$, $P=0.031$), explaining almost 50% of the variation in hornbill density. Monthly estimates of fig biomass also had a significant positive effect on mean monthly flock size (range = 1 - 101, $F=52.02$, $d.f.=1,20$, $P<0.001$), showing that hornbills congregated in flocks during periods of high fig abundance. Finally, the density of reproductive fig trees influenced the spatial distribution of red-knobbed hornbills; density was higher in hectare blocks with high fig-tree densities ($F=5.02$, $d.f.=1, 67$, $P=0.028$) after controlling for effects of habitat type and breeding season. During the breeding season, radio tracking of males attending nests in the study area showed that although males ranged widely (up to 15 km²), average daily travel distance declined significantly with increasing fig biomass.

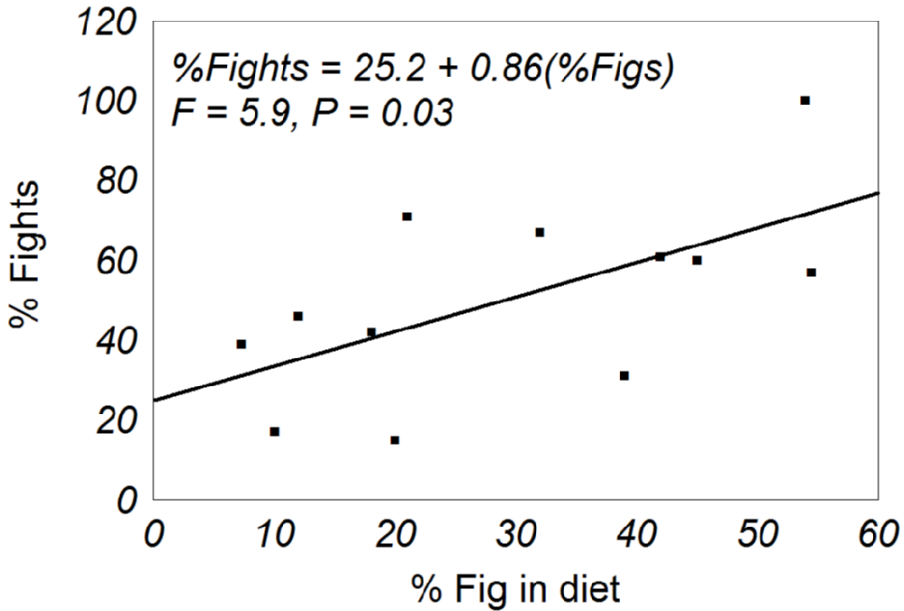


Figure 10. Regression of intergroup fights and % fig in diet for crested black macaques.

On Sumatra, wreathed hornbills appear to react strongly to fluctuations in the abundance and biomass of figs but not other hornbill fruits. Monthly density estimates of wreathed hornbills ranged from 0 to 8 birds/km² and were significantly correlated with changes in ripe fig biomass ($r = 0.37, P=0.011$). Ripe fig biomass was significantly lower ($T=2.88$ $df = 39.7, P=0.006$) in months when wreathed hornbill densities were <1.0 (14 of 46 months).

Among *Buceros* and *Rhinoplax* hornbills, the results were less clear cut. Helmeted hornbill densities fluctuated between 0 and 6.5 birds/km². Densities fell below 1 bird/km² in 9 of 46 months and density exceeded 2 birds/km² in 25 months. Helmeted hornbill densities did not show significant fluctuations with fig biomass on a monthly basis; however, they responded weakly to ripe fig biomass. Ripe fig biomass was lower in the months when density declined below 1 bird/km² ($T=1.92, P= 0.06$). Although we have no evidence that helmeted hornbills are territorial, helmeted hornbills have been observed defending fruiting figs against conspecifics (Kinnaird et al., 2003). The defense involves spectacular aerial jousts in which hornbills fly toward one another and collide casque to casque. These jousts usually involve male-male pairs and usually occur near fruiting figs. Rhinoceros hornbill density ranged from 0 to 4.1 birds/km². This species responded more strongly to monthly fluctuations in the ripe fruit crop of non-fig hornbill foods ($r = 0.34, P=0.02$) than monthly fluctuations in figs.

Table 3. Hornbill community density, biomass and diet for Sulawesi and Sumatra.

Site	Hornbill	Territorial	Density (ind/km ²)	Wt. (kg)	Biomass (kg/km ²)	% fruit in diet	% fig in fruit diet
Sulawesi	<i>A. cassidix</i>	No	51	2.36	120.36	89	88
	<i>P. exarhatus</i>	Yes	2.84	0.46	1.31	85	33
	Total				121.67		
Sumatra	<i>R. undulatus</i>	No	2.28	2.54	5.79	97	73
	<i>A. corrugatus</i>	No	rare	1.59		?	?
	<i>B. rhinoceros</i>	No	1.5	2.58	3.87	98	77
	<i>R. vigil</i>	No	2.3	3.1	7.13	98	100
	<i>B. bicornis</i>	No	rare	3.0		86	66
	<i>B. comatus</i>	Yes	0.76	1.3	0.99	>50	25
	<i>A. galeritus</i>	Yes	1.8	1.17	2.11	81	18
Total					19.89		

Fig density and hornbill communities

We next asked if hornbill density and biomass was related to the density of figs across Southeast Asia and Wallacea. We compared fig densities at eight locations in Southeast Asia and six locations in Wallacea to the density and biomass of the hornbill community at these sites. Fig density had a significant positive effect on hornbill density and abundance irrespective of the number of species involved and the mix of territorial and non-territorial species in the hornbill community (Figure 11). Hornbill density was more closely related to fig density than hornbill biomass.

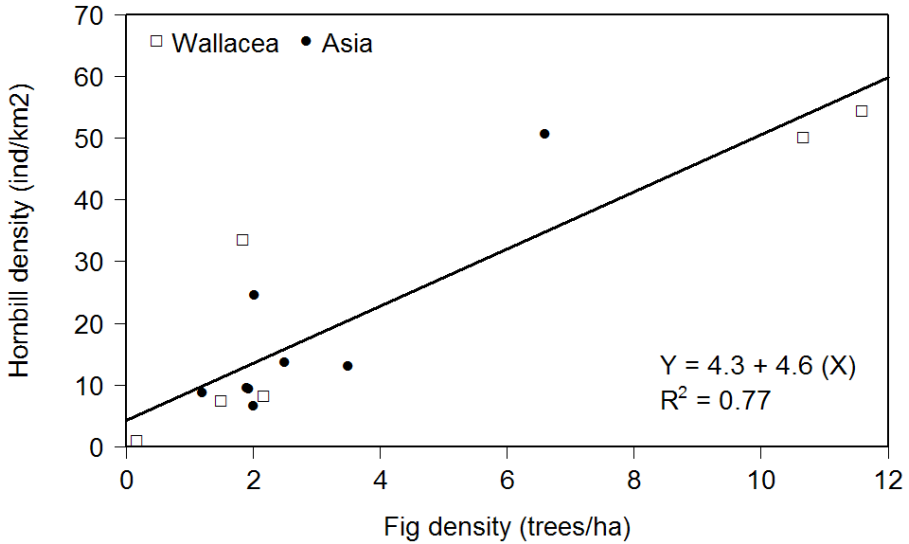


Figure 11. Regression of hornbill density on fig density for Asian and Wallacean hornbill communities.

Figs as strong interactors

We compared the percentage of major tree families in hornbill and primate fruit diets to fruit tree density for the 10 most important hornbill and primate fruits including Anacardiaceae, Annonaceae, Burseraceae, Clusiaceae, Ebenaceae, Euphorbiaceae, Lauraceae, Meliaceae, Moraceae (figs only), and Myristicaceae to test the impact of figs relative to other fruits (Table 2; Figure 12). If diet is proportional to density, we expect that hornbill and primate diets should fall along the diagonal reference line. Fruit families with points falling below the line are considered weak interactors (Powers & Mills, 1995) and those falling high above the line can be considered strong interactors. Contribution to the diets by all families are low relative to abundance, except for the Anacardiaceae, which contribute to macaque and siamang diets as expected given the density. The fig portion of the diet is above the reference line for all species indicating a strong interaction between fig fruits and diets of primates and hornbills.

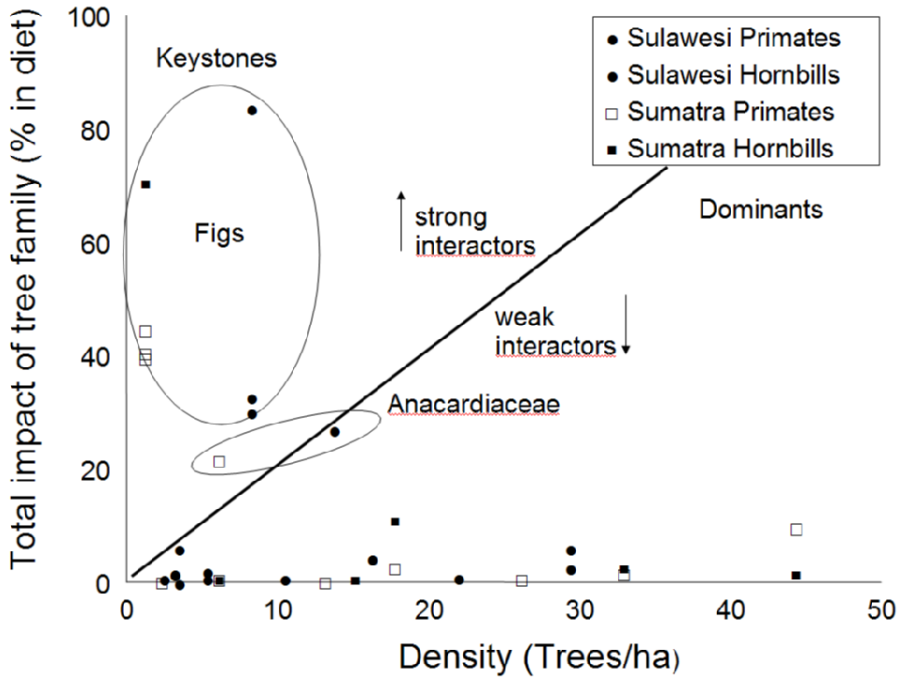


Figure 12. The impact of figs on hornbill and primate communities compared to nine other diet families. Points represent percent of family in diet relative to the density for the family. The diagonal line represents expected % in diet if fruits are consumed proportional to density. Weak interactors are defined as species that are consumed less than expected based on density and strong interactors are species that consumed more than expected based on density. The figure illustrates that common plant species may be dominant in diet but still not be keystone resources.

DISCUSSION

A popular perception of figs is that they attract a diverse group of generalist frugivores that provide poor quality dispersal services in return for a 'low quality' fig reward (Shanahan, 2001), but this is not the case (Kinnaird et al., 1999; O'Brien et al., 1998). Figs appear to be strong interactors in the sites where we work. Our studies have shown that figs affect a number of aspects of hornbill and primate ecology, including community biomass, density fluctuations, diet, movements and social behavior. Our results also point out important differences in fruiting phenologies between Wallacea and Southeast Asia and between forests dominated by dipterocarps and other forest types in Southeast Asia.

In general, fruit production is higher on Sulawesi than on Sumatra. This is true whether we measure production by the number of trees in fruit, the number of fruits produced, or the biomass of fruits produced. Higher fruit biomass may lead to the higher biomass of primates and hornbills as well as the other fruit-eating species we have observed. Sulawesi also produces more fruit consumed by primates and hornbills, as well as a host of other frugivorous birds and mammals. Not surprisingly, densities of pigeons and fruit doves are higher on Sulawesi (Kinnaird et al., 1999, unpublished data) than Sumatra (Rombang, 1999), as are the densities of wild pigs (*Sus celebensis* = 12/km², *Sus scrofa* = 5/km²; O'Brien & Kinnaird, 1996; O'Brien et al. in review). Neither site suffers from the strong and pronounced seasonal effects in fruit production comparable to Barro Colorado Island or Cocha Cashu in the Neotropics (see Milton, this volume, and Stevenson, this volume). Also, neither site suffers from prolonged periods of fruit shortage, as has been reported for dipterocarp dominated forests of Borneo (Leighton and Leighton, 1983) and Malaya (Chivers, 1974).

Fig production is more constant on Sulawesi and Sumatra than has been reported for many sites (Foster, 1982; Kinnaird & O'Brien, 1999; Leighton, 1983; van Schaik, 1996; Terborgh, 1986). On Sulawesi, the high diversity and relatively high density of strangling figs assures that on average, 1 strangling fig is in fruit every month for every 1.3 ha, resulting in 7-10 ripe figs/km² on any given day (Kinnaird et al., 1999). On Sumatra, figs occur at lower densities (@ 1 fig in fruit per month per 6 ha) but many of the strangling figs produce very large crops of large figs, and figs dominate overall fruit production. This is unlike the Neotropics (Janzen, 1979; Terborgh, 1986) where figs fruit asynchronously in populations but synchronously within trees. On Sulawesi and Sumatra we find fig communities composed of aseasonal and asynchronous species, as well as coordinated and highly seasonal species. We also see asynchronous fruiting within a tree and variable temporal fruiting patterns within trees (Kinnaird et al., 1999). Clearly, fig fruiting phenologies are complex and encompass the gamut of possibilities.

The extreme reliance on figs by non-territorial primates and hornbills suggests that seasonal movements may reflect tracking of fig resources (Kinnaird et al., 1996) rather than tracking general fruit production (van Schaik, 1996; Terborgh, 1986) or other specialized subsets of fruits (e.g. lipid rich fruits, Leighton, 1983). Resource tracking may take place over a local scale (a few km² or tens of km²: Kinnaird et al., 1996) or a regional scale (100's to 1,000's of km²: Curran & Leighton, 2000). Tracking supra-annual fruit production through migration (sometimes called nomadism) requires a reliable environmental cue that assures a shift in location will result in finding a resource (e.g. food or reproductive sites). Should an environmental cue fail to provide the proper information, the cost of long distance movement may be starvation or reproductive failure. The patterns of supra-annual fruiting that seem characteristic of trees in eastern Borneo (Leighton, 1983), western Borneo (Curran et al., 2001) and northern Sumatra (van Schaik, 1996) are much more difficult to track regionally or locally compared to seasonal variation in fruit production. Wandering over a large landscape in search of localized fruiting peaks associated with weather phenomena such as ENSO events (Curran & Leighton,

2000) does not seem an efficient strategy when ENSO events occur at 3-6 year intervals (Strahle et al., 1998; Curran & Leighton, 2000). Counter-intuitively, the asynchrony of fig fruiting may produce the most dependable fruit resource in an ecosystem characterized by short booms in fruit production followed by long periods of low fruiting. Wandering over a localized landscape of 10-50 km² in search of fruiting figs may be a more viable alternative for surviving boom and bust cycles of fruit production.

Fig specialization is more widespread in the Old World than in the Neotropics and more widespread in Asia and Australasia than in Africa (Shanahan et al., 2001; Chapman et al., this volume). In Asia, the evolution of a host of fig specialists, including hornbills, *Chloropsis* leafbirds, fairy bluebird, *Treron*, *Ducula*, and *Ptilinopus* pigeons, barbets, birds of paradise, Asian koel, channel-billed cuckoo, several parrots, gibbons, binturongs, *Pteropus* and *Cynopterus* fruit bats suggest that tracking keystone figs resources is a viable strategy. Evolution of food specialization requires a certain stability of resources such that dependencies can develop and this indirectly argues that figs represent a stable food source.

Territoriality by tropical frugivores also requires reliable fruit production in small areas, often less than 1-2 km², or the ability to subsist on alternate diet items. Territorial species that utilize supra-annual fruit resources will have to rely primarily on small fruit crops within a territory, or have the ability to shift to alternate food sources, such as animal prey, leaves or gum. Many small-bodied, territorial hornbills appear to follow this strategy, but still manage to find figs for a substantial portion of their diet (Leighton, 1982; O'Brien, 1997; Poonswad et al., 1987). Alternatively, if fig densities are sufficient, territorial defense may develop around figs whenever a species can successfully exclude conspecifics from the resources. The reliance on a diverse array of small fruit crops then becomes a strategy for getting through times of fig scarcity rather than the other way around. Given the unreliability of fruit production in Southeast Asia, it is hard to envision large frugivorous birds and mammals becoming territorial, yet all gibbon species are territorial and among Asian hornbills there are more territorial than non-territorial species. We suspect that figs play a keystone role in filling the fruit shortfall for territorial frugivores in Asian forests.

The overwhelming contribution of figs to the diets of primates (orangutans, gibbons, macaques) and hornbills, and the attempted defense of figs by primates and hornbills (Kinnaird et al., 2003; Leighton 1982) strongly suggest that figs have played a fundamental role in shaping the frugivore communities of Southeast Asia and Wallacea. This in turn may have profound indirect effects on the rest of the fruit tree community via dispersal services of frugivores that, while relying on figs, consume and disperse the seeds of other rainforest plants. Kinnaird (1998) demonstrated that Sulawesi red-knobbed hornbills moved seeds of 33 diet species to germination sites while feeding primarily on fig fruits. Studies of fruit delivery to the nest suggest similar dispersal capabilities for many other hornbill species (Kinnaird & O'Brien, unpublished data; O'Brien, 1997; Poonswad et al., 1987). Primates also are well known seed dispersers. Siamang, for example, swallow seeds of *rao* and *Polyalthia* spp whole and move them hundreds of meters throughout

their home ranges (O'Brien & Kinnaird, unpublished data; Rusmanto, 2002). Macaques typically stuff their cheek pouches with whole fruits, and move away from the parent trees where they scrape the mesocarp and deposit seeds intact. In Tangkoko, macaque groups' daily movement patterns often are between fruiting figs, and they feed on other species en route.

Finally, figs are strong interactors. They are important relative to abundance and relative to gross nutrient award. While other fruits may yield higher energetic rewards, long handling times and problems of digestibility may reduce the attractiveness of many fruits, and small fruit crops may increase search times relative to figs. Therefore, it makes sense that figs should be preferred wherever they are abundant enough to be locally reliable resources. The question then becomes what is the density threshold for reliability.

To be a territorial species and rely on figs, a species probably needs enough figs in the territory to produce at least one fruit tree every month. Territory size, therefore, may be a function of fig density. For a territorial hornbill to rely on figs for a third of the diet may require that a fig be producing ripe fruit for approximately 10 days per month. A minimum density of 12 figs/home range will suffice, on average, if the probabilities of fruiting are equal for all months. Higher densities improve the probability of ripe fig availability. At some point fig density is so low that the asynchrony and aseasonality of fig production becomes a cost rather than a benefit because figs become unreliable fruit sources or the territory becomes undefendable. The question of context dependency will only be resolved by replicated studies of territorial and nonterritorial frugivore species across a range of sites characterized by different densities of fig resources.

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