

POPULATION FLUCTUATION IN SULAWESI RED-KNOBBED HORNBILLS: TRACKING FIGS IN SPACE AND TIME

MARGARET F. KINNAIRD¹, TIMOTHY G. O'BRIEN¹,
AND SUER SURYADI²

¹Wildlife Conservation Society, 185th and Southern Blvd., Bronx, New York 10460, USA; and

²Center for Biodiversity and Conservation Studies, Faculty of Mathematics and Sciences,
University of Indonesia, Depok 16424, Indonesia

ABSTRACT.—We studied spatial and temporal variation in a population of Sulawesi Red-knobbed Hornbills (*Aceros cassidix*) in relation to availability of fruit resources over a two-year period in the Tangkoko DuaSudara Nature Reserve, North Sulawesi, Indonesia. Fruit production did not show any discernable patterns over 22 months of study, in spite of the strong seasonality of rainfall. Figs were available in all months of the year, and fig biomass exceeded ripe nonfig-fruit biomass in 10 of 22 months. Hornbill densities fluctuated dramatically over time (\bar{x} = 51 birds·km⁻², range 9.3–82.7) and among habitats. Spatial and temporal variation in hornbill numbers was best explained by habitat selection and the abundance and distribution of figs. Hornbill numbers were higher in those areas with greater densities of fig trees, and monthly hornbill densities and mean flock size increased with increasing fig biomass. Because Sulawesi Red-knobbed Hornbills appear to track fig production over potentially large distances, and include a mix of other rainforest tree species in their diet, we hypothesize that they may play an important role as agents of rainforest regeneration. Received 22 June 1995, accepted 13 September 1995.

AVIAN POPULATION FLUCTUATIONS have been shown to arise primarily from random demographic processes (Karr 1982, Boag and Grant 1984, DeSante and Geupel 1987) and movement of individuals within and among habitats (Greenberg 1981, Karr and Freemark 1983, Wheelwright 1983). Individuals move in response to seasonal climatic changes (Root 1988), breeding (Robinson 1992), or the temporal and spatial variation in food resources (Wheelwright 1983, Levey 1988, Blake and Loiselle 1991, Powell and Bjork 1994). Studies in the New World tropics emphasized the importance of fruit-resource availability on the spatial and temporal population fluctuations of frugivorous birds (Skutch 1967, Karr 1982, Stiles 1985, Levey 1988, Blake and Loiselle 1991, Loiselle and Blake 1991). In the Old World tropics, particularly Asia, studies providing concurrent data on fluctuations in both frugivore populations and fruit abundance are lacking (but see Leighton and Leighton 1983). This results in part from extremely low capture rates for frugivorous birds in Asian forests (Fogden 1972, Wong 1985), which in turn may be due to the low percentage of understory and canopy trees bearing edible fruit species relative to the Neotropics (Fogden 1972, Medway 1972).

Communitywide fluctuations in fruit resources may not be sufficient to explain fluctuations in populations of avian frugivores that specialize on a subset of the fruit community, or are capable of switching to invertebrate prey. Wheelwright (1983) illustrated the importance of one family (Lauraceae) in the diet of Resplendent Quetzals (*Pharomachrus mocinno*); fluctuations in abundance of Lauraceae triggers altitudinal migrations in search of these fruits (Powell and Bjork 1994). Plant taxa that fruit outside community peaks in fruit production, such as figs (*Ficus* spp.) or palms, may be important in maintaining populations of more sedentary frugivores (Terborgh 1986, Lambert and Marshall 1991).

Lambert and Marshall (1991) argued that figs play an important role in maintaining populations of frugivores like flowerpeckers (Dicaeidae) and green pigeons (*Treron* spp.) during periods of general fruit scarcity. Leighton (1986) discussed responses to fig availability by a community of Bornean hornbills. Species that include large quantities of figs in their diet, such as the Wreathed Hornbill (*Aceros undulatus*), are believed to move long distances in search of patchy fruit resources, producing local fluctuations in population size. Territorial hornbills,

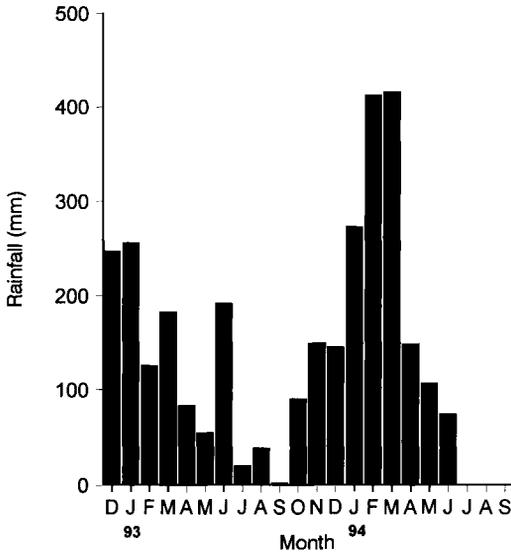


Fig. 1. Monthly rainfall (mm) in study area over 22 months.

such as the Bushy-crested Hornbill (*Anorrhinus galeritus*), increase the proportion of invertebrate prey in the diet during periods of fruit scarcity, and population size remains relatively constant.

The Sulawesi Red-knobbed Hornbill (*Aceros cassidix*; formally *Rhyticeros cassidix* and hereafter referred to as the Red-knobbed Hornbill) is a large (2.5 kg), canopy-fruit specialist endemic to the Indonesian island of Sulawesi (White and Bruce 1986). It is nonterritorial and sympatric with only one other hornbill, the Sulawesi Tarictic Hornbill (*Penelopides exarhatus*). Recent studies have focussed exclusively on breeding biology (Kinnaird and O'Brien 1993, Kinnaird in prep.) and feeding ecology (Suryadi et al. 1994). Red-knobbed Hornbills nest in natural cavities of large forest trees and are capable of attaining high nesting densities. Breeding begins in late June during the dry season; fledging occurs from late December through early January, soon after the onset of the wet season (Kinnaird and O'Brien 1993). Fledging success is typically high (Kinnaird unpubl. data). Red-knobbed Hornbills are a major component of the Sulawesi frugivore community and, although they prefer ripe fig fruits (*Ficus* spp.), they consume fruits and presumably disperse the seeds of a wide range of tree species (Kinnaird and O'Brien 1993, Suryadi et al. 1994).

We collected data on the spatial and temporal variation of a population of Red-knobbed Horn-

bills in North Sulawesi. Concurrently, we collected data on fruit production and asked if population fluctuation and patterns of hornbill distribution could be explained by the abundance and distribution of fruit resources. Because of the importance of figs in the Red-knobbed Hornbill diet (Kinnaird and O'Brien 1993, Suryadi et al. 1994), we compared the response of the hornbill population to fluctuations in figs (i.e. synchronia) versus nonfig fruit resources.

METHODS

Study area.—We conducted our research in the Tangkoko DuaSudara Nature Reserve on the northernmost tip of the Indonesian island of Sulawesi (1°34'N, 125°14'E). The Reserve encompasses approximately 8,900 ha and is isolated from other forests by sea and 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 (Fig. 1), with occasional droughts. The reserve is dominated by three volcanoes: Tangkoko, the recent ash cone Batu Angus, and the twin peaks of DuaSudara. Our study was conducted within a 441-ha area on the north slope of Tangkoko Volcano. The study area is characterized by a mosaic of habitat types and disturbance regimes (O'Brien and Kinnaird unpubl. data). Disturbance regimes include: (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 (e.g. Anacardiaceae and Euphorbiaceae; 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.

Hornbills.—We used line-transect surveys to estimate monthly distributions and densities of hornbills over 24 months (October 1992–September 1994). Line transect method is appropriate for Red-knobbed Hornbills because they are large and easily seen and call loudly; also, during flight they produce a loud sound as air passes through the primaries that can be heard up to 100 m away. Red-knobbed Hornbills are sexually dimorphic in size, plumage, and vocalizations, allowing easy classification of sexes during censuses. One day of each month we surveyed 10 trails, each 2 km in length. Surveys began at 0600 and ended before 1000. Five observers simultaneously walked

east-west trails 200 m apart and noted time, initial cue (visual, vocal or wing beat), number, age and sex (when possible), and estimated perpendicular distance from trail to bird or flocks. To prevent double counting, a maximum strip width was used (100 m on a side) to map each bird. All mapped data were compared by location and time of observation and possible double counts were eliminated.

Fruit.—Beginning December 1992, fruit resources were estimated each month just prior to a hornbill census. We monitored 2,015 trees for fruit, representing about 168 species, in 22 0.25-ha plots. An additional 2.1-km transect was established specifically to monitor fruiting of fig trees that were underrepresented in the plots. For each fruiting tree, the number of ripe and unripe fruits was estimated on an exponential scale following Leighton (1982, 1993). Monthly biomass of ripe and unripe fruit was calculated by multiplying a species' mean fruit wet mass (O'Brien unpubl. data) by its fruit crops, then summing across species. We calculated monthly fruit biomass for the entire community and then partitioned biomass estimates for figs and nonfigs.

Fig census.—To calculate distribution and density of fig (*Ficus* spp.) trees, we counted all canopy-sized figs within 15 m of either side of 20 trails for a total of 42 km. Figs were identified by species and density estimates for all species combined were calculated for each hectare block. *Ficus variegatus*, the most common fig species, was not included in the census because it was known not to be important to hornbills.

Analyses.—We used the computer program DISTANCE (Laake et al. 1993) to calculate monthly hornbill densities. Data were grouped into 10-m intervals and evaluated using three models to fit detection-probability functions: uniform, half-normal and hazard. Each model used cosine-adjustment terms; models were fit sequentially until no further improvement was gained by adding cosine terms. We chose models that minimized the coefficient of variation associated with density estimates. Data were insufficient to calculate monthly densities by habitat using DISTANCE models. To evaluate the monthly distribution of hornbills by habitat, we calculated observed densities per month in each habitat by summing all hornbills observed in hectare blocks of a given habitat and divided by the total number of hectares represented by each habitat.

We used analysis of covariance (ANCOVA; Sokal and Rohlf 1981) to examine the effect of habitat type and breeding season on monthly hornbill densities, using fig-tree density as a covariate. Fig-tree density was estimated monthly for only those hectare blocks in which birds were observed. We eliminated hectare blocks with zero observations because we were concerned with habitat choices on a monthly basis. Inclusion of blocks with no birds in the estimate of fig densities eliminates monthly variability. This analysis, therefore, assumes that birds are choosing hectare blocks within a habitat that have a high probability

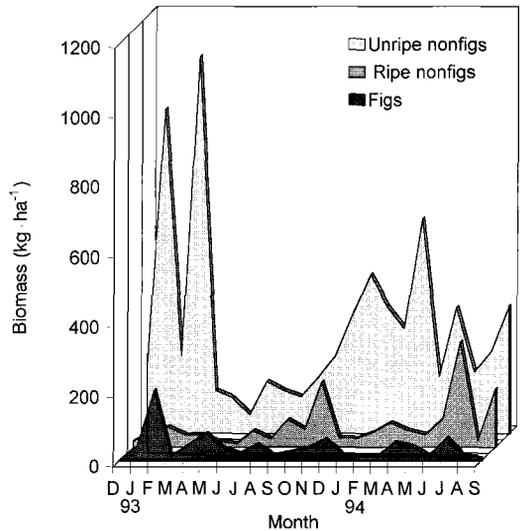


Fig. 2. Monthly estimates of fruit biomass for fig and nonfig fruits. Nonfig fruits are partitioned into estimates of ripe- and unripe-fruit biomass.

of a fruit crop in a given month. Significant differences among habitat types and between the breeding and nonbreeding seasons were examined using Duncan's multiple range tests. The ANCOVA model was tested using Type III sums of squares.

We examined relationships between monthly hornbill densities and estimates of fruit biomass for figs and nonfig-fruit trees using multiple-regression analysis. Because hornbills feed preferentially on fleshy fruits or husked fruits with fleshy arils (Leighton 1982, Suryadi et al. 1994) in the canopy and mid-canopy, we eliminated all wind-dispersed, understory and leguminous species from estimates of monthly nonfig-fruit biomass. The remaining sample comprised 85 species of which 732 individuals of 66 species fruited at least once. The fig sample was comprised of 18 species, represented by 73 individuals of which 59 fruited during the study. Nonfig-fruit biomass was partitioned into ripe and unripe biomass. Because fig crops tend to ripen quickly and simultaneously (Janzen 1979, Lambert and Marshall 1991), estimates of unripe fig biomass were not analyzed separately. We also examined relationships between mean numbers of hornbills in flocks and estimates of fruit biomass using correlation and regression analyses. We used Statistical Analysis System software (SAS Institute 1985) for all analyses.

RESULTS

Fruits.—Total fruit biomass varied over time, but did not show any discernable patterns over 22 months of study, in spite of the strong seasonality of rainfall (Figs. 1 and 2). Nonfig-fruit

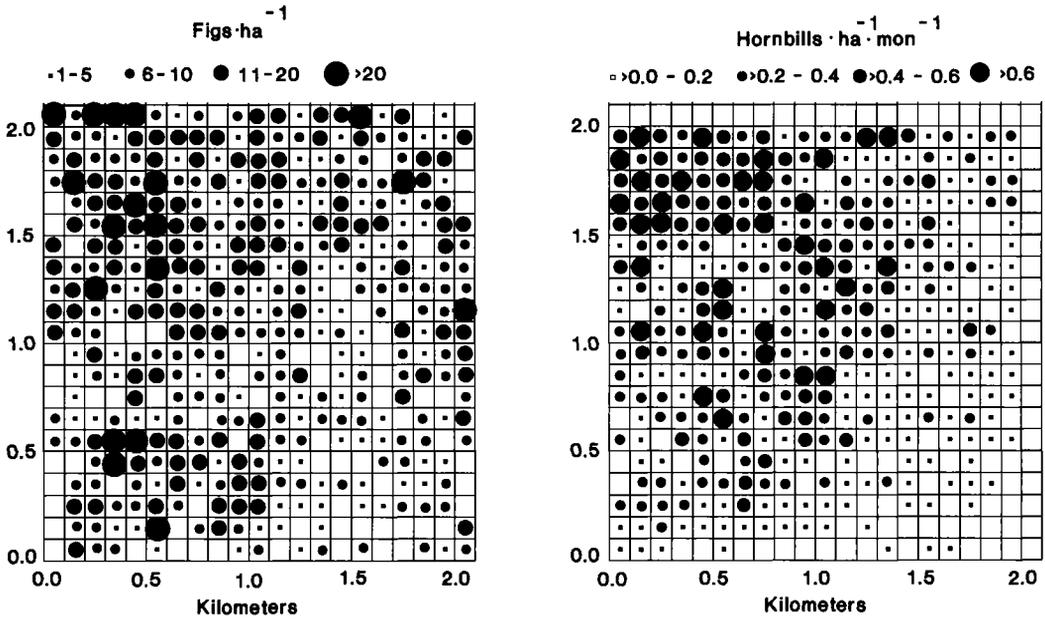


Fig. 3. Distribution of *Ficus* trees and mean monthly hornbill sightings in study area.

production fluctuated more widely than that for figs, and these fluctuations suggested a weak association with monthly rainfall, although the association did not reach statistical significance (Spearman's $r = 0.402$, $P = 0.06$, $n = 22$). Major

peaks in ripe-fruit production were less than 6 months apart, with 10 months of generally low fruiting before the first peak. Unripe-fruit biomass was higher than ripe-fruit biomass in all months except July 1994. This reflects the dominance of a few species with extremely large crops that mature slowly and nonsynchronously within a tree (e.g. *Dracontomelum dao* and *Palaequium amboinense*). The fig community exhibited an asynchronous fruiting phenology, with no recurrent annual pattern. Figs were available in all months of the year; crops often ranged from 100,000 to 1,000,000 fruits per tree for large, strangling figs (e.g. *F. virens*). Fig-fruit biomass exceeded ripe nonfig-fruit biomass in 10 of the 22 months of study.

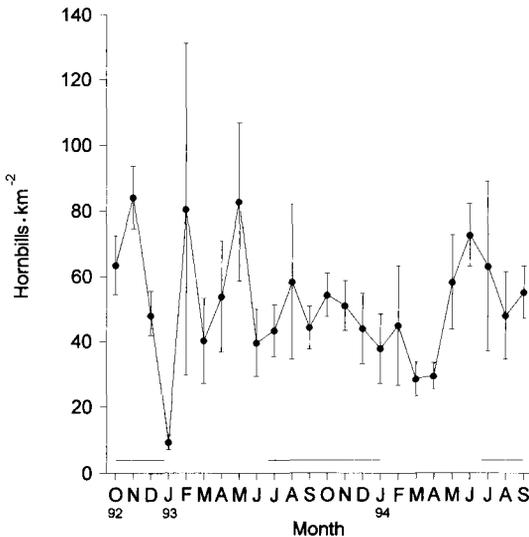


Fig. 4. Mean (\pm SD) monthly Red-knobbed Hornbill densities. Horizontal lines denote breeding season.

Fig trees are patchily distributed throughout the study area, with densities ranging from 0 to 27 trees·ha⁻¹ (Fig. 3). Mean fig densities are higher in primary forest ($\bar{x} = 10.28$ trees·ha⁻¹) than secondary forests ($\bar{x} = 8.28$ trees·ha⁻¹) or burned forests ($\bar{x} = 8.25$ trees·ha⁻¹), but these differences are not significant. Regenerating agricultural areas had significantly fewer fig trees than all other habitats ($\bar{x} = 5.34$ trees·ha⁻¹; $F = 3.68$, $df = 3$ and 437 , $P = 0.012$).

Hornbills.—Hornbill densities varied spectacularly over time (Fig. 4), ranging from a low of 9.3 birds·km⁻² in January 1993 to a high of 84.1

TABLE 1. Monthly Red-knobbed Hornbill density estimates^a and DISTANCE-model parameters with associated standard errors.

| Month | <i>n</i> | No. hornbills·km ⁻² | Mean strip width | Mean cluster size |
|-------------|----------|--------------------------------|------------------|-------------------|
| 1992 | | | | |
| October | 75 | 63.4 ± 8.9 | 51.4 ± 2.0 | 1.4 ± 0.16 |
| November | 108 | 84.1 ± 9.5 | 50.0 ± 0.91 | 1.8 ± 0.18 |
| December | 68 | 48.1 ± 6.8 | 51.1 ± 1.9 | 1.7 ± 0.17 |
| 1993 | | | | |
| January | 24 | 9.3 ± 2.2 | 100.0 ± 0.0 | 2.1 ± 0.39 |
| February | 40 | 80.5 ± 50.7 | 51.0 ± 2.5 | 7.1 ± 4.4 |
| March | 45 | 40.2 ± 13.1 | 67.7 ± 8.8 | 3.1 ± 1.2 |
| April | 56 | 53.8 ± 17.1 | 71.6 ± 7.7 | 2.3 ± 1.5 |
| May | 46 | 82.7 ± 24.1 | 51.7 ± 2.8 | 5.0 ± 1.6 |
| June | 35 | 39.6 ± 10.3 | 79.6 ± 4.9 | 4.5 ± 1.3 |
| July | 67 | 43.4 ± 8.0 | 53.0 ± 2.9 | 1.8 ± 0.31 |
| August | 44 | 58.3 ± 23.8 | 40.4 ± 4.4 | 3.1 ± 1.2 |
| September | 70 | 44.2 ± 6.6 | 53.1 ± 2.8 | 1.6 ± 0.17 |
| October | 91 | 54.3 ± 6.7 | 54.3 ± 2.9 | 1.5 ± 0.89 |
| November | 64 | 51.0 ± 7.7 | 50.0 ± 1.2 | 1.9 ± 0.23 |
| December | 42 | 43.9 ± 10.8 | 56.9 ± 5.2 | 2.6 ± 0.67 |
| 1994 | | | | |
| January | 45 | 37.9 ± 10.6 | 66.0 ± 8.2 | 2.6 ± 0.74 |
| February | 40 | 44.9 ± 18.3 | 54.6 ± 4.4 | 3.2 ± 1.8 |
| March | 38 | 28.5 ± 5.3 | 50.0 ± 1.5 | 1.6 ± 0.22 |
| April | 68 | 29.4 ± 4.1 | 87.6 ± 3.5 | 1.7 ± 0.15 |
| May | 63 | 58.2 ± 14.5 | 55.9 ± 3.9 | 2.8 ± 0.75 |
| June | 93 | 72.5 ± 9.5 | 54.1 ± 2.8 | 1.8 ± 0.19 |
| July | 56 | 63.0 ± 25.9 | 50.0 ± 1.3 | 3.4 ± 1.4 |
| August | 52 | 47.9 ± 13.4 | 52.2 ± 2.9 | 2.5 ± 0.78 |
| September | 81 | 55.1 ± 8.0 | 54.9 ± 3.2 | 1.5 ± 0.19 |

^a All calculated using uniform model, except for April and June 1993 and April 1994, which were calculated using hazard model.

birds·km⁻² in November 1992, with an overall mean of 51.4 birds·km⁻² ± SE of 17.7 (Table 1). We usually chose monthly density estimates generated using a uniform density function with a first-order cosine-adjustment term for the detection-probability model; estimated mean strip width was relatively constant within and among months (Table 1). Monthly mean cluster size was generally low (1–3 birds/cluster), indicating that hornbills tend to occur as individuals (60% records) or pairs (30% records). The remaining 10% of sighting records were of flocks; flocks ranged in size from 3 birds in October 1993 to 101 birds in February 1993.

The sex ratio (female:male) of hornbills fluctuated among months and reflected the general chronology of the breeding season (Fig. 5). Sex ratios were male dominated from June to December when females were sealed in nest cavities, and near unity only during the nonbreeding season (January–early June).

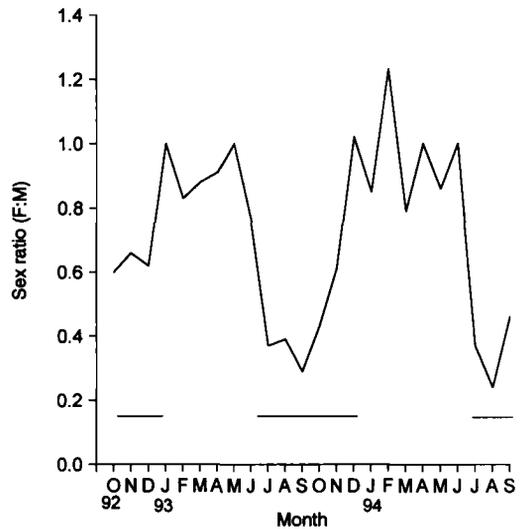


Fig. 5. Observed sex ratio (female : male) by month. Horizontal lines denote breeding season.

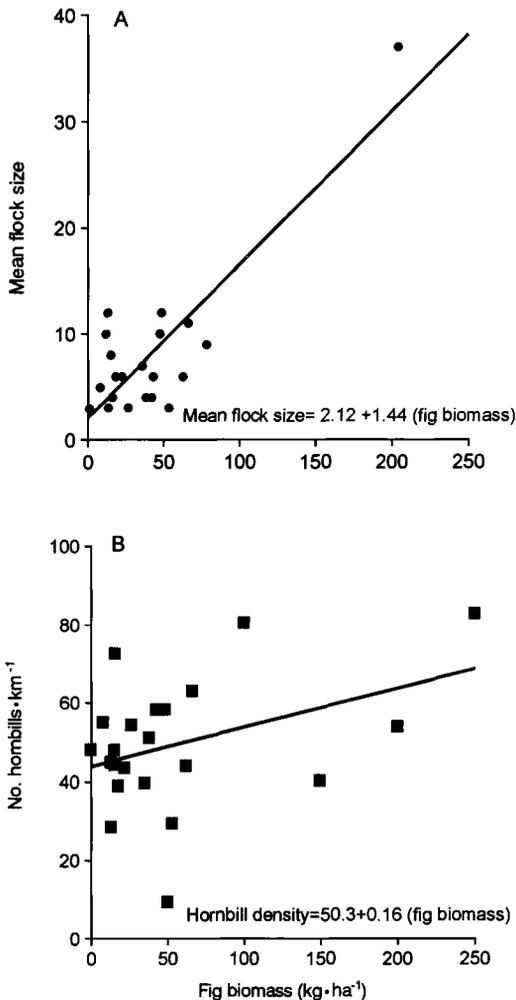


Fig. 6. Relationship of monthly estimates of fig-fruit biomass to (A) number of hornbills·km⁻² and (B) mean flock size.

Hornbills and fruit resources.—Monthly estimates of fruit biomass explained 47% of the temporal variance in hornbill densities ($F = 5.33$, $df = 3$ and 18 , $P = 0.005$). Monthly hornbill densities increased significantly with increasing fig-fruit biomass ($F = 5.43$, $P = 0.031$; Fig. 6), but declined as biomass of unripe nonfig-fruits increased ($F = -7.18$, $P = 0.015$). There was no significant effect of ripe nonfig-fruit biomass on monthly hornbill densities. Monthly estimates of fig-fruit biomass also had a significant positive effect on mean monthly flock size ($F = 52.02$, $df = 1$ and 20 , $P < 0.001$; Fig. 6). Estimates of ripe and unripe nonfig-fruit biomass were not correlated with flock size. The

relationships of biomass, hornbill density, and flock size, however, are strongly influenced by unusually high fig production and hornbill numbers in February 1993 (Fig. 6). Removal of this month reduces the fig-hornbill density relationship to a positive but statistically nonsignificant association ($0.1 > P > 0.05$), although the overall model remains significant. The relationship between mean flock size and fig biomass also is reduced to the point at which it is no longer statistically significant.

The spatial distribution of hornbills was significantly affected by habitat type ($F = 9.20$, $df = 2$ and 67 , $P < 0.001$) and the density of reproductive fig trees ($F = 5.02$, $df = 1$ and 67 , $P = 0.028$). Hornbills preferred primary forest ($\bar{x} = 0.41$ birds·ha⁻¹) over secondary ($\bar{x} = 0.27$ birds·ha⁻¹) and burned forest ($\bar{x} = 0.21$ birds·ha⁻¹). Regenerating gardens were eliminated from the analysis because hornbills were never detected in this habitat type. After controlling for habitat, hornbill density was higher in hectare blocks with high fig-tree densities (Fig. 3). Although hornbill densities were higher during the nonbreeding than during the breeding season (nonbreeding, $\bar{x} = 0.34$ birds·ha⁻¹ vs. breeding, $\bar{x} = 0.25$ birds·ha⁻¹), the difference was not statistically significant.

DISCUSSION

Red-knobbed Hornbill densities in the Tangkoko DuaSudara Nature Reserve fluctuate dramatically over time and space. Our data indicate that, although these fluctuations are influenced by breeding, when a large proportion of females enter nest cavities and are removed from the census population, the distribution and abundance of fruiting figs are the overriding factors affecting these fluctuations. Monthly fig-fruit biomass was significantly related to estimates of hornbill density and the size of hornbill flocks. The importance of fig production in explaining the rise and fall of Red-knobbed Hornbill numbers is further underscored by the lack of relationship between hornbill densities and ripe-fruit production by the nonfig community.

Nonfig-fruits however are not unimportant to hornbills. Nearly 20% of the breeding season diet is composed of ripe nonfig species (Kinnaird and O'Brien 1993). Although we did not explore the possibility, other subsets of the nonfig community that fruit outside the community

peak may influence hornbill numbers. For example, Leighton (1982) showed that less than one-half of the nonfig-tree species important to Bornean hornbills fruited during the peak of community fruiting. Nevertheless, in contrast to figs, most of these fruiting species are rare and fruit at relatively long intervals (Leighton and Leighton 1983). Nonfig species in the Tangkoko DuaSudara Nature Reserve typically occur in small crops and mature slowly, such that only a few ripe fruit are available on a given day and are rapidly selected by a guild of large frugivores including Red-knobbed Hornbills, imperial pigeons (*Ducula* spp.), and crested black macaques (*Macaca nigra*).

Our data demonstrate that the distribution of fig trees influences spatial patterns in hornbill densities. Red-knobbed Hornbills prefer primary habitat over secondary habitat, burned forests, or regenerating agricultural lands and, irrespective of habitat, they choose areas with high fig-tree densities. Other studies have demonstrated similar preference among hornbill species. Kalina (1988) found Black-and-white-casqued Hornbills (*Bycanistes subcylindricus*) at significantly higher densities in primary forest than selectively logged areas in East Africa, but observed temporary influxes of hornbills into heavily logged areas when two species of *Ficus* (*F. dawei* and *F. natalensis*) were in fruit. Surveys of Southeast Asian hornbills in primary and logged forests show that hornbills use secondary habitats, but occur at lower densities than in comparable primary habitats (Kemp and Kemp unpubl. report, Wilson and Johns 1982). Johns (1983, 1987) documented a numerical decline in some hornbill populations after selective logging of forests in Sungai Tekam, Peninsular Malaysia and speculated that the decline was tied in part to a reduction in densities of *Ficus* growing on commercially important hosts in the logged forests.

Although primary habitat in the Tangkoko DuaSudara Nature Reserve does not have significantly more fig trees relative to other habitats, primary habitat is characterized by generally larger canopied trees and may contain larger figs that bear larger crops, or species that are highly preferred diet items (e.g. *F. altissima*; Suryadi et al. 1994). Because figs show patterns of asynchronous fruiting both within and among species (Janzen 1979, van Schaik 1986, Lambert and Marshall 1991), high fig-tree density improves the probability that at least one fig will

be producing fruits at any given time. On average, $19.29 \pm \text{SD of } 4.8$ of the figs in our phenological sample were in fruit each month. With a mean density of $8.3 \text{ figs} \cdot \text{ha}^{-1}$, this translates into $1.6 \text{ fruiting figs} \cdot \text{mon}^{-1} \cdot \text{ha}^{-1}$, or up to $160 \text{ figs} \cdot \text{km}^{-2}$ with ripe fruit during any given month.

Fig densities and the resulting fruit production in the Reserve are exceptionally high relative to reports from other Southeast Asian forests. Leighton and Leighton (1983) reported a mean of $6.6 \text{ figs} \cdot \text{ha}^{-1}$ in primary forest of East Kalimantan, Lambert (1991) calculated an average of $2.5 \text{ figs} \cdot \text{ha}^{-1}$ in primary forest of Sabah, Malaysia, and Johns (1983) estimated $2 \text{ trees} \cdot \text{ha}^{-1}$ in forests of Peninsular Malaysia. In Kuala Lompat, Malaysia, Lambert and Marshall (1991) estimated between 1 and $13 \text{ Ficus} \cdot \text{km}^{-2}$ with ripe figs on any particular day.

We believe that high fig densities in Tangkoko DuaSudara Nature Reserve are responsible for maintaining the overall high population density of Red-knobbed Hornbills. Forest hornbills, in general, are found at relatively low densities. Some of the highest densities for single species in Asia have been reported by Leighton (1982) and van Schaik (1991) for the Bushy-crested Hornbill (Table 2). If we compare biomass estimates for entire Asian hornbill communities, the Tangkoko DuaSudara Nature Reserve ranks highest in hornbill biomass (Table 2). Only biomass estimates from the Kutai community approach biomass estimates for the Reserve; this is due primarily to the occurrence of large flocks of Wreathed Hornbills and Wrinkled Hornbills (*A. corrugatus*) that were believed to be tracking fig resources (Leighton 1982). The Kutai study area also has the second-highest reported fig-tree density next to what we found in the Reserve.

Figs, combined with numerous tree cavities may explain the extraordinary Red-knobbed Hornbill breeding densities in the Reserve. Approximately 70% of the Red-knobbed Hornbill's breeding season diet is composed of figs (Kinnaid and O'Brien 1993) and the preferred nest tree, *Palaquium amboinense*, is common and prone to heart-rot, resulting in frequent cavity formation. During the 1993–1994 breeding season, we counted 60 active nest cavities in approximately 600 ha, yielding a nesting density of 10 Red-knobbed Hornbill pairs $\cdot \text{km}^{-2}$. Breeding studies of other hornbill species have reported lower densities. In Thailand, Poonswad et al.

TABLE 2. Comparison of hornbill^a densities and biomass among four South East Asian study sites.

| Species | No. hornbills·km ⁻² | Mean body mass (kg) | Hornbill biomass·km ⁻² |
|--|--------------------------------|---------------------|-----------------------------------|
| Krau Game Reserve, Malaysia (Whitmore 1984) | | | |
| Helmeted Hornbill | 0.5 | 3.10 | 1.55 |
| Rhinoceros Hornbill | 0.5 | 2.58 | 1.29 |
| Oriental Pied Hornbill | 1.0 | 0.74 | 0.74 |
| Malay Black Hornbill | 2.0 | 1.05 | 2.10 |
| Bushy-crested Hornbill | 2.5 | 1.17 | 2.93 |
| White-crowned Hornbill | ? ^b | 1.31 | ? |
| Total | | | >8.61 |
| Gunung Leuser National Park, N. Sumatra (van Schaik unpubl. report) | | | |
| Helmeted Hornbill | 0.83 | 3.1 | 2.57 |
| Rhinoceros Hornbill | 3.11 | 2.58 | 8.02 |
| Wrinkled Hornbill | 0.10 | 1.59 | 0.17 |
| Wreathed Hornbill | 1.05 | 2.54 | 2.67 |
| Bushy-crested Hornbill | 4.28 | 1.17 | 5.02 |
| Total | | | 18.45 |
| Kutai National Park, E. Kalimantan (Leighton 1982) | | | |
| Helmeted Hornbill | 0.3 | 3.1 | 0.93 |
| Rhinoceros Hornbill | 1.1 | 2.58 | 2.84 |
| Malay Black Hornbill | 2.7 | 1.05 | 2.84 |
| Bushy-crested Hornbill | 6.2 | 1.172 | 7.27 |
| White-crowned Hornbill | 4.2 | 1.31 | 5.50 |
| Wrinkled Hornbill | 5-21 | 1.59 | 20.67 ^c |
| Wreathed Hornbill | 10-46 | 2.54 | 71.12 ^c |
| Total | | | 111.17 |
| Tangkoko DuaSudara Nature Reserve, Sulawesi (this study; O'Brien and Kinnaird 1994) | | | |
| Red-knobbed Hornbill | 51.40 | 2.36 | 120.36 |
| Tarictic Hornbill | 2.84 | 0.46 | 1.30 |
| Total | | | 121.66 |

^a Helmeted Hornbill (*Buceros vigil*), Rhinoceros Hornbill (*B. rhinoceros*), Oriental Pied Hornbill (*Anthracoceros albirostris*), Malay Black Hornbill (*A. malayanus*), Bushy-crested Hornbill (*Anorrhinus galeritus*), White-crowned Hornbill (*Aceros comatus*), Wrinkled Hornbill (*A. corrugatus*), Wreathed Hornbill (*A. undulatus*), Red-knobbed Hornbill (*A. cassidix*), and Tarictic Hornbill (*Penelopides exarhatus*).

^b Species present, but density estimates not available.

^c Denotes biomass calculations using midpoint of range of densities.

(1987) reported a nesting density of less than 1 pair·km⁻² for four hornbill species. Kalina (1988) reported maximum densities of 5.6 cavities·km⁻² for Black-and-white-casqued Hornbills of Kibale Forest, Uganda.

The well-documented aseasonality, intrapopulation asynchrony, and resulting year-round availability of *Ficus* often are cited as the key factors allowing figs to gain such importance to frugivore communities (Foster 1982, Milton et al. 1982, Leighton and Leighton 1983, Terborgh 1986). As Lambert and Marshall (1991) and Kan-

nan (1994) pointed out however, it is not the intrapopulation asynchrony per se that gives this taxon such importance, but a combination of other attributes. Fig crops tend to be large and frequently are available during periods of general fruit scarcity (Lambert and Marshall 1991). Figs also form a unique subset because of their short crop persistence and synchronous maturation within a tree. Crop persistence is an important indicator of daily fruit availability: the shorter the duration, the greater the mean proportion of fruits available per day during the fruiting period (Lambert and Marshall 1991). Crop persistence for figs monitored on daily basis in the Tangkoko DuaSudara Nature Reserve was short, with minimum persistence as low as five days. The ease of harvest and nutritional content of *Ficus* are added benefits. Most figs are succulent, soft, and can be easily swallowed. Figs are energy-rich foods and have higher caloric values than nonfig-fruits, as well as adequate protein levels (Wrangham et al. 1993; but see Bronstein and Hoffmann 1987). Data from the Tangkoko DuaSudara Nature Reserve demonstrate that figs are an excellent source of natural calcium (Kinnaird et al. unpubl. data) required for growth and development. The fact that several avian frugivores are capable of subsisting almost entirely on figs (e.g. green pigeons [*Treron* spp.] and barbets [*Megalaima* spp.], Lambert 1991; Helmeted Hornbills [*Buceros vigil*], Leighton 1982; Great Pied Hornbills [*B. bicornis*], Kannan 1994) supports the hypothesis that, given year-round availability, figs constitute an adequate diet for some frugivores.

Although the spectrum of fig production generally reflects year-round availability to Red-knobbed Hornbills, it is apparent from the data that figs may be locally scarce at some times of the year (Fig 1). During this time Red-knobbed Hornbills rely more heavily on other fruit resources and invertebrate prey, or make large-scale movements to adjacent habitats in search of figs. Large-scale movements by Wreathed Hornbills in Thailand have been documented by Poonswad and Tsuji (1994), and data from on going radio-telemetry studies show that Red-knobbed Hornbills cover daily distances of up to 13 km during the nonbreeding season. Use by Red-knobbed Hornbills of secondary forests and burned habitats in close proximity to primary forest may promote regeneration of disturbed sites if hornbills are depositing viable seeds. Although we have not demonstrated seed viability or effectiveness of dispersal, we hy-

pothesize that Red-knobbed Hornbills may be important and effective dispersers because: (1) they move seeds away from seed shadows of parent trees; (2) they are capable of carrying up to 500 g in one load; (3) fruits are processed and seeds are spit or defecated intact; and (4) seeds of fruits delivered to nests often sprout underneath (pers. obs.). Removal of figs (Johns 1983, 1987, Lambert 1991) or reduction of fig populations to nonviable sizes (McKey 1989) will have serious repercussions for Red-knobbed Hornbill populations and the forest ecosystems in which they live.

ACKNOWLEDGMENTS

This work was conducted under the auspices of the Wildlife Conservation Society in collaboration with the Indonesian Directorate General for Nature Preservation and Forest Protection (PHPA) and Puslitbang Biologi of the Indonesian Institute of Science (PB/LIPI). Funding was provided by the Wildlife Conservation Society, the National Geographic Society (grant no. 4912-92), and the Conservation Food and Health Foundation. We thank Soetikno Wiryoatmodjo (PB/LIPI), Dedi Darnaedi (PB/LIPI), Romon Palete (PHPA, North Sulawesi), and Jatna Supriatna (University of Indonesia) for their kind help throughout our time in Indonesia. Denand Kakauhe, Nelman Kakauhe, Jukber Lambaihang and Yopi Manderos are thanked for assisting with data collection. Finally, we thank Carlos Martinez, Gary Stiles, and Adrian Marshall for constructive criticism of an earlier draft of the manuscript.

LITERATURE CITED

- BLAKE, J. G., AND B. A. LOISELLE. 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. *Auk* 108: 114-130.
- BOAG, P. T., AND P. R. GRANT. 1984. Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos: Breeding and feeding ecology in a climatically variable environment. *Ecol. Monogr.* 54:463-489.
- BRONSTEIN, J. L., AND K. HOFFMANN. 1987. Spatial and temporal variation in frugivory at a Neotropical fig, *Ficus pertusa*. *Oikos* 49:261-268.
- DESANTE, D. F., AND G. R. GEUPEL. 1987. Landbird productivity in central coastal California: The relationship to annual rainfall, and a reproductive failure in 1986. *Condor* 89:636-653.
- FOGDEN, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114:307-342.
- FOSTER, R. B. 1982. The seasonal rhythm of fruit fall on Barro Colorado Island. Pages 151-172 in *The ecology of a tropical forest: Seasonal rhythms and long-term change* (E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, Eds.). Smithsonian Institution Press, Washington, D.C.
- GREENBERG, R. 1981. Frugivory in some migrant tropical forest wood warblers. *Biotropica* 13:215-223.
- INTERNATIONAL UNION FOR CONSERVATION OF NATURE. 1991. Atlas of tropical rainforests. IUCN Special Publication. Gland, Switzerland.
- JANZEN, D. H. 1979. How to be a fig. *Annu. Rev. Ecol. and Syst.* 10:13-52.
- JOHNS, A. 1983. Ecological effects of selective logging in a West Malaysian rain forest. Ph.D. dissertation, Cambridge Univ., Cambridge.
- JOHNS, A. 1987. The use of primary and selectively logged rainforest by Malaysian hornbills (*Bucerotidae*) and implications for their conservation. *Biol. Conserv.* 40:1679-190.
- KALINA, J. 1988. Ecology and behavior of the Black-and-white Casqued Hornbill (*Bycanistes subcylindricus subquadratus*) in Kibale Forest, Uganda. Ph.D. dissertation, Michigan State Univ., Lansing.
- KANNAN, R. 1994. Ecology and conservation of the Great Pied Hornbill (*Buceros bicornis*) in the western Ghats of Southern India. Ph.D. dissertation, Univ. Arkansas, Fayetteville.
- KARR, J. R. 1982. Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology* 63:1975-1978.
- KARR, J. R., AND K. E. FREEMARK. 1983. Habitat selection and environmental gradients: Dynamics in the "stable" tropics. *Ecology* 64:1481-1494.
- KINNAIRD, M. F., AND T. G. O'BRIEN. 1993. Preliminary observation on the breeding biology of the endemic Sulawesi Red-knobbed Hornbill (*Rhyticeros cassidix*). *Trop. Biodiv.* 1:107-112.
- LAAKE, J. L., S. T. BUCKLAND, D. R. ANDERSON, AND K. P. BURNHAM. 1993. DISTANCE user's guide, version 2.0. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State Univ., Fort Collins.
- LAMBERT, F. 1991. The conservation of fig-eating birds in Malaysia. *Biol. Conser.* 58:31-40.
- LAMBERT, F. R., AND A. G. MARSHALL. 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *J. Ecol.* 79:793-809.
- LEIGHTON, M. 1982. Fruit resources and patterns of feeding, spacing and grouping among sympatric Bornean hornbills (*Bucerotidae*). Ph.D. dissertation, Univ. California, Davis.
- LEIGHTON, M. 1986. Hornbill social dispersion: Variations on a monogamous theme. Pages 108-130 in *Ecological aspects of social evolution* (D. I. Rubenstein and R. W. Wrangham, Eds.). Princeton Univ. Press, Princeton, New Jersey.
- LEIGHTON, M. 1993. Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. *Int. J. Primatol.* 14:257-313.
- LEIGHTON, M., AND D. R. LEIGHTON. 1983. Vertebrate responses to fruiting seasonality within a Bor-

- nean rain forest. Pages 181–196 in *Tropical rain forest: Ecology and management* (S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, Eds.). Blackwell Scientific Publications, Cambridge, United Kingdom.
- LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecol. Monogr.* 58:251–269.
- LOISELLE, B. A., AND J. G. BLAKE. 1991. Resource abundance and temporal variation in fruit-eating birds along a wet forest elevational gradient in Costa Rica. *Ecology* 72:180–193.
- McKEY, D. 1989. Population biology of figs: Applications for conservation. *Experientia* 45:661–673.
- MEDWAY, LORD. 1972. Phenology of a tropical rain-forest in Malaya. *Biol. J. Linn. Soc.* 4:117–146.
- MILTON, K., D. M. WINDSOR, D. W. MORRISON, AND M. A. ESTRIBI. 1982. Fruiting phenologies of two Neotropical *Ficus* species. *Ecology* 63:752–762.
- O'BRIEN, T. G., AND M. F. KINNAIRD. 1994. Notes on the density and distribution of the endemic Sulawesi Tarictic Hornbill (*Penelopides exarhatus*) in the Tangkoko-DuaSudara Nature Reserve, North Sulawesi. *Trop. Biodiv.* 2:252–260.
- POONSWAD, P., AND A. TSUJI. 1994. Ranges of males of the Great Hornbill *Buceros bicornis*, Brown Hornbill *Ptilolaemus tickelli* and Wreathed Hornbill *Rhyticeros undulatus* in Khao Yai National Park, Thailand. *Ibis* 136:79–86.
- POONSWAD, P., A. TSUJI, AND C. NGAMPONGSAI. 1987. A comparative study on breeding biology of sympatric hornbill species (Bucerotidae) in Thailand with implications for breeding in captivity. Pages 250–315 in *Proc. Jean Delacour/IFCB Symposium. Breeding birds in captivity*. International Foundation for the Conservation of Birds, North Hollywood, California.
- POWELL, G. V. N., AND R. D. BJORK. 1994. Implications of altitudinal migration for conservation strategies to protect tropical biodiversity: A case study of the Resplendent Quetzal *Pharomacrus mocinno* at Monteverde, Costa Rica. *Bird Conserv. Int.* 4:161–174.
- ROBINSON, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pages 408–418 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagen III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- ROOT, T. 1988. Energy constraints on avian distributions and abundances. *Ecology* 69:330–339.
- SAS INSTITUTE. 1985. *SAS users guide: Statistics*, Version 5 ed. SAS Institute, Inc., Cary, North Carolina.
- SKUTCH, A. 1967. Life histories of Central American highland birds. *Nuttall Ornithol. Club* 7.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman and Co., San Francisco.
- STILES, F. G. 1985. On the role of birds in the dynamics of Neotropical forests. Pages 49–59 in *Conservation of tropical forest birds* (A. W. Diamond and T. E. Lovejoy, Eds.). International Council for Bird Preservation, Tech. Publ. 4.
- SURYADI, S., M. F. KINNAIRD, T. G. O'BRIEN, J. SUPRIATNA, AND S. SOMADIKARTA. 1994. Food preferences of the Sulawesi Red-knobbed Hornbill during the non-breeding season. *Trop. Biodiv.* 2:377–383.
- TERBORGH, J. 1986. Keystone plant resources in the tropical forest. Pages 33–44 in *Conservation biology: The science of scarcity and diversity* (M. E. Soulé, Ed.). Sinauer Associates, Sunderland, Massachusetts.
- VAN SCHAIK, C. P. 1986. Phenological changes in a Sumatran rain forest. *J. Trop. Ecol.* 2:327–347.
- WHEELWRIGHT, N. T. 1983. Fruits and the ecology of Resplendent Quetzal. *Auk* 100:286–301.
- WHITE, D. M. N., AND M. C. BRUCE. 1986. The birds of Wallacea (Sulawesi, the Moluccas and Lesser Sunda Islands, Indonesia): An annotated checklist. *British Ornithologists' Union*, London.
- WHITMORE, T. C. 1984. *Tropical rainforests of the Far East*, 2nd ed. Clarendon, Oxford.
- WILSON, W. L., AND A. D. JOHNS. 1982. Diversity and abundance of selected animal species in undisturbed forest, selectively logged forest and plantations in East Kalimantan, Indonesia. *Biol. Conserv.* 24:205–218.
- WONG, M. 1985. Understorey birds as indicators of regeneration in a patch of selectively logged West Malaysian rainforest. Pages 249–263 in *Conservation of tropical forest birds* (A. W. Diamond and T. E. Lovejoy, Eds.). International Council for Bird Preservation Tech. Publ. 4.
- WRANGHAM, R. W., N. L. CONKLIN, G. ETOT, J. OBUS, K. D. HUNT, M. D. HAUSER, AND A. P. CLARK. 1993. The value of figs to chimpanzees. *Int. J. Primatol.* 14:243–255.