SPECIAL FEATURE Interspecific segregation and attraction in forest birds

The effects of food-supply on Southeast Asian forest birds

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ORNITHOLOGICAL SCIENCE

Abstract Southeast Asian forests are being lost at an alarming rate. This unprecedented deforestation is resulting in avifauna losses. Despite this, Southeast Asian avifauna remains poorly studied. A few studies measured the food-supply and correlated it with the Southeast Asian forest bird ecology. These correlative studies (qualitative as well as quantitative) show that food-supply can affect the bird diversity, abundance/density, breeding ecology, body condition, ranging behaviour and/or flocking behaviour. However, there has been no experimental study conducted to determine the effects of food-supply on the forest bird ecology. In this geographic area, exciting research avenues remain available to study the avian feeding ecology and to explore a relationship between food-supply and forest bird ecology. Descriptive, correlative as well as experimental data on these aspects are required to enhance the knowledge of avian ecology as well as for avian conservation purposes.

Key words Bird ecology, Food-supply, Rainforest birds, Southeast Asia, Tropics

Southeast Asia (primarily containing Myanmar, Thailand, Cambodia, Laos, Vietnam, Malaysia, Singapore, Brunei and Indonesia) is a region of high bird diversity with over 1200 bird species present (Inskipp et al. 1996, Robson 2000). Within this region, at least 70% of resident bird species may be partly or exclusively dependent upon the primary forest (Wells 1985). The percentage of threatened species restricted to forested areas within Southeast Asia varies from 17% (Singapore) to 72% (Indonesia) (Collar et al. 1994). Despite this, forest loss in Southeast Asia has been extensive; with rate of deforestation three times higher here than other tropical areas (Food and Agriculture Organization 1999). This forest loss has probably resulted in concomitantly heavy avian extinctions (Diamond et al. 1987, Castelletta et al. 2000).

The avian extinctions do not appear to occur randomly following forest loss (e.g. Karr 1980, Brash 1987). Frugivores and insectivores, for example, are particularly vulnerable to extinctions after deforestation (Castelletta et al. 2000). One of main contributing factors in such cases could be a decline in food-supply. Therefore, it may be critical to understand the relationships between the ecology of forest birds (depending on primary or old secondary forest to survive) and food abundance/density. My objectives here are to: 1) summarize results of studies exploring food-supply and bird ecology relationships, 2) identify if there are any general patterns based on previous studies and 3) provide some future directions for studies to determine the effects of food-supply on bird ecology. Only studies where food abundance/density was quantitatively measured and related with Southeast Asian bird ecology are discussed here. Published studies were searched by using various databases such as the Web of Science and BIOSIS. These searches were supplemented by gleaning through the literature cited by relevant studies and searching through some of the regional journals such as Tropical Biodiversity. Bird classification used in this manuscript follows Sibley & Monroe (1990).

CASE STUDIES

1) Malaysia

Fogden (1972) estimated fruit and insect abundance in the Semengo Forest Reserve (Sarawak, Malaysia). He qualitatively related the food abundance with various aspects of bird ecology. Birds' breeding in December to May coincided with a period when insects were more abundant. Frugivorous

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bird species had similar breeding phenology as insectivorous bird species despite the fact that fruits were not consistently abundant during any particular time of the year. This may be due to the fact that many frugivorous species supplement their diets with protein rich insects during the breeding season.

In Semengo, insects were least abundant in November and most bird species finished moulting by the end of October (Fogden 1972). Exception to this included the species for which insect abundance was suspected not to vary widely such as bark-foraging woodpecker species (e.g. the Rufous Woodpecker *Celeus brachyurus*) and leaf-litter foraging babbler species (e.g. the Short-tailed Babbler *Malacocincla malaccensis*).

Two bulbul species (*Pycnonotus* spp.) in Semengo fed on both insects as well as fruits (Fogden 1972). Fruits must have constituted an important part of the diet for these bulbuls because they consumed them even when insects were plentiful. Probably fruits represent an easily harvestable source of energy. These two bulbul species had suppressed breeding activity in low fruit abundance year than in high fruit abundance year. The proportion of juveniles in the population was seven fold higher in high fruit abundance year (14%) than in low fruit abundance year (2%). There also seemed to be a recovery in the body masses of these bulbul species when fruits abundance increased (Fogden 1972). Thus, Fogden's qualitative study implies broad consequences of food-supply on the bird ecology.

Wong (1986) studied the effect of food resources (flowers, fruits and arthropods) on understory bird communities in primary versus disturbed (regenerated) areas of the Pasoh Forest Reserve (Peninsular Malaysia). Wong found that the number of plant individuals that produced flowers or fruits used by birds was at least three times higher in primary than in the disturbed forest. Foliage arthropod abundance did not differ between the primary and disturbed areas but the period of low arthropod abundance was four months longer in disturbed than in the primary forest. Both, bird species richness (73 versus 83 species) and abundance (575 versus 703 individuals), were lower in disturbed than in the primary forest. Wong argued that this was because lower resource abundance could support fewer birds in disturbed than in the primary forest.

In Pasoh, foliage arthropods did not show marked temporal and spatial variation as shown by fruiting and flowering plants. Therefore, frugivores would have to range over wider areas than insectivores. Consistent with this prediction, Wong (1986) found that the abundance of frugivores varied twice more than that of insectivores both in primary and the disturbed forest. Wong's study highlights the importance of food-supply on the avian community diversity and abundance.

2) Indonesia

Leighton and Leighton (1983) monitored fruit density in the Kutai Nature Reserve (Kalimantan, Indonesia). In a semi-quantitative manner, they correlated fruit density with frugivore behaviour and movements. Leighton and Leighton found that all hornbill species (the Rhinoceros Hornbill *Buceros rhinoceros*, Helmented Hornbill *Rhinoplax vigil*, Bushy-crested Hornbill *Anorrhinus galeritus*, Black Hornbill *Anthracoceros malayanus*, White-crowned Hornbill *Aceros comatus*, Wrinkled Hornbill *A. corrugatus* and Wreathed Hornbill *A. undulates*) only bred when the fruit density peaked (January to May). Based on bird sightings, it appeared that the Green Imperial Pigeon *Ducula aenea*, Jambu Fruit Dove *Ptilinopus jambu*, Hill Myna *Gracula religiosa*, Green Broadbill *Calyptomena virdis*, *A. undulates* and *A. corrugatus* emigrated from the study area during low fruit density periods (September-October). These results suggest that birds may be adjusting their breeding activities and/or foraging areas by tracking food resources.

Kinnaird et al. (1996) studied the effect of temporal and spatial differences in fruit abundance on the Sulawesi Red-knobbed Hornbill (*Aceros cassidix*) in the Tangkok DuaSundra Nature Reserve (Sulawesi, Indonesia). The Sulawesi Red-knobbed Hornbill feeds on fruits in the forest canopy. Kinnaird et al. (1996) found that fig (*Ficus* spp.)-fruit biomass correlated significantly with the temporal population fluctuations of the hornbill. The flock size also increased during months when fig-fruit biomass was high. Additionally, hornbill densities were higher in areas with higher than in lower fig-tree densities (Kinnaird et al. 1996). In line with some previous studies (e.g. Wong 1986), food-supply seemed to effect population dynamics in this case.

3) Singapore

Sodhi et al. (in press) studied the effects of food abundance on bird abundance in two large (>480 ha) forest fragments, MacRitchie and Nee Soon, in Singapore. Line transects of approximately four and half km were surveyed eight times at each site between 14 July and 24 September 1997. All surveys were made during fair weather conditions and between 0700 and 0930 h. Foliage along the transects was sweep sampled for the presence of understorey arthropods. Each transects was sampled for arthropods on five different occasions. Sweep sampling was conducted at intervals of 150 m and 16 sweeps using butterfly net were made at each sampling station. Sampling stations were changed for subsequent samplings. All arthropods found were used in calculating their mean abundance. The number of fruiting trees along the transect was also counted twice.

Sodhi et al. found that the mean number of understory insectivore bird individuals (belonging to species: the White-rumped Shama *Copsychus malabaricus*, Dark-necked Tailorbird *Orthotomus atrogularis*, Abbott's Babbler *M. abbotti*, Short-tailed Babbler and Chestnut-winged Babbler *Stachyris arythroptera*) did not differ significantly between MacRitchie (73.63±5.76 [standard error] individuals) and Nee Soon (87.88±7.57 individuals). And as expected, the mean number of foliage arthropods also did not differ between the two forests (11.8±0.39 [standard error] and 9.66±0.67 individuals, respectively). However, more frugivore bird individuals (belonging to species: the Red-crowned Barbet *Magalaima rafflesii*, Long-tailed Parakeet *Psittacula longicauda* and Pink-necked Green-Pigeon *Treron vernans*) were found in MacRitchie (maximum number=45) than in Nee Soon (10). More fruiting trees were also available in MacRitchie (maximum number=352) than in Nee Soon (285).

Castelletta (unpubl. data) measured the arthropod abundance and insectivore bird density in 13 forest patches (7–935 ha) in Singapore. Eleven insectivorous bird species that feed in the understory were considered (the Laced Woodpecker *Picus vittatus*, Oriental Magpie Robin *Copsychus saularis*, White-rumped Shama, Yellow-bellied Prinia *Prinia flaviventris*, Common Tailorbird *Orthotomus sutorius*, Dark-necked Tailorbird, Rufous-tailed Tailorbird *O. sericeus*, Ashy Tailorbird *O. ruficeps*, Abbott's Babbler, Chesnut-winged Babbler and White-chested Babbler *Trichastoma rostratum*). Castelletta analysed correlations between the mean insectivore density (all species combined) and all arthropod abundance. Separate analyses were conducted for arthropods less than 1 cm and those more than 1 cm in length. No significant correlation was found between the mean density of insectivores and arthropod abundance for all the comparisons. One of the reasons for this lack of correlation may be that the diet of the study species is poorly understood thus making the analyses crude. However, Castelletta found that arthropod abundance was highest during the peak of the breeding season (April to September) of insectivorous forest birds. The studies from Singapore show that some food types can effect bird abundances and breeding season while others may either exert minimal effect or their effect may be difficult to demonstrate.

WHAT ARE THE GENERAL PATTERNS?

Only a few studies have been conducted on the effects of food-supply on Southeast Asian forest birds. However, these limited number of studies imply the importance of food-supply on forest bird ecology (Table 1). Timing of breeding and moulting, bird diversity and abundance/density, ranging behaviour and flock size seem to be effected by food-supply. The only study that found no significant correlative effect of food-supply on forest bird abundance is from Singapore (Catelletta unpublished data). As mentioned, this study suffers from the fact that the diet of the studied bird species remained poorly documented. Some of the studies also imply or show that different prey types exert different influences on the bird ecology. Arthropod resources usually do not show remarkable temporal and spatial variation in abundance as shown by other resource types such as fruits and flowers. The temporal and spatial variation in the abundance of fruits particularly effects the distribution, dispersal and movements of the frugivores (e.g. Fogden 1972, Wong 1986, Kinnaird et al. 1996).

FUTURE DIRECTIONS

One of the problems with Southeast Asian forest birds is that basic descriptive data are lacking even to conduct critical correlative studies. For example, the diet composition of many birds is poorly understood and data on breeding ecology (e.g. clutch sizes) are not readily available.

All the studies determining the effects of food-supply on Southeast Asian forest birds are either qualitative or at the best correlative. Demonstrating a precise effect of food-supply on bird ecology may be difficult from correlative studies and there may be a need to conduct well-designed experiments (Newton 1998). Correlative studies do however, present hypotheses and ideas for experimental testing. As men-

Table 1. The number of studies correlating the food-supply with Southeast Asian forest bird ecology.

Bird ecology	Total no. of studies	No. of studies with quantitative comparisons	No. of studies with experimental evidence
Population characteristics			
Diversity	1	1	0
Abundance/density	4	4	0
Breeding ecology			
Phenology	3	0	0
Reproductive success	1	0	0
Other ecological aspects			
Body condition	1	0	0
Moulting	1	0	0
Flocking	1	1	0
Ranging behaviour	2	0	0

tioned, even correlative studies linking the food-supply with Southeast Asian forest bird ecology are few. There is an urgent need to conduct the studies that attempt to find a correlation between food supply and bird movements, reproductive success and recruitment. With relatively well-developed radio-tracking techniques, it is now possible to track selected bird species and determine how they use home ranges or territories in relation to food distribution.

Mass flowering or fruiting is a striking feature of dipertocarp forests of Southeast Asia (Ashton et al. 1988). This phenomenon occurs during irregular intervals of 2–10 years and it causes many different families to flower simultaneously. While the ecological causes of this phenomenon are poorly understood (Corlett 1990), such an event can have profound impacts on bird ecology and adaptations. To my knowledge, the effects of mass flowering or fruiting on Southeast Asian forest bird ecology remains poorly documented.

To my knowledge no experimental study has been conducted to determine the effects of food-supply on Southeast forest birds (Table 1). For some of the relatively well-studied species, food supplementation (e.g. addition of fruits to a frugivore's range) or food reduction (e.g. removing or killing of exotic vegetation) experiments should be carried out. Therefore, in summary, exciting research avenues remain available on the feeding ecology and on the effects of food-supply on Southeast Asian forest bird ecology. In light of heavy deforestation, descriptive, correlative as well as experimental data are urgently needed on these research aspects. Researchers can rely for theoretical and methodological considerations on the research conducted on the effects of food-supply on forest birds in other geographic areas (e.g. Holmes & Schultz 1988, Rodenhouse & Holmes 1992, Burke & Nol 1998).

CONCLUSIONS

As mentioned, forests within Southeast Asia are lost at an unprecedented rate. Previous studies reveal that forest loss and fragmentation can cause local extinctions in birds in this region (e.g. Ford & Davison 1996, Castelletta et al. 2000). Despite this, the ecology of Southeast Asian forest birds remain poorly studied. Because reduction in food-supply may be one of the variables causing the decline or local extinction of Southeast Asian forest birds, it is critical to understand the relationships between food-supply and bird ecology. Avian extinctions may occur over 100 years following habitat loss (Brooks et al. 1999). Therefore, following habitat loss and degradation, there may be time to save some of the avifauna through proper conservation actions. For example, some of the supplemental food experiments may be critical to determine if the conservation of some of the threatened birds is feasible (e.g. maintaining or increasing their abundance with supplemental food).

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