

A Tropical Montane Forest in Borneo as a Source of Fruit Supply for Frugivorous Birds

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Abstract

An altitudinal survey of correspondences between fruiting phenology of fleshy-fruited tree species and seasonal dynamics of frugivorous birds was carried out for 50 weeks across three vegetation types on Mt. Kinabalu, Borneo: a hill forest (800 m a.s.l.), a lower montane forest (1,700 m a.s.l.) and a subalpine forest (3,100 m a.s.l.). In the hill forest, a large fruiting peak following the general flowering period was observed during October–November in 1996 and a marked fruitless period was observed during February–April in 1997. During the fruitless period, the number of resident frugivorous birds decreased in some families. In the lower montane forest, a bimodal fruiting pattern was observed. A large number of frugivorous temperate migrants occurred and removed a lot of the fruit when the fruiting peak occurred. The number of resident frugivorous birds increased and several lowland bird species were observed when the number of resident birds decreased in the hill forest. In the subalpine forest, more continuous and irregular fruiting patterns without outstanding peaks were observed and the number of resident frugivorous birds was more stable throughout the year. These suggested (1) temperate migrants visited mainly the lower montane forest to obtain fruit resources and (2) altitudinal movements of lowland bird species to montane vegetation might occur seasonally, revealing that seasonal movements and migrations to track fruit resources might be common among frugivorous birds occurring on Mt. Kinabalu.

Key words: altitudinal migrant, frugivorous bird, fruiting seasonality, lower montane forest, Mt. Kinabalu, temperate migrant.

1. Introduction

Frugivorous birds move and migrate tracking fruit resources (Corlett, 1990; Karr, 1976; Leighton & Leighton, 1983; Levey, 1988; Loiselle & Blake, 1991; van Schaik *et al.*, 1993; Wich & van Schaik, 2000). In temperate regions, migratory frugivorous birds which have finished breeding in the north arrive when fruiting species bear abundant fruit, and consume a large amount of the fruit (Fuentes, 1992; Herrera, 1984, 1998; Kominami, 1987; Okamoto & Kitajima 1992; Sorensen, 1981; Stapanian, 1982; Thompson & Willson, 1979). In subtropical and tropical regions where most of the temperate migrants overwinter, fruiting species produce fruit during their overwintering period and provide fruit resources for them (Noma & Yumoto, 1997). However, tracking movements of temperate migrants were observed even where they were the overwintering (Loiselle & Blake, 1991). Also resident frugivorous birds were observed moving locally within their habitats (Leighton & Leighton, 1983; Levey, 1988; Loiselle &

Blake, 1991; van Schaik *et al.*, 1993), although the destinations, seasonality and periodicity have not been clarified for the most part.

In Southeast Asia, a tropical montane area has been noticed as a destination for migratory frugivorous birds. Leighton & Leighton (1983) reported that the number of inhabiting hornbills and pigeons decreased with decreasing number of fruiting species in a lowland forest of Borneo. They suggested montane regions as one of the destinations of the disappearing birds. Wells (1990) noted that in the Greater Sunda regions, frugivorous birds, including temperate migrants, were often observed in montane regions, and suggested that fruit resource conditions might be more comfortable in the montane regions. However, no provable study has been reported associating a seasonal change in fruiting conditions with seasonal dynamics of frugivorous birds in montane regions of Southeast Asia.

In this paper, the correspondence between fruiting phenology and seasonal dynamics of frugivorous birds are investigated in three forest types located from the

foothills to the mountainside of a Bornean tropical mountain, in order to clarify the tracking movements of frugivorous birds on a tropical mountain in South-east Asia.

2. Study Sites

Mt. Kinabalu is located at 6°5'N and 160°33'E in northern Borneo (Fig. 1). The mountain is 4,095 m high and several vegetation types appear and disappear altitudinally from the foothills to the summit. The vegetation types had been classified by several researchers. This study followed the classification by Kitayama (1992).

Fieldwork was carried out in Kinabalu Park established in 1964 surrounding the mountain area. Three study sites were placed in three vegetation types, that is, subalpine forest, lower montane forest and hill forest. The highest site was Paka Cave (PAKA) located at an altitude of 3,100 m in a subalpine forest. Conspicuous canopy trees were *Dacrydium kinabaluensis* (Wasscher) de Laubenfels, *Ilex*, *Leptospermum recurvum* Hook. f., *Lithocarpus havilandii* (Stapf) Barnett, *Myrica javanica* Bl., and *Phyllocladus hypophyllus* Hk.f. Small trees and shrubs, *Ardisia*, *Drymis piperita* (Hook.f.) Miers., *Ilex*, *Photinia*, *Rapanea*, *Schefflera*, *Rhododendron*, *Rubus* and *Vaccinium* are common. The second site was Park Headquarters (PHQ) located at an altitude of 1,700 m

in a lower montane forest, below the lower limit of the cloud belt. *Agathis*, *Castanopsis*, *Caulophyllum*, *Dacrydium*, *Dacrydium*, *Magnolia*, *Palaquim*, *Payena*, *Phyllocladus hypophyllus*, *Lithocarpus*, *Schima wallichii* (DC.) Korth., *Symplocos*, *Syzygium* and *Tristaniopsis* trees were dominant in the forest canopy and subcanopy. Numerous small trees and shrubs, *Ardisia*, *Diplycosia*, *Ficus*, *Litsea*, *Medinilla*, *Psychotria*, *Rhododendron*, *Symplocos* and *Vaccinium* occurred. The lowest site was Poring (PORING) located at an altitude of 800 m in a hill forest. The forest canopy reached 40-50 m in height. *Parashorea*, *Shorea* and *Dipterocarpus* of the Dipterocarpaceae, *Koompassia*, and *Pangium* were conspicuous canopy trees. The Canopy Walkway System was useful for observations, with walkways spanning 158 m in total length at 5-40 m above the ground.

Mt. Kinabalu is located in a humid tropical climate. The daily mean air temperature is roughly constant all year round (Kitayama, 1992). There is no dry season, although severe droughts have occurred once every several years and have been reported to cause damage to vegetation (Kitayama, 1996; Kudo & Kitayama, 1999).

One observation period of this study (from July 1996 to June 1997) appeared to be under normal seasonal trends (Kitayama *et al.*, 1998). Figure 2 shows month-to-month changes in the mean air temperature and the monthly rainfall derived from the

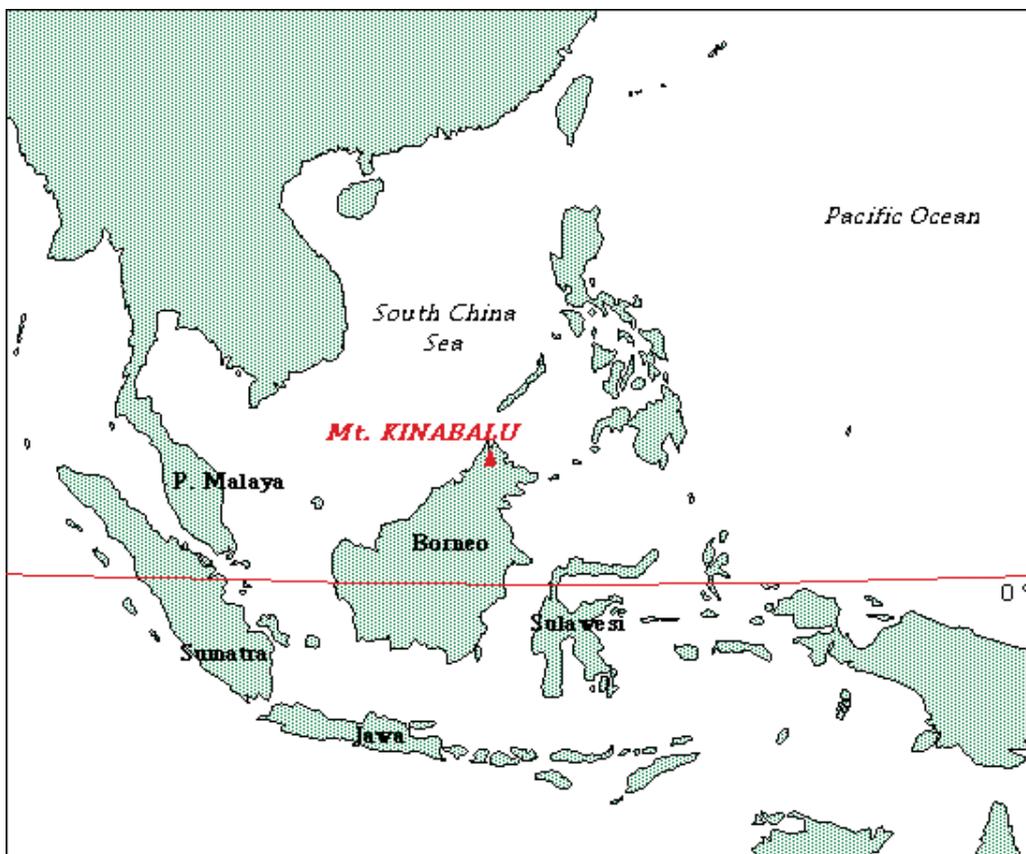


Fig. 1 Location of Mt. Kinabalu in the Greater Sunda region.

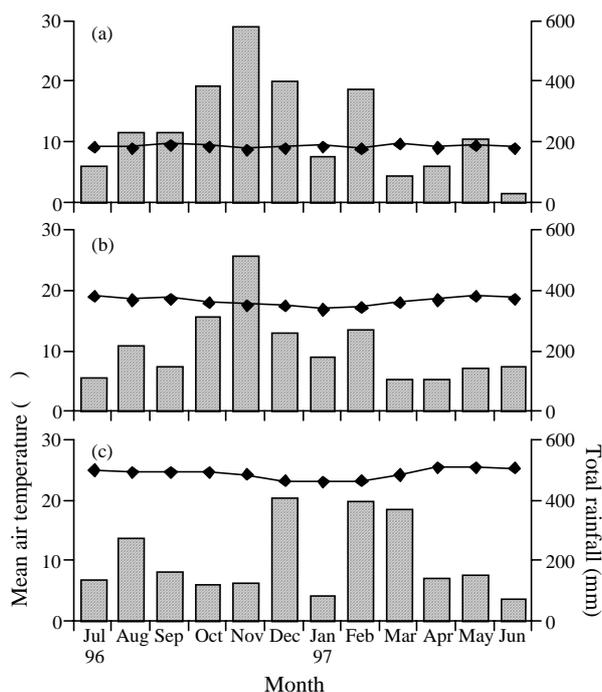


Fig. 2 Seasonal changes in the monthly mean air temperature (line) and total rainfall (bar) at the three study sites on Mt. Kinabalu, after Kitayama *et al.* (1999). From the top, (a) PAKA, (b) PHQ and (c) PORING.

climate stations which had been set up in an open place at the median altitude of each vegetation zone (Laban Rata [3,300 m], PHQ [1,700 m] and PORING [800 m]), after Kitayama *et al.* (1998). The temperature changed little during the entire observation period at all sites, although a very slight depression of temperature was recorded from December to March at PHQ and PORING. Annual total rainfall ranged from *ca.* 2,500 mm to 3,000 mm at all sites. A synchronous change in rainfall was observed between Laban Rata and PHQ; prominent peaks occurred in November and February. The pattern of rainfall at PORING was different from the others; prominent peaks occurred in December and February-March. Although there was no defined dry season, the monthly rainfall did not reach 100 mm in March and June in Laban Rata and January and June at PORING.

3. Methods

3.1 Fruiting phenology

The fruiting phenology of fleshy-fruited plant species at the three sites was shown based on records of 398 trees/shrubs bearing mature fleshy fruit which were observed biweekly from July 1996 until June 1997. We defined 'fruiting species' as those in which at least one individual was bearing fruit for each census, and calculated the ratio of the number of the fruiting species to the total number of observed species at each site.

"Fleshy-fruited plants" in this study means ones which have seeds surrounded by or attached to an edible part. Voucher specimens were collected from

most of the marked trees and were identified by matching them to specimens in the herbaria of Kinabalu Park and the Forest Research Centre, Sabah Forestry Department, Sandakan, Malaysia.

To find trends of fruiting phenology in the plant community of each site, I recognized six types of fruiting frequency based on frequencies of flowering and fruiting during the study period, referring to Newstrom *et al.* (1994). These types were 'continuous (c-) type', 'biannual (a2-) type', 'annual (a1-) type', 'annual with only fruiting (a1/fr-) type', 'no reproduction (nr)' and 'others'. The c-type included plants that bore fruit without a clear intermittence of reproduction. The a2- and a1-types bore fruits twice and once a year, respectively. The plants of the a1/fr-type were only observed to fruit during the observation period as the result of flowering in the previous period. The 'others' included species which flowered without fruiting. We defined the fruiting frequency types for particular species based on the individuals which reproduced most frequently.

3.2 Bird census

Biweekly bird censuses were conducted in order to investigate seasonal changes in frugivorous birds at all study sites. The majority of birds recorded in Borneo were distributed in the region of Mt. Kinabalu (MacKinnon & Phillipps, 1993). A total of 326 species have been documented in Kinabalu Park, and they have been categorized into three groups based on their altitudinal zonations: lowland, lower montane and upper montane (Biun, 1999), corresponding to the three study sites.

Methods were as follows: at PAKA and PHQ, route censuses were conducted from 0600 to 0800 along a census route 2 km in length. The route was the summit trail from Laban Rata (3,300 m) to Carson Camp (2,700 m) and the road near PHQ (*ca.* 1,700 m). In the censuses, the number and species of birds appearing or singing within a radius of 25 m from observation points were recorded. At PORING, I started at 0600 and observed for 30 min each from three fixed points: at an edge of the forest, inside the forest (forest understorey), and on the Canopy Walkway System (forest canopy). Birds which appeared within a semi-circle with a radius of 25 m from the fixed point were recorded.

The reason for applying a different method at PORING was that it was too difficult to identify birds in the forest canopy from the ground because the canopy trees were too tall and because subcanopy trees hindered my upward view. This method revealed seasonal changes in birds better, covering more bird species than route censuses would have done, although this does not allow comparison of the bird density at PORING with the others.

Very few specific descriptions associated with diets of birds on Mt. Kinabalu are available. Accordingly, we chose major frugivorous species which are

highly or more frugivorous and minor frugivorous species which are partially frugivorous (Appendix, after Kimura *et al.*, 2001), referring to Corlett (1998), Davison (1992), Leighton & Leighton (1983), MacKinnon & Phillipps (1993) and Smythies (1999) and my observations on their feeding behaviour.

Nine families including major frugivores were recognized: Columbidae (doves and pigeons), Bucerotidae (hornbills), Megalaimidae (barbets), Eurylaimidae (broadbills), Aegithinidae (leafbirds), Pycnonotidae (bulbuls), Turdidae (thrushes), Dicaeidae (flowerpeckers), and Corvidae (treepies).

Frugivorous species were categorized into three groups based on the scale of their seasonal movement (Loiselle & Blake, 1991). The first was 'resident' which included resident species of Borneo that occur in a specific vegetation type all year round. The second was 'altitudinal migrant' which was also resident species but occurred seasonally across vegetation zones on Mt. Kinabalu. The third was 'temperate migrant' which bred in the temperate regions and appeared in the tropical regions during their non-breeding seasons. Most of the temperate migrants in the regions come from the north (MacKinnon & Phillipps, 1993). Wells (1990) recorded two temperate migrants, *Turdus obscurus* Gmelin and *Zoothera sibirica* (Pallas), which eat fruit in the mountains of the Greater Sunda regions. *T. obscurus* is a regular winter visitor to hill and mountain forests of northern Borneo, but *Z. sibirica* is a rare visitor to northern Borneo.

4. Results

4.1 Fruiting frequency types of fleshy-fruited plants

Different compositions of fruiting frequency types of fleshy-fruited plant species were clarified among the three sites (Table 1). Annual fruiting types represented by the a2-type and a1-type were the most frequent at all sites, although there was no significant difference among sites. The proportion of the annual types at PHQ was 49.3%, the highest among the sites. The occurrence of the c-type was significantly higher in PAKA (Chi-square test, $\chi^2=14.0$, $df=2$, $p<0.01$). At PORING, c-type species were not observed and the

occurrence of the a1/fr-type was overwhelmingly higher than those at the montane sites (Chi-square test, $\chi^2=19.8$, $df=2$, $p<0.001$). Fleshy-fruited plant communities at PAKA included more plants with unclear fruiting seasons. Those at PHQ included more plants with clear fruiting seasons, while, those at PORING included more plants with clear fruiting seasons in a supra-annual cycle.

4.2 Fruiting phenology of fleshy-fruited plants

Seasonal patterns in the total number of fruiting species at the three sites were divided mainly into three groups by the results of Spearman's rank correlation test. The first was a montane group at PAKA and the second was a lowland group at PORING. The seasonality of the montane group was that fruiting was less marked and there was no fruitless period, while that of the lowland group was highly marked and there was a fruitless period (Fig. 3). The last group was found at PHQ having an intermediate pattern between these two groups because its seasonal changes had significant positive correlations with the all other sites. The seasonality of PHQ showed a balanced bimodal pattern with no fruitless period.

Detailed explanations about the seasonality are as follows (Fig. 3):

PAKA – Several peaks occurred throughout the year, but there was no outstanding one. Seasonal patterns of fruiting frequency types except for the a1/fr-type had significant positive correlations with the pattern of total fruiting species (Spearman's rank correlation test, $p<0.05$). Although a2- and a1-type species should exhibit clear fruiting seasons, they did not show an aggregated fruiting trend at the community level but synchronized with the seasonal pattern of the c-type.

PHQ – A bimodal pattern was observed, with peaks in October-December 1996 and April 1997. The seasonal pattern of the a1-type had a very strong positive correlation with the pattern of total fruiting species (Spearman's rank correlation test, $p<0.0001$), although those of c-type, sc-type and a2-type species also had significant positive correlations.

PORING – An unbalanced bimodal pattern was observed; large outstanding peaks during October-November 1996 and a very small peak in May 1997. A fruitless period was observed from February to April 1997. Seasonal patterns of the a1-type and

Table 1 Number of fleshy-fruited plant species observed at the three study sites on Mt. Kinabalu.

Study site	N	Fruiting frequency types					
		c	a2	a1	a1/fr	nr	others
PAKA	37 (143)	10	8	7	2	5	5
PHQ	73 (166)	7	9	27	5	10	15
POR	46 (89)	0	5	12	17	8	4

c: continuous, a2: biannual, a1: annual, a1/fr: annual (only fruiting), nr: no reproduction, others: species which flowered without fruiting.
(): number of observed individuals.

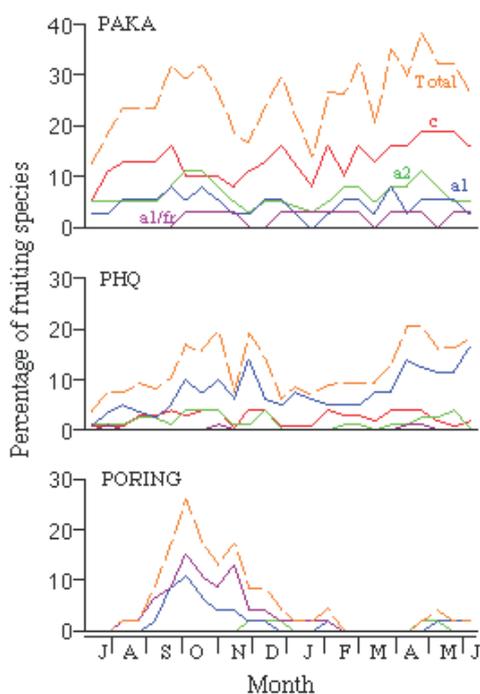


Fig. 3 Seasonal changes in proportion of fruiting species to the total reproducing species at the three study sites, showing seasonal changes of respective types of fruiting frequency; c - continuous, a2 - biannual, a1 - annual, and a1/fr - annual (only fruiting).

a1/fr-type had strong positive correlations with the pattern of total fruiting species (Spearman's rank correlation test, $p < 0.0001$), but major fruiting seasons of both types were different. The major fruiting peak of the a1-type occurred at the end of September and the peaks of a1/fr-type occurred at that time and in the middle of November.

4.3 Seasonal dynamics of frugivorous birds

Thirty-nine bird species of nine frugivorous families were recorded in the censuses and six more species were observed out of censuses at all sites (Table 2). The greater part of frugivorous species of Bucerotidae, Megalaimidae, Eurylaimidae, Aegithi-

nidae, Pycnonotidae and Dicaeidae occurred in PORING. While, the frugivorous species of Turdidae and Corvidae tended to occur at the montane sites, in particular, one of thrushes, *Turdus poliocephalus* Latham, was unique to PAKA. Forty-four species were residents. Only one species, *Turdus obscurus*, which was a temperate migrant and occurred at PHQ and PAKA.

Columbidae, Megalaimidae, Aegithinidae, Pycnonotidae, and Turdidae species were frequently observed eating fruit of various fleshy-fruited species: *Ilex* (Aquifoliaceae), *Schefflera* (Araliaceae), *Daphniphyllum* (Daphniphyllaceae), *Elaeocarpus* (Elaeocarpaceae), *Vaccinium* (Ericaceae), *Macaranga* (Euphorbiaceae), *Lindera* and *Litsea* (Lauraceae), *Medinilla* (Melastomataceae), *Myrica* (Myricaceae), *Ficus* (Moraceae), *Ardisia* (Myrsinaceae), *Syzygium* (Myrtaceae), *Olea* (Oleaceae), *Dacrycarpus* and *Dacrydium* (Podocarpaceae), *Photinia* and *Rubus* (Rosaceae), *Symplocos* (Symplocaceae), *Boehmeria* (Urticaceae), *Drymis* (Winteraceae), and so on (unpublished data).

Major frugivorous resident species occurred at all sites but no major frugivorous temperate migrants were observed at PORING. Seasonal changes in the number of residents and temperate migrants are shown in Fig. 4:

PAKA – There was no prominent seasonal change in the number of major frugivorous resident species. Four resident species, *Macropygia ruficeps*, *Megalaima pulcherrima*, *Turdus poliocephalus* and *Pycnonotus flavescens* were common members. Two to four resident species appeared in every census except July under windy conditions. *Turdus poliocephalus* occurred in every census and *Pycnonotus flavescens* often occurred. A temperate migrant species (*T. obscurus*) was observed in early December 1996.

The number of major frugivorous resident species fluctuated irregularly through the year. The number increased in September-October, December, January-February and April. The highest number was in early December 1996 when four individuals of *T. obscurus* occurred.

Table 2 Observed number of frugivorous bird species of nine families at the three study sites.

Family	Taxonomic groups	Site			Total
		PAKA	PHQ	POR	
Columbidae	Pigeons & Doves	1	3	2	4
Bucerotidae	Hornbills	1(1)	1	3(2)	3(1)
Megalaimidae	Barbets	1	2	6(1)	8(1)
Eurylaimidae	Broadbills	0	1	3(1)	4(1)
Aegithinidae	Leafbirds & Bluebirds	0	2(2)	4	4
Pycnonotidae	Bulbuls	1	3(1)	10(2)	12(1)
Turdidae	Thrushes	4(2)	3	1	4
Dicaeidae	Flowerpeckers	0	2(1)	4(1)	5(2)
Corvidae	Treepies	1	1	1(1)	1
Total		9(3)	18(4)	25(8)	45(6)

(): number of species observed out of the census.

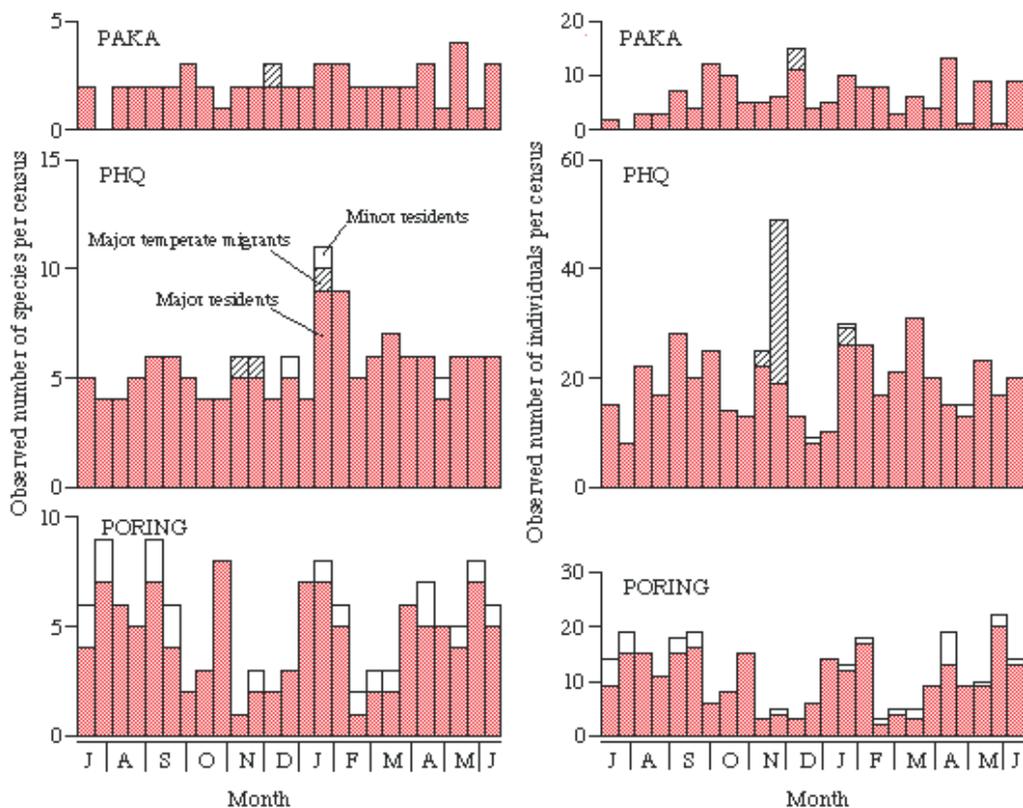


Fig. 4 Seasonal changes in the number of frugivorous bird species (left) and individuals (right) observed at the three study sites: major frugivorous residents (red), minor frugivorous residents (white) and temperate migrants (slash).

PHQ – The number of major resident frugivorous species from the end of January to March exceeded six species (*Ducula badia*, *Macropygia ruficeps*, *Megalaima pulcherrima*, *Alphoixus ochraceus*, *Dicaeum monticulum* and *Dendrocitta cinerascens*) which was estimated as the number of regular species of the censuses. This increase was caused by a concentration of occurrences of irregular montane species and by the rare occurrences of lowland species, that is, *Macropygia phasianella*, *Rhyticeros undulatus* and *Pycnonotus atriceps*.

The number of individuals of major resident frugivorous species increased during August-October and January-March. The former period was due to particularly large numbers of Columbidae species (*D. badia* and *M. ruficeps*). The latter was caused by an increase in the number of species.

The occurrence of *T. obscurus*, a major frugivorous temperate migrant, produced a large peak of individuals in November 1996. The number of individuals in the peak reached 30, more than the summed number of individuals of all major frugivorous residents in that census. They were observed from November 1996 to March 1997 at all sites according to the census data and non-census data. During the five months, they overwintered in the Kinabalu region.

PORING – The number of major frugivorous

resident species fluctuated irregularly through the year. Outstanding decreases in the number were recorded during November-December and February-March when only one or two species occurred. The two periods of decline resulted from fewer observations of major frugivorous taxonomic groups, such as barbets, leafbirds and bulbuls.

The seasonal pattern of the number of individuals mirrored the pattern of species. Prominent decreases were observed during November-December and February-March.

4.4 Seasonal dynamics of each frugivorous bird family

Seasonal changes in the number of individuals of nine families including major frugivorous species are shown in Fig. 5. Major frugivorous species of Columbidae, Megalaimidae and Pycnonotidae were observed at all sites. Individuals of these families occurred frequently at PHQ and PORING. However, there were some periods when the number of individuals decreased at PORING but increased at PHQ or PAKA: during January-March in Columbidae, during February-March in Megalaimidae and during November-December and February-March in Pycnonotidae. The increases during the latter period at montane sites were caused not only by an increase in

individuals of regular species but also an influx of individuals of lowland species, such as a dove (*Macropygia phasianella*) and a bulbul (*Pycnonotus atriceps*).

Bucerotidae species were rarely observed at PHQ and PORING. A few individuals of *Rhyticeros undulatus* were observed during January-March in PHQ or moving up or down along the mountain slope. Only a single individual of *Anthracoceros malayanus* occurred in February 1997 at PORING. Away from the study sites, I saw *R. undulatus* in July 1996 and *Buceros vigil* in September 1996 and March 1997 in the foothills of Mt. Kinabalu.

Eurylaimidae, Aegithinidae and Dicaeidae were observed occasionally at PHQ and PORING. Two major frugivorous broadbills, *Calyptomena viridis* and *C. whiteheadi* are common residents in lowland and montane forests, respectively (Smythies, 1999). However, I had few records because they live mainly deep in the forests and are difficult to observe. One

major frugivorous species of Aegithinidae, *Chloropsis cochinchinensis*, was observed eating fruit of *Daphniphyllum* sp. in April 1997 at PHQ, though no individual of Aegithinidae was recorded during the census.

The major frugivorous species of Turdidae and Corvidae were common at the montane sites. Individuals of Turdidae occurred less frequently and more seasonally at PHQ than at PAKA. Temperate migrants of *T. obscurus* amounting to seven times more than those at PAKA came to PHQ in November 1996. After November 1996, a few individuals of *T. obscurus* were sometimes observed out of censuses until March 1997. Individuals of the Corvidae also occurred more commonly at PHQ than at PAKA.

It was probable that the Columbidae, Megalaimidae, Pycnonotidae, Bucerotidae and Aegithinidae included altitudinal migrants. In the case of the Columbidae, Megalaimidae and Pycnonotidae, the increase in the number of individuals at PHQ corresponded with a decrease in the number of individuals at

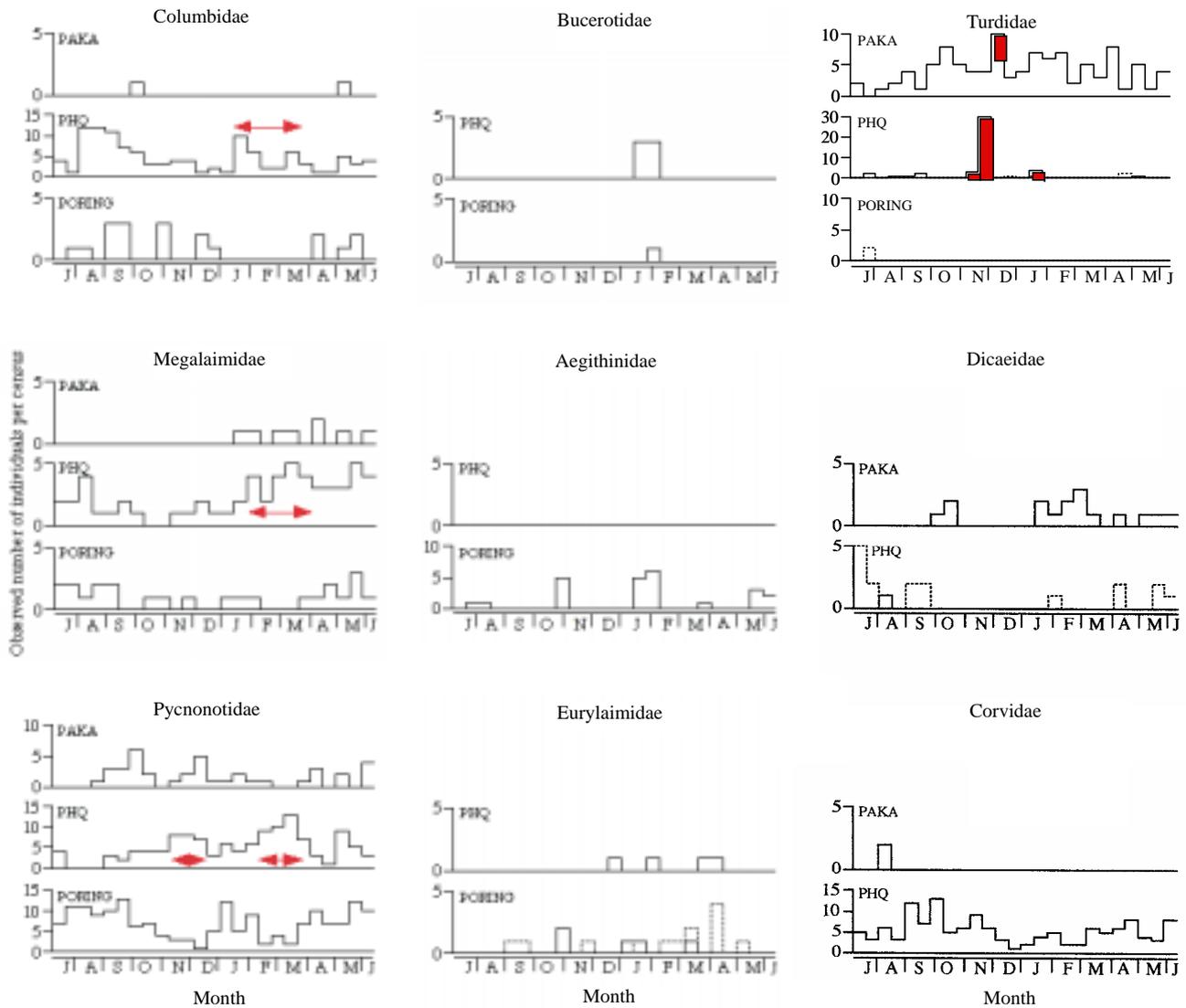


Fig. 5 Seasonal changes in the number of individuals of nine families which include major frugivorous species at the three study sites. Three categories of frugivore are shown; major frugivorous residents (line), minor frugivorous residents (dotted line) and temperate migrants (red). Arrows indicate periods when the observed number at PHQ increased as the number decreased at PORING.

PORING during the fruitless period at PORING. Some individuals of lowland species of the Aegithinidae were also observed at PHQ during the fruitless period. *M. phasianella*, *P. atriceps* and *C. cochinchinensis*, were likely to be altitudinal migrants. Species of Bucerotidae inhabiting mainly the lowlands departed the study sites during the fruitless period. Among them, *R. undulatus* moved over a wider range altitudinally. *Megalaima monticola*, which usually occurs below 1,600 m, was also likely to be an altitudinal migrant.

4.5 Relationship between fruiting seasons and migration periods of temperate migrants

A relationship emerged between the seasonal dynamics of fruiting events and migration periods. We tried to find the relationship at PHQ by dividing the observation period into four terms: pre-migration term (the first 9 censuses), migration term (the next 3 censuses), overwintering term (the next 8 censuses) and post-overwintering term (the last 5 censuses). Table 3 shows the number of start/end of fruiting events in each term. The number of 'start-of-fruiting events' means the number of trees that bore mature fruit newly in each census, and the number of 'end-of-fruiting events' means the number of individuals that had all of their fruit removed or lost in each census.

There was no significant difference in the start of fruiting events among the four terms as indicated by a chi-squared test, showing that there was no seasonal trend in the number of start-of-fruiting events throughout the year. However, when the overwintering term was combined with the migration term, there was a significantly smaller number in the combined period ($\chi^2=6.80$, $df=2$, $p<0.05$). As for end-of-fruiting events, only the migration term had a significant large number ($\chi^2=11.3$, $df=3$, $p<0.01$). This suggests that fruit removal from trees might be concentrated when temperate migrants arrived at PHQ.

Comparison with the fruiting phenology at PHQ revealed the following scenario: start-of-fruiting events accumulated during the pre-migration period,

Table 3 The number of starts and ends of fruiting events of fleshy-fruited plants at PHQ during the four terms.

	Pre-migration term	Migration term	Over-wintering term	Post-over-wintering term	Total
Duration (number of censuses)	9	3	8	5	25
Starts of fruiting events	28	4	16	20	68
Ends of fruiting events	13	13	9	14	49

and the accumulated events formed a fruiting peak in October 1996. In November 1996, mainly temperate migrants removed the fruit. Accumulated fruiting events during the migration period formed a fruiting peak in December 1996, and fruit removal by temperate migrants occurred again. After the second fruit removal in December 1996, a smaller amount of fruit corresponding to a smaller number of start-of-fruiting events was consumed by a small number of residents and temperate migrants staying at PHQ.

5. Discussion

The difference in fruiting phenologies among the three sites played an important role in dietary support of frugivorous birds which were seen in the Mt. Kinabalu region. In particular, the fruiting phenological groups observed in the lower montane forests were very important for altitudinal migrants from the lowlands and temperate migrants.

In hill forests, regular fruiting seasons and fruitless seasons occurred with a large year-to-year fluctuation in the number of fruiting species. This fluctuation was caused by a mast fruiting (mass flowering) phenomenon, which is common in lowland forests of Southeast Asia and is unpredictable because the phenomenon occurs once every several years (Appanah, 1985; Ashton *et al.*, 1989; Kitayama *et al.*, 1998; Sakai *et al.*, 1999). These unstable fruiting conditions make lowland frugivorous birds move or change their diet. This study showed the movement of lowland birds tracking fruit resources, suggesting that an altitudinal difference in fruiting seasonality encouraged the birds to move to montane forests (van Shaick *et al.*, 1993) (Fig. 6). In Costa Rica, the

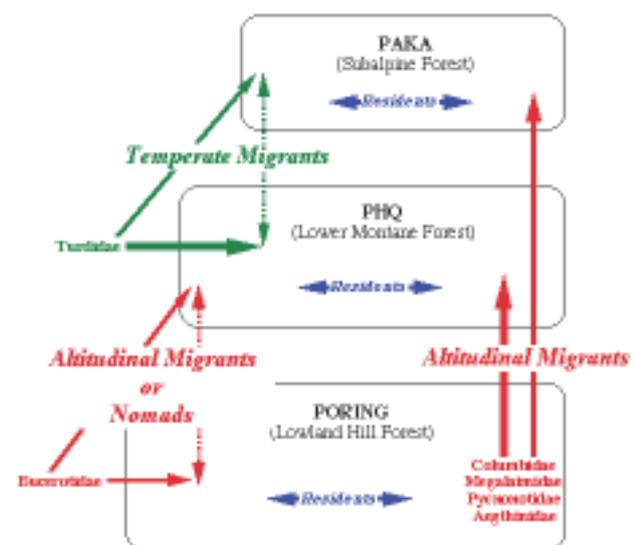


Fig. 6 A scheme of tracking movements of frugivorous birds on Mt. Kinabalu. Arrows indicate the direction of movements of residents (blue), temperate migrants (green) and altitudinal migrants (red) from their breeding regions. Dotted arrows indicate their probable movements.

opposite direction of movement from montane area to lowlands was reported (Loiselle & Blake, 1991). These altitudinal migrations corresponding to local fruit conditions suggest the behaviour of frugivorous birds tracking fruit resources might be flexible.

Some studies indicated that a tropical montane region was one of the destinations supplying fruit resources during periods of fruit scarcity in lowland forests of the Greater Sunda region (Leighton & Leighton, 1983; van Schaik *et al.*, 1993; Wells, 1990). The present study supports these studies. The montane region of Mt. Kinabalu was probably one of the destinations because the increase in the number of species and individuals at montane sites was not so prominent, suggesting that the scale of altitudinal movements was not so large. Many studies explained that large lowland birds such as hornbills and pigeons were possible altitudinal migrants because of their expected long flying range (Leighton & Leighton, 1983). However, small birds such as barbets, bulbuls and leafbirds moved up to montane regions, although surrounding geographical features may have influenced their movements.

Not only altitudinal migrants but also temperate migrants utilized montane forests for their feeding sites (Fig. 6). The fruiting peak in November 1996 at PHQ was explainable as very convenient for the arriving temperate migrants. The lower montane forests which have regular fruiting seasons leading to a predictable fruit supply would be a favorable visiting and overwintering site for regular temperate migrants. This result supports the previous description by Wells (1990) that frugivorous temperate migrants often occurred in montane area in the Greater Sunda region.

T. obscurus must be an important fruit consumer and seed disperser in lower montane forests of Mt. Kinabalu, although its quality as a consumer and disperser should be more thoroughly investigated. Thrushes are important as migratory birds in fruit-bird relationships in Asia (Kwok & Corlett, 1999; Noma & Yumoto, 1997; Wells, 1990) as well as on the other continents of the Northern Hemisphere (Blake & Loiselle, 1992; Herrera, 1995; Herrera & Jordano, 1981; Loiselle & Blake, 1991; Sorensen, 1981; Thompson & Willson, 1979; Willson & Whelan, 1993).

It was strange that most temperate migrants were observed in lower montane forests, even though there was mature fruits during the migration and overwintering period in hill forests and subalpine forests. It may be that the seasonal dynamics of temperate migrants in the two forests may be influenced by the density and habits of resident species. In hill forests, a number of mature fruits were certainly removed by residents during the fruiting peak, although the fruiting peak had occurred before the migration period of temperate migrants. Actually, many residents visited fruiting trees one after another to remove fruits of

Macaranga hypoleuca (Reichb. f. & Zoll.) Muell. and *Ardisia corolata* Roxb. (unpublished data). In other words, the carrying capacity of fruit resources for frugivores might have been saturated even in a mast fruiting year. While in subalpine forests, the number of frugivorous birds might not reach a level matching the amount of available fruit, because an influx of lowland frugivores and temperate migrants was also observed. As an alternative to the carrying capacity, it is probable that *T. obscurus* competes for fruit resources against closely related species sharing the same feeding guild (Wells, 1990), such as *T. poliocephalus* as a resident in the forests.

Tropical montane forests of Mt. Kinabalu hold more regular and stable conditions in fruit resources and provide temporal 'refugia' for many frugivorous birds. The role as refugia may be very important because there are more montaneous areas in Southeast Asia (Whitmore, 1994). It is predictable that, for many lowland frugivorous birds, the tropical montane forests will be more precious in non-mast-fruiting years because the shortage of fruit resources in hill forests will be more severe in non-mast-fruiting years than in mast fruiting years such as the study period. In addition, tropical montane forests, especially lower montane forests, must provide a more precious overwintering area for many frugivorous temperate migrants in fruitless years in the north.

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