POLLINATION OF HEMIPARASITES (LORANTHACEAE) BY SPIDER HUNTERS (NECTARINIIDAE) IN THE CANOPY OF A BORNEAN TROPICAL RAIN FOREST

TAKAKAZU YUMOTO[1, 2]

Faculty of Science, Kobe University, Nada, Kobe 657, Japan

TAKAO ITINO

Faculty of Agriculture, Kagawa University, Kagawa 761–07, Japan

HIDETOSHI NAGAMASU

Faculty of Integrated Human Studies, Kyoto University, Kyoto 606, Japan

ABSTRACT. We observed pollination process of three hemiparasites, Loranthaceae, *Amylotheca duthieana* (King) Danser, *Trithecanthera sparsa* Barlow and *T. xiphostachys* Tiegh. Flowers of these three species were cylindrical with different corolla lengths. Flowers of *A. duthieana, T. sparsa* and *T. xiphostachys* were reddish orange, yellow, and pink in color, respectively. Flowers lacked odor, nectar guides, and landing places for visitors. Long-billed spider hunters (*Arachnothera robusta*) were main visitors to flowers of all three species, although little spider hunters (*Arachnothera longirostra*) foraged on *A. duthieana* and *T. sparsa* in much less frequency. Aggressive behavior of the long-billed spider hunter might have modified the other nectarivorous birds' foraging pattern. Long-billed spider hunters visited *A. duthieana* flowers only in the early morning, but visited *T. sparsa* flowers rather constantly from the morning to noon. Flowers of *T. xiphostachys* were visited by them at most only two times a day. Diurnal patterns of nectar production and nectar level in the corolla fit well to the above visit patterns to these three species. The utilization of pollinators by three species of mistletoes may be partitioned along a diurnal dimension.

INTRODUCTION

A large number of vascular epiphytes characterizes humid tropical forests. In the vertical stratum of tropical rainforests, the light intensity decreases exponentially as one comes down from the upper canopy. The forest floor receives up to a few percent of the irradiance of the upper canopy. Epiphytism can be understood as a plant strategy which spreads their foliage in the better light condition without investing a large cost in constructing the trunk as do the canopy trees.

But epiphytes suffer from the stress of water and nutrient shortage. Many epiphytes possess stout-walled epidermal cells covered by a thick evaporation-retarding cuticle as xerophytes in the drier climatic conditions. Epiphytic orchids have developed specialized water-storage organs. For the nutrient shortage, some epiphytes belonging to *Myrmecodia* (Rubiaceae) and *Dischidia* (Asclepiadaceae) are ant fed: a plant provides nest sites for ants and these ants supply it with nutrients. Some epiphytic ferns belonging to *Drynaria* (Polypodiaceae) and *Asplenium* (Aspleniaceae) have special foliage structures which catch debris for collecting nutrients. Gen-

try and Dodson (1987) pointed out that the abundance of epiphytes correlates with the soil richness and that in tropical Asia the epiphyte flora is much poorer than those in tropical America because of soil nutrients. Poor-nutrient soil can limit the nutrient supply to epiphytes by low nutrient cycling rate which determines the amount of organic materials deposited in the canopy layer.

Another mode of life for epiphytism to acquire nutrients is parasites. Mistletoes invade host vasculature and get nutrients directly from the host trees. The Loranthaceae is a family of mistletoes with 65 genera and some 900 species distributed mostly in the tropics (Benzing 1990). Their habits are aerial, hemiparasitic shrubs growing on host trees to which individuals are attached either by a single massive club-like haustorium or by a network of surface runners which at intervals give rise to a haustorium.

A wide prevalence of ornithophily among the Loranthaceae has been recognized by a number of field botanists since the late 19th century (Evans 1895, Volkens 1899, Werth 1900, 1915, Winckler 1906, Docters van Leeuwen 1954). As a highly adapted character for ornithophily, the explosive flower-opening mechanisms of the Loranthaceae, flowers that do not open until they explode under the impact of a nectar-seeking bird, was investigated in particular species by

Goebel (1920), Docters van Leeuwen (1931), Vogel (1954) and Feehan (1983, 1985). The success of the Loranthaceae as a group in tropical ecosystems is due as much to their remarkable mutualistic relationship with nectar-feeding birds and floral adaptations which they have evolved in connection with this as it is to their precarious hemiparasitism in the canopy (Feehan 1985).

It is, however, still difficult to observe the pollination process of the Loranthaceae *in situ* because they grow in the canopy layer of rain forests >35 m above the ground. In the Canopy Biology Program in Sarawak (CBPS) we constructed the canopy observation system to observe interactions between plants and animals at canopy and emergent layers (Inoue *et al.* 1995). This study aims to identify the pollinators *in situ* of three species of the Loranthaceae; *Amylotheca duthieana* (King) Danser, *Trithecanthera sparsa* Barlow and *T. xiphostachys* Tiegh., and to discuss the guild structure of nectarivorous birds which are attracted to mistletoes and diurnal partitioning of pollinators among mistletoes, with special reference to nectar secretion pattern.

MATERIALS AND METHODS

Our study plot was situated in Lambir Hills National Park, Sarawak (113°8′E, 3°4′N). The vegetation of the study site is a typical lowland mixed dipterocarp forest at altitudes of 100 to 200 m above sea level (Ashton 1991; Ashton & Hall 1992). The height of emergent trees exceeds 70 m above the ground. We set the canopy biology plot and constructed two tree towers connected by 9 spans of aerial walkways (see Inoue *et al.* 1995). There is another tree tower available, the Operation Raleigh Tower, which is situated 500 m away from the canopy biology plot.

All plants observed parasited on the Dipterocarpaceae trees; *A. duthieana* was on a branch and two species of *Trithecanthera* were on the trunks. They were very conspicuous by standing out clearly against the foliage of the hosts.

Amylotheca duthieana (8.4 cm in diameter at the connecting part to the host) parasited on *Shorea acuta* Ashton (40.8 cm in DBH: diameter at 1.3 m height, 37 m total height) at 27 m in height above the ground. The plant had more than 2600 leaves which spread an extent of 3 m × 4 m × 0.8 m, and about 450 flowers which opened from 1 to 8 August, 1992.

Two plants of *T. sparsa* (6.8 cm and 7.2 cm in diameter at the connecting part to the host, respectively) parasited on *Dipterocarpus globosus* Vesque (99.8 cm in DBH, 62 m total height).

A plant of 7.2 cm in diameter had 36 leaves which spread an extent of 1.7 m × 0.5 m × 0.5 m parasited on the host tree at 32 m in height; the other of 6.8 cm in diameter had 18 leaves which spread an extent of 0.6 m × 0.6 m × 0.6 m parasited at 29 m in height. Those plants had about 200 and 120 flowers respectively, and bloomed from 7 to 12 August, 1992.

Trithecanthera xiphostachys (2.6 cm in diameter at the connecting part to the host) parasited on *Shorea smithiana* Sym. (68.4 cm in DBH, 34 m total height) at 12 m in height above the ground. The plant with 25 leaves which spread an extent of 0.7 m × 0.4 m × 0.4 m had 52 flowers in an inflorescence which bloomed from 2 to 16 March, 1994. One to seven flowers in the inflorescence per day opened successively.

Observations were made for *A. duthieana* and *T. sparsa* from 5 to 10, August, 1992. We used the Operation Raleigh Tower which is about 27 m in height from the ground for the observation. As for *T. xiphostachys*, observations of *T. xiphostachys* were made from 4 to 10 March, 1994 using the walkway No. 6 which is about 12.2 m in height from the ground. Herbarium specimens of the three species are deposited in the herbariums of Sarawak Forest Department, Kuching, Sarawak, Malaysia (SAR) and of Faculty of Science, Kyoto University, Kyoto, Japan (KYO).

Samples of floral nectar were taken by microcapillary tubes. Nectar sampling was conducted in the morning (from 0900 to 1000) and at noon (from 1100 to 1200) for the three species in bagged condition. The nectar level in the total corolla length was estimated by holding flowers to the light. The sugar concentration as sucrose equivalents of nectar was measured by a pocket refractometer (Belingham & Stanley Ltd., BS-R70) and refractive index was converted into the sugar percentage (weight/weight). The size of the flowers was measured by slide calipers, based on 5 to 20 flowers for each species.

We observed the flower-visiting animals from 0600 hr to 1700 hr. The total observation hours were 24 hours, 26 hours and 41 hours for *A. duthieana*, *T. sparsa* and *T. xiphostachys*, respectively. We recorded animal species, staying time and the number of flowers visited at each visit. The foraging animals were observed by a pair of binoculars (Nikon, 12 × 40, 5.5 °WF) and the identification of birds was made by the field marks in Smythie (1960) and MacKinnon & Phillipps (1993). The scientific names of birds followed MacKinnon & Phillipps (1993).

The bill length (upper mandible length), bill width (gape width), head width and the total length of the observed bird species were measured for the specimens collected in the Sarawak

TABLE 1.   Floral characteristics of three Loranthaceae species. Thickness of flower wall was measured at the bottom of flowers.

Species	Floral color	Sample size	Collora length (Mean, s.d)		Lobe	Number of lobes	Lobe length	Thickness of flower wall
			(mm)	(mm)				
Amylotheca duthieana	Reddish orange	20	45.8	0.2	Reflexed	6	4	0.3
Trithecanthera sparsa	Yellow	10	77.2	0.3	Suberect	6	18	0.6
Trithecanthera xiphostachys	Pink	4	167.8	2.4	Patent	5	23	1.1

Museum. These specimens were collected in Sarawak, mainly around Kuching.

RESULTS

Flower Shapes and Anthesis

Flowers of *A. duthieana*, *T. sparsa* and *T. xiphostachys* were reddish orange, yellow, and pink in color, respectively (TABLE 1). All flowers were cylindrical with corollas of different lengths. The longest corolla and lobes were *T. xiphostachys*, *T. sparsa* was intermediate, and the shortest were *A. duthieana* (FIGURE 1). The lobes of *A. duthieana* were reflexed, *T. sparsa* suberect and *T. xiphostachys* patent. Flowers of these three species lacked odor and nectar guides. They were sessile and reflexed upwards. The inflorescence of *T. xiphostachys* is a spike of flowers in oblique whorls, the axis was 33 cm long with a 20 cm long sterile tip. These flowers lacked lips and margin, i.e., no perch or landing place on the flower itself for pollinators. Flowers showed diurnal anthesis. Each flower of *T. xiphostachys* opened before 0400 hr and dropped its corolla by 1600 hr. They had thick flower walls: 0.3 mm, 0.6 mm and 1.1 mm at the bot-
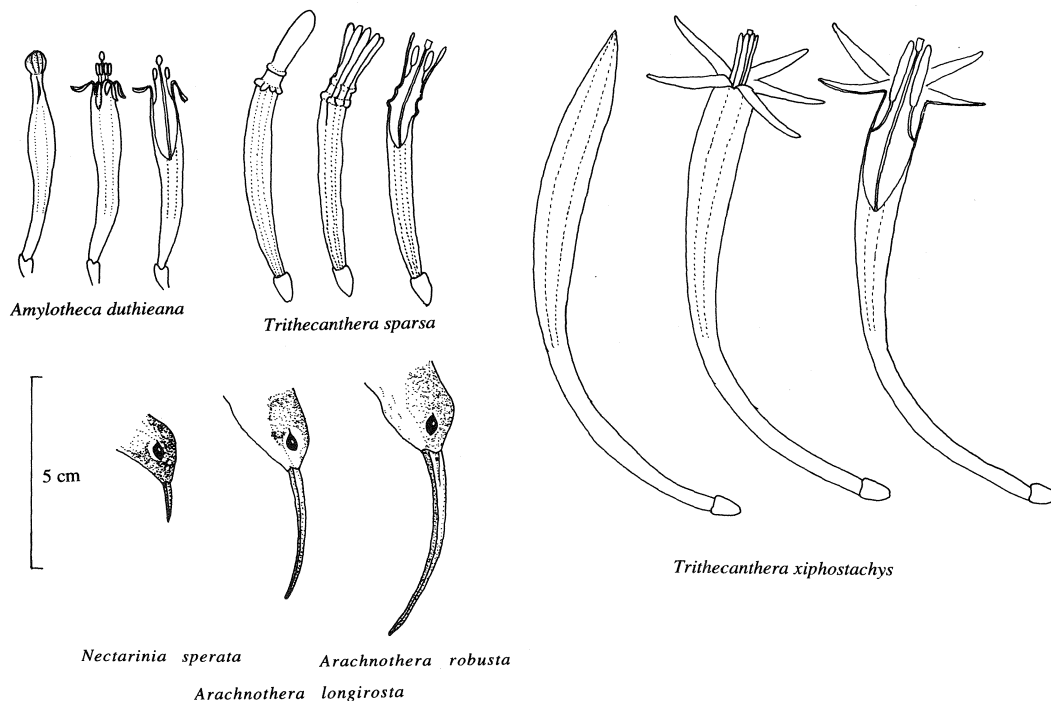

FIGURE 1.   Flower shapes of three mistletoes, *Amylotheca duthieana*, *Trithecanthera sparsa* and *T. xiphostachys,* and bill shapes of three nectarivorous birds, *Arachnothera robusta, A. longirosta* and *Necatrinia sperata* in a scale. Flowers in bud, in bloom, and the position of anthers and stigma are shown in each species.

TABLE 2. Amounts, sugar concentration and energy per flower of floral nectar of three Loranthaceae species without consumption. The mean values and the range are shown for each sampling.

Species (sample number)	Morning (0800–0900)			Noon (1100–1200)		
	Amount (μl)	Sugar concentration (%)	Energy (cal./ flower)	Amount (μl)	Sugar concentration (%)	Energy (cal./ flower)
Amylotheca duthieana (N = 20)	2.8 (0.5–6.0)	8.0 (5–10)	0.83	1.0 (0–2.3)	1.2 (0–4)	0.04
Trithecanthera sparsa (N = 10)	4.4 (1.6–16.5)	16.0 (15–17)	2.60	15.8 (0.3–69.2)	14.0 (11–15)	8.14
Trithecanthera xiphostachys (N = 3)	149.4 (130.4–155.6)	17.5 (17–18)	96.73	230.6 (184.8–267.7)	17.0 (17)	145.05

tom of flowers for *A. dulthieana, T. sparsa* and *T. xiphostachys,* respectively.

Flowers of all three species were bisexual and homogamous. Anthers were situated as high as the tip of the lobes, and the stigma was slightly higher than the top of the stamen. The separation of anthers and stigma in space, herkogamy, was apparent for those three species.

Explosive flower opening was found in *A. duthieana,* but not in the two *Trithecanthera* species. As for *A. duthieana,* tensions within the stamens caused the tubular corolla to split along the petal junctions to form window-like fenestrae.

Nectar Secretion

The mean nectar volume and sugar concentration of *A. duthieana* dropped between morning and noon samplings (TABLE 2). The nectar level in the corollas was from ¼ to ⅓ of the total length of the corolla. For *T. sparsa* and *T. xiphostachys,* the mean nectar volume increased between morning and noon, while sugar concentrations decreased albeit slightly. The nectar level increased for both species between morning and noon. The highest nectar level of *T. sparsa* was ¼ of the corolla length at the morning sample and that at the noon sampling was ⅕. The nectar level of *T. xiphostachys* increased from ⅓ to ⅖ at the morning sample up to ½ to ⅔ for the noon sample.

Flower Visitors

A. duthieana was visited by mainly the long-billed spider hunter, *Arachnothera robusta* (TABLE 3, PHOTO 1a, 1b). The little spider hunter, *Arachnothera longirostra,* and purple-throated sunbird, *Nectarinia sperata* (male), were observed to visit the flowering plants in less frequencies. Both the little spider hunter and pur-

TABLE 3. Flower visitors of three Loranthaceae species. Number of visits per hour, staying time per visit and flowers visited per visit are shown.

Species (observed hours)	Arachnothera robusta			Arachnothera longirostra			Nectarinia sperata		
	No./hour	Time/ visit (min.)	# Flowers/visit	No./hour	Time/ visit (min.)	# Flowers/visit	No./hour	Time/ visit (min.)	# Flowers/visit
Amylotheca duthieana (24 hours)	0.5	1.93	27.2	0.04	0.55	18.0	0.04	0.25	0
Trithecanthera sparsa (26 hours)	1.0	0.88	9.3	0.04	3.53	34.0	0	0	0
Trithecanthera xiphostachys (41 hours)	0.12	2.34	6.8	0	0	0	0	0	0

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PHOTO 1. Flowers of three mistletoes and visitation by *Arachnothera robusta*: (a) flowers of *Amylotheca duthieana* and *A. robusta*; (b) *A. robusta* sucking nectar from a flower of *A. duthieana*; (c) *A. robusta* sucking nectar from a flower of *Trithecanthera sparsa*; (d) *A. robusta* sitting on a twig of *Trithecanthera sparsa*; (e) inflorescence of *Trithecanthra xiphostachys* with a long fertile tip; and (f) two *A. robusta* visiting flowers of *T. xiphostachys.*
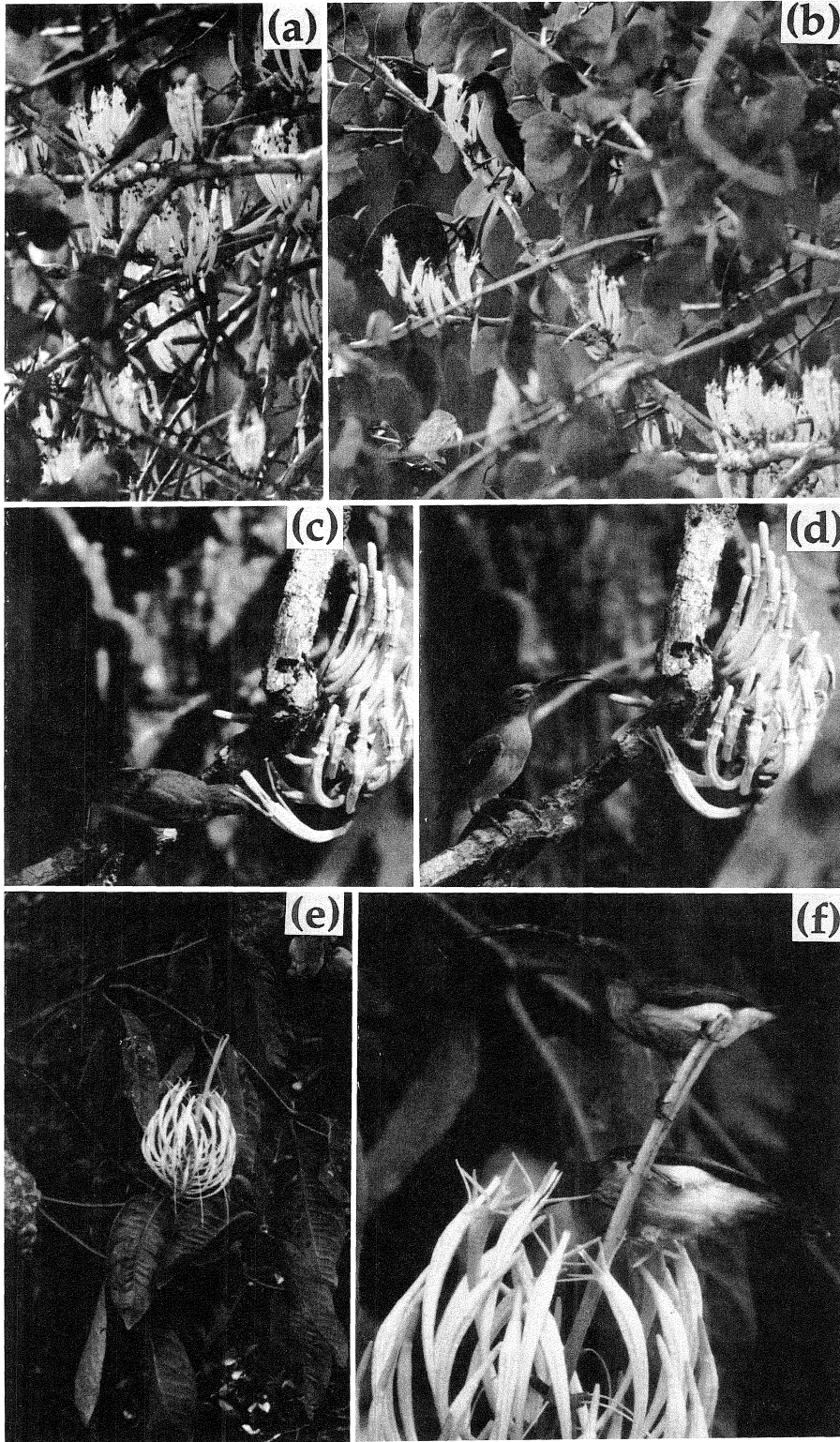
TABLE 4. Bill length, bill width, head width and total length of three bird species measured of the specimens collected in the Sarawak Museum.

Species (sex)	Sample number	Bill length		Bill width		Head width		Total length	
		Mean (mm)	s.d.	Mean (mm)	s.d.	Mean (mm)	s.d.	Mean (mm)	s.d.
Arachnothera robusta (male)	8	56.2	2.09	9.3	0.75	16.8	0.86	18.8	1.53
Arachnothera robusta (female)	17	55.2	2.65	9.1	0.62	16.4	1.06	18.3	0.80
Arachnothera longirostra (male)	15	37.2	1.19	6.8	0.37	13.1	0.95	14.5	0.92
Arachnothera longirostra (female)	11	34.5	1.83	6.5	0.39	13.2	1.02	13.2	1.21
Nectarinia sperata (male)	17	12.3	0.57	4.2	0.36	10.9	0.98	8.9	0.53
Nectarinia sperata (female)	11	11.4	0.63	4.1	0.38	10.8	0.52	8.4	0.35

ple-throated sunbird visited only once for each of the observation periods, and nectar sucking was observed only by a little spider hunter. Long-billed spider hunters stayed on *A. duthieana* for an average 1'56" and visited on 27.2 flowers (n = 12) when the mistletoe had ca. 250 flowers in bloom. Long-billed spider hunters probed the flower tube in a regular jagging motion that lasted 0.5–1 second. A little spider hunter visited 18 flowers of *A. duthieana* and a male of purple-throated sunbird visited no flower. Some flowers of *A. duthieana* had a hole caused by an insertion of the beak of birds visiting flowers. But no bird was observed to suck nectar from the holes.

Flower visitors of *T. sparsa* were also long-billed spider hunter (PHOTO 1c, 1d). They visited 9.3 flowers (n = 26) when 65 flowers were in bloom. On each flower, the regular jagging motion lasted about one second. A little spider hunter was observed to visit flowers once during two days observation of *T. sparsa*. It visited 34 flowers. Both spider hunter species were observed to suck nectar. A visit by long-billed spider hunter made a slit in the corolla of *T. sparsa*.

For *T. xiphostachys*, only long-billed spider hunters were observed to visit the flowers (PHOTO 1f). At every observation, birds visited every open flower in the inflorescence. On each flower, the regular jagging motion lasted about 7–8 seconds. No other birds could be seen even near the plant.

When a long-billed spider hunter visited on the flowers of *A. duthieana* and *T. sparsa*, it perched on the twig near the flowers. But when it visited *T. xiphostachys*, it always perched on a sterile tip of the inflorescence (PHOTO 1e). Spider hunters seldom showed hovering flight around the flowers. Only two cases were observed of long-billed spider hunters hovering to suck nectar of *T. sparsa*'s flower in short duration.

For all of three Loranthaceae species, the pollen was observed to attach to the feathers at the base of bill, and on the forehead and the crown of both long-billed and little spider hunters. Less pollen was attached to the feather of the chin. No nectar sucking nor pollen attachment was observed on the body of the purple-throated sunbird.

Long-billed spider hunters had the longest bills. Based on the specimens in the Sarawak Museum, the mean length was 56.2 mm for males and 55.2 mm for females (TABLE 4). A long-billed spider hunter in our study area was estimated from a photograph to have a 55 mm long bill. Bill length of little spider hunters was apparently shorter than that of long-billed spider hunters (36.0 mm ± 1.9 mm), based on the specimens at the Sarawak Museum. A little spider hunter which was dead in Lambir Hills National Park had a 36.4 mm bill with an elongated tongue 12 mm beyond the tip of bill. The bill of the male purple-throated sunbird averaged 12.3 mm. A male purple-throated sunbird in our study area was estimated from a photograph to have a 12 mm long bill.

As for insects, an unidentified skipper butterfly (Hesperiidae) was observed to visit on the flowers of *A. duthieana* and *T. sparsa*. They tried to suck nectar, but we could not confirm their success. Many stingless bees flew around the flowers of *A. duthieana* and *T. sparsa*, but we never observed them touching the anther or stigma. During a two-day observation of *T. sparsa*, a Rajah Brooke's birdwing butterfly (*Ornithoptera brookeana*) tried to visit the flowers once but failed. No insects were observed to visit the flowers of *T. xiphostachys*.

Daily Visitation Pattern of Long-billed Spider Hunters

Visits of long-billed spider hunter on *A. duthieana* were limited to a short period from 0626 to 0806 hr (FIGURE 2). They visited on *T. sparsa* more constantly, 0726 to 1342 hr. As for *T. xiphostachys*, long-billed spider hunters were ob-
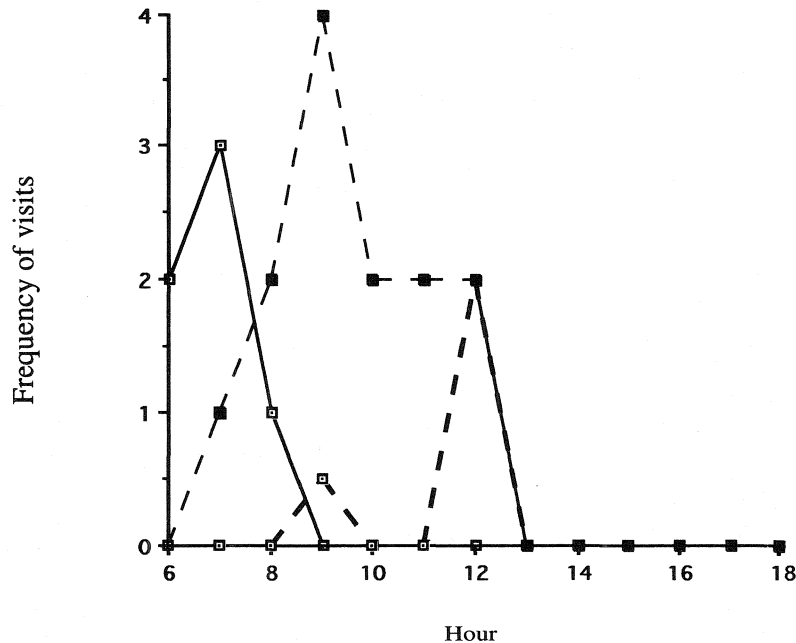
FIGURE 2. Daily visitation pattern of *Arachnothera robusta* to three mistletoes, *Amylotheca duthieana* (solid line), *Trithecanthera sparsa* (dot line) and *T. xiphostachys* (bold dot line). Frequencies of visits in each hour are shown from 0600 to 1800.

served to visit only three times at most a day. Out of four days observation, no bird visitation was observed on the first day. On the second day, a pair of long-billed spider hunters visited at 1206 hr. They stayed for three and a half minutes, and both of them foraged on each of seven flowers in bloom. On the third day, a long-billed spider hunter came to the flowers at 0931 hr, and on the fourth day at 0941 hr and 1311 hr.

Three species of mistletoes received the visitation of long-billed spider hunters at different times in the day. Long-billed spider hunters visited *A. duthieana* flowers only in the early morning, but visited *T. sparsa* flowers rather constantly from the morning to noon. Flowers of *T. xiphostachys* were visited by them at most only two times a day, usually at noon.

DISCUSSION

Bird-pollination in a Bornean Tropical Rainforest

Generally bird-pollination in tropical rainforests is more common than in the temperate regions. Adaptation to flower utilization has been developed independently in hummingbirds (Trochilidae) in the Neotropics, sunbirds (Nectariniidae) in the Paleotropics, honey-creepers (Drepanididae) in Hawaii, and honey-eaters (Meliphagidae) in the Indo-Australian region (Faegri & van der Pijl 1979).

In Central and South American mountains, the number of ornithophilous species in the flora is quite large. The data from a tropical montane forest indicate that 100 out of estimated 600 flowering plant species are pollinated by hummingbirds (Feinsinger 1983). Even in a lowland tropical rain forest of Costa Rica, 39 species out of 220 which flowered in the subcanopy and understory, and two species out of 52 in the canopy had a bird-pollination system (Bawa 1990).

But in our plot of Lambir Hills National Park, only one species (*Ganua* sp., Sapotaceae) out of 228 tree species (Momose & Inoue 1994) and eight species of the Zingiberaceae out of 34 species (S. Sakai, pers. comm.) had the syndromes of bird-pollination. Although bird-pollination among *Rhododendron* species can be observed in high mountains (Argent *et al.* 1988) and some understory plants of the Musaceae in lowland rain forests (Itino *et al.* 1991), ornithophily syndromes are still much less common in Southeast Asia. Flowers of the Loranthaceae, together with the Zingiberaceae, can be said to form the main frame of a special guild of bird-pollinated plants in the Asian lowland tropical rain forests.

Interference Competition in the Guild of Nectarivorous Birds

Nectarivorous birds show strong interference competition as well as exploitation competition among a guild (Wolf 1969, Gill and Wolf 1975a, 1975b, Wolf *et al.* 1975, Feinsinger 1976). Feinsinger (1976) concluded that the behavior of one territorial species modified all other species' foraging patterns within a guild of hummingbirds in a montane forest of Costa Rica. Size plays an important role in interspecific dominance among hummingbirds (Wolf 1970, Stiles & Wolf 1970). In Australia, a large bodied, aggressive honeyeater rigorously excludes smaller species when it visits the flowers of the Loranthaceae (Bernhardt 1982).

In Lambir Hills National Park at least six species of the Nectariniidae were recorded besides the three species mentioned here: plain sunbird (*Anthreptes simplex*), ruby-cheeked sunbird (*A. singalensis*), purple-naped sunbird (*Hypogramma hypogrammicum*), crimson sunbird (*Aethopyga siparaja*), yellow-eared spider hunter (*Arachnothera chrysogenys*) and grey-breasted spider hunter (*A. affinis*) (Bransbury 1993). Long-billed spider hunters are the largest among them. Little spider hunters and purple-throated sunbirds were very watchful when they approached the flowering plants, and they stayed only a short time. Little spider hunters looked around carefully with a warning note "jwe, jwe." A long-billed spider hunter was observed to chase a little spider hunter that was flying near the flowering mistletoes.

Little spider hunters have the long bill and tongue suitable to suck nectar from flowers of *A. duthieana, T. sparsa* and probably *T. xiphostachys,* and to pollinate them. The morphological characteristics of long-billed spider hunters, with the longest and thick curved bill, seem to be best adapted among nectarivorous birds in the study site for long corolla of flowers. But the aggressive behavior of long-billed spider hunters have possibly limited the frequency of visits of other nectarivorous species to these Loranthaceae.

Densities, Fecundities and Energetics of the Loranthaceae

Because Loranthaceae are epiphytes growing more than 35 m from the ground, estimation of their densities was very difficult even in the canopy observation system. When we observed flowers of *A. dulthieana* and *T. sparsa,* there were no flowering mistletoes within at least 1 ha. Within about 3 ha around our canopy observation system, we found four *A. dulthieana,* but only one *T. sparsa.* Approximately 100 m away from the *T. sparsa* observed in this study, another *T. sparsa* bloomed in August, 1993. No *T. xiphostachys* were observed in bloom within 4 ha.

The ratio of fruit set for *A. dulthieana* and *T. sparsa* was unknown because we did not mark individual flowers. From the photographs taken after 3 months of observation, the fruit set ratio of *A. dulthieana* was estimated to be over 50%, and *T. sparsa* over 60%. The inflorescence of *T. xiphostachys* bore 38 fruits out of 46 flowers, so the fruit set ratio was 82.6%.

Flowers of all three species were bisexual and homogamous, but showed apparent herkogamy, so that it is incapable morphologically of mechanical autogamy. Some Australian mistletoes of the genus *Amyema* (Loranthaceae) were self-incompatible (Bernhardt *et al.* 1980) and another case of *Amyema* was vector-mediated self-compatible (Bernhardt and Calder 1981b). We cannot conclude whether the three Loranthaceae species in this study bore fruits with high fecundity by autogamy (or geitonogamy) or xenogamy. Experimental studies are needed.

The energetics of pollination presented by Heinrich and Raven (1972) suggested that the caloric rewards provided by flowers and the energy expended by pollinators should balance if cross-pollination is maximal. The energy cost of foraging is affected by body size, flight distance and temperature. The intake energy during a visit to flowering plants was calculated as: the mean nectar volume per flower × the mean sugar concentration × caloric value per sucrose weight × the number of flowers visited per visit, assuming that birds can suck all amount of nectar of flowers they visited. Results are 22.6 cal (*A. dulthieana* in the morning), 75.7 cal (*T. sparsa* at noon) and 986.3 cal (*T. xiphostachys* at noon).

The three mistletoes in this study received bird visitations at different times in a day, so the effect of temperature was considered first. Gill and Wolf (1975a, 1975b), Wolf (1975) and Wolf *et al.* (1975) studied the energetics of nectarivorous birds when they foraged on flowers. The standard metabolism value for the African golden-winged sunbird (*Nectarinia reichenowi*) was calculated from the equation: ml O_2/g h = 7.93 − 0.17 T (°C), assuming a constant overnight temperature of 15°C. Values were similar to those calculated from the thermal conductance equations using a body temperature of 41°C. This means that sunbirds need more energy for foraging at low temperatures in the morning. The difference in nectar secretion among three mistletoe species cannot be explained by the energy requirements at different temperature.

As shown, the density of *A. dulthieana* was high, and *T. xiphostachys* was the lowest. The energetics of pollination predicts that the rarest mistletoes should have the most plentiful nectar. The energy intake calculated in this study supports this prediction.

Diurnal Partitioning of Pollinators among Mistletoes

Long-billed spider hunters visited the flowers of *A. duthieana* only in the morning, those of *T. sparsa* continuously from morning to noon, and those of *T. xiphostachys* mainly at noon. Diurnal patterns of nectar production and nectar level in the corolla can attempt to explain the visit patterns to these three species. The mean standing nectar volume of *A. duthieana* peaked in the morning and decreased at noon. On the other hand, the mean nectar volume of *T. sparsa* increased from morning to noon. The nectar volume of *T. xiphostachys* was abundant in the morning, but the nectar level in the corolla was still low (⅓ to ⅖). It increased toward noon but with a constant sugar concentration, and the nectar level became high (½ to ⅔) enough for the long-billed spider hunters to suck nectar.

Since the same species of nectarivorous birds visited flowers of the different species at different times of day, the utilization of pollinators by plants may be partitioned diurnally. The pollinators are affected by the nectar secretion pattern and corolla length and subsequently forage on flowers at different times in a day. The longer the corolla, the more the nectar was secreted and the later the birds visited the flowers. This partitioning of pollinators among plants was also similar in relation to flowering phenology. Some authors stressed that plants which flower at different times of the year reduce the competition for pollinators, but there are strong arguments against such a partition of flowering time (see Cole 1981). Actually, the extreme low densities of the three Loranthaceae and their very short flowering periods do not support the long-billed spider hunter's population. So no evidence of reciprocal coevolution between birds and mistletoes is suggested.

It is notable that the three Loranthaceae had flowers of different color and corolla length. Interspecific hybridization of mistletoes were reported in Australia (Bernhardt and Calder 1981a). For all three Loranthaceae species, the pollen was observed to have attached to almost the same part of the bird body. Differences in secretion patterns of floral nectar promotes reproductive isolation, and the difference of morphology in color and corolla length can aid in the recognition of species by birds.

Then how has the extreme long corolla of *T. xiphostachys* evolved? A possible case of reciprocal coevolution was reported between a hummingbird species, *Ensifera ensifera,* which has a very long bill as long as 105 mm, and *Passiflora mixta,* whose corolla is as long as 114 mm (Snow and Snow 1980). *P. mixta* may have evolved its long corolla in an elongation race like the one proposed earlier for long-tongued hawkmoths and their food plants (Feinsinger 1983). But again, low availability in time and space of the flowers of *T. xiphostachys* make such a reciprocal coevolution unlikely.

The energetics of pollination may provide an explanation: the low density of *T. xiphostachys* needs a large amount of floral nectar kept in a long corolla to make pollinators fly long distances between individual plants. The bright color and long corolla of an inflorescence can also attract pollinating birds from a long distance. The ratio of fruit set of *T. xiphostachys* was the highest among three species; nevertheless the flower density was low. The long corolla of *T. xiphostachys* may have selected for the relatively low density of nectar storage but the attractive flag for pollinators.

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