BIRD ACTIVITY AND SEED DISPERSAL IN TWO NEOTROPICAL TREES: *Guarea macrophylla* AND *Trichilia quadrijuga* (MELIACEAE)

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In Manu National Park, Peru, I investigated bird activity on and seed dispersal of two sympatric neotropical rain forest trees: *Guarea macrophylla* and *Trichilia quadrijuga*. Of 24 bird species that consumed *Guarea* fruits, only four (*Catharus ustulatus*, *Myoidynastes luteiventris*, *Pipra coronata*, and *P. fasciicauda*) consistently visited and dispersed its seeds. Of three bird species that consumed *Trichilia* fruits, two (*P. fasciicauda* and *P. chloromeros*) regularly visited and dispersed its seeds. As *Catharus* and *Myiodynastes* are northern migrants, their consumption of *Guarea* fruit might partially account for the distribution of this plant in Amazonian South America.

I also investigated the time of visit for each bird, the length of the visit, whether the bird perched on the fruiting tree, its method of plucking a pulp unit (aril plus seed), number of pulp units ingested per visit, method of ingestion, and whether seeds were dropped under the parent tree or carried away from the canopy after ingestion. I measured and weighed pulp units and seeds of *G. macrophylla* and *T. quadrijuga* and compared these measurements with bill

dimensions of bird species to determine if the size of the pulp unit or seed could be correlated with any aspect of bird feeding behavior or seed dispersal.

Variance in the time spent at fruiting trees across and within bird species was high. Most bird activity occurred between 700 h and 1000 h. With few exceptions, all visiting birds perched in the observed tree and either removed fruit in flight or from a nearby perch. The number of ingested pulp units per visit ranged from 0 to six depending on the bird. Few seeds were dropped under the parent tree. The mean measurements for *Guarea* pulp units were 10.4 mm long, 7.2 mm wide, and 5.6 mm deep; whereas, *Trichilia* pulp units were 12.7 mm long and 5.9 mm in diameter. Pulp units of both tree species had a mean weight of 0.27 g.

The observations of bird activities did not support the idea of tight coevolution between these Meliaceae plants and their seed dispersers since the fruits were small enough to be ingested by many species of birds and because the most reliable dispersers are not uniquely frugivorous.

INTRODUCTION

Tropical rain forests support the richest terrestrial biodiversity on earth. Many complex population interactions exist among the thousands of plants, animals, and fungi that form part of this large biome. Among tropical rain forests, those in the Neotropics boast some of the highest diversity of plants in the world (Gentry 1993). Little is known about growth rates, annual production, phenology, population densities, interspecific interactions, reproduction (agents of pollination and seed dispersal) and evolution of many of these plants. Information about these processes is essential for a better understanding of forest dynamics and community ecology.

The agents of seed dispersal for a vast number of tropical rain forest trees have never been recorded or studied in detail. Yet many frugivorous animals play an essential role in the reproductive biology of the plants whose fruits they consume. This mutualistic relationship has sparked recent interest in the evolutionary consequences of frugivory and seed dispersal for animals and plants (Howe and Smallwood 1982, Herrera 1985, Estrada and Fleming 1986, Fleming and Estrada 1993). McKey (1975) argued that large-seeded plants and their specialized seed dispersers, as well as small-seeded plants and their generalist visitors, are coevolved. Factors such as weak selective pressures on seed dispersers, temporal and spatial unpredictability of suitable germination sites and disperser behavior, extensive plant gene flow resulting from distant dispersal, and slow rates of plant evolution relative to those of dispersers, render close coevolution of plant and disperser species unlikely (Howe 1981, Herrera 1986).

I list the birds that visited each plant species and differentiate seed dispersers from seed predators or cheaters. This information, along with that collected by many others (e.g., Foster 1977, Howe 1977, Foster and McDiarmid 1983, Murray 1988) will aid conservation biologists in the identification of important birds that contributed to the overall health and maintenance of forests. Additionally, these should assist them in making better-informed decisions regarding wildlife conservation and management, habitat protection, and sustainable harvesting of natural resources.

METHODS

The study site. Observations were made in the mature floodplain forest around Cocha Cashu Biological Station in Manu National Park, Peru (11° 54' S, 71° 18' W, elevation approximately 400 m). Located on the fringes of the equatorial zone, the climate at the station has a well-defined wet season from mid October to April, followed by a dry season from May through September. The mean annual temperature is between 23° C and 24° C, and rainfall exceeds 2000 mm (Terborgh et al. 1990). Three major habitat types occur in the vicinity of Cocha Cashu: Riparian succession bordering the Rio Manu; lacustrine succession adjacent to oxbow lakes left by the changing course of the river; and high-ground forest in the more interior sections of the meander belts. Riparian succession can be divided into four stages: 1) even-aged stands of *Tessaria* sp. (Asteraceae); 2) riparian canebreaks of 10 m-tall stands of caña brava (*Gynerium sagittum*, Poaceae) overtopped by a canopy of *Cecropia leucophaia* (Moraceae); 3) successional forest dominated by *Ficus insipida* (Moraceae), *Cedrela odorata* and *Guarea* sp. (Meliaceae), *Erythrina* spp. (Leguminosae), *Casearia* sp. (Flacourtiaceae), and *Sapium* sp. (Euphorbiaceae); and 4) flood-disturbed forest of varied structure and composition. Lacustrine succession can be divided into late successional forest of high species diversity (most of it seasonally flooded), late successional forest dominated by *Cedrela* *odorata*, and fig-swamp forest dominated by *Ficus trigona*. High-ground forest is a mature forest with emergents, such as *Dipterix micrantha* (Leguminosae), *Ceiba pentandra* (Bombacaceae), and *Ficus perforata* (Moraceae), attaining heights of 50 or 60 m. A thorough description of the study site, including climate, vegetation, and fruiting phenology can be found in Terborgh (1983).

Study Species. Observations were made on avian seed dispersal for two Neotropical plant species: *Guarea macrophylla* Vahl ssp. *pachycarpa* (hereafter referred to as *Guarea*) and *Trichilia quadrijuga* Kunth in HBK ssp. *quadrijuga* (hereafter referred to as *Trichilia*), both members of the Family Meliaceae, that reach heights of 25 m and 30 m, respectively (Roosmalen 1985). I collected data at the end of the dry season and beginning of the rains, between 14 October and 16 November, 1998. During this period, both *Guarea* and *Trichilia* came into fruit.

Limited information is available on the natural history of these Meliaceae plants. The genus *Guarea* is represented by 35 Neotropical and five African species (Gentry 1993) that range from understory to canopy trees that are widespread in the lowland Neotropics. *Guarea macrophylla* is divided into five subspecies: *macrophylla*, *tuberculata*, *spicaeflora*, *pachycarpa*, and *pendulispica* (Pennington 1981). The subspecies studied here, *Guarea macrophylla pachycarpa*, is a tree of lowland rain forest and riversides. Up to 25 m tall, it is found in permanently and seasonally-flooded forests. Most collections of this widely distributed subspecies are from the Amazon delta in Para (Brazil) and from Cayenne (Guyane). It is also found in the coastal rain forests of Bahia and Espiritu Santo, Brazil. Its distribution expands from central Amazonia, where its occurrence is spotty, to Amazonian Peru and Bolivia, where it occurs at elevations up to 800 m (Pennington 1981). In Surinam and French Guiana, it is very rare, inhabiting upland rain forest, especially in bauxite hills (Roosmalen 1985). Along the Javari River, which divides Brazil from Peru, *macrophylla* is the common *varzea* species of *Guarea.* Flowering has been recorded in Bahia during two seasons: in April-May and again in November. In other areas, flowering has been recorded most often from July to October (Pennington 1981).

The genus *Trichilia* is represented by 70 Neotropical and 16 Old World species (Gentry 1993). Its members range in size from understory to canopy trees. *Trichilia quadrijuga* is divided into two subspecies: *quadrijuga* and *cinerascens* (Pennington 1981). The subspecies studied (*quadrijuga*) is distributed from Panama across northern South America to Para and Maranhao in northeastern Brazil, extending to the Atlantic coastal forests of Bahia. It is also found throughout central Amazonia as far west as Amazonian Ecuador, Peru, and Bolivia (Pennington 1981) including Manu National Park. *Trichilia quadrijuga quadrijuga* is a tree of lowland forest usually on non-flooded land but often recorded from riverbanks and only rarely from periodically flooded sites. Trees are up to 30 m high, though the highest individuals recorded at Cocha Cashu are 8 m tall. Most records of flowering are from June to November, and fruit ripening occurs from September to April (Pennington 1981).

Study trees. I selected three large fruiting trees of *G. macrophylla* and three individuals of *T. quadrijuga*. Trees of these sympatric species produce dehiscent fruit. The plants were identified by their fruits and leaves (Roosmalen 1985). I also compared them to photocopies of herbarium sheets in the collections of the Field Museum of Natural History, Chicago: Specimen *R. B. Foster 3218* (*Guarea macrophylla pachycarpa*) collected near Rio Alto Madre de Dios, in forest near Chacra of S. Carpio, halfway between Shintuya and Manu; and specimen *R. B. Foster & J. Terborgh 5063* (*Trichilia quadrijuga quadrijuga*) collected in the vicinity of the Cocha Cashu Biological Station. From two additional trees of *T. quadrijuga*, I collected fruit for aril and seed measurements. The number of hours each tree was observed, along with approximate height, forest or habitat type, and approximate number of arillate seeds available (i.e., in dehisced exocarps) per individual per day are listed in Table 1. I positioned myself 10 to 15 m from the trunk of each tree to minimize disturbance to visiting birds, and observed each plant from a minimum of 20 h to as many as 33 h depending on its size and quantity of fruits available. I did not observe trees from which I collected fruit. I covered five terminal racemes on each of two different trees of *G. macrophylla* with a thin, green, cotton netting and counted the number of dehisced fruits in each mesh bag at the beginning of each observation day. To estimate the number of available pulp units each day, the number of open exocarps per raceme was multiplied by six, the average number of units per exocarp (see "*Fruit*" in the "Results" section, below), times a rough count of racemes per branch, times the number of branches per tree (Table 1).

Fruits. I collected, weighed, and measured pulp units and seeds of 100 *G. macrophylla* and 51 *T. quadrijuga* arillate seeds, using an Acculab electronic digital scale (model 221) with graduation of 0.01g, and a SPi caliper (model 30-410) with accuracy of 0.05 mm. For *G. macrophylla*, each pulp unit was plucked from the fruit and weighed whole. Length, width, and thickness were then measured. Next, the thin, oily aril was carefully and completely removed to expose the smooth yellow-white seed, which was weighed and measured. I computed means, standard deviations, maximum and minimum values for all the measurements above. For *T. quadrijuga*, each pulp unit was weighed and then length and diameter measured. After this, the fleshy aril was removed, and the seeds were counted, weighed, and measured. Three measurements were taken for each seed: length, width, and depth. I calculated means, standard deviations, maximum, and minimum values from the above measurements. The total mass per pulp unit carried by birds after ingestion and the actual mass consumed after the seed was expelled were estimated from the above measurements. I performed t-tests for total seed mass among *Trichillia* fruits containing one, two or three seeds.

Table 1. Characteristics of trees studied at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998. Forest types after Terborgh, 1983.

Tree	Species	Hours observed	App. Height (m)	App. No. available pulp units per day	Forest type
1	*G. macrophylla*	30	10	> 500	Mature high-ground
2	*G. macrophylla*	30	7	> 300	Flood-disturbed
3	*G. macrophylla*	33	7	> 300	Mature high-ground
4	*T. quadrijuga*	28	4	20	Late successional
5	*T. quadrijuga*	23	3	15	Flood-disturbed
6	*T. quadrijuga*	20	3	10	Late successional
7	*T. quadrijuga*	0	2.5	3	Flood-disturbed
8	*T. quadrijuga*	0	4	6	Late successional

Birds. Before I recorded my observations, I watched each tree for a whole day in order to assess bird activity and best times of the day for observation. Birds ate all observed ingested fruits, although other animals may also consume them (see below). Bird activity was highest in the morning. Birds were identified with the use of 10 X 42 Bausch & Lomb Elite binoculars and several field guides (Terborgh et al. 1984, Hilty and Brown 1986, Ridgely and Tudor 1994). During observation periods, I identified birds that visited each tree and recorded the length of their stay in seconds with a stopwatch, and recorded time of day. I noted whether the bird perched in the tree, its feeding behavior (in air or sallying, perching and reaching down, perching and reaching up), number of pulp units ingested per visit (if any), method of ingestion (swallow whole, bite or mash), whether seeds were dropped under the tree or carried away, and whether the bird traveled beyond the canopy after ingestion. When more than one bird visited the tree, I kept the stopwatch running and stopped it after the last bird had flown away. During these occasions, I simply recorded the bird species present, any ingested fruits that I determined with certainty, and estimated the length of visit in seconds for each bird as follows: If the first bird to arrive was not the last to leave, I divided the total recorded time for all visitors by the total number of birds in that period. Otherwise, If the first bird to arrive was also the last one to leave, I used the total time recorded as the length of the visit for that bird, and for all others I used an approximate intermediate length of time.

Keeping track of the number of pulp units ingested by each bird was often difficult due to the small size of some birds, fruit height, or obscuring foliage. Ingested fruit was counted only as determined with certainty. This was seldom a problem for *T. quadrijuga*. The observed trees were small, had few open fruits relatively close to the ground, and each fruit included only one pulp unit. In *G. macrophylla* however, it was sometimes difficult to determine whether a bird had plucked and swallowed a pulp unit from the exocarp. For the most part, birds would sally to a fruit, pluck an arillate seed, and then perch on a nearby branch where I could see them ingesting the fruit. On a few occasions, a bird would sally to a fruit and then fly away to a point where I could not see it. In both cases, I counted a pulp unit as ingested. Bill wiping was observed following ingestion of fruits as well as frustrated attempts at plucking a pulp unit, so when I witnessed bill wiping alone, I did not count it as an ingestion. On several occasions, I was unable to identify the bird species with certainty. Usually this was due to the short time of the visit, blocking foliage, or similarity to other species. Female manakins of the genus *Pipra*, for instance, were at times particularly hard to distinguish because of their similarities in size, color, and shape. When unsure, I used the categories 'unidentified manakin' (Pipridae) or 'unidentified species.'

I measured bills for all bird species that actually ate fruit from either of the two trees, using specimens from the Museum of Natural History in Baton Rouge, Louisiana. I measured bill length and bill width for five males and five females of each species. Most of the measured specimens had been collected in southeastern Peru, but when not available, specimens from other geographical locations were used. I determined that bill gape measurements from museum specimens were inconsistent, subjective, and unrepeatable, and therefore ignored that dimension.

RESULTS

Fruit. Table 1 shows the approximate number of available pulp units per day for each species. The means were significantly different ($t = 7.28$, $df = 6$, $P < 0.0005$). Fruits of *G. macrophylla* are borne on racemes on the terminal ends of branches. They have a thick, woody, uneven, dull purple-brown exocarp. When the fruit is ripe, the capsule dehisces longitudinally forming four sections and exposing from 4 to 10 bright red-orange arillate seeds (Table 2). The arillate seeds are plucked and ingested whole by birds, the oily red arils stripped off, and the yellow-white seeds regurgitated intact. Seeds without aril weighed an average of 0.24 g, which means that the mean maximum mass of food intake per arillate seed was 0.034 g (SD= 0.01, n = 100) or about 13% of total pulp-unit mass.

Table 2. Mean pulp unit dimensions and weights for *Guarea* fruits collected at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998.
Number of pulp units n= 100.

	Length (mm)	Width (mm)	Depth (mm)	Seed + Aril mass (g)	Seed mass (g)	Aril mass (g)
Mean	10.4	7.26	5.64	0.27	0.23	0.034
S.D.	0.87	0.49	0.35	0.047	0.043	0.012
Max.	13.05	8.45	7.2	0.38	0.34	0.07
Min.	8	6.2	5	0.18	0.15	0.01

The exocarp of a *T. quadrijuga* fruit is relatively thin, soft, smooth, bright orange in color and is borne singly at the tips of panicled branches. When ripe, the three-part capsule dehisces to expose a single juicy, bright red pulp unit (Table 3). As in *Guarea*, these are plucked and ingested by birds, and the juicy red flesh is stripped from the olive-green seeds which are regurgitated or excreted. Fruits have from zero to three seeds (e.g., 8% no seed, 41% one, 41% two, and 10% three, n = 51). Fruits with more than three seeds have also been observed (M. S. Foster, *pers. communication*). The mean aril mass is 54% of total pulp unit mass. Seed numbers per fruit, dimensions, and weight are given in Table 4. Seed sizes and weights changed with number of seeds per fruit (Table 5). Individual seed mean masses between fruits containing one or two seeds were not significantly different ($t = 1.11$, $df = 61$, $P > 0.1$). However, the means for individual seed masses between fruits containing one or three seeds ($t = 3.11$, $df = 34$, $P < 0.001$) or between fruits containing two or three seeds ($t = 3.74$, $df = 55$, $P < 0.0005$) were significantly different. Similarly, means for total seed mass between fruits containing one or two seeds ($t = 4.63$, $df = 40$, $P < 0.0005$) or between fruits with one or three seeds ($t = 3.59$, $df = 24$, $P < 0.001$) were significantly different. Means for total seed mass for fruits containing two or three seeds were not significantly different ($t = 1.70$, $df = 24$, $P < 0.1$). Thus, seed mass in single-seeded fruits was larger on average than individual seed masses in double- or triple-seeded fruits. On the other hand, total average seed mass in fruits with two or three seeds is almost twice as large as the total seed mass of single-seeded fruits.

Table 3. Mean pulp unit dimensions and weights for *Trichilia* fruits collected at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998.
Number of pulp units n= 51.

	Length (mm)	Diameter (mm)	Seed + aril mass (g)	Total seed(s) mass (g)	Aril mass (g)
Mean	12.68	5.87	0.27	0.14	0.14
S. D.	2.5	1.3	0.13	0.07	0.08
Max.	20.8	9.05	0.69	0.29	0.4
Min	8.5	3.1	0.07	0.03	0.05

Table 4. Mean number of seeds per pulp unit, and mean seed dimensions and mass for all *T. quadrijuga* seeds collected at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998. Number of pulp units n= 51.

	No. of Seeds per fruit	Seed length (mm)	Seed width (mm)	Seed depth (mm)	Seed mass (g)
Mean	1.53	9.80	4.25	2.86	0.085
S. D	0.78	1.81	0.57	0.61	0.035
Max.	3	16.1	5.5	4.35	0.17
Min.	0	7.0	2.95	2.0	0.02

Table 5. Mean seed dimensions and mass for *T. quadrijuga* fruits according to the number of seeds per fruit. Fruits were collected at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998. Number of pulp units n= 51.

Number of fruits (n)	Number of seeds per fruit	Seed length in mm (SD)	Seed width in mm (SD)	Seed depth in mm (SD)	Individual Seed mass in g (SD)	Total seed mass in fruit in g (SD)
4	0	0	0	0	0	0
21	1	9.7 (1.5)	4.2 (0.58)	3.6 (0.47)	0.097 (0.04)	0.097 (0.04)
21	2	10.1 (2.1)	4.4 (0.59)	2.6 (0.37)	0.087 (0.03)	0.17 (0.06)
5	3	9.0 (0.61)	4.0 (0.40)	2.4 (0.35)	0.062 (0.02)	0.18 (0.07)

Bird Activity. Number of birds per visit to trees ranged from 1 to 8 (Table 6). Eighty-two and sixty percent of observations for *Guarea* and *Trichilia*, respectively, were of visits by a single bird. The number of birds visiting either species was not significantly different ($t = 1.04$, $df = 14$, $P > 0.1$) in spite of smaller *Trichilia* individuals with fewer available fruits for birds.

Table 6. Frequency of visits by one or several birds at *Guarea* or *Trichilia* trees at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998.

Number of birds	*Guarea*	*Trichilia*	Total instances
1	329	39	368
2	41	20	61
3	14	6	20
4	11	0	11
5	4	0	4
6	2	0	2
7	0	0	0
8	1	0	1
Total	402	65	467

In order to assess bird activity, I recorded the time of visit for each bird. Because observations were not made equally across all hours of the day, due to rain or lack of available fruit, I divided the total number of recorded visits during each hour by the number of hours for which observations were made during that hour (Fig. 1). Clearly, bird activity at *G. macrophylla* was greater than that at *T. quadrijuga*. The highest bird activity at *Guarea* trees occurred between 800 h and 1000 h, with a maximum between 800 h and 900 h. A lower peak activity period occurred in mid afternoon. In *Trichilia*, bird activity was highest in the early part of the morning between 700 h and 800 h and early afternoon between 1400 h and 1500 h.

Visiting birds. A total of 18 bird species of six families fed on fruits of *G. macrophylla* trees while only three bird species of one family ate fruits of *T. quadrijuga* plants. Some important bill and size characteristics of these birds are listed in Table 7. An additional five species (*Momotus momota*, Momotidae; *Paroaria gularis*, Emberizinae; *Ramphocelus carbo* and *Tangara schrankii*, Thraupinae; and *Hylophilus ochraceiceps*, Vireonidae) visited *Guarea* but ate no fruits, and one species (*Momotus momota*, Momotidae) visited *Trichilia* but did not eat fruits. The three species of the *Pipra* genus that frequently visited *Trichilia* trees were also regular visitors of *Guarea.* The shortest and narrowest bills were found in males of the Blue-crowned Manakin, *Pipra coronata*. Male Sulphur-bellied flycatchers, *Myiodynastes luteiventris,* had the longest and widest bills.

Seed dispersal and predation. Table 8 shows the total number of bird visits and ingested fruits per bird species, the total number of seeds dropped under the crown, and the average time per visit in seconds for *Guare*a plants. The most frequent visitors were Swainson's Thrush (*Catharus ustulatus*) 21% of visits, Blue-crowned Manakin (*Pipra coronata*), 16% of visits, Band-tailed Manakin (*P. fasciicauda*), 13% of visits, and Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*), 11% of visits. These bird species also ingested the largest number of pulp units, 27%, 13%, 14% and 13%, respectively. None of these species is uniquely frugivorous. While a large percentage of the diets of manakins is made up of fruit complemented with insects (Snow 1971), *Catharus* eats a variety of animal matter and is very frugivorous during migration, and *Myiodynastes* specializes in large insects but is often highly fruigivorous (Hilty and Brown, 1986).

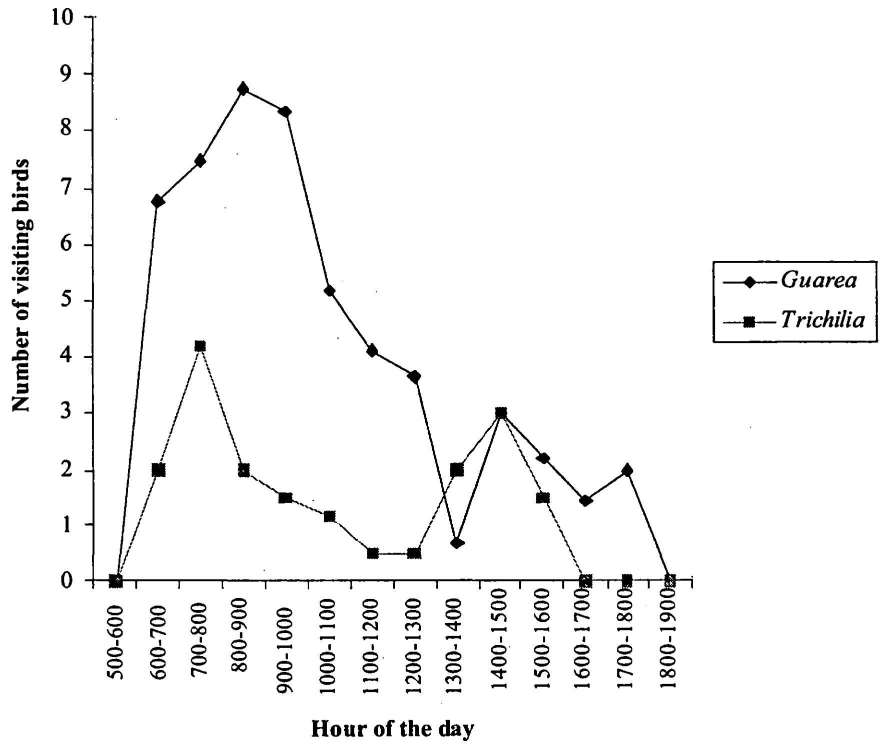

Figure 1. Average number of bird visitors to *Guarea* and *Trichilia* trees per hour at different times of day, observed at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998.

Species of visitors varied noticeably among *Guarea* trees. For instance, the most frequent visitors to tree #1, located in mature high-ground forest, were *Pipra fasciicauda*, Round-tailed Manakin (*P. chloromeros*), *C. ustulatus*, and *P. coronata*, accounting for 34%, 14%, 10%, and 7.5% of all visits, respectively. In contrast, the most frequent visitors to tree # 2, located in flood-disturbed forest along the Rio Manu, were *C. ustulatus* and *M. luteiventris* with 36% and 25% of all visits, respectively. Most other visitors were tyrannid flycatchers. Other visitors were Black-spotted Barbet (*Capito niger*), Pale-vented Thrush (*Turdus hauxwelli*), Collared Trogon (*Trogon collaris*), and Blue-gray Tanager (*Thraupis episcopus*), which are often seen in more open areas. No manakins visited tree # 2. Finally, tree #3, located in high-ground mature forest next to a small creek was visited by *P. coronata*, *P. fasciicauda*, *C. ustulatus*, White-necked Thrush (*Turdus albicollis*), and *T.*

hauxwelli, with 53%, 11%, 8%, 7%, and 7% of all visits, respectively. Only two bird species (*C. ustulatus* and *T. hauxwelli*) visited all three plants.

Table 7. Mean body weights and mean bill dimensions of birds that visited *Guarea macrophylla* and *Trichilia quadrijuga* trees at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998. For bill measurements, five males and five females were used. All bird specimens were collected in Peru, except as noted below. All weights from Terborgh et al. (1990), unless otherwise noted.

Taxon	Body Weight (g)	Male Bill Length mm (SD)	Male Bill Width mm (SD)	Female Bill Length mm (SD)	Female Bill Width mm (SD)
TROGONIDAE					
Trogon collaris	59	10.7 (0.5)	9.3 (0.6)	10.2 (0.6)	9.0 (0.6)
CAPITONIDAE					
Capito niger	64	16.4 (0.7)	8.5 (0.4)	16.0 (0.8)	8.6 (0.6)
TYRANNIDAE					
Myiodynastes luteiventris *		16.4 (0.3)	10.0 (0.4)	16.2 (0.5)	9.9 (0.7)
Ochthornis littoralis (1)		8.4 (0.2)	5.2 (0.5)	7.8 (0.7)	4.8 (0.6)
Tyrannus melancholicus	40 **	16.2 (0.3)	9.5 (0.4)	16.8 (0.7)	9.7 (0.5)
Myiozetetes similis (2)		9.3 (0.9)	5.9 (0.4)	9.3 (0.4)	6.1 (0.3)
Myiozetetes luteiventris (3)		8.2 (0.6)	5.7 (0.5)	7.6 (0.6)	5.4 (0.4)
Myiarchus tuberculifer	20	12.8 (0.8)	7.2 (0.1)	11.9 (0.6)	7.1 (0.3)
Sirystes sibilator (4)	38	13.4 (0.4)	8.7 (0.3)	13.6 (0.5)	8.9 (0.3)
Attila bolivianus	45	16.3 (0.6)	8.4 (0.6)	15.9 (0.8)	7.6 (0.5)
PIPRIDAE					
Pipra fasciicauda (5)	17	6.7 (0.4)	4.2 (0.3)	7.2 (0.3)	4.7 (0.2)
P. coronata	9	5.9 (0.4)	3.7 (0.3)	6.3 (0.2)	4.4 (0.3)
P. chloromeros	17	6.6 (0.3)	4.2 (0.4)	6.8 (0.3)	4.6 (0.4)
Tyranneutes stolzmanni (6)	9	6.3 (0.4)	4.0 (0.3)	6.6 (0.3)	4.3 (0.7)
TURDINAE					
Catharus ustulatus	27	8.7 (0.4)	4.6 (0.2)	8.3 (0.5)	4.9 (0.2)
Turdus albicollis	52	10.7 (0.7)	4.9 (0.2)	10.3 (0.8)	5.1 (0.3)
T. hauxwelli	72	12.8 (0.6)	5.7 (0.3)	12.7 (0.7)	5.8 (0.6)
THRAUPINAE					
Thraupis episcopus	32 **	8.9 (0.5)	6.3 (0.4)	9.0 (0.6)	6.4 (0.3)

* Specimens from Costa Rica, Guatemala, Ecuador and Bolivia.

** Weights from Moermond and Denslow (1985).

(1) One female from Bolivia, all others from Peru.

(2) Specimens from Venezuela, Colombia, Ecuador, Peru and Brazil.

(3) Four males and one female from Bolivia. All others from Peru.

(4) One male and one female from Brazil. All others from Argentina.

(5) All specimens from Bolivia.

(6) One female from Ecuador, all other specimens from Peru.

The average length of visits to *Guarea* varied considerably both among and within bird species. Among species, the average time spent in a tree per visit ranged from as little as 44 s for *Ochthornis littoralis* to as long as 175 s for *Trogon collaris*. Single visits ranged from as little as 1 s when a *Tyrannus melancholicus* sallied to a fruit, plucked a pulp unit and flew away, to as long as 1004 s (about 17 minutes) when an individual *C. ustulatus* fed and rested in tree # 1. This same bird regurgitated seven seeds under the canopy, thus decreasing the probability of their survival and germination (Janzen, 1970). Two *Capito niger* individuals visited tree #2 on a single occasion, swallowing a total of 12 units and regurgitating six of them under the canopy.

In all but five cases, fruits were swallowed immediately after plucking. If a fruit was plucked by a bird in flight, the bird usually landed in the same tree, positioned the seed within its bill, and swallowed it whole. Birds that plucked fruits while perched always swallowed them at the same spot. On four occasions, an individual Dwarf Tyrant-Manakin (*Tyranneutes stolzmanni*) sally-plucked a pulp unit, landed on a nearby branch, and then appeared to bite the pulp unit very hard. In all cases, the arillate seed fell to the ground under the canopy. It was difficult to determine if the bird actually ingested any aril. In these instances the pulp unit appeared too large for the bird to manipulate it. On another occasion, another *Tyranneutes* plucked an arillate seed and carried it away beyond the canopy, effectively dispersing it.

Moermond and Denslow (1985) found most bird species use one capturing technique over another, even though most birds occasionally used the other technique as well. In general, smaller birds gathered most fruit in flight while larger birds gathered fruit in flight or from a perch. Manakin species removed between 70 and 100% of ingested fruit in flight. Larger birds such as *C. ustulatus*, *Turdus albicollis*, *T. hauxwelli*, *Myiodynastes luteiventris*, and *Myiarchus tuberculifer* (Dusky-capped Flycatcher) commonly used both techniques (Table 9).

The most notable exception was *Trogon collaris*, which at 59 g is considerably heavier than most Piprids, yet it exclusively removed *Guarea* fruit in flight. Sample sizes for the other species were too small to provide significant percentages.

Table 10 shows the total number of bird visits and total number of ingested fruits per bird species, total number of seeds dropped under the crown and average time per visit in seconds for *Trichilia* trees. The two most frequent visitors were *Pipra fasciicauda* and *P. chloromeros* which made 82% and 13% of the visits, respectively. *Pipra fasciicauda* accounted for 89% of the observed fruit removed. I did not observe any of these birds regurgitate seeds under the canopy. The number of pulp units ingested per visit was quite low for all birds, reflecting the fact that birds did not always feed when they visited the tree (Table 10). A group of three *P. fasciicauda* males visited tree # 4 often and displayed dominance behavior interactions (Robbins 1983, 1985) while two *P. chloromeros* males used tree # 6 for similar purposes. The average time per visit among birds that actually fed on fruit was lowest for *P. coronata* (45 s), and highest for *P. chloromeros* (144 s). With three exceptions, birds gathered fruits in flight and landed on a nearby branch of the same tree to swallow it. The exceptions were two *P. fasciicauda* individuals that plucked one and two fruits, respectively, by perching and reaching down, and a *P. chloromeros* individual that plucked two fruits in the same manner.

Table 8. Mean number of bird visits, total and mean number of ingested and regurgitated pulp units, and average time per visit observed in *Guarea macrophylla* trees at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998.

Taxon	Total number of visits (n)	Pulp units removed	Pulp units removed per visit	Seeds dropped under tree	Seeds dropped per visit	Average time per visit s (SD)	Range (s)
TROGONIDAE							
Trogon collaris	6	17	2.8	0	0	175 (112)	66 - 327
CAPITONIDAE							
Capito niger	2	12	6	5	2.5	142	142
TYRANNIDAE							
Myiodynastes luteiventris	60	95	1.6	0	0	106 (85)	2 - 414
Ochthornis littoralis	31	29	0.9	0	0	44 (32)	3 - 125
Tyrannus melancholicus	17	19	1.1	0	0	59 (50)	1 - 127
Myiozetetes similis	15	16	1.1	0	0	109 (117)	15 - 448
Myiozetetes luteiventris	7	12	1.7	0	0	69 (66)	5 - 199
Myiarchus tuberculifer	4	5	1.2	0	0	70 (31)	45 - 105
Sirystes sibilator	4	7	1.7	0	0	94 (74)	45 - 204
Attila bolivianus	1	2	2	0	0	103 (101)	32 - 175
PIPRIDAE							
Pipra fasciicauda	70	100	1.4	1	0.01	97 (65)	25 - 319
P. coronata	87	93	1.1	3	0.03	95 (103)	15 - 840
P. chloromeros	22	33	1.5	0	0	102 (60)	26 - 219
Tyranneutes stolzmanni	7	14	2	4	0.6	96 (57)	30 - 186
unidentified Manakin	25	11	0.4	0	0	75 (35)	15 - 139
TURDINAE							
Catharus ustulatus	114	198	1.7	11	0.1	105 (143)	2 - 1004
Turdus albicollis	19	33	1.7	1	0.05	190 (257)	33 - 900
T. hauxwelli	15	25	1.7	0	0	83 (47)	29 - 210
THRAUPINAE							
Thraupis episcopus	1	2	2	2	2	226	
unidentified species	16	14	0.8	0	0	108 (136)	15 - 480
Totals	537	737	1.4	27	0.05		

Table 9. Feeding behavior of the most common visitors to *Guarea macrophylla* at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998.

Taxon	Body Weight (g)	Total Number of ingested fruits (n)	% ingested from perch	% ingested in flight
TROGONIDAE				
Trogon collaris	59	17	0	100
CAPITONIDAE				
Capito niger	64	12	100	0
TYRANNIDAE				
Myiodynastes luteiventris		95	39	61
Ochthornis littoralis		29	10	90
Tyrannus melancholicus	40	19	0	100
Myiozetetes similis		16	25	75
Myiozetetes luteiventris		12	8	92
Myiarchus tuberculifer	20	5	40	60
Sirystes sibilator	38	7	0	100
Attila bolivianus	45	2	100	0
PIPRIDAE				
Pipra fasciicauda	17	100	24	76
P. coronata	9	93	17	83
P. chloromeros	17	33	30	70
Tyranneutes stolzmanni	9	14	0	100
unidentified Manakin		11	9	91
TURDINAE				
Catharus ustulatus	27	198	42	58
Turdus albicollis	52	33	67	33
T. hauxwelli	72	25	64	36
THRAUPINAE				
Thraupis episcopus	32	2	100	0
unidentified species		14	0	100

Table 10. Mean number of visits, total and mean number of ingested and regurgitated pulp units, and average time per visit observed in *Trichilia quadrijuga* plants at Cocha Cashu Biological Station in Manu National Park, Peru, between 14 October and 16 November, 1998.

Taxon	Total number of visits (n)	Pulp units removed	Pulp units removed per visit	Seeds dropped under tree	Seeds dropped per visit	Average time per visit s (SD)	Range (s)
PIPRIDAE							
Pipra fasciicauda	80	42	0.5	0	0	68 (67)	2 - 405
P. coronata	1	1	1	0	0	45	
P. chloromeros	12	4	0.3	0	0	144 (74)	59 - 281
Totals	93	47	0.5	0	0		

DISCUSSION

McKey (1975) argued for the existence of two general patterns of coevolution between fruits and dispersal agents: Evolution of fruits whose seeds can be dispersed by many species of animals, most of which are generalists and perform low-quality seed dispersal, and the evolution of fruits adapted to a few specialized frugivores that perform high-quality seed dispersal. His arguments are briefly summarized as follows: Plants that produce a few large and costly fruits consisting of large seeds with soft seed coats and pulp with high protein and lipid content, prevent generalist birds from feeding on them since they are physically unable to eat these large fruits. Instead, these plants attract fruit specialists capable of ingesting large fruits and of providing high-quality seed dispersal. High-quality seed dispersers faithfully visit fruit crops, ingest many seeds of the same tree species, carry them beyond the canopy, and regurgitate them unharmed in suitable sites ready for germination. On the other hand, plants that produce many small and inexpensive fruits including seeds with relatively hard seed coats, and pulp low in protein and lipids but high in carbohydrates attract generalist and opportunist feeders that provide low-quality seed dispersal. Low-quality seed dispersers are unreliable visitors to fruit crops, often damage seeds as they travel through the gut, and drop seeds in unfavorable sites, sometimes very near the parent tree. McKey argued that large-seeded plants and their specialized seed dispersers, as well as small-seeded plants and their generalist visitors are coevolved. Although these interactions seem intuitive, two major assumptions must be met for such coevolution to occur: 1) That interactions between a particular plant and its seed disperser occur in a world where they are the only inhabitants, and 2) that plant characteristics relevant to dispersal undergo measurable evolutionary change in a reasonable time frame in response to ecological conditions. Neither of these assumption is supported (Herrera 1986). Factors such as weak selective pressures on seed dispersers, temporal and spatial unpredictability of suitable germination sites and disperser behavior, extensive plant gene flow resulting from distant dispersal, and slow rates of plant evolution relative to those of dispersers, render close coevolution of plant and disperser species unlikely (Howe 1981, Herrera 1986). Indeed, Herrera (1995) argued that extremely efficient plant-disperser mutualisms do not require coevolution between the participants. Both *Guarea* and *Trichilia* have relatively small pulp units and would be expected to attract opportunistic feeders. However, because *Guarea* aril appears to be richer than *Trichilia* in lipid (and perhaps in protein) content, its larger seeds should be expected to be dispersed by specialist feeders. Based on my observations, generalist and opportunist birds feed on fruits of both tree species. Little evidence supports coevolution between these trees and their bird agents of dispersal.

Many times, I was able to identify a bird but was not able to ascertain that it had eaten seeds (especially when several birds were visiting the same tree simultaneously). As a result, the average number of seeds swallowed by each bird species per visit might be underestimated. There was not a single instance of more than three birds visiting the same *Trichilia* plant (Table 3), perhaps a result of the smaller size of the observed trees. Size and available fruit discrepancies between observed *Guarea* and *Trichilia* trees may also explain the higher bird activity in the former species.

The most reliable seed dispersers of *G. macrophylla* are *Catharus ustulatus*, *Pipra coronata*, *P. fasciicauda* and *Myiodynastes luteiventris*. Not only were they the most common and consistent visitors, they also ingested the largest number of pulp units and, with a few exceptions, carried seeds beyond the canopy of the parent tree. Piprids are primarily frugivorous birds that complement their diets with some insects (Snow 1971). *Guarea* may provide some essential protein and lipids to these birds. While *C. ustulatus* is a ground feeder and specializes in arthropods and *M. luteiventris* specializes in aerial insects, both species are facultative frugivores, complementing their diets with some fruit (Hilty and Brown 1986), such as *Guarea* aril. On the other hand, the most common dispersers of *Trichilia* seeds are *P. fasciicauda* and *P. chloromeros*. As in the case of *Guarea*, these birds were the most consistent visitors throughout the observation period, ate the largest numbers of fruits, and always carried seeds away from the canopy of the parent tree. Further studies on how seeds are treated in the bird's gut, and how viable they are once regurgitated or defecated will further elucidate the quality of dispersal that these birds provide for *Guarea* and *Trichilia* seeds.

I observed *Ochthornis littoralis* feed on fruits of *Guarea* (Table 8). These birds inhabit steep banks of rivers and are considered totally insectivorous. Tree # 2 was located next to a steep bank of the Rio Manu and a total of 29 of its pulp units were removed by these birds. This is the first record of *Ochthornis littorali* feeding on fruit.

Regarding plant distributions, it is noteworthy that *Catharus ustulatus* and *Myiodynastes luteiventris* are known northern migrants while *Pipra coronata*, *P. fasciicauda*, and *P. chloromeros* are resident species. Whereas, *Myiodynastes* breeds from Arizona to southern Costa Rica and winters in eastern Peru and Bolivia, *Catharus* breeds in North America and winters in South America south to northern Argentina and western Brazil (Hilty and Brown 1986). Such large distributions combined with consistent and reliable removal of *Guarea* seeds might ensure long distance dispersal and a large geographical range for this plant, provided that the trees are fruiting during the same period that the birds are migrating. If the birds only encounter trees in fruit once they have reached their wintering grounds and stay at one site all winter, they can only account for short distance dispersal. Alternately, if *C. ustulatus* and *M. luteiventris* wander around the Amazon basin all winter, they may partially account for the distribution of this *Guarea* ssp which has been found only in Amazonian South America. These birds feed on insects and other fruits to sustain them during their long migrations, and might drop all ingested *Guarea* seeds in marginal habitat sites beyond the present range of this subspecies. Similar reasoning would predict that since in my observations *Trichilia quadrijuga* fruit was eaten and dispersed by resident species, its range might coincide with that of *P. fasciicauda* and *P. chloromeros*. Plants of *T. quadrijuga* have been found in Panama and in parts of South America where neither bird species is encountered. Given the small size of *Trichilia* trees found at Cocha Cashu, and the few bird species observed removing its fruit, there must be other bird species that regularly feed on its arillate seeds. These birds might have larger distributions than the piprids mentioned above. Alternately, the large distribution of *Trichilia* can be explained by many visiting bird species with small ranges that overlap, at least partially, and with each successive species being distributed further north or south. Larger trees with more fruits need to be observed for longer periods in order to determine more accurately seed dispersal agents for *Trichilia.*

Average bill lengths for the major seed dispersers of *Guarea* ranged from 5.9 mm in *P. coronata* males to 16.4 mm in *M. luteiventris* males; whereas, the average pulp unit length was 10.4 mm. Similarly, mean bill widths ranged from 3.7 mm in *P. coronata* males to 10.0 mm in *M. luteiventris* males, while the average pulp unit width was 7.3 mm. Birds often ingested *Trichilia* fruits with several seeds which probably disassociated in the gut and were regurgitated or excreted singly. As a result, the most interesting dimensions and masses are those of the largest seeds, which ultimately determine the minimum digestive tract diameter for the seed to pass through safely. When all seeds collected, whether singles, doubles, or triples were combined to calculate means, standard deviations were rather large (Table 4). When separated into categories according to the number of seeds per fruit, standard deviations were smaller. Average bill lengths for the major seed dispersers of *Trichilia* ranged from 6.6 mm in *P. chloromeros* males to 7.2 mm in *P. fasciicauda* females, while average pulp unit length was 12.7 mm. Similarly, mean bill widths ranged from 4.2 mm in both piprid males to 4.7 mm in *P. fasciicauda* females, while average pulp unit diameter was 5.9 mm. Lack of correlation between fruit lengths, widths and diameters with bird bill measurements is an indication that these birds may be gape-limited foragers (Wheelwright 1985). If average gape widths are larger than fruit widths, these birds may not be limited at all with regard to *Guarea* or *Trichilia* fruits. Unfortunately, gape measurements are not available. It is not surprising, however, that feeding behaviors observed at both species of Meliaceae were quite similar. This is perhaps the result of similarities in fruit size and weight, in fruit display, and in common bird visitors to both plant species.

Nutritional analyses of *Guarea* and *Trichilia* aril are needed to determine the costs to the plants in terms of lipid, protein, and carbohydrate content and the benefits obtained by seed dispersers. Given an average aril mass of 0.034 g for *Guarea*, a sizeable number of these arillate seeds may be needed in order to obtain sufficient dry weight material for laboratory analysis. This may also be a problem with *Trichilia*. In spite of its larger average pulp mass per fruit (0.14 g), its aril appears very high in liquid content

Catharus and *Myiodynastes* breed in temperate North America and do not depend on *Guarea* or *Trichilia* during their reproductive cycles. A *P. fasciicauda* female was seen incubating at Cocha Cashu in late September, at the end of the dry season and before this study was initiated (M. S. Foster, *pers. communication*). There is little evidence that *P. coronata*, *P. fasciicauda* or *P. chloromeros* depend heavily on either Meliaceae fruit during their reproductive cycles.

Guarea and *Trichilia* aril is also consumed by other animals. Dusky titi monkeys (*Callicebus moloch*) eat both fruits occasionally (F. Bossuyt, *pers. communication*), but there is not enough information to determine if they are seed predators or seed dispersers. A troop of brown capuchin monkeys (*Cebus apella*) visited *Guarea* tree #2, but none of the troop members was observed feeding on the pulp units. Rodents ate some fruit samples of both species left in the laboratory after measurement. They consumed the arils and partially destroyed the seeds, acting in essence as seed predators. *Trichilia* fruits also appear to be animal-distributed by howler monkeys (*Alouatta* spp), spider monkeys (*Ateles* spp), and cotingas (*Cotinga* spp), and their seeds are often predated by saki monkeys (*Pithecia* spp and *Chiropotes* spp) and macaws (*Ara* spp) (Roosemalen 1985). Given that neither *Guarea* nor *Trichilia* possesses fruit fragrance or color that would typically attract bats, it is unlikely that bats eat fruits or disperse seeds of either tree species.

Future research on the effectiveness of avian dispersal of *Guarea* and *Trichilia* seeds should concentrate on seed germination experiments, on better ways to determine how far seeds are carried away from parent trees, on relative percentages of seeds regurgitated or defecated, and on time of seed passage through the gut of each bird species. Additional information can be also be gained by performing observations at more trees of each species, at larger *Trichilia* trees for longer periods of time, and by setting seed traps in the forest.

LITERATURE CITED

Estrada, A. and T. H. Fleming, editors. 1986. Frugivores and seed dispersal. W. Junk, Dordrecht, The Netherlands.

Fleming, T. H. and A. Estrada, editors. 1993. Frugivory and seed dispersal: Ecological and evolutionary aspects. W. Junk, Dordrecht, The Netherlands.

Foster, M. S. 1977. *Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source.* Ecology **58**, 73-85.

Foster, M. S. and R. W. McDiarmid. 1983. *Nutritional value of the aril of Trichilia cuneata, a bird-dispersed fruit.* Biotropica **15**, 26-31.

Gentry, A. H. 1993. A field guide to the families and genera of woody plants of Northwest South America (Colombia, Ecuador, Peru) with supplementary notes on herbaceous taxa. Conservation International, Washington, DC, USA.

Herrera, C. M. 1985. *Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates.* Oikos **44**, 132-41.

Herrera, C. M. 1986. *Vertebrate-dispersed plants: Why they don't behave the way they should.* In A. Estrada and T. H. Fleming, editors. Frugivores and seed dispersal. W. Junk, Dordrecht, The Netherlands.

Herrera, C. M. 1995. *Plant-vertebrate seed dispersal systems in the Mediterranean: Ecological, Evolutionary, and Historical Requirements.* Annual Review of Ecology and Systematics. **26**, 705-727.

Hilty, S. L. and W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, USA.

Howe, H. F. 1977. *Bird activity and seed dispersal of a tropical wet forest tree.* Ecology **58,** 539-550.

Howe, H. F. 1981. *Dispersal of a Neotropical nutmeg (Virola sebifera) by birds.* Auk **98,** 88-98.

Howe, H. F. and J. Smallwood. 1982. *Ecology of seed dispersal.* Annual Review of Ecology and Systematics. **13**, 201-228.

Janzen, D. H. 1970. *Herbivores and the number of tree species in tropical forests.* Am. Nat. **104**, 501-528.

McKey, D. 1975. *The ecology of coevolved seed dispersal systems.* pp. 159-191 in L. E. Gilbert and P. H. Raven, editors. Coevolution of animals and plants. University of Texas Press, Austin, Texas, USA.

Moermond, T. C. and J. S. Denslow. 1985. *Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection.* Ornithological Monographs. **36**, 865-897.

Murray, K. G. 1988. *Avian seed dispersal of three neotropical gap-dependent plants.* Ecological Monographs. **58**, 271-298.

Pennington, T. D. 1981. *Meliaceae.* Flora Neotropica. Monograph No. **28**. The New York Botanical Garden, Bronx, New York, USA.

Ridgely, R. S. and G. Tudor, 1994. The birds of South America. Vols. **1**, **2**. University of Texas Press, Austin, Texas, USA.

Robbins, M. B. 1983. *The display repertoire of the Band-tailed Manakin (Pipra fasciicauda).* Wilson Bulletin. **95**, 321-342.

Robbins, M. B. 1985. *Social Organization of the Band-tailed Manakin (Pipra fasciicauda).* Condor. **87**, 449-456.

Roosmalen, M. G. M. van. 1985. Fruits of the Guianan flora. Drukkerij Veenman B. V., Waginingen, The Netherlands.

Snow, D. W. 1971. *Evolutionary aspects of fruit-eating by birds.* Ibis. **113**, 194-202.

Terborgh, J. 1983. Five New World primates: a study in comparative ecology. Princeton University Press, Princeton, New Jersey, USA.

Terborgh, J., J. W. Fitzpatrick, and L. Emmons. 1984. *Annotated checklist of bird and mammal species of Cocha Cashu Biological Station, Manu National Park, Peru.* Fieldiana (Zoology, New Series) **21**, 1-29.

Terborgh, J., S. K. Robinson, T. A. Parker III, C. A. Munn, and N. Pierpont. 1990. *Structure and organization of an Amazonian forest bird community.* Ecological

Monographs. **60**, 213-238.

Wheelwright, N. T. 1985. *Fruit size, gape width, and the diets of fruit-eating birds.* Ecology **58**, 539-550

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