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FEEDING BEHAVIOR, BIRD VISITATION, AND SEED DISPERSAL IN *GUAREA MACROPHYLLA* AND *TRICHILIA QUADRIJUGA* (MELIACEAE)

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Resumen. – Comportamiento alimenticio, visita de aves y dispersión de semillas en *Guarea macrophylla* y *Trichilia quadrijuga* (Meliaceae). - Estudié en el Parque Nacional Manu, Perú, el comportamiento alimenticio, la actividad de aves y la dispersión de semillas en dos árboles simpátricos neotropicales de selva húmeda, *Guarea macrophylla* y *Trichilia quadrijuga*. Los números de individuos, de especies visitantes y de semillas removidas correlacionaron directamente con el tamaño de la cosecha de frutas disponibles en cada especie de planta. De 18 especies de aves que consumieron frutos de Guarea, solo cuatro (*Catharus ustulatus*, *Myiodynastes luteiventris*, *Lepidothrix coronata*, y P*ipra fasciicauda*) la visitaron consistentemente y dispersaron sus semillas. De tres especies de aves que consumieron frutos de Trichilia, dos (*Pipra fasciicauda* y *P. chloromeros*) visitaron y dispersaron sus semillas regularmente. La variación en la cantidad de tiempo en los árboles frutales entre y dentro de cada especie fue alta. La mayor actividad ocurrió entre las 07:00 hs y las 10:00 hs. Con pocas excepciones, todas las aves visitantes se posaron en el árbol observado y removieron frutos en vuelo o desde una percha cercana. El número de unidades de pulpa ingeridas varió de cero a seis, dependiendo del ave. Pocas semillas cayeron bajo el árbol.

Abstract. – In Manu National Park, Peru, I investigated feeding behavior, bird activity on and seed dispersal of two sympatric Neotropical rain forest trees, *Guarea macrophylla* and *Trichilia quadrijuga*. The numbers of individual visitors, visiting species, and seeds removed were directly correlated to the available fruit crop for each plant species. Of 18 bird species which consumed *Guarea* fruits, only Swainson's Thrush (*Catharus ustulatus*), Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*), Blue-crowned Manakin (*Lepidothrix coronata*), and Band-tailed Manakin (*Pipra fasciicauda*) consistently visited and dispersed its seeds. Of three bird species which consumed *Trichilia* fruits, only Band-tailed and Round-tailed Manakins (*P. chloromeros*) regularly visited and dispersed its seeds. Variance in the time spent at fruiting trees across and within bird species was high. Most bird activity occurred between 07:00 h and 10:00 h. With few exceptions, all visiting birds perched in the observed tree and then removed fruit either in flight or by reaching from a nearby perch. The number of ingested pulp units per visit ranged from zero to six depending on the bird. Few seeds were dropped under the parent tree. *Accepted 25 February 2014.*

Key words: Sulphur-bellied Flycatcher, Swainson's Thrush, Pipridae, *Guarea macrophylla*, *Trichilia quadrijuga*, avian seed dispersal, migrant bird visitation.

INTRODUCTION

Many frugivorous animals play an essential role in the reproductive biology of the plants whose fruits they consume. This mutualistic relationship has sparked interest in the evolutionary consequences of frugivory and seed dispersal for animals and plants (McKey 1975,

Howe 1981, Howe & Smallwood 1982, Herrera 1985, 1986; Estrada & Fleming 1986, Fleming & Estrada 1993). In spite of the tremendous effort to understand frugivory and seed dispersal, however, observational data on many tropical tree species is sparse. A few *Guarea* and *Trichilia* (Meliaceae) species have received attention: *G. glabra* (Howe & De Steven 1979, Wheelwright *et al.* 1984, Wenny 1999), *G. kunthiana* (Wenny 1999), *G. tonduzii*, *G. tuisiana*, and *T. havanensis* (Wheelwright *et al.* 1984), *T. cuneata* (Leck 1969, Foster & McDiarmid 1983), and *T. micrantha* (Argel-de-Oliveira 1992). Knowledge of seed dispersal in *G. macrophylla* and *T. quadrijuga* is lacking. I chose to study these two ornithochorous plants because: a) they belong to the same family, b) they have similar fruit types, i.e., capsules that dehisce to expose seeds covered with bright red-orange or red arils, c) they have an equal average arilloid (seed with aril) mass of 0.27 g, and d) they fruit in the study site at roughly the same time. These plant species, however, differ in average aril mass (see below), and apparent nutritional value of the aril (*Guarea* oily, *Trichilia* watery).

Fruits of *G. macrophylla* are borne on racemes on the terminal ends of branches. They have a thick, woody, bumpy, 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. These are plucked and ingested whole by birds, the oily red arils stripped off, and the yellow-white seeds regurgitated or defecated intact. The average food intake is 0.034 g or 12.6% of the pulp unit (Prado 1999).

The exocarp of a *T. quadrijuga* fruit is relatively thin, soft, smooth, bright orange in color and is borne singly at the tips of small branches. When ripe, the three-part capsule dehisces to expose a single juicy, bright red pulp unit. As in *Guarea*, these are plucked and swallowed 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, although fruits with more than three seeds have also been observed (Foster pers. comm.). Mean food intake from this fruit is 0.14 g or 54% of pulp unit mass (Prado 1999).

Here I list the birds that visited these plant species, try to differentiate seed dispersers from seed predators, and note avian feeding behavior and bird activity at trees of these species. The data reported here will be useful to researchers studying plant and bird congeners in other places, and will also serve as useful baseline data for anyone carrying out a longitudinal study of plant-frugivore interactions at Manu National Park.

METHODS

Study site. Observations were made in the mature floodplain forest around Cocha Cashu Biological Station in Manu National Park, Peru (11°53'17"S, 71°24'27"W, approximately 400 m a.s.l.). 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). A thorough description of the study site, including climate, vegetation, habitat types, and fruiting phenology can be found in Terborgh (1983).

Study species. Two Neotropical plants, *Guarea macrophylla* Vahl ssp. *pachycarpa* and *Trichilia quadrijuga* Kunth in HBK ssp. *quadrijuga*, family Meliaceae, were observed. The species 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. Further information on the natural history and distributions of these two genera can be found in Pennington (1981) and Gentry (1993).

Study trees. I selected three large fruiting trees of *G. macrophylla* (trees # 1, 2, and 3) and three individuals of *T. quadrijuga* (trees # 4, 5, and 6). The plants were identified by their fruits and leaves (Roosmalen 1985) and by comparisons to photocopies of herbarium sheets. 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 and forest type are as follows: tree # 1(30 h, 10 m, mature high-ground), tree # 2 (30 h, 7 m, flood-disturbed), tree # 3 (33 h, 7 m, mature high-ground), tree # 4 (28 h, 4 m, late successional), tree # 5 (23 h, 3 m, flood-disturbed), and tree # 6 (20 h, 3 m, late successional). Observations were made at a distance of 10 to 15 m from each tree to minimize disturbance to visiting birds, and for a time proportional to tree 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 trees of *G. macrophylla* with thin 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, and then by a rough count of racemes per branch, and the number of branches per tree.

Birds. Before I recorded my observations, I watched each tree for a whole day (EST 06:00–18:00 h) in order to assess bird activity and best times of the day for observation. Birds were identified using 10 x 42 binoculars, two field guides (Hilty & Brown 1986, Ridgely & Tudor 1994), and the bird checklist for the station (Terborgh *et al.* 1984). During watching periods, I identified birds that visited each tree, recorded the length of their stay in seconds with a stopwatch, and recorded time of day. Observations were not made equally across all hours, due to rain or lack of available fruit. To estimate bird activity throughout the day, I divided the total number of recorded visits during each hour by the number of hours for which observations were made during that hour.

I noted whether each bird perched in the tree, its feeding behavior (in air or sallying, perching and reaching up or down), 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 (i.e., beyond the tree crown). 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 approximate intermediate lengths 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 a pulp unit from the exocarp and swallowed it. For the most part, birds sallied to a fruit, plucked

an arillate seed, and then perched on a nearby branch ingesting it. If a bird sallied to a fruit and then flew away with it out of my sight, I counted the pulp unit as ingested. Birds bill-wiped following ingestion of fruits as well as unsuccessful attempts to pluck 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. Female manakins of the genus *Pipra* were particularly hard to distinguish because of their similar sizes, colors, and shapes. Such birds were recorded as 'unidentified manakin' (Pipridae) or 'unidentified species.'

RESULTS

Visiting birds. A total of 18 bird species from six families removed 737 pulp units of *G. macrophylla* trees in 537 visits (Table 1) whereas birds of only three species from one family swallowed 47 fruits of *T. quadrijuga* in 93 visits. The three species of manakin that frequently visited *Trichilia* trees were also regular visitors to *Guarea*. Table 1 shows mean body mass, numbers of bird visits, numbers of removed pulp units, feeding behavior, regurgitated seeds, and average times per visit in seconds for *Guare*a plants. The most frequent visitors were: Swainson's Thrush 21% of visits, Blue-crowned Manakin 16%, Band-tailed Manakin 13%, and Sulphur-bellied Flycatcher 11%. These bird species also ingested the largest number of pulp units: 27%, 13%, 14% and 13%, respectively. None of these species is an obligate frugivore.

Species of visitors varied noticeably among *Guarea* trees. For instance, the most frequent visitors to tree #1, located in mature high-ground forest, were Band-tailed Manakin, Round-tailed Manakin, Swainson's Thrush and Blue-crowned Manakin, 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 Swainson's Thrush and Sulphur-bellied Flycatcher 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 Blue-crowned Manakin, Band-tailed Manakin, Swainson's Thrush, White-necked Thrush (*Turdus albicollis*), and Pale-vented Thrush, with 53%, 11%, 8%, 7%, and 7% of all visits, respectively. Only two bird species (Swainson's Thrush and Pale-vented Thrush) visited all three plants.

The average length of visits to *Guarea* varied considerably both among and within bird species, ranging from as little as 44 s for Drab Water-Tyrant (*Ochthornis littoralis*) to as long as 175 s for Collared Trogon. Individual bird visits ranged from as little as 1 s, when a Tropical Kingbird (*Tyrannus melancholicus*) sally-plucked a pulp unit and flew away, to as long as 1004 s (about 16 min) when a Swainson's Thrush fed and rested in tree # 1. This same bird regurgitated seven seeds under the crown, where the probability of their survival and germination is reduced (Janzen, 1970).

Bird activity. Birds visited trees singly or in groups of up to 8 as follows: one bird (*Guarea* 329 times, *Trichilia* 39 times), two birds (*Guarea* 41, *Trichilia* 20), three (*Guarea* 14, *Trichilia* 6), four (*Guarea* 11, *Trichilia* 0), five (*Guarea* 4, *Trichilia* 0), six (*Guarea* 2, *Trichilia* 0), seven (*Guarea* 0, *Trichilia* 0), and eight (*Guarea* 1, *Trichilia* 0). Eighty-two and 60% of observations for *Guarea* and *Trichilia*, respectively, were of visits by a single bird. Bird activity was greater at *G. macrophylla* than at *T. quadrijuga*. *Guarea* experienced highest bird activity between 08:00 h and 10:00 h. A lower peak

TABLE 1. Mean body mass, numbers of bird visits, total numbers of pulp units removed and seeds regurgitated, feeding behavior, and average visit lengths of visitors observed to *Guarea macrophylla* trees at Cocha Cashu Biological Station, Manu National Park, Peru, between 14 October and 16 November, 1998. Body masses obtained from Terborgh *et al.* (1990), Moermond & Denslow (1985), and Dunning (2008), respectively.

Bird species	Body mass (g)	Number of visits (n)	Pulp units removed	% removed from perch	% removed in flight	Seeds dropped under tree	Average length of visits (SD)
Trogon collaris (Collared Trogon)	59	6	17	0	100	0	175 (112)
Capito niger (Black-spotted Barbet)	64	2	12	100	0	5	142
Myiodynastes luteiventris (Sulphur-bellied Flycatcher)	46	60	95	39	61	0	106 (85)
Ochthornis littoralis (Drab Water-Tyrant)	13	31	29	10	90	0	44 (32)
Tyrannus melancholicus (Tropical Kingbird)	40	17	19	0	100	0	59 (50)
Myiozetetes similis (Social Flycatcher)	28	15	16	25	75	0	109 (117)
Myiozetetes luteiventris (Dusky-chested Flycatcher)	19	7	12	8	92	0	69 (66)
Myiarchus tuberculifer (Dusky-capped Flycatcher)	20	4	5	40	60	0	70 (31)
Sirystes sibilator (Sirystes Flycatcher)	38	4	7	0	100	0	94 (74)
Attila bolivianus (Dull-capped Attila)	45	1	2	100	0	0	103 (101)
Pipra fasciicauda (Band-tailed Manakin)	17	70	100	24	76	1	97 (65)
Lepidothrix coronata (Blue-crowned Manakin)	9	87	93	17	83	3	95 (103)
Pipra chloromeros (Round-tailed Manakin)	17	22	33	30	70	0	102 (60)
Tyranneutes stolzmanni (Dwarf Tyrant-Manakin)	9	7	14	0	100	4	96 (57)
Catharus ustulatus (Swainson´s Thrush)	27	114	198	42	58	11	105 (143)
Turdus albicollis (White-necked Thrush)	52	19	33	67	33	1	190 (257)
T. hauxwelli (Pale-vented Thrush)	72	15	25	64	36	0	83 (47)
Thraupis episcopus (Blue-gray Tanager)	32	1	2	100	0	2	226
Unidentified manakin	-	25	11	9	91	0	75 (35)
Unidentified species	-	16	14	0	100	0	108 (136)
Totals		537	737			27	

occurred in mid-afternoon. In *Trichilia*, bird activity was highest in the early morning between 07:00 h and 08:00 h and early afternoon between 14:00 h and 15:00 h (See also Prado 1999).

Seed dispersal and predation at Guarea. In all but five cases, fruits were swallowed immediately after plucking. Birds that plucked a pulp unit in flight usually landed in the same tree, positioned the pulp unit within the bill, and swallowed it whole. Birds that plucked pulp units while perched always swallowed them without moving. 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 seed with attached aril 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. On another occasion, another Dwarf Tyrant-Manakin plucked an arillate seed and carried it away beyond the canopy, effectively dispersing it. Two Black-spotted Barbets visited tree #2 once, swallowing a total of 12 pulp units and regurgitating five seeds under the canopy.

Bird visits, feeding behavior, seed dispersal and predation at Trichilia. Total numbers of bird visits, pulp units ingested, seeds dropped under the tree crown per bird species, and average lengths of visit (± SD) for *Trichilia* trees were as follows: Band-tailed Manakin (80; 42; 0; x = 68 ± 67 s, range 2–405 s), Blue-crowned Manakin (1; 1; 0; 45 s), and Round-tailed Manakin (12; 4; 0; x = 144 ± 74 s, range 59–281 s). Band-tailed and Round-tailed Manakins made 82% and 13%, respectively, of all visits. Band-tailed Manakin accounted for 89% of the observed pulp units removed. 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. Three Band-tailed Manakin males used tree # 4 and two Round-tailed Manakin males used tree # 6 for intraspecific dominance displays (Robbins 1983, 1985). Blue-crowned Manakins had the shortest visit (45 s) among birds that actually fed on fruit, and Round-tailed Manakin averaged the longest (144 s). Most birds plucked pulp units in flight and landed on a nearby branch of the same tree to swallow it. Exceptions were two Band-tailed Manakins and a Round-tailed Manakin that plucked one, two, and two fruits, respectively, by perching and reaching down.

Fruit crop. The approximate number of available pulp units (individual seed and its aril consumed individually and separately from other such units contained in the same fruit) per tree per day was as follows: tree # 1 > 500, tree # 2 > 300, tree # 3 > 300, tree # 4 = 20, tree # 5 = 15, and tree # 6 = 10. The plant species thus differed in observed crop size (much larger for *Guarea* than for *Trichilia*).

DISCUSSION

I expected a heterogeneous assemblage of frugivorous birds to feed from both plant species, as Howe & De Steven (1979) found for *G. glabra*, but a much larger assembly at *Guarea* than at *Trichilia.* Indeed, a taxonomically diverse assemblage of birds (18 species in 6 families) removed *G. macrophylla* pulp units, whereas only three piprids removed *T. quadrijuga* fruits. Differences in the numbers of individual visitors, visiting species, and seeds removed between *Guarea* and *Trichilia* probably reflect: a) large differences in the sizes of their fruit crops size (> 300 pulp units for *Guarea* trees and < 20 pulp units for *Trichilia* = 7% of the *Guarea* crop), b) taller *Guarea* trees which passively may "intercept" more species than *Trichilia* trees, c) a more

diverse set of habitats (tree locations) for *Guarea*, d) differences in aril nutritional content, and/or e) differences in aril masses. Species composition among the three individual *Guarea* trees varied considerably, probably reflecting different habitat preferences of the visiting birds. Thus, the observed visitors at *Guarea* generally reflected the avian assemblage that feeds on this tree. Manakins tend to avoid open areas, whereas thrushes and flycatchers are frequently observed in such habitat. Nevertheless, all three manakin species ate fruits of both plant species, which probably indicates that these birds obtain different nutrients from each plant. The average number of seeds swallowed by each bird species per visit is probably a low estimate due to inaccurate counts when the trees were visited by more than three individuals at the same time. Not once did more than three birds visit the same *Trichilia* plant simultaneously, perhaps again a result of their lower heights and smaller crop sizes.

Moermond & Denslow (1985) found that most bird species use one removal technique primarily and others only occasionally. In general, smaller birds gathered most fruit in flight whereas larger birds gathered fruit in flight or when perched. Manakin species removed between 70 and 100% of ingested fruit in flight. Swainson's Thrush, White-necked Thrush, Pale-vented Thrush, Sulphur-bellied Flycatcher, and Dusky-capped Flycatcher (*Myiarchus tuberculifer*) commonly used both techniques (Table 1). The most notable exception was Collared Trogon, which at 59 g is considerably heavier than manakins, removed *Guarea* fruit exclusively in flight. Sample sizes for the other species were too small for meaningful comparisons. The feeding behavior patterns I observed are thus in general agreement with Moermond & Denslow's (1985) findings.

Terborgh *et al.* (1990) reported that out of a total 319 bird species recorded in a 97-ha plot at Cocha Cashu Biological Station, 30 species were obligate arboreal frugivores, 2 species obligate terrestrial frugivores, and 44 species arboreal omnivores. The remaining 243 species form all other known guilds. Not included in this list are six bird species that I observed removing *Guarea* fruit: Sulphur-bellied Flycatcher, Drab Water-Tyrant, Tropical Kingbird, Social Flycatcher (*Myiozetetes similis*), Dusky-chested Flycatcher (*Myiozetetes luteiventris*), and Blue-gray Tanager. Thus in this Amazonian forest community, a total of 82 out of 325 (25.2%) of the bird species regularly or occasionally eat fruit at this time of the year. Among those, the most reliable seed dispersers of *G. macrophylla* are Swainson's Thrush, Blue-crowned Manakin, Band-tailed Manakin, and Sulphur-bellied Flycatcher. Piprids are primarily frugivorous birds that may complement their diets with some insects (Snow 1971). *Guarea* fruits may provide some essential protein and lipids to these birds. Although the Swainson's Thrush is a ground feeder that specializes in arthropods and the Sulphur-bellied Flycatcher specializes in aerial insects, both species are facultative frugivores (Hilty & Brown 1986). These four species (4.8% of the 82 at least partially frugivorous bird species at Cocha Cashu) accounted for 67% of the pulp units removed, and 62% of the visits to *Guarea* trees. Three of the 82 at least partially frugivorous species at Cocha Cashu (3.6%) fed on *Trichilia* fruits. This suggests that both *Guarea macrophylla* and *Trichilia quadrijuga* may depend on a few specialized bird species to disperse their seeds.

Two migrant species, Swainson's Thrush and Sulphur-bellied Flycatcher, removed 40% of *G. macrophylla* pulp units. The thrush breeds in temperate North America and migrates south from late July to early October, arriving in the Amazon basin in October. The Sulphur-bellied Flycatcher breeds from the southwestern United States to Costa Rica and is a winter resident of South America from

October to April (Ridgely & Tudor 1994). Thus, the arrival of the two migrant species in the Peruvian Amazon coincides with the fruiting phenology of *G. macrophylla*. Howe & De Steven (1979) showed that the fruiting of *G. glabra* in Panama coincides with the northern migration of several bird species, including Swainson's Thrush, which was one of the most frequent visitors to trees of that species. It would be interesting to gather more data and explore whether *Guarea*'s fruiting phenology is adaptively synchronized to the arrival of these North American migrants or is simply timed to match higher abundance of fruit-eating birds locally, potentially increasing the number of bird species consuming its fruits. Alternatively, *Guarea*'s fruit phenology may be constrained by its flowering phenology or by abiotic conditions such as the end of the rainy season.

Blake & Loiselle (1992) recorded 63 fruit species (none in the Meliaceae family) in fecal samples of Swainson's Thrush in Costa Rica. We can thus add *G. glabra* and *G. macrophylla* to the diet of this species. Sulphur-bellied Flycatcher has been observed removing pulp units of *T. cuneata* in Guanacaste province in Costa Rica (Leck 1969). There is little evidence that any of the manakins observed in this study depend heavily on either Meliaceae fruit during their reproductive cycles.

I observed Drab Water-Tyrant feeding on fruits of *Guarea* (Table 1). These birds inhabit steep banks of rivers and are considered mostly insectivorous (Foster pers. comm.). To my knowledge, this is the first record of this species feeding on fruit.

Guarea macrophylla and *T. quadrijuga* arils are also consumed by other mammals and birds. Dusky Titi Monkeys (*Callicebus moloch*) eat both fruits occasionally (F. Bossuyt pers. comm.), but whether they are seed predators or dispersers is not known. 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. Swallow-tailed Manakin (*Chiroxiphia caudata*), Helmeted Manakin (*Antilophia galeata*), Red-tailed Amazon (*Amazona brasiliensis*), Black-fronted Piping Guan (*Pipile jacutinga*), and Araçari spp. (*Pteroglossus azara, P. inscriptus, P. pluricinctus*) have been observed eating *G. macrophylla* fruit (Marini 1992, Martuscelli 1995, Galetti *et al.* 1997, Holbrook 2003, Fadini & De Marco 2004). Howler monkeys (*Alouatta* spp.), spider monkeys (*Ateles* spp), and cotingas (*Cotinga* spp) also appear to disperse *T. quadrijuga* seeds, whereas their seeds are often preyed on by Saki Monkeys (*Pithecia* spp and *Chiropotes* spp) and macaws (*Ara* spp.) (Roosmalen 1985, Roosmalen *et al.* 1988). Neither *G. macrophylla* nor *T. quadrijuga* fruits are fragrant nor are their pulp colors likely to attract bats.

Future research on the effectiveness of avian dispersal of *G. macrophylla* and *T. quadrijuga* seeds should focus on seed germination experiments, percentages of seeds regurgitated or defecated, on better ways to determine how far seeds are carried away from parent trees, and time of seed passage through the gut of each bird species. More information can be also be gained by performing observations at more trees of each species in locations other than Manu, at larger *Trichilia* trees for longer periods, and by setting seed traps in the forest. *Guarea* species occur throughout the Neotropics, and it would be useful to study the fruiting phenology of these species throughout their ranges, their relationships with their seed dispersers, and the role this genus may play in the diets and movements of North American migrants. Studies of the treatments of seeds in the bird's gut, and their viability following regurgitation or defecation will further elucidate the quality

of dispersal that these birds provide for *Guarea* and *Trichilia* seeds.

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