

DISPERSAL OF A NEOTROPICAL NUTMEG (*VIOLA SEBIFERA*) BY BIRDS

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ABSTRACT.—Feeding assemblages of birds were observed at a Panamanian population of *Viola sebifera* (Myristicaceae) in order to test the hypothesis that plants producing especially nutritious fruits in limited supply should be efficiently dispersed by a small set of obligate frugivores. *Viola sebifera* produces an encapsulated arillate seed that is swallowed by birds shortly after dehiscence. The aril (54% lipid, 7% protein, 8% usable carbohydrate) is retained; the seed is regurgitated intact within 10–30 min. The plant produces 1–96 (\bar{x} = 24) ripe arillate seeds each day, of which 40–89% (\bar{x} = 76%) are taken within a few hours of dawn. The visitor assemblage consists of six resident frugivores. Three [Chestnut-mandibled Toucan (*Ramphastos swainsonii*), Keel-billed Toucans (*R. sulfuratus*), and Masked Tityra (*Tityra semifasciata*)] are “regulars,” likely to visit all trees; three [Slaty-tailed Trogon (*Trogon massena*), Rufous Motmot (*Baryphthengus martii*), and Collared Aracari (*Pteroglossus torquatus*)] are common throughout the Barro Colorado Forest but do not consistently use *Viola sebifera*. The Chestnut-mandibled Toucan is responsible for 43% of the seeds removed by birds, although it is also responsible for more seed waste (regurgitation under the tree crown) than other visitors. Rapid depletion of available fruits each morning and active defense of the crowns by toucans suggest a limited and preferred food resource for “regulars” in the assemblage.

A review of recent work indicates that the assemblage visiting *Viola sebifera* is similar to that frequenting its larger congener (*V. surinamensis*) but is far smaller and more specialized than those visiting other fruiting trees in the same forest. Received 28 April 1980, accepted 31 July 1980.

MANY tropical trees bear fleshy fruits adapted for the attraction of dispersal agents, and many tropical birds eat fruits and either disperse or destroy seeds. The most quantitative work has been life-history studies of fruit-eating birds (e.g. Snow 1962a, b; Bourne 1974) or censuses of fruiting and visitation phenologies (e.g. Snow 1965, Medway 1972, Crome 1975). Coevolutionary problems are relatively unexplored. Snow (1971) suggests that natural selection favors plants that attract the largest number and variety of dispersal agents possible, thereby scattering seeds to the widest variety of sites possible. McKey (1975) and Howe and Estabrook (1977) discuss the possibility of dichotomous dispersal strategies in which small-seeded species attract a variety of opportunistic frugivores with fruits of individually low nutritional quality, while large-seeded species attract specialists with smaller displays of highly nutritious fruits. The advantage of “opportunistic” dispersal by a large pool of potential dispersal agents may be offset if some generalists are more wasteful at removing seeds than others. The advantage of dispersal by specialists is reliable visitation by efficient dispersal agents; a possible cost is dependence on one or a few species that may vary dramatically in abundance in time and space (see Baker and Hurd 1968).

This paper examines the relationship between avian visitation and seed removal from an overstory nutmeg, *Viola sebifera* Aubl. (Myristicaceae) on Barro Colorado Island, Panama. The brilliant red aril indicates a classic bird fruit (Fig. 1; see Van der Pijl 1972). The aril is one of the most nutritious per gram dry weight yet described, with high proportions of fats and proteins (see Snow 1962b, White 1974). One prediction from the strategic dichotomy presented above is that such a “high

investment" tree should be visited by a small assemblage of regular specialists (McKey 1975). A second is that dispersal agents should vie for a limited resource, as evidenced by rapid depletion of the crop as it is presented and perhaps by aggressive encounters among visitors (Howe and Estabrook 1977). A third prediction is that primary dispersal agents, when faced with rare episodes of fruit abundance, should "selfishly" eat fruits without dispersing seeds (Howe and Estabrook 1977). Such sedentary behavior should be evident for any dispersal agent large enough to be immune from most predators (Howe 1979). The framework utilized here presumes that the interaction between fruiting tree and dispersal agent involves reproductive competition within each population, as well as a facultative mutualism between populations that may lead to variations in the benefits or costs accrued to either bird or plant.

METHODS

I sampled 14 female *V. sebifera* trees for fruit production between late September 1977 and late February 1978. Fruit debris was collected with 1-m² traps of nylon mesh and plastic (PVC) tubing raised 0.2–0.5 m above the forest floor, depending on underlying topography. Traps were placed in a randomized design under the crowns, with coordinate locations drawn from a random-number table (Rohlf and Sokal 1969). Biweekly collections included unopened fruits, dehisced capsules, and undispersed seeds. Each set of traps sampled approximately 10% of the area under the crown of each tree; estimates of each category of debris were made by dividing the number of pieces in each category for each tree by the proportion of area sampled for that tree. The number of seeds dispersed for each tree is estimated by subtracting the estimate of the seeds dropped under the tree from the estimate of capsules dropped (see above). The method is similar to that used in more extensive studies (Howe in press) and far superior to the combination of traps and transects attempted earlier (Howe 1977).

Commercial nutrient extractions were obtained for a composite sample of 20 arils freeze-dried in the field and analyzed at Colorado State University. Standard techniques included pentane extractions of lipids, colorimetric evaluation of protein content, and calorimetry (summarized in Allen 1974). Individual analyses are infeasible, as each sample requires 2.00–3.00 g dry weight, and individual arils average 0.12 g.

Bird activity and the presentation and depletion of fruits were monitored with five continuous watches between 0600 and 1100 (dawn is ca. 0610) at each of six trees in a transect from the edge of the laboratory clearing to 2.5 km into the forest. During these 150 h of observation (25 at each plant) the number of visits, the number of aggressive encounters, and the number of arils eaten and seeds regurgitated or dropped were recorded for each bird species. Observation trees were selected for maximum visibility from some point on the ground; none was in an unusual location (e.g. clearings), but all were more visible than others in the sample. The number of capsules that opened each day was also monitored during these watches. Where possible, watches were spaced throughout individual fruiting seasons.

RESULTS

Natural history of the tree.—*Viola sebifera* is a widespread, dioecious, wet-forest tree of essentially unknown reproductive biology. The species occurs from Nicaragua to Peru, Bolivia, and Brazil and is an abundant component of both new (60+ yr) and old (150+ yr) forest on Barro Colorado Island (Croat 1978). Mature fruits dehisce from September through late February, with a dramatic peak in November and December, a season somewhat more extended than that of a smaller sample from Costa Rica (Frankie et al. 1974). In this study, 14 trees matured crops of 19–3,567 fruits ($\bar{x} = 948 \pm 181$ SE) over individual fruiting periods lasting 6–18 weeks ($\bar{x} 12 \pm 1$). Many fruits reaching mature size aborted because of insect (weevil and fly) infestations; mortality ranged from 5 to 96% ($\bar{x} = 41 \pm 5\%$). Trees in this sample succeeded in maturing 5–2,163 fruits in a season ($\bar{x} = 594 \pm 158$). This sample appeared representative of other trees of this species.



Fig. 1. Newly dehisced fruits of *Virola sebifera*. A single gray seed of moderate size (10×14 mm) is surrounded by a laciniate aril of brilliant red color. Left: fruit as presented to birds; middle: seed with aril peeled away; right: empty capsule.

The fruit is single-seeded and surrounded by a protective capsule (Fig. 1). Capsules dehisce to expose a 14×10 -mm elliptical seed surrounded by a netlike red aril less than 1 mm thick. The seed weighs 0.69 ± 0.04 g fresh, the aril 0.23 ± 0.01 g ($n = 20$). The aril is 97.5% organic matter and 2.5% ash. Most organic matter is digestible fat (53.7%), protein (7.1%), and usable carbohydrate (8.4%). Gross energetic content is 6,888 cal/g, or 826 cal for an average aril of 0.12 g dry weight. All birds observed eating these arillate seeds regurgitated intact seeds after stripping the arils; nine seeds recovered from Chestnut-mandibled Toucans (*Ramphastos swainsonii*) germinated in 8–10 weeks. There is little likelihood that birds increase germination of such seeds, other than by removing arils that might mold, because the seeds do not pass through the digestive tract (Howe in press). Agoutis (*Dasyprocta punctata*) chew up and kill seeds under trees but do not bury or carry off seeds. Juvenile plants are rare under adult crowns.

Fruit presentation and depletion.—Fruit capsules dehisce from before dawn until mid-morning, and arillate seeds are either removed, dropped, or regurgitated in place by mid-morning. Over the 30 observation periods of 5-h duration, $1-96$ ($\bar{x} = 24 \pm 4$) fruits opened daily on each tree, and 85% were removed by birds. The remainder were eaten and regurgitated in situ (5%), were dropped by birds (3%), or spontaneously fell off the tree (7%). Independent determinations of dispersal success from fruit traps under these same six plants showed that over the entire fruiting season 84% of the seeds were removed. The entire sample of 14 plants showed 40–89% dispersal ($\bar{x} = 76 \pm 4\%$).

Assemblage characteristics.—Direct observations indicate an unusually small assemblage of six resident bird species and one incidental migrant, representing a total of five families and spanning a size range of 32 to 639 g (Table 1).

Fruits are open at dawn (ca. 0605–0615), and visitation starts immediately (Fig. 2). More than half of the total visits occur before 0800. The three species that

TABLE 1. Taxa, migratory status, and weights of seven species of birds seen eating arilloids of *Virola sebifera*.

Family Common name	Status	<i>n</i>	Weight (g ± SD) ^a
Trogonidae Slaty-tailed Trogon	Resident	10	145 ± 12
Motmotidae Rufous Motmot	Resident	5	185 ± 20
Ramphastidae Collared Aracari	Resident	10	299 ± 11
Chestnut-mandibled Toucan	Resident	7	639 ± 45
Keel-billed Toucan	Resident	15	399 ± 35
Cotingidae Masked Tityra	Resident	15	84 ± 7
Turdidae Swainson's Thrush	Migrant	15	32 ± 2

^a Weights are from labels of museum specimens collected in Panama and Costa Rica.

occurred only at one to three trees in the sample [Slaty-tailed Trogon (*Trogon masena*), Rufous Motmot (*Baryphihengus martii*), and Collared Aracari (*Pteroglossus torquatus*)] tended to be early visitors. On two occasions a motmot fed on fruits before dawn; the number eaten could be monitored by watching the silhouette against the sky. Three regular visitors throughout the forest [Keel-billed Toucan (*Ramphastos sulfuratus*), Chestnut-mandibled Toucan, and Masked Tityra (*Tityra semifasciata*)] visited throughout the morning, although the first Chestnut-mandibled Toucan visits were always within 10 min of dawn at trees with more than 15 fruits available. In view of the fact that 28% of the Keel-billed Toucan visits ended with

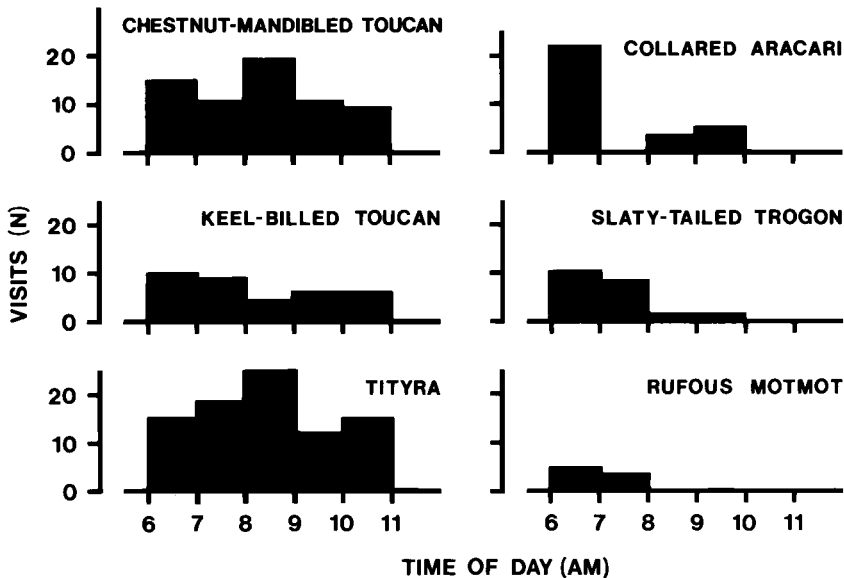


Fig. 2. Daily visitation patterns of the six common dispersal agents of *Virola sebifera* on Barro Colorado Island. "Regular" species seen throughout the forest are on the left; "local" species that heavily use some plants, but not others, are on the right.

TABLE 2. Handling attributes (per visit) of seven birds observed eating *Virola sebifera* arilloids.

Species	n	Seeds			
		Seeds eaten ($\bar{x} \pm SE$) ^a	regurgitated ($\bar{x} \pm SE$) ^{a,b}	Seeds dropped ($\bar{x} \pm SE$) ^{a,b}	Seeds removed ($\bar{x} \pm SE$) ^{a,b}
Slaty-tailed Trogon	20	1.4 ± 0.4 (0-8)	0.1 ± 0.1 (0-1)	0.1 ± 0.1 (0-1)	1.3 ± 0.4 (0-8)
Rufous Motmot	8	4.0 ± 0.9 (1-8)	none	none	4.0 ± 0.9 (1-8)
Collared Aracari	16	3.6 ± 0.7 (0-8)	none	0.1 ± 0.1 (0-1)	3.5 ± 0.7 (0-8)
Chestnut-mandibled Toucan	61	4.0 ± 0.6 (0-18)	0.2 ± 0.1 (0-2)	0.4 ± 0.2 (0-11)	3.6 ± 0.6 (0-18)
Keel-billed Toucan	35	0.5 ± 0.1 (0-3)	— (0-1)	none	0.5 ± 0.1 (0-3)
Masked Tityra	86	1.5 ± 0.2 (0-5)	— (0-2)	— (0-1)	1.5 ± 0.2 (0-5)
Swainson's Thrush	1	1.0 (1)	none	none	1.0 (1)

^a Range in parentheses.

^b "None" means the event was not observed. A dash means that the value has too few significant figures to show in the table.

displacement by Chestnut-mandibled Toucans (see below), it is noteworthy that the distributions of visits of the two large toucans are different ($\chi^2 = 10.53$, 4 df, $P < 0.05$). Keel-billed Toucans tend to avoid the peak visitation times of their larger congeners. Distributions of visits of Chestnut-mandibled Toucans and Masked Tityras are indistinguishable ($\chi^2 = 1.21$, 4 df, $P > 0.9$). Displacements of the tityras are less frequent (ending 14% of the tityra visits) and are qualitatively different. Chestnut-mandibled Toucans almost always drive other toucans out of the area; the smaller tityras often dodge into neighboring trees and resume feeding after the toucans leave.

These species are potentially effective dispersal agents, because they swallow arillate seeds whole and regurgitate intact seeds. They show dramatic differences, however, in potential and average seed ingestion per visit, as well as in the extent to which they drop or regurgitate seeds under the tree crown (Table 2). Grand means pooled over all observations and trees may be used, because measurable differences between trees are not detectable. Complete feeding observations are available for a subset of the total visitation record. The relative importance of each species to *Virola sebifera* dispersal may be calculated roughly using the mean number of seeds taken each visit and the slightly larger sample of all recorded visits to the study trees (Table 3). Despite the fact that Chestnut-mandibled Toucans regurgitated and

TABLE 3. Relative dispersal importance of seven bird species observed eating fruits of *Virola sebifera*.

Species	Visits (n)	Eaten	Total seeds handled (n)			Percent- age of total taken ^a
			Regur- gitated	Dropped	Taken	
Slaty-tailed Trogon	20	28	2	2	26	5
Rufous Motmot	8	32	0	0	32	6
Collared Aracari	30	105	0	3	105	19
Chestnut-mandibled Toucan	65	260	26	13	234	43
Keel-billed Toucan	35	18	0	1	18	3
Masked Tityra	86	129	0	0	129	24
Swainson's Thrush	1	1	0	0	1	—

^a Refers to the percentage of the total seeds removed by birds; ca. 15% of those available are not removed.

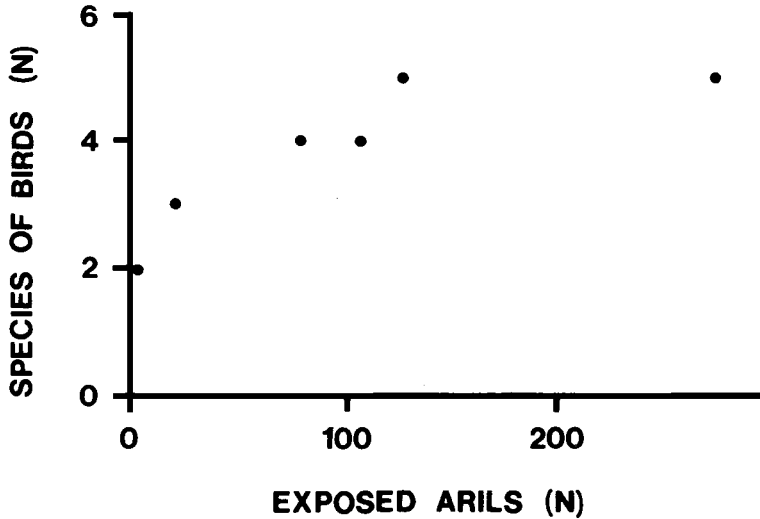


Fig. 3. Plot of the number of species observed against the sum of the fruits available during 25 h of observation at each of six *Virola sebifera* trees. No more than five species visited any one tree, indicating the smallest assemblage recorded at a tropical tree. At least 40 partly or wholly frugivorous birds and mammals occur in the study area.

dropped more seeds in place than other visitors, they were responsible for a much higher proportion of seeds removed than other birds (43%). The Masked Tityra, the smallest regular visitor in the assemblage, also visited most trees in high frequency and took a respectable proportion of seeds (24%). The high proportion recorded for Collared Aracaris (19%) is misleading, as all visits were to one individual tree next to the laboratory clearing. These birds failed to visit trees in the primary forest, even when feeding within meters of them; on one occasion a small flock ate legume flowers from a vine in a tree crown that intermingled with the branches of a *Virola* tree without eating the fruits. Such behavior could indicate particularly distasteful fruits on some trees, but it is more likely due to entirely different feeding regimes in different parts of the forest. Keel-billed Toucans ate few fruits despite frequent visitation; trogons and motmots did not visit most trees (see below).

Despite the smallness of the assemblage, visitation varied at different individual trees. Chestnut-mandibled Toucans and Keel-billed Toucans were the only species recorded from all six 25-h observational series; Masked Tityras missed one tree with very low production. Such birds appeared to be "regulars," likely to find and use any fruiting *Virola sebifera* in the forest. Motmots and aracaris were recorded at only one tree each, while Slaty-tailed Trogons visited one *Virola* heavily and two others one and three times, respectively. Such birds appeared to be "locals" that heavily used some plants, but not others. All three are abundant throughout the forest inhabited by *Virola* but evidently have different feeding regimes in different areas. One visit by a Swainson's Thrush (*Catharus ustulatus*) was incidental. From an individual plant's perspective, the recorded assemblage never exceeded five species. The number of visits to different plants increased with the number of fruits available ($r = 0.84$, $P < 0.05$), but the number of species quickly plateaued (Fig. 3).

Some frugivores common in the vicinity of *Virola sebifera* trees did not visit them.

TABLE 4. Seeds removed per visit for birds displaced by Chestnut-mandibled Toucans, compared with those removed by undisturbed foragers.

Species	Displaced		Undisturbed	
	Range	Mean (\pm SE)	Range	Mean (\pm SE) ^a
Chestnut-mandibled Toucan	0-4	1.1 \pm 0.5	0-16	3.8 \pm 0.7*
Keel-billed Toucan	0-3	0.3-0.3	0-3	0.5 \pm 0.2*
Masked Tityra	0-3	0.4-0.3	0-4	1.6 \pm 0.2**

^a One-tailed *U*-test: * = $P < 0.05$, ** $P < 0.01$.

Notable was a group of four Crested Guans (*Penelope purpurascens*) that habitually roosted between two fruiting *Virola* trees. Though never farther than 10 m from trees laden with fruits early in the morning, the guans never visited the plants. The same birds ate *Eugenia* (Myrtaceae) fruits in a tree within 2 m of a fruiting *Virola*. Purple-throated Fruitcrows (*Querula purpurata*) habitually roosted as a family group (one adult of each sex, two juvenile birds) within 15 m of another fruiting *Virola* without visiting the plant. Both of these bird species were common elsewhere in the forest and failed to visit the small nutmeg; guans did eat fruits of the larger congener (*V. surinamensis*; see Howe in press). A Blue Cotinga (*Cotinga nattererii*) frequented another fruiting tree (Melastomaceae) 20 m from a *Virola* without visiting the study plant. Howler monkeys (*Alouatta palliata*), white-faced monkeys (*Cebus capucinus*), and marmosets (*Saguinus geoffroyi*) frequented the vicinities of *Virola* trees without eating the fruits; the howler monkey even ate the leaves without touching fruits. All of these primates are known frugivores (e.g. Hladik and Hladik 1969, Milton 1977, Howe 1980). Spider monkeys (*Ateles geoffroyi*) were not seen eating *Virola sebifera* during the 1977-1978 season, although K. Milton (pers. comm.) did observe them eating fruits of this species during a season of exceptionally heavy fruit fall in 1979. No bats ate fruits during crepuscular hours nor have any been recorded at this species during long-term studies of bat frugivory (e.g. Morrison 1978). No arboreal fruit-eating birds known to have been common on Barro Colorado Island in the past are now thought to be extinct (Willis and Eisenmann 1979). A few frugivores thus appear to prefer *Virola sebifera* fruits; other species ignore them.

Interactions among visitors.—A particularly nutritious resource in limited supply might be expected to promote active defense among visitors. The first issue is whether such defense occurs. The largest visitor, the Chestnut-mandibled Toucan (Table 1), excluded conspecifics and other species with which it co-occurred at fruiting trees. Exclusion was by a direct chase, usually accompanied by a hoarse croak. All attempts were successful in driving the intruder from the tree. Such displacements involved 8 conspecifics, 10 Keel-billed Toucans, 12 Masked Tityras, and 3 Rufous Motmots. Exceptions to the rule of automatic displacement were pairs of males and females that arrived and fed together (sexes were distinguishable by bill size); such pairs fed together in a manner analogous to pair cooperation in hummingbirds (Wolf and Stiles 1970). No groups of toucans visited *Virola sebifera*, as frequently happens at species of trees with substantially larger fruit crops. Displacements had an obvious effect on the foraging success of the affected birds; birds chased from trees ate (and removed) fewer seeds than those feeding during the absence of aggressive Chestnut-mandibled Toucans (Table 4). Aggressive toucans ate 0-18 seeds per visit (\bar{x} =

5.8 ± 1.7), which is more than were eaten by conspecifics that they displaced (*U*-test, $P < 0.025$; see Table 4).

A second question is whether such displacements enhance or inhibit seed removal. Aggressive toucans spent 218 min in *Virola* trees during 15 visits, as compared with 279 min spent by undisturbed birds during 38 visits ($\chi^2 = 4.8$, 1 df, $P < 0.05$). These aggressors regurgitated 19 seeds in situ, while those birds in 38 uneventful feeding bouts regurgitated only 8 ($\chi^2 = 12.8$, 1 df, $P < 0.001$). These totals reflect a positive correlation between visit duration and the number of seeds regurgitated in situ ($r_s = 0.43$, $P < 0.001$). Even such rough calculations give indirect evidence that the sedentary behavior encouraged by aggressive exclusion of potential competitors depresses dispersal. The longer a bird stays in a tree, the more likely it will regurgitate seeds in place rather than disperse them.

DISCUSSION

These results reflect upon the aptness of the "low investment" and "high investment" dichotomy for the explanation of patterns of fruit production and depletion at *Virola sebifera*, and they provide a needed backdrop for a general discussion of the adequacy of current theory in explaining patterns of frugivory on Barro Colorado Island and in comparable forests (cf. McKey 1975, Howe and Estabrook 1977). A related insight of general interest concerns the issue of coevolution and co-occurrence of frugivores and fruiting trees in tropical communities.

As predicted, a small set of obligate frugivores reliably depletes a tree with protein- and lipid-rich fruits. *Virola sebifera* produces one of the most nutritious arils known (see Snow 1962b, White 1974), and its seeds are primarily dispersed by three "regulars," which visit most or all plants in the population. As adults, Chestnut-mandibled and Keel-billed toucans and Masked Tityras depend primarily upon fruit for food (Van Tyne 1929; Skutch 1946, 1971). Three other resident bird species were abundant throughout the forest but simply neglected most *Virola sebifera* trees. A migrant thrush was incidental. The dramatic depletion of fruits within hours of dawn and the aggressive exclusion of some visitors by others suggest that the nutmeg aril is a preferred food in limited supply (cf. Leck 1972), not a superabundant resource (Willis 1966). Sedentary visitors tended to regurgitate more seeds in place than did birds visiting for short periods. The proclivity of Chestnut-mandibled Toucans to defend tree crowns can, under conditions of exceptionally large fruit crops, work against the dispersal of the seeds, because the birds tend to remain in trees long enough to process fruits and regurgitate seeds in place rather than to remove them. Consistent behavior of this sort would favor individual plants that produce limited numbers of fruits each day over those that produce so many as to promote territoriality and sedentary habits among visitors (Howe and Estabrook 1977).

Parallel studies support the distinction between "high investment" and "low investment" dispersal systems (Table 5). In Costa Rican dry forest, a vireo (*Vireo flavoviridis*) removes 65% of the oily arillate seeds of *Casearia corymbosa* that are handled by birds. Overall, 91% of the seeds are taken by mid-morning. An assemblage similar to that at *V. sebifera* occurs at the larger congener, *V. surinamensis*, which reaches peak fruit production on Barro Colorado in June and July. The only assemblage differences are the addition of the spider monkey to the *V. surinamensis* assemblage and the change in the functional role of the Masked Tityra from an active dispersal agent to a fruit thief. The tityra is too small to swallow the large

TABLE 5. Assemblage size and dispersal success of neotropical trees visited by birds or birds and mammals.

Tree species	<i>n</i>	Frugivore species (<i>n</i>)	Crop taken (%)	Source
High investment				
<i>Casearia corymbosa</i>	17	14	91	Howe and Vande Kerckhove (1979)
<i>Virola sebifera</i>	14	7	75	This study
<i>Virola surinamensis</i>	19	8	62	Howe (in press)
Low investment				
<i>Guarea glabra</i>	12	19	? ^a	Howe and De Steven (1979)
<i>Tetragastris panamensis</i>	19	23	28 ^b	Howe (1980)

^a Seed traps were not used.

^b Of the 28% removed, a maximum of 4% of the total escaped seedling mortality in fecal clumps of seeds left by mammals.

(up to 5 g) seeds of this species and simply knocks off and consumes the aril, letting the seed fall under the parent tree. These small and efficient assemblages contrast with those using two other trees on Barro Colorado, at which a small reward is associated with both a large assemblage and low dispersal success (Table 5). At *Guarea*, a paper-thin aril attracts numerous migrant and resident birds. *Tetragastris* produces a bulky aril of sugar and water and attracts nearly two dozen species of resident birds and mammals. In both systems, much of the crop ends up under the parent trees. Quantitative estimates of *Tetragastris* dispersal indicate that only 28% of the crop leaves the vicinity of the parent, and less than 4% of the total escapes intense seedling competition under parental crowns or in bouquets of seedlings that emerge from mammal droppings. Quite in contrast to the *Virola* systems, assemblage richness increases linearly with crop size at *Guarea* and *Tetragastris*. In such cases, the "high investment" and "low investment" dichotomy appears real.

Recent ornithological studies indicate, however, that McKey's (1975) framework is sometimes insufficient. Some oily fruits are eaten by a wide variety of birds, and some migrant "opportunists" specialize on certain fruits. Nearly all of the small seeds of *Stemmadenia donnell-smithii* are consumed by at least 22 species of birds in secondary habitats in Costa Rica (McDiarmid et al. 1977). This compound fruit contains an average of 132 seeds imbedded in an oily matrix (64% fat, 11% protein, 17% usable carbohydrate). The assemblage is larger than expected and includes several birds normally considered "generalists." The number of species visiting the plant is probably even greater than that reported, because only a few days were sampled in an 8–10 month fruiting season (cf. Frankie et al. 1974). The relative importance of the various frugivores visiting *Stemmadenia* has yet to be clarified, because records over an entire season may show some visitors to be far more regular than others (e.g. Howe 1977, *contra* Howe and Primack 1975). A well-documented instance of anomalous specialization is reported by Greenberg (in press), who found that two North American warblers (*Dendroica castanea* and *D. pensylvanica*) visited *Miconia* and *Lindackeria* trees far out of proportion to the abundance of the birds in the forest. Both plants produce small fruits in overabundance, and both seem to be visited by insectivorous birds that are expected to feed on fruits opportunistically. *Lindackeria*, in fact, appears to be a "warbler tree."

In short, McKey's (1975) "strategic dichotomy" is a useful guide to field research, but it is not a sufficient conceptual framework. Reward richness does influence

dispersal success and assemblage diversity, but interactions between birds and fruiting trees appear more diverse than the framework predicts.

Have *Virola sebifera* and the birds that eat its fruits coevolved with one another? The likelihood of obligate coevolution is low. The contribution to seed removal by the principal dispersal agent, the Chestnut-mandibled Toucan, is substantial but not overwhelming, and the "selfish" behavior of the bird at particularly fecund trees belies a "finely-tuned" obligate mutualism. Perhaps more important, ranges of the tree and the bird do not overlap in much of South America (Ridgely 1976, Croat 1978). Comparative investigations of other trees show that far greater degrees of local interdependence are facultative; vireos and tityras that disperse *Casearia corymbosa* in Costa Rica resemble each other more in abundance, behavior, and effect than in taxonomic affinity (Howe and Vande Kerckhove 1979). In other cases, comparative evidence may suggest loose coevolution between sets of related species, as has been inferred for plants and insects herbivores (Ehrlich and Raven 1965). Insofar as nutmegs present similar rewards and digestive challenges to birds, and toucans and aracarís provide similar qualities of dispersal to nutmegs, the two groups may have a widespread and evolved interdependence. *Virola surinamensis* is dispersed by toucans in northern South America (Bourne 1974) and Central America (Howe in press), as is *V. koschnyi* in eastern Costa Rica (Howe 1977, pers. obs.). Several birds eat *V. sebifera* fruits, but the most effective regulars are toucans. More comparative evidence is needed, but it appears likely that coevolution normally involves taxonomic categories wider than species and genera. The first level of analysis in a field study should be determination of the extent to which different birds disperse, destroy, or waste seeds and of the nutritional properties of fruits. At this first level, the question of coevolution is moot. A second level of analysis, based on comparative evidence, may point to the presence or absence of proclivities in use and dependence between related species of birds and related species of plants. This second level allows one to infer the absence of coevolution, as indicated in the *Casearia* studies, or the possibility of coevolution between one broad taxonomic group and another, as suggested by the *Virola* studies.

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