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ARILS AS FOOD OF TROPICAL AMERICAN BIRDS

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ABSTRACT.—In Costa Rica, 16 kinds of trees, lianas, and shrubs produce arillate seeds which are eaten by 95 species of birds. These are listed and compared with the birds that feed on the fruiting spikes of *Cecropia* trees and berries of the melastome *Miconia trinervia*.

In the Valley of El General, on the Pacific slope of southern Costa Rica, arillate seeds and berries are most abundant early in the rainy season, from March to June or July, when most resident birds are nesting and northbound migrants are leaving or passing through. The oil-rich arils are a valuable resource for nesting birds, especially honeycreepers and certain woodpeckers, and they sustain the migrants. Vireos are especially fond of arils, and Sulphur-bellied Flycatchers were most numerous when certain arillate seeds were most abundant.

Many species of birds take arils from the same tree or vine without serious competition. However, at certain trees with slowly opening pods, birds vie for the contents while largely neglecting other foods that are readily available.

Although many kinds of fruits eaten by birds may be distinguished morphologically, functionally they fall into two main types, exemplified by the berry and the pod containing arillate seeds. Berries and berrylike fruits are generally indehiscent; no hard or tough integument keeps animals away from the edible tissue. In contrast to a berry, which develops from the ovary, an aril is an outgrowth of the ovule, or of the funicle which attaches it to the placenta. An aril may partly or completely cover the seed. Accordingly, each seed has its own aril, although, when seeds are many and small, their arils may be massed together. Arillate seeds are commonly enclosed in tough or woody pods or capsules, which protect them until mature, at which time the pods split open to expose the seeds prominently. Arils and pods are often of contrasting colors: an aril may be white in a red or yellow pod, or red between yellow valves, the whole conspicuous amid green foliage, easily found by hungry animals, who may disperse the seeds.

Rarely, as in granadillas or maypops (*Passiflora* spp.), arillate seeds are enclosed in a thin, indehiscent pod. Arils of certain passion flowers are also exceptional in being sweetish, although most others that I have tasted have no evident sugar but are often slightly bitter. Many arils are poor in starch but rich in lipids and proteins (McDiarmid et al. 1977). Oils or fats are the chief nonnitrogenous reserves of many seeds, and arils develop from the seeds themselves. Within the soft aril is a seedcoat that is often hard, or somehow able to resist digestion during the short time that the seed remains in the alimentary tract of a small bird.

Wallace (1872) described how the Blue-tailed Imperial Pigeon (*Ducula concinna*) swallows the seed of the nutmeg (*Myristica fragrans*) and, after digesting the aril or mace, casts up the seed uninjured. Several species of large fruit pigeons (*Ducula myristicivora*, *D. luctuosa*, *D. bicolor*, and *D. spilorrhoa*) are sometimes known as "nutmeg pigeons," and the last two are reported to eat wild nutmegs (Goodwin 1967). The Many-colored Fruit Dove (*Ptilinopus perousii*) of Samoa and neighboring islands is also known as the "nutmeg dove." Pijl (1952) recognized the role of arils in the dispersal of seeds of tropical plants by birds, and gave several examples, including species of New World origin. In a long list of fruits eaten by tanagers and honeycreepers on Trinidad, Snow and Snow (1971) included many species with arillate seeds, belonging to the genera *Clusia*, *Sloanea*, *Protium*, *Alchornea*, *Sapium*, *Davilla*, and *Lacistema*, but they did not give special attention to arils.

I present here my own observations on arils and the birds that eat them, amplifying my earlier account (Skutch 1971). Unless otherwise stated, my observations were made at "Los Cusingos," which is situated between Santa Elena and Quizarrá in the Valley of El General, on the Pacific slope of southern Costa Rica, at about 750 m above sea level. These records have been gathered over many years, but more intensively during the last four. For comparison, I list the birds that I have seen eat two other at-

TABLE 1. Some aril-bearing woody plants at Los Cusingos.

Species	Habit	Main fruiting season	Color of capsule	Color of aril	Size in mm and (no. of seeds)[a]
Virola Koschnyi	Big tree	June–Aug.	Brownish	Bright red	23–26 × 15 (1)
Compsoneura Sprucei	Small tree	April–May	Pale yellow	Bright red	28 × 22 (1)
Siparuna nicaraguensis	Straggling shrub	March–June	Pale red	Bright red	5 (many)
Zanthoxylum procerum	Medium tree	Oct.	Green	Black	3 (1)
Protium sp.	Tall tree	Sept.–Oct.	Red	White	20–22 × 13–16 (1–4)
Alchornea latifolia	Tall tree	April	Green	Bright red	6 (2)
Dipterodendron elegans	Tall tree	April–May	Greenish	White	10 (1, rarely 2)
Davilla Kunthii	Liana	April–May	Yellowish brown	White	6 (1, rarely 2)
Doliocarpus dentatus	Liana	April–May	Red	White	9 (2)
Souroubea guianensis	Liana	June–July	Pale green	Bright red	3 (many)
Clusia spp.	Small trees	March–July	Green to dull red	Red to orange	Tiny (many)
Casearia sylvestris	Small tree	March	Green	Orange	2 (1–7)
Casearia arborea	Slender tree	Sept.	Green or brownish	Yellow	2 (1–15)
Lacistema aggregatum	Small tree	April–June	Glossy red	White	6–7 (1)

[a] Size with aril attached; (number of seeds in capsule).

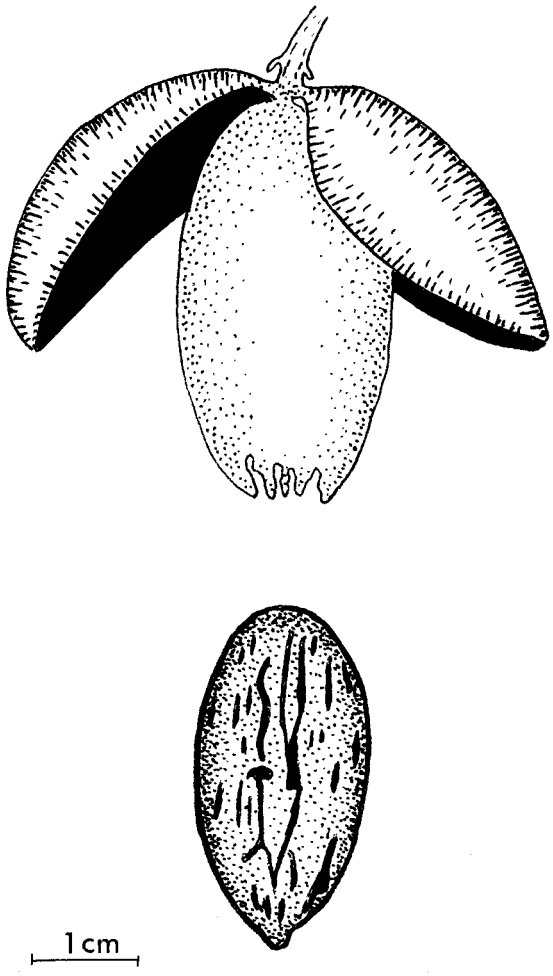

FIGURE 1. *Compsoneura Sprucei.* Above: A seed enclosed in its bright red aril hangs between the two pale yellow valves of the open pod. Below: A seed removed from its aril. It is pale brown, mottled with deep brown.

tractive plant foods, the berries of a melastome and the pistillate spikes of *Cecropia* trees. Lacking means to make quantitative analyses of arils, I tested for starch by the iodine reaction and looked for globules or larger flows of oil in microscopic preparations. Scientific names of birds not given in the text will be found in Table 2.

THE ARILLATE SEEDS AND THE BIRDS THEY ATTRACT

Virola spp. (Myristicaceae). These big trees of humid forests at low altitudes bear ellipsoid capsules that, while still attached to the twigs, split into two valves, between which hangs a single, large arillate seed. The bright red aril divides near the base into narrow or broad, strap-shaped branches, between which the shiny, brown seed is partly

visible (Table 1). The aril contains much oil but little or no starch. To me, it is pleasantly spicy when ripe but painfully hot and peppery when not quite mature. I have seen only fairly large birds swallow these big seeds. In El General, those of *V. Koschnyi* are taken by Blue-diademed Motmots, Rufous Pihas, Masked Tityras, Gray's Thrushes, and White-throated Thrushes. The thrushes try strenuously to eat the whole, aril-covered seed, sometimes failing to do so.

In the Panamá Canal Zone, I have seen Collared Araçaris (*Pteroglossus torquatus*) and Massena Trogons (*Trogon massena*) eat the slightly smaller seeds of *V. panamensis*; Chapman (1929) reported their consumption by the Rufous Motmot (*Baryphthengus ruficapillus*) and Chestnut-mandibled Toucan, and Van Tyne (1929) included them among the fruits eaten by the Keel-billed Toucan. Seeds of *V. surinamensis* are eaten by the Red-billed Toucan (*Ramphastos tucanus*) (Bourne 1975), Capuchinbird or Calfbird (*Perissocephalus tricolor*; Snow 1972) and Bearded Bellbird (*Procnias averano*; Snow 1970).

Compsoneura Sprucei (Myristicaceae). This small, slender tree, up to 12 m high, is widely scattered through the rain forest at Los Cusingos. Its pale yellow pods open by two valves, exposing a single, bright red, arillate seed (Fig. 1). Unlike the aril of the related *Virola,* this aril, about 0.5 mm thick, is almost entire, covering like a sleeve the pale brown seed, mottled with deeper brown (Table 1). The open fruits, hanging beneath slender leafy twigs, are conspicuous. Of all the arils that I have examined, only these contain much starch, as well as a fair amount of oil. They would appear to be most attractive to birds; yet, I have never seen any bird pluck them, probably because each tree bears too few to draw many visitors, and to watch it in dense forest one must stand too near. I have seen Blue-diademed Motmots carry many of the seeds to nestlings, who left some uneaten in their burrow. Placed on a feeder, these nutritious arils were neglected by the birds; and domestic chickens disdained them.

Siparuna nicaraguensis (Monimiaceae). This straggling shrub of lush second-growth thickets bears pale red, strongly lemon-scented globes 17–24 mm in diameter (Fig. 2). At maturity, the thick, fleshy wall splits irregularly and flattens out, exposing numerous small seeds (Table 1). Each shiny gray seed, about 5 mm long, is about half covered with a bright red aril, which has a spicy taste and is rich in oil but contains little or no starch. Ochre-bellied Pipromorphas, Blue Honeycreepers, and Blue-black Grosbeaks (*Cyanocompsa cyanoides*) pluck the seeds one by one from the pale red inner surface of the receptacle.

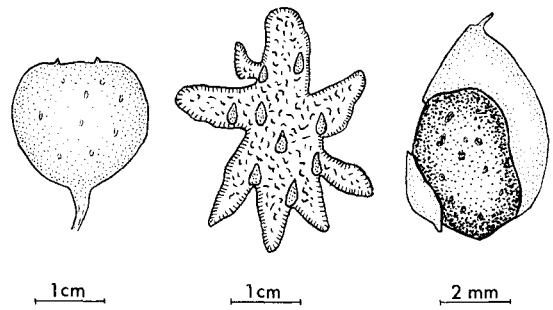

FIGURE 2. *Siparuna nicaraguensis.* Left: A pale red ripe receptable. Center: A receptacle that has opened exposing nine seeds attached to the rough, pale red inner surface. Right: A single shiny gray seed, with a bright red aril covering half its surface, and a small red caruncle at its lower left.

Zanthoxylum spp. (Rutaceae). These trees with thorny trunks bear large panicles of small capsules, which in some species are so covered by projecting oil glands that they resemble miniature strawberries. At maturity each pod splits into two valves, permitting the single black, shiny seed to slip out and stand above it upon the short, thread-like funiculus (Table 1). The thin, oil-rich, black aril, nearly tasteless to me, covers a hard, indigestible seed coat. In October 1936, on the northern side of the Valley of El General at an altitude of about 890 m, I watched a tree as its seeds (3 mm in diameter) were sought by Blue Honeycreepers, who came in groups of three to six or seven individuals. Other birds that ate these seeds included the Scarlet-thighed Dacnis (*Dacnis venusta*), Golden-masked Tanager, and Ochre-bellied Pipromorpha.

At a *Zanthoxylum* tree of another species, growing at about 1,700 m in the Costa Rican mountains, in March 1938, the tiny black seeds were eaten by Gray-capped Flycatchers, Vermilion-crowned Flycatchers, Sulphur-bellied Flycatchers, Ochre-bellied Pipromorphas, Mountain Thrushes (*Turdus plebejus*), and, above all, by Mountain Elaenias (*Elaenia frantzii*). In November 1964, in the vicinity of San José, Costa Rica, at about 1,200 m, *Zanthoxylum* seeds were taken by Crimson-fronted Parakeets (*Aratinga finschi*), wintering Scissor-tailed Flycatchers (*Muscivora forficata*), and wintering Rose-breasted Grosbeaks.

Protium spp. (Burseraceae). The low or tall trees of this genus at Los Cusingos ripen their fruits in the rainy season. Like many forest trees, they tend to flower and fruit in alternate years. The hard, woody capsule may contain as many as four fertile cells, but sometimes the number is reduced to one. Each cell opens by one valve, exposing its single pure white seed, which contrasts with the dull red exterior and bright red interior of the pod, to the apex of which it clings (Table 1). The thick, pasty, white aril is tasteless or slightly sweetish, and it contains little if any starch, and no oil that I could detect. The ripe fruits have a strong, not unpleasant odor.

Among the birds that I have seen eat these arils (Table 2), Fiery-billed Araçaris and Blue-diademed Motmots swallow them whole, but smaller birds find them too big. Boat-billed Flycatchers, Rufous Pihas, Gray-headed Tanagers, and Buff-throated Saltators pluck a seed and carry it away in the bill. Still smaller birds, including Green Honeycreepers, Silver-throated Tanagers, Speckled Tanagers, and Bay-headed Tanagers, peck pieces from an aril while the seed remains attached to its pod; accordingly, they are not disseminators. Scarlet-rumped Tanagers sometimes peck pieces from an attached seed and sometimes carry a whole seed away. Fallen seeds attract agoutis (*Dasyprocta punctata*), who sometimes gnaw out the embryo after they eat the aril.

In Trinidad, Snow and Snow (1971) saw 10 species of tanagers and honeycreepers eat seeds of *P. heptaphyllum*, and Snow (1962a, b) watched two kinds of manakins eat them. Capuchinbirds eat seeds of *P. neglectum* and *P. Schomburgkianum* (Snow 1972), Keel-billed Toucans those of *P. sessiliflorum* (Van Tyne 1929), and Red-billed Toucans those of *P. crenatum* (Bourne 1975).

Alchornea latifolia (Euphorbiaceae). This broad-leaved tree grows in old forest, where it may attain a height of 27 m, and in clearings, where it usually remains much lower. The fruits are borne in panicles that hang below the lateral branches and may become 30 to 38 cm long. When ripe, usually in April but sometimes in November, each of the green pods splits into four valves, conspicuously exposing twin seeds in bright red arils (Table 1). Among the most numerous visitors to these trees (Table 2) are wintering Yellow-throated and Philadelphia vireos and, in April, migrating Swainson's Thrushes. These and most of the other birds listed in Table 2 swallow seeds whole, but a few have special methods. Chestnut-sided Warblers nibble into the arils. Rose-breasted Grosbeaks break the seeds in their thick bills.

Alchornea costaricensis (Euphorbiaceae). A medium-sized tree of this smaller-leaved species grew beside a stream in an open part of the forest at "La Selva," in the Caribbean lowlands of northern Costa Rica. In early June 1967, it ripened red arillate seeds similar to those of the preceding species. The 24 kinds of birds that I saw eating them in a few hours of watching are listed in Table 2. In Trinidad, Black-and-White Manakins (*Manacus manacus*) and Golden-headed Manakins (*Pipra erythrocephala*) take seeds of *A. triplinervia* (Snow 1962a, b).

Sapium sp. (Euphorbiaceae). In early May 1972, a tall tree bore pea-sized green pods in slender spikes. Migrating Red-eyed Vireos searched until they found an opening pod, from which they extracted the small seed covered by a red aril. Yellow-green Vireos, Blue Honeycreepers, and a single male Scarlet-thighed Dacnis also ate these seeds. Golden-headed Manakins take seeds of *S. aucuparium* (Snow 1962b).

Dipterodendron elegans (Sapindaceae). This tall tree of forest and clearings bears drooping panicles of pods that are irregular globes, about 2 cm long by nearly as broad. Although two-celled, a pod rarely contains more than one good seed, which is ellipsoid and about 1 cm long. At maturity, the pod splits into two thick, fleshy valves, exposing the seed (Table 1). The basal two thirds of each shiny black seed is surrounded, as by a sleeve, with a thin white aril. Rich in oil but poor in starch, these arils are nearly tasteless; such flavor as I could detect was slightly unpleasant.

The seeds are highly attractive to birds, most of whom feed in the early morning. These birds spent much effort trying to extract seeds from closed or barely open pods, and supplanting each other at promising situations. Meanwhile, bananas spread for them at a feeder less than 30 m away remained hardly touched. Likewise, these birds seldom ate the more easily gathered ripe berries of several kinds of arborescent melastomes growing nearby. Probably the birds were drawn not by the quantity of nourishment that the thin arils contained, but by some special substance or enticing taste undetectable by me.

The birds differed in the ways that they procured the *Dipterodendron* seeds. Of the 31 species that ate these seeds (Table 2),

TABLE 2. Arillate seeds and fruits eaten by Central American birds.[1]

Species	*Protium* spp.	*Alchornea latifolia*	*A. costaricensis*	*Dipterodendron elegans*	*Davilla Kunthii*	*Souroubea guianensis*	*Clusia* spp.	*Casearia sylvestris*	*Lacistema aggregatum*	*Cecropia* spp.	*Miconia trinervia*
Gray-headed Chachalaca											
Ortalis cinereiceps										+	
Short-billed Pigeon											
Columba nigrirostris										+	
White-crowned Parrot											
Pionus senilis				+							
Black-throated Trogon											
Trogon rufus			+								
Violaceous Trogon											
Trogon violaceus										+	
Citreoline Trogon											
Trogon citreolus										+	
Baird's Trogon											
Trogon bairdi										+	
Blue-diademed Motmot											
Momotus momota	+			+							
Fiery-billed Araçari											
Pteroglossus frantzii	+			+		+			+	+	
Keel-billed Toucan											
Ramphastos sulfuratus			+							+	
Chestnut-mandibled Toucan											
Ramphastos swainsonii										+	
Golden-naped Woodpecker											
Melanerpes chrysauchen				++	+		++			+	+
Black-cheeked Woodpecker											
Melanerpes pucherani			++								
Red-crowned Woodpecker											
Melanerpes rubricapillus		+		++		+	++			+	
Chestnut-colored Woodpecker											
Celeus castaneus			+								
Lineated Woodpecker											
Dryocopus lineatus							+				
Blue-crowned Manakin											
Pipra coronata						+		+			+
Red-capped Manakin											
Pipra mentalis			+					+	+		++
White-ruffed Manakin											
Corapipo altera											+
Orange-collared Manakin											
Manacus aurantiacus		+			+		+	+	+		+
White-collared Manakin											
Manacus candei			+								
Bright-rumped Attila											
Attila spadiceus			+	+	+						
Rufous Mourner											
Rhytipterna holerythra			+								
Rufous Piha											
Lipaugus unirufus	+										+
White-winged Becard											
Pachyramphus polychopterus				+							
Masked Tityra											
Tityra semifasciata			++	++							
Black-crowned Tityra											
Tityra inquisitor			+	+							
Eastern Kingbird											
Tyrannus tyrannus				+						+	
Tropical Kingbird											
Tyrannus melancholicus		+		++	+						
Piratic Flycatcher											
Legatus leucophaius		+		+	+					+	+
Sulphur-bellied Flycatcher											
Myiodynastes luteiventris				++	+						

TABLE 2. Continued.

Species	*Protium* spp.	*Alchornea latifolia*	*A. costaricensis*	*Dipterodendron elegans*	*Davilla Kunthii*	*Sourouboea guianensis*	*Clusia* spp.	*Casearia sylvestris*	*Lacistema aggregatum*	*Cecropia* spp.	*Miconia trinervia*
Streaked Flycatcher											
Myiodynastes maculatus		+									
Boat-billed Flycatcher											
Megarhynchus pitangua	+	+	+	+							+
Vermilion-crowned Flycatcher											
Myiozetetes similis				++	+		+	+	+		+
Gray-capped Flycatcher											
Myiozetetes granadensis		+	+	++			+			+	+
Wied's Crested Flycatcher											
Myiarchus tyrannulus				+							
Olivaceous Flycatcher											
Myiarchus tuberculifer								+			
Yellow-bellied Flycatcher											
Empidonax flaviventris								+			
Yellow-bellied Elaenia											
Elaenia flavogaster		+							++		+
Lesser Elaenia											
Elaenia chiriquensis		+			+			+	+		++
Greenish Elaenia											
Myiopagis viridicata					+			+			
Ochre-bellied Pipromorpha											
Pipromorpha oleaginea		+	++		+		++	++			
Brown Jay											
Psilorhinus morio										+	
Gray's Thrush											
Turdus grayi		+		++	+	+	++		+	+	++
White-throated Thrush											
Turdus assimilis											++
Swainson's Thrush											
Catharus ustulatus		++		+					++		++
Orange-billed Nightingale-Thrush											
Catharus aurantiirostris							+				+
Yellow-throated Vireo											
Vireo flavifrons		++						+			+
Red-eyed Vireo											
Vireo olivaceus		+		++	++		++	+	+		+
Yellow-green Vireo											
Vireo flavoviridis		+		++	+		++	+	+		+
Philadelphia Vireo											
Vireo philadelphicus		++			++			++			
Scrub Greenlet											
Hylophilus flavipes							+				
Gray-headed Greenlet											
Hylophilus decurtatus		+									
Green Honeycreeper											
Chlorophanes spiza	+		++	+		++	++	++		+	++
Blue Honeycreeper											
Cyanerpes cyaneus		+		++		++	++	+		+	++
Shining Honeycreeper											
Cyanerpes lucidus			++	+		++	++	++			+
Blue Dacnis											
Dacnis cayana			+	+		++	+	+			+
Bananaquit											
Coereba flaveola									++		
Tennessee Warbler											
Vermivora peregrina		+								+	++
Chestnut-sided Warbler											
Dendroica pensylvanica		+						+			++
Bay-breasted Warbler											
Dendroica castanea											+

TABLE 2. Continued.

Species	*Protium* spp.	*Alchornea latifolia*	*A. costaricensis*	*Dipterodendron elegans*	*Davilla Kunthii*	*Souroubea guianensis*	*Clusia* spp.	*Casearia sylvestris*	*Lacistema aggregatum*	*Cecropia* spp.	*Miconia trinervia*
Mourning Warbler											
Oporornis philadelphia									+		
Chestnut-headed Oropendola											
Psarocolius wagleri			+								
Montezuma Oropendola											
Psarocolius montezuma			+							+	
Scarlet-rumped Cacique											
Cacicus uropygialis			+								
Baltimore Oriole											
Icterus g. galbula		+		+			+	+		+	
Tawny-bellied Euphonia											
Euphonia imitans	+					+					
Speckled Tanager											
Tangara guttata	+	+		++		++	+	+			++
Silver-throated Tanager											
Tangara icterocephala	+					++	+			+	++
Golden-masked Tanager											
Tangara larvata		+	+			+	+	+		+	++
Bay-headed Tanager											
Tangara gyrola	+					++	+	+	+	+	++
Blue Tanager											
Thraupis episcopus						+	+			+	++
Palm Tanager											
Thraupis palmarum		+	+			+	+			+	+
Scarlet-rumped Tanager											
Ramphocelus passerinii	+	+				++	+		++	+	++
Summer Tanager											
Piranga rubra		+						+			+
Scarlet Tanager											
Piranga olivacea				+							
Red-crowned Ant-Tanager											
Habia rubica											+
White-shouldered Tanager											
Tachyphonus luctuosus								++			
Gray-headed Tanager											
Eucometis penicillata	+										+
Dusky-faced Tanager											
Mitrospingus cassinii			+								
Buff-throated Saltator											
Saltator maximus	+	+	+	++		+	++	+	++	+	++
Streaked Saltator											
Saltator albicollis		+		++		+	+	++	++		+
Black-faced Grosbeak											
Caryothraustes poliogaster			+								
Rose-breasted Grosbeak											
Pheucticus ludovicianus		+		++				++			
Yellow-faced Grassquit											
Tiaris olivacea											+
Variable Seedeater											
Sporophila americana										+	++
Black-striped Sparrow											
Arremonops conirostris									+		+
TOTALS 87	12	29	24	31	14	18	26	27	17	28	41

[1] Includes only plants the seeds or fruits of which were eaten by 12 or more species of birds. Other records are given in the text. A double plus (++) indicates very frequent feeding. See Table 1 for names of plants.

Fiery-billed Aracaris gathered them most easily. Unlike the smaller birds, they could neither cling to the thin, drooping panicles nor pluck the seeds in flight, but, while perching on fairly stout twigs, they reached far out or down and seized a pod in the tip of the great bill, thereby demonstrating the utility of its length. Often they forced a pod open, then extracted the seed and threw it back into the throat with an upward toss of

the head. They ate so many in a short while that they never stayed long in the tree. White-crowned Parrots could also remove a seed from a closed pod, which they held in a foot. Probably, in the manner of parrots, which are poor disseminators, they preferred the embryos to the arils. Blue-diademed Motmots repeatedly tried without success to open pods.

The two kinds of woodpeckers clung back-downward beneath a pod while trying to open it. Often they failed, but when successful they swallowed the seed whole. With their slender bills, vireos, honeycreepers, and Gray's Thrushes often extracted fragments of arils from slightly open pods. Sometimes as many as six thrushes were simultaneously present. When a vireo could obtain a whole seed, it swallowed it, later regurgitating the seed divested of its aril. The two species of tityras and most of the flycatchers plucked the seeds either while hovering or perching beside the pods, and swallowed them whole. When a saltator of either species secured a seed, it laid it on a horizontal branch while it removed and ate the aril, then dropped the seed, much as it did with the *Protium* seeds. Rose-breasted Grosbeaks carried their seeds into the neighboring woods. Strangely, the abundant tanagers, except for the Speckled Tanager, took little interest in the *Dipterodendron* seeds, probably because, with bills that were neither long nor strong, and little ability to hover, they could not compete successfully with the other birds. Speckled Tanagers swallowed whole seeds, and a male gave one to his mate.

The great attraction of a particular *Dipterodendron* tree was evident in its effect on migrants. In 1975, when it fruited profusely, one of the several Rose-breasted Grosbeaks that frequented it, a female, continued to visit it until the exceptionally late date of 29 April. Sulphur-bellied Flycatchers, usually rare spring transients here, were never more abundant, and became exceptionally adept at snatching seeds in flight, as did the Piratic Flycatcher and White-winged Becard. Sometimes five or six Sulphur-bellied Flycatchers were present together; some remained until 5 May, when the fruits were almost exhausted. In 1976, when this tree failed to flower and set fruit, I saw not a single Sulphur-bellied Flycatcher on the farm. In 1977, when the tree fruited but the diseased arils were shriveled and blackish, I noticed very few of these flycatchers, as likewise in 1978, when again the tree did not flower.

Davilla Kunthii (Dilleniaceae). This liana is abundant at Los Cusingos, where it grows in tall second-growth thickets, at the forest's edge, and on riverside trees. Masses of fragrant, evanescent, golden flowers adorn it at the height of the dry season (Skutch 1971). These are followed by arillate seeds that ripen in April and May (Fig. 3). Each flower produces a single, tiny, black seed, rarely two, surrounded by a white aril containing much oil but little or no starch (Table 1). Of the 14 species of birds that I have seen eat these seeds (Table 2), the most frequent were migrating Red-eyed and Philadelphia vireos, followed by resident Yellow-green Vireos and Tropical Kingbirds.

In Trinidad, Snow and Snow (1971) saw three species of tanagers eat seeds of *D. aspera*, and D. Snow (1962b) found Golden-headed Manakins taking them.

Doliocarpus dentatus (Dilleniaceae). In April and May, this vigorous liana displays masses of vivid red pods high in trees of primary and second-growth woodland. The globose pods, 10-14 mm in diameter, open by hemispheric valves. Each pod contains two flattish, hard, black seeds, enclosed in soft, waxy-white, slightly sweetish arils (Table 1). The vines often form such dense tangles, high in trees, that it is difficult to see the birds who enter them. Of those that I have detected, migrating Swainson's Thrushes were the most frequent. Others were Orange-collared Manakins, Orange-billed Nightingale-Thrushes, Scarlet-rumped Tanagers, Buff-throated Saltators, and the only Gray Catbird (*Dumetella carolinensis*) that I have seen in El General in over 40 years. It spent much time in a vine tangle, swallowing seeds whole. In Trinidad, Snow and Snow (1971) saw Blue and Palm tanagers, and D. Snow (1962a, b) saw Black-and-White and Golden-headed manakins eat seeds of this same species.

Souroubea guianensis (Marcgraviaceae). This glossy-leaved, epiphytic vine burdens trees in forest and clearings. The depressed-globose fruits, up to 22 mm in diameter, are pale green, finely sprinkled with minute brown scales. In June and July, these pods dehisce by five hard, fleshy valves, 7–8 mm thick, which fall away, often when touched by a bird, exposing the bright red arillate seeds (Table 1). Arils grow not only from the developed seeds in a pod but also from the many abortive seeds, and all are tangled together in a coherent mass (10 mm in diameter), in which the seeds are wholly or partly embedded. They contain no starch but some oil or fat. The 18 species of birds

that I have seen eat this food are listed is Table 2. Unlike some other arils, these are as attractive to tanagers as to honeycreepers, doubtless because their complete exposure in large masses makes them easy for short-billed birds to gather.

In the Costa Rican highlands, the minute seeds of *Marcgravia rectiflora* are borne on and in a scarlet mass of soft, juicy tissue that is sweetish and pleasant to eat. The structure resembles the seed mass of *Souroubea* but it may be the placenta rather than a cluster of arils. It was sought by Prong-billed Barbets (*Semnornis frantzii*), Blue-throated Toucanets (*Aulacorhynchus prasinus*), and other frugivorous birds.

Clusia spp. (Guttiferae). Clusias are epiphytic shrubs or small trees that usually grow on trees or rocks but sometimes stand on the ground, after the decay of the trunk that originally supported them. In wet Costa Rican forests they occur in a bewildering variety of forms, whose fruits range in size from that of an olive to that of an apple. At maturity, these green or red-tinted pods dehisce by from four to a dozen valves (according to the species) that spread out like the petals of a flower (Fig. 4). Along the inner side of each valve is an elongate mass of lobed, coherent arils, in which the small seeds are embedded (Table 1). These fringelike arils contain a single large oil globule in many of their cells but have little or no starch.

Clusias with many small or middle-sized fruits, from which the seeds are more easily removed, attracted more of the 26 species of birds listed in Table 2 than did the species with the largest but fewest fruits, *C. rosea*, at which competition for seeds was keenest. Here, where the birds waited for the valves to separate just far enough to extract seeds through a chink, those with slender, sharp bills had the advantage over short-billed tanagers and finches, which rarely tried to compete with them. Most successful in procuring seeds were the Golden-naped and Red-crowned woodpeckers, who could cling back-downward beneath a pod and reach them through a tiny cleft. Slender-billed honeycreepers also clung inverted, or hovered beneath a fruit long enough to remove arils.

In the competition to procure this enticing food the moment it became available at a particular *C. rosea* tree, a hierarchy developed. Dominant over all others were the Golden-naped Woodpeckers, who could displace even Red-crowned Woodpeckers from a fruit. Both kinds of woodpeckers took

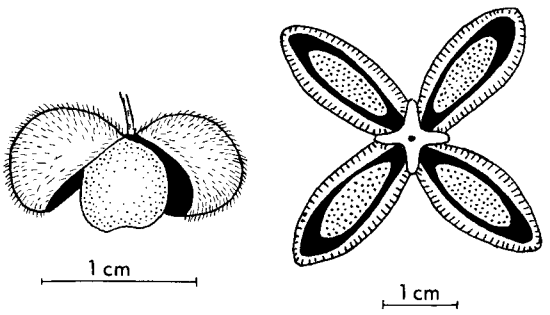

FIGURE 3. (Left) *Davilla Kunthii*. A single seed, enclosed in a pure white aril, is exposed between the two yellowish brown inner sepals, which serve as a pod.

FIGURE 4. (Right) *Clusia* sp. An open pod, exposing a mass of tiny seeds enclosed in red arils (stippled), lying above each of the four valves, which are externally green. In the center, the four-armed axis of the fruit.

precedence over the honeycreepers, of which the Green could displace the Shining and the latter could displace the Blue. Although Blue Honeycreepers were the most numerous of the visitors, they were clearly subordinate to all the others. They sometimes tried to intercept arils that a parent Golden-naped Woodpecker was passing to well-grown young but I never saw this ruse succeed. Sometimes a bird displaced another of its own kind from an opening pod; even members of the same closely knit Golden-naped Woodpecker family supplanted each other with mild pecks. But I saw only one brief, inconsequential fight, between a female Shining Honeycreeper and a female Blue Honeycreeper. Near this tree a feeder offered bananas, which all these honeycreepers and woodpeckers freely eat. Clearly, these birds contended for the arils because they liked them, not because they lacked food.

In Trinidad, Snow and Snow (1971) recorded four kinds of honeycreepers, but no tanagers, eating the seeds of several species of *Clusia*.

Casearia sylvestris (Flacourtiaceae). In mid-March 1977, I watched a slender tree, 15 m high, that grew in tall second-growth woods and was fruiting profusely. Each pod, 4.5 mm in diameter, opened by three valves to expose hard, shiny, brown seeds covered by thin orange arils (Table 1). Rich in oil and lacking starch, the arils contained numerous minute chromoplasts, apparently of carotene. I found them tasteless, but they were so attractive to birds that on four mornings I saw them taken by the 27 species listed in Table 2. The most frequent were Shin-

ing Honeycreepers, Philadelphia Vireos, and Ochre-bellied Pipromorphas.

Casearia arborea (Flacourtiaceae). This slender tree, up to 18 m high, grows both in old forest and young second growth. I found it fruiting in September 1976 but not during 1977. The green or brownish pods, slightly larger than those of *C. sylvestris*, measure 5–6 mm in diameter and contain 1 to 15 blackish, shining seeds (Table 1). Attached to the side of each is an aril with irregular lobes that contract into fine, crooked filaments, which become entangled with the filaments of adjacent seeds to form a loose, yellow mass about 4 mm in diameter. Tasteless to me, these arils contain some starch and much oil. They were eaten by five resident species (Orange-collared Manakin, Blue-crowned Manakin, Gray-headed Greenlet, White-shouldered Tanager, and Buff-throated Saltator) and four recently arrived migrants (Yellow-bellied Flycatcher, Red-eyed Vireo, Blackburnian Warbler [*Dendroica fusca*], and Chestnut-sided Warbler). With the exception of the last-mentioned, the migrants came to eat the arils more often than the residents.

In the lowlands of northeastern Costa Rica, Howe and Primack (1975) saw five species of birds eat the arillate seeds of *C. nitida*.

Lacistema aggregatum (Flacourtiaceae [Burger 1977]). These slender, glossy-leaved trees, up to 16 m high, grow in wet forests as well as in second growth and hedgerows. They tend to flower and fruit most abundantly in alternate years, ripening large numbers of glossy, red, globose fruits about 8 mm in diameter. Each capsule opens by two valves, exposing a single, thin, white aril that surrounds a hard, smooth, brown seed (Table 1). The aril contains no starch, but many of its cells are packed with granules that appear to be lipid.

The 17 species of birds (Table 2) fed in various ways. Orange-collared and Red-capped manakins plucked seeds in flight and swallowed them whole. Most of the others gathered the seeds while perched; even Yellow-bellied Elaenias only exceptionally seized one in flight. Araçaris, flycatchers, thrushes, and vireos swallowed whole seeds. Saltators and tanagers plucked an arillate seed, mandibulated it, and dropped something white. Often, through binoculars, it appeared that they discarded the aril and swallowed the hard seed. However, from the ground I picked up many freshly fallen seeds with much of the arils removed, but enough remaining to make the seeds appear white. Evidently, these thick-billed birds ate part of the aril but did not succeed in removing all from the seed coat. Neither these birds nor Bananaquits disseminated the seeds. The latter, a very frequent attendant, pressed out juice or perhaps ate very small fragments, from arils of seeds that they did not detach. Domestic chickens ate fallen seeds still in their arils, and I strongly suspect that White-fronted Doves (*Leptotila verreauxi*) and Ruddy Quail-Doves (*Geotrygon montana*) did likewise.

In Trinidad, Snow and Snow (1971) saw five species of tanagers, the Green Honeycreeper, and the Blue Dacnis eat seeds of *L. aggregatum*. Surprisingly, although the same two honeycreepers occur here, I did not see either eat *Lacistema*.

Passiflora sp. (Passifloraceae). The only bird that I have seen eat a granadilla is the Brown Jay, which, years ago in Guatemala, I watched peck a hole in the side of a green hanging fruit and remove large billfuls of the seeds enclosed in soft arils.

BIRDS ATTRACTED TO *CECROPIA* AND *MICONIA*

Cecropia spp. (Moraceae). Among the important food plants of tropical American birds are the cecropias or guarumos, tall, spindly trees that spring up in newly cleared lands in humid regions, and in openings in the forest made by landslides or the fall of great trees (Skutch 1977). Their finger-thick, long or short, green pistillate spikes, covered with innumerable minute achenes, are sought by birds ranging from diminutive honeycreepers and seedeaters to big toucans and chachalacas, especially in the dry season, when more succulent fruits are often scarce. The smaller birds cling to the spikes and consume them from the apex upward. Most of the 28 species listed in Table 2 as eating these spikes did so in El General, but a few were seen in other parts of Central America. Eisenmann (1961) saw 22 species of birds eat cecropia fruits in Panamá; and Snow and Snow (1971) watched 10 kinds of tanagers and honeycreepers take them in Trinidad. D. Snow (1962a) also saw Black-and-White Manakins eat them.

Miconia trinervia (Melastomaceae). In the Valley of El General, as in other humid regions of tropical America, the melastome family is an important source of food for small frugivorous birds, apparently supplying more nourishment than any other family of plants. No genus of this large and varied family is more generous to birds than *Mi-*

conia, whose multitudinous species include shrubs and low or tall trees of woodland and clearings, although never, in my experience, massive giants of the rain forest. Some of the miconias that yield most food for birds flower synchronously, all the shrubs or trees in a locality concentrating their anthesis within the same one or two days. They become covered with fragrant masses of tiny, white, short-lived, nectarless flowers that swarm with pollen-gathering, stingless bees and other small insects. After some weeks or months, the same plants may bloom again, also synchronously. Nevertheless, the ripening of fruits from the same flowering is not simultaneous but spread over several weeks, thus providing a continuing source of berries for birds.

Among the abundant melastomes at Los Cusingos is *Miconia trinervia* (*M. scorpioides* in Standley 1938), a small tree with scorpioid inflorescences that in March or April yields large crops of deep purple or black berries, about 6 mm in diameter. In contrast to arils, these berries are slightly sweetish but contain little, if any, oil or starch. The 41 species of birds that I have seen eat them (Table 2) proceed differently. Nearly all pluck the berries while perching; even the flycatchers and Rufous Pihas only exceptionally snatch one in flight, which only the manakins do consistently. Most birds swallow their berries whole, although the larger tanagers and finches mandibulate them, often dropping the skins. Tiny Variable Seedeaters, which are among the most constant attendants at these miconia trees, nibble at attached berries instead of swallowing them whole, as do Yellow-faced Grassquits, who come more seldom. With their sharp bills, Tennessee Warblers pierce the skin and extract juice, or possibly fragments of flesh, from berries that remain attached. Chestnut-sided Warblers, who come frequently, have a different method; they pluck and mandibulate a berry before swallowing it.

Although birds take many other kinds of melastome berries, those listed in Table 2 as eating fruits of *M. trinervia* include all the species that I have recently seen eat any kind of melastome fruit, except the Philadelphia Vireo and the Orange-chinned Parakeet (*Brotogeris jugularis*). In Guatemala, Land (1963) saw 20 species eat berries of *M. trinervia*. In Trinidad, Snow and Snow (1971) found 14 species of tanagers and honeycreepers taking berries of *Miconia*. One, the Silver-beaked Tanager, (*Ramphocelus carbo*) ate berries of no less than 11 species of *Miconia*. Fifteen species of *Miconia* contributed to the diet of the Black-and-White Manakin (Snow 1962a).

CONCLUSIONS

From Table 2 it is evident that most, if not all, of the birds recorded as eating arillate seeds also take fruits (as different as melastome berries and the achenes of *Cecropia*) and insects. I know of no birds that eat only arils. Arillate seeds are most plentiful from March to June; although some kinds, including those of *Virola Koschnyi*, *Protium* spp., *Zanthoxylum*, and *Casearia arborea* are available later in the year. In certain years, some of the several species of *Clusia* open their pods late, although they do so most freely in April, May, and June. This is also the period when berries are most abundant. In April 1978, seven kinds of plants, including four arboreal or arborescent species of *Miconia*, the vine *Tournefortia glabra*, a rubiaceous shrub with cobalt-blue berries, and *Lacistema aggregatum*, all growing spontaneously within 100 m of our house, were competing for birds to eat their fruits and disseminate their seeds. Moreover, mistletoes (Loranthaceae) were ripening berries attractive to euphonias and the Paltry Tyrannulet (*Tyranniscus vilissimus*). This abundance of fruits early in the rainy season, together with multitudes of insects on fresh foliage, coincides with the peak of nesting, from March to June or July (Skutch 1950, 1976). As the rainy season progresses to its climax in September–November, food becomes much scarcer and very few birds breed.

Arils help nesting birds to nourish their young. Above all, the honeycreepers, including the Green, the Blue, the Shining, and the Blue Dacnis, fly to their nests with many conspicuous billfuls of the red or orange arillate seeds of *Clusia*. I have seen Golden-naped Woodpeckers so stuff their nestlings with this food that the young could take no more. The oil-rich arils, so plentiful when migrants are passing northward, must help these birds to fatten for their long flights. No birds seem more eager for them than Philadelphia Vireos preparing to leave after wintering in El General, and Red-eyed Vireos, Swainson's Thrushes, and Sulphur-bellied Flycatchers passing through the valley after wintering farther south. Doubtless, it was no accident that the only Gray Catbird that I have seen here was eating arils of *Doliocarpus*; and transient Sulphur-bellied Flycatchers were most numerous when *Dipterodendron* seeds were most

abundant. Even a raptor, the Swallow-tailed Kite (*Elanoides forficatus*) eats arils—those of *Matayba oppositifolia* (Sapindaceae) (Buskirk and Lechner 1978).

Only at the *Dipterodendron* tree, and at the large-fruited *Clusia rosea*, did I notice much competition for food. The thick pods of these trees opened slowly and the birds seemed impatient for the contents. Even here, no bird tried to exclude others from the trees' narrow, rather open crowns; what I witnessed was simply supplanting at particular pods, with almost never any physical contact between two individuals. At other kinds of trees with an abundance of smaller fruits, the visitors of many kinds, whatever their size, ate with little interference. Likewise, McDiarmid et al. (1977) stated that interspecific displacements were rare at fruits of *Stemmadenia Donnell-Smithii*.

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