# Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by Birds

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## ABSTRACT

The dispersal ecology of *Stemmadenia donnell-smithii* was studied in the tropical dry forest zone of northwestern Costa Rica. Fruit was most abundant late in the dry season and was eaten by 22 species of birds, many of which are primarily insectivorous. Stomach-content analyses substantiated our observations. Total crop size per tree and rate of fruit opening were greatest in pasture-edge trees and smallest in forest trees. Rates and percent of seed germination were highest for seeds from which the surrounding aril was removed, scarified seeds, and seeds which had passed through the digestive tract of a bird. The mean compositions of the fruit tissues were, aril: 7.9% ash, 63.9% lipid, 10.9% protein, 16.8% carbohydrate; seed: 3.4% ash, 31.4% lipid, 10.9% protein, 54.2% carbohydrate; husk: 17.0% ash, 24.0% lipid, 11.2% protein, 47.6% carbohydrate.

The foraging behavior of birds taking *S. donnell-smithii* included hovering, and perching and reaching. Rates of pulp utilization in each habitat were relatively constant; all pulp plus seeds were removed in only a few hours. Calculations of daily energy expenditures suggest that *Stemmadenia* may provide up to 25 percent of the total energy requirement of individuals of several bird species. Interspecific displacements of birds at fruit were rare.

Characteristics of *S. donnell-smithii* that enhance dispersal include peak fruit availability in dry season, slow rate of opening, seed protection until maturation by husk, bright color of arils, relative accessibility and ease of separation of seed from husk and aril from seed, and high nutritive value of aril. Energetically the plant expends the most calories for protection (husk), followed by expenditures for germination (seed) and dispersal (aril). However, on a calorie-per-gram, ash-free, dry-weight basis, the plant puts the greatest amount of energy into aril for dispersal, followed by seed for germination, and then husk for protection. Percent nutrient composition and caloric content of seeds and husk were relatively uniform, whereas lipid, protein, and caloric content of aril tissue varied among samples from different fruits, habitats, and years. This variation may be important in allowing the plant to maintain protection and seed quality while maximizing seed production under varying environmental conditions.

THE NATURE OF PLANT-ANIMAL INTERACTIONS has been the focus of extensive work for hundreds of years. Many studies on the mutualistic aspects of plant-animal interactions (Gilbert and Raven 1975) emphasize the intricate associations of plants and animals in pollination systems (e.g., Faegri and Pijl 1971). Ecological studies on the interactions between plants and animals with regard to seed dispersal are scarce (McKey 1975). Among vertebrates, birds are perhaps most commonly associated with seed dispersal (Pijl 1972). Their fruit-eating habits are well known (e.g., Lein 1972, Brown 1974), and some tropical species have evolved obligate frugivory (Morton 1973). Although several studies have described the utilization of fruit by birds at various tropical localities (e.g., Land 1963, Willis 1966, Leck 1969, 1972, Haverschmidt 1971), little is known about the energetics of the relationships between birds and the plants whose seeds they disperse, or about the mechanisms used by plants to promote seed dispersal.

This study considers the interaction between *Stemmadenia donnell-smithii* (Rose) Woodson and the several species of birds which utilize its fruit. In the dry region of northwestern Costa Rica, the large conspicuous fruits of *Stemmadenia* are fed upon by birds for several months during the dry season and early wet season. We were able to determine rates of utilization of fruits by birds and the caloric value of fruit produced by the plant. We also discuss the peculiar structure of the fruit in the context of adaptations for seed dispersal. Finally, we comment on the relative "quality" of seed dispersal in *Stemmadenia* and speculate on its importance to the community of dispersal agents.

## METHODS AND MATERIALS

Most observations were made between 18 and 26 April 1971 during the Organization for Tropical Studies Course: Habitat Exploitation and Diversity: An Ecological Approach with Vertebrates. Additional data were collected in 1972 and 1973 as time permitted.

Germination experiments were conducted in May 1971 as follows: scarified seeds were nicked at one end with a scalpel; acid-treated seeds were placed in sulfuric acid (pH 2) for 3 minutes. Seeds were stored in a cool, dark place between layers of moist paper towel in plastic boxes, the sides of which were perforated to allow air circulation.

In June 1972 fruits collected at random from many of the trees observed in 1971 were weighed and measured. Five were separated into husk, aril, and seed components in the field and dried. Four others were taped shut, frozen, and returned to Florida where components were separated in the laboratory. The components of four other fruits (two from a pasture tree, 23 May; one each from two forest edge trees, 20 and 21 June) were separated in the field in 1973. All samples were vacuum desiccated over concentrated sulfuric acid in the laboratory. Dried material was ground in a Wiley Mill before analyzing organic components.

Ash content was determined by incinerating subsamples in a muffle furnace for four hours at 500°C. The total lipid content of the husk, aril, and seed was determined by chloroform-methanol extraction (Freeman *et al.* 1957). The percent total protein was determined using Vasu's (1965) modification of Lowry *et al.'s* (1951) colorimetric method with alanine as the standard. Soluble carbohydrate was determined by using the phenol-sulfuric acid method of Dubois *et al.* (1956) with glycogen as the standard. Structural carbohydrates were determined by subtraction (Merrill and Watt 1973). The ash-free dry weights of each component were converted into caloric units using: 9.45 kcal/ash-free g lipid, 5.65 kcal/ash-free g protein, and 4.10 kcal/ash-free g carbohydrate (Paine 1971).

Voucher specimens of *S. donnell-smithii* are deposited in the University of South Florida Herbarium, Tampa. In this report, the term pulp includes both seeds and arils. One pulp unit consists of one seed plus its aril. Fruit refers to the entire reproductive structure, including the husk, seeds, and arils.

STUDY AREA.—Field observations were made near the Río Higuerón, 1.6 km SE of Estación Experimental Enrique Jiménez Nuñez (Finca Jiménez) agricultural station located 12 km SW Cañas, Guanacaste Province, Costa Rica. The general area, sometimes referred to as Taboga, was described by Orians and Paulson (1969) and Janzen (1973a). The study site lies in the Tropical Dry Forest (Tosi 1969) and has a seasonal climate. Much of the region surrounding Finca Jiménez is devoted to cattle production, sugar cane, and other agricultural development. Remnants of dry forest are still found on the hills behind the station.

Rainfall averages 1725 mm per year ($\bar{x}$ of four years) and is highly seasonal in distribution (fig. 1). In most years, little or no rain falls during the dry season, which begins in November and continues through April. The wet season (May to October) is interrupted by a short dry period (Veranillo de San Juan) of a few weeks to a month in July or August. In 1971 the rains began early in April and had slowed by late June (fig. 1). Much of the community activity ceased as birds abandoned nests and trees dropped their newly formed leaves. Near-normal rains began again in August and continued through October (fig. 1). This unusual year was followed by a very long dry season beginning in November of 1971 and essentially continuing into 1973. In 1972 there was essentially no wet season. Both the total amount and distribution of rain falling from June through October were reduced greatly (fig. 2).

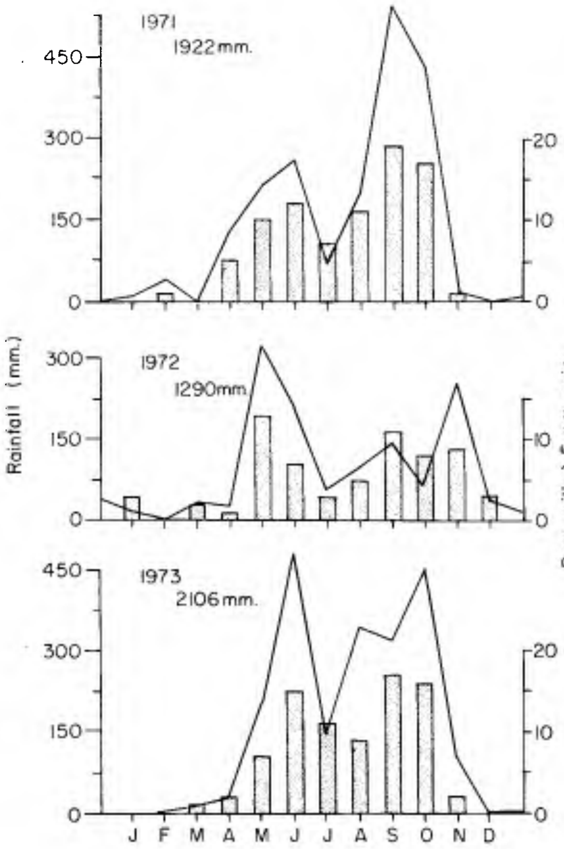


FIGURE 1. Monthly distribution of rainfall at Finca Jiménez in 1971 (top), 1972 (middle), and 1973 (bottom). Total amount (left) and number of days with more than 5 mm of rainfall (right) are shown. Data taken from records on file at the station.

The relatively large amounts falling early (May) and late (November) in the wet season of 1972 (fig. 1) were not adequate to break the drought. During this year the entire northwestern part of Costa Rica experienced a severe drought. By 1973 the drought had ended, and rainfall during the wet season was near normal.

A riparian forest with a maximum canopy height between 30 and 35 meters (Holdridge *et al.* 1971, Janzen 1973a) persists along the Río Higuerón. Although this forested area is relatively small and has been subject to varying degrees of disturbance, some sections remain relatively natural. A 10 m understory of palms, mainly *Scheelea rostrata* (Holdridge *et al.* 1971), and the presence of many evergreen trees reduce the light level in the forest during the dry season as compared to nearby non-riparian forests.

The presence of many large mammals, including mountain lion *(Felis concolor)*, margay *(Felis wiedii)*, jaguaroundi *(Felis yagouaroundi)*, white-tailed deer *(Odocoileus virginianus)*, collared peccary *(Tayassu tajacu)*, and agouti *(Dasyprocta punctata)*, and large birds, including crested guans *(Penelope purpurascens)*, indicates that some of the forest is still relatively undisturbed. The remainder of the vertebrate fauna is diverse and contains most of the species known from similar habitats in dry forest sites in northwestern Costa Rica.

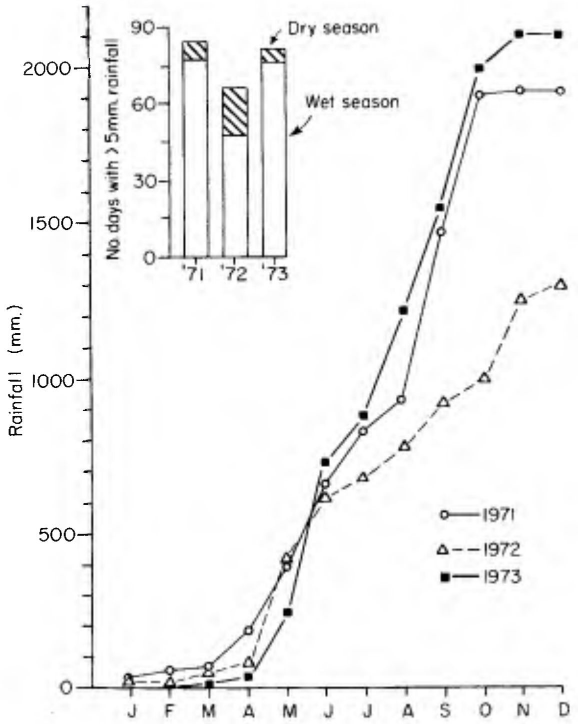


FIGURE 2. Seasonal distribution of rainfall by year (above) and cumulative amount by month (below) showing the relative drought conditions in the wet season of 1972.

## TREE ECOLOGY

SIZE, DISTRIBUTION AND FLOWERING PERIODICITY.—*Stemmadenia donnell-smithii*, a widespread member of the family Apocynaceae, is found at low elevations from eastern and southern México (Pennington and Sarukhán 1968) through Central America, to Panama (Nowicke 1970). It is a medium-sized (to 20 m) tree common in the middle strata of semi-evergreen forests of México (Pennington and Sarukhán 1968, Gómez-Pompa 1973) and Central America (our observations) but is able to grow in relatively open areas and commonly is found in second growth and pastures (Allen 1956). It has opposite, lanceolate leaves with terminal inflorescences of 1 to 5 yellow flowers about 3-4 cm deep, and large, paired fruits (fig. 3). The latter account for the colorful local name "huevos de caballo." The tree exudes copious, sticky, white latex from the branches, leaves, flowers, and fruits.

Individual trees occurred in pasture, open forest, and forest habitats at the study site. Two trees, located in a large pasture at the forest edge, measured 0.17 and 0.21 m in diameter at breast height (DBH), 9 and 13 m in height, and 4.5 and 6.1 m in crown width. Both were in full sun; each was shorter and had a broader crown relative to its diameter than other trees in forest habitats. Fourteen trees included in the open-forest group grew either along a forest trail and fence row or under a large opening in the canopy. Most of these trees were partially shaded by taller canopy trees. They measured 0.07 to 0.36 m DBH, 7 to 15 m in height, and 3 to 6.7 m in crown width. Trees in the forest group were surrounded by other vegetation and usually were shaded by canopy trees. A few taller individuals that formed part of the sub-canopy received more sunlight. Fifteen in this group ranged from 0.14 to 0.28 m DBH, 8 to 14 m in height, and 3.5 to 7.0 m in crown diameter. The forest trees generally had small crowns relative to their DBH. No obvious relationship between tree size and location was noted except for the broader canopy in pasture trees compared to forest trees with the same DBH.

Flowering varies considerably between sites and among individuals at a site. Pennington and Sarukhán (1968) reported flowers of *S. donnell-smithii*

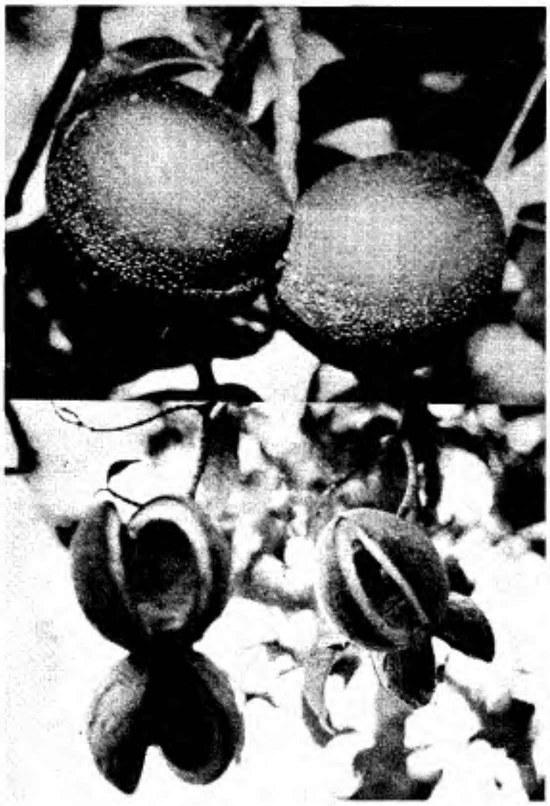

FIGURE 3. Mature, unopened fruit (above) and recently opened and emptied husks (below) of *Stemmadenia donnell-smithii* on trees along forest trail near Finca Jiménez, April 1971.

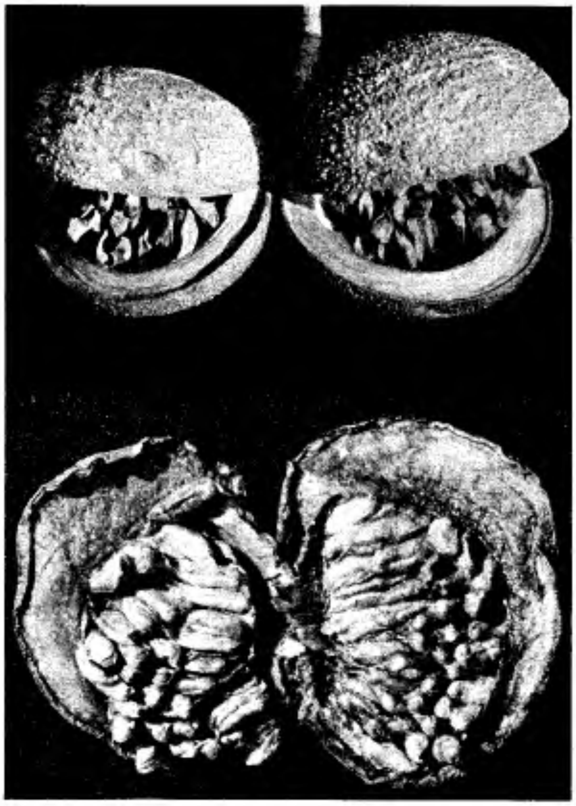

FIGURE 4. Newly opened, normal fruit from forest tree (above) and shrivelled, dried fruit from pasture tree (below) near Finca Jiménez, June 1973.

primarily in the wet season (May to December) in México. Allen (1956) reported trees in bloom in March and April (end of dry season and beginning of wet season) near Palmar Norte, Costa Rica. Janzen (pers. comm.) recorded flowers in June, July, and August in Guanacaste. We found flowers present in March, April, and August; we do not have data from other months. Of 28 trees censused in April 1973, eight were flowering, and all but one bore mature fruit. Apparently individuals of *S. donnell-smithii* may bloom almost anytime of year, the variation in flowering and fruit ripening time being related to climate. In 1973, following a major drought year, the first fruits matured two months later than in previous years (May instead of March). Many fruits had pale-yellow instead of bright-orange aril on opening, and some fruits shrivelled on the tree before ripening (fig. 4).

FRUIT DESCRIPTION.—Fruits, usually paired, are large (6.9 to 9.3 cm long by 5.6 to 7.6 cm diam.), heavy (52.6 to 215.2 g wet weight, $\overline{x} = 143.7$, $N = 20$), and terminal on branches (fig. 3). The follicles are obliquely, broadly ovoid with an obtuse apex. The greenish-brown skin is slightly rugose. The somewhat woody husk (=fruit wall) is 1.0 to 1.6 cm thick (fig. 4) and accounts for 77 to 88 percent of the wet weight of the fruit. Ripe fruits dehisce along the distal margin (fig. 4), opening over a period of a day or more to a width of about 10 cm. The width of the opening rarely exceeds 1 to 2 cm before all the pulp is removed by animals. Ripe fruit occurs from August through March in México (Pennington and Sarukhán 1968), in August and September at Palmar Norte (Allen 1956), and from March to September, at least, in Guanacaste. The peak of fruit production apparently coincides with the dry season at Taboga. A fleshy bright red-orange aril nearly encloses each of the seeds (fig. 4). A slit in the aril that often exposes the seed facilitates separation of the aril and seed. The aril is somewhat stringy and very oily, traits that readily identify

*Stemmadenia* in stomach contents. The seeds are longitudinally grooved, narrowly ovoid, and often irregularly shaped. Twenty seeds selected randomly from one fruit averaged 8.3 mm in length (range, 7.2-9.2) and 3.7 mm in diameter (range 3.4-3.9). When wet, the seeds are dark brown to nearly black and contrast sharply with the bright aril.

The thick husk and sticky white latex apparently prevent insect damage to the immature fruits. No insects were found in more than 40 mature fruits opened. Stingless bees (*Trigona* sp.) were attracted to the exposed edges of the natural opening and apparently collected the latex. Once the fruit opens, latex flow from the husk is greatly reduced and perhaps terminated. Large numbers of a small beetle apparently were feeding on open husks even while they remain on the tree.

Most likely, the husk and the terminal position of the unripe fruit protect it from vertebrate frugivores. Of more than 700 fruits observed on the trees, only five had been opened by vertebrates. Marks on the fruit indicated parrots, even though none of the four species of parrots known to occur commonly in the area was seen in *Stemmadenia* trees. On a few occasions, one of us (MSF) observed White-faced Capuchins *(Cebus capucinus)* pick and eat fruit. The monkeys bit through and spit out the husk to get to the interior of the fruit; however, we do not know if they ate the aril, the seeds, or both. Evidence of openings made by monkeys were characterized by their shape and tooth marks. Small numbers of fruits with such openings were observed regularly on the ground throughout the fruiting seasons of 1973 and 1974.

The number of fruits on 20 trees counted on 21 April 1971 varied from 16 to 135. A similar count of 25 trees in April 1973 revealed 0 to 348 fruits (table 1). The relationship between trunk diameter and fruit crop (fig. 5) was significant ($p < .05$) in both 1971 ($F_{1,18} = 10.4337$) and 1973 ($F_{1,22} = 7.9451$). However, only 36.7 and 26.5 percent of the variation in size of the fruit crop was attributable to variation in tree DBH in the two years, respectively. In addition, the variance about the regression lines differed significantly between 1971 and 1973 ($p < .05$, $F_{22,18} = 4.9367$). This variation may reflect differences among individuals in timing of fruit production. As might be expected, the average fruit crop increased in size from forest to open forest to pasture trees in both years. On the average the pasture trees had fruit crops 2.5 to 11 times larger than those of forest trees (table 1). Similar responses in fruit crop have been noted in other tropical forest trees growing in pastures or on forest edges where they receive more sunlight (Janzen, pers. comm.).

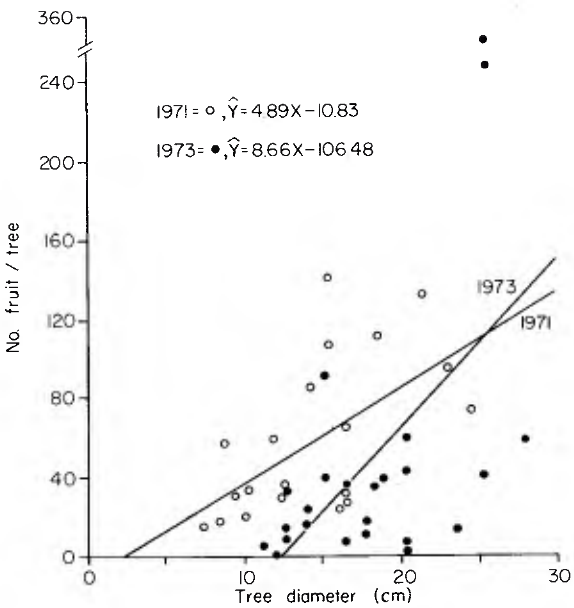


FIGURE 5. Number of fruit per tree as a function of tree diameter in 1971 and 1973 censuses. Differences between years are significant ($p < 0.05$).

Fruit size varied on a single tree, but the range of sizes did not differ noticeably between trees within or between habitats. Seeds averaged 132.5 per fruit (SD = 57.0, range = 31-199, median = 160, N = 30). We found no significant correlation between seed size or number and fruit weight, between mean seed weight and seed number, or between mean aril weight per seed and seed number, based on both wet and dry weights. For each fruit, total seeds and total aril were weighed and divided by seed number to obtain mean seed weight and mean aril weight per seed. These values were then averaged for all fruits. Seeds weighed an average of 0.094 g wet weight (N = 15 fruit) and 0.054 g dry weight (N = 4 fruit). Aril per seed averaged 0.079 g wet weight (N = 15 fruit) and 0.017 g dry weight (N = 4 fruit).

RATE OF FRUIT OPENING.—The rate at which fruit opened, thereby making pulp available to birds, was determined for 13 trees in the three habitats during intervals of four to seven days. The average daily rate of fruit opening per tree varied from 0.0 to 10.29, the greatest rates being recorded for pasture trees (table 2). Both relative and absolute rates of opening varied with crop size and increased from forest and open forest to pasture (table 2). Thus, a large tree with a sizable fruit crop will have freshly opened fruit available during most of the fruiting season. The proportion of available fruits opening was nearly 70 percent higher in the forest than in open forest, though both rates were considerably lower than that for the pasture trees. This variation probably reflects temporal or spatial variability in flowering and/or fruit ripening among individuals in the forest habitats.

AGENTS OF SEED DISPERSAL.—Although 132 fruits dehisced during the 1971 study period, few fruits with seeds were found on the ground beneath the trees. To determine if seeds could be dispersed from fruits on the ground, 21 open fruits were distributed on the ground in the three habitats. Eight were placed beneath *Stemmadenia* trees, and 13 were placed from 5 to 150 meters from the trees. After two days, the seeds had been removed from only two of the eight fruits placed under the trees. The other 19 fruits retained nearly all their seeds, but the aril around the seeds had been removed by ants. From this it is evident that *Stemmadenia* is dispersed by flying animals. In food samples collected from 132 bats of 15 species examined (Howell and Burch 1974) at Taboga in April 1971, only one individual of the bat *Tonatia sylvicola* had evidence of *Stemmadenia*. Whether the orange aril found in the bat stomach was from *S. donnell-smithii* or from fruit of some other local species with a similar aril (e.g., *Tabernaemontana amygdalifolia*) is unknown. The occasional fruits that fell to the ground almost never were cleared of their pulp. During the dry season, these fruits dried rapidly. In the wet season fallen fruits often were covered with mold, and the rotting pulp was inhabited by fly larvae. Newly hatched larvae were white, but with age they became orange, apparently from feeding on *Stemmadenia* arils.

GERMINATION.—A series of experiments evaluated the effect of bird ingestion on germination of *S. donnell-smithii* seeds. Seven treatments using 25 seeds each were run for 18 days (table 3). Seeds were collected from ripe fruit on trees in the field and tested in the laboratory. The best germination was obtained with 1) intact seeds with or without aril, 2) seeds from which the aril was removed and the seed coat scarified, and 3) seeds that had been passed through the digestive tract of a Yellow-green Vireo (*Vireo flavoviridis*). Intact and scarified seeds treated in acid had poor germination. Because hydrochloric acid was not available, we used sulfuric acid (pH 2) that was somewhat weaker than the stomach acids of birds (Ziswiler and Farner 1972). Acid-treated seeds also supported a growth of mold which may have influenced their viability. Seeds taken from rotted fruit on the forest floor had maggots in the aril and did not germinate. The germination of seeds consumed by the vireo and, especially, with intact

TABLE 1. *Fruit crop of trees from three habitats censused in 1971 and 1973 at Finca Jiménez, Guanacaste Province, Costa Rica.*

| Habitat | Year | N | $\bar{x}$ | Range |
|---|---|---|---|---|
| Forest | 1971 | 10 | 41.5 | 16-95 |
| | 1973 | 12 | 26.2 | 0-60 |
| Open forest | 1971 | 8 | 73.0 | 30-135 |
| | 1973 | 11 | 30.7 | 6-92 |
| Pasture | 1971 | 2 | 100.0 | 66, 134 |
| | 1973 | 2 | 298.5 | 249, 348 |

TABLE 2. *Rate of fruit opening of* Stemmadenia donnell-smithii *in three habitats at Finca Jiménez, Guanacaste Province, Costa Rica, in April 1971.*

| Habitat | Trees | Days | Number of fruit | | | Fruit opening | | |
|---|---|---|---|---|---|---|---|---|
| | | | total | studied | opening | No./tree/day | $\bar{x}$ No./tree/day | No./100 fruit available/ habitat/day |
| Forest | 1 | 5 | 21 | 21 | 4 | 0.80 | | |
| | 2 | 5 | 16 | 16 | 3 | 0.60 | | |
| | 3 | 5 | 18 | 18 | 3 | 0.60 | | |
| | 4 | 5 | 57 | 57 | 4 | 0.80 | 0.70 | 1.92 |
| | 5 | 5 | 29 | 29 | 8 | 1.60 | | |
| | 6 | 5 | 95 | 95 | 4 | 0.80 | | |
| | 7 | 5 | 30 | 30 | 2 | 0.40 | | |
| | 8 | 5 | 25 | 25 | 0 | 0.00 | | |
| Open forest | 9 | 7 | 34 | 34 | 2 | 0.29 | | |
| | 10 | 7 | 112 | 112 | 10 | 1.43 | 0.87 | 1.13 |
| | 11 | 4 | 108 | 60 | 2 | 0.90 | | |
| Pasture | 12 | 7 | 134 | 134 | 72 | 10.29 | 6.43 | 6.43 |
| | 13 | 7 | 66 | 66 | 18 | 2.57 | | |

aril was delayed 5-10 days compared to the germination of cleaned seeds.

NUTRITIONAL VALUE OF FRUIT.—The ash, lipid, protein, and carbohydrate contents of the husk, aril, and seed obtained from fruits collected in May and June 1972 and 1973 are presented in table 4. Percent lipid, ash, and structural carbohydrate in the arils varied considerably between trees. The other components of the arils and particularly the composition of the seeds and husks were more uniform. The low lipid content of the aril from pasture fruits (samples 1 and 2; one-half to one-third that for other fruits) was balanced by larger proportions of

TABLE 3. *Results of germination experiments with seeds of* Stemmadenia donnell-smithii.

| Treatment | N | Seeds germinating Cumulative total by day[a] 1 | 2-3 | 4 | 6 | 7 | 8-9 | 10 | 11-12 | 13-14 | 15 | 16-25 | Total | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Seed + aril (F)[b] | 25 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 9 | 11 | 20 | 23 | 23 | 92 |
| Seed + aril (R) | 25 | 0 | 0[c] | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Seed only (F) | 25 | 0 | 0 | 0 | 18 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 100 |
| Seed only, scarified (F) | 25 | 0 | 0 | 3 | 16 | 20 | 23 | 23 | 24 | 24 | 24 | 24 | 24 | 96 |
| Seed only, acid treated (F) | 25 | 0 | 0 | 0 | 4[d] | 5 | 8 | 9 | 9 | 9 | 9 | 9 | 9 | 36 |
| Seed only, acid treated & scarified (F) | 25 | 0 | 0 | 1 | 9[d] | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 36 |
| Seed only, from Yellow-green Vireo feces (F) | 25 | 0 | 0 | 0 | 1 | 1 | 2 | 11 | 19 | 22 | 24 | 24 | 24 | 96 |

[a] Seeds not checked on Day 5.
[b] F = taken from fresh, newly opened fruits on the tree; R = taken from rotten fruit on the ground.
[c] Maggots first observed in aril.
[d] Mold first observed on seeds.

TABLE 4. *Nutrient composition of fruits of* Stemmadenia donnell-smithii *from trees at Finca Jiménez, Guanacaste Province, Costa Rica. Values expressed as % per gram dry weight of tissue.*

| Tissue | Sample[a] | % ash | % lipid | % protein | % TCA-Soluble Carbohydrate | % Structural Carbohydrate |
|---|---|---|---|---|---|---|
| Aril | 1 | 17.3 (4)[b] | 24.4 (4) | 16.4 (4) | 15.2 (4) | 26.7 (4) |
| | 2 | 20.95 (4) | 31.1 (4) | 17.65 (6) | 9.5 (4) | 20.8 (4) |
| | 3 | 18.5 (6) | 58.2 (6) | 12.1 (4) | 4.0 (4) | 7.2 (4) |
| | 4 | 9.4 (6) | 62.8 (6) | 8.2 (4) | 10.3 (4) | 9.6 (4) |
| | 5 | 5.05 (8) | 67.4 (8) | 16.5 (8) | 9.4 (8) | 2.8 (8) |
| | 6 | 3.3 (10) | 79.3 (10) | 4.4 (10) | 6.7 (10) | 6.4 (10) |
| | $\bar{x}$ (N=13)[c] | 7.9 | 63.9 | 10.95 | 8.5 | 8.3 |
| Seed | 1 | 3.6 (4) | 26.0 (4) | 11.4 (4) | 17.2 (4) | 41.85 (4) |
| | 2 | 3.2 (3) | 31.6 (5) | 10.3 (4) | 20.3 (3) | 34.5 (4) |
| | 3 | 3.6 (4) | 36.0 (4) | 11.7 (4) | 15.7 (4) | 33.0 (3) |
| | 4 | 3.05 (4) | 32.1 (4) | 10.35 (4) | 18.6 (4) | 35.9 (4) |
| | $\bar{x}$ (N = 4) | 3.36 | 31.4 | 10.9 | 17.95 | 36.3 |
| Husk | 1 | 11.3 (6) | 24.4 (4) | 9.9 (4) | 9.65 (4) | 44.1 (4) |
| | 2 | 23.2 (4) | 26.65 (4) | 11.8 (4) | 8.15 (4) | 30.2 (4) |
| | 3 | 16.3 (4) | 28.7 (4) | 12.4 (4) | 9.6 (4) | 33.05 (4) |
| | 4 | 17.3 (4) | 16.25 (4) | 10.6 (4) | 9.9 (4) | 45.9 (4) |
| | $\bar{x}$ (N = 4) | 17.0 | 24.0 | 11.2 | 9.3 | 38.3 |

[a] 1 = Pasture tree 1, fruit 1; 2 = pasture tree 1, fruit 2; 3 = open forest tree 1, fruit 1; 4 = open forest tree 2, fruit 1; 5= trees from all habitats (pasture, open forest, forest) combined, field prepared, 4 fruits, aril only; 6 = trees from all habitats, laboratory prepared, 5 fruits, aril only.
[b] Figures in parentheses specify numbers of samples analyzed.
[c] N = total number of fruits analyzed.

ash and structural carbohydrate compared to samples 3 and 4 (table 4). The difference between field-prepared fruits (sample 5) and laboratory-prepared fruits (sample 6) in percent lipid and percent protein may reflect differences in conditions under which they were prepared. Field preparation of aril samples resulted in unavoidable loss of some oily material on fingers, instruments, and collecting paper. The oily component of arils prepared after freezing and partial thawing was more viscous, and much less was lost. All other samples (1-4) were prepared in the field. Thus component analyses probably underestimate lipid content and show a corresponding overestimate of the other constituents.

The lipid level of the aril of *S. donnell-smithii* ($\bar{x} = 63.9\%$, range 24.4-79.3) is one of the highest reported for any plant material (Altman and Dittmer 1968, Snow 1971, Morton 1973, White 1974). Among edible plant tissues, only the avocado, several nuts, and the fruit pericarps of several tropical species are comparable to *Stemmadenia.* Our highest values are similar to those reported for the oil palm (Morton 1973). The lipid level of the seeds averaged 31.4 percent, essentially identical to the mean value (31.16%) reported for six species of Apocynaceae by Levin (1974).

The allocation of wet and dry weight to husk, seed, and aril (fig. 6) shows that although the husk makes up the bulk of the fruit, the seeds still constitute a substantial proportion of the dry weight. The aril comprises the smallest portion of the weight of the fruit, but its caloric value is relatively high because of the high proportion of lipid (table 5). For caloric values, as for the distribution of components (table 4), the greatest variation occurs in the aril. Variations in seed and husk values are negligible.

## BIRD ECOLOGY

AVIFAUNA AND FORAGING BEHAVIOR.—Of the nearly 300 species of birds reported from the general region (all habitats) of Finca Jiménez, we observed 20 species feeding on *S. donnell-smithii* fruit during April 1971. Individuals of two additional species had *Stemmadenia* pulp in their stomachs. The birds known to eat *Stemmadenia,* and where data are available, the total time spent by individuals of each species feeding in trees in each habitat, and the number of pulp units removed and/or eaten during the total time are detailed in table 6. Observations were made at the forest and pasture sites from 0600 to 1800 hours on 24 April, at the open-forest sites from 0740 to 0840 and from 1200 to 1230 on 25 April, and irregularly on several other occasions in 1972-1974. Few, if any, birds visiting the tree were missed.

Hoffmann's Woodpeckers, Magpie Jays, Tropical Kingbirds, Swainson's Thrushes, Red-legged Honeycreepers, and Yellow-green Vireos ate 77 percent of the fruit pulp consumed. Other species, such as the Yellow-olive Flycatcher, Greenish Elaenia, Grey-headed Greenlet, and Chestnut-sided Warbler, visited

TABLE 5. *Weights and caloric values of aril, seed and husk of four fruits of* Stemmadenia donnell-smithii.

| Tissue | Sample[a] | Wet wt. (g) | Dry wt. (g) | Ash-free dry wt.(g) | kcal[c]/ash-free g dry wt. |
|---|---|---|---|---|---|
| Aril | 1 | 2.796 | 0.344 | 0.284 | 5.986 |
| | 2 | 12.887 | 1.363 | 1.077 | 6.551 |
| | 3 | 17.315 | 3.757 | 3.062 | 8.151 |
| | 4 | 8.900 | 2.416 | 2.196 | 7.936 |
| | | | | | $\bar{x}$ 7.156 |
| Seed[b] | 1 | 3.384 | 1.632 | 1.5735 | 5.725 |
| | 2 | 16.351 | 8.443 | 8.169 | 6.014 |
| | 3 | 20.910 | 10.768 | 10.380 | 6.286 |
| | 4 | 8.979 | 4.891 | 4.742 | 6.037 |
| | | | | | $\bar{x}$ 6.015 |
| Husk | 1 | 46.341 | 7.543 | 6.640 | 5.757 |
| | 2 | 120.060 | 11.675 | 8.966 | 6.195 |
| | 3 | 174.754 | 9.865 | 8.261 | 6.143 |
| | 4 | 125.500 | 10.040 | 8.298 | 5.351 |
| | | | | | $\bar{x}$ 5.866 |

[a] Samples described in legend, table 4.
[b] Seed nos. per sample: 1=31; 2=171; 3=190; 4=84.
[c] For conversion factors, see text (after Paine 1971).

the trees so infrequently that they can be listed as occasional exploiters and of only minor importance to seed dispersal. Some species, particularly the Pale-billed Woodpecker, which visit the trees infrequently but consume a large amount of pulp at each visit, must be relatively important among the species that utilize the fruit and disperse the seeds.

Observations by D. Bradford (1971) on three *Stemmadenia* trees at the pasture edge on 21 April 1971 were similar to ours. In 300 minutes of observation he recorded 12 species utilizing the fruits (table 7). He calculated an intensity of bird-feeding activity of 31.2 bird minutes/hour in 16.8 visits/hour versus our rate for two pasture trees of 55 bird minutes/hour. The Pale-billed Woodpecker made one prolonged visit during Bradford's observations of pasture trees, whereas we recorded it only once in the forest habitat. In both instances it consumed a large amount of pulp.

Foraging behavior of species observed feeding on *S. donnell-smithii* is summarized in Appendix I. Pulp was removed by one of two foraging techniques: in one, the birds hover below the fruit and reach in to pick out the pulp; in the second, individuals perch on the fruit, its pedicel, or a nearby branch, and reach in to remove the pulp. Most small birds and all flycatchers hover-feed. The perch feeders include most large birds, such as the woodpeckers and jays. The woodpeckers particularly were adept at perching on the fruit, often suspended upside down, and feeding for long periods.

Different birds disperse seeds to different degrees. Some species swallowed whole pulp units and presumably passed seeds through the gut. Others swallowed whole pulp units and later regurgitated the cleaned seeds. A few species separated the aril from the seed at the feeding site. A few species sometimes swallowed pulp whole and at other times separated seed and aril.

Availability of pulp units in each habitat was calculated from rates of fruit opening and total fruit crops (table 2). Seed availability expressed per tree, per 100 fruits, and per total fruit observed and rate of visits and pulp consumption by birds in each habitat are summarized in table 8. The estimated proportion of seeds consumed (pulp units taken/hour) to seed availability (per total crop/day) was 42 to 51 percent and did not vary with habitat. This finding implies that all available seeds are removed in only a few hours. Our estimates of utilization rates are probably low owing to difficulties in estimating pulp consumption by the more voracious feeders. Because most fruits were completely emptied (fig. 3) before they dropped from the tree, utilization of the pulp by birds probably approached 100 percent.

INTERACTIONS AT THE TREE.—Two or more species of birds occurred in a tree simultaneously 16 percent of 321 bird species minutes of observation, during which 12 interspecific interactions involving 7 species were noted (table 9). Most of these did not result in displacement from the trees of either interacting individual. The Tropical Kingbird, Hoffmann's Woodpecker, and Northern Oriole were clearly dominant species; the Yellow-green Vireo and Red-legged Honeycreeper were clearly subordinate.

STOMACH ANALYSIS.—We examined stomach contents of 20 individuals of 18 species collected in the study area. Remains of *Stemmadenia* arils were found in eight (table 10). Individuals of three species (Yellow Warbler, Swainson's Thrush, Yellow-olive Flycatcher) known to feed on the fruit (table 6) did not contain *Stemmadenia* remains in their stomachs. A Gray-headed Tanager had remains of fruit in its stomach but had not been seen feeding on *Stemmadenia* during the observation periods. In addition, several Long-tailed Manakins passed *Stemmadenia* seeds when they were removed from mist nets. *Stemmadenia* seeds also have been found beneath manakin display perches and in manakin stomachs. Therefore, we have added the Long-tailed Manakin to our list of dispersal agents, although we did not observe it feeding on *Stemmadenia.*

## DISCUSSION

Dispersal is an important event in the plant life cycle (Janzen 1969, 1970, 1971, Pijl 1972, McKey 1975). It enables plants to establish their progeny in suitable, newly available patches of habitat and may form an important avenue of escape from seed predation (Janzen 1970). In addition, seed dispersal promotes gene flow between populations and is important in maintaining variability (Levin and Kerster 1974). Because *Stemmadenia* seeds can germinate after passing through the avian digestive tract, birds that consume aril and seed together are potentially effective long-distance dispersal agents. Because the presence of an aril delays germination and reduces percent germination, *Stemmadenia* probably is dependent on birds for its perpetuation in addition to its dispersal.

The characteristics of plants related to the dispersal of their seeds by birds are: 1) the temporal and spatial availability of the resource; 2) attractiveness of the edible aril and its associated seed to the bird; 3) accessibility of the pulp; and 4) nutritive

TABLE 6. *Time spent feeding on* Stemmadenia donnell-smithii *and number of pulp units taken by birds observed at three sites, Finca Jiménez, Guanacaste Province, Costa Rica, in April 1971.*

| Species | Status[a] | Forest[b] Bird min.[e] | Forest[b] pulp u. | Open-forest[c] Bird min. | Open-forest[c] pulp u. | Pasture[d] Bird min. | Pasture[d] pulp u. | Totals Bird min. | Totals pulp u. | Relative Efficiency pulp u./min. feeding |
|---|---|---|---|---|---|---|---|---|---|---|
| Hoffmann's Woodpecker *Centurus hoffmannii* | R | 7 | 21 | 15 | 6 | 48 | 124 | 70 | 151 | 2.16 |
| Magpie Jay *Calocitta formosa* | R | 0 | 0 | 0 | 0 | 21 | 91 | 21 | 91 | 4.33 |
| Tropical Kingbird *Tyrannus melancholicus* | R | 11 | 1 | 4 | 0 | 73 | 75 | 88 | 76 | 0.86 |
| Swainson's Thrush *Catharus ustulatus* | M | 49 | 44 | 25 | 17 | 2 | 1 | 76 | 62 | 1.23 |
| Red-legged Honeycreeper *Cyanerpes cyaneus* | R | 19 | 32 | 0 | 0 | 54 | 27 | 73 | 59 | 0.81 |
| Yellow-green Vireo *Vireo flavoviridis* | B | 30 | 15 | 16 | 6 | 70 | 33 | 116 | 54 | 0.47 |
| Yellow Warbler *Dendroica petechia* | W | 0 | 0 | 2 | 2 | 92 | 31 | 94 | 33 | 0.35 |
| Northern Oriole *Icterus galbula* | W | 0 | 0 | 4 | 2 | 35 | 28 | 39 | 30 | 0.77 |
| Pale-billed Woodpecker *Phloeoceastes guatemalensis* | R | 5 | 27 | 0 | 0 | 0 | 0 | 5 | 27 | 5.40 |
| Turquoise-browed Motmot *Eumomota superciliosa* | R | 0 | 0 | 22 | 11 | 20 | 14 | 42 | 25 | 0.59 |
| White-collared Seedeater *Sporophila torqueola* | R | 0 | 0 | 0 | 0 | 7 | 7 | 7 | 7 | 1.00 |
| Dusky-capped Flycatcher *Myiarchus tuberculifer* | R | 10 | 5 | 2 | 1 | 0 | 0 | 12 | 6 | 0.50 |
| Rufous-naped Wren *Campylorhynchus rufinucha* | R | 0 | 0 | 0 | 0 | 7 | 6 | 7 | 6 | 0.86 |
| Sulfur-bellied Flycatcher *Myiodynastes luteiventris* | R | 0 | 0 | 6 | 4 | 0 | 0 | 6 | 4 | 0.66 |
| Streaked Flycatcher *Myiodynastes maculatus* | R | 0 | 0 | 0 | 0 | 10 | 3 | 10 | 3 | 0.30 |
| Yellow-olive Flycatcher *Tolmomyias sulphurescens* | R | 0 | 0 | 0 | 0 | 4 | 2 | 4 | 2 | 0.50 |
| Greenish Elaenia *Myiopagis viridicata* | R | 0 | 0 | 2 | 2 | 0 | 0 | 2 | 2 | 1.00 |
| Gray-headed Greenlet *Hylophilus decurtatus* | R | 0 | 0 | 2 | 2 | 0 | 0 | 2 | 2 | 1.00 |
| Lineated Woodpecker[f] *Dryocopus lineatus* | R | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — |
| Chestnut-sided Warbler[f] *Dendroica pensylvanica* | W | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — |
| Long-tailed Manakin[g] *Chiroxiphia linearis* | R | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — |
| Gray-headed Tanager[g] *Eucometis penicillata* | R | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — |
| Total | | 131 | 145 | 100 | 53 | 443 | 442 | 674 | 640 | |
| Per hr. observed | | 16 | 18 | 67 | 35 | 55 | 55 | | | |

[a] R: resident year-round; M: migrant, transient; B: breeding resident; W: migrant and winter resident.
[b] 6 trees; 8 hr observation.
[c] 8 trees; 1.5 hr observation.
[d] 2 trees; 8 hr observation.
[e] Times rounded to nearest whole minute.
[f] Rarely observed or observed at other times or places.
[g] Record based on stomach analyses only.

value of the aril to the bird (Snow 1971). Each of these characteristics is discussed in detail.

AVAILABILITY.—Competition among trees for dispersal agents should be intense (Janzen 1975) and may result in staggered reproduction of trees of one species over a year (e.g., *Ficus*) or, more commonly, in reproductive synchronization of individuals of a tree species to part of a year with several species (e.g., *Miconia*) staggering their reproduction and together spanning the entire year (Snow 1965, Smythe 1970). *S. donnell-smithii* apparently has fruit for up to six months at Finca Jiménez with peak abundance in the dry season. It is one member of a series of species in the area with a staggered sequence of fruiting that is important to certain frugivorous birds (e.g., Long-tailed Manakin). Fruiting in the dry season may increase utilization of dispersal agents (Janzen 1967). One frequently cited but never demonstrated advantage of a frugivorous diet is the relative abundance of fruit compared to insects (e.g., Morton 1973), particularly during periods of insect scarcity. During the dry season in Guanacaste, insect density is considerably reduced in all but riparian habitats which serve as mesic refugia (Janzen 1973a, 1973b). Because the peak of fruit ripening in *Stemmadenia* occurs in the late dry season, fruit is most abundant when birds, especially insectivores, which comprise a majority of the species exploiting *Stemmadenia,* are concentrated along the edges of riparian forest. Selection also may favor fruit maturation just prior to the beginning of the wet season, which is suspected to be optimal for germination (Janzen 1967).

The methods of seed dispersal by various bird species undoubtedly have important consequences for the plant. Frugivorous birds tend to be forest dwellers, a circumstance probably related to the high proportion of second-growth plants with small wind-dispersed seeds and fruits. Conversely insectivorous

TABLE 7. *Birds feeding in three* Stemmadenia donnell-smithii *trees at Finca Jiménez, Guanacaste Province, Costa Rica, on 21 April 1971.*[a]

| Species | No. minutes observed | No. visits |
|---|---|---|
| Yellow Warbler | 33.21 | 17 |
| Yellow-green Vireo | 29.01 | 20 |
| Hoffmann's Woodpecker | 20.02 | 22 |
| Pale-billed Woodpecker | 19.25 | 1 |
| Tropical Kingbird | 13.66 | 6 |
| Northern Oriole | 12.83 | 2 |
| Red-legged Honeycreeper | 8.80 | 4 |
| Magpie Jay | 8.67 | 3 |
| Turquoise-browed Motmot | 4.68 | 2 |
| Swainson's Thrush | 2.42 | 2 |
| Yellow-olive Flycatcher | 2.08 | 2 |
| Streaked Flycatcher | 0.76 | 2 |
| Unidentified bird | 0.42 | 1 |
| | 155.81 | 84 |

Total observation time — 300 minutes.
Intensity of feeding activity — 31.2 bird minutes/hour.
16.8 visits/hour.

[a] Data from Bradford (1971).

TABLE 8. *Availability and utilization of seeds and pulp of* Stemmadenia donnell-smithii *in three habitats at Finca Jiménez, Guanacaste Province, Costa Rica, April 1971.*

| Habitat | Index of seed availability No. seeds/hr. | | | $\bar{x}$ bird min./hr. observation[b] | $\bar{x}$ pulp u. taken/hr. observation[b] |
|---|---|---|---|---|---|
| | A[a] | B[a] | C[a] | | |
| Forest (6 trees)[c] | 7 | 17 | 43 | 16 (8) | 18 (8) |
| Open forest (8 trees)[d] | 9 | 12 | 69 | 67 (1.5) | 35 (1.5) |
| Pasture (2 trees) | 66 | 66 | 131 | 55 (8) | 55 (8) |

[a] Calculated as product of ($\bar{x}$ no. seeds/fruit) times ($\bar{x}$ no. fruits opening, A = per tree/day; B = per 100 fruits/day; C = per total crop/day). Values rounded to nearest whole no. Based on 132.53 seeds/fruit and 13 hr daylight/day.
[b] Total hrs observation in parentheses.
[c] Trees 1 and 2 omitted because bird observations not available.
[d] Including 5 trees not listed in table 2, with a total fruit crop of 400 fruits. Rate of fruit opening was assumed to be identical to other open-forest trees (1.13/100 fruit/day).

TABLE 9. *Recorded aggressive interactions among birds observed at* Stemmadenia donnell-smithii *trees.*

| Species | Intra-specific | Interspecific Displaces | Displaced |
|---|---|---|---|
| Hoffmann's Woodpecker | 1 | 2 | 0 |
| Tropical Kingbird | 5 | 2 | 0 |
| Swainson's Thrush | 1 | 0 | 1 |
| Yellow-green Vireo | 1 | 3 | 4 |
| Red-legged Honeycreeper | 0 | 1 | 5 |
| Yellow Warbler | 0 | 1 | 1 |
| Northern Oriole | 0 | 3 | 1 |
| Totals | 8 | 12 | 12 |

| Displaced \ Displacer | HW | TK | ST | YGV | RLH | YW | NO |
|---|---|---|---|---|---|---|---|
| HW | 1 | | | | | | |
| TK | | 5 | | | | | |
| ST | | | 1 | 1 | | | |
| YGV | 1 | 1 | | 1 | 1 | 1 | |
| RLH | | | | 2 | | | 3 |
| YW | | 1 | | | | | |
| NO | 1 | | | | | | |

birds, especially the sallying and hovering flycatchers (Orians 1969), are relatively more abundant along forest edges and in second-growth habitats. The utilization of both insectivorous and frugivorous birds by *Stemmadenia* increases the total habitats to which seeds are dispersed. It also increases the total area of dispersal since birds from many home ranges could learn the location of fruiting trees. If disperser diversity is advantageous to the tree, then edge trees probably are contributing more to colonization of new areas than forest trees, especially by insectivorous birds. We have shown that edge-pasture trees attract the greatest number of birds and have the greatest fruit crop and rate of fruit opening. We also have shown that most of the birds attracted are insectivorous and common along forest edges. This situation may account in part for the relative commonness of trees of *S. donnell-smithii* along edges and in second-growth areas today (Allen 1956).

The slow rate of opening of *Stemmadenia* (table 2) could enhance dispersal 1) by maintaining bird populations over the entire dry season when insects are least abundant in most habitats, 2) by allowing birds to incorporate visits to fruit trees into daily movement patterns and thereby provide regular fruit utilization, and 3) by ensuring that fruit does not become overly abundant and that all seeds are dispersed. The last point is supported directly by our findings and may explain the rarity of encounters between birds in the trees. Aggressive interactions at an open fruit were minimal since birds apparently came into the area singly. Leck (1969) found that intraspecific feeding encounters in a *Trichilia* tree in the wet season also were low and resulted in few displacements.

ATTRACTIVENESS.—In his studies on color preference in fruit- and seed-eating birds, Turček (1963) showed that red or black diaspores were taken significantly more often than predicted by their availability. He concluded that bird-dispersed fruit frequently would be one of these colors. In *S. donnell-smithii,* the greenish-brown fruit splits open at maturity to expose the bright red-orange aril. The dark brownish-black seeds, often visible through the aril, increase the contrast. The difficulty we experienced in finding recently open fruits with untouched contents even shortly after dawn attests to the effectiveness of the advertising color in eliciting a rapid response from birds.

ACCESSIBILITY.—For bird-dispersed plants, easy access to the fruit and ease of harvesting edible parts with seeds are important components of the dispersal strategy. The fruits of *S. donnell-smithii* are large and terminally placed on branches. For birds perched on those branches access to the fruit pulp is difficult because the fruit splits along the surface facing away from the attachment point (fig.3). Furthermore, the slit is relatively small initially. These characteristics apparently restrict accessibility primarily to 1) birds large enough to perch on the fruit and reach around

TABLE 10. *Summary of stomach analyses of birds collected at Finca Jiménez, 25 April 1971.*

| Species | Locality | Stomach[a] | Contents | *Stemmadenia* |
|---|---|---|---|---|
| Orange-chinned Parakeet | Edge | Full | Fruit | No |
| Black-headed Trogon | Forest | Full | Fruit | No |
| Turquoise-browed Motmot | Edge | Nearly empty | Fruit | Yes |
| Hoffmann's Woodpecker | Edge | Fragments | Fruits; Arthropods | Yes |
| Barred Antshrike | Forest | Half-full | Insects | No |
| Black-capped Tityra | Edge | Fragments | Insects | No |
| Tropical Kingbird | Edge | Mostly fragments | Fruit; Insects | Yes |
| Boat-billed Flycatcher | Forest | Nearly empty | Insects | No |
| Boat-billed Flycatcher | Edge | Full | Insects | No |
| Dusky-capped Flycatcher | Edge | Nearly empty | Fruit; Insects | Yes |
| Yellow-olive Flycatcher | Forest | Nearly empty | Insects | No |
| Greenish Elaenia | Forest | Mostly fragments | Fruit; Insects | Yes |
| Swainson's Thrush | Forest | Nearly empty | Mostly fruit | No |
| Yellow-throated Vireo | Forest | Nearly empty | Fruit seeds | Probable |
| Yellow-green Vireo | Edge | Mostly fragments | Fruit; Insects | Yes |
| Red-legged Honeycreeper | Forest | Fresh | Fruit; Arachnids; Gastropods | Yes |
| Red-legged Honeycreeper | Forest | Fresh | Fruit; Insects | Yes |
| Yellow Warbler | Edge | Mostly fragments | Mostly insects | No |
| Gray-headed Tanager | Forest | Full | Fruit; Insects | Yes |
| Orange-billed Sparrow | Forest | Mostly fragments | All seed coats | No |

[a] Fragments refer to condition of insect parts, usually in stomachs that were nearly empty.

to the pulp (e.g., jays); 2) birds which can hang from the fruit, often upside down, and feed (e.g., woodpeckers); 3) large, hover-feeding birds with long, relatively narrow bills (e.g., flycatchers and motmots); and 4) small hover-feeding birds which can insert their heads at least part way into the fruit opening (e.g., honeycreepers, manakins). Even so, the pulp is generally accessible. The pulp is easily freed from the husk, and the aril is easily separated from the seed. The fruits are firmly attached to the branches and support the weight of large birds.

During the study, many species of birds seen and netted in forest and edge habitats were never observed to feed on *Stemmadenia*. Among the more conspicuous of these were the Orange-chinned Parakeet *(Brotogeris jugularis)*, Collared Araçari *(Pteroglossus torquatus)*, Masked Tityra *(Tityra semifasciata)*, Citreoline Trogon *(Trogon citreolus)*, Kiskadee Flycatcher *(Pitangus sulphuratus)*, Boat-billed Flycatcher *(Megarhynchus pitangua)*, Social Flycatcher *(Myiozetetes similis)*, and Scrub Euphonia *(Tanagra affinis)*. All these species except the parakeet were recorded at the same site by Leck (1969) who observed them feeding on *Trichilia cuneata* (Meliaceae) whose dehiscent fruit is clustered, about 10 mm diameter, and covered by a thin but relatively tough yellowish-orange husk (=pericarp). The two to four straw-colored seeds found in each *Trichilia* fruit are covered by a bright red-orange aril which is exposed when the fruit is ripe. With respect to color, position, availability, and size, the fruit and/or seed of *Trichilia* is similar to that of *Stemmadenia*. Chemical analysis of the aril of six samples, each sample containing 10 fruits, of *Trichilia cuneata* indicates that they also are similar nutritionally. The dry weight composition of *Trichilia* aril is 3 percent ash, 60 percent lipid, 22 percent carbohydrate, and 15 percent protein.

At Taboga, ripe fruits of *Trichilia* are most abundant in July, during the wet season, a month or more after the peak fruit availability for *Stemmadenia*. The two tree species share many dispersers, including Hoffmann's Woodpecker, Yellow-green Vireo, Red-legged Honeycreeper, Streaked Flycatcher, and Magpie Jay. Species common at *Trichilia* but absent from *Stemmadenia* were the Masked Tityra, Citreoline Trogon, Boat-billed Flycatcher, and the Collared Araçari. Of these species all but the Boat-billed Flycatcher (best described as omnivorous) are characteristically frugivorous, and their absence from *Stemmadenia* seems paradoxical.

To determine whether the morphology of a species imposed a constraint on the types of fruit that it could exploit, we divided the common species at Taboga into three groups based on intensity of utilization of *Stemmadenia* (great, slight, none). The groups were compared on the basis of body weight, ratio of wing length to tarsus length, and ratio of culmen length to culmen width. We presumed that these traits would reflect the ability of birds to hover under the *Stemmadenia* fruit and to insert their bills into the narrow opening in the husk. The analysis failed to detect any notable differences in morphology among the species in the three groups. Thus it seems unlikely that fruit utilization and, therefore, selection by birds depend upon external morphological characteristics related to feeding or, in this case, flight. However, the structure of the digestive tract may be shown to be an important factor. We were not able to determine why so many frugivorous birds at Taboga did not utilize *Stemmadenia*.

NUTRITIVE VALUE.—The aril of *Stemmadenia* contains a large proportion of lipid (table 4), as much as any other similar plant tissue. The protein level of the aril (11%) is also greater than most similar fleshy fruit tissues, but it is not as great as that of insects (Morton 1973). As a source of calories and nitrogen, the aril of *S. donnell-smithii* undoubtedly satisfies the qualitative requirements of adult birds. To determine the approximate quantitative importance of *Stemmadenia* to the diet, we estimated the proportion of total calories provided by *Stemmadenia* to the 10 species that utilized the fruit most regularly (table 11). Our estimates are based on (1) the average weight of an adult bird, (2) the minimum number of individuals that utilized the fruit, determined by the largest number of individuals seen at one time in a tree, and (3) the estimated number of pulp units removed in the three study areas in 17.5 hours of observations. The corrected daily rate of pulp unit utilization per individual (4) was based on a 13-hour day. Because all fruit was removed by birds, we multiplied the estimated pulp extraction rate by 2.25 to bring the exploitation rate up to the production rate of the trees. The estimated metabolizable energy of fruit consumed by birds (5) was based on a value of 0.10 kcal/pulp unit (aril only) calculated from data in table 5 and based on a dry weight of 0.017 g per aril. We assumed an assimilation efficiency of 80 percent and metabolizable energy equivalents of 9.45 kcal/g lipid, 4:30 kcal/g protein and 4.14 kcal/g carbohydrate (Ricklefs 1974). The estimated daily energy expenditure (DEE) of individuals (6) was calculated from the relationship.

$$\text{DEE (kcal/day)} = 317.7 \text{ weight (kg)}^{0.7052}$$

(King 1974). Although these calculations are tentative, they suggest that *Stemmadenia* fruit may provide up to one-quarter of the total energy requirements of individuals of several species. In seven of the ten species that most frequently utilize *Stemmadenia,* the fruit provides an estimated 16-25 percent of DEE. The percentages listed in column (7) of table 11 probably are exaggerated because the number of individuals of each species utilizing the fruit almost certainly was greater than our conservative estimates and because observed rates of pulp extraction were probably more accurate than corrected rates for small birds that removed one unit at a time. Furthermore, our conversion factor for metabolizable energy per aril is based on many unknown or poorly sampled factors and may be too large.

Because *Stemmadenia* fruit, as with most other fruits, has relatively little protein per kilocalorie of energy, it may not be a suitable food for young rapidly growing birds (Morton 1973, White 1974). We observed a pair of Hoffmann's Woodpeckers feeding young of unknown number and age near the pasture study area. Of 96 trips by the parents to the nest recorded during three hours of observations, only five are known to have followed feeding on the fruit of *Stemmadenia.*

For effective seed dispersal, plants which rely upon animals as dispersal agents must provide a food resource of adequate nutritional value so as to attract potential dispersal agents. Attractiveness and hence seed dispersal presumably vary in direct relation to nutritive value of the pulp. Some balance, however, must exist between the allocation of resources to seed dispersal and the allocation to other aspects of reproduction. In *Stemmadenia,* the nutritional and energetic costs of producing fruit are partitioned among the husk for protection, the arils for dispersal, and the seeds for germination and early seedling survival. The alternatives—whether a tree is better off making a few, large, predator-free seeds that have a moderate probability of being dispersed and of germinating into viable seedlings or making many seeds, many of which will be destroyed by predators, some of which will be dispersed, and a few of which will germinate successfully—were discussed by Harper *et al.* (1970) and McKey (1975). It generally is agreed that primary forest trees follow the first strategy while second-growth species commonly follow the second (Harper *et al.* 1970, Pijl 1972). Even though *Stemmadenia* is common in edge situations, it has a primary forest-tree strategy.

The investment by the tree in each fruit component was estimated by taking the product means of the caloric value/ash free g dry weight multiplied by the ash free dry weight (table 5) for each sample. This procedure assumes that the cost of producing a caloric equivalent in a seed, an aril, and a husk is equal. From these calculations it is obvious that the greatest total number of calories are expended by the tree for fruit protection (husk = 47.230 kcal/total ash free g dry wt.), followed by germination (seed = 38.003) and dispersal (aril = 12.785). This pattern essentially reflects the percentage dry weight of an average fruit made up by the three components (fig. 6). However, it should be emphasized that qualitatively the components are quite different (e.g., aril contains a much higher percent lipid than other components). Thus, the caloric

TABLE 11. *Estimates of the proportion of daily energy expenditure provided by feeding on the fruit of* Stemmadenia donnell-smithii.

| Species | (1) Adult weight (g) | (2) Min. no. indiv. | (3) Rate of fruit extraction Observed (u/17.5 h.) | (4)[a] Corrected (u/13h/ind) | (5)[a] (kcal/ind/day) | (6)[a] Est. DEE (kcal/ ind/day) | (7)[a] Energy value of fruit (% DEE) |
|---|---|---|---|---|---|---|---|
| Hoffmann's Woodpecker | 82 | 2 | 151 | 126 | 12.6 | 54.5 | 23.1 |
| Magpie Jay | 224 | 3 | 91 | 51 | 5.1 | 110.6 | 4.6 |
| Tropical Kingbird | 42 | 2 | 76 | 64 | 6.4 | 34.0 | 18.8 |
| Swainson's Thrush | 31 | 2 | 62 | 52 | 5.2 | 27.4 | 19.0 |
| Red-legged Honeycreeper | 14 | 3 | 59 | 33 | 3.3 | 15.7 | 21.0 |
| Yellow-green Vireo | 18 | 2 | 54 | 45 | 4.5 | 18.7 | 24.0 |
| Yellow Warbler | 10 | 2 | 33 | 28 | 2.8 | 12.3 | 22.8 |
| Northern Oriole | 35 | 1 | 30 | 50 | 5.0 | 29.9 | 16.7 |
| Pale-billed Woodpecker | 229 | 1 | 27 | 45 | 4.5 | 112.4 | 4.0 |
| Turquoise-browed Motmot | 64 | 3 | 25 | 14 | 1.4 | 45.7 | 3.1 |

[a] Note: $(4) = \frac{(3) \times 2.25 \times 13}{(2) \times 17.5}$; $(5) = (4) \times 0.10$ kcal/pulp unit; $(6) = 317.7 \times \text{weight (kg)}^{0.7052}$; $(7) = 100 \times (5)/(6)$. See text.

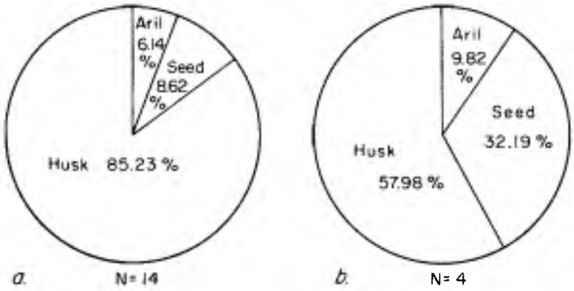


FIGURE 6. Percent distribution of total fruit weight among aril, seed, and husk of *Stemmadenia donnell-smithii*. A = wet weight, B = dry weight. Values calculated as means for fruits sampled.

values per ash free gram dry weight of tissue of each component show a trend opposite to that of total expenditure with the plant investing the greatest amount/gram of aril tissue ($\bar{x} = 7.156$ kcal), followed by the seed ($\bar{x} = 6.015$ kcal) and the husk ($\bar{x} = 5.866$ kcal). While protection from seed predators is provided primarily by the husk, dispersal also is a means of escaping seed predation.

The constancy of composition of the seed and husk contrasts with variation in the composition of the aril (table 4). Levin (1974) reported that lipid content of seeds was relatively constant within a species, and, although exceptions exist (e.g., Snell 1976), the lipid content of most species is not influenced by density, climate, or soil minerals. Selection should constrain the quality of the seed closely because the seed's properties determine the survival of an individual. Optimum seed quality should vary according to habitat (Harper *et al.* 1970). The composition of the husk may also be constrained by structural requirements for adequate protection from seed predators. Over short intervals, the quality of the aril is not, however, rigidly constrained. The feeding behavior of birds probably does not respond directly to variation in nutritional quality of fruit among individual trees unless this variation is consistently associated with habitat or some other environmental cue.

How then can we explain the variation in aril quality reflected in the variation in lipid, protein and caloric content among samples from different fruits, habitats, and years (tables 4, 5)? In our opinion, flexibility should be expected here. We are not suggesting that dispersal is less important to the plant than protection or germination. In fact, we suspect the opposite. Rather we suggest that the nature of the dispersal system in *Stemmadenia* promotes retention of flexibility and provides a mechanism of promoting exploitation of favorable environmental changes and of minimizing detrimental ones. Most of the avian dispersers of *Stemmadenia* are thought to be primarily insectivorous although a few species (e.g., manakins) are primarily frugivorous. An environmental change, such as the formation of a natural light gap in the forest, may enable a tree (subject to that change) to produce a fruit crop larger than usual compared to other trees in the forest. Any chance overproduction of fruit would be wasted if the dispersal community was entirely frugivorous in nature. An increase in community size could be accomplished by an increase in the number of fruit eaters, but this would require a concomitant overproduction of fruit for all trees in the area through the year. Such a phenomenon is unlikely. A temporally isolated increase in frugivores also could be accomplished by the presence of a highly mobile frugivore community, such as reported for mixed feeding flocks, that could shift its activity spatially to exploit a short-lived superabundance of fruit. This practice is unlikely in the Taboga area due to the rarity of mixed feeding flocks of frugivores as evidenced by the low frequency of co-occurrence of bird species in fruit trees. However, the increased availability of *Stemmadenia* fruit does not go unexploited because species which are typically insectivorous and frequent in light gaps become opportunistic, partial frugivores and rapidly use this temporarily abundant resource. Likewise, a tree which energetically is capable of producing a larger fruit crop than normal but is limited by nutrient availability or some other factor can produce fruits whose arils are of lower quality (less calories, lower oil content) than average but make up for lower quality per pulp unit by increasing the total number of units (availability) and thus maintain an adequate dispersal community. We offer this as one explanation to account for some of the difference in the composition of arils from pasture versus forest fruits in the 1973 sample (table 4). Pasture trees consistently had the largest crops and arils with the lowest lipid content of all fruit sampled. It is also possible that the effect of the drought of 1972 (figs 1, 2) was manifested in the 1973 fruit crop, especially in the pasture trees (fig. 4). If the effects of the drought through some influence on tree physiology were manifest as decreased lipid production, we would expect it to be expressed most in quality of the aril and to be most severe in pasture trees. Drought conditions also would affect the food supply of insectivorous birds and promote utilization of an alternate food resource, in this case *Stemmadenia* fruit.

Finally, the morphological characteristics and the relative high nutritional quality of *Stemmadenia* fruit seem to support the idea that this species has evolutionarily captured a large number of opportunistic "insectivorous" species of birds for seed dispersal. Reliance on such species has pre-adapted the tree to grow in second-growth habitats where insectivorous birds are common, and may account for the relative success of *Stemmadenia* in disturbed habitats today.

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## APPENDIX

APPENDIX 1. *Notes on the Foraging Behavior of Birds at* Stemmadenia *Fruit.*

TURQUOISE-BROWED MOTMOT. Removes pulp while hovering, always swallowing both seed and aril; hovering time variable according to ease with which the pulp is removed.

LINEATED WOODPECKER. Perches on the fruit, often suspended from the underside. Takes large amounts of pulp at one time without removing seeds. Visits trees infrequently.

HOFFMANN'S WOODPECKER. Perches on the fruit or its pedicel, often hanging from the distal surface of the fruit to remove pulp. May swallow pulp or may remove seeds swallowing aril only.

PALE-BILLED WOODPECKER. Perches on the fruit, often hanging from the distal surface. Takes large amounts of pulp at one time without removing seeds. Visits trees infrequently.

TROPICAL KINGBIRD. Removes pulp while hovering below fruit. Swallows pulp without separating seeds and aril.

SULPHUR-BELLIED FLYCATCHER. Hovers below fruit while removing pulp which is swallowed unseparated.

STREAKED FLYCATCHER. Hovers below fruit to remove pulp which is swallowed unseparated.

DUSKY-CAPPED FLYCATCHER. Removes pulp while hovering below fruit. Swallows pulp unseparated.

YELLOW-OLIVE FLYCATCHER. Hovers beneath fruit to feed.

GREENISH ELAENIA. Hovers beneath fruit to feed.

MAGPIE JAY. Perches on the fruit and reaches around into opening beneath. Removes a great deal of pulp at one time; swallows it unseparated. Visits trees infrequently.

RUFOUS-NAPED WREN. Hovers beneath fruit to feed. Swallows seed and aril.

SWAINSON'S THRUSH. Feeds while hovering below fruit, or perches on adjacent branch and reaches into nearby fruit. Swallows pulp unseparated.

YELLOW-GREEN VIREO. Usually hovers below fruit, often for long periods. Sometimes picks out pieces of aril without seeds.

GRAY-HEADED VIREO. Hovers beneath fruit to feed.

RED-LEGGED HONEYCREEPER. Feeds while hovering below fruit. Picks out pieces of aril or occasionally swallows unseparated pulp. Often plucks pulp and manipulates it roughly with the bill to remove seed but also losing much aril at the same time.

YELLOW WARBLER. Hovers below fruit to feed. Picks out pieces of aril. Probably never swallows seeds.

CHESTNUT-SIDED WARBLER. Hovers beneath fruit to feed.

NORTHERN ORIOLE. Perches on the fruit and reaches around into opening beneath, or perches on adjacent branch and reaches into nearby fruit. Removes pulp unseparated and often holds it underfoot on a perch while pecking at it. Loses up to half the aril.

WHITE-COLLARED SEEDEATER. Hovers below fruit to feed. On one occasion held pulp underfoot on perch while removing aril. May feed on the seed rather than the aril.

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