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# Fig-Seed Predation and Dispersal by Birds

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## ABSTRACT

Observations of birds eating the figs of a single *Ficus continifolia* (H.B.K.) tree in Costa Rican lowland deciduous forest indicate that a crop of *ca* 100,000 figs was exhausted in five days, of which 95,000 were removed during the first three days. Birds processed an estimated average of 20,828 figs/day (65.1% of the total daily consumption), and the difference (34.9%) represented fruits consumed by mammals and/or those falling to the ground. Parrots were responsible for 78 percent of the total taken by birds and 50.6 percent of the figs leaving the tree per day. Use by these seed predators represents fruit (and seed) waste. The "true" avian dispersers (*e.g.,* orioles, tanagers, trogons, flycatchers) took only *ca* 4600 figs/day. An estimated $4.42 \times 10^6$ fig seeds were lost each day, 36.2 percent of them to parrots and 63.8 percent to destruction by invertebrates (mostly agaonid wasps). Only 6.3 percent of the seeds leaving the tree per day are actually dispersed undamaged by birds.

FIGS HAVE LONG BEEN RECOGNIZED as an important food for vertebrate frugivores in tropical habitats (Hladik *et al.* 1971, Leck 1972, Fleming *et al.* 1977, Bonaccorso 1979). In spite of being a prominent element in tropical woody vegetation, the relative contribution of the various consumer organisms to the seed shadow is poorly known (Janzen 1979b).

I report here observations of birds eating the fruits of a single *Ficus cotinifolia* (H.B.K.) tree in the lowland deciduous forest of Santa Rosa National Park (Guanacaste Province, Costa Rica). A description of study area may be found in Fleming *et al.* (1977). The study tree was located close to the park's access road, on the border between a dry-deciduous forest stand and a large area covered with African pasture grass, *Hyparrhenia rufa,* Stapf., and scattered shrubs (e.g., *Acacia collinsii,* Safford; *Eugenia* sp.). The tree was 10 m high, and horizontal crown protection was approximately 15 m in diameter. At the time of observation, the crown was leafless and bore numerous figs. New leaves started to flush when the fig crop had been exhausted by frugivores.

## METHODS

I watched the tree crown between 3 and 7 March 1980, spending *ca* 20 h observing the foraging behavior of birds visiting it. For each individual bird, the total time spent in the crown, the number of fruits eaten, and the type of foraging behavior were recorded whenever possible. Observations were coded either as "total," if including all the visit length, or "partial," if only a part of the visit was observed. Only total observations were used to compute mean visit length, but both were employed to calculate feeding rates.

Specific visitation rates for the principal species were estimated from scores derived during the observation period. However, owing to the enormous visitation rates, which made it impossible to record all entrances and exits, and the difficulty of watching the whole crown from any single observation point, the scores were bucked as follows: <5 visits/h, 5–10, 10–20, 20–40, and 40–80 visits per hour; then specific visitation rates were obtained by taking the midpoints for each of the above intervals (*i.e.,* 2.5, 7.5, 15, 30, and 60 visits/h).

Fresh, ripe figs were obtained from the tree, measured (length and width) and weighed (to the nearest 0.1 g) in the field. Total dry weight (to the nearest 0.01 g), number of seeds (both intact and with wasp exit holes or wasp inside), total dry weight of seeds ("seed load"), and pulp dry weight ("pulp load") were obtained in the laboratory after drying the sample at 60°C for 48 h. A pulp sample was prepared to obtain nutrient contents by standard analytical procedures. Measurements are given as mean ± one SD (Table 1).

## RESULTS

Crop size on 3 March was estimated at 100,000 figs, which made up about 95 percent of the total crop, 29.1 ± 15.8 percent of them being ripe (based on 287 figs on 20 branch counts). Thus, the figures reported below are to be referred to the entire crop, as only a few fruits were missing when the observations started. Standing crop size decreased dramatically to 100–500 unripe figs by 7 March, mainly due to direct consumption by frugivores but also by an unquantified fall to the ground. On 5 March, only 5000 figs, mainly unripe, were available on the tree. From the above figures I estimate that nearly 100,000 fruits left the crown during the five days of observation. However, about 95,000 of them were exhausted during the first three days, representing an average daily "fruit exit" of about 32,000 figs.

Fresh, ripe figs measure 9.5 ± 0.8 mm long and 11.6 ± 0.9 mm wide ($N = 15$). The average fruit has a

TABLE 1. *Nutrient composition of pulp of* Ficus cotinifolia *figs from the study tree, Santa Rosa National Park, Guanacaste Province, Costa Rica.*

| | Lipid | Protein[a] | Soluble[b] carbohydrates | Fiber | Ash |
|---|---|---|---|---|---|
| Average dry wt. (g) per fig | 0.004 | 0.007 | 0.081 | 0.033 | 0.012 |
| Percent[c] | 2.7 | 5.3 | 59.5 | 23.7 | 8.8 |

[a] N × 6.25.
[b] Obtained by difference.
[c] On a dry-weight basis.

fresh weight of 0.6 g, of which 66.4 percent is water, and contains 238 ± 42 seeds of 0.25 ± 0.06 mg. Mean dry weight of individual figs is 0.21 ± 0.05 g, of which 0.14 ± 0.03 g represents the pulp. Table 1 shows the relative nutrient content of the pulp, representing a gross caloric content of 0.54 Kcal/fruit (computed using conversion factors of 9.5, 5.7, and 4.0 Kcal/ash-free g for lipids, protein, and total carbohydrate, respectively [Kleiber 1961]).

Twenty-one species of bird were common visitors which ate figs or fig parts (Table 2), and the following species were recorded eating figs at least once: *Leptotila verreauxi, Piaya cayana, Trogon elegans, Myiozetetes similis, Piranga rubra,* and *Penelope purpurascens,* all with <2.5 visits/h. Three species of parrots, *Brotogeris jugularis, Aratinga canicularis,* and *Amazona albifrons,* were the most frequent and conspicuous visitors. They usually mandibulated both ripe and unripe figs with the aid of their feet, dropping pieces of the fruit wall (with an unknown amount of seeds attached) under the crown. Consumption by parrots accounted for 77.7 percent of the figs taken daily by birds. Parrots are to be considered seed predators rather than dispersers, as they usually crack and/or digest all the fig seeds ingested (Olson and Blum 1968, Janzen 1981). In contrast other species (including

TABLE 2. *Body sizes, visit rates, and statistics of feeding rates of the principal bird species recorded at a* Ficus cotinifolia *(H.B.K.) tree in Santa Rosa National Park, Guanacaste Province, Costa Rica. Figures are means ± SD, sample size in parentheses. Bracketed figures refer to partial observations only (see Methods).*

| | Body weight[a] (g) | Behavior[b] | Visit length (sec) | Fruits/visit[c] | Visit rate (vis/h) | Estimated[d] % fruits removed | Fruits/minute |
|---|---|---|---|---|---|---|---|
| Orange-fronted parakeet *Aratinga canicularis* | 85 | G, M, P | 195.6 ± 117.8 (8) | 14.8 ± 9.5 (8) 4–31 | 30 | 25.3 | 4.1 ± 1.6 (8) |
| Orange-chinned parakeet *Brotogeris jugularis* | 60 | G, M, P | (e) | [12.7 ± 11.6 (10)] [2–37] | 60 | 43.5 | 4.5 ± 1.3 (10) |
| Black-headed trogon *Trogon melanocephalus* | 93 | F, I, D | 96.8 ± 35.4 (9) | 2.8 ± 0.4 (9) 2–4 | 7 | 1.1 | 2.5 ± 1.3 (11) |
| Hoffman's woodpecker *Centurus hoffmanni* | 82 | G, I, D | — | [3.1 ± 1.5 (7)] [1–5] | 7 | 1.2 | 3.2 ± 2.0 (7) |
| Magpie jay *Calocita formosa* | 224 | G, I, D | 101.0 ± 55.2 (5) | 7.2 ± 2.8 (5) 3–10 | 7 | 2.9 | 5.2 ± 2.1 (9) |
| Baltimore oriole *Icterus galbula* | 35 | G, M, I, D | 147.2 ± 34.2 (4) | 7.0 ± 1.6 (4) 5–[14] | 15 | 5.8 | 3.0 ± 0.8 (9) |
| Western tanager *Piranga ludoviciana* | 32 | G, I, D | 159.9 ± 79.3 (9) | 5.9 ± 3.5 (9) 2–14 | 30 | 10.1 | 2.3 ± 0.9 (13) |
| Boat-billed flycatcher *Megarhynchus pitangua* | 75 | F, I, D | — | [3.3 ± 0.9 (3)] [2–4] | 5 | 0.9 | 2.5 ± 0.2 (3) |
| White-fronted parrot *Amazona albifrons* | 202 | G, M, P | (e) | [9.5 ± 6.2 (4)] [4–20] | 15 | 8.1 | 3.3 ± 1.4 (4) |
| Others[f] | | D | — | — | 2.5 | 0.9 | — |

[a] Sources for bird weights: McDiarmid *et al.* 1977, Howe 1977, Howe and Steven 1979, Willis 1980, and specimen labels in the museum of the Escuela de Biología, San José, Costa Rica.
[b] M, mandibulates the fruit; I, ingests the whole fruit; G, gleaning; F, flycatching; D, seed disperser; P, seed predator.
[c] Both minimum and maximum number of fruits ingested/visit are given, bracketed figures for partial observations.
[d] Fruits/visit × visit rate as a percentage of total number of fruits eaten daily by birds.
[e] Visits of variable duration, never being <300 sec.
[f] Including *Euphonia affinis, Muscivora forficata, Myarchus nuttingi, Ramphastos sulfuratus, Turdus grayi,* and *Cyanerpes cyaneus.*

*Piranga ludoviciana, Icterus galbula, Calocitta formosa, Centurus hoffmanni, Trogon melanocephalus,* and *Megarhynchus pitangua*) showed the characteristic behavior of true dispersers: ingesting the whole fruit, and leaving the tree after relatively short visits with no reason to believe that the seeds were damaged (Olson and Blum 1968). Among these species, the commonest visitors were *P. ludoviciana* and *I. galbula,* taking together 15.9 percent of the fruits consumed daily by birds. The remaining species (see Table 2) made negligible contributions to fig removal, owing to their infrequent visits, but they too are probably true dispersers.

Transportation by birds is only one of the ways for fig seeds to leave the parent tree, for bats are well known for their high dependence on figs for food (Fleming *et al.* 1977, Morrison 1978, Bonaccorso 1979). I also observed a coati (*Nasua nasua*) ingesting up to 400 figs over a period of 40 minutes, and these mammals occur in groups of up to 10 individuals foraging in the early morning. I also recorded *Odocoileus virginianus* and *Tayassu tajacu* foraging directly below the tree crown, probably for fallen figs. Aside from the deer, both peccaries and coatis pass seeds intact and, at least for peccaries, nearly 100 percent germination is obtained from seeds in faeces (Janzen, pers. comm.).

The number of figs eaten daily by birds was estimated (data presented in Table 2), by multiplying visitation rates by specific mean ingestion rates per visit. This calculation yields a conservative estimate because only partial observations are available for some species and thus the number of figs taken per visit is underestimated. Furthermore, only 10 of the 21 species recorded were considered due to the negligible importance of the removal by the remaining 11 species (Table 2). Birds processed an estimated 20,828 figs/day, representing 65.1 percent of the total number of figs disappearing from the tree each day. According to this estimate, the figs consumed by mammals and/or fallen to the ground made up the remaining 34.9 percent. The points to be emphasized are, firstly, that about 78 percent of the fruits taken daily by birds are taken by predatory parrots, a loss constituting about 50 percent of the figs leaving the tree each day; and secondly, the genuine avian dispersers take only 22.1 percent of the fruit taken by birds and only 14.5 percent of the fruit leaving the crown.

## DISCUSSION

This fig-consumer assemblage is among the most diverse reported for tropical trees with regard to species number and taxonomic affinities. The robust stems with sessile or subsessile figs allow both small and large potential dispersers to have access to the fruit by a variety of foraging behaviors. It is remarkable that the avian consumers recorded at this tree ranged in body weight from 8 to 800 g.

The small seeds may represent an escape from the high seed-predation pressure by animals which mandibulate the fruit and may crack some seeds (*e.g.,* deer and coatis). However, this strategy also enables the small consumers with gape widths smaller than the figs to mandibulate and/or peck the fruit to remove pulp with some seeds, as if they were ingesting a smaller fruit. These adaptations may account for the high-diversity consumer assemblage noted above.

Janzen (1979b) argued that the absence of toxic compounds in the fruit pulp may also contribute to the high consumer diversity observed at fig trees. Large consumers can ingest the maximum fruit loads at each visit, without decrease in the assimilation efficiency which follows the presence of digestion-inhibitors (*e.g.,* tannins) and other compounds. However, the fig pulp is very rich in fiber (up to 23.7% dry weight) which has a negative correlate with digestibility, and has very low protein and fat contents. Figs probably represent a readily utilizable source of calories and water (0.54 Kcal and 0.40 g water per fruit), but fail to provide a balanced diet to frugivores feeding on them (Morrison 1978). Thus, several species recorded at the fig tree (*e.g.,* tanagers, guans, trogons, and jays) were observed feeding on other fruits available at that time (*e.g., Muntingia calabura,* L., *Bursera simarouba* (L.) Sarg., *Ardisia revoluta,* Humboldt, Bonpland and Kunth).

If different individual trees were widely dispersed in the habitat (Fleming *et al.* [1977] report 0.6 individuals per hectare for *F. cotinifolia*) and asynchronous in their fruiting (Morrison 1978), they probably interact with different sets of consumers. Thus, the avian assemblages of conspecific *F. cotinifolia* trees fruiting some weeks later or earlier from the one observed could lack important North American true dispersers. Fig-tree populations may also show a high between-crop consumer diversity.

In addition to seed destruction by birds in the dispersal phase, another characteristic feature of the reproductive pattern of fig trees is the very large fraction of the seed crop lost during the period from flower development to seed dispersal. Janzen (1979a) has shown that seed destruction by wasps in wild figs from Santa Rosa ranged from 41 to 77 percent, averaging about 55 percent. My own data indicate that 56.6 percent of the fig seeds ingested by a bird are unsound. How many seeds were sacrificed for the pollination and dispersal of this tree's seeds? This question can only be answered partially for I have quantified only avian activity at the tree. The main results are summarized in Table 3. On a daily basis, the fig tree pays $4.42 \times 10^6$ seeds in dispersal by birds, 36.2 percent of them in parrot predation plus the remaining 63.8 percent destroyed in advance by invertebrates (mostly agaonid wasps). Only 9.8 percent of the

TABLE 3. *Summary of the estimated number of seeds leaving daily the crown of the* Ficus cotinifolia *tree studied in Santa Rosa National Park, Guanacaste Province, Costa Rica. Figures were calculated assuming an average of 238 seeds/fig. See text for explanation.*

| Removed by birds | Number of seeds | % |
|---|---|---|
| Parrots | $3.8 \times 10^6$ | 50.0 |
| Invertebrate predation | $2.2 \times 10^6$ | 28.9 |
| Parrot predation | $1.6 \times 10^6$ | 21.1 |
| "True" dispersers | $1.1 \times 10^6$ | 14.5 |
| Invertebrate predation | $6.2 \times 10^5$ | 8.2 |
| Voided undamaged | $4.8 \times 10^5$ | 6.3 |
| Total by birds | $4.9 \times 10^6$ | 64.5 |
| Total estimated daily output | $7.6 \times 10^6$ | 100.0 |
| Not accounted for[a] (by difference) | $2.7 \times 10^6$ | 35.5 |

[a] Presumably due to consumption by mammals and/or fallen to the ground.

seeds removed from the tree by birds are actually dispersed undamaged (see Table 3). However, if birds select individual figs on the basis of the overall size or the amount of pulp/fig, then they actually ingest those figs with more viable seeds inside, as both fig dry weight and pulp dry weight/fig are negatively correlated with the percent seeds damaged by invertebrates ($r = -0.57$, $P < 0.05$ and $r = -0.72$, $P < 0.01$, respectively). This condition should result in more seeds being defecated undamaged in spite of parrots also selecting the more "rewarding" figs.

The fig tree lost more seeds during the dispersal stage. Figs on the ground below the parent's canopy are readily attacked by lygaeid bugs, which may destroy all their seeds (Slater 1972). An important fraction of the figs on the ground may be "recovered" and subsequently dispersed by ground-foraging mammals such as peccaries and coatimundis. However, like the variable seed losses during pollination shown by conspecific fig trees (Janzen 1979a), seed losses during the dispersal stage probably also show high intertree variability, as crops separated both in time and space interact with different sets of dispersers and predators. More information is needed on intercrop impact of seed predators and dispersers, as well as quantifications of fruit fall and activity of nocturnal consumers.

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