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# Fruiting and frugivores at a strangler fig in the tropical rain forest of Los Tuxtlas, Mexico

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ABSTRACT. Diurnal and nocturnal censuses were conducted on animal visitors at a single strangler *Ficus* aff. *cotinifolia* (H.B.K.) tree during the entire period of ripe fruit availability. Fruit fall to the ground was measured with fruit traps, and chemical analyses were conducted on the figs. Fourteen species of birds, four species of nonvolant mammals and two species of bats consumed the figs. Of the total number of ripe figs accounted for during the sampling period ($N = 1.9 \times 10^5$), 42% fell to the ground, 45% were removed by mammals and 13% by birds. Frugivores such as the howling monkey *Alouatta palliata*, the cacomistle *Bassariscus sumichrasti*, the keel-billed toucan *Ramphastos sulphuratus* and fruit-eating bats removed the largest amounts of figs from the tree and deposited seeds of 13 plant species other than figs below the tree crown.

RESUMEN. Se llevaron a cabo censos diurnos y nocturnos de los animales que visitaron un higo estrangulador, *Ficus* aff. *cotinifolia* (H.B.K) durante el periódo completo de disponibilidad de higos maduros. La lluvia de higos bajo la sombra de la copa del àrbol se medió por medio de trampas de colecta de frutos y muestras de los higos fueron sometidas a anàlisis quimicos. Catorce especies de aves, cuatro especies de mamiferos no voladores y dos especies de murcielagos fueron observados alimentandose de los higos en la copa. Del total de higos contados durante el periódo de frutación ($N = 1.9 \times 10^5$), 42% cayeron al suelo, 45% fueron removidos por mamiferos y 13% por aves. Frugivoros como el mono alluador (*Alouatta palliata*), el cacomixtle (*Bassariscus sumichrasti*), el tucàn (*Ramphastos sulphuratus*) y murcielagos consumidores de frutos retiraron la mayor cantidad de higos durante sus visitas al àrbol y depositaron las semillas de 13 especies de plantas bajo la sombra de la copa.

KEY WORDS: *Ficus*, frugivory, México, seed dispersal, tropical rain forest.

## INTRODUCTION

Fruiting fig trees attract highly diverse frugivore assemblages that disperse huge numbers of seeds over large areas (August 1981, Breitwisch 1983, Janzen 1979a, Jordano 1983). Although figs do not seem to be especially nutrient rich and contain considerable amounts of indigestable fibre (Milton 1980, Morrison 1978), they are an important food item in the diet of fruit bats (Bonaccorso 1979, Morrison 1978), primates (Estrada & Coates-Estrada 1984, Milton 1980) and other frugivores. In spite of the ubiquitous nature of fig trees in tropical forests the world over, studies of frugivore assemblages at fruiting fig trees are few (Breitwisch 1983, Jordano 1983, Wheelwright *et al.* 1984) and have not considered fruit fall, the foraging activity of all animal visitors (diurnal and

nocturnal), or the possible consequences of frugivore activity for dispersal success. The aim of this paper is to report fruit fall as well as fig-eating activity of diurnal and nocturnal consumers during rip fruit production of a single strangler *Ficus* aff. *cotinifolia* (H.B.K.) (Moraceae).

## METHODS

*Study site.* The study was conducted at the biological reserve Los Tuxtlas in southern Veracruz, Mexico (95° 04′ W, 18° 34′ N; elevation 150–530 m). The dominant vegetation type is tall evergreen rain forest (Miranda & Hernandez 1963). The climate is hot and humid with mean annual temperature of 25°C; mean annual precipitation is 4900 mm (see Estrada & Coates-Estrada 1984).

*Fruit production.* The 30 m tall strangler *Ficus* tree we studied was located in primary forest and had become self-supporting; the death of the host tree (*Brosimum alicastrum*, Moraceae) occurred years earlier. The tree had an estimated crown projection of 1350 $m^2$. Observations were conducted from 3 March to 30 May 1983. To estimate fruit fall, 135 circular fruit traps (0.5 m in diameter and 0.5 m above ground level) were placed on the ground under the area of the crown. Contents of the fruit traps were collected every two days and there was no evidence of fruit removal by terrestrial vertebrates. Fruits were sorted (fig and non-fig), counted, and weighed before and after oven-drying at 60°C for 24 hours. Chemical analysis of the nutrient content of the fruit wall and florets (seeds excluded) using standard techniques (Flores 1981) were conducted at the Animal Nutrition Laboratory, Veterinary School, University of Mexico.

*Animal visitors.* We conducted diurnal and nocturnal scan censuses every two days during the tree's fruiting period. The day scans (0600–1800 hrs) were conducted with the aid of binoculars (8 × 30) 30 m from the trunk where at least 50% of the crown was visible. On each observation day 24 scans (2 per hr of 15 min duration each) were completed. At night, 8 scans were completed (2 per hr) between 1900 and 2300 hrs (a peak of animal activity: A. Estrada, personal observation) with the aid of binoculars, lantern, and sometimes a night viewing device (Javelin Electronics, model 221) from the same vantage point. During diurnal and nocturnal observations intervals of one half-hour occurred between scans. In each scan all animals detected foraging were followed visually until they were out of sight. When a flock of birds arrived, we concentrated on one individual bird at a time. For each animal visitor (except bats), we recorded the following: identity, number of figs ingested per minute, time spent feeding and, for birds, flight direction (within the crown or away from the trees). To obtain identity of some of the bat species visiting the trees we placed two mist nets 3.0 m above ground under the crown for three consecutive non-lunar nights (1900–2300 hrs) on two separate occasions.

In total, we completed 156 and 52 hours of diurnal and nocturnal observations spaced throughout the fruiting period of the tree. Fig removal by animal

visitors was calculated as follows: (visits per hr) X (12 hr observation day or 4 hr observation night) X (number of days the animal was observed feeding at the tree) X (visitation length in minutes) X (fruits removed per minute). To obtain data on fig consumption by bats, we counted the number of feeding passes per unit time to the part of the crown under observation. Fruit removal by these volant mammals was estimated as follows: (passes per hr) X (10 days of records) X (125 fruits = 75 g). The 125 fruits represent 75 g of fruit required per night by a 50 g bat to maintain metabolic balance assuming the bat only consumed figs. These calculations were based on the food intake requirements reported for *Artibeus jamaicensis* (Morrison 1980) and therefore represent a crude estimate of fig removal because other larger (e.g. *Artibeus lituratus*) and smaller (e.g. *Vampyrodes major*) bat species were also known to consume figs.

## RESULTS

*Fruit characteristics.* The figs of the tree were small (x = 1.0 SD ± 0.01 cm in diameter; N = 100) and dark red in colour when ripe. Mean (± SD) fresh weight of a fig was 0.60 ± 0.20 g and dry weight was 0.13 ± 0.05 g; water content was 78%. The mean (± SD) number of seeds per fruit was 240.6 ± 15.6 (N = 100). Chemical analysis (means ± SD of five replicates in each case) of the figs indicated moderate amounts, on a dry weight basis, of nutrients such as protein (N X 6.25; 8.0 ± 1.9%), lipids (7.7 ± 0.6%), soluble carbohydrates (52.3 ± 3.0%) and metabolizable energy (13.3 kJ); the fibre content of figs was relatively high (25.6 ± 1.0%).

*Fruit fall.* Fruit fall lasted 52 days owing to the gradual ripening of figs. A major peak occurred between the 15th and 21st days after the onset of fruiting. This peak contributed to 43% of the total estimated fruit fall for the entire crown ($N = 8.0 \times 10^4$ figs) (Figure 1).

*Visitor guild.* Twenty-eight species of animals were recorded visiting the tree. Of these, 20 were observed feeding on the figs during the observation periods. Fourteen were bird species (eight additional bird species were observed foraging for insects only) of which six were North American migrants, four were non-volant mammals and two were bats (Table 1). Mist-nets captured the bats *Artibeus jamaicensis, Artibeus lituratus, Carollia brevicauda,* and *Glossophaga soricina.* The only species which showed conclusive signs of fig consumption, either by seed defecation or fruit pulp in mouth, were *A. jamaicensis* and *A. lituratus.* The number of captures for *A. jamaicensis* was greater than that for *A. lituratus* (6 vs 1).

Very little ground-feeding activity was noted on the fallen figs. On two different occasions an agouti, *Dasyprocta mexicana*, was observed foraging under the tree crown. Two doves, *Geotrygon montana* and *Leptotila rufaxilla*, were observed, each on separate days, feeding on fallen figs. Sherman live-traps placed under this tree and baited with ripe figs captured the rodents *Peromyscus mexicanus* and *Heteromys desmarestianus.* Determination of ingestion rates

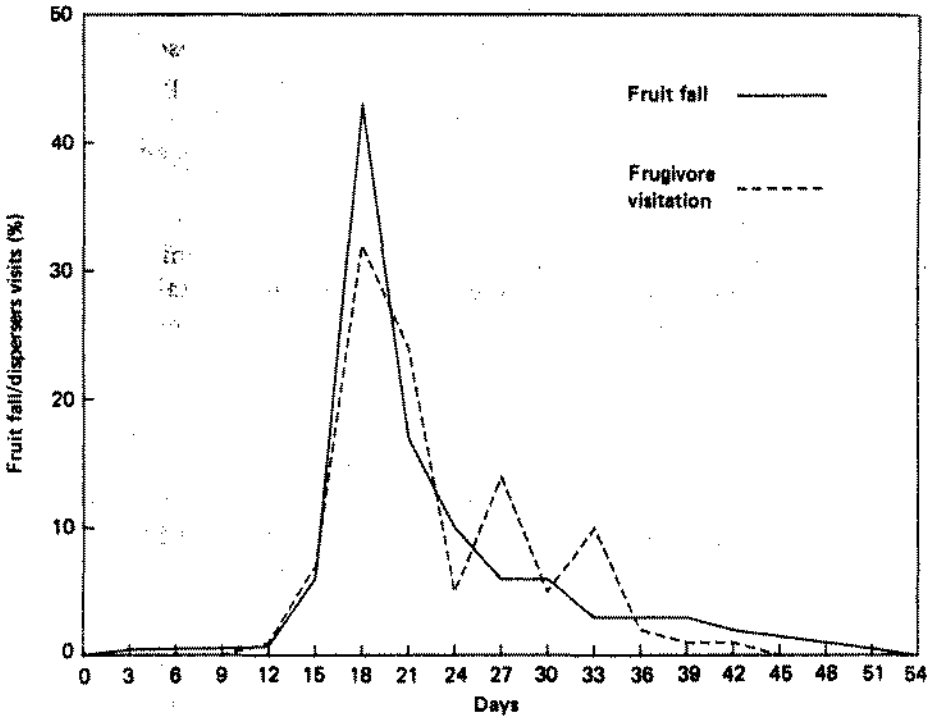


**Figure 1. Fruit fall ($N = 8.0 \times 10^4$) and frugivore visitation ($N = 20$ species) at a strangler fig during the entire fruiting period.**

by these species was not possible. Disturbance resulting from our presence may have caused other terrestrial animals to avoid the tree. We found that the figs were readily taken by captive coatis, *Nasua narica*, collared peccaries, *Tayassu tajacu*, and tayras, *Eira barbara*.

*Frugivore visits and fruit removal.* Percent of figs ingested by frugivores and visits to the tree per hour were positively correlated with frugivore body weight ($r_s = 0.76$, $P < 0.05$, $N = 19$; $r_s = 0.58$, $P < 0.05$, $N = 18$) indicating that this is a major variable affecting fruit ingestion rates at the fig tree. Of the total number of ripe figs accounted for throughout the fruiting period (figs removed by animals + figs dropped to the ground = $1.9 \times 10^5$), 13% and 45% were taken by birds and mammals respectively and 42% fell to the ground (Table 1). On a daily basis about $7.1 \times 10^3$ figs were removed from the tree by birds and mammals and increased foraging activity by frugivores to the tree matched the observed peak in fruit fall (Figure 1). The most important fig removers were *Alouatta palliata* (23%), *Bassariscus sumichrastri* (17%), *Ramphastos sulfuratus* (6%), *Columba nigrirostris* (4%) and *Pteroglossus torquatus* (2%) (Table 1).

Three species of birds that ate the figs possessed either bill morphology or digestive adaptations for seed crushing (*Columba nigrirostris, Caryothraustes poliogaster* and *Cyanacompsa parellina*) and removed 5% of all ripe figs; they may have destroyed some of the seeds they ingested (about $1.0 \times 10^6$ seeds daily); of these, *C. nigrirostris* was the most important as it removed 33% of the

Table 1. List of animals observed feeding on ripe figs of the strangler fig tree.

| Taxa | Weight (g) ($\bar{x}$)[a] | Fruits per min $\bar{X} \pm SD$ | Visits per hr | Visit length (min) $\bar{X} \pm SD$ | Fruits removed %[b] | Flight away % |
|---|---|---|---|---|---|---|
| **BIRDS** | | | | | | |
| COLUMBIDAE | | | | | | |
| *Columba nigrirostris* (Short-billed Pigeon) | 162 (5) | 5.0 ± 1.0 | 1.8 | 8.3 ± 5.7 | 4.0 | 20 |
| RAMPHASTIDAE | | | | | | |
| *Pteroglossus torquatus* (Collared Aracari) | 198 (4) | 7.0 ± 0.8 | 1.0 | 7.2 ± 3.2 | 2.0 | 100 |
| *Ramphastos sulphuratus* (Keel-billed Toucan) | 235 (5) | 9.0 ± 1.5 | 2.0 | 5.0 ± 2.3 | 6.0 | 67 |
| MUSCICAPIDAE | | | | | | |
| *Catharus ustulatus* (Swainson's Thrush)* | 33 (15) | 5.0 ± 0.2 | 0.2 | 5.0 ± 0.2 | 0.03 | – |
| *Hylocichla mustelina* (Wood Thrush)* | 46 (15) | 5.5 ± 0.6 | 0.2 | 5.6 ± 1.1 | 0.02 | – |
| *Turdus grayi* (Clay-coloured Robin) | 74 (9) | 4.5 ± 1.2 | 0.4 | 5.0 ± 2.0 | 0.11 | 100 |
| VIREONIDAE | | | | | | |
| *Vireo bellii* (Bell's Vireo)* | 8 (1) | 1.5 ± 0.1 | 0.2 | 5.0 ± 0.2 | 0.005 | – |
| EMBERIZIDAE | | | | | | |
| *Cynanerpes cyaneus* (Red-legged Honey-creeper | 19 (1) | 1.0 ± 0.1 | 0.3 | 4.0 ± 0.1 | 0.01 | 100 |
| *Euphonia hirundinacea* (Yellow-throated Euphonia) | 14 (5) | 1.0 ± 0.5 | 1.8 | 5.2 ± 2.5 | 0.54 | 20 |
| *Piranga rubra* (Summer Tanager)* | 28 (2) | 5.0 ± 1.0 | 0.4 | 4.2 ± 1.5 | 0.06 | – |
| *Piranga olivacea* (Scarlet Tanager)* | 27 (2) | 5.0 ± 0.2 | 0.8 | 4.2 ± 1.5 | 0.26 | – |
| *Caryothraustes poliogaster* (Black-faced Grosbeak) | 35 (5) | 5.5 ± 1.1 | 0.6 | 5.0 ± 0.1 | 0.20 | – |
| *Cyanocompsa parellina* (Blue Bunting) | 16 (3) | 5.5 ± 0.7 | 0.4 | 5.0 ± 0.1 | 0.04 | 100 |
| *Icterus galbula* (Northern Oriole)* | 37 (6) | 5.0 ± 0.9 | 0.4 | 5.0 ± 0.1 | 0.07 | – |
| **MAMMALS** | | | | | | |
| DIDELPHIDAE | | | | | | |
| *Didelphis marsupialis* (Opossum) | 1500 (8) | 7.5 ± 1.5 | 1.0 | 7.5 ± 1.7 | 1.0 | |
| PHYLLOSTOMIDAE | | | | | | |
| *Artibeus* spp. (Neotropical Fruit Bats) | 50 (6) | – | 0.9[c] | – | 2.0 | |
| CEBIDAE | | | | | | |
| *Alouatta palliata* (Howling Monkey) | 7500 (11) | 12.0 ± 3.1 | 1.2 | 25.0 ± 3.4 | 23.0 | |
| SCIURIDAE | | | | | | |
| *Sciurus deppei* (Tree Squirrel) | 250 (5) | 6.0 ± 1.4 | 1.0 | 6.2 ± 1.6 | 1.0 | |
| PROCYONIDAE | | | | | | |
| *Bassariscus sumichrasti* (Cacomistle) | 1000 (3) | 8.0 ± 2.5 | 2.5 | 21.0 ± 1.8 | 17.0 | |

a: Mean weights obtained at the study site from capture-mark-release studies (sample size).
b: Total number of fruits removed = $1.1 \times 10^5$.
c: Number of passes per hour.
*: North American migrants.

figs taken by birds. *Sciurus deppei*, a mammal seed/fruit eater, removed 1% of all ripe figs ($2.6 \times 10^5$ seeds daily) removed by frugivores (Table 1).

*Frugivore behaviour and seed dispersal.* Flights away from the fig tree immediately after fig ingestion were scored for only seven species of birds (Table 1). The two toucans (*R. sulfuratus* and *P. torquatus*) were the most important dispersers since more than 60% of their flights after feeding on ripe figs were away from the tree. The other species were observed to remain perching after

feedings and very likely defecated or regurgitated the seeds under the crown. The arboreal mammals remained in the tree for an average of 20 minutes, but since their food passage rates are generally slower than those of birds (18 hrs in *A. palliata*, 3–4 hrs in *B. sumichrasti* and *D. marsupialus*; Estrada & Coates-Estrada 1984 and unpublished data), the seeds they ingested were probably deposited away from the tree. Bats do not usually consume the figs in the tree but rather carry them away to feeding roosts (Morrison 1978). If we consider that, on average, about 50% of the seeds in figs are destroyed by wasps before dispersal (Janzen 1979b, Jordano 1983), we estimate that the number of seeds leaving the fig crown daily via birds and mammals was about $4.1 \times 10^3$.

*Foreign seeds.* The seeds of 13 other plant species were collected in the fruit traps placed under the tree crown [Moraceae - *Trophis mexicana* 28, *Pseudolmedia oxyphyllaria* 18; Meliaceae - *Guarea grandifolia* 25; Loganiaceae - *Strycnos tabascana* 7; Araceae - *Syngonium podophyllum* 6; Annonaceae - *Cymbopetalum baillonii* 6; Burseraceae - *Bursera simaruba* 5; Sapindaceae - *Paullinia pinnata* 3, *Cupania dentata* 2, *Allophylus campostachis* 1; Malpighiaceae - *Bunchosia lindeniana* 4; unidentified species 2 (three seeds)]. These seeds dispersed by avian and/or mammalian frugivores came from other fruit sources consumed concurrently with figs.

## DISCUSSION

*Frugivory and seed dispersal.* Of the many species that visited the strangler *Ficus* tree to consume the fruit and/or seeds, the most important seed dispersers were the howling monkey, *A. palliata*, and the cacomistle, *B. sumichrasti*. *A. palliata* is capable of ingesting many more figs than a bird per single feeding bout, has a slow food transit time through its digestive system, and moves variable distances daily in search of leaves and/or fruit, depositing viable fig seeds more than 200 m away from the original site of ingestion (Estrada & Coates-Estrada 1986). Smaller than a monkey, *B. sumichrasti* displayed short feeding bouts, was highly mobile, and conceivably dispersed most of the seeds it ingested. Fruit-eating bats such as *Artibeus* spp., are reported to have relatively fast food passage rates and consume the fruit, dropping and/or defecating the seeds, at feeding roosts located several dozens to hundreds of metres away from the fruiting tree (August 1981, Bonaccorso *et al.* 1980, Fleming & Heithaus 1981, Morrison 1978, 1980).

Important avian dispersers were the toucans *R. sulphuratus* and *P. torquatus*. Not only did they remove more figs than the other bird species, but they were the most frequent avian visitors and usually moved away from the tree soon after feeding. Several other species (e.g. the Scarlet Tanager, *Piranga olivacea*, and the Yellow-throated Euphonia, *Euphonia hirundinacea*) visited the tree frequently and removed moderate amounts of fruit but usually remained perched in the tree after feeding. Consequently, most of the seeds they ingested were either regurgitated or defecated below the tree crown. In contrast, some

species with low fruit removal rates (e.g. the Clay-coloured Robin, *Turdus grayi*, and the Red-legged Honeycreeper, *Cyanerpes cyaneus*) moved directly away from the tree after feeding and deposited the fig seeds away from their origin. Resident species were apparently the most important avian dispersers of the fig seeds. North American migrants ate about 9% of all figs consumed by birds and 2.5 % of figs eaten by all frugivores. Their contribution to the dispersal of the fig seeds, however, was probably minimal as they remained in the crown of the tree after feeding (Table 1).

Seeds of other fruit sources were defecated and/or regurgitated by frugivores beneath the crown of the fig tree, and fig seeds were probably deposited under other tree species, thus resulting in frugivore-created heterogenous seed shadows under the crowns of many trees (Fleming & Heithaus 1981). It has been suggested that animals consume figs as they are a source of ready energy, water and some protein, but other essential dietary needs are satisfied by consuming other fruits each day [the ripe fruits apparently contain few defensive compounds (Janzen 1979a)].

*Fruit waste and seed predation.* Many figs fell to the ground as a result of movements of frugivores in the crown. Furthermore, frugivores that remained in the crown after feeding dropped partly eaten figs and/or defecated or regurgitated the seeds to the ground below. Once on the ground many figs rotted or were quickly attacked by fungi. Fig seeds that fall under the crown are eaten not only by vertebrates (e.g. *Peromyscus* and *Heteromys* rodents) but also by invertebrates (e.g. lygaeid bugs; Slater 1972). This destruction leaves few seeds available for dispersal, especially to arboreal sites, by terrestrial frugivores.

*Frugivore activity and dispersal success.* Epiphytic and hemiepiphytic figs are established by seed germination on branches in the crowns of host trees after dispersal by animals that dwell in the canopy (Croat 1978). Although some seeds under the crown may be dispersed by terrestrial frugivores these seeds would not be deposited on an aerial structure which the seedling could use as support for growth. For these reasons, dispersal of the strangler fig seeds by canopy frugivores is most important in the establishment ecology of these plants.

The few studies available of fruit phenology of tropical rain forest trees indicate that figs fruit asynchronously at the population level (Estrada & Coates-Estrada 1985, Foster 1982, Frankie *et al.* 1974, Janzen 1979a, Leighton & Leighton 1983, Milton *et al.* 1983). It has been suggested that this trait may lower intraspecific competition for dispersal services and maximize dispersal success (Milton *et al.* 1983). However, while asynchronous fruiting may indeed lower intraspecific competition for dispersers, fruit removal is not equivalent to dispersal success. Successful or unsuccessful dispersal will depend on the post dispersal fate of the seed which, like the dispersal event itself, is subjected to a large environmental variance (see Herrera 1985).

The probability that a seed of a strangler fig will be deposited in an adequate microsite in the canopy for germination and growth depends in part upon

whether or not (i) the microsites are available, (ii) the faecal or regurgitated matter is intercepted by vegetation, and (iii) the seeds embedded in this matter adhere to the branches or are trapped in fissures of the tree bark. In addition, non-disperser organisms may have an important effect on the fate of seeds defecated by animals. Field evidence indicates that animal faecal material intercepted by tree trunks, branches and leaves or the ground, is a resource assiduously sought after by dung processing organisms (e.g. Coleoptera, Diptera, Dermaptera, etc.). The foraging and nesting behaviours of some of these organisms (e.g. dung beetles) could result in further movement of the animal-dispersed seed to another microsite where it may or may not become established (Estrada & Coates-Estrada 1986).

Fruiting fig trees could be considered as 'pivotal' (Howe 1984) or 'keystone' (Gilbert 1980) for the persistence of many plant and animal species in the tropical forest. As a result of their asynchronous fruiting, fig trees seem to be a comparatively constant source of food whereas other species of fruit are distinctly seasonal. At Los Tuxtlas, many of the frugivores that consumed the figs are important seed dispersal agents for many other species in the Moraceae (other *Ficus* species, *Poulsenia armata, Brosimum alicastrum, Pseudolmedia oxyphyllaria, Cecropia obtusifolia*), Lauraceae (*Nectandra ambigens*), Araliaceae (*Dendropanax arboreus*) and Annonaceae (*Cymbopetalum baillonii*) plant families among others (Coates-Estrada, unpublished data).

The results of our study suggest that in spite of presenting a very diverse frugivore coterie, only a few frugivores may be efficient dispersal agents for the seeds of the *Ficus* tree. In general and from a conservation viewpoint, the disappearance of fig trees as a result of deforestation may bring about serious local consequences for the survival of several important ecological links in the biologically depauperate remnants of tropical rain forests in southern México.

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## LITERATURE CITED

AUGUST, P. 1981. Fig consumption and seed dispersal by *Artibeus jamaicensis* in the llanos of Venezuela. *Biotropica* 13:70–76.

BONACCORSO, F. J. 1979. Foraging and reproductive ecology in a Panamanian bat community. *Bulletin of the Florida State Museum Biological Sciences* 24:59–408.

BONACCORSO, F. J., GLANZ, W. G. & SANDFORD, C. M. 1980. Feeding assemblages at fruiting *Dipteryx panamensis* (Papilionaceae) trees in Panama: seed predation, dispersal and parasitism. *Revista de Biología Tropical* 28:61–72.

BREITWISCH, R. 1985. Frugivores at a fruiting *Ficus* vine in a southern Cameroon tropical rain forest. *Biotropica* 15:125–128.

CROAT, T. 1978. *Flora of Barro Colorado Island.* Stanford University Press, Stanford, California. 960 pp.
ESTRADA, A. & COATES-ESTRADA, R. 1984. Fruit-eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. *American Journal of Primatology* 6:77–91.
ESTRADA, A. & COATES-ESTRADA, R. 1985. A preliminary study of resource overlap between howling monkeys (*Alouatta palliata*) and other arboreal mammals in the tropical rain forest of Los Tuxtlas, Mexico. *American Journal of Primatology* 9:27–37.
ESTRADA, A. & COATES-ESTRADA, R. 1986. Frugivory in howling monkeys (*Alouatta palliata*) at Los Tuxtlas: seed dispersal and fate of seeds. Pp. 93–104 in Estrada, A. & Fleming, T. H. (eds). *Frugivores and seed dispersal.* Dr W. Junk Publishers, The Hague. 392 pp.
FLEMING, T. H. & HEITHAUS, E. R. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica* 13:45–53.
FLORES, J. A. M. 1981. *Bromatologia animal* (2nd edition). Editorial Limusa, Mexico City, Mexico. 930 pp.
FOSTER, R. 1982. The seasonal rhythm of fruit fall on Barro Colorado Island. Pp. 151–172 in Leigh, E. G., Rand, A. S. & Windsor, D. M. (eds). *The ecology of a tropical forest: seasonal rhythms and long term changes.* Smithsonian Institution Press, Washington DC. 468 pp.
FRANKIE, G. W., BAKER, H. G., OPLER, P. A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 63:881–919.
GILBERT, L. E. 1980. Food web organization and the conservation of neotropical diversity. Pp. 11–33 in Soulé, M. E. & Wilcox, B. A. (eds). *Conservation biology: an evolutionary-ecological perspective.* Sinauer Associates, Sunderland, Mass. 512 pp.
HERRERA, C. M. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos* 44:132–141.
HOWE, H. F. 1984. Implications of seed dispersal by animals for tropical reserve management. *Biological Conservation* 30:261–281.
JANZEN, D. H. 1979a. How to be a fig. *Annual Review of Ecology and Systematics* 10:13–51.
JANZEN, D. H. 1979b. How many babies do figs pay for babies? *Biotropica* 11:48–50.
JORDANO, P. 1983. Fig-seed predation and dispersal by birds. *Biotropica* 15:38–41.
LEIGHTON, M. & LEIGHTON, D. R. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. Pp. 181–196 in Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds). *Tropical rain forest: ecology and management.* Blackwell Scientific Publications, Oxford. 498 pp.
MILTON, K. 1980. *The foraging strategy of howler monkeys: a study in primate economics.* Columbia University Press, New York, NY. 165 pp.
MILTON, K., WINDSOR, D. M., MORRISON, D. W. & ESTRIBI, M. A. 1983. Fruiting phenologies of two neotropical *Ficus* species. *Ecology* 63:72–762.
MIRANDA, F. & HERNANDEZ, E. 1963. Los tipos de vegetación de México y su clasificación. *Boletín de la Sociedad Botánica de México* 29:29–129.
MORRISON, D. W. 1978. Foraging ecology and energetics of the frugivorous bat *Artebeus jamaicensis.* *Ecology* 59:716–723.
MORRISON, D. W. 1980. Efficiency of food utilization by fruit bats. *Oecologia* 45:270–273.
SLATER, J. A. 1972. Lyaegid bugs (Hemiptera:Lyaegidae) as seed predators of figs. *Biotropica* 4:145–151.
WHEELWRIGHT, N. T., HABER, W. A., MURRAY, K. G. & GUINDON, C. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16:173–192.

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