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SHORT COMMUNICATION

# Frugivores at a fruiting *Ficus* in south-eastern Peru

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In neotropical forests, 50–90% of the canopy trees bear fruits adapted for animal dispersal whereas close to 100% of the shrubs and sub-canopy trees produce fleshy fruits (Howe & Smallwood 1982). It has been suggested that during periods of fruit scarcity, some plant species perform a critical role in the forest ecosystem by sustaining frugivorous animals that are important dispersal agents for seeds of many other trees during other seasons of the year (Howe 1984, Terborgh 1986*a*). Loss or absence of those seed dispersers would have strong negative consequences for tree species, thereby affecting the health of the entire ecosystem, over time. For that reason, plant species that sustain frugivores (= seed dispersers) during periods of resource scarcity have been called 'keystone species' (Gilbert 1980, Howe 1984, Terborgh 1983, 1986*a*, *b*; van Schaik *et al*. 1993). For example, in the tropical rain forest of Manu National Park, Peru, Terborgh (1983) found that figs, palm nuts and nectar are resources of great importance for the primate community during periods of fruit scarcity. During that season, three species of fig were identified as keystone resources maintaining nearly 40% of the animal biomass in the ecosystem (Terborgh 1983). The asynchronous character of fruit production by figs that guarantees a continuous supply of fruit throughout year, and the huge crop of fruits that figs produce enhance the importance of these plants to the entire forest system. Although their central role in vertebrate diets is well known (August 1981, Breitwisch 1983, Bronstein & Hoffmann 1987, Coates-Estrada & Estrada 1986, Jordano 1983, Lambert 1989*a*, *b*; Leighton & Leighton 1983, Snow 1981, Terborgh 1983), little is known of the relative contribution of the various frugivores, principally birds, to the seed shadow. Some birds tend to be more effective seed dispersers than mammals because they swallow the entire fruit, and thus transport seeds away from parent plants, whereas some mammals, especially primates, separate seeds from pulp and drop the seeds directly under the parent (Howe 1980, Howe & Smallwood 1982). In this paper, I report observations of diurnal vertebrates eating figs of a single *Ficus pertusa* L. f. *sensu lato* (Moraceae) tree, including estimates of visitation and feeding rates as well as relative contributions of seed dispersal for the most common species visiting this tree. *Sensu lato* is used here because there is some debate as to whether this individual tree belongs to *F. pertusa* or may constitute a new species (R. Foster, *pers. comm.*).

The observations were made in an undisturbed lowland wet forest at Cocha Cashu Biological Station (11°54′S, 71°18′W), elevation *c*. 400 m asl, Manu National Park, Department of Madre de Dios, south-eastern Peru. Mean temperature at the station is 23–24 °C, and rainfall averages about 2000 mm annually (Terborgh *et al*. 1990). Rainfall is concentrated during a 5-mo rainy season extending from late November to early May. On average, less than 100 mm of rain falls monthly during the dry season.

An individual *Ficus pertusa s. l.* tree was monitored for a total of 160 h over a 21-d period from 10–30 August 1994. The hemi-epiphytic fig tree was about 15 m high, situated on the branches of a 45 m emergent tree (*Luehea cymulosa* Spruce ex Benth., Tiliaceae). I estimated projection of the fig crown onto the forest floor as circular, about 15 m in diameter, and the vertical space occupied in the supporting tree about 5 m. Crop size on 9 August was estimated at 200 000 figs, with about 10–15% of them ripe (based on 200 figs on 10 branch counts). Standing

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crop size decreased to about 60 000 figs by 27 August; the other figs were eaten by vertebrate frugivores or dropped to the ground. By 16 September, fewer than 1000 figs were available in the tree. Fresh ripe figs were obtained from the tree, measured (diameter to the nearest 0.05 mm), weighed (to the nearest 0.1 g), and the number of seeds counted. Ten 1-$m^2$ fruit traps were placed under the canopy for estimation of the quantity of fruits falling under the tree crown. Traps were checked daily between 06h00 and 07h00. Fruit characteristics (small fruit ripening red and asynchronous ripening of the fruits within the crop) suggest a bird dispersal syndrome (Bronstein & Hoffmann 1987, Kalko *et al*. 1996, Korine *et al*. 2000).

I observed bird and mammal visitors from 06h00 to 17h45. For each individual visitor, the total time spent in the crown, the number of fruits eaten and the type of foraging behaviour were recorded whenever possible. Observations were coded either as total, if including the entire 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. Estimations of feeding rates were corrected for average group size. Feeding-rate calculations yield a conservative estimate because only partial observations are available for some species, and thus the number of figs taken per visit is underestimated. Values presented are means ± SE.

Fresh, ripe figs (syconia) of this species have a diameter of 9.02 ± 0.05 mm (n = 157). They are spheroidal, and red-yellow with dark red dots when ripe. The average fig has a fresh weight of 0.35 ± 0.01 g (n = 102), and contains 55.13 ± 1.87 seeds (n = 102).

I recorded 44 species of diurnal vertebrates eating figs from this single tree (Table 1). Birds accounted for 91% and primates for 9% of the recorded species. Body masses of frugivorous vertebrates visiting this fig tree range from 9 g in *Pipra coronata* to 10 500 g in *Ateles paniscus*. Forty-eight per cent of the frugivorous species swallowed the entire fig (manakins, cotingas, trogons, thrushes etc.) showing the characteristic behaviour of effective dispersers; that is, they ingested the whole fruit, and left the tree after relatively short visits (Olson & Blum 1968) (Table 1). Among those species, *Pipra chloromeros* and *Lipaugus vociferans* visited most frequently (Table 1). Forty-three per cent handled the figs by mashing them, ingesting pulp and juice, and dropping the remains (all primates and tanagers). The remaining 9% of visitors belong to bird groups (parrots and pigeons) that have been suggested to be seed predators rather than dispersers (Janzen 1981, Jordano 1983, Lambert 1989*b*).

The number of figs eaten daily by vertebrates was estimated by multiplying average number of visits per day for each species by its species-specific average number of fruits ingested per visit, corrected for group size, and then summing across all species (Tables 2 and 3). I considered only 26 of the 44 recorded species because observations and/or importance of removal by the remaining 18 species were negligible. The four species of primate processed an estimated 721 figs $d^{-1}$, representing 43.3% of the estimated number of figs leaving the tree each day. Birds processed an estimated 615.3 figs $d^{-1}$, representing 36.9%. The remaining 19.8% (330.9 figs) was made up of figs that fell to the ground under the tree usually owing to activity of vertebrates moving in the tree. Fruit trap counts of figs showing signs of being mashed represented 53.9% of the total figs removed daily by the 'mashers' (primates and tanagers) (872.6 figs), and 35.2% of the total figs removed daily by all vertebrates (1336.7 figs).

It has been argued that the absence of toxic compounds (Janzen 1979*b*) and the high calcium content (O'Brien *et al*. 1998) in the fruit pulp may contribute to the high consumer diversity observed at fig trees. However, fig pulp is also very rich in fibre, which has a negative effect on digestion rates, and has very low protein and fat content (Jordano 1983). This may explain why several of the observed fig consumers (43%) avoid swallowing the whole fig and instead processed figs by mashing the fruit and dropping the rest. This feeding behaviour may help to minimize the amount of indigestible matter ingested with the pulp and juice, but will also influence the effectiveness of the vertebrate as a seed disperser, by reducing the amount of seeds moved away from the tree.

In addition to seed destruction by some groups of birds (parrots and pigeons) in the dispersal phase, it has been shown that an average of 55% of *Ficus* seed crops are destroyed by parasitic wasps (Janzen 1979*a*, Jordano 1983). Using this average, an estimate of number of seeds that are lost in the pollination and dispersal of this tree's seeds can be made (Table 3). On a daily basis, $0.39 \times 10^5$ seeds destroyed in advance by invertebrates (mostly agaonid wasps), are eaten by vertebrates. In addition, $0.009 \times 10^5$ seeds are damaged owing to parrot/pigeon predation. This leaves only 42.9% ($0.3 \times 10^5$) of the seeds removed by vertebrates that are potentially dispersed undamaged (see Table 3). Data on the frequency of mashed fruits collected in the fruit traps allowed us to estimate the daily number of figs that were dropped by vertebrates that mash the figs instead of swallowing them. These estimates represent 35.2% of the total figs/seeds removed by vertebrates. Therefore, of the estimate $0.3 \times 10^5$ undamaged seeds removed by vertebrates daily, only $0.2 \times 10^5$ seeds are potentially dispersed away from the tree, which represents 28.6% of the total fig/seeds removed daily by vertebrates.

An estimated 19.8% of the daily fig/seed output is lost when figs fall to the ground owing to the daily frugivore activity on the tree. Because trumpeters (*Psophia*

**Table 1.** Body weights, behavioural characteristics, total number of observations of each species (n), and mean number of individuals/species/observation.

| Common name | Scientific name | Body weight (g)[1] | FCM[4] | FHM[5] | n | Mean indiv. per obs. |
|---|---|---|---|---|---|---|
| spider monkey | *Ateles paniscus* Linnaeus | 10 500[2] | P | M | 8 | 5.0 ± 1.3 |
| weeping capuchin | *Cebus apella* Linnaeus | 3100[2] | P | M | 6 | 5.8 ± 1.7 |
| white-fronted capuchin | *Cebus albifrons* Humboldt | 2400[2] | P | M | 13 | 8.4 ± 1.9 |
| squirrel monkey | *Saimiri sciureus* Linnaeus | 1000[2] | P | M | 9 | 21.4 ± 2.4 |
| common piping-guan | *Aburria pipile* Jacquin | 1200 | P | S | 8 | 2.0 ± 0.0 |
| pale-winged trumpeter | *Psophia leucoptera* Spix | 990 | G | S | 23 | 5.4 ± 0.6 |
| crested oropendola | *Psarocolius decumanus* Pallas | 289 | P | S | 4 | 1.5 ± 0.3 |
| plumbeous pigeon | *Columba plumbea* Vieillot | 210 | P | Pr | 36 | 2.0 ± 1.0 |
| curl-crested aracari | *Pteroglossus beauharnaesii* Wagler | 203 | P | S | 2 | 4.0 |
| ivory-billed aracari | *Pteroglossus azara* Vieillot | 135 | P | S | 2 | 2.0 |
| purple-throated fruitcrow | *Querula purpurata* Muller | 125 | A | S | 5 | 2.0 ± 0.0 |
| black-tailed trogon | *Trogon melanurus* Swainson | 122 | A | S | 30 | 2.0 ± 0.0 |
| screaming piha | *Lipaugus vociferans* Wied-Neuwied | 81 | A | S | 183 | 1.2 ± 0.1 |
| rock parakeet | *Pyrrhura rupicola* Tschudi | 75 | P | Pr | 7 | 2.8 ± 0.4 |
| Hauxwell's thrush | *Turdus hauxwelli* Lawrence | 72 | P | S | 19 | 1.0 ± 0.0 |
| cobalt-winged parakeet | *Brotogeris cyanoptera* Salvadori | 67 | P | Pr | 4 | 2.0 ± 0.0 |
| painted parakeet | *Pyrrhura picta* Statius Muller | 67 | P | Pr | 3 | 4.5 ± 0.5 |
| black-spotted barbet | *Capito auratus* Dumont | 64 | P | S | 3 | 2.0 ± 0.0 |
| black-billed thrush | *Turdus ignobilis* Sclater | 60[3] | P | S | 27 | 1.0 ± 0.0 |
| collared trogon | *Trogon collaris* Vieillot | 59 | A | S | 5 | 2.0 |
| white-necked thrush | *Turdus albicollis* Vieillot | 52 | P | S | 34 | 1.0 ± 0.0 |
| bright-rumped attila | *Attila spadiceus* Gmelin | 35 | A | S | 1 | 1.0 |
| paradise tanager | *Tangara chilensis* Vigors | 24 | P | M | 29 | 2.9 ± 0.1 |
| opal-crowned tanager | *Tangara callophrys* Cabanis | 23 | P | M | 1 | 2.0 |
| green-and-gold tanager | *Tangara schrankii* Spix | 20 | P | M | 77 | 2.3 ± 0.1 |
| white-browed purpletuft | *Iodopleura isabellae* Parzudaki | 20[3] | A | S | 1 | 1.0 |
| white-winged shrike-tanager | *Lanio versicolor* Orbigny & Lafresnaye | 19 | P | M | 21 | 2.4 ± 0.2 |
| turquoise tanager | *Tangara mexicana* Linnaeus | 19 | P | M | 1 | 2.0 |
| green honeycreeper | *Chlorophanes spiza* Linnaeus | 18 | P | M | 2 | 2.0 |
| round-tailed manakin | *Pipra chloromeros* Tschudi | 17 | A | S | 197 | 1.5 ± 0.2 |
| band-tailed manakin | *Pipra fasciicauda* Hellmayr | 17 | A | S | 49 | 1.0 ± 0.0 |
| masked tanager | *Tangara nigrocincta* Bonaparte | 17 | P | M | 2 | 2.0 ± 0.0 |
| yellow-crested tanager | *Tachyphonus rufiventer* Spix | 17 | P | M | 1 | 2.0 |
| golden-bellied euphonia | *Euphonia chrysopasta* Sclater & Salvin | 15 | P | M | 55 | 2.0 ± 0.0 |
| rufous-bellied euphonia | *Euphonia rufiventris* Vieillot | 15 | P | M | 38 | 2.0 ± 0.0 |
| red-eyed vireo | *Vireo olivaceus* Linnaeus | 15 | P | S | 1 | 1.0 |
| thick-billed euphonia | *Euphonia laniirostris* Orbigny & Lafresnaye | 15[3] | P | M | 11 | 2.0 |
| orange-bellied euphonia | *Euphonia xanthogaster* Sundevall | 14 | P | M | 133 | 2.0 ± 0.3 |
| blue-naped chlorophonia | *Chlorophonia cyanea* Thunberg | 13 | P | M | 9 | 2.0 ± 0.0 |
| black-faced dacnis | *Dacnis lineata* Gmelin | 13 | P | M | 1 | 2.0 |
| forest elaenia | *Myiopagis gaimardii* Orbigny | 12 | A | S | 2 | 2.0 |
| white-vented euphonia | *Euphonia minuta* Cabanis | 10 | P | M | 9 | 2.0 ± 0.0 |
| dwarf tyrant-manakin | *Tyranneutes stolzmanni* Hellmayr | 9 | A | S | 88 | 1.0 ± 0.0 |
| blue-crowned manakin | *Pipra coronata* Spix | 9 | A | S | 3 | 1.0 ± 0.0 |

[1]Data from Terborgh *et al*. (1990) except as noted; [2]Data from Emmons (1990); [3]Data from Dunning (1993); [4]FCM = fruit capture mode; A = in air, G = from ground, P = from perch; [5]FHM = fruit handling mode; S = swallow whole, M = mash, Pr = seed predator. The last two abbreviations follow Moermond & Denslow (1985).

*leucoptera*) feed opportunistically on figs that are knocked and dropped to the ground by primates (Sherman 2002), these figs have a good chance to be processed before lygaeid bugs (Slater 1972) or carabid beetles (Paarmann *et al*. 2001) attack their seeds. My observations suggest that trumpeters may subsequently disperse some of the seeds contained in these fallen figs. Trumpeters processed an average of 211.2 figs $d^{-1}$, which represented 63.8% of the total number of fruits falling under the tree daily. Overall, trumpeters constituted one of the most important fig removers accounting for 15.8% of the total number of figs removed daily by vertebrates (Table 2).

The assemblage of frugivores recorded at this fig tree represents perhaps the most diverse ever reported for a single individual tropical tree with regard to species number and taxonomic breadth. The robust stems of the tree allowed both small and large potential dispersers to have access to the figs by a variety of foraging behaviours. The species observed at the tree represent 25% and 31%, respectively, of the total number of frugivorous birds and primate species that have been recorded at Cocha Cashu (Terborgh *et al.* 1984), illustrating the importance of figs for the vertebrate community of this tropical wet forest. These results are consistent with the general perception of

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**Table 2.** Visit rates and statistics of feeding rates of the principal diurnal vertebrate species recorded at a *Ficus pertusa s. l.* tree.

| Species | Visit rate (visits $d^{-1}$) | Visit length (min) | Figs per visit | Removal rate (figs $min^{-1}$) | Estimated[1] % figs removed |
|---|---|---|---|---|---|
| **Primates** | | | | | |
| *Saimiri sciureus* | 0.7 | 14.6 ± 3.0 (9) | 17.1 ± 4.9 (7) | 1.4 ± 0.4 (7) | 18.5 |
| *Cebus albifrons* | 1.0 | 17.4 ± 4.6 (12) | 21.8 ± 6.9 (8) | 1.4 ± 0.4 (8) | 13.3 |
| *Ateles paniscus* | 0.6 | 33.8 ± 10.0 (8) | 55.5 ± 16.0 (6) | 1.9 ± 0.8 (6) | 12.5 |
| *Cebus apella* | 0.5 | 12.8 ± 3.9 (5) | 49.5 ± 19.4 (4) | 3.2 ± 0.5 (4) | 9.7 |
| **Birds** | | | | | |
| *Psophia leucoptera* | 1.7 | 9.2 ± 1.7 (15) | 22.7 ± 7.4 (6) | 3.0 ± 1.8 (6) | 15.8 |
| *Lipaugus vociferans* | 13.7 | 2.0 ± 0.5 (137) | 4.1 ± 0.4 (61) | 4.6 ± 1.0 (57) | 5.2 |
| *Euphonia xanthogaster* | 10.0 | 5.6 ± 0.6 (101) | 2.9 ± 0.5 (14) | 0.7 ± 0.2 (12) | 4.4 |
| *Columba plumbea* | 2.7 | 7.7 ± 1.2 (32) | 7.6 ± 1.9 (16) | 1.3 ± 0.4 (15) | 3.1 |
| *Pipra chloromeros* | 14.8 | 1.4 ± 0.2 (103) | 1.7 ± 0.2 (49) | 2.8 ± 0.5 (42) | 2.8 |
| *Aburria pipile* | 0.6 | 19.7 ± 5.0 (8) | 28.0 ± 3.8 (6) | 2.4 ± 0.6 (6) | 2.5 |
| *Tangara schrankii* | 5.8 | 2.8 ± 0.4 (61) | 2.2 ± 0.3 (19) | 3.4 ± 1.0 (17) | 2.2 |
| *Euphonia chrysopasta* | 4.1 | 5.0 ± 0.7 (42) | 3.3 ± 0.6 (12) | 1.3 ± 0.5 (12) | 2.1 |
| *Trogon melanurus* | 2.3 | 2.4 ± 0.7 (27) | 2.7 ± 0.6 (16) | 5.0 ± 1.9 (16) | 1.7 |
| *Euphonia rufiventris* | 2.9 | 3.9 ± 0.5 (29) | 2.6 ± 0.4 (8) | 1.5 ± 0.5 (8) | 1.1 |
| *Tangara chilensis* | 2.2 | 3.3 ± 0.4 (26) | 2.3 ± 0.4 (7) | 1.0 ± 0.3 (7) | 1.1 |
| *Tyranneutes stolzmanni* | 6.6 | 4.0 ± 1.4 (43) | 1.5 ± 0.1 (23) | 1.9 ± 0.5 (17) | 0.9 |
| *Pipra fasciicauda* | 3.7 | 3.7 ± 1.8 (33) | 2.5 ± 0.3 (25) | 1.9 ± 0.3 (24) | 0.7 |
| *Turdus ignobilis* | 2.0 | 5.1 ± 1.7 (21) | 3.5 ± 0.4 (10) | 1.9 ± 0.5 (10) | 0.5 |
| *Pyrrhura rupicola* | 0.5 | 5.5 ± 1.8 (7) | 4.0 ± 1.4 (4) | 0.9 ± 0.52 (4) | 0.4 |
| *Turdus albicollis* | 2.6 | 10.3 ± 3.0 (27) | 2.8 ± 0.5 (12) | 1.7 ± 1.1 (11) | 0.3 |
| *Euphonia minuta* | 0.7 | 3.6 ± 1.3 (7) | 3.3 ± 1.0 (4) | 3.8 ± 2.3 (4) | 0.3 |
| *Querula purpurata* | 0.4 | 4.7 ± 2.4 (5) | 4.5 ± 1.3 (4) | 1.4 ± 0.6 (4) | 0.3 |
| *Brotogeris cyanoptera* | 0.3 | 8.2 ± 4.2 (4) | 5.0 ± 2.0 (3) | 0.5 ± 0.1 (3) | 0.2 |
| *Turdus hauxwelli* | 1.4 | 3.8 ± 0.9 (16) | 4.8 ± 1.1 (13) | 1.8 ± 0.5 (13) | 0.2 |
| *Euphonia laniirostris* | 0.8 | 2.9 ± 0.8 (9) | 1.3 ± 0.3 (4) | 0.5 ± 0.1 (4) | 0.2 |
| *Trogon collaris* | 0.4 | 3.4 ± 1.8 (4) | 2.7 ± 1.2 (3) | 1.8 ± 1.0 (3) | 0.1 |

[1] Fruits/visit × visit rate × average number of individuals/visit as a percentage of total number of fruits eaten daily by vertebrates.

**Table 3.** Summary of the estimated number of figs/seeds leaving daily the crown of a *Ficus pertusa s. l.* tree. Total number of figs/seeds removed daily by vertebrates was estimated from species-specific visitation rates, figs per visit, and the average number of individuals per visit. Seeds figures were calculated assuming an average of 55 seeds per fig. Pre-dispersal invertebrate predation was estimated using an average value of 55% from Janzen (1979*a*) and Jordano (1983).

| Category | Number of figs | Number of seeds | % |
|---|---|---|---|
| Total removed by diurnal vertebrates | 1336 | $0.7 \times 10^5$ | 77.8 |
| Primates | 721 | $0.4 \times 10^5$ | 44.6 |
| Estimated invertebrate seed predation | – | $0.22 \times 10^5$ | 24.5 |
| Voided undamaged | – | $0.18 \times 10^5$ | 20.1 |
| Birds | 615 | $0.3 \times 10^5$ | 33.2 |
| Swallowers | 414 | $0.2 \times 10^5$ | 22.1 |
| Estimated invertebrate seed predation | – | $0.11 \times 10^5$ | 12.2 |
| Voided undamaged | – | $0.09 \times 10^5$ | 9.9 |
| Mashers | 151 | $0.08 \times 10^5$ | 8.9 |
| Estimated invertebrate seed predation | – | $0.044 \times 10^5$ | 4.9 |
| Voided undamaged | – | $0.036 \times 10^5$ | 5.0 |
| Seed predators | 50 | $0.02 \times 10^5$ | 2.2 |
| Estimated invertebrate seed predation | – | $0.011 \times 10^5$ | 1.2 |
| Estimated vertebrate seed predation | – | $0.009 \times 10^5$ | 1.0 |
| Total fallen to the ground | 331 | $0.2 \times 10^5$ | 22.2 |
| Removed by trumpeters | 211 | $0.12 \times 10^5$ | 14.2 |
| Left under the tree | 120 | $0.08 \times 10^5$ | 8.0 |
| Total observed daily output | 1667 | $0.9 \times 10^5$ | 100.0 |

the role of figs as keystone species as well as variation in dispersal effectiveness among frugivores.

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## LITERATURE CITED


AUGUST, V. A. 1981. Fig fruit consumption and seed dispersal by *Artibeus jamaicensis* in the llanos of Venezuela. *Biotropica* 13(suppl.):70–76.

BREITWISCH, R. 1983. Frugivores at a fruiting *Ficus* vine in a southern Cameroon tropical wet forest. *Biotropica* 15:125–128.

BRONSTEIN, J. L. & HOFFMANN, K. 1987. Spatial and temporal variation in frugivory at a Neotropical fig, *Ficus pertusa*. *Oikos* 49:261–268.

COATES-ESTRADA, R. & ESTRADA, A. 1986. Fruiting and frugivores at a strangling fig in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 2:349–357.

DUNNING, J. B. (ed.). 1993. *CRC Handbook of avian body masses*. CRC Press, Ann Arbor, Michigan. 371 pp.

EMMONS, L. E. 1990. *Neotropical rainforest mammals: a field guide*. University of Chicago Press, Chicago. 281pp.

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 and ecological perspective*. Sinauer Associates, Sunderland.

HOWE, H. F. 1980. Monkey dispersal and waste of a Neotropical fruit. *Ecology* 61:944–959.

HOWE, H. F. 1984. Implications of seed dispersal by animals for tropical reserve management. *Biological Conservation* 30:261–281.

HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal of a tropical tree. *Ecology* 60:180–189.

JANZEN, D. H. 1979*a*. How many babies do figs pay for babies? *Biotropica* 11:13–51.

JANZEN, D. H. 1979*b*. How to be a fig. *Annual Review of Ecology and Systematics* 10:13–51.

JANZEN, D. H. 1981. *Ficus ovalis* seed predation by an orange-chinned parakeet (*Brotogeris jugularis*) in Costa Rica. *Auk* 98:841–844.

JORDANO, P. 1983. Fig-seed predation and dispersal by birds. *Biotropica* 15:38–41.

KALKO, E. K. V., HERRE, E. A. & HANDLEY, C. O. 1996. Relation of fig fruit characteristics to fruit-eating bats in the new and old world tropics. *Journal of Biogeography* 23:565–576.

KORINE, C., KALKO, E. K. V. & HERRE, E. A. 2000. Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. *Oecologia* 123:560–568.

LAMBERT, F. 1989*a*. Fig-eating by birds in a Malaysian lowland rain forest. *Journal of Tropical Ecology* 5:401–412.

LAMBERT, F. 1989*b*. Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. *Ibis* 131:521–527.

LEIGHTON, M. & LEIGHTON, D. R. 1983. Vertebrates 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 Publishing, Oxford.

MOERMOND, T. C. & DENSLOW, D J. S. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs* 36:865–897.

O'BRIEN, T. G., KINNAIRD, M. E. & DIERENFELD, E. S. 1998. What's so special about figs? *Nature* 392:668.

OLSON, S. L. & BLUM, K. E. 1968. Avian dispersal of plants in Panama. *Ecology* 49:565–566.

PAARMANN, W., ADIS, J., STORK, N., GUTZMANN, B., STUMPE, P., STARITZ, B., BOLTE, H., KÜPPERS, S., HOLZKAMP, K., NIERS, C., & DA FONSECA, C. R. V. 2001. The structure of ground beetle assemblages (Coleoptera: Carabidae) at fig fruit falls (Moraceae) in a terra firme rain forest near Manaus (Brazil). *Journal of Tropical Ecology* 17:549–561.

SHERMAN, P. T. 2002. Desire under the figs: an Amazonian bird's unusual diet results in an even more unusual mating system. *Natural History* 111:28–32.

SLATER, J. A. 1972. Lygaeid bugs (Hemiptera: Lygaeidae) as seed predators of figs. *Biotropica* 4:145–151.

SNOW, D. W. 1981. Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13:1–14.

TERBORGH, J. 1983. *Five new world primates*. Princeton University Press, Princeton. 260 pp.

TERBORGH, J. 1986*a*. Keystone plant resources in the tropical forests. Pp. 330–344 in Soulé, M. E. (ed.). *Conservation Biology II*. Sinauer Associates, Sunderland.

TERBORGH, J. 1986*b*. Community aspects of frugivory in tropical forests. Pp. 371–384 in Estrada, A. & Fleming, T. H. (eds). *Frugivores and seed dispersal*. Dr W. Junk Publishers, Dordrecht.

TERBORGH, J. W., FITZPATRICK, J. W. & EMMONS, L. 1984. Annotated checklist of bird and mammal species of Cocha Cashu Biological Station, Manu National Park, Peru. *Fieldiana Zoology New Series No.* 21. 29 pp.

TERBORGH, J. W., ROBINSON, S. K., PARKER, T. A., MUNN, C. A. & PIERPONT, N. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60:213–238.

VAN SCHAIK, C. P., TERBORGH, J. W. & WRIGHT, S. J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–377.

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