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FRUIT SIZE AND FRUGIVORE SPECIES RICHNESS: ADDITIONAL EVIDENCE FROM OBSERVATIONS AT A LARGE *FICUS* TREE

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Frugivorous birds make up a large proportion of any tropical forest avifauna (Fleming *et al.* 1987) and play an important role in the dispersal of tropical tree seeds (Howe 1993, Levey *et al.* 1994). The interactions between fruiting trees and frugivorous birds can, however, take different routes. On the one hand, trees may use different strategies (Howe 1993, Schupp 1993, and references therein). Some trees may offer relatively few, large, and highly nutritious fruits while others may produce large numbers of small, less nutritious fruits. Larger fruits can often only be taken by larger bird species which are morphologically adapted to handling such fruits, e.g., have a wide enough gape (even though some smaller bird species may eat such fruits piecemeal, *cf.* Moermond & Denslow 1985, Levey 1987). Smaller fruits, however, can usually be taken by both larger and smaller species. Therefore, one might expect a negative correlation between the fruit size of a tree species and the number of frugivorous bird species visiting it (Ertan 1999, Hamann & Curio 1999, Heindl & Curio 1999).

On the other hand, not all of the visiting bird species may be 'seed dispersers', i.e., deposit intact seeds away from the parent tree (Schupp 1993, Levey *et al.* 1994). Rather, some species may be 'seed thieves' which eat the fruit and drop the remaining seeds under the parent trees or even 'seed predators' which digest the seeds for their nutritional value (Janzen 1981). Using observations of fruit handling, one can try to estimate what percentage of seeds are actually dispersed away from the parent tree by the visiting birds.

To study fruiting tree – frugivore interactions, studies in species-rich ecosystems like rainforests are needed (Howe 1993). For example, Ertan (1999) recorded bird visitors to several rainforest fruiting trees at a field site in southern Venezuela. As predicted, she found a negative correlation between fruit size and frugivorous bird species richness (Fig. 1). To further test this relationship, I observed frugivorous bird visitors at a large *Ficus* tree producing many small fruits at the same Venezuelan study site in two successive years. Since the tree was standing in a garden so that the entire canopy was visible from the ground, a complete census during the observational period was possible. Thus, it was not just possible to record all visiting species, but also to get a rough estimate of their abundance. Abundance of frugivore species may correlate with the numbers of fruits taken and may thus indicate which species predominantly disperse seeds (see Methods).

METHODS

Fieldwork was conducted in Esmeralda, Estado Amazonas, southern Venezuela (65°32'W, 3°11'N, altitude ca. 110 m a.s.l.) which lies in the catchment area of the upper Orinoco. Esmeralda is a small Indian village located within a patch of lowland grassland and

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scrub surrounded by lowland and flooded tropical evergreen, river-edge, river island, gallery, palm and second-growth forests (Stotz *et al.* 1996). It is found almost at the center of the Alto Orinoco-Casiquiare Biosphere Reserve, which has so far been spared from severe human disturbance. The most prevalent anthropogenic influences are hunting and slash-and-burn agriculture of the local Indian populations (Anhuf & Winkler 1999).

Average daily temperatures are approximately 26 °C, and average annual precipitation is around 3000 mm (1000–4000 mm) (Anhuf & Winkler 1999). The rainy season usually lasts from April to November. However, large fluctuations in precipitation patterns were recorded, partly due to large climatic events such as the La Niña and El Niño phenomenons, in 1996 and 1997–98 (Rütger Rollenbeck, pers. comm.).

The study tree is situated 20 m north of the Orinoco River and 50 m east of the landing site of the shuttle boats for the Surumoni Crane-Project. The tree's habitat probably used to be river-edge forest, but it is now surrounded by several smaller trees, small houses and gardens. The nearest patch of continuous lowland river-edge rainforest is a few hundred meters away, but large and small trees in gardens and along the river bridge this gap. This tree fruited for about 1–2 weeks in May 1998 and March-April 1999. As rainfall patterns probably dictate fruiting times, the irregular rainfall patterns during 1998 and 1999 most likely produced these markedly different fruiting times. In April 1999, samples of the tree's branches, leaves and fruits were obtained, and the tree was identified as a *Ficus* species. Rough extrapolations made from these samples put the number of small fruits (diameter mean 0.6 cm, range 0.4–0.8 cm, mass < 1 g) on this tree at several tens of thousands.

I observed the tree for about 10 hours in 1998 and about 6 hours in 1999. Exact observations times were in 1998: 11:10–13:10 h and 15:05–16:50 h on 21 May, 13:05-15:50 h and 16:50-18:00 h on May 22, 8:50–11:00 h on 23 May; and in 1999: 7:20–10:20 h on 25 March, and 10:20–13:15 h on 27 March. To observe this large tree (23 m high, 25 m canopy diameter), I sat 10–15 m away from the trunk (1.5 m diameter) and scanned the canopy in a clockwise direction every 5 minutes, counting all individual birds and recording the species and, if possible, sex and age. In addition, any bird entering the tree during the 5-minute interval was also recorded. Abundance was thus scored as the cumulative number of individuals present during successive 5-minute intervals. This protocol causes birds to be recorded several times during successive intervals if they remain in the tree for longer periods. Therefore, abundance does not reflect number of bird visitors; rather, it should roughly reflect the percentage time spent in the tree by different bird species. Percentage time may or may not correlate with the number of fruits taken, but it is more likely to correlate with fruit consumption than just the number of visits.

RESULTS

In 1998, 15 species were observed to take fruits (Table 1). The most abundant species were *Brotogeris cyanoptera, Thraupis episcopus, Ramphocelus carbo*, and one *Elaenia* sp., which together accounted for 56% of 5-minute-interval observations. *Euphonia* spp. accounted for another 23% of observations, but these were divided among two identified and at least one unidentified species (however, the following species are likely candidates as (1) they were previously identified in the area and (2) females, for which some of the correct field marks were observed, fed in the tree: *E. chlorotica* or *E. chrysopasta*).

In 1999, 15 species were again observed to take fruits. However, considerable species turnover took place as five new species were observed. The most abundant species were again *Brotogeris cyanoptera, Thraupis episcopus*, and *Ramphocelus carbo*, which accounted for 68% of observations. Surprisingly, *Euphonia* spp. accounted for only 3% of observations in 1999.

Summing over both years, at least 20 species took fruits, of which the most abundant were *Brotogeris cyanoptera, Thraupis episcopus*, and *Ramphocelus carbo* (57% of observations). At least four *Euphonia* spp. accounted for another 13% of observations.

Ertan's (1999) systematic observations showed that the following species swallow fruits and therefore probably qualify as seed dispersers: *Capito niger, Tyrannus melancholicus, Vireo* sp., *Cacicus cela*, the two *Cyanerpes* spp. and *Thraupis palmarum* (Table 1). My own observations indicate that the *Elaenia* sp., *Icterus chrysocephalus*, the two *Dendroica* warblers and the three larger tanagers *Thraupis episcopus, Ramphocelus carbo* and *Schistochlamys melanopis* all swallow the relatively small *Ficus* fruits and therefore also probably qualify as seed dispersers (although they may be seed thieves for larger fruits, *cf.* Moermond 1983, Levey 1987). Concurrent with my observations, *Bro-*

togeris cyanoptera, *Nannopsittaca panychlora* and the four *Euphonia* spp. observed by Ertan (1999) all mash the fruits and drop the seeds. Therefore, the euphonias of this study probably qualify as seed thieves while the parrots are probably even seed predators (*cf.* Janzen 1981). Using these categories, 14, 4 and 2 species were seed dispersers, thieves and predators respectively. However, the number of observations for these three categories were 662 (59.0%), 144 (12.8%) and 317 (28.2%) respectively. Therefore, probably more than half the seeds were dispersed away from the parent tree.

Multiple regression analysis showed that the number of birds present during a 5-minute interval was influenced by date and time of day. In 1998, both date and time of day had a negative effect on bird abundance (Fig. 2; n = 118 intervals; date: $R^2 = 0.14$, $P < 0.0001$; time of day: $R^2 = 0.09$, $P < 0.0004$). In 1999, however, only time of day had a negative effect on bird abundance (n = 70 intervals; date: $R^2 = 0.001$, $P = 0.78$; time of day: $R^2 = 0.18$, $P < 0.0002$).

DISCUSSION

The observed *Ficus* tree attracted at least 20 frugivorous bird species. The actual species richness is probably much higher. For example, most *Euphonia* females and juveniles could not be positively identified and were conservatively summarized under *Euphonia* spp. (*cf.* Table 1). Furthermore, the tree was not ob-

TABLE 1. Abundance of frugivorous bird species visiting a single large *Ficus* tree in Southern Venezuela in two successive years (1998 and 1999). 'Abundance' represents the cumulative number of individuals recorded during successive 5-minute intervals (see Methods). The last column presents the percentage of the total abundance of each species, i.e., the number presented in the fifth column divided by the total abundance of 1123 individuals of all species counted during 188 5-minute intervals. English and Latin names were taken from Sibley & Monroe (1990), except for the correct genus name *Schistochlamys* (Isler & Isler 1999). Mean body mass (in grams) were taken from Bennett (1986), Dunning (1993) and, whenever possible, from own data. Superscripts denote seed dispersers[1], seed thieves[2] (Ertan's 1999 and own observations) and seed predators[3] (Janzen 1981).

Avian taxa	Body mass	Abundance 1998	1999	total	%
Cobalt-winged Parakeet (*Brotogeris cyanoptera*)[3]	67.0	113	174	287	25.6
Tepui Parakeet (*Nannopsittaca panychlora*)[3]	42.0	30	0	30	2.7
Black-spotted Barbet (*Capito niger*)[1]	60.5	1	13	14	1.2
Tropical Kingbird (*Tyrannus melancholicus*)[1]	37.8	30	0	30	2.7
Elaenia sp.[1]	-	58	1	59	5.2
Vireo sp.[1]	-	0	2	2	0.2
Yellow-rumped Cacique (*Cacicus cela*)[1]	74.0	3	42	45	4.0
Moriche Oriole (*Icterus chrysocephalus*)[1]	41.2	0	13	13	1.2
Yellow Warbler (*Dendroica petechia*)[1]	10.3	0	24	24	2.1
Blackpoll Warbler (*Dendroica striata*)[1]	13.0	0	18	18	1.6
Short-billed Honeycreeper (*Cyanerpes nitidus*)[1]	7.9	19	0	19	1.7
Purple Honeycreeper (*Cyanerpes caeruleus*)[1]	9.9	18	0	18	1.6
Orange-bellied Euphonia (*Euphonia xanthogaster*)[2]	13.0	0	1	1	0.1
White-vented Euphonia (*Euphonia minuta*)[2]	8.9	5	0	5	0.4
Violaceous Euphonia (*Euphonia violacea*)[2]	14.7	39	6	45	4.0
Euphonia spp.[2]	-	83	10	93	8.3
Blue-grey Tanager (*Thraupis episcopus*)[1]	35.2	87	149	236	21.0
Palm Tanager (*Thraupis palmarum*)[1]	38.3	17	45	62	5.5
Silver-beaked Tanager (*Ramphocelus carbo*)[1]	28.2	58	60	118	10.5
Black-faced Tanager (*Schistochlamys melanopis*)[1]	32.1	2	2	4	0.4

served during its entire fruiting period, so most likely several species were missed. The tree was also not observed at night. However, few if any frugivorous bird species are active at night (a possible exception is the Oilbird *Steatornis caripensis*), and all birds tended to arrive at dawn and leave at dusk (*cf.* Leck 1969). Finally, several species which would have been expected in continuous rainforest were not observed, probably because they were reluctant to enter secondary growth used by humans. For instance, Ertan (1999) observed several Ramphastinae, Cotinginae, and Piprinae at similar trees in the rainforest, none of which were observed at the *Ficus* tree. Therefore, the total spectrum of bird species using this tree is probably substantially higher than the recorded 20 species. Nevertheless, the recorded species richness supports Ertan's (1999) findings that trees with large numbers of small, nutrient-poor fruits attract more bird species than trees offering small numbers of large, nutritious fruits. Moreover, the relatively high species richness (relative to other tree species, see Fig. 1) further supports the hypothesis that *Ficus* trees are an important 'keystone' resource for tropical frugivores (Goodman & Ganzhorn 1997, Goodman *et al.* 1997, Heindl & Curio 1999).

The considerable species turnover between years is partly attributable to the different fruiting times, as the migratory warblers observed in March 1999 were probably not present in May 1998. However, it was mostly attributable to turnover of rare species. The overall seven most abundant species were observed in both years, while 10 out of the 12 least abundant species were observed during only one of the two years (Table 1, excluding the multi-species data for *Euphonia* spp.). Therefore, even in this small system, one may make a distinction between the "core" avifauna which regularly uses the tree and the "noncore" avifauna which only occasionally uses it (Remsen 1994). Of course, other birds, which did not eat fruits, also used the tree, e.g., the insectivorous *Myiozetetes cayanensis* and *Troglodytes aedon*, *Galbula galbula*, which hawked for dragonflies, or *Buteo magnirostris*, whose arrival caused all other birds to leave.

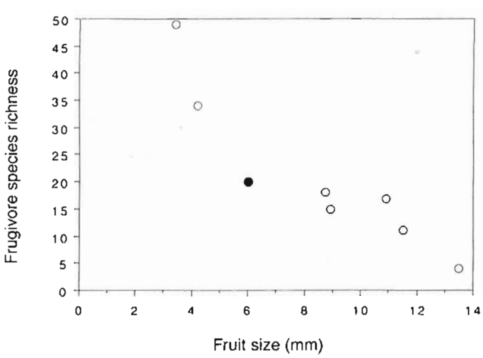

FIG. 1. Plot of fruit size against observed frugivore species richness for eight tree species (Spearman-Rank correlation, rho = - 0.98, $P = 0.01$). All data taken from Ertan (1999) except the data point filled black which represents the tree observed in this study.

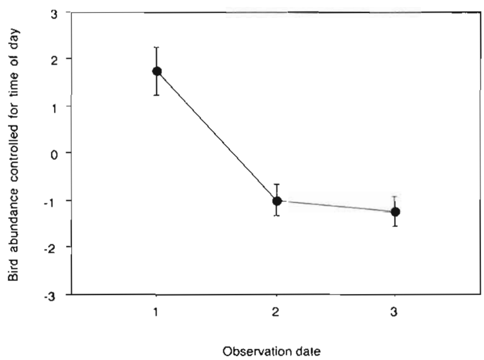

FIG. 2. Plot of observation date in 1998 against bird abundance. Bird abundance during each 5-minute interval was controlled for the effect of time of day by taking residuals of time of day versus abundance. Error bars denote one standard error.

Despite the considerable fruit numbers, the fruits were quickly consumed (in about two weeks), which was reflected in the rather dramatic decrease in bird abundance (Fig. 2). This effect was not observed in the following year, perhaps because the timing of the observation period was different relative to the peak of fruit ripening. Bird abundance also decreased during the day which may also partly reflect decreasing fruit numbers. However, it is more likely that bird activity overall decreases during the day, especially during the hot afternoon, with a short rise of activity before dusk (Walther, in press).

The tree's fitness is partially dependent on seed disperses and may suffer from seed thieves and predators (Howe 1993, Schupp 1993). Assuming that bird abundance roughly reflects fruit consumption, approximately 60% of the seeds were dispersed away from the parent tree. However, this estimate presumes that the disperser categories indeed reflect the degree to which bird species disperse seeds. Some species may swallow fruits but defecate the seeds while still at the parent tree, while others may destroy many seeds, but also disperse some (Levey *et al.* 1994). Therefore more detailed observations of frugivore behavior after fruit consumption will be needed to substantiate the above estimate.

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