BIOTROPICA 23(1): 29–40 1991

# How Long do Fruit-eating Birds Stay in the Plants Where They Feed?[1]

**Nathaniel T. Wheelwright**

Department of Biology, Bowdoin College, Brunswick, Maine 04011, U.S.A.

## ABSTRACT

The foraging behavior of fruit-eating birds influences the reproductive success of the plants whose seeds they disperse.

of the same predictions as the marginal value theorem (Charnov 1976), namely, that birds should prefer and spend more time in "good" than in "poor" patches.

Howe (1979) proposed that the overall risk of attack should increase the longer a bird stays in a fruiting tree because such trees attract frequent and conspicuous visits by fruit-eating birds, making the tree a rich and predictable patch from the perspective of a predator (Snow & Snow 1986). Birds that are small relative to predators should be especially vulnerable to predation and should therefore spend less time in fruiting trees than larger, less vulnerable birds (Howe 1979). The duration of visits by "fearful frugivores" should be negatively correlated with fruit crop size because rich fruit patches should attract predators as well as fruit-eaters (Howe 1979).

Pratt and Stiles (1983) considered three additional factors besides nutritional needs and body size: crypsis, diet, and breeding system. Following

reasoned that cryptically colored birds should be less

(Wheelwright *et al.* 1984). In this study I focus mainly on eight lauraceous tree species (hereafter called "focal tree species") for which I have adequate numbers of feeding observations. The purpose of a comparative approach involving a single plant family is to control for major interspecific differences in fruit and patch characteristics. The focal tree species vary somewhat in phenology, fruit mass, and crop size, but they are very similar in other fruit traits such as the color and nutritional value of their lipid-rich, single-seeded fruits (Table 1; Wheelwright *et al.* 1984, Wheelwright 1985a).

Eighteen bird species feed on the fruits of the Lauraceae (Wheelwright *et al.* 1984). This paper concentrates on four bird species (hereafter called "focal bird species") that together accounted for the vast majority of all visits by birds to lauraceous trees. The species—resplendent quetzal (*Pharomachrus mocinno*), three-wattled bellbird (*Procnias tricarunculata*), emerald toucanet (*Aulacorhynchus*

differ widely in morphology, breeding system, for-

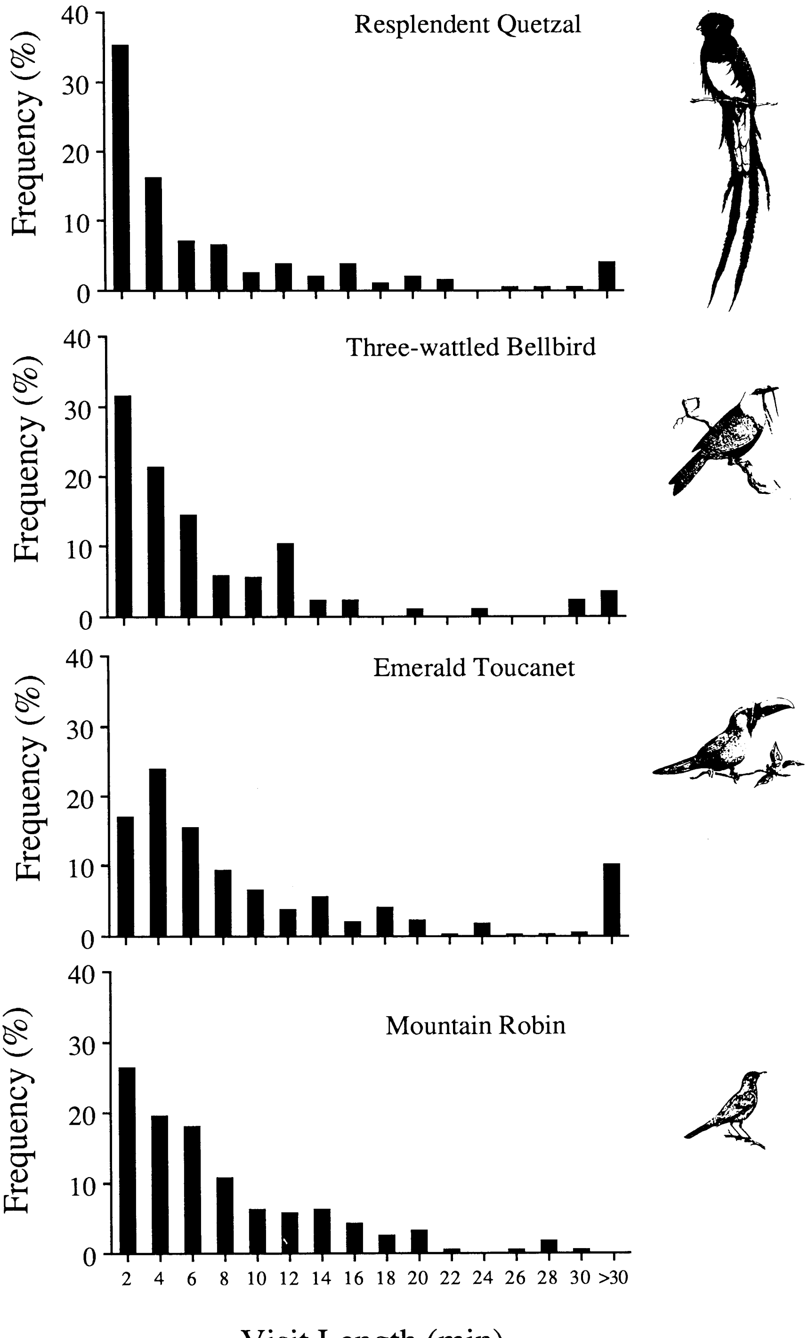


FIGURE 1. Frequency distribution of amount of time spent per foraging visit to fruiting trees of all species of Lauraceae combined by four major fruit-eating bird species at Monteverde, Costa Rica.

TABLE 1. *Reproductive characteristics of fruiting trees of eight focal species in the family Lauraceae at Monteverde, Costa Rica. Crop size and fruit mass are means for the species; kJ/fruit is estimated from data on dry pericarp mass and chemical composition in Wheelwright* et al. *(1984).*

| Tree species | Mean crop size | Mean mass of fruit (g) | Estimated kJ/fruit | Visits per min |
|---|---|---|---|---|
| *Phoebe "cinnamomifolia"*[a] | 15,000 | 0.93 | 2.9 | 0.19 |
| *Ocotea insularis* | 50,000 | 1.34 | 4.4 | 0.48 |
| *Phoebe cinnamomifolia* | 25,000 | 2.04 | 4.0 | 0.33 |
| *Ocotea floribunda* | 19,000 | 2.94 | 5.7 | 0.17 |
| *Ocotea monteverdensis* | 12,000 | 5.50 | 15.8 | 0.14 |
| *Nectandra salicina* | 7000 | 7.42 | 22.2 | 0.16 |
| *Ocotea valeriana* | 1000 | 9.28 | 9.1 | 0.04 |
| *Beilschmiedia pendula* | 2000 | 12.89 | 17.1 | 0.04 |

names listed above correspond to the following species described in Wheelwright *et al.* (1984) and Wheelwright (1985a, b): *Phoebe* sp. AF, *Ocotea tonduzii, Phoebe mexicana, Ocotea wachenheimii, Nectandra hypoglauca, Nectandra salicina, Ocotea* sp. FL, and *Beilschmiedia costaricensis,* respectively.

sometimes obscured birds momentarily or large aggregations of birds arrived simultaneously (see Pratt

representative branches or quadrants within a tree, counting the number of fruits through binoculars teverde bear ripe fruits. Counting all tree species, I conducted at least 15 hr of observations in every month except November (0 hr) and December (2

lauraceous trees in fruit (Wheelwright 1985a). The median amount of time spent observing each focal tree species was 19.0 hr (range 7.0–29.9 hr). These observations were supplemented by biweekly cen-

ficiency and catabolized completely and by multiplying the mean per-fruit mass of lipids by 39.8 kJ/g; of carbohydrates by 17.2 kJ/g; and of pro-

almost certainly overstate the actual caloric value of eating fruits. The daily energy expenditure ($E_{TOT}$) of birds was estimated from Walsberg's (1983) equation, $\ln(E_{TOT}) = \ln 13.05 + 0.06052 \ln(M_B)$,

*the Lauraceae at Monteverde, Costa Rica. Sample sizes in parentheses*
*terisks indicate that the bird species is known to feed on fruits of that*

| ecies | | | | |
|---|---|---|---|---|
| *onte-sis* | *Nectandra salicina* | *Ocotea valeriana* | *Beilschmiedia pendula* | All eight tree spp. |
| 0 | 4.00 (46) | 2.17 (7) | 1.75 (15) | 2.92 (184) |
| 7 | 2.00 (14) | 1.79 (2) | * | 3.17 (89) |
| 9 | 6.63 (44) | 1.33 (7) | 8.83 (8) | 4.67 (366) |
| | — | — | — | 4.00 (371) |
| | * | * | 3.75 (7) | 1.60 (58) |
| 7 | 4.00 (104) | 2.00 (16) | 3.63 (30) | 3.75 (1068) |

of avian activity at fruiting trees, one might have expected that predators on fruit-eating birds would have been common. During 276 hours of obser- [illegible]

plant families, I never observed predation attempts by hawks although I often heard and saw bird-eating hawks elsewhere. Nonetheless, after entering trees and while foraging for fruits, most birds appeared wary (as evidenced by frequent visual scans over their shoulders). Many birds seemed to coordinate their arrival times at fruiting trees, entering and leaving relatively synchronously with other species, although they rarely formed multispecies flocks outside fruiting trees (N. T. Wheelwright, pers. comm.; *cf.* Powell 1985).

[illegible]

visit length differed temporally, even within bird or tree species. Changes in the amount of time birds spent per visit over the course of each tree species' [illegible]

trends in foraging behavior. Toucanets spent progressively longer periods per visit in successive 10-day intervals during the fruiting season at 6 of 8 tree species, but the correlation between visit length and interval was significantly positive at only 1 of the 8 tree species; it was significantly negative at 2 of the tree species (Spearman Rank Test: $P < 0.05$). None of the other three focal bird species showed consistent trends in the amount of time they spent in fruiting trees over the course of the fruiting season. Birds spent no less time in fruiting trees during the breeding season (Feb.–July) than in the nonbreeding [illegible]

Table 4. *Mean processing times for fruits (time between ingestion and regurgitation of seeds, in min) of various species in the Lauraceae by different bird species at Monteverde, Costa Rica. Numbers in parentheses represent ±1 SD, followed by sample sizes for observed processing times. Estimated processing times, based on the elapsed time between successive visits to fruiting trees by birds, are designated by asterisks. Dashes indicate no observations. (See Table 1 for alternative species names.)*

| | Bird species | | | |
|---|---|---|---|---|
| Plant species | Resplendent quetzal | Three-wattled bellbird | Emerald toucanet | Mountain robin |
| *Phoebe "cinnamomifolia"* | 44* (—, 1) | — | 33* (±1, 2) | 37* (±11, 13) |
| *Ocotea insularis* | 19* (±7, 2) | 34 (±4, 5)<br>28* (±8, 21) | 25 (—, 1)<br>27* (±8, 13) | 34* (±9, 9) |
| *Phoebe cinnamomifolia* | 41* (±9, 18) | — | 24 (—, 1)<br>42* (±2, 4) | 43* (±9, 19) |
| *Ocotea floribunda* | 27* (±9, 6) | 44* (±7, 6) | 29 (±4, 7)<br>34* (±4, 11) | — |
| *Ocotea monteverdensis* | 53* (±10, 26) | 50* (±13, 21) | 59* (±14, 11) | — |
| *Ocotea tenera* | — | — | 52 (±0, 2) | — |
| *Nectandra salicina* | 59* (±19, 11) | — | 47* (±14, 13) | — |
| *Ocotea valeriana* | 45* (±13, 4) | — | 32 (—, 1) | — |
| *Beilschmiedia pendula* | 65 (±6, 3)<br>67* (±5, 7) | — | 35 (±2, 3)<br>73* (—, 1) | — |

larger species per visit unless they stayed in the tree until they had regurgitated the seed from the previously ingested fruit. Quetzals, toucanets, and bellbirds could simultaneously process as many as three medium-sized fruits (*O. monteverdensis, N. sali-*

of these species per visit ($\bar{x}$ = 1.5 fruits, $N$ = 49 observations). At tree species with small fruits (*P. "cinnamomifolia," O. insularis*), birds larger than

the mass of the fruit; about 75 percent of the pulp is water. Thus, a 10 g fruit yields only about 1.2 g dry weight of edible pulp. On a dry weight basis, lipids comprise about 20–35 percent of the pulp of lauraceous fruits, proteins 6–18 percent and car-

The maximum estimated energetic value of a single fruit of the eight focal species therefore ranges from 2.9 to 22.2 kJ. Although large fruits have higher trees and regurgitate or defecate seeds from previous visits during the short time they are in the tree.

Median visit lengths by birds of different species foraging at the same tree species were strikingly

suggest that birds pay close attention to the possibility of predation. Although I never observed a predation attempt at a fruiting tree, the costs of ignoring even rare predation risks are great (Howe

breeding system, diet, gut capacity, feeding methods, energetic requirements, and body size (*cf* Hoppes 1987). Mean visit lengths in this study (5.5–11.7

birds are common (Snow & Snow 1986). Nonetheless, in this study, if cryptic birds were less at risk than conspicuous birds, they did not take adimportant claims on their time besides eating. Quetzals, for instance, spend up to 40 percent of the day during the breeding season incubating, brooding young, or guarding the nest (Wheelwright 1983). Male bellbirds pass twice that proportion of time attending display perches during the breeding season (Snow 1977). Time may also be usefully spent censusing future food supplies or diversifying the diet (Foster 1978). Preliminary data suggest that toucanets forage widely early in the day, eating a variety of small-seeded, carbohydrate-rich fruits before directing their attention to a subset of trees with "higher quality" fruits (*sensu* McKey 1975). Birds may sacrifice immediate foraging gains (*e.g.*, bypassing more nutritious fruits) in order to sample fruits from a wide area to estimate their density and quality, or to explore for newly ripening fruits, since fruit availability varies in space and time (Levey 1988). The nutritional inadequacy of fruits may demand that birds diversify their fruit diets (Johnson *et al.* 1985); once the immediate requirements for energy or essential elements are attended to, birds may concentrate on species that are high in energy or particular nutrients. All of these factors would place a premium on short visits to fruiting trees. Evidence against the importance of time minimi-

fruits because they assume 100 percent digestive efficiency (*cf.* Walsberg 1975). They also overlook energetic losses to specific dynamic action, and assume nonstop feeding at maximal rates during a 13 hr day. Even ignoring the problems of overestimation, if these values are compared to the calculated daily energy expenditure (DEE) of the four focal bird species, it appears that birds cannot digest the larger species of lauraceous fruits rapidly enough to meet their energetic demands. Estimated DEE ranges from 205.4 to 331.9 kJ for the four bird species. The disparity between energetic needs and ability to satisfy them is greater with males than with the smaller females, and greater in larger birds (quetzals and bellbirds) than smaller birds (toucanets and especially mountain robins). Because of the long processing time of lauraceous fruits and limitations on the number that can be eaten simultaneously, it may be that large birds would starve even if given a superabundant supply of lauraceous fruits and unlimited foraging time during the day. Additional evidence comes from numerous instances of birds repeatedly regurgitating partially digested fruits, catching them in their bills, and reswallowing them. To illustrate by recounting one observation, after a toucanet in the field swallowed two *O. tenu*-

bird may be able to process more small-seeded fruits over the course of a foraging day, which is the more relevant time span from the perspective of birds and bird-dispersed plants.

the lengthy processing times required to handle large-seeded fruits. In short, fruit-eating birds that are "loafing" may be "busy doing nothing—efficiently" (Krebs & Harvey 1986).

Many fruit-eating birds appear to devote relatively little time to foraging. Manakins and cotingas

playing (Snow 1962, Snow 1977). Frugivory may have facilitated the evolution of polygynous breeding systems because females can raise young unaided and "liberated" males can concentrate on courtship

## ACKNOWLEDGMENTS

This research was funded by grants from the National Science Foundation, New York Zoological Society, Chapman Fund, and Sigma Xi, and supported by the Organization for Tropical Studies–University of Washington