

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

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ABSTRACT

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

One important aspect of their behavior is the amount of time they spend in the plants where they feed.

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

(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

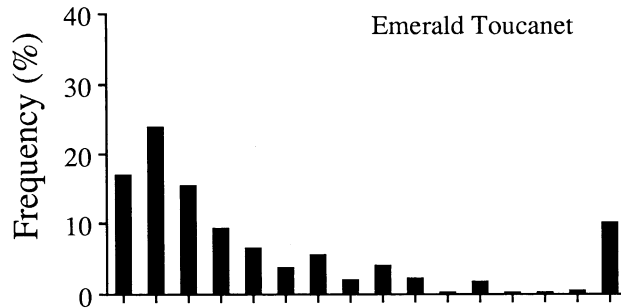
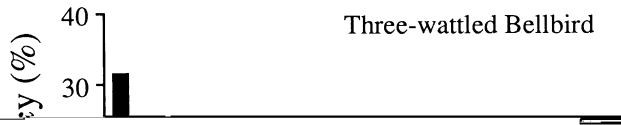
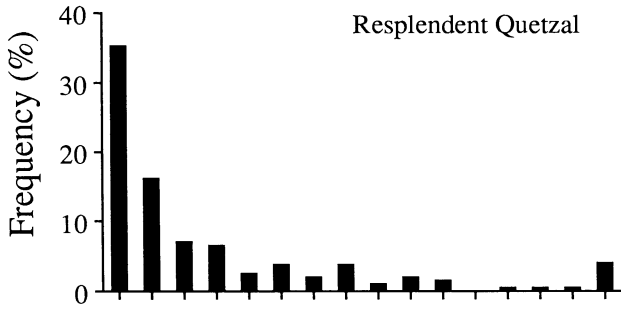


TABLE 1. Reproductive characteristics of fruiting trees of eight focal species in the family Lauraceae at Monteverde, Costa Rica. Crop size and fruit mass are means for the species; kJ/fruit is estimated from data on dry pericarp mass and chemical composition in Wheelwright et al. (1984).

Tree species	Mean crop size	Mean mass of		Visits per min
		fruit (g)	Estimated kJ/fruit	
<i>Phoebe</i> "cinnamomifolia" ^a	15,000	0.93	2.9	0.19
<i>Ocotea insularis</i>	50,000	1.34	4.4	0.48
<i>Phoebe cinnamomifolia</i>	25,000	2.04	4.0	0.33
<i>Ocotea floribunda</i>	19,000	2.94	5.7	0.17
<i>Ocotea monteverdensis</i>	12,000	5.50	15.8	0.14
<i>Nectandra salicina</i>	7000	7.42	22.2	0.16
<i>Ocotea valeriana</i>	1000	9.28	9.1	0.04
<i>Beilschmiedia pendula</i>	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 hr) months during which it is difficult to find any

efficiency 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 protein by 22.6 kJ/g (Gosselink 1977). Total energy

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 censuses of about 300 trees over a 14-month period

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, $\ln(E_{TOT}) = \ln 13.05 + 0.06052 \ln(M_B)$, where M_B is body mass (g). Mean M_B of *C. caeruleus*

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

species

Species	<i>Nectandra salicina</i>	<i>Ocotea valeriana</i>	<i>Beilschmiedia pendula</i>	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-

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'

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

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

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.)

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

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 carbohydrates 5–20 percent (Wheelwright *et al.* 1984).

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 ad

important 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 preening and displaying perches during the breeding season

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 cal

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 coringas

... (Snow 1962, Snow 1977). ...

ACKNOWLEDGMENTS

WHEELWRIGHT, M. D. 1926. F. L. G. 1926. F. L. G. 1926. F. L. G. 1926.