

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. One important aspect of their behavior is the amount of time they spend in fruiting plants. Qualitative models based on a bird's predation risk, diet, and breeding system have been proposed by Howe (1979) and Pratt and Stiles (1983) to explain how much time birds spend in fruiting trees. These models predict that relatively large body size and cryptic plumage should make birds less vulnerable to predation and enable them to spend longer time in fruiting trees. Additionally, they predict that birds that specialize on a narrow fruit diet or have monogamous breeding systems should also spend more time in fruiting plants because they do not have to leave plants to diversify their diet or attend leks or display perches.

This study presents data on the behavior of four bird species which were responsible for more than 94 percent of all feeding visits to eight bird-dispersed tree species in the family Lauraceae in the lower montane forests of northwestern Costa Rica. Despite prominent differences in size, coloration, diet, method of foraging for fruits, and breeding system, the birds spent about the same amount of time per foraging visit (median visit lengths = 2.9–4.7 min) and ate about the same number of fruits (1–3) per visit. Differences between sexes within bird species were slight or nonexistent. Single factors such as crypsis, diet, or breeding system were ineffective in predicting how long birds spent in fruiting plants.

An analysis of fruit processing times and caloric value in relation to birds' metabolic rates indicates that fruits may not be the "free lunch" they are often reputed to be. Birds may not be able to meet their energetic demands on a pure diet of the large, lipid-rich fruits of the Lauraceae because gut space is limited and it takes so long to process individual fruits.

THE BEHAVIOR OF FRUIT-EATING BIRDS has important consequences for the evolution of reproductive traits in many plant species because of the role birds play as seed dispersers (Snow 1971, McKey 1975, Thompson 1982, Howe 1986). How birds handle fruits, which fruits they choose, where they move and feed during the course of a day or year, and even what kind of breeding system they have will influence where seeds land and hence the reproductive success of bird-dispersed plants (Trainer & Will 1984, Levey 1987, Moermond & Denslow 1985, Fogden 1972, Katak 1981, Wheelwright 1983, Martin & Karr 1986, Hoppes 1987, Murray 1988, Beehler & Pruett-Jones 1983). One major aspect of the behavior of fruit-eating birds that affects their suitability as seed dispersers is the amount of time they spend in fruiting plants during foraging trips. Presumably, the more time birds spend in a plant, the more seeds they deposit beneath the plant, where seeds and seedlings suffer higher mortality (Janzen 1971, Howe & Estabrook 1977, Clark & Clark 1984, Howe & Schupp 1985). If birds' visits are short, they are more likely to carry seeds away

from the parent plant, make more visits per day, and produce a less clumped distribution of seeds (Howe & Estabrook 1977).

Traditional models of patch foraging behavior, which have been widely successful in predicting when animals ought to leave a patch in order to maximize their long-term average rate of intake of a resource such as energy (Charnov 1976, Stephens & Krebs 1986), have not been applied to fruit-eating birds because many of the assumptions of the simpler models (*e.g.*, patch depletion, prey capture costs, ability to meet nutritional needs within a patch, etc.) are inaccurate or incomplete (Martin 1985). Instead, models specific to fruit-eating birds have been proposed to explain the behavior of fruit-eating birds in "patches." Howe and Estabrook (1977) proposed that fruit-eating birds should remain in trees until they were satiated (*i.e.*, their guts were full) or the supply of ripe fruits was exhausted; in the latter case, they envisioned depletable patches such as trees with arillate fruits enclosed in capsules, only a small number of which open at a time. They hypothesized that visit lengths should increase with crop size in "frugivores whose actions are governed solely by nutritional need and reward" (Howe 1979). This reasoning leads to some

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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: cypsis, diet, and breeding system. Following Howe's (1979) emphasis on predation risk, they reasoned that cryptically colored birds should be less vulnerable to predation and should spend more time per visit in fruiting trees than conspicuously colored birds. Also, birds that can sustain themselves on a diet of fruits alone because of their specialized digestive adaptations should linger longer in fruiting trees than birds that must forage elsewhere for invertebrates to balance their diet. Finally, monogamous species should spend more time in fruiting trees than polygamous species because the latter have to devote more time to courtship (Pratt & Stiles 1983).

This paper presents data on the amount of time fruit-eating birds spend per foraging bout in trees in the family Lauraceae in a lower montane forest in Costa Rica. The results are considered in the context of the models of Howe and Estabrook (1977), Howe (1979), and Pratt and Stiles (1983). I also present evidence suggesting that many fruits may not be the "free lunch" they are often reputed to be because of lengthy processing times.

METHODS

The study area, Monteverde, Costa Rica, includes 15 km² of lower montane wet and rain forests and pastures at an elevation of 1350–1500 m in the Cordillera de Tilarán (10°18'N, 84°48'W) (see Lawton and Dryer [1980] and Wheelwright [1985a] for a more complete description of the site).

Birds have been observed feeding on the fruits of at least 171 plant species at Monteverde, including 23 species in the avocado family (Lauraceae)

(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 (*Pharomacrus mocinno*), three-wattled bellbird (*Procnias tricarunculata*), emerald toucanet (*Aulacorhynchus prasinus*), and mountain robin (*Turdus plebejus*)—differ widely in morphology, breeding system, foraging mode, body size, and migratory habits (Fig. 1, Table 2). Although the number of focal tree and bird species observed in this study is small, they vary in the traits highlighted by Howe, Pratt and Stiles. Differences in the amount of time birds spend in fruiting plants therefore can be used as a preliminary evaluation of the predictions of those models.

At regular intervals I conducted 1–6 hr watches of birds feeding in fruiting trees, including a mean of 4.4 individual trees per species for each of the eight focal plant species. Trees on the edges of light gaps, in ravines, or along pasture edges provided the best opportunity to observe birds and quantify their foraging behavior accurately. Trees vary in fruit crop size and visit rates by different bird species even over small spatial scales (Martin & Karr 1986, Murray 1987, Bronstein & Hoffman 1987, Frost 1980), but differences in the behavior of birds (*e.g.*, visit lengths) as a function of habitat or time of day or season were not observed.

From a distance of 20–40 m, a distance far enough away that the behavior of birds was unaffected, I observed birds through binoculars or a 15× spotting scope. Observations were dictated into a portable tape recorder and later transcribed. For each bird entering a fruiting tree, I recorded species, sex and age class (if distinctive), time of entry and departure (to the nearest 5 sec), number of fruits eaten, and food handling behavior. The duration of a bird's visit was defined as the time of departure minus the time of entry. It was not always possible to follow every bird because dense foliage

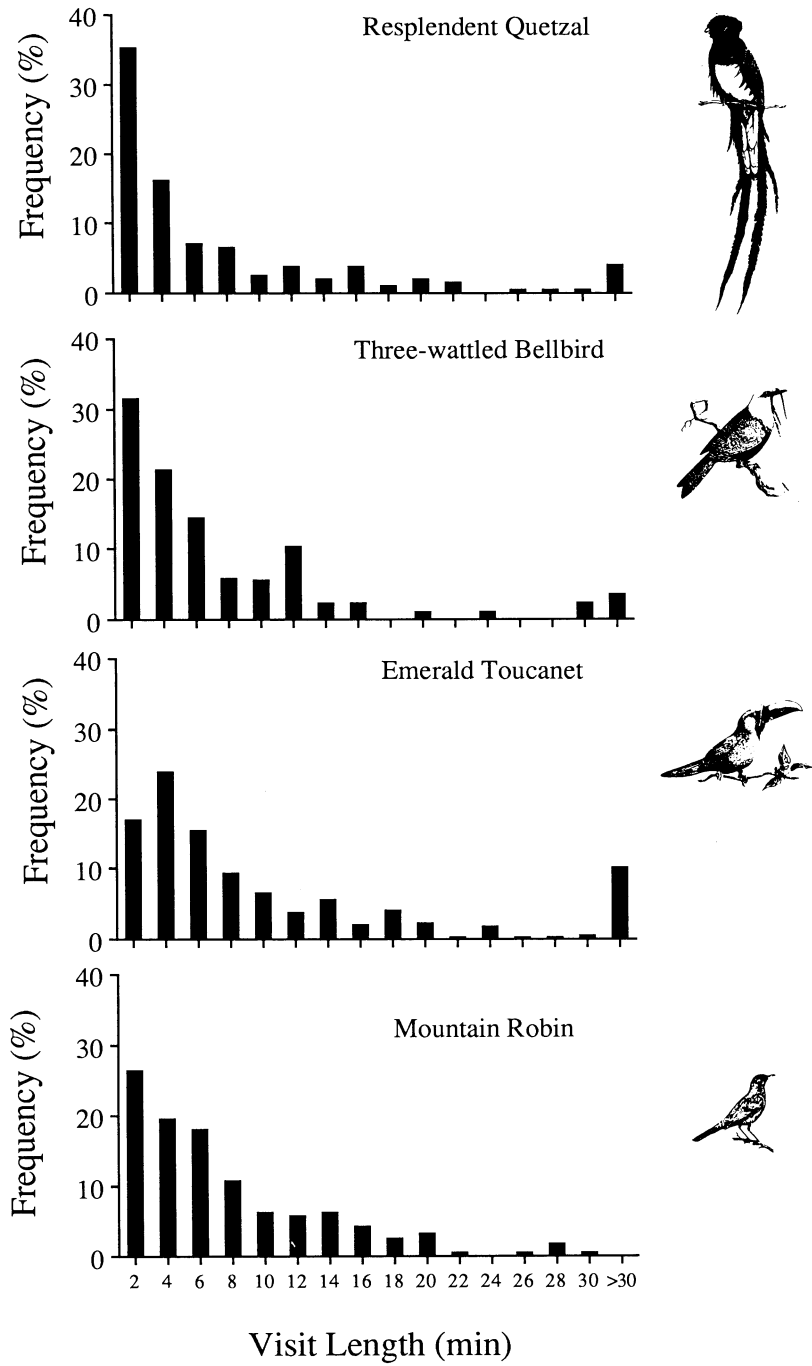


FIGURE 1. Frequency distribution of amount of time spent per foraging visit to fruiting trees of all species of Lauraceae combined by four major fruit-eating bird species at Monteverde, Costa Rica.

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
<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

^a The taxonomy of the Lauraceae of Costa Rica has recently been clarified by Burger and van der Werff (1990). The 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 hypoglaucula*, *Nectandra salicina*, *Ocotea* sp. FL, and *Beilschmiedia costaricensis*, respectively.

sometimes obscured birds momentarily or large aggregations of birds arrived simultaneously (see Pratt & Stiles 1983, Wendelken & Martin 1987). This problem never occurred with quetzals, which typically entered and left alone and conspicuously, and only rarely with toucanets and adult male bellbirds. Most incomplete observations (less than half of all visits) involved mountain robins. Observations in which I could not determine the identity of the bird, the time it entered the tree, or the time it departed were excluded from analyses of visit duration. Thus, sample sizes vary between comparisons. Fruit crop sizes were estimated by haphazardly selecting several

representative branches or quadrants within a tree, counting the number of fruits through binoculars or a spotting scope, and extrapolating that fruit density over the entire tree.

The research in Monteverde began in June 1979. Most of the observations on which this study are based occurred during 17 months between 1979 and 1981, although they incorporate data gathered through 1990. In total I spent 208 hr at lauraceous trees, including 137 hr at the eight focal species. Over half of all observations took place between 0700 and 1000 hr and in the first months of the rainy season, when most lauraceous plants at Mon-

Table 2. *Ecological characteristics of the four major bird species feeding on fruits of trees in the family Lauraceae at Monteverde, Costa Rica.*

Bird species	Body mass (g)	Coloration	Diet	Foraging group size	Breeding system
Resplendent quetzal					
Male	206	conspicuous	chiefly fruits	solitary, small groups	monogamy
Female	189	intermediate	chiefly fruits	solitary, small groups	monogamy
Three-wattled bellbird					
Male	210	conspicuous	chiefly fruits	solitary	polygyny
Female	148	cryptic	chiefly fruits	solitary	polygyny
Emerald toucanet					
Male	162	intermediate	fruits, invertebrates, vertebrates	solitary, small to medium flocks	monogamy
Female	162	intermediate	fruits, invertebrates, vertebrates	solitary, small to medium flocks	monogamy
Mountain robin					
Male	95	cryptic	fruits, invertebrates	small to large flocks	monogamy
Female	95	cryptic	fruits, invertebrates	small to large flocks	monogamy

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 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, monthly censuses for an additional 12 months, and annual censuses for an additional 8 years.

All birds in this study regurgitate the relatively large seeds of lauraceous fruits after removing the surrounding pulp in their proventriculus or gizzard. I determined fruit-processing time directly by following individual birds continuously in the field and recording when they swallowed a fruit and when they next regurgitated a seed of the same species. Lauraceous seeds, which weigh as much as 9 g, are very conspicuous when dropped from the canopy. In the case of large-seeded fruits, which completely occupied the stomach and could be processed only one fruit at a time (see below), I could relate with certainty a given feeding event with subsequent regurgitation and quantify processing times precisely. Field observations yielded similar results to observations of toucanets during captive feeding trials. For other species, rough estimates of fruit-processing times were made by measuring intervals between repeat visits to the same fruiting tree by individual birds. Estimates of fruit-processing times derived from repeat visit intervals can be confounded by the problems of uncertainty in recognizing unmarked individuals and potential overestimation of processing times because birds may regurgitate seeds away from the tree or visit other trees before returning. Alternatively, they may underestimate processing times because birds often return to fruiting trees before regurgitating seeds (Wheelwright 1983). Therefore, I used repeat visit intervals to estimate fruit-processing times only when I was confident that I was observing the same birds and that they were not feeding at other trees in the interim (*i.e.*, they flew into a neighboring tree from which I saw no birds depart until birds returned to the tree under observation). In most cases such estimates were in the same range as other methods (see below).

Nutritional values of fruits are presented in Wheelwright *et al.* (1984). From these I derived estimates of maximum possible energetic content of individual fruits by assuming conservatively that all compounds were assimilated with 100 percent ef-

iciency 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 proteins by 23.6 kJ/g (Gordon 1977). Such estimates 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 the focal bird species is given in Wheelwright *et al.* (1984).

For statistical analyses I used SAS (SAS 1985); ANOVAs were performed using the GLM procedure. All other tests are nonparametric except where noted. Unless ANOVAs revealed significant differences in feeding behavior (duration of visits, fruit processing times) between sexes and age classes within a bird species, I combined sexes and age classes. I report both mean and median visit durations. Means are useful to reflect the total time a bird species spent in trees and they allow comparison with other published data, but they are disproportionately influenced by a few extreme values, which is a problem when distributions are highly skewed, as in the distribution of visit lengths (see below). Therefore, median visit lengths are reported because they give a better indication of a typical visit length and behavior of birds in fruiting trees.

RESULTS

VISIT FREQUENCIES.—Birds entered fruiting lauraceous trees at an average rate of 0.17 arrivals/min ($N = 2119$ visits). Mean visit frequencies at different tree species varied from 0.04 to 0.48 arrivals/min (Table 1). The four focal tree species whose fruits weighed less than 3.5 g and whose crop size typically exceeded 10,000 fruits attracted an average of 0.36 birds/min, whereas the four tree species whose fruits weighed more than 5.0 g and whose mean fruit crop size was less than 5000 drew an average of only 0.09 birds/min (Mann–Whitney *U*-Test: $P < 0.05$; crop sizes represent the total number of fruits on a plant, 20–70% of which might be ripe at any one time, irrespective of fruit size). Four bird species—mountain robins, emerald toucanets, resplendent quetzals, and three-wattled bellbirds—accounted for 94 percent of all visits to lauraceous trees; 13 other birds species accounted for the remaining visits. Mountain robins, the species with the smallest gape width of the four, fed at only three of the eight focal tree species (Table 3; Wheelwright 1985b).

Because of a conspicuous and predictable amount

Table 3. Median amount of time (min) spent by fruit-eating birds per visit in individual fruiting trees in the Lauraceae at Monteverde, Costa Rica. Sample sizes in parentheses below. Dashes indicate that the bird species was not recorded foraging at a particular species; asterisks indicate that the bird species is known to feed on fruits of that lauraceous species but visits were not timed. (See Table 1 for alternative species names.)

Bird species	Tree species								All eight tree spp.
	<i>Phoebe</i> "cinnamomi- folia"	<i>Ocotea</i> <i>insularis</i>	<i>Phoebe</i> <i>cinna-</i> <i>momifolia</i>	<i>Ocotea</i> <i>floribunda</i>	<i>Ocotea</i> <i>monte-</i> <i>verdensis</i>	<i>Nectandra</i> <i>salicina</i>	<i>Ocotea</i> <i>valeriana</i>	<i>Beilschmiedia</i> <i>pendula</i>	
Resplendent quetzal	1.67 (9)	3.83 (13)	1.83 (30)	2.25 (17)	3.50 (47)	4.00 (46)	2.17 (7)	1.75 (15)	2.92 (184)
Three-wattled bellbird	—	4.08 (9)	*	2.00 (15)	3.67 (49)	2.00 (14)	1.79 (2)	*	3.17 (89)
Emerald toucanet	5.83 (36)	4.88 (44)	2.33 (64)	9.00 (113)	3.79 (50)	6.63 (44)	1.33 (7)	8.83 (8)	4.67 (366)
Mountain robin	5.75 (33)	4.00 (246)	2.83 (92)	—	—	—	—	—	4.00 (371)
Other bird species	2.67 (12)	1.25 (25)	1.58 (14)	*	*	*	*	3.75 (7)	1.60 (58)
All bird species combined	5.67 (90)	3.83 (337)	2.33 (200)	5.00 (145)	3.67 (146)	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 observation at fruiting trees of the Lauraceae and other 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).

AMOUNT OF TIME SPENT IN FRUITING TREES.—Birds spent a mean of 8.1 min per visit at lauraceous trees ($N = 1068$ visits; Table 3), but most visits were half that length (<4 min), irrespective of tree species, fruit size, or fruit crop size (Fig. 1). The distribution of visit lengths by individual bird species feeding at different tree species were highly skewed to the right in all cases (Fig. 1). The median visit length for all bird visits to lauraceous trees was 3.8 min (Table 3). On rare occasions, toucanets stayed up to 4 hr in a single tree, feeding at approximately hourly intervals. Quetzals seldom remained as long as 1 hr within a tree. No other bird species was recorded spending more than 40 min per visit. Visits tended to be longer in lauraceous species with large fruits and correspondingly long processing times (see below).

The median length of time that birds spent per visit varied only slightly between bird species, despite the birds' distinct breeding systems, foraging modes, and body sizes (Fig. 1, Table 2). Quetzals spent a median of 2.9 min/visit, as compared to bellbirds (3.2 min/visit), toucanets (4.7 min/visit), and mountain robins (4.0 min/visit) (Table 3). Tree species, despite their differences in phenology, fruit crop size, and fruit size (Table 1, Wheelwright *et al.* 1984), also varied relatively little in the amount of time birds spent per visit; median visit lengths ranged from 2.0 to 5.7 min at the eight focal lauraceous species (Table 3). A two-way ANOVA (using log-transformed data) revealed significant sources of variation in visit length due to bird species ($P < 0.001$), tree species ($P < 0.001$), and bird species–tree species interaction ($P = 0.01$), but the magnitude of differences in visit lengths were slight (Table 3).

There were few consistent patterns in the way

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' fruiting season illustrated the lack of predictable 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 season (Mann–Whitney U -Test: $P > 0.05$). Diurnal patterns of visit lengths also showed no consistent trends.

Of the four focal bird species, only quetzals and bellbirds are sexually dimorphic enough to allow comparisons between sexes. Male and female quetzals spent about the same amount of time per visit to fruiting trees ($N = 74$ and 77 visits, respectively). At none of the eight focal tree species did they differ significantly in visit lengths (Mann–Whitney U -Test: $P > 0.05$), nor did they differ when records at all tree species were combined ($P = 0.86$). Male bellbirds ($N = 25$ visits), in contrast, spent more time per visit than females and juveniles collectively ($N = 36$); differences were significant when records at all tree species were combined ($P = 0.03$) and at one of two tree species for which I had samples adequate for statistical analysis, but not at the other ($P = 0.01$, $P = 0.42$, respectively).

There was a tendency for visit lengths to be longer at large-fruited trees than small-fruited trees when bird species were considered collectively ($N = 689$ and 467 visits, respectively; Mann–Whitney U -Test: $P = 0.02$). The differences were not significant when bird species were considered separately and sample sizes were reduced.

FRUITS EATEN PER VISIT, FRUIT DIGESTION TIMES AND ENERGETIC VALUE OF FRUITS.—Birds generally ate 1–3 fruits per visit ($N = 203$ observations of fruit consumption). A single fruit of the larger species (*B. pendula*, *O. valeriana*) is too large to be eaten by mountain robins and totally fills the stomachs of the other birds, based on dissections of three toucanets, two mountain robins, and one quetzal (Wheelwright 1983, 1985b). As a consequence, birds never swallowed more than one fruit of the

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</i> "cinnamomifolia"	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 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 mountain robins could eat as many as seven fruits, but typically ate far fewer (\bar{x} = 2.2 fruits, N = 99 observations).

The time between ingestion of a fruit and regurgitation of its seed depended on fruit size. Large fruits required much longer digestion times than small fruits, and fewer could be processed at a time (Table 4). The shortest digestion time observed was 24 min for captive toucanets eating *P. cinnamomifolia* fruits. The longest time was 71 min spent by a quetzal observed processing a single *B. pendula* fruit (Table 4). On average, processing lauraceous fruits took about 30–40 min.

From observations on the number of fruits eaten per visit, the processing times per fruits, and the caloric content of fruits, one can estimate the maximum daily rate of energy intake a bird would gain by feeding exclusively on the fruits of each of the eight focal tree species. Mean fruit mass varies from 0.9 to 12.9 g in the eight focal species (Table 1; Wheelwright *et al.* 1984). The relatively large single seed of lauraceous fruits contributes about half of

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). 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 absolute energetic values than small fruits, they yield relatively less energy per g whole fruit mass. Maximum estimated daily energy gain from feeding on different lauraceous fruits ranges nearly an order of magnitude, from 154 to 1156 kJ (Table 1).

DISCUSSION

Most visits by birds to fruiting lauraceous trees in the lower montane forest of Monteverde, Costa Rica, were short. Half lasted less than 4 min, irrespective of tree species. Fruit digestion times were never less than 24 min, and, typically, birds regurgitated seeds after at least 30 min. Very rarely did birds stay so long in trees that they dropped seeds from that particular foraging bout. Nonetheless, one commonly finds seeds dropped by birds beneath fruiting trees (Wheelwright, pers. obs., although see Murray 1988). In light of the brevity of foraging bouts and the duration of fruit processing times documented in this study, it appears that birds often return to

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 similar, in spite of differences in the birds' coloration, 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 min) were similar to visit lengths by New Guinean passerines (4.5–12.5 min; Pratt & Stiles 1983) and within the range of visit lengths of birds at a neotropical fig (1.9–19.7 min, with most birds between 3.3 and 8.5 min; Bronstein and Hoffman 1987) in spite of the fact that very different bird and plant species were involved (see also Wendelken and Martin 1987). Temperate zone birds observed feeding at shrubs seemed to spend less time per visit (Herrera & Jordano 1981, Herrera 1984, Hoppes 1987), a discrepancy probably attributable to the difference between trees and shrubs rather than the tropics and temperate zone (Wheelwright 1988).

Do the slight differences between species reflect ecologically important underlying factors, such as predation risk, diet, and breeding system, as proposed by Howe (1979) and Pratt and Stiles (1983)? In spite of the small number of focal species studied, it is worth considering whether the results of this study are consistent with existing models of the foraging behavior of fruit-eating birds. Howe's (1979) model in its simplest form predicts that larger birds, which were presumably safer from predators, should spend more time in fruiting trees than smaller birds. That turned out not to be the case with bellbirds and quetzals, which spent the same amount of time per visit as the smaller toucanets and robins. These results are confounded by differences in foraging mode (Santana & Milligan 1984) and crypsis, and the size range of birds included in this study may not be broad enough to reveal an effect of differential predation risk due to size differences.

Nor was there an obvious relationship between plumage coloration and visit lengths, as shown by comparing ages and sexes within bird species. Female and juvenile bellbirds are exceedingly cryptic, yet they spent significantly less time in fruiting trees than the conspicuous male bellbirds. Gaudy male quetzals spent about the same amount of time in trees as female quetzals, which are relatively inconspicuous. This is not to say that fruit-eating birds are unconcerned with the risk of predation. On the contrary, their wariness and the apparent synchrony of their arrivals and departures from fruiting trees

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 1979). In other habitats, attacks on fruit-eating birds are common (Snow & Snow 1986). Nonetheless, in this study, if cryptic birds were less at risk than conspicuous birds, they did not take advantage of their relative safety by spending more time in fruiting trees.

Controlling for tree species, I did not find that birds whose diet consisted predominantly of fruits spent longer in fruiting trees than more facultative fruit-eaters, unlike Pratt and Stiles (1983). Mountain robins and emerald toucanets stayed as long per visit as resplendent quetzals and three-wartled bellbirds, species with more specialized fruit diets (Wheelwright *et al.* 1984). Breeding system appeared to have little influence on visit lengths, in contrast to the results of Pratt and Stiles (1983). Bellbirds, the only polygynous species observed, spent an intermediate amount of time in fruiting trees, instead of the expected shortest time.

Although this study does not provide support for the models of Howe (1979) and Pratt and Stiles (1983), the small sample sizes (four bird species, eight tree species) and the many confounding variables (size, coloration, diet specialization) do not allow their rejection either. The models are reasonable and based on well-documented natural history observations. Coloration, diet, breeding system, and risk of predation almost certainly influence birds' foraging behavior, although this study suggests that their influence is either more subtle or less important than thought. The way such factors interact, however, may result in a surprising convergence in the amount of time spent in fruiting trees by such ecologically distinct species as bellbirds and toucanets or in such distinct habitats as Costa Rica and New Guinea. If subsequent studies show that unrelated tropical fruit-eating birds behave similarly in distinct habitats, the kinds of general models proposed by Howe (1979) and Pratt and Stiles (1983), appropriately modified, may reveal the common factors underlying their behavior.

Perhaps we would learn more by rephrasing the question "how long do fruit-eating birds stay in the plants where they feed" to "why do they leave?" Certainly, more attention should be paid to what they do when not in fruiting trees. Three general hypotheses, none mutually exclusive, appear possible: time minimization, predation risk, and decline in patch quality. The first recognizes that birds have

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 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 minimization to birds comes from the lack of differences in time spent by birds with broad vs narrow diets, between breeding season visits and visits during the nonbreeding season, and between monogamous and polygamous bird species.

Birds spend little time in fruiting trees, typically leaving to digest fruits in nearby trees, which supports the second hypothesis, minimization of the risk of predation (Howe 1979). Yet in this study conspicuous males spent as much or more time as inconspicuous females, and small birds as much as large birds over the size range studied.

The third hypothesis, a decline in "patch quality" (Charnov 1976), proved to be unimportant in this study because of the lack of seasonal or diurnal trends in visit lengths (despite changing fruit densities), the fact that the abundance of ripe fruits in lauraceous trees far exceeded the number that could be eaten by one bird, or even a flock of birds, during individual foraging bouts, and the persistence of ripe but uneaten fruits for weeks or months (Wheelwright 1985a, pers. obs.).

One of the unexpected outcomes of this study was the fact that fruits seem not to be the "free lunch" they are often reputed to be. The calculations of energy gain presented above almost certainly overestimate the energetic value of eating lauraceous

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. tenera* fruits, it regurgitated, caught, and reswallowed one or both of the incompletely digested fruits at 20 min, 30 min, 43 min, 45 min, and 49 min, before it finally liberated the seeds from the pulp and ejected them, 51 and 52 min after having first swallowed the fruits.

In retrospect, such a result should not be surprising, given the potential conflict between species in most mutualistic interactions (Wheelwright & Orians 1982, Boucher 1985, Herrera 1985). Fruits are easily procured, but the hidden cost of a fruit diet is the lengthy time it takes to digest them, especially the large-seeded fruits examined in this study. It is often noted that fruits whose seeds are regurgitated can be processed more rapidly than fruits with small seeds that are defecated (Sorenson 1984). Yet an often overlooked advantage of small-seeded fruits is that they can be eaten and processed continuously; the digestive tract is a flow-through system. Large-seeded fruits, on the other hand, must be eaten one or a few at a time because seeds generally have to be regurgitated before subsequent fruits are eaten. A single large-seeded fruit may be processed more quickly in some cases than a small-seeded fruit (that is, seeds that are regurgitated reappear faster than seeds that travel the length of the digestive tract and are defecated). However, a

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.

Many fruit-eating birds appear to devote relatively little time to foraging. Manakins and cotingas sometimes spend over 90 percent of the day displaying (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 (Snow 1971). Nonetheless, this study suggests that fruit-eating birds, while sitting around or displaying, may be minimizing energy expenditures or indulging in activities that do not compete with feeding while they wait until pulp and seeds are separated and space is evacuated in the gut for the next meal (*cf.* Karasov *et al.* 1986). On an *ad libitum* diet of nothing but lauraceous fruits, it may not be easy for them to satisfy their metabolic demands, given

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).

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