

Four Constraints on Coevolution Between Fruit-eating Birds and Fruiting Plants: a Tropical Case History

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Abstract

Few researchers currently expect to find evidence of tight coevolution between fruit-eating birds and the plants whose seeds they disperse, despite the intuitive appeal and logic of earlier theories about the direction of evolutionary change in mutualistic interactions. Obligate, specialized relationships between avian seed dispersers and plants are probably rare, because coevolution is constrained in four ways: (a) weak selection; (b) inconsistent selection; (c) antagonistic selection; and (d) limitations on evolutionary responses. These factors are illustrated with data from research on fruit-eating birds and bird-dispersed plants in the family Lauraceae at Monteverde, Costa Rica, from 1979 to 1986. I describe seasonal and individual differences in fruit choice in Three-wattled Bellbirds (*Procnias tricarunculata*) and Long-tailed Manakins (*Chiroxiphia linearis*) and present the results of field experiments on seed predation by spiny pocket mice. Despite clear constraints on coevolution, patterns such as the correspondence between fruit color and birds' visual perception or between fruit size and the trophic morphology of avian seed dispersers strongly implicate the importance of coevolution at higher taxonomic levels than species-species interactions.

Introduction

McKey (1975) was an influential proponent of the notion that tight coevolution occasionally occurs between fruit-eating birds and fruiting plants, an intuitively appealing theory based on the recognition that avian seed dispersers positively influence the fitness of plants, and vice versa (Howe and Estabrook 1977). Nonetheless, few of McKey's (1975) original predictions on dietary specialization or dispersal quality have been supported by subsequent empirical studies (Worthington 1982; Herrera 1982; Wheelwright 1985a). Furthermore, the theory

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has been strongly challenged on theoretical grounds (Wheelwright and Orians 1982; Schemske 1983; Howe 1984; Herrera 1985a). Critics of the theory maintain that coevolution between avian seed dispersers and plants is constrained for four general reasons: (a) weak selection; (b) inconsistent selection; (c) antagonistic selection; and (d) limitations on evolutionary responses (Wheelwright and Orians 1982).

Similar constraints apply to evolutionary change in general, but in this paper I shall illustrate them with examples from interactions between plants and their avian seed dispersers. The theoretical bases for expecting these constraints on coevolution between birds and plants are the following. First, natural selection for an intimate association between a particular bird species and a particular plant species should be weak when ecological or behavioral differences between the bird species and alternative seed dispersers are too slight to produce distinguishable effects on plant fitness. The force of selection promoting tight pairwise associations should be diminished even further in complex systems, where pollination, seed predation, and other types of interactions have the effect of diluting the seed-dispersal interaction (Herrera 1985a). Second, natural selection should be inconsistent in space and time, as birds' diets or behaviors as seed dispersers vary in different habitats, in different portions of their geographical range, in different seasons, and in different years. The extinction of one or both of the interacting populations represents an extreme example of temporal inconsistency in species' interactions. Third, natural selection for particular plant reproductive traits that promote tight associations between birds and plants, such as large fruit-crop size or conspicuous fruit displays, may be opposed because of antagonistic selection by seed or fruit predators attracted to large or conspicuous fruit crops. Finally, even when natural selection is strong, consistent, and unopposed, it may not result in the evolution of fine-tuned, species-specific, coevolved associations between birds and plants because of a lack of genetic variability in relevant traits, genetic correlations between traits, or intrinsic features of the interaction that prevent or slow the evolution of precise mutual adaptations (Wheelwright and Orians 1982; Schemske 1983; Howe 1984; Herrera 1985a).

The aim of this paper is to consider some of the evidence for each of these hypothetical constraints on coevolution. Since 1979 I have been conducting research on fruit-eating birds and their food plants in a lower montane forest in northwestern Costa Rica. My research, like that of other researchers (Howe and Vande Kerckhove 1979; Herrera 1984a; Moermond and Denslow 1985), suggests that tight coevolution between such birds and plants is indeed uncommon and that the rarity of specialized, obligate associations is due in large part to the constraints predicted above. In this paper, I will describe temporal and spatial changes in the diets of several specialized fruit-eating birds and present the results of several experiments on seed predation following dispersal. I will also briefly summarize some of the main conclusions of research previously published in order to illustrate the constraints on coevolution and to give a general overview of the dynamics of interactions between fruit-eating birds and fruiting plants at one tropical site.

Methods

Study Area

The study area encompasses approximately 15 km² of undisturbed lower montane wet and rain forests (Holdridge 1967), small cattle pastures, and woodlots in Monteverde, Costa Rica (10°18'N, 84°48'W). It also includes the Monteverde Cloud Forest Reserve (now 4000 ha) and abuts the 33 000-ha Arenal Forest Preserve. Monteverde sits on a plateau along the continental divide at an elevation of 1350–1550 m. The rich volcanic soils support a diverse forest (an ongoing study at Monteverde suggests that the forest contains as many as 2000 vascular plant species; W. Haber, pers. commun.). Of the 1000 or so woody plant species, over half produce fleshy fruits that are eaten by birds. The avifauna of Monteverde is also quite rich (see Buskirk 1976, Feinsinger 1978, and Powell 1979 for reports on other aspects of avian ecology at Monteverde) and includes over 85 species of fruit eaters (Wheelwright *et al.* 1984) besides parrots and pigeons, which probably rarely disperse viable seeds (Janzen 1981). For a more complete description of the climate and forest of the area, see Lawton and Dryer (1980) and Wheelwright (1986).

Plant Species

When this study began, coevolution between plants and seed dispersers was believed to occur most commonly in the tropics, where species in the family Lauraceae were held up as prime examples of fruiting plants that had evolved a special relationship with their seed dispersers (Snow 1973; McKey 1975; Snow 1980). Therefore, to explore this proposed special relationship for evidence for or against coevolution, I chose to focus on the Lauraceae in Monteverde, Costa Rica, and on the bird species that feed on lauraceous fruits.

At least 23 bird-dispersed species in the Lauraceae occur in the same or adjoining habitats in Monteverde (Fig. 1). Because of their overlapping or proximate ranges and the vagility of fruit-eating birds (Wheelwright 1983), individual birds can potentially feed on the fruits of each tree species, assuming that they can swallow the bulky fruits of the largest Lauraceae (Wheelwright 1985a). However, only four to five bird species at Monteverde are large enough to feed on the entire size range of lauraceous fruits, which range in diameter from 8 to 25 mm; these large-gaped birds consume fruits of most or all of the lauraceous species at Monteverde (Wheelwright *et al.* 1984).

Ripe fruits of at least one lauraceous species were available in every month of the year between 1980 and 1982 (Wheelwright 1985b) and in every year between 1979 and 1986 (Wheelwright 1986). At most times, several species bear ripe fruits. During the late dry – early rainy season (April–June), ripe fruits of as many as 15 species may be found (Wheelwright 1985b). The physical and nutritional characteristics of lauraceous fruits and other fruits commonly eaten by birds at Monteverde are described in detail in Wheelwright *et al.* (1984). Mean annual crop sizes of lauraceous tree species (except for two understory trees with small crops) range from 1000 to as many as 100 000 fruits. The number of fruits produced by individual trees fluctuates annually (Wheelwright 1986).

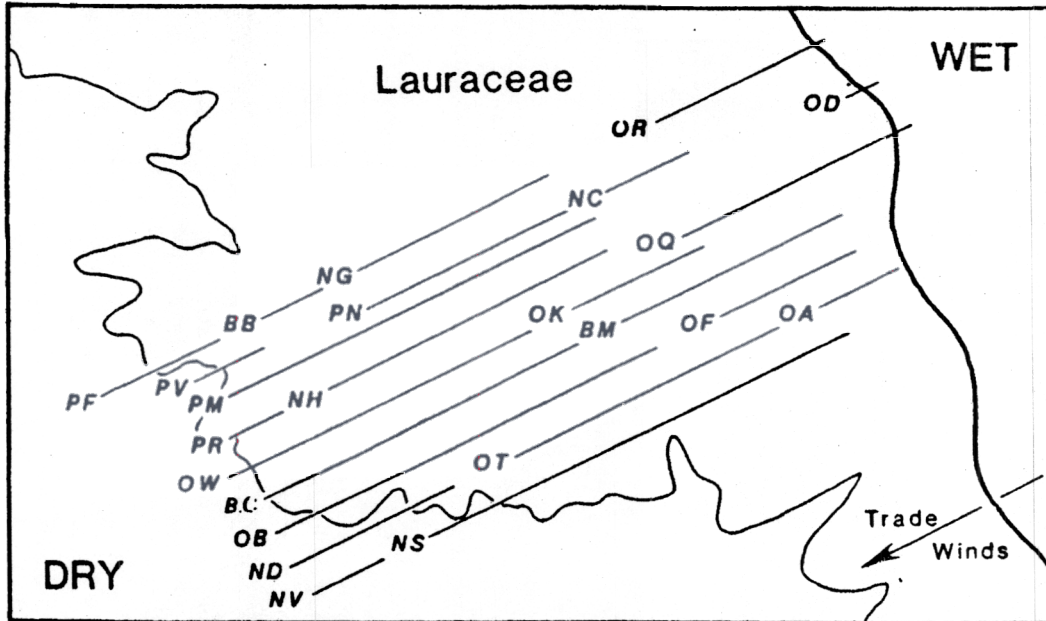
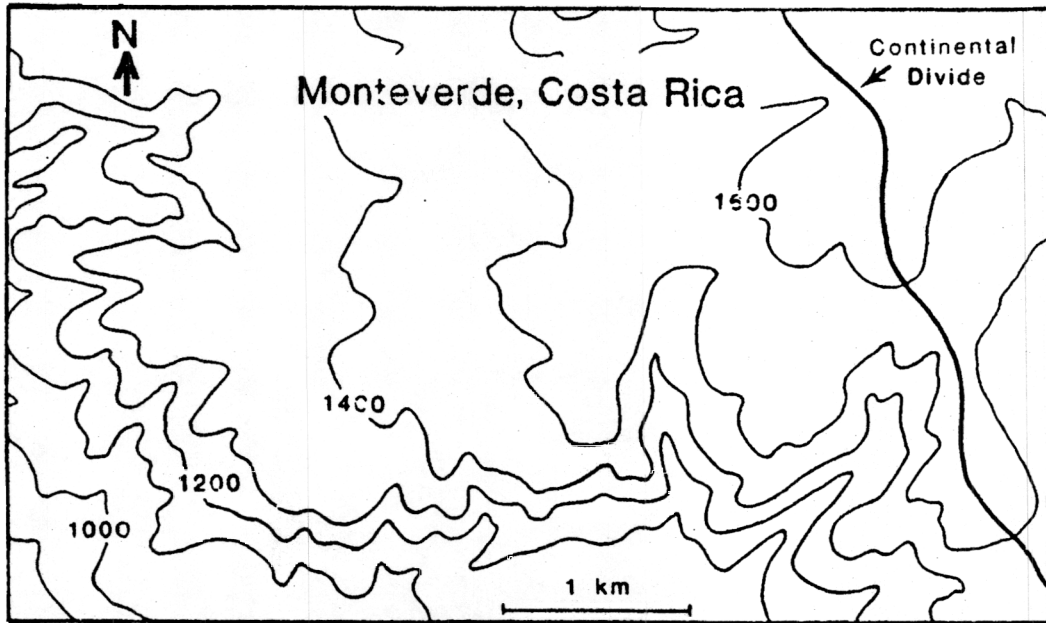


Figure 1. (Upper) Topographic map of the study area. (Lower) Distribution of 23 bird-dispersed Lauraceae tree species in the study area. The northeast trade winds create a steep moisture gradient across the study area. Lines indicate the NE-SW extent of trees' ranges along this gradient.

For example, an *Ocotea tonduzii* tree bore about 65 000 1.4-g fruits in 1979, 0 in 1980, 55 000 in 1981, 10 000 in 1982, 10 000 in 1983, 60 000 in 1984, 0 in 1985, and 60 000 in 1986 (mean for 8 yr. = 32 500 per year); over a reproductive life span of 100 yr (cf. Brokaw 1982), such a tree might produce more than 3 million fruits.

Bird Species

Birds that feed on lauraceous fruits at Monteverde do not seem to be united by any peculiar behavioral or morphological features other than larger-than-average body and gape size. Nonetheless, they are not a random sample of the avifauna: the most important avian consumers of lauraceous fruits represent only five families (Cracidae, Trogonidae, Ramphastidae, Cotingidae, and Muscicapidae [Turdinae]). Birds of other families of common fruit-eating birds rarely (Tyrannidae) or almost never (Columbidae, Momotidae, Picidae, Corvidae, Ptilonotidae, Vireonidae, and Emberizidae [Thraupinae]) eat lauraceous fruits at Monteverde.

Four birds species were responsible for over 95% of feeding visits to lauraceous trees during 192 h of observation ($n = 2119$ visits) and several thousand censuses of more than 300 marked individual trees. The four species (Resplendent Quetzal [*Pharomachrus mocinno*]; Three-wattled Bellbird [*Procnias tricarunculata*]; Emerald Toucanet [*Aulacorhynchus prasinus*]; and Mountain Robin [*Turdus plebejus*]) also consumed over 97% of the lauraceous fruits observed eaten by birds ($n = 418$ fruits) (NTW, unpublished data). Bellbirds and, to a lesser extent, quetzals (Wheelwright 1983) show marked seasonal altitudinal migrations. Mountain Robin flocks move readily between habitats on a daily basis; the seasonal timing of their more extensive movements from 1200 to 1800 m is unknown. Toucanets are relatively sedentary except during extreme food shortages, when they may migrate to the Costa Rican lowlands (F.G. Stiles, pers. commun.).

Field Observations

From 1979 to 1986, I spent 21 months in Monteverde sampling birds' diets by using "seed traps" (Snow 1970), watching for 1- to 5-h periods at fruiting trees, spot-censusing fruiting trees, following feeding flocks, and observing birds in captivity. The methods, and the biases inherent in such methods, are discussed in detail in Wheelwright *et al.* (1984) and Wheelwright (1985a). Large samples of seeds were collected from March through June 1981 beneath four display perches of bellbirds sampled simultaneously and beneath six leks of Long-tailed Manakins (*Chiroxiphia linearis*) sampled simultaneously.

Results

Weak Selection: Negligible Differences in the Behavior of Seed Dispersers

The four main avian consumers of lauraceous fruits vary conspicuously in their morphology and most aspects of their foraging behavior (Table 1; Santana and Milligan 1984), but they appear to differ only slightly in terms of characteristics that might affect their suitability as seed dispersers (with the exception of male bellbirds: see below). All the birds regurgitate lauraceous seeds without damaging them; germination rates of lauraceous seeds uninfested by weevil larvae approach 100%, irrespective of disperser or even whether the fruit pulp has been removed by hand (NTW, unpublished data). Seeds remain in the birds' digestive tracts for a relatively short time (24–52 min for most lauraceous species except

Table 1. Characteristics of the four main avian seed dispersers of lauraceous plants at Monteverde, Costa Rica.

Species	Mass (g)	Foraging	Social system
Resplendent Quetzal	205 (males) 190 (females)	Solitary to loose groups of up to ten birds	Monogamy
Three-wattled Bellbird	210 (males) 150 (females)	Solitary	Polygyny
Emerald Toucanet	160	Solitary to flocks of up to 30 birds	Monogamy
Mountain Robin	95	Solitary to flocks of up to 200 birds	Monogamy

Beilschmeidia spp., which may require more than 1 h to process; NTW, unpublished data). During most of this time, the seed is protected from digestive enzymes by the fruit pericarp. All the bird species under consideration have a simple gut and soft-lined gizzard. Consequently, processing by different birds does not noticeably affect germination speed, which takes two to six weeks in most lauraceous species (Wheelwright 1985b). Different bird species feeding on the same lauraceous fruits require similar amounts of time to regurgitate seeds (NTW, unpublished data).

No one has succeeded in measuring actual patterns of seed dispersal produced by different bird species for any bird-dispersed plant species (Smith 1975; Howe and Primack 1975). Even if we could determine where birds dropped all seeds, it would still be difficult to rank different bird species according to dispersal quality because so little is known about seedling and sapling microhabitat requirements. For the present, we are left with comparing features of birds' behavior that presumably influence the success of seed dissemination. Bird species spent significantly different amounts of time in fruiting lauraceous trees at Monteverde ($P < 0.001$) and in other tree species ($P < 0.001$). Nonetheless, absolute differences in visit duration were slight and biologically unimportant, relative to the lengthy processing times of lauraceous fruits: quetzals spent a median of 2.9 min per visit ($n = 184$), bellbirds 3.2 min ($n = 89$), toucanets 4.7 min ($n = 366$), and Mountain Robins 4.0 min ($n = 371$) (NTW, unpublished data).

The interaction between seed dispersers and plants is overshadowed by intense postdispersal seed predation, chiefly by *Heteromys demarestianus*. Of 520 *Nectandra davidsoniana* seeds placed at different densities and distances from conspecific plants, none survived 5 d (Fig. 2; Janzen 1971).

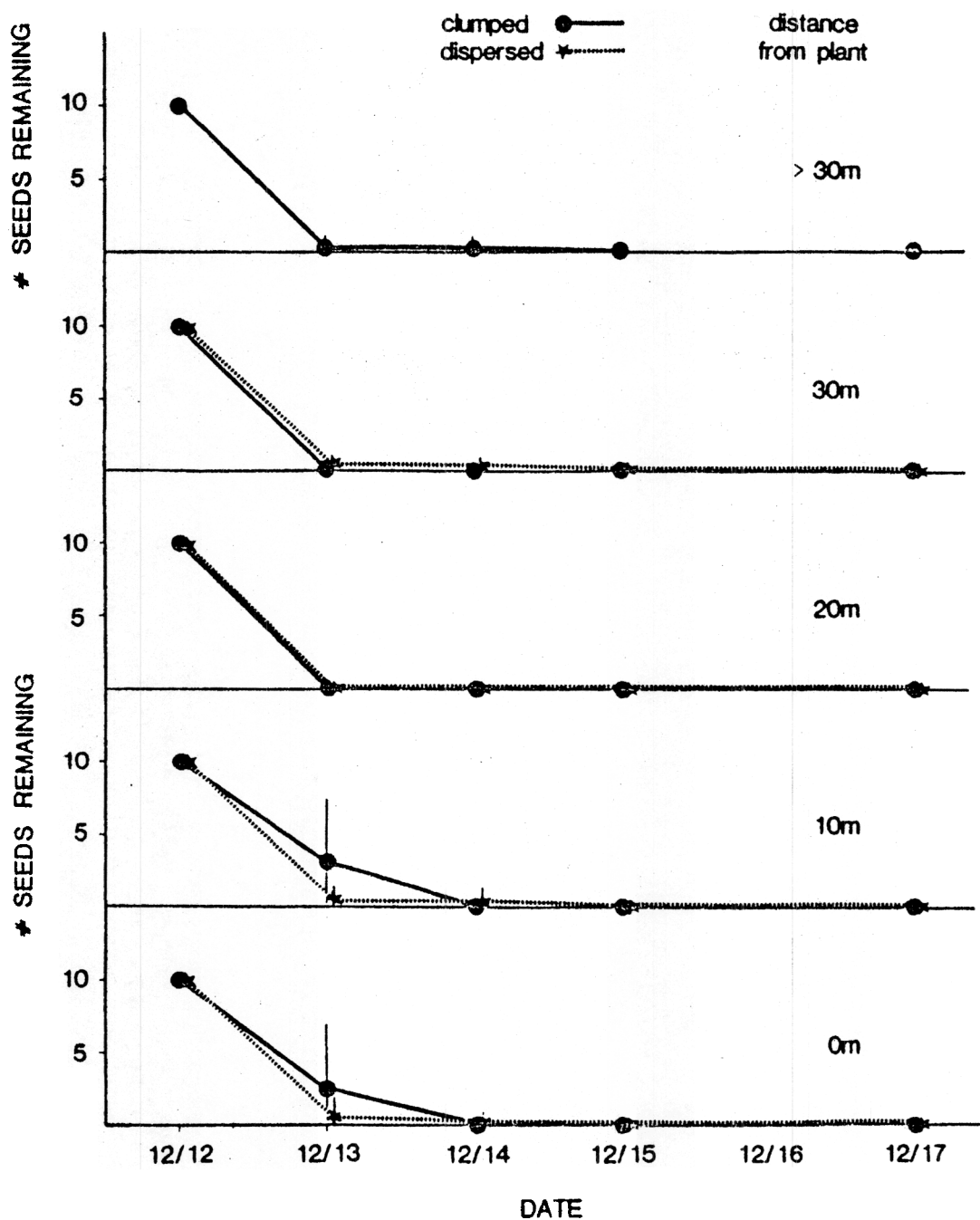


Figure 2. Removal of seeds of *N. davidsoniana* placed at different densities and distances from conspecific fruiting trees in December 1980. Seeds were placed in groups of ten, with eight replicate groups placed at each distance (except > 30 m, where there were only six replicates) for the dispersed treatment, and four replicate groups placed at each distance for the clumped treatment (except > 30 m, where seeds were not placed in clumps).

Inconsistent Selection: Spatial and Temporal Variation in the Diets of Fruit-eating Birds

During the breeding season, male Three-wattled Bellbirds, which are polygynous, spend about 80% of the day calling from a single perch of an emergent canopy tree, beneath which fall the seeds that they regurgitate (Snow 1977). Although bellbirds were not individually marked, some have distinctive plumage patterns (F. Joyce, pers. commun.). Each perch is occupied by only one male (visited occasionally by various females, neighboring males, and juvenile males, who typically spend less than 1 min per visit), judging from the facts that a perch is occupied for most of the day by a displaying male and that males can be observed calling simultaneously from different perches. Display perches were separated by 100–3000 m. Thus, seeds collected beneath a particular perch presumably reflect fruit choice by a single male bellbird. At four display perches monitored at the same time over a 3.5-month period, each male fed on different fruit species in different proportions (Fig. 3; Wheelwright 1986). It should be noted that fruits of all species that ripen during the breeding season could be found within the home ranges of each bellbird; at the highest elevations, I sometimes recovered seeds of plant species that grow only in the Guanacaste foothills 10 km away. Fruits of the Lauraceae predominated in the diet of all bellbirds (60–78% of fruits; Wheelwright 1986).

The diet of bellbirds also shifted seasonally. Certain fruit species gradually were dropped from the diet to be replaced by others (Fig. 4). In some cases, bellbirds shifted to different fruit species even though a previously eaten species was still available. In other cases, fruits were eaten until they were depleted.

Similar spatial and temporal variability in fruit choice was shown by manakins at seven sites (Figs. 5 and 6). Population studies of marked manakins (D. McDonald, pers. commun.) demonstrate that widely spaced display perches correspond to individual male pairs, so seeds collected beneath a perch reflected the diet of a pair of males. (As in bellbirds, a small fraction of the seeds deposited beneath display perches presumably resulted from the visits of females and occasional tertiary males.) Each pair of males fed mainly on a different fruit species at the same time of year (Fig. 5). The population of about 200 manakins that occurs in an 80-ha portion of the study area is continuous with respect to breeding (females range widely over the entire area; D. McDonald, pers. commun.) but subdivided with respect to the birds' interactions with plant species. As with bellbirds, fruits declined in importance in the diet as a function of plant phenologies, fruit removal rates, and the availability of preferred fruits.

At much larger spatial and temporal scales, interactions between fruit-eating birds and plants are also inconsistent. As an example of spatial inconsistency, toucanets were responsible for 72% of all visits ($n = 186$) by birds to four trees of *Ocotea floribunda* (= *O. wachenheimii* in previous publications) observed for 18 h (NTW, unpublished data). Toucanets also consumed more of the 2.9-g fruits per visit (mean = 2.5 fruits, $n = 10$ visits) than any bird species except Black Guans (*Chamaepetes unicolor*) and regurgitated seeds widely, rapidly (mean = 29 min per seed, $n = 7$), and in viable condition. At Monteverde, at least, toucanets are the chief dispersers of *O. floribunda*, and

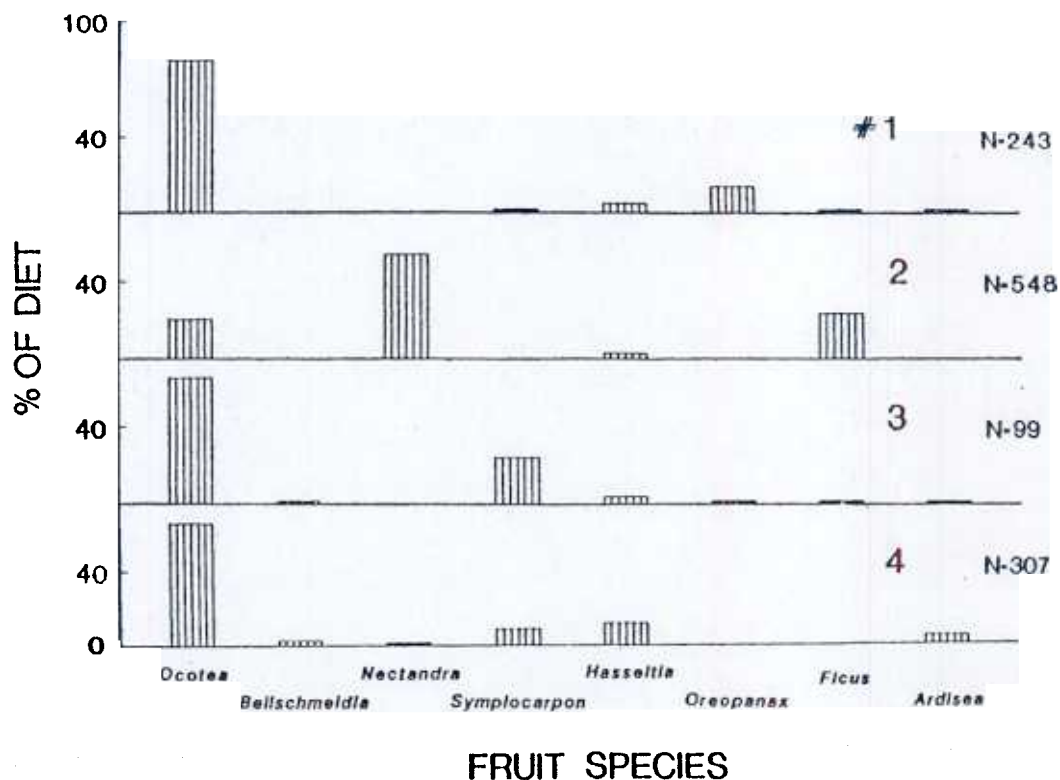


Figure 3. Proportion of diet comprised by different fruit species (corrected for distinct number of seeds per fruit) at four different Three-wattled Bellbird display perches.

O. floribunda fruits are the major food of toucanets for several months per year. Yet Emerald Toucanets are absent from most of the range of *O. floribunda* (Bernardi 1962), and *O. floribunda* is an important food source for Emerald Toucanets in only a fraction of the birds' range (Fig. 7).

As an example of temporal inconsistency, more than half of the fruits eaten by bellbirds at Monteverde (judging from seed-trap results) were *Ocotea tonduzii* during the breeding season in 1981, a year when most trees of that species had massive fruit crops. The previous year and again in 1985, very few *O. tonduzii* trees bore fruit at all (Wheelwright 1986), and bellbirds were forced to feed on other fruit species. Interactions between birds and plants are inconsistent over even longer time scales, of course. For example, Crested Guans (*Penelope purpurescens*) and Bare-necked Umbrellabirds (*Cephalopterus glabricollis*), undoubtedly important seed dispersers of the Lauraceae at Monteverde in the past, have recently become locally extinct. Relatively little is known about the animal-dispersed flora of Monteverde, but presumably similar population turnovers have taken place among plants.

Antagonistic Selection: Fruit Choice, Seed Size, and Seed Predation

Two examples will illustrate how different sources of selection with opposite effects may constrain coevolution. The first example concerns factors that favor and disfavor increasing seed and fruit size. Large seeds produce more vigorous

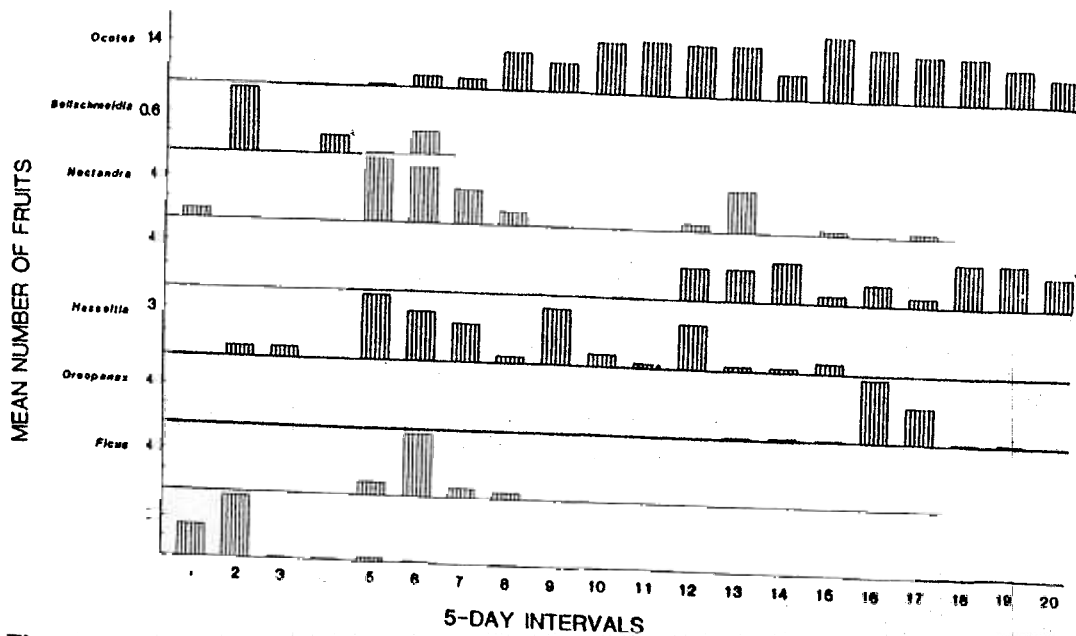


Figure 4. Proportion of diet comprised by different fruit species (corrected for distinct number of seeds per fruit) at all four Three-wattled Bellbird display perches at 5-d intervals.

seedlings than small seeds (Howe *et al.* 1985). Furthermore, they may be less susceptible to predation by rodents (NTW, unpublished data; cf. Janzen 1971). An increase in seed size, however, demands an increase in fruit size. Birds, which swallow most fruits whole, are "gape-limited"; plants with large fruits attract fewer potential seed dispersers than small-fruited plants (Wheelwright 1985a). Although the gape widths of some birds may respond evolutionarily to accommodate increased fruit sizes (Snow 1973), the morphology of most bird species is probably constrained. A reduction in the number and ecological diversity of seed dispersers is thought to result in slower rates of fruit removal (and higher predispersal rates of seed predation; Thompson and Willson 1978), as well as dispersal to a narrower range of microhabitats (Wheelwright and Orians 1982). Another cost of producing large-seeded fruits is that they are likely to be dropped uneaten beneath fruiting trees by birds that cannot swallow them (Wheelwright 1985a).

Seed dispersal by male bellbirds illustrates a second example of antagonistic selection. In some respects, bellbirds are excellent disseminators of seeds. Because they have broad gapes, they can carry large-seeded fruits, one criterion listed by McKey (1975) for high-quality seed dispersal. They account for over a third of all visits ($n = 242$) to *Nectandra hypoglauca* and 8–17% of all visits to *O. floribunda*, *O. sp.*, and *N. salicina* ($n = 397$). At each tree species, bellbirds remove approximately as many fruits as other bird species except toucanets (NTW, unpublished data). They are reliable dispersers (*sensu* McKey 1975), spend relatively little time per visit in fruiting trees, and regurgitate seeds in viable condition.

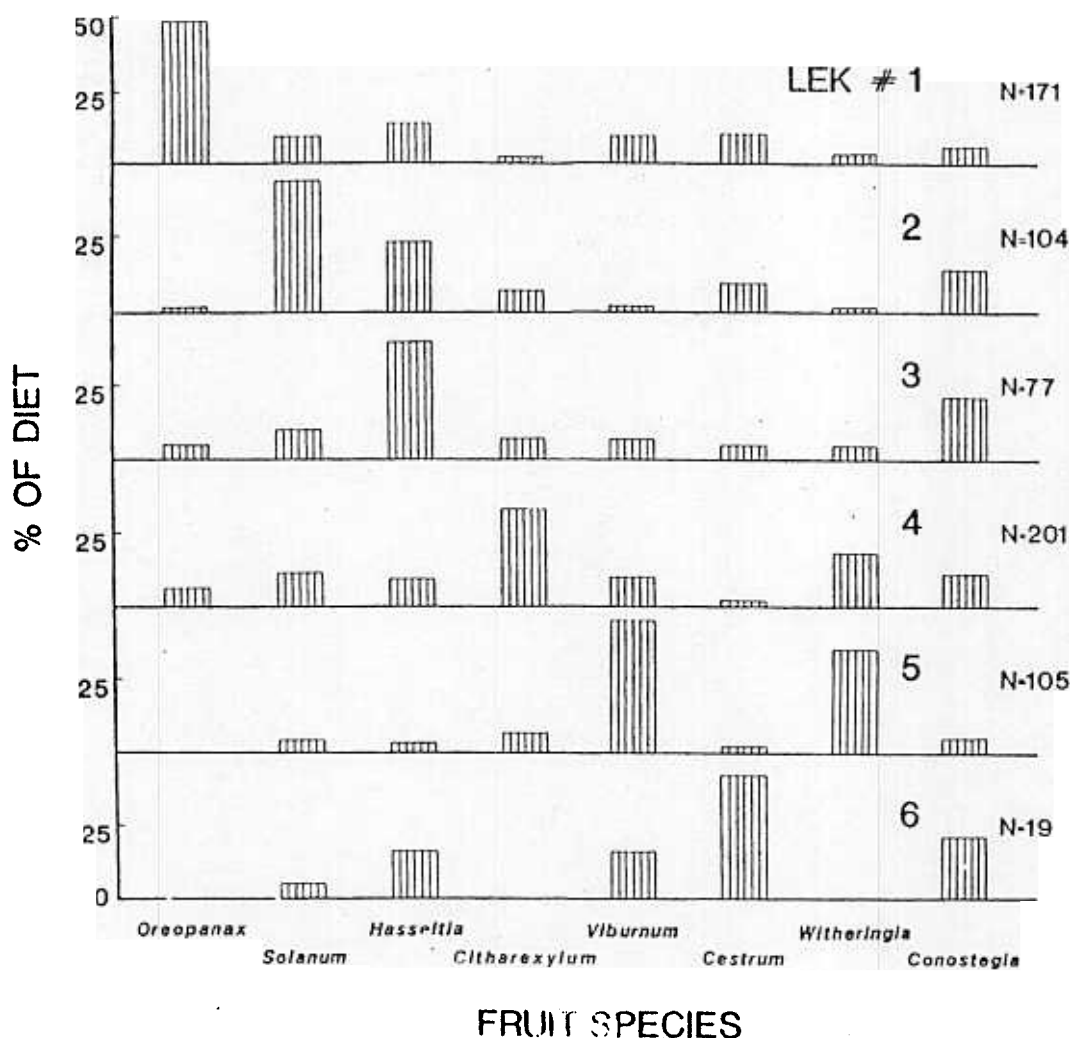


Figure 5. Proportion of diet comprised by different fruit species (corrected for distinct number of seeds per fruit) at six different Long-tailed Manakin display perches.

Yet displaying male bellbirds deposit most seeds in sites that guarantee their failure. Most of the breeding season is spent perched in a single spot, from which a rain of seeds falls. Such behavior produces a clumped distribution of seeds, out of which at most a single seed is likely to survive to reproductive maturity. Seed predators quickly learn to respond to the predictable rain of seeds. I tested the hypothesis that seed predation is higher beneath bellbird perches than at randomly located sites. On the ground below three bellbird perches at 5-d intervals I scattered *O. tonduzii* seeds as bellbirds might have dropped them (ca. 20 per square meter). Similar numbers of seeds were simultaneously deposited approximately 20 m away. Seed removal (and presumed seed predation) was 100% in every trial beneath bellbird perches. In randomly located sites, on the other hand, seeds were not discovered until the fourth trial; in all subsequent trials, 100% of the seeds were removed (Fig. 8).

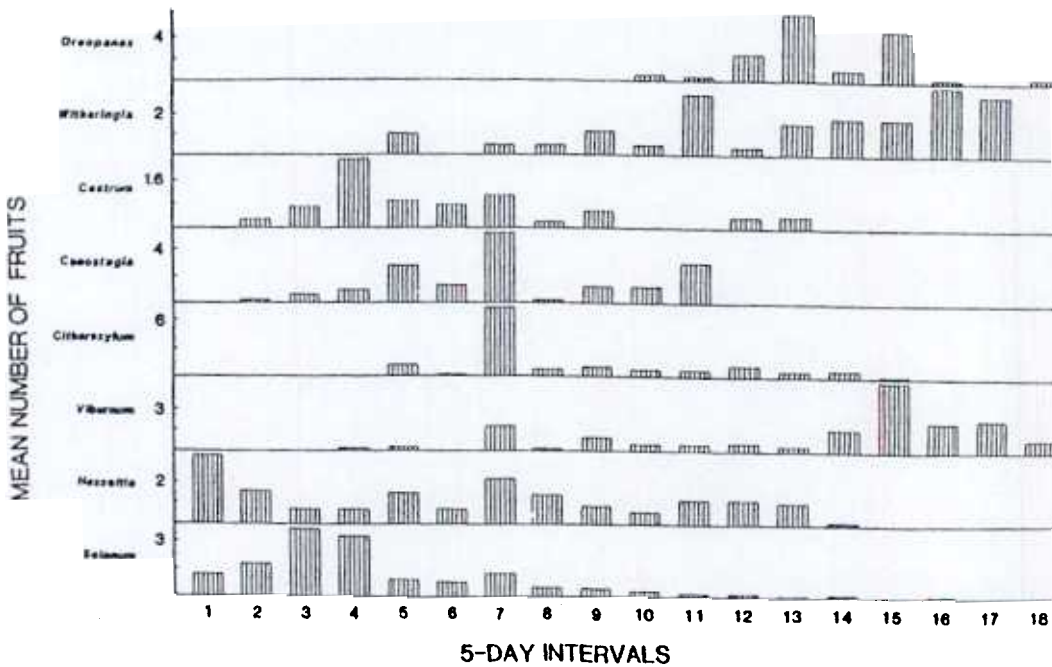


Figure 6. Proportion of diet comprised by different fruit species (corrected for distinct number of seeds per fruit) at all six Long-tailed Manakin display perches at 5-d intervals.

Limitations on Evolutionary Responses: Intrinsic and Genetic Constraints

Limitations on evolutionary responses of species involved in a mutualistic interaction are easy to imagine but more difficult to demonstrate empirically. They fall into two classes—intrinsic and genetic. The first category includes features of the mutualism that unavoidably prohibit finely tuned behaviors on the part of plants or dispersers. For example, the success of dispersed seeds has an enormous stochastic element. Success depends on many features (e.g., allelopaths, the occurrence of future light gaps, root competition, density of seed predators) indeterminable to the seed disperser, no matter how much the disperser might benefit (e.g., by harvesting future fruits; Herrera 1985b) by delivering high-quality seed dispersal. In this regard, seed dispersal is quite different from pollen dispersal, and such limitations may in part explain the relative rarity of tight associations between fruit-eating birds and the plants whose seeds they disperse (Wheelwright and Orians 1982).

Another intrinsic limitation is illustrated by the contrast in behavior between male and female bellbirds. Displaying males deliver high-quality seed dispersal in some respects and poor-quality dispersal in others, as discussed above. Female bellbirds share the same morphological and behavioral traits that make males good seed dispersers, yet females do not present the drawback (from the plant's perspective) of spending most of their time calling from a single spot, causing a clumped seed-dispersion pattern and entraining seed predators. I presume that female bellbirds are excellent dispersers of lauraceous seeds. But response to selection for a tight association between female bellbirds and lauraceous trees is constrained by the correlation between male and female traits.

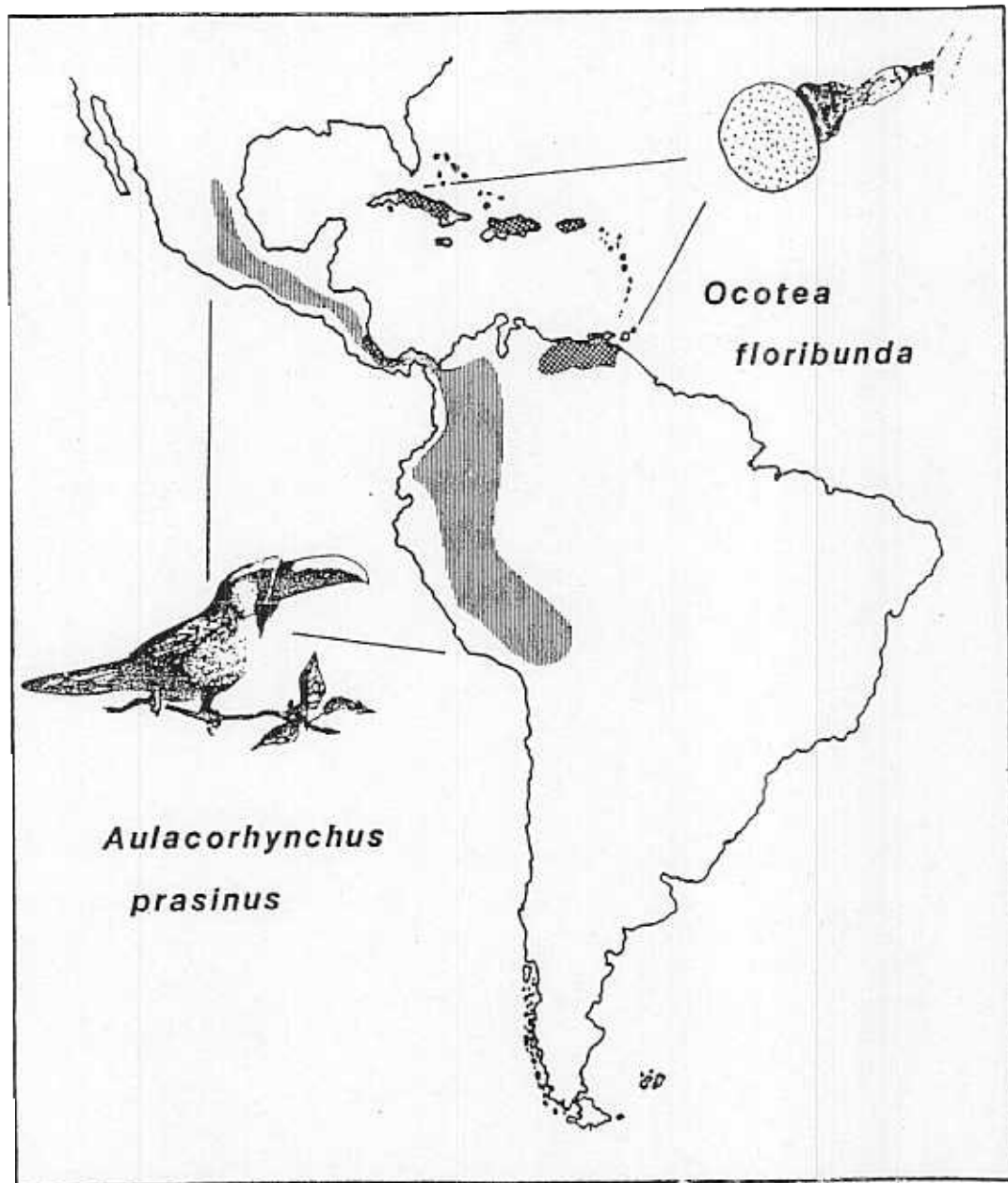


Figure 7. Geographic ranges of Emerald Toucanets and *Ocotea floribunda*, whose fruits are seasonally a major part of toucanets' diets where the ranges of the two species overlap. Toucanets are also the chief seed dispersers of *O. floribunda* at Monteverde.

In other words, plants are in an evolutionary bind because they are under selective pressure to appeal to one disperser and discourage another that shares similar physiology, morphology, and genome except for the sex chromosome. Asymmetrical dependence of plants and birds on one another, as well as their distinct generation times, exemplify inescapable features of the seed disperser – plant relationship that represent intrinsic limitations on evolutionary responses (Herrera 1985a).

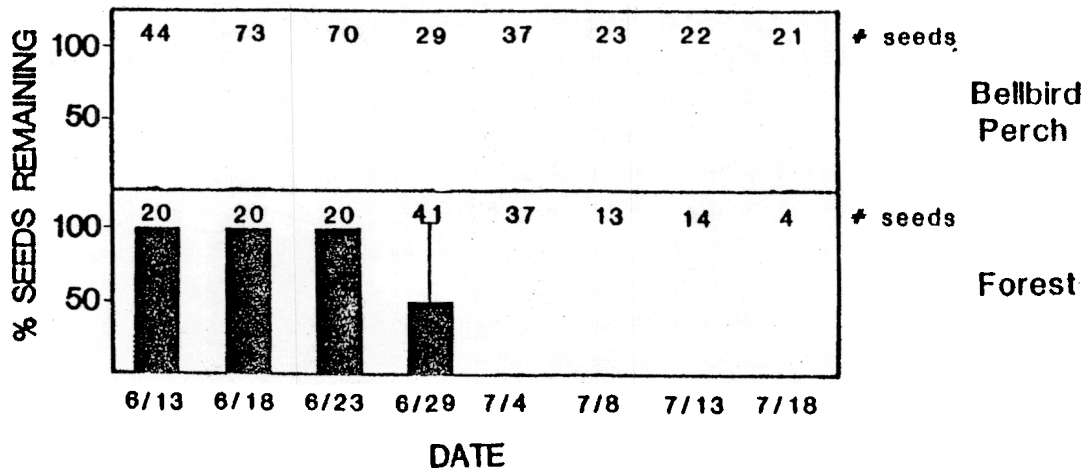


Figure 8. Removal rates of *Ocotea tonduzii* seeds (a major component of the diet of Three-wattled Bellbirds during the breeding season) placed beneath bellbird display perches compared with removal rates at nearby randomly located sites. “# seeds” refers to the total number of seeds placed at all sites in each experiment. Error bar = 1 s.d.

The second class of limitations includes the same factors that slow evolution of any kind—for example, pleiotropy, lack of genetic variation, and developmental constraints (Futuyma 1979). Little is known about the genetics of animal-dispersed plants or fruit-eating birds or their response to selection for traits important in mutualistic interactions (e.g., fruit-crop size, phenology, dispersal behavior, gape size, and digestion time). Until the difficult, long-term experiments on the heritability of such traits have been completed, we can only assume that genetic and developmental constraints are important factors in explaining the paucity of finely tuned, coevolved interactions between plants and their seed dispersers.

Discussion

Coevolution between fruit-eating birds and fruiting plants has infrequently, if ever, led to the kinds of specialized, obligate associations predicted only a decade ago (McKey 1975; Howe and Estabrook 1977). The reasons for the rarity of such coevolutionary outcomes may be the four constraints illustrated in this paper: weak selection, inconsistent selection, antagonistic selection, and limitations on evolutionary responses. The literature on fruit-eating birds, which has grown explosively in the last decade in large part due to the stimulating papers of Snow (1971), McKey (1975), and Howe and Estabrook (1977), contains additional evidence for these constraints. For example, many of the dispersers of *Casearia corymbosa* seeds are absent during part of the fruiting season (Howe 1977), illustrating temporal inconsistency (Martin and Karr 1986). Research on the same tree species also documents spatial inconsistency: a distinct suite of bird species serves as seed dispersers at a different Costa Rican site (Howe and Vande Kerckhove 1979). T. Keeler-Wolf (unpublished data) discovered geographic variation in plant interactions with avian seed dispersers between

populations of three tree species found on both Trinidad and Tobago, which he suggests led to evolution in fruit traits. Various studies on the importance of North American migrants as seed dispersers for neotropical trees (Leck 1972; Howe and De Steven 1979; Greenberg 1981) demonstrate that the dynamics of seed dispersal must change seasonally as the principal fruit feeders at certain trees leave the area during the fruiting season. Fogden's (1972) and Leighton and Leighton's (1983) observations suggest variation in fruit availability within and between years in relatively aseasonal tropical forests (Bullock 1980; Howe 1983). Fruit pigeons in tropical Australia ignore certain fruit species when favored fruits are available (Crome 1975).

Herrera's (1984a) work is relevant to the question of limitations on evolutionary responses as well as weak directional selection, because of the dilution of the plant-disperser interaction due to herbivores, seed predators, and competing plants. Other studies have shown that patterns of fruit removal and seed dispersal depend on a variety of factors extrinsic to the plant and thus are unlikely to be selected for (Stapanian 1982; Willson *et al.* 1982; Beehler 1983; McDonnell and Stiles 1983; Manasse and Howe 1985; Denslow, *in press*).

Yet it would be a mistake to ignore the intricate adaptations that some fruit-eating birds show or the nonrandom relationships that exist between some taxa of birds and plants (Snow 1980). Recent examples are Janson's (1983) confirmation of van der Pijl's (1969) fruit "syndromes" in a neotropical forest and the discovery of broad character syndromes (in spite of an "outstanding lack of specificity"; Gautier-Hion *et al.* 1985) in animal-dispersed plants in Gabon (Stiles 1980; the correspondence between fruit diameter and gape width: Wheelwright 1985a; the convergent evolution of fruit-color patterns in unrelated floras: Wheelwright and Janson 1985). Different bird species show consistent preferences for distinct fruit taxa, often with accompanying morphological specializations (Davidar 1983; Moermond and Denslow 1985). Some examples of mutual congruency between birds and plants (e.g., Herrera 1982) may reflect "epiphenomena" rather than coevolution (Herrera 1984b). Nonetheless, there is growing evidence that fruit choices by birds are based in part on shared evolutionary history and diffuse coevolution with plants (Janzen 1980). In diffuse coevolution, the constraints described in this paper become less important. "Tanager fruits" or "flycatcher fruits" (Levey, *pers. commun.*) may owe their origin to diffuse coevolution with higher taxa of birds. The larger pool of interacting species admitted by diffuse coevolution damps the effects of population oscillations and the inconsistency of selection for congruous traits in classes of fruiting plants and their seed dispersers. Antagonistic selection and intrinsic limitations on evolutionary responses remain real barriers for the evolution of specialized features in seed-dispersal mutualisms; however, when more species are involved in diffuse plant - seed disperser interactions, there may be more opportunities to overcome such constraints. For example, the collective selective effect of fruit choice and seed dispersal by many bird species that individually have only a weak or inconsistent effect may be strong enough to direct the evolution of plant reproductive traits, with the result that birds and plants develop general mutual adaptations.

With a better understanding of the constraints on coevolution, future research should be directed toward documenting the importance of "core taxa" (Fleming 1986) in birds' diets and describing patterns of seed dispersal that different birds produce feeding on the fruits of different plants.

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References

- BEEHLER, B.M. 1983. Frugivory and polygamy in birds of paradise. *Auk*, **100**: 1-12.
- BERNARDI, L. 1962. Lauraceae. Universidad de Los Andes, Merida, Venezuela.
- BROKAW, N.V.L. 1982. Treefalls: frequency, timing, and consequences. *In* The ecology of a tropical forest. E.G. Leigh, A.S. Rand, and D.M. Windsor (eds.). Smithsonian Institution Press, Washington, D.C.
- BULLOCK, S.H. 1980. Dispersal of a desert palm by opportunistic frugivores. *Principes*, **24**: 29-32.
- BUSKIRK, W.H. 1976. Social systems in a tropical forest avifauna. *Am. Nat.* **110**: 293-310.
- CROME, F.H.J. 1975. The ecology of fruit pigeons in tropical northern Queensland. *Aust. Wildl. Res.* **2**: 155-185.
- DAVIDAR, P. 1983. Birds and neotropical mistletoes: effects on seedling recruitment. *Oecologia (Berlin)*, **60**: 271-273.
- DENSLow, J.S. Fruit removal rates from clumped and isolated bushes of the red-berried elder, *Sambucus pubens*. *Can. J. Bot.* (in press).
- FEINSINGER, P. 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecol. Monogr.* **48**: 269-287.
- FLEMING, T.H. 1986. Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. *In* Frugivores and seed dispersal. A. Estrada and T.H. Fleming (eds.). W. Junk, Amsterdam.
- FOGDEN, M.P.L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis*, **114**: 307-343.
- FUTUYMA, D.J. 1979. Evolutionary biology. Sinauer Associates, Inc., Sunderland, Mass. 565 pp.
- GAUTIER-HION, A., J.-M., DUPLANTIER, R. QURIS, F. FEER, C. SOURD, J.-P. DECOUX, G. DUBOST, L. EMMONS, C. ÉRARD, P. HECKERSWEILER, A. MOUNGAZI, C. ROUSSILLON, and J.-M. THIOLLAY. 1985. Fruit characters as a basis for fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia (Berlin)*, **65**: 324-337.

- GREENBERG, R. 1981. Frugivory in some migrant tropical forest wood warblers. *Biotropica*, **13**: 215-223.
- HERRERA, C.M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology*, **63**: 773-785.
- HERRERA, C.M. 1984a. A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecol. Monogr.* **54**: 1-23.
- HERRERA, C.M. 1984b. Seed dispersal and fitness determinants in wild rose: combined effects of hawthorn, birds, mice, and browsing ungulates. *Oecologia (Berlin)*, **63**: 386-393.
- HERRERA, C.M. 1985a. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos*, **44**: 132-141.
- HERRERA, C.M. 1985b. Habitat-consumer interactions in frugivorous birds. *In* *Habitat selection in birds*. M.L. Cody (ed.). Academic Press, New York. pp. 341-365.
- HOLDRIDGE, L. 1967. Life zone ecology. Tropical Science Center Publication, San José, Costa Rica.
- HOWE, H.F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology*, **58**: 539-550.
- HOWE, H.F. 1983. Annual variation in a neotropical seed-dispersal system. *In* *Tropical rain forest: ecology and management*. S.L. Sutton, T.C. Whitmore, and A.C. Chadwick (eds.). Blackwell, Oxford. pp. 221-227.
- HOWE, H.F. 1984. Constraints on the evolution of mutualisms. *Am. Nat.* **123**: 764-777.
- HOWE, H.F., and D. DE STEVEN. 1979. Fruit production, migrant bird visitation, and seed dispersal of *Guarea glabra* in Panama. *Oecologia (Berlin)*, **39**: 185-196.
- HOWE, H.F., and G.F. ESTABROOK. 1977. On intraspecific competition for avian dispersers in tropical trees. *Am. Nat.* **111**: 817-832.
- HOWE, H.F., and R.B. PRIMACK. 1975. Differential seed dispersal by birds of the tree *Casearia nitida* (Flacourtiaceae). *Biotropica*, **7**: 278-283.
- HOWE, H.F., and G.A. VANDE KERCKHOVE. 1979. Fecundity and seed dispersal of a tropical tree. *Ecology*, **60**: 180-189.
- HOWE, H.F., E.W. SCHUPP, and L.C. WESTLEY. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology*, **66**: 781-791.
- JANSON, C.H. 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science*, **219**: 187-189.
- JANZEN, D.H. 1971. Seed predation by animals. *Annu. Rev. Ecol. Syst.* **2**: 465-492.
- JANZEN, D.H. 1980. When is it coevolution? *Evolution*, **34**: 611-612.
- JANZEN, D.H. 1981. *Ficus ovalis* seed predation by an Orange-chinned Parakeet (*Brotogeris jugularis*). *Auk*, **98**: 841-844.
- LAWTON, R., and V. DRYER. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia*, **18**: 101-116.
- LECK, C.F. 1972. Seasonal changes in feeding pressures of fruit- and nectar-feeding birds in Panama. *Condor*, **74**: 54-60.
- LEIGHTON, M., and D.R. LEIGHTON. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. *In* *Tropical rain forest: ecology and management*. S.L. Sutton, T.C. Whitmore, and A.C. Chadwick (eds.). Blackwell, Oxford. pp. 181-196.

- MARTIN, T.E., and J.R. KARR. 1986. Temporal dynamics of neotropical birds with special reference to frugivores in second-growth woods. *Wilson Bull.* 98: 38-60.
- MCDONNELL, M.J., and E.W. STILES. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* (Berlin), 56: 109-116.
- MCKEY, D. 1975. The ecology of coevolved seed dispersal systems. *In* *Coevolution of animals and plants*. L.E. Gilbert and P.H. Raven (eds.). Univ. of Texas Press, Austin. pp. 155-191.
- MOERMOND, T.C., and J.S. DENSLow. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. *In* *Neotropical ornithology*. P.A. Buckley, M.S. Foster, E.S. Morton, R.S. Ridgely, and F.G. Buckley (eds.). *Ornithol. Monogr.* No. 36.
- POWELL, G.V.N. 1979. Structure and dynamics of interspecific flocks in a neotropical mid-elevation forest. *Auk*, 96: 375-390.
- SANTANA, C.E., and B.G. MILLIGAN. 1984. Behavior of toucanets, bellbirds, and quetzals feeding on Lauraceous fruits in Costa Rica. *Biotropica*, 16: 152-154.
- SCHEMSKE, D.W. 1983. Limits to specialization and coevolution in plant-animal mutualisms. *In* *Coevolution*. M.H. Nitecki (ed.). Univ. of Chicago Press, Chicago. pp. 67-109.
- SMITH, A.J. 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. *Ecology*, 56: 19-34.
- SNOW, B.K. 1970. A field study of the Bearded Bellbird in Trinidad. *Ibis*, 112: 299-329.
- SNOW, B.K. 1977. Territorial behavior and courtship of the male Three-wattled Bellbird. *Auk*, 94: 623-645.
- SNOW, D.W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis*, 113: 194-202.
- SNOW, D.W. 1973. Distribution, ecology and evolution of the bellbirds (Procnias, Cotingidae). *Bull. Br. Mus. (Nat. Hist.)* 25: 369-391.
- SNOW, D.W. 1980. Regional differences between tropical floras and the evolution of frugivory. *Proc. Int. Ornithol. Congr.* 17: 1192-1198.
- STAPANIAN, M.A. 1982. A model for fruiting display: seed dispersal by birds for mulberry trees. *Ecology*, 63: 1432-1443.
- STILES, E.W. 1980. Patterns of fruit presentation and seed dispersal in bird-dispersed woody plants in the Eastern deciduous forest. *Am. Nat.* 116: 670-688.
- THOMPSON, J.N., and M.F. WILLSON. 1978. Disturbance and the dispersal of fleshy fruits. *Science*, 200: 1161-1163.
- VAN DER PIJL, L. 1969. Principles of dispersal in higher plants. Springer-Verlag, New York. 161 pp.
- WHEELWRIGHT, N.T. 1983. Fruits and the ecology of Resplendent Quetzals. *Auk*, 97: 268-282.
- WHEELWRIGHT, N.T. 1985a. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology*, 66: 808-818.
- WHEELWRIGHT, N.T. 1985b. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. *Oikos*, 44: 465-477.
- WHEELWRIGHT, N.T. 1986. A seven-year study of individual variation in fruit production in tropical bird-dispersed tree species in the family Lauraceae. *In* *Frugivores and seed dispersal*. A. Estrada and T.H. Fleming (eds.). W. Junk, Amsterdam. pp. 19-35.

- WHEELWRIGHT, N.T., and C.H. JANSON. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. *Am. Nat.* **126**: 777-799.
- WHEELWRIGHT, N.T., and G.H. ORIANI. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *Am. Nat.* **119**: 150-164.
- WHEELWRIGHT, N.T., W.A. HABER, K.G. MURRAY, and C. GUINDON. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica*, **16**: 173-191.
- WILLSON, M.F., E.A. PORTER, and R.S. CONDIT. 1982. Avian frugivore activity in relation to forest light gaps. *Caribb. J. Sci.* **18**: 1-4.
- WORTHINGTON, A. 1982. Population sizes and breeding rhythms of two species of manakins in relation to food supply. *In* The ecology of a tropical forest. E.G. Leigh, A.S. Rand, and D.M. Windsor (eds.). Smithsonian Institution Press, Washington, D.C. pp. 343-360.