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## *Frugivory: An Overview*

Douglas J. Levey, Timothy C. Moermond, and Julie Sloan Denslow

Seed dispersal by vertebrates may have been responsible for the spread and domination of angiosperms (Corner 1964; Regal 1977; Snow 1981; but see Herrera 1989). Its modern importance in tropical forests is reflected in the diversity and abundance of animal-dispersed plants. Several studies have estimated that more than 80% of tree and shrub species in tropical wet forests are animal dispersed (Frankie et al. 1974a; Croat 1975; Hilty 1980; Opler, Frankie, et al. 1980; Gentry 1982a; Stiles 1985b; Willson et al. 1989). These plants provide enough fruit to support large populations of fruit-eating birds and bats (Snow 1971; Snow and Snow 1971; Heithaus et al. 1975). In fact, fruit resources alone may account for approximately 20% of the difference between temperate and tropical avian species diversity (Karr 1971; Remsen 1985). Estimates of the tropical vertebrate biomass supported by fruits range from 50% (for birds) to 80% (birds plus mammals, Willis 1980; Terborgh 1986a; Janson and Emmons 1990).

The importance of tropical frugivory extends beyond its role in community structure. As a mechanism for seed dispersal, frugivory is hypothesized to be important in maintaining high species diversity of tropical plants (Janzen 1970). The advantages of dispersal include escape from high seed and seedling mortality near the parent (Janzen 1970; Connell 1971; D. A. Clark and Clark 1984), colonization of regeneration sites (Thompson and Willson 1978; Culver and Beattie 1978), and increased gene flow (Levin and Kerster 1974). Without dispersal agents fruiting plants may become prone to extinction (Howe 1977, 1984a; Temple 1977; D. A. Clark and Clark 1981). Nevertheless, little is known about the relative importance of selective forces that promote dispersal (Howe and Smallwood 1982; Howe 1986).

From an ecological perspective fruits offer an opportunity to monitor seasonal changes in abundance of an important food resource. Unlike other food items fruits are made for consumption. Hence, they are conspicuous and relatively easy to count. Documenting temporal variation in fruit abundance helps us understand population dynamics of frugivores. Currently, we know very little about what causes population fluctuations of any tropical vertebrate even though such fluctuations are common (Fogden 1972; Toft 1980b; Martin and Karr 1986b; chaps. 15, 16). Understanding these fluctuations is especially important in management of tropical forests. At a minimum one needs to estimate how much habitat is necessary to maintain frugivore populations. Failure to preserve a

key fruiting plant species or disperser may have cascading effects through the community as other species are affected by the loss of a mutualistic link (Gilbert 1980; Janzen and Martin 1982; Howe 1984b; Terborgh 1986b).

From an evolutionary perspective fruits represent an interesting compromise between conflicting strategies (Snow 1971). The conflict arises because the aspects of seed dispersal that are beneficial to fruiting plants represent costs to frugivores who transport seeds without benefiting from their nutrient content. Similarly, what is beneficial to frugivores is a cost to fruiting plants, which must produce fruit pulp to attract seed dispersers. Examination of these costs and benefits allows one to explore the basis of plant-frugivore coevolution. Of particular interest is the question of how closely fruiting plants and frugivores are coevolved. Clearly, the interaction between these groups is mutualistic. However, we have yet to determine the level of interaction between the groups and the mechanisms underlying their coevolution (Howe 1984a; Futuyma and Slatkin 1983; Herrera 1986; Jordano 1987).

Here we present an overview of frugivory at La Selva. More general reviews of frugivory are provided by Howe (1986), Willson (1986), Fleming et al. (1987), Wheelwright (1988), and Jordano (1992). Our goal is to put La Selva work in the perspective of frugivory in general and tropical frugivory in particular. We begin with a general description of fruits and frugivores at La Selva and compare them with other tropical forests. Then we address the following questions: What factors influence fruit choice? What is the role of fruit handling in successful dispersal? How do spatial and temporal variation in fruit abundance affect frugivore populations? Given information on fruit choice, fruit handling, and spatial/temporal variation in bird and fruit abundance, what can one deduce about the coevolutionary patterns and constraints in fruit-frugivore interaction? In each section we present a brief review and then focus on what is known about the topic at La Selva. In this chapter we focus on avian frugivory only because it has received so much attention at La Selva.

### GENERAL DESCRIPTION OF FRUITS AND FRUGIVORES

#### Fruits

We distinguish between fruits produced by shrubs and treelets and those produced by trees. This dichotomy follows similar

divisions proposed by Smythe (1970), McKey (1975), and Janson (1983).

**Fruits of Shrubs and Treelets.** Ninety-five percent of 154 species of shrubs and treelets surveyed by Opler, Frankie, et al. (1980) at La Selva bore small fleshy fruits (Opler, Frankie, et al. 1980). Members of the Rubiaceae, Melastomataceae, Palmae, Piperaceae, and Gesneriaceae are found commonly in fruit in the understory and areas of second growth. Within the forest significantly more species and individuals are found to bear fruit in tree-fall gaps than in shaded understory (Marquis 1988; Levey 1988b, 1990). Three generalizations made about these small fruits are not well supported at La Selva. First, small-fruited species are usually envisioned as prolific fruit producers (Land 1963; Willis 1966; McKey 1975). Such plants often do produce large crops when in high light environments, but in the understory crop sizes are typically quite small, usually fewer than one hundred fruits per plant (Bullock 1982; Denslow et al. 1986; Murray 1987). For example, 69% of fifty fruiting plants found in fifty 100 m<sup>2</sup> quadrats had fewer than ten ripe fruits per plant per census period (Denslow et al. 1986). Similarly, small crop sizes have been observed in other tropical communities (Fleming 1981; Leighton and Leighton 1983; Terborgh 1983). Second, small-fruited species are often characterized as having numerous small seeds (Harper et al. 1970; McKey 1975). Exceptions at La Selva include three dominant families (Heliconiaceae, Arecaceae, and Rubiaceae), whose members all produce fruits with one-to-several large seeds. Third, fruits are thought to "advertise" their presence by being brightly colored (Snow 1971; Van der Pijl 1982). At La Selva the most common ripe fruit color among 101 understory species is very dark blue/black (table 22.1; see also Wheelwright and Janson 1985). Although the dark fruits may appear inconspicuous, their relative visibility (brightness; see Willson and Hoppes 1986) has yet to be determined. In most species with dark fruits contrasting colors provided by the infructescence or neighboring unripe fruit make the fruit display quite visible to the human eye (table 22.1).

Bat- and bird-consumed fruits display many differences (Van der Pijl 1982). Although these differences are pronounced, it is important to note they are not exclusive. Many birds, for example, take *Piper* fruits, and bats readily take "bird" fruits (Fleming et al. 1985; Dinerstein 1987; Palmeirim et al. 1989). Despite these exceptions the syndromes provide an interesting basis of comparison.

In general, fruits eaten by birds are small and spherical, are in brightly colored displays held close to foliage, and are without an odor. Common examples at La Selva are species of Melastomataceae and Rubiaceae. These watery fruits are typically low in proteins and lipids but high in carbohydrates (White 1974; Moermond and Denslow 1985); they tend to rot quickly. In contrast, other bird-dispersed species, such as those of *Heliconia*, produce dense, lipid-rich fruits that often remain on the plant for long periods with little sign of decay (White 1974; Moermond and Denslow 1985). Fruits dispersed by bats are typically green, odoriferous, and presented away from foliage. The most common examples at La Selva are in the Piperaceae.

**Table 22.1** Fruit types and display characteristics of shrubs and treelets compared with trees at La Selva

Characteristics	Shrubs and Treelets <sup>a</sup> (No. Species)	Trees <sup>b</sup> (No. species)
Fruit type		
Arillate	27	23
Berry <sup>c</sup>	70	7
Other	4	1
Color of ripe fruit <sup>d</sup>		
Red/orange	24	12
Light blue	12	0
Dark blue/black	50	11
White	10	7
Green	5	1
Source of contrasting colors <sup>e</sup>		
Infructescence structure	21	16
Ripening fruits	44	6

Sources: Denslow et al. 1986; Levey 1988a.

Note: The sample of 132 species is based on censuses of all fruiting plants occurring in 50 quadrats (100 m<sup>2</sup>) and along 150 transects (12 m × 1 m).

<sup>a</sup>Height less than 10 m.

<sup>b</sup>Height more than 10 m.

<sup>c</sup>Functionally defined as a soft, watery fruit.

<sup>d</sup>Colors originally determined by reference to color swatches based on the Munsell system.

<sup>e</sup>Species without sharply contrasting colors not listed.

**Tree Fruit.** Ninety percent of the 185 tree species surveyed by Frankie et al. (1974a; see chapter 11) produce fleshy fruits. Seeds of approximately 50% of these species are probably dispersed by birds, 13% by bats, and the remainder by other mammals (Hartshorn 1978). Wind dispersal, which is almost absent among understory species (Opler, Frankie, et al. 1980), is also rare among trees (see also Gentry 1982a). Only 6% of the surveyed tree species are adapted for wind dispersal and 83% of these are canopy species (e.g., *Ceiba pentandra*, *Pterocarpus officinalis*).

Fruit production in the canopy is more seasonal than in the understory (Frankie et al. 1974a; Croat 1975; Opler, Frankie, et al. 1980). Species that produce small, berrylike fruits are rare; large-seeded arillate species predominate (table 22.1). Most of the large-seeded fruits are protected by a husk that opens when ripe to expose an arillate seed. The arils are typically white, orange, or red. Bright colors in other structures associated with infructescences are less common among trees than among understory plants, in which relatively inconspicuous fruits are associated with brightly colored accessory structures (table 22.1).

Examples of common trees with bird-dispersed seeds are *Protium* spp., *Virola* spp., and *Guarea* spp. Many species with especially large seeds (e.g., *Dipteryx panamensis*, *Lecythis ampla*) are dispersed by bats. Monkeys feed on numerous canopy fruits (e.g., *Welfia georgii*, *Dendropanax* spp.) but frequently drop, rather than disperse large seeds (Hladik and Hladik 1969). As in understory plants, canopy species are often dispersed by more than one type of disperser. Some species such as *Cecropia obtusifolia* and *Ficus* spp. are eaten and dispersed by almost all groups of frugivores.

Although wind dispersal is common among tropical forest

epiphytes and lianas (Croat 1975; Opler, Baker, et al. 1980; Gentry 1982a) many bear vertebrate-dispersed seeds (e.g., *Monstera*, *Syngonium* and other genera of Araceae). These fruits are often similar to those of understory shrubs (e.g., *Anthurium* spp.). Further, most canopy trees support many fleshy-fruited epiphytes (J. Denslow and D. Levey unpublished data). Although crop sizes are typically small, the abundance of epiphytes probably makes them an important component of the fruiting plant community.

Understory species are typified by a disproportionate number of berry-producing species, whereas canopy species are dominated by arillate fruits ( $\chi^2 = 22.1$ , d.f. = 1,  $p < 0.001$ ; table 22.1). Similarly, color of ripe fruit and plant growth-form are not independent ( $\chi^2 = 8.3$ , d.f. = 3,  $p < 0.05$ ; Table 22.1; White and Green categories combined). An examination of the residuals in the chi-square table reveals that most of the deviation from the expected distribution is the result of the relative abundance in the understory, and absence in the canopy, of light-blue fruits. Wheelwright and Janson (1985) found that species with brightly colored fruits were significantly more common in the understory in another Costa Rican forest. The evolutionary basis of such patterns remains largely unexplored (Willson and Whelan 1990; Cipollini and Levey 1991).

### Frugivores

Here we define a frugivore as any organism whose diet includes more than 50% fruit. We stress that this definition, which follows Terborgh (1986a) and Fleming et al. (1987), is arbitrary and artificially imposes a dichotomy on a continuum of fruit dependency. Although many animals at La Selva eat fruit, probably none rely only on fruit. Animals that consume almost entirely fruit (e.g., some phyllostomid bats; T. Fleming pers. comm.) apparently must supplement their diets with insects, pollen, or other sources of protein (Morton 1973; Foster 1978). Note that under our definition, consumption of fruit is the only criterion by which frugivory is defined. We purposefully do not distinguish between frugivores that disperse seeds and those that destroy them because the distinction is usually unclear (Howe 1986). Research on the predation end of the spectrum (the destruction of fruit and seeds) is covered in chapter 21.

Fruit-eaters transcend taxonomic and trophic boundaries (table 22.2). Many carnivores will eat fruit. Swallow-tailed kites (*Elanoides forficatus*), for example, take fruit (Buskirk and Lechner 1978) and all Costa Rican Carnivora, except otter (*Lutra longicaudus*) and mountain lion (*Felis concolor*), "are known or alleged to consume large amounts of fruit" (Janzen and Wilson 1983, 430). Most granivores also depend on fruit if only for a source of seeds. Nearly all flycatchers will eat fruit (Traylor and Fitzpatrick 1982); wrens and vultures take fruit (McDiarmid et al. 1977; Willis 1980); and even some rails and antbirds are fruit-eaters (Skutch 1933; Morton 1973; Keeler-Wolf 1986; D. Levey pers. observation). In short, most vertebrates at La Selva probably take advantage of fruit resources. This is not surprising given that most fleshy fruits are conspicuous and provide an easily accessible energy source. What is surprising is that some mammals and birds (e.g., woodcreepers) apparently never eat fruit.

Here we briefly describe vertebrate frugivores at La Selva.

For discussion of invertebrate frugivores, which are most likely seed predators, refer to chapter 21. It is likely that all vertebrate frugivores disperse at least some seeds but their efficacy as dispersers varies tremendously (e.g., Levey 1987b). In the following sections we state when possible whether a given animal is likely to disperse seeds. We augment, where possible, descriptions of the behavior and role of frugivores that have received little study at La Selva with observations of the same species elsewhere in Central America.

**Birds.** Understory frugivores are extremely common at La Selva, accounting for approximately 50% of individual mist net captures (Levey 1988b; Blake and Loiselle 1991; D. Levey unpublished data). Approximately 28% of the resident species are frugivores (Stiles 1985b), and it is likely that all of these species supplement their diets with protein-rich food sources. We follow Moermond and Denslow (1985) in classifying these by the nonfruit portion of their diets, insects and seeds.

At La Selva most frugivorous species also eat insects. Only a few species seem to eat almost exclusively fruits. In particular, three manakins (*Pipra mentalis*, *Manacus candei*, and *Corapipo altera*) and one tanager (*Euphonia gouldi*) almost always have pulp or seeds in their feces (100% occurrence of pulp and/or seeds in more than 250 total samples; D. Levey unpublished data). All common La Selva tanagers are frequent fruit-eaters. They probably disperse most small (<2 mm) seeds but are likely to drop larger seeds under or near the parent plant (Levey 1987b). Large flycatchers (e.g., *Pitangus*, *Megarynchus*, *Myiodynastes*, *Myiozetetes* spp.) commonly consume fruits. In contrast, relatively few of the many smaller flycatcher species regularly take fruit (e.g., *Mionectes* spp., *Ornithion*, and *Zimmerius* do take fruits). Cotingas are primarily frugivorous (Snow 1982) but little is known about their feeding behavior at La Selva because they spend most of their time in the canopy where observation is difficult. Finally, species of Ramphastidae, Picidae, Trogonidae, Icterinae, and Turdinae are also commonly observed eating fruit. Although Turdinae are usually uncommon at La Selva, they may be important dispersers during fall migration when they are abundant. In October 1983, for example, three species of *Catharus* constituted 32% of all frugivore mist net captures and fecal analysis revealed that they were eating many fruits (D. Levey unpublished data).

The most common seed-eating frugivores at La Selva are emberizine finches (e.g., *Caryothraustes poliogaster* and *Arremon aurantirostris*). These birds have strong bills and crack some seeds, but many seeds are dropped during fruit handling or ingested and defecated still intact (Levey 1986). Ground-feeding species such as tinamous, curassows, and ground- and quail-doves feed on fallen fruits, and most seeds are probably destroyed in the muscular gizzard. In the canopy pigeons and parrots are the most common seed-eating frugivores (Loiselle 1988). Pigeons (*Columba* spp.) eat both ripe and unripe fruit and are assumed to be primarily seed predators although their effect on seeds remains undetermined. Parrots usually eat large-seeded fruits (e.g., *Dendropanax*, *Guarea*), destroying the seeds and rarely ingesting pulp or aril. They also destroy many small seeds (e.g., *Ficus* spp., Janzen 1981a; Jordano 1983) but may defecate some intact (Fleming et al. 1985).

Table 22.2 Families of vertebrates at La Selva and their relative dependence on fruit, including seeds

Vertebrate Families	Total Species	Frugivory <sup>a</sup>	Seed Treatment <sup>b</sup>	Abundance <sup>c</sup>
<b>Birds</b>				
Tinamidae	3	+++	-	3
Cathartidae	3	+	?	2
Accipitridae	24	+	?	2
Cracidae	3	+++	+/- <sup>d</sup>	2
Aramidae	7	+	?	3
Columbidae	11	++++	+/-	4
Psittacidae	8	++++	-	4
Trogonidae	5	+++--++++	+	4
Motmotidae	2	+++	+	4
Ramphastidae	5	++++	+	3
Picidae	7	++	+	3
Cotingidae	13	+++	+	3
Pipridae	6	++++	+	5
Tyrannidae	41	+--+++	+	4
Hirundinidae	6	+	+	3
Corvidae	1	++	+	1
Mimidae	1	+++	+	2
Muscicapidae	8	++++	+	3
Vireonidae	8	+++	+	3
Emberizidae	85	+--++++ <sup>e</sup>	+/- <sup>f</sup>	2-4 <sup>g</sup>
<b>Mammals</b>				
Didelphidae	3	+++	+	3
Phyllostomidae	40	+--++++ <sup>h</sup>	+	1-5 <sup>g</sup>
Cebidae	3	+++	+/-	3-4
Edentata	3	+	?	3
Sciuridae	4	+++	-	2
Heteromyidae	1	+--+++	-	4
Erethizontidae	1	++?	?	1
Dasyproctidae	2	+++	-	4
Echimyidae	2	+++?	-?	2
Muridae	5	+++?	-	2?
Mustelidae	4	+--+++	+	2
Procyonidae	2	++++	+	3
Felidae	5	++?	+	1
Tayassuidae	2	++++	-	2
Cervidae	1	+++?	-?	1
Tapiridae	1	+++	-	1
<b>Reptiles and amphibians</b>				
Emydidae	2	++?	+	2
Iguanidae	13	++	?	3

Sources: Janzen 1983c; Macdonald 1984; T. Fleming pers. comm.; and D. Levey, T. Moermond pers. observations.

<sup>a</sup>+ = fruit rarely included in the diet; ++ = fruit included occasionally; +++ = fruit included regularly; ++++ = fruit dominates the diet.

<sup>b</sup>+ = probably disperses most seeds from fruits consumed; - = probably does not disperse most seeds from fruits consumed (but may, nonetheless, be an important disperser).

<sup>c</sup>1 = very rare; 2 = uncommon; 3 = common; 4 = very common; 5 = abundant.

<sup>d</sup>Guans and Chachalacas defecate viable seeds. Curassows appear to destroy most ingested seeds (R. Buchholz pers. comm.).

<sup>e</sup>A diverse group in degree of frugivory and abundance at La Selva. Major subfamilies that are heavily frugivorous are Icterinae (twelve spp.), Thraupinae (twenty-one spp.), Cardinalinae (seven spp.) and Emberizinae (ten spp.).

<sup>f</sup>Seed treatment heavily dependent on seed size relative to bird size (see text).

<sup>g</sup>A diverse group in degree of frugivory and abundance at La Selva. Major subfamilies that are heavily frugivorous are Caroliinae (three spp.) and Stenodermatinae (thirteen spp.). Both of these subfamilies are generally abundant. One subfamily, Desmodontinae, takes no fruits.

**Mammals.** Until the late 1980s, mammalian frugivory at La Selva received little attention. A project begun in the late-1980s by A. Campbell (unpublished data), along with researchers at other Central American sites, suggests that fruit may be an important resource to most La Selva mammals.

Phyllostomid bats in the subfamilies Caroliinae and Stenodermatinae largely depend on fruit and are extremely common in Costa Rica and Panama (Fleming et al. 1972; Heithaus et al. 1975; Heithaus and Fleming 1978; Morrison 1978; Bonaccorso 1979; Fleming 1988). La Selva has three species of

*Carollia* and thirteen species in the Stenodermatinae, including the common Jamaican fruit bat (*Artibeus jamaicensis*). At other sites this species primarily feeds on canopy figs and has a large home range (Heithaus et al. 1975; Morrison 1978; Bonaccorso 1979). Other members of the Stenodermatinae are also canopy frugivores (Bonaccorso 1979). In contrast, *Carollia* spp. are understory frugivores that feed mainly on *Piper* spp. and have comparatively small home ranges (Heithaus et al. 1975; Heithaus and Fleming 1978; Bonaccorso 1979; Fleming 1981).

Fruits in the following genera are common at La Selva and frequently eaten by bats elsewhere: *Ficus*, *Piper*, *Spondias*, *Solanum*, *Dipteryx*, *Quararibea*, *Astrocaryum*, *Markea*, *Clusia*, and *Cecropia* (Heithaus et al. 1975; Heithaus and Fleming 1978; Bonaccorso 1979; Fleming and Heithaus 1981). Many of these fruits (e.g., *Ficus*, *Cecropia*, *Solanum*, *Piper*) are also taken by birds (Palmeirim et al. 1989). Curiously absent from most bat diets are fruits of Melastomataceae and Rubiaceae, both of which are primarily eaten by birds at La Selva.

Even highly frugivorous bat species depend on other food resources (Heithaus et al. 1975). Nevertheless, the correlation between bat breeding seasons and periods of high fruit abundance suggests that fruit is a critical resource to these bats (Fleming et al. 1972; Heithaus et al. 1975; Bonaccorso 1979; Dinerstein 1987).

Bats rarely ingest fruits in fruiting trees; instead they carry fruits to feeding sites or roosts where seeds are dropped or defecated in dense piles (Morrison 1978; Bonaccorso 1979; Fleming 1981; Fleming and Heithaus 1981). Seed and seedling mortality is high in these piles (Janzen 1971b). Some seeds, however, are undoubtedly dropped or defecated away from roosts (Morrison 1978; Fleming 1981; Fleming and Heithaus 1981).

Monkeys consume large quantities of fruit. Three primates occur at La Selva: white-faced Capuchins (*Cebus capucinus*), howler (*Alouatta palliata*), and spider (*Ateles geoffroyi*) monkeys. Howlers are known to consume fruits of numerous species at La Selva including *Ficus*, *Cecropia*, *Cordia*, *Brosimum*, *Spondias*, *Dendropanax*, and *Tetragastris* (Opler et al. 1975; Howe 1980; Milton 1980; Estrada et al. 1984; D. Levey pers. observation). On Barro Colorado Island, Panama, figs are their favored fruit; 36% of their feeding time was spent in fig trees (Milton 1980; see also Estrada and Coates-Estrada 1984). Spider monkeys are primarily frugivorous (Eisenberg 1983) and take a wide variety of fruits common at La Selva (e.g., *Ficus*, *Trichilia*, *Tetragastris*, *Welfia*, *Swartzia*, and *Virola*; Boucher 1981; Howe 1980, 1982; Eisenberg 1983). White-faced Capuchins often forage near the ground and, perhaps, include more smaller fruits in their diets. Oppenheimer (1982) and Freese (1977, 1983) report them feeding on *Neea*, *Siparuna*, *Ficus*, *Miconia*, and *Dendropanax*. At La Selva they feed heavily on *Welfia* (T. Fleming pers. comm.; D. Levey pers. observation). In general, monkeys are probably not good dispersers. They drop large seeds under the parent tree and defecate small seeds in dense clumps (Vandermeer et al. 1979; Howe 1980; Freese 1983; Estrada and Coates-Estrada 1984). Nevertheless, the huge number of seeds they ingest and defecate (Hladik and Hladik 1969) ensures that a few will be deposited in good sites for germination.

Among other La Selva mammals known to eat fruit are armadillos (*Dasypus novemcinctus*, Wetzel 1983), Tayras (*Eira barbara*, Brosset and Erard 1986, Janzen 1983c), coatis (*Nasua narica*, Kaufmann 1962, 1983; Opler et al. 1975; Jordano 1983), kinkajoes (*Potos flavus*, Vandermeer et al. 1979), margays (*Felis wiedii*, Koford 1983) and most other Carnivora (Janzen and Wilson 1983). The three opossum species at La Selva may at times be important frugivores and seed dispersers (cf. Charles-Dominique et al. 1981), but little is known of their diets or abundance. Agoutis (*Dasyprocta punctata*, Smythe 1970; Vandermeer et al. 1979), squirrels (especially *Sciurus granatensis*, Heaney and Thorington 1978; Glanz et al. 1982; Heaney 1983), peccaries (*Tayassu tajacu*, Kiltie 1981b; Sows 1983), and heteromyid rodents (especially *Heteromys desmarestianus*, Fleming 1974a) feed on seeds but also cache or defecate intact seeds (Janzen 1971b; Sows 1983). Hence, these species are probably dispersers as well as seed predators (Smythe 1970, 1986; Janzen 1971b; Charles-Dominique et al. 1981). With the exception of bats and monkeys, however, extremely little is known about the effectiveness of mammalian seed dispersal.

**Reptiles and Fish.** Brown land turtles (*Rhinoclemmys annulata*) "relish" fruits (Ernst 1983, 416); the basilisk lizard (*Basiliscus basiliscus*) consumes *Ardisia*, *Cordia*, *Spondias*, *Ficus*, and *Sloanea* (Van Devender 1983); and iguanas (*Iguana iguana*) are also reported to eat fruit (Rand 1978). Some fish (e.g., *Brycon*; Characidae) apparently wait under fruiting *Ficus glabrata* trees to catch fruits that fall into the water; such fruits are found and consumed in seconds (chap. 14). Nothing is known about seed dispersal via these fish at La Selva but in the seasonally inundated forests of the Amazon, many fish clearly play an important role in seed dispersal (Gottsberger 1978; Goulding 1980). They may also be important dispersers of riparian species at La Selva.

## FRUGIVORE COMMUNITIES: LA SELVA COMPARED WITH OTHER RAIN FORESTS

The taxonomic composition of assemblages of frugivores differs among tropical regions of the world. Such differences offer fertile ground for speculation and future work. A few such differences suggest particularly important evolutionary divergences in seed dispersal systems (see also Fleming et al. 1987; Gentry 1990a). Delineating the ultimate causes behind these differences is beyond the scope of this chapter; we refer the reader to Willson et al. (1989) for alternative hypotheses. Our comparisons will be limited to selected groups of birds and mammals because these groups are the best studied and also appear to be by far the most important seed-dispersers in all tropical wet forests (Gentry 1982a; Whitmore 1984; Gautier-Hion et al. 1985; Stiles 1985b; Howe 1986).

### Birds

A great variety of birds feed on fruits in all major tropical forest regions. David Snow (1980, 1981) has provided a thorough Pan-tropical comparison of avian frugivores and their food plants. His comparison emphasizes the fruit-eaters that take large fleshy fruits. Each major tropical region has one or more groups of birds in this category, most drawn from widely

disparate taxonomic groups. Cotingas (Cotingidae), toucans (Ramphastidae), and trogons (Trogonidae) are the major representatives of this group in the Neotropics. Hornbills (Bucerotidae) and fruit pigeons (*Ptilinopus*, *Ducula*, *Treron*, and related genera) are the predominant elements in the Paleotropics (e.g., Crome 1975; Leighton and Leighton 1983), and in New Guinea, many birds-of-paradise (Paradisaeidae) are similarly important (Beehler 1981; Pratt and Stiles 1985; Diamond 1986). Even some apparent similarities among regions may be illusory. The trogons of the Paleotropics do not appear to be as frugivorous as those of the Neotropics, particularly *Pharomachrus* spp. (Wheelwright 1983); the African species may eat fruit only very rarely (Brosset and Erard 1986). Nor should hornbills be taken as ecological equivalents of toucans. Some species are much larger than toucans, and many small hornbills are highly insectivorous (Kemp 1979; Brosset and Erard 1986). Among fruit pigeons, *Treron* spp. and *Columba* spp. are thought to be seed predators because of the action of their well-developed gizzards (Goodwin 1970; F. G. Stiles pers. comm.).

In all regions one can find a large number of small frugivore-insectivore species that consume small watery fruits (e.g., Thraupinae, Pycnonotidae, Muscicapidae). This category of fruit-eaters is by far the most species rich. The species richness of these birds varies among regions (see Karr 1976a, 1976b, 1980; Pearson 1977), with a particularly high diversity in the Neotropics and New Guinea. Despite the large number of species, this group contributes little to the biomass of tropical forest systems, especially in contrast to mammalian frugivores (Terborgh 1986a). Because of their small size and mixed diet, these frugivore-insectivores have received relatively little attention in most studies of frugivory. Yet they play an important role in seed dispersal in the Neotropics (Wheelwright et al. 1984; Loiselle and Blake 1990), and we suspect that they will be shown to be important components of Paleotropical dispersal systems also (e.g., Beehler 1981).

Data on possible regional differences in fruit-feeding behavior and fruit selection are almost totally lacking. A preliminary study of fruit-eating behavior of some central African fruit-eating birds (T. C. Moermond unpublished data) suggests that the small African species do not encompass the wide range of fruit-taking behavior described for small Neotropical fruit-eaters (see Moermond and Denslow 1985). For example, in the Neotropics manakins and tyrant flycatchers take fruit by hover gleaning, but in the Paleotropics no birds apparently forage in this manner. Lacking also in the Paleotropics are birds that crush fruits in their bills while eating, a common behavior among Neotropical tanagers and emberizids.

### Mammals

The situation is much more complicated in mammals than in birds. We have divided them into seven major groups: small nocturnal rodents, terrestrial herbivores, carnivores, marsupials, squirrels, bats, and primates. Because the degree of frugivory and manner of seed handling of most mammals are poorly studied, mammalian groups undoubtedly include seed dispersers as well as seed predators and do not include all the mammals that take fruits.

Small, nocturnal rodents are often implicated as seed pred-

ators but may occasionally serve as seed dispersers through "sloppy" seed handling, seed caching, or, more rarely, through defecation of viable seeds. Although rodents are potential dispersers in every tropical region, studies of their fruit eating and potential seed dispersal are rare or nonexistent (but see Janzen 1986b). Nearly the same situation exists for the herbivores that feed on fallen seeds in almost every tropical wet forest (cf. Smythe 1986). This group includes the large caviomorph rodents, peccaries (Tayassuidae), and deer (Cervids) in the Neotropics (cf. species accounts in Janzen 1983b); pigs (Suidae), antelopes and chevrotains in the Afrotropics (Dubost 1984); pigs, mouse-deer (Tragulidae) and deer in the Asian tropics (Medway 1978, Payne et al. 1985); and wallabies (Macropodidae) in the Australian tropics (Strahan 1983). Tapirs (Tapiridae) in the Neotropics and Indo-Malaysian tropics, and elephants in African and Asian forests may also play important roles as dispersers (Alexandre 1978; Janzen 1983b, 1986b; Gautier-Hion et al. 1985). In addition, extinct mammals may have played an important role in all regions (e.g., Proboscideae, Ursidae, Diprodonidae; Janzen and Martin 1982, Pratt 1983; but see Howe 1985).

At La Selva we know that small rodents probably play a role in seed dispersal (Denslow and Moermond 1982; S. Hermann unpublished data). Large rodents such as agoutis are common but little studied (cf. Smythe 1978; Hallwachs 1986). Tapirs (*Tapirus bairdii*) are rare at La Selva, as is common for large mammals in forests near significant human populations.

Many carnivores have been noted to take occasional fruits; nevertheless, the species identified as regular frugivores are few. They include two mustelids (*Eira* and *Mephitis*) and three procyonids (*Potos*, *Bassaricyon*, and *Nasua*) in the Neotropics (Charles-Dominique et al. 1981; Janzen 1983b), and the palm civets (Paradoxurinae, Viverridae) in the Old World tropics (*Nandinia* for Africa [Charles-Dominique 1978] and *Paguma*, *Paradoxurus*, *Arctogalidia*, and *Arctictis* for Indo-Malaysia [Medway 1978; Payne et al. 1985]).

Charles-Dominique et al. (1981) present extensive data on diet and ranging patterns of five species of Didelphidae in Cayenne, French Guyana. Other Neotropical marsupials are poorly studied but are likely to consume fruit and disperse seeds. *Caluromys* spp., in particular, are heavily frugivorous and probably disperse many seeds (B. McNab pers. comm.). In New Guinea and Australia the phalangers (Phalangeridae) and many of the possums (Pseudocheiridae) eat fruits (Strahan 1983) but only as a minor part of the diet; most species are folivores (Smith and Hume 1984).

Squirrels (Sciuridae) are present in Neotropical, Afrotropical, and Indo-Malaysian forests. Although poorly studied, they appear to be primarily seed-predators (MacKinnon 1978; Emmons 1981; Glanz et al. 1982; Heaney 1983). Some species may contribute to seed dispersal of certain plants (Leighton and Leighton 1983; Becker and Wong 1985).

Bats are clearly important frugivores and seed dispersers (Fleming 1979, 1981, 1988; Marshall 1983; Charles-Dominique 1986; and others cited previously). The frugivorous bats of the Neotropics are small and in one family (Phyllostomidae) of the Microchiroptera. In contrast, the Microchiroptera of the Paleotropics are insectivorous or carnivorous (McNab 1971). In the Paleotropics frugivory in bats is generally confined to the large Megachiroptera (McNab 1971;

Medway 1978; Marshall 1983). In addition to size difference between the Old and New World frugivorous bats the two groups have apparently radiated differently with respect to foraging zones. Whereas Neotropical phyllostomids forage throughout the forest, Paleotropical pteropodids are generally canopy or forest edge feeders and do not commonly forage in the understory (Fleming et al. 1987).

Primates are often a dominant element among tropical forest frugivores. In particular, diverse assemblages of primates dominate the frugivore biomass in many Paleotropical communities (Terborgh 1986a). Neotropical rain forests have fewer, but often still quite numerous, species of primates (e.g., Panama [Hladik and Hladik 1969], Surinam [Mittermeier and Roosmalen 1981], Peru [Terborgh 1983; Janson and Emmons 1990]). An important difference between the frugivory system at La Selva, with only three primate species, and other rain forest sites is, thus, likely to be reduced significance of frugivory by primates. Indeed, "monkey fruits" appear much less common at La Selva than reported in Peru (Janson 1983; Terborgh 1983). Data to substantiate this impression, however, are lacking.

Primates are extremely variable in their effectiveness as dispersers (Howe 1980; Hladik and Hladik 1969; Gautier-Hion 1984; Terborgh 1983; Corlett and Lucas 1990). Old World primates are generally more folivorous than New World primates (Terborgh 1986a), but the degree of folivory compared to frugivory varies from region to region (Gautier-Hion 1983). The degree of folivory appears to be positively correlated with body weight in Malaysia (Chivers 1980), Gabon (Gautier-Hion et al. 1980), Panama (Hladik and Hladik 1969), and Peru (Terborgh 1983). Another difference between New and Old World primates is that New World primates are almost exclusively arboreal but many Old World primates are markedly terrestrial (Fleming et al. 1987).

It is particularly interesting to note that the New World Callitrichidae, which are all much smaller than the cebids or the cercopithecids, are heavily insectivorous with many species also frugivorous (Terborgh 1983; Rylands 1984). Two *Saguinus* species in Peru appear to eat primarily small, sugary "bird" fruits, which are typically found in small, widely dispersed patches in the understory (Terborgh 1983; Garber 1986). These small, sometimes abundant primates, have no direct parallel in Africa or Asia. In Madagascar frugivorous lemurs have similar feeding patterns (Tattersall 1982). Although the Old World lorises are in the same small size range, only a few are notably frugivorous (*Galago alleni* and *Pterodicticus potto* in Africa [Charles-Dominique 1971, 1977] and *Nycticebus coucang* in Southeast Asia [Payne et al. 1985]). Their solitary, nocturnal behavior and relatively low population densities offer a very different picture from that of the diurnal and abundant tamarins and marmosets of the Neotropics.

## FRUGIVORES AS SEED DISPERSERS

To understand the ecological and evolutionary importance of frugivores as seed dispersers, we need to know how dispersal affects plant fitness (Herrera 1986; Willson 1991; Jordano 1992). This is a difficult question especially because appropriate plant fitness estimators vary among plant species (Mur-

ray 1987). The ecological and evolutionary consequences of dispersal are beyond the scope of this chapter and have been reviewed elsewhere (Howe and Smallwood 1982; Beattie 1985; Howe 1986). Instead, we focus on one dimension of seed dispersal that we suggest is of universal importance—whether seeds are carried away from the parent plant. From this perspective seed dispersal has two important components. First, fruits must be chosen for consumption and then they must be handled in such a way that seeds are ingested and dispersed. Work at La Selva has focused on these components of dispersal among frugivorous birds.

## Fruit Choice by Birds

**Fruit and Fruit Display Attributes.** Fruit choice by birds is influenced by a variety of fruit attributes: fruit size (Moermond and Denslow 1983; Wheelwright 1985b), seed size (Sorensen 1984), dry pulp mass (Johnson et al. 1985), pulp to seed ratio (Howe and Vande Kerckhove 1980; Herrera 1981), pulp taste (Sorensen 1983), sugar concentration (Levey 1987c), caloric content (Sorensen 1984; Jordano 1988), fruit color (Morden-Moore and Willson 1982; Willson and Thompson 1982), and ripeness (Moermond and Denslow 1983). In addition, other factors such as fruit crop size (Howe and De Steven 1979; Howe and Vande Kerckhove 1979; Stapanian 1982; Foster 1990), distance to nearest fruiting neighbors (Manasse and Howe 1983; Levey et al. 1984; Denslow 1987a; Sargent 1990) and nutritional content of other fruits (Jordano 1988) affect fruit choice on another level by influencing which fruiting plants are visited. How birds integrate these factors when choosing among fruits is complex and largely unknown (Martin 1985a; Moermond et al. 1987). We have been able, however, to examine the underlying decision-making process in fruit choice by offering captive birds pairwise choices of fruits on artificial infructescences (Moermond and Denslow 1983). These birds make consistent and transitive choices among fruits. This means that fruit choices are consistent with a maximization principle (McCleery 1978). Our working hypothesis is that this maximization principle is, in turn, based upon weighing costs and benefits associated with each fruit type. The spectrum of costs and benefits, and their relative importance, remains unclear but almost certainly includes fruit availability and bird morphology. Under a framework of cost-benefit analysis we discuss these factors and how they are weighed against each other in determining fruit choice in birds.

**Fruit Availability.** Fruit abundance, detectability, and accessibility are components of fruit availability. They define the context in which fruits are encountered by birds, and they influence fruit removal rates and frugivore abundance (Thompson and Willson 1978; Manasse and Howe 1983; Martin and Karr 1986b; Loiselle 1988; Loiselle and Blake 1990). If, as hypothesized previously, frugivores employ a cost-benefit approach in choosing fruits, then we would predict that fruit choice depends on context. A fruit preferred in one situation may not be taken when encountered in a different context.

We have examined how one component of fruit availability, accessibility, affects fruit choice (Moermond et al. 1986, 1987). Accessibility is a measure of how easily a fruit can be



taken from an infructescence. It includes proximity of a fruit to a perch and perch diameter, angle, and flexibility. If a bird is given a choice between a fruit close to a perch and a fruit of the same species far from a perch, it chooses the closer, more accessible fruit (Denslow and Moermond 1982; Moermond and Denslow 1983). Similarly, birds will choose fruits adjacent to large, sturdy perches over identical fruits near small, flexible perches (Moermond et al. 1986).

What if both accessibility and fruit quality are varied by presenting a bird with a choice between a low-ranked, easily accessible fruit and a high-ranked, less-accessible fruit? Can birds simultaneously weigh both fruit quality and accessibility when selecting fruits? We have addressed this question by "titrating" fruit quality against accessibility. A bird is first presented with two equally accessible fruits, A and B. It usually shows a preference for one, say A, by taking it first. If A is then made less and less accessible over a series of trials, the bird usually switches its behavior and takes B before A (Moermond and Denslow 1983; Levey et al. 1984; Moermond et al. 1986). These switches are reversible and consistent among trials. Highly preferred fruits must be made very inaccessible before the less desirable but more accessible fruit is taken first. These results indicate that birds weigh fruit quality against accessibility in choosing among fruits. Thus, they appear to employ a cost-benefit assessment; costs of access are weighed against relative benefits of different fruits.

If birds are most likely to take easily accessible fruits, why are so many fruits placed on terminal infructescences where they are relatively inaccessible? Denslow and Moermond (1982) suggest that terminal infructescences reduce seed predation by arboreal rodents. Although fruit removal by birds may also be reduced, they argue that because rodents are less agile than birds, probability of predation by rodents decreases more rapidly than probability of dispersal by birds as fruits become more inaccessible. An alternative explanation of terminal fruit presentation may be that fruits are produced where flowers are placed, and flowers are placed to maximize pollination success.

**Bird Morphology.** Fruits that are accessible to individuals of one bird species may be relatively inaccessible to another because of differences in the birds' morphology and associated effects on foraging behavior. Avian frugivores at La Selva separate into two morphological groups (Moermond and Denslow 1985; Moermond et al. 1986; Levey 1987b). The first group is represented by the subfamilies Thraupinae and Emberizinae. Its members have relatively strong feet, narrow gapes, and long, stout bills. The second group contains Pipridae, Cotingidae, Trogonidae, and Tyrannidae. Members of this group generally have weak feet, wide gapes, short, flat bills, and short, broad and/or highly slotted wings. Whereas members of the first group usually reach for fruit from perches, members of the second group often take fruits during flight and can thereby remove fruits that would be difficult to reach from a perch. Consequently, perch structure is less important to them than to members of the first group (Moermond et al. 1986; D. Levey unpublished data). They tend to be more selective than birds in the first group (Moermond et al. 1986). This high selectivity may be related to the higher costs of taking fruit on the wing.

Integrating the factors responsible for fruit choice poses a challenging problem (Martin 1985a). In this section we have presented evidence that birds select fruits by balancing disparate costs and benefits. Alternative ideas need further attention (e.g., Worthington 1989; Loiselle and Blake 1990). We conclude that birds are selective but their choices depend on context. Because the contexts in which fruits are found are extremely variable, the costs and benefits associated with taking particular fruits will also vary, resulting in a dynamic fruit selection process. This conclusion yields two insights: first, little opportunity for specialization and coevolution exists because fruit choice by birds depends heavily on variables that are beyond the control of individual fruiting plants; second, the wide diet breadth of fruit-eating birds and overlap among species (Snow 1962a, 1962b; Leck 1971; Snow and Snow 1971; Worthington 1982; Wheelwright et al. 1984; Moermond and Denslow 1985) should not necessarily be interpreted as a lack of discrimination by birds. Instead, it is a likely consequence of the complex decisions underlying fruit selection. An alternative hypothesis is offered by Worthington and Olberg (1990).

### Handling of Fruits and Seeds

Handling fruit and seeds has important consequences for both the bird and fruiting plant. From a frugivore's perspective seeds represent useless bulk. Yet they often constitute much of each fruit and if not processed efficiently could result in high costs of ballast or gut volume displacement. From a plant's perspective seed processing is critical because it determines how effectively seeds are dispersed. For example, Howe (1977) and Howe and Primack (1975) documented different methods of seed handling by birds feeding on *Casearia*. Some species carried seeds away from the parent tree, whereas others deposited them below the tree where survivorship was lower than for dispersed seeds (see also Augspurger 1984b; D. A. Clark and Clark 1984; Howe et al. 1985).

At one extreme of seed-handling techniques are granivores. It is important to note that although these species are usually assumed to be seed predators, many may also be seed dispersers; the two groups are not distinct (Janzen 1971b; Levey and Byrne in press). For example, at La Selva, two species of emberizid finches consume and defecate many small seeds in viable condition. In fact, these finches may be better dispersers of small seeds than tanagers and manakins because the seeds have longer passage times and are distributed among more defecations (Levey 1986).

Even among those frugivores that are unlikely to digest seeds, there are important differences in fruit and seed-handling techniques. Differences between the two morphological groups mentioned earlier are especially evident (Moermond and Denslow 1985; Moermond et al. 1986). The group with strong bills (henceforth, "mashers") thoroughly mandibulate fruits, often extracting and dropping seeds, especially large seeds (Levey 1987b). Birds with weak bills (henceforth, "gulpers") and wide gapes usually swallow fruit whole, ingesting all seeds regardless of size. Mashers also have higher ingestion rates (number of fruits eaten per feeding bout), longer handling times, are more sensitive to taste cues, take a wider range of fruit sizes than gulpers of equivalent size, and can suction drink (Moermond 1983; Levey 1987b, 1987c).

Large seeds are handled efficiently by mashers because

minimal cost is incurred in dropping them. Cost to the plant, however, is high because most seeds are dropped near the parent where relatively few will survive (Howe and Primack 1975; D. A. Clark and Clark 1984). Even though gulpers ingest large seeds, the seeds are still processed rapidly. In contrast to small seeds, which are defecated by both mashers and gulpers, large seeds are regurgitated (Levey 1987b). Regurgitation is a much faster method of voiding seeds than defecation (Johnson et al. 1985; Sorensen 1984; Levey 1986, 1987b). In most cases seeds are defecated within thirty minutes and regurgitated within fifteen minutes. Both mashers and gulpers can internally separate seeds from fruit pulp and pass the seeds before the pulp (Levey 1986; Levey and Grajal 1991).

## VARIATION IN FRUIT AND FRUGIVORE ABUNDANCE

### Spatial Variation

At La Selva production of fleshy fruits by shrubs and treelets is higher in secondary than mature forest (Opler, Frankie, et al. 1980; Blake and Loiselle 1991). Abundance of understory bird-dispersed fruits is also significantly higher in early second growth than in tree-fall gaps and significantly higher in gaps than in adjacent understory (Denslow et al. 1986; Levey 1988a; see also Martin 1985b; Blake and Loiselle 1991). These differences are primarily the result of higher densities and crop sizes in the higher light environments (Bullock 1982; Marquis 1988; Levey 1990; Blake and Loiselle 1991).

The diversity of fruiting plant species also varies across habitats. Opler, Frankie, et al. (1980) recorded more fruiting species in mature than secondary forest (ninety-one and forty-three species, respectively), but this pattern is confounded by a greater sampling effort in mature forest. Other studies have documented a higher species diversity of plants with fruit in second growth and gaps than in mature forest understory (Denslow et al. 1986; Levey 1988b; Blake and Loiselle 1991).

Spatial variation in fruit abundance apparently affects frugivore abundance; fruit-eating bird abundance mirrors fruit abundance (Levey 1988b; Blake and Loiselle 1991; Loiselle and Blake 1991). The concentration of fruits and frugivores in tropical tree-fall gaps suggests that gaps may be "hotspots" of frugivore activity and seed dispersal (Willson et al. 1982; Herrera 1985b; Levey 1988a, 1990). This conclusion has several important implications: First, the disparity in fruit crop sizes between gap and understory conspecifics (Marquis 1988; Levey 1990) suggests that shrubs may produce a large proportion of their lifetime output of fruit during the relatively short time they are in a gap (Levey 1990). Second, although gaps represent rare opportunities for understory plants to produce large crops and attract many dispersers (Denslow and Moermond 1982; Blake and Hoppes 1986; Martin and Karr 1986a), competition with neighboring plants for dispersers is probably severe because frugivores are most selective under such circumstances (Levey et al. 1984). Thus, pronounced neighborhood effects (Manasse and Howe 1983; Herrera 1986; Sargent 1990) may be typical of gaps. Third, the abundance of frugivores and high rates of fruit removal in gaps (Thompson and Willson 1978; Denslow and Moermond 1982;

Piper 1986) coupled with rapid seed-passage times (Levey 1986; Murray 1988; Worthington 1989) suggest that frugivores do not select fruits and disperse seeds randomly within tropical forests (Murray 1988; Schupp et al. 1989; Willson and Crome 1989; see also Hoppes 1988; Malmberg and Willson 1988). Instead, we hypothesize that they are most likely to take fruits from and disperse seeds into (or near) gaps. The consequences of such dispersal are complex and remain largely unresolved (e.g., Augspurger 1984b; Augspurger and Kelly 1984; Dirzo and Domínguez 1986; Webb and Willson 1985; Willson 1988; Schupp 1988b; Schupp and Frost 1989).

### Temporal Variation

Fruit abundance at La Selva has been monitored for more than eleven years over a twenty-year period (Frankie et al., 1974a; Opler, Frankie, et al., 1980; Denslow et al. 1986; Levey 1988b; Loiselle and Blake 1991). To compare fruiting phenology at La Selva to BCI, another tropical site with almost equally extensive data, we standardized by dividing each monthly value into the range of monthly values reported (see the figure legend for sources). If data for more than one understory habitat or plant form were reported in a study, fruiting activity was calculated for each and then averaged across months.

In general, there is a single peak in fruit abundance in September–October and a period of relative fruit scarcity during the dry season (January–March; fig. 22.1). This single-peak pattern contrasts with double peaks of annual fruit abundance reported elsewhere in Costa Rica, Panama, and Peru (Frankie et al. 1974a, Croat 1975, Opler, Frankie, et al. 1980; Foster 1982b; Janson and Emmons 1990; fig. 22.1). Even during the period of relative fruit scarcity, however, ripe fruit is not uncommon. Frankie et al. (1974a, 902) concluded that "a continual source of food was . . . provided to resident frugivorous animals" throughout their three-year study.

The magnitude of seasonal shifts in fruit abundance depends on habitat (fig. 22.1). Individuals in the canopy, second growth, and gaps tend to display large, synchronous changes in fruiting activity (Frankie et al. 1974a; Levey 1988b). Understory fruit production, on the other hand, is much less seasonal (Frankie et al. 1974a; Opler, Frankie, et al. 1980; Levey 1988b). Because understory species tend to produce fruit over brief periods (Opler, Frankie, et al. 1980) the aseasonality of understory fruit abundance is apparently caused by many short, nonoverlapping fruiting episodes. Still, the understory is an area of relative fruit scarcity; most sites are without fruit for at least four months of each year (Denslow et al. 1986). Despite large communitywide fluctuations in fruit abundance in gaps, individuals of at least several species produce fruit nearly continuously in gaps, whereas conspecifics in the understory do not (Bullock 1982; Marquis 1988; Levey 1990).

The abundance of fruit-eating birds also displays seasonal fluctuations (Loiselle 1987a, 1988; Levey 1988b; Loiselle and Blake 1991). Large numbers of frugivores, mostly temperate and altitudinal migrants, start to appear in October–November when fruits are abundant. Frugivore abundance remains high through January–February and then drops during the dry season period of relative fruit scarcity. These concurrent shifts in frugivore abundance suggest that many frugivorous birds track changes in fruit availability through altitudinal migration

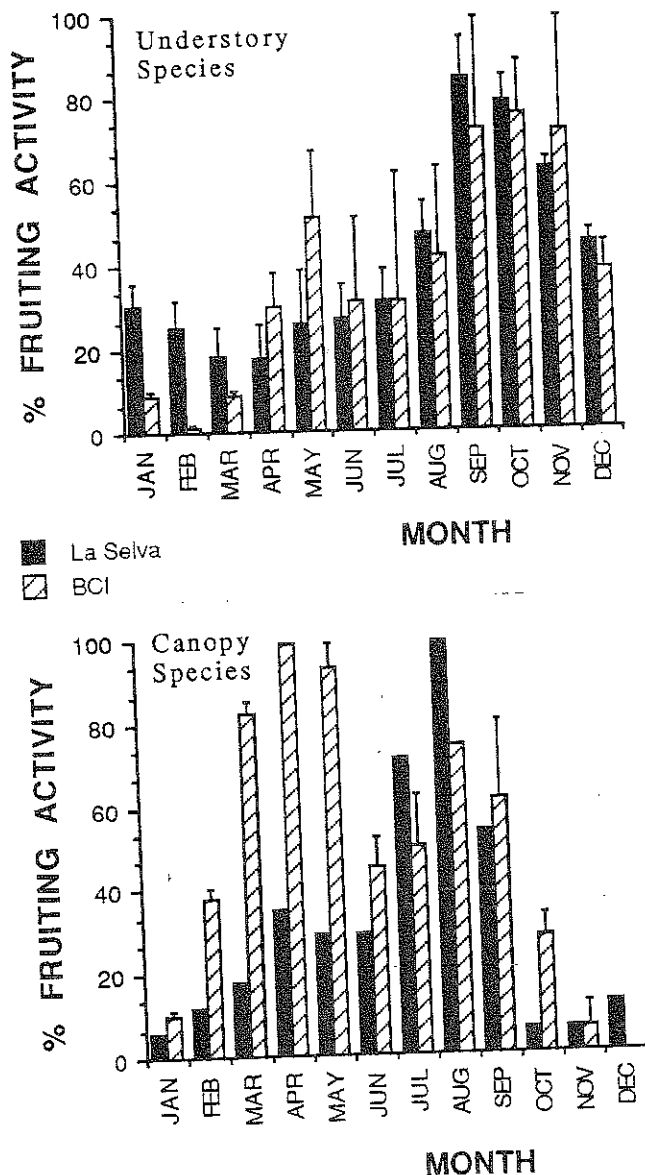


Fig. 22.1. Seasonal patterns of (top) understory and (bottom) canopy fruiting activity on Barro Colorado Island and La Selva. Fruiting activity reflects either the number of individuals in fruit per area or proportion of community bearing fruit, depending upon the data base. Bars are standard errors (each data base contributed only once per habitat to their calculation). (Data from Frankie et al. 1974a; Croat 1975; Opler, Frankie, et al. 1980; Foster 1982b; Denslow et al. 1986; Loiselle 1987a; Levey 1988b.)

(Rosselli 1989; Loiselle and Blake 1991). Movements of birds, bats, and primates at other tropical sites also appear tied to seasonal shifts in fruit abundance (Crome 1975; Marshall 1983; Leighton and Leighton 1983; Innis 1989; Te Boekhorst et al. 1990).

Temporal variation in frugivore abundance is likely to affect fruit removal rates. *Hamelia patens*, for example, produces ripe fruit continuously and experiences dramatic changes in disperser abundance (Leck 1972; Levey 1987a). During some periods its fruits rot on the tree, whereas at other times they are removed while still unripe. Fruits of *Hamelia* ripen more rapidly during periods of rapid fruit removal

(Levey 1987a). Denslow and Moermond (1982) reported higher fruit removal rates during a season of fruit scarcity than during a season of fruit abundance (see also Leck 1972). Similarly, Vandermeer et al. (1979) documented highest fruit removal rates of *Welfia georgii* from individuals that fruited slightly out of synchrony with the rest of the population. Croat (1974) and Snow (1965) argue that some species may shift their fruiting periods in response to changes in frugivore feeding activity. The extent to which such shifts are a cause or an effect of correlated shifts in frugivore activity, however, remains unclear.

Breeding activity and mortality patterns in many types of frugivores have been linked to seasonal changes in fruit availability (Kaufmann 1962; Fleming 1981; Smythe 1978; Bonaccorso 1979; Glanz et al. 1982; Oppenheimer 1982; Smythe et al. 1982; Russell 1982; Terborgh 1983). Widespread famine among frugivores during fruit shortages has been reported elsewhere in Central and South America (Foster 1977, 1982a; Terborgh 1986a) but has not yet been reported at La Selva. During the dry season of 1981, however, we observed fifteen species of frugivorous birds eating unripe or partially ripe fruits. Some species were using unusual foraging methods (e.g., *Ramphocelus* tanagers hopping on the ground), and we noticed more aggressive interactions at fruiting trees than usual (D. Levey unpublished data). Foster (1982a) estimates that severe fruit shortages occur on Barro Colorado Island approximately every ten years following unusually wet dry seasons. Indeed, January and February of 1981 were unusually wet—over a twenty-seven-year period only three Januaries and two Februaries were wetter (chap. 3).

During periods of extremely low fruit availability, the few species in fruit may be responsible for maintaining the entire frugivore community. Figs are often identified as such “key-stone” mutualists (Leighton and Leighton 1983; Terborgh 1983, 1986b). At La Selva, we have not noticed any such key-stone species. Figs, in particular, do not appear to play as important a role as elsewhere (see also Gautier-Hion and Michaloud 1989). Howe (1984b) suggested, however, that *Casearia corymbosa* may be a critical resource for *Tityra semifasciata* during times of fruit scarcity at La Selva.

## FRUIT-FRUGIVORE COEVOLUTION

The importance of tropical fruits as resources for birds was well documented in the 1960s (Snow 1962a, 1962b; Land 1963; Willis 1966; Leck 1969) but a theoretical framework to explain the diversity of fruits and frugivores was lacking. Van der Pijl (1982) noted several syndromes among fruiting plants. Fruits commonly eaten by bats, for example, were different in predictable ways from those eaten by birds. These syndromes seemed to be clear evidence of coevolution, but the underlying mechanisms generating them were unclear. The first explanation (McKey 1975) was based on Snow's (1971) work and was later expanded by Howe and Estabrook (1977). It emphasized a continuum of evolutionary and ecological dependence between species of birds and fruiting plants and focused attention on the end points of the continuum.

At one end of the hypothesized continuum were closely interdependent *specialists*. Plants in this group produced rela-

tively small crops of large-seeded, nutritious fruits and attracted a few species of uncommon but "reliable" dispersers. These birds were thought to eat only *specialist* fruits and disperse their seeds to favorable germination sites. At the other end of the continuum were *generalist* plants, producing large crops of small-seeded fruits. Because these fruits contained little more than sugar-water and seeds, birds feeding on them were necessarily generalists, taking a wide variety of fruits and insects. Hence, the birds were seen as opportunistic foragers that displayed little selectivity among the many species of fruits they ate.

The generalist-specialist hypothesis has generally lacked both theoretical and empirical support (Wheelwright and Orians 1982; Howe 1984a; Moermond and Denslow 1985; Herrera 1986). We review the difficulties encountered by the theory and suggest a current view of fruit-frugivore coevolution that is consistent with the results of recent studies.

Detailed studies of foraging behavior by frugivores quickly revealed many inconsistencies between predicted and observed patterns. First, generalist frugivores do not feed on small fruits opportunistically or haphazardly. Instead, they are highly selective in choosing among fruits and apparently weigh disparate costs and benefits of different fruits found in various contexts (Moermond and Denslow 1983; Moermond et al. 1986, 1987; Loiselle and Blake 1990). Second, large specialized birds do not rely exclusively on a few specialized fruits but, in fact, often take many species of fruits over a wide range of sizes, including Melastomataceae and Moraceae (refs. in Moermond and Denslow 1985; Wheelwright 1985b). Third, small generalist birds are not low-quality dispersers. Viable seeds have been found in the feces of almost all tanagers and manakins and even supposed seed predators (e.g., *Arremon*) captured in mist nets at La Selva (D. Levey unpublished data). Small birds, in general, (and tanagers, in particular) are usually active and, hence, are likely to disperse seeds away from the parent plant. Furthermore, they appear to be "reliable"; color-banded individuals return regularly to specific fruiting trees (Pratt 1984; D. Levey pers. observation). Fourth, "specialist" frugivores often do not provide effective dispersal. Trogons at La Selva and Monteverde (Costa Rica) frequently regurgitate seeds under or near the parent tree (Wheelwright 1983); oilbirds deposit many seeds in their roosting caves (Snow 1962c); and toucans may often be fruit "thieves" (Howe 1977). Fifth, it is often inaccurate to label a bird species as a high- or low-quality disperser because how well it disperses seeds may not be an inherent attribute of the bird but instead depend upon seed size, pulp texture, or other fruit traits (Levey 1987b). A tanager, for example, may be an excellent disperser of small seeds but may seldom ingest large seeds even though it feeds on large-seeded fruits. Finally, species interactions may change dramatically from site to site, a phenomenon not accounted for by the theory. Similar species of *Casearia* are dispersed by specialists at La Selva but by generalists elsewhere (Howe 1977; Howe and Vande Kerckhove 1979). These observations suggest that the theoretical framework proposed by McKey (1975) and Howe and Estabrook (1977) does not adequately describe tropical fruit-frugivore interactions.

How closely are fruiting plants and frugivores coevolved? We do not expect tight, species-specific coevolution for sev-

eral reasons. Plants have little control over where frugivores deposit their seeds. Because birds are "rewarded" for taking fruits rather than dispersing seeds, there is no direct mechanism for the evolution of dispersal to especially good germination sites (Wheelwright and Orians 1982; Howe 1984a). In addition, spatial and temporal variation in dispersal effectiveness and fruit supply may often be high enough to swamp evolution of species-specific interdependence (Howe and Smallwood 1982; Howe 1984a; Herrera 1985a, 1986; Denslow et al. 1986). Dynamic fruit-frugivore associations such as those at La Selva preclude close coevolution. If there are no clear or consistent differences among dispersers in their effectiveness, there is little chance of selection for specialization with the best disperser. Finally, genetic constraints on quantitative traits are little understood but may hinder the evolution of tight fruit-frugivore mutualisms (Howe 1984a; Herrera 1985a, 1986).

For these reasons coevolution in the strict sense (mutual shifts in gene frequencies in two interacting populations) is undoubtedly rare between plants and fruit-eating birds. It is simply unclear how either group would benefit from species-specific interactions (Wheelwright and Orians 1982). The few examples of close coevolution that apparently do exist beg further study. These examples nearly all involve mistletoes (Wetmore 1914; Ridley 1930; Ali 1931; Sutton 1951; Doctors van Leeuwen 1954; Parker 1981; Davidar 1983; Reid 1986; Restrepo 1987). In this case sticky viscin clinging to each seed often results in birds wiping their vents against branches to dislodge the seeds, thereby "planting" it on the branch, the best potential germination site for a mistletoe. This may represent one of the very few cases where a plant in part determines its dispersal site, thereby satisfying one of the seldom met criteria for coevolution toward a more specific fruit-frugivore interaction (Wheelwright and Orians 1982).

On a very general level the syndromes described by Ridley (1930) and Van der Pijl (1982) do exist although their distinctness is blurred (see Howe 1986; Fleming et al. 1987). Differences between fruits typically consumed by birds, bats, rodents and monkeys are well-documented (Van der Pijl 1982; Janson 1983; Gautier-Hion et al. 1985; see also Willson et al. 1989; Jordano 1992). Within these groups are still further divisions of consumers and fruit types. At La Selva, for example, *Euphonia gouldi* eats mostly fruits of epiphytic plants (especially *Anthurium* spp.) and *Mionectes oleagineus* is clearly a specialist on arillate fruits (Loiselle and Blake 1990; D. Levey unpublished data). Clearly, patterns exist among frugivores of who eats what fruits. The fact that proposed theoretical constructs (McKey 1975; Howe and Estabrook 1977) are inadequate should not detract attention from these patterns; they still need to be explained. Indeed, fruit syndromes suggest that differences among dispersers have been important in the evolution of fruit attributes (Janson 1983; Gautier-Hion et al. 1985; Levey 1987b; Levey and Grajal 1991) and that reciprocal selection pressures are likely among groups of plants and groups of frugivores. Thus, seed-dispersal systems exemplify "diffuse" coevolution (Janzen 1980b) where evolutionary changes result from interactions between groups of species rather than between individual species.

The species groups responsible for the diffuse nature of

fruit-frugivore coevolution remain unclear. To delineate them one must keep a historical perspective (Janzen and Martin 1982; Howe 1985). More importantly, biologists need a more thorough understanding of how plant fitness and demography are tied to dispersal by different frugivores (Howe 1984a, 1989; Jordano 1987). If, as suggested earlier, dispersal of seeds away from a parent plant is an important and ubiquitous selective force, then the masher-gulper dichotomy may represent a level of diffuse coevolution between birds and fruiting plants. Because mashers drop most large seeds, large-seeded plants may have methods of increasing the probability of gulpers feeding on their fruits while simultaneously decreasing the possibility of mashers doing so. Predicted mechanisms for such selectivity have been described, tested, and generally supported (Levey 1987d; Rosselli and Stiles in press).

## AVENUES FOR FUTURE RESEARCH

### Nonavian Frugivory

Little is known about nonavian frugivory at La Selva. In particular, bats are an important but poorly understood group of frugivores and seed dispersers at La Selva that have only recently received attention (T. Fleming unpublished data). Given the wealth of detailed information on diets, foraging patterns, and annual cycles of frugivorous bats in more seasonal Neotropical sites (Fleming et al. 1972; Heithaus et al. 1975; Morrison 1978; Bonaccorso 1979; Foresta et al. 1984; Fleming 1988), work on frugivorous bats at La Selva would provide important comparative data. In addition, several similarities and differences between frugivorous bats and birds merit further attention. First, radiotelemetry studies of bats and birds in Cayenne suggest that dispersal of seeds by bats is more homogeneous than by birds (Foresta et al. 1984). Second, bats may display altitudinal migrations similar to those observed in frugivorous birds (see Marshall 1983; Bonaccorso and Humphrey 1984; Dinerstein 1987). Third, the seed-handling techniques of mashing and gulping described for birds appear also characteristic of Neotropical bats (Fleming 1986; Bonaccorso and Gush 1987).

Invertebrate frugivores have been almost universally overlooked (Janzen 1977b; Herrera 1982, 1984). Yet from a coevolutionary perspective the interactions between these fruit-consumers and their hosts are probably more intricate than between vertebrate frugivores and fruiting plants (Thompson 1982; Herrera 1984, 1986; Sallabanks and Courtney 1992). The interaction between pathogens and fruiting plants is especially interesting because it may directly affect the probability of a vertebrate frugivore feeding on a fruit and dispersing its seeds (Borowicz 1988; Jordano 1989; Buchholz and Levey 1990). On the one hand, secondary compounds that protect ripe fruits against nonmutualist frugivores are also liable to discourage potential seed dispersers. On the other hand, seed dispersers may sometimes prefer insect-damaged fruit because the insects increase the amount of available protein (Redford et al. 1984; Piper 1986; Drew 1988). In any case, the large proportion of damaged fruits on many plants strongly suggests that pathogens may be an important selective force for many fruit traits and, consequently, influence seed dispersal.

### The Role of Spatial and Temporal Variation

Gaps at La Selva host high concentrations of fruiting shrubs and foraging frugivores and, thus, can be considered arenas of fruit-frugivore interactions. Yet researchers know little about the consequences of such intense, localized activity. Do birds and bats that feed in gaps bring seeds from other gaps? Are seeds that they take deposited nonrandomly in gaps? and if so, What are the consequences for seedling survival? Because gaps tend to enlarge (Hubbell and Foster 1986b; Runkle and Yetter 1987; Young and Hubbell 1991), if frugivores commonly deposit seeds around the perimeter of gaps (Hoppes 1988), then seed dispersal of many plants may be "directed" to an area of high potential for seedling establishment (Levey 1988a; Malmberg and Willson 1988; Schupp et al. 1989).

This mechanism for seedling recruitment into gaps presently lacks supporting data, but we feel it is likely important at La Selva. In other tropical forests, however, it probably does not operate. For example, in a Panamanian forest neither fruit-eating birds nor fruiting plants are prevalent in gaps (Schemske and Brokaw 1981; Willson et al. 1982). Such basic differences between geographically proximate forests remain unexplained.

As emphasized earlier, the impact of fruit seasonality on frugivore populations is poorly understood. Of particular interest is the extent to which annual cycles of frugivores are tied to fruit abundance and how closely frugivores track changes in fruit availability. Tracking may occur on a small scale (habitat shifts; Karr and Freemark 1983; Blake and Loiselle 1991) or on a large scale (altitudinal and latitudinal migration; Morton 1977; Levey 1988b; Rosselli 1989; Loiselle and Blake 1991; Levey and Stiles 1992 chap. 17). The degree to which frugivores can and do track fruits has important implications for conservation because large areas of contiguous forest may be necessary to maintain viable populations. How much forest will sustain viable populations of highly transient species is, however, unknown. For management of more sedentary species it is important to identify "keystone" species, if, indeed, they exist (DeSteven and Putz 1984; Terborgh 1986b; Gautier-Hion and Michaloud 1989). At La Selva we suggest that tree-fall gaps, which always seem to support relatively high levels of fruits, may be more important than specific keystone species in maintaining frugivores through periods of fruit scarcity (Levey 1990).

### Integrating Multiple Factors at the Level of the Plant Species

Perhaps the most challenging task is framing frugivory and seed dispersal in the context of the many other components of a plant's life history (Schupp et al. 1989). A first step is to determine the relationship between fitness and patterns of seed dispersal; researchers need to move beyond studies of frugivore behavior and link such studies with plant demography (Howe 1989; Jordano 1992). How, for example, do seed deposition patterns influence seed and seedling survival (Howe et al. 1985; Fleming 1988; Schupp 1988a; Willson and Whelan 1990)? Only a handful of studies at La Selva have focused on postdispersal seed fates (Schupp and Frost 1989; Loiselle 1990; Byrne and Levey in press; Levey and Byrne in press). This is a critical area of research because both demographic and experimental studies have demonstrated that pre-

dition on seeds and seedlings can be the major limitation to recruitment in some tropical species (Sarukhán 1978; Augspurger 1984b; Howe et al. 1985; Sork 1987; Schupp 1990).

Seed dispersal also needs to be integrated with the many other factors affecting plant fitness. For example, how do gap dependence, pollination, herbivory, and seed predation influence fruit and seed attributes and, hence, dispersal success? Large seeds may be required for vigorous, shade-tolerant seedlings but may also increase risk of predation and decrease dispersibility (Snow 1971; Howe and Richter 1982). Similarly, fruiting phenology may be dictated by flowering phenology and, thus, constrained by pollinator abundance and/or weather rather than tied solely to disperser abundance. Hence, examining only seed dispersal or frugivory may yield conclusions that are misleading when placed in the broader context of the plant's autecology and evolution.

## CONCLUSIONS

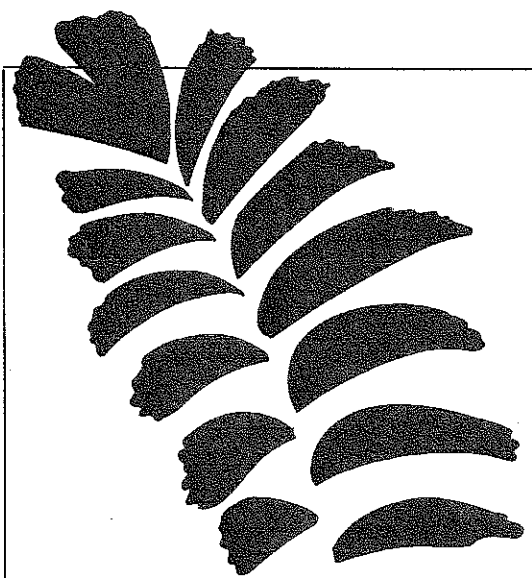
Fruiting plants and frugivores are a critical part of the La Selva ecosystem; most dicots rely on frugivores for seed dispersal, and most vertebrates rely on fruit resources for at least part of their energetic requirements. The central role of frugivory is apparently typical of other tropical wet forests as well, but the types of dominant fruits and frugivores vary widely. At La Selva small fruits are especially common, and the birds that feed on them have received much attention. These birds are

selective in their choice of fruits, yet their choices are context dependent and their fruit-handling techniques vary in important ways. Thus, the major dispersers of a given plant species are often unpredictable. This type of fruit-frugivore interaction precludes close coevolution. Instead, the important selective pressures probably occur between groups of species, such as those determined by fruit type or fruit-handling technique.

Spatial and temporal heterogeneity in fruit and frugivore abundance emphasize the importance of long-term and large-scale studies. There are obviously times and places of intense frugivore and fruiting activity. Yet the impact of such variation is unclear, especially for the most common frugivores (small birds and bats) and fruiting plants (shrubs, treelets, lianas, epiphytes, and herbaceous plants).

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# LA SELVA

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