

Chapter 6

Fruits and Frugivory

Pedro Jordano

Estación Biológica de Doñana, CSIC, Apdo. 1056, Sevilla, Spain

Jordano, P. 2000. Fruits and frugivory. In: Fenner, M. (ed.). *Seeds: the ecology of regeneration in plant communities*, 2nd edition. CABI Publ., Wallingford, UK. Pages 125-166.

Introduction

The pulp of fleshy fruits, with the soft, edible, nutritive tissues surrounding the seeds, is a primary food resource for many frugivorous animals, notably mammals and birds, but also reptiles (Howe, 1986). These animals either regurgitate, defecate, spit out or otherwise drop undamaged seeds away from the parent plants; they are the seed dispersers that establish a dynamic link between the fruiting plant and the seed-seedling bank in natural communities. Therefore, frugivory is a central process in plant populations where natural regeneration is strongly dependent upon seed dissemination by animals.

Early conceptual contributions to the study of frugivory emphasized dichotomies in frugivory patterns and fruit characteristics that presumably originated by co-evolved interactions (Snow, 1971; McKey, 1975; Howe and Estabrook, 1977; Howe, 1993). Fruits with pulps of a high energetic content and nutritive value surrounding a single large seed would be one extreme of specialization by interacting with specialized frugivores providing high-quality dispersal; fruits with succulent, watery, carbohydrate-rich pulps occupy the other extreme by having their numerous small seeds dispersed by opportunist frugivores. Subsequent work during the last two

decades has centred around this seminal paradigm and there is a wealth of information about patterns of frugivory in particular taxa, variation in fruit characteristics and detailed descriptions of plant/frugivore interactions for particular plant species or communities (for recent reviews, see Howe, 1984, 1993; Estrada and Fleming, 1986; Herrera, 1995; Corlett, 1998). However, studies of frugivory have rarely been linked conceptually with demographic patterns in the plant population; also, the evolutionary consequences of frugivore choices, fruit processing and movement patterns have seldom been examined in an explicit evolutionary context, where fitness differentials in plant populations are measured and associated with individual variation in dispersal-related traits. Frugivory and dispersal influence the evolution of plant traits through effects on population processes, but predictive frameworks that link frugivory patterns, associated differences in seed/seedling mortality and differential reproductive success with demographic patterns in natural plant populations are very scarce (Howe, 1989; Jordano and Herrera, 1995; Schupp and Fuentes, 1995; Wenny and Levey, 1998).

Recent reviews of seed dispersal and frugivore ecology show that, for most frugivores, fleshy fruits are a non-exclusive food resource, which is supplemented with

animal prey, vegetative plant parts, seeds, etc. (Hladik, 1981; Moermond and Denslow, 1985; Fleming, 1986; Howe, 1986; Willson, 1986; Corlett, 1998). Very few vertebrates rely totally on fruit food, but many species are 'partial' frugivores, which consume other prey together with various amounts of fruit; dietary habits among these species range from sporadic fruit consumption to almost totally frugivorous diets. For example, only 17 families of birds (15.6%) can be considered as strictly frugivorous, but at least 21 families (19.3%) consume a mixed diet with a large proportion of fruits and a minor contribution of animal prey; and 23 families (21.1%) mix, in roughly equal proportions, fruits and other material in their diets (see Snow, 1981). Total frugivory among mammals is non-existent. Among bats, only pteropodids (Old World bats) and phyllostomids (New World fruit-bats) can be considered largely frugivorous (Gardner, 1977; Marshall, 1983; Fleming, 1986), supplementing fruit food with insects (Courts, 1998) and/or leaves (Kunz and Diaz, 1995). Fruit is the most widely used type of food among primates, found in the diets of 91% of the species examined to date (Harding, 1981; Hladik, 1981), and certain frugivorous forest ungulates, such as brocket deer (*Mazama* spp.) and African cephalophines (*Cephalophus* spp.), can include up to 85% of fruit material in their diet (Dubost, 1984; Bodmer, 1989a, 1990). However, partially frugivorous mammals include opossums, phalangers, kangaroos, lemurs, lorises, apes, foxes, bears, elephants, horses and other ungulates (Harding, 1981; Janzen, 1983; Howe, 1986). Finally, among reptiles, tortoises, lizards and iguanids can have an important role as seed dispersers, even with infrequent and non-obligate frugivory (Barquín and Wildpret, 1975; Losos and Greene, 1988).

Frugivorous animals, relying sporadically or obligately on fruits for food, have a central role in demography and plant community evolution because: (i) their interaction with plants takes place at the final stage of each plant reproductive episode, having a potential to 'screen off' or nullify

previous effects of the pollination and fruit growth phases (Herrera, 1988a; Jordano, 1989); (ii) by directing the early spatial distribution of the seeds, i.e. the 'seed shadow' (Janzen *et al.*, 1976), they provide a template over which future spacing patterns of adult plants will build up; and (iii) seed deposition patterns by frugivores directly affect patterns of early seed survival and seedling establishment (Howe *et al.*, 1985; Katusic-Malmberg and Willson, 1988; Schupp, 1988; Willson, 1988; Herrera *et al.*, 1994).

The purpose of this chapter is to dissect this fleshy-fruit/frugivore interface, which brings up both characteristics of the fruits as 'prey items', which must be sought, handled and efficiently processed, and the ability of frugivores to perform these tasks, with consequences for the plants themselves. Throughout the chapter, any mention of fruits will be with reference to fleshy fruits, loosely defined to include any structure enclosing seeds surrounded by a fleshy, edible, pulp layer (Howe and Smallwood, 1982). Most references to frugivorous animals will be to birds, primates, ungulates and bats that behave as seed dispersers. The first section of the chapter describes fruits as prey items from the perspective of the foraging animal, and examines their characteristics, temporal and spatial patterns of availability and intrinsic traits, such as design and nutritive value. The second part reviews frugivore traits that influence fruit choice, fruit and seed processing and foraging movements that have implications for seed deposition patterns.

Fruit production and availability

Fleshy fruits are, for the organisms consuming them, discrete food items available in an extremely diverse array of spatial and temporal configurations. The various characteristics (Table 6.1) include those that define their spatial distribution and the temporal patterns of availability, both seasonally and between years, and their food value as prey that must be processed as

Table 6.1. Summary of major characteristics of fleshy fruits as food resources for frugivorous vertebrates.

A. Availability characteristics	
	Marked seasonal changes in abundance
	Non-renewable in the short term
	Strong between-year changes in availability for certain species
	Heterogeneous spatial distribution: highly clumped; local superabundance; few species available at the same particular location
B. 'Intrinsic' characteristics as prey items	
	High water content
	Strong imbalance between energetic and protein components
	Presence of voluminous mass of indigestible material (seeds)
	Presence of secondary metabolites

discrete items. Availability characteristics influence overall abundance of frugivores in particular habitat patches, their foraging movements and important aspects of their annual cycles. Intrinsic features determine fruit and seed processing and, consequently, how the seeds reach the ground. Both groups of traits ultimately influence seed deposition patterns, because they determine the movement patterns of frugivores foraging for fruits in relation to the mosaic of habitat patches.

Production and abundance of fruits

Variation among communities in the frequency of endozoochorous seed dispersal

is broadly associated with variation in precipitation and moisture (Gentry, 1982), and a latitudinal gradient is also evident. Vertebrate seed dispersal is very common among woody plants in neotropical (70–94% of woody species), Australian (82–88%) and African rainforests (approximately 80%) (Table 6.2). Mediterranean scrubland and some tropical dry and humid forests and woodlands usually range between 50 and 70%; temperate coniferous and broad-leaved forests vary within 30–40% of animal-dispersed woody species. Frugivory and endozoochorous seed dispersal are virtually absent or unimportant in grasslands, extreme deserts, alpine vegetation and certain types of scrublands on nutrient-poor sites.

Table 6.2. Percentages of woody species adapted for endozoochorous seed dispersal by vertebrates in different vegetation types.

Vegetation type	Mean (Range)	References ^a
Temperate coniferous forest	41.8 (33.3–56.5)	1–4
Temperate deciduous forest	35.4 (9.5–53.8)	1–5
Savannah woodland	41.2 –	6
Mediterranean scrubland (Spain)	56.1 (47.1–64.3)	7, 8
Mediterranean scrubland (Chile)	41.9 (20.0–55.1)	9
Mediterranean scrubland (California)	34.4 (16.7–43.3)	9
Mediterranean scrubland (Australia)	22.5 (10.0–50.0)	9–11
Neotropical dry forest	46.2 (27.0–58.7)	12–14
New Zealand lowland forest	64.0	15
Subtropical humid forest	69.4 (65.2–73.5)	16, 17
Neotropical and palaeotropical humid forest	74.7 (62.1–82.1)	5, 18–22
Tropical rainforest	89.5 (70.0–93.5)	5, 22–24

^a References: 1, Johnson and Landers (1978); 2, Marks and Harcombe (1981); 3, Schlesinger (1978); 4, Franklin *et al.* (1979); 5, Howe and Smallwood (1982) and references therein; 6, Poupon and Bille (1974); 7, Herrera (1984b); 8, Jordano (1984); 9, Hoffmann and Armesto (1995); 10, Milewski (1982); 11, Milewski and Bond (1982); 12, Gentry (1982); 13, Frankie *et al.* (1974b); 14, Daubenmire (1972); 15, Burrows (1994); 16, Frost (1980); 17, Boojh and Ramakrishnan (1981); 18, Charles-Dominique *et al.* (1981); 19, Alexandre (1980); 20, Lieberman (1982); 21, Tanner (1982); 22, Willson *et al.* (1989) and references therein; 23, Putz (1979); 24, Janson (1983).

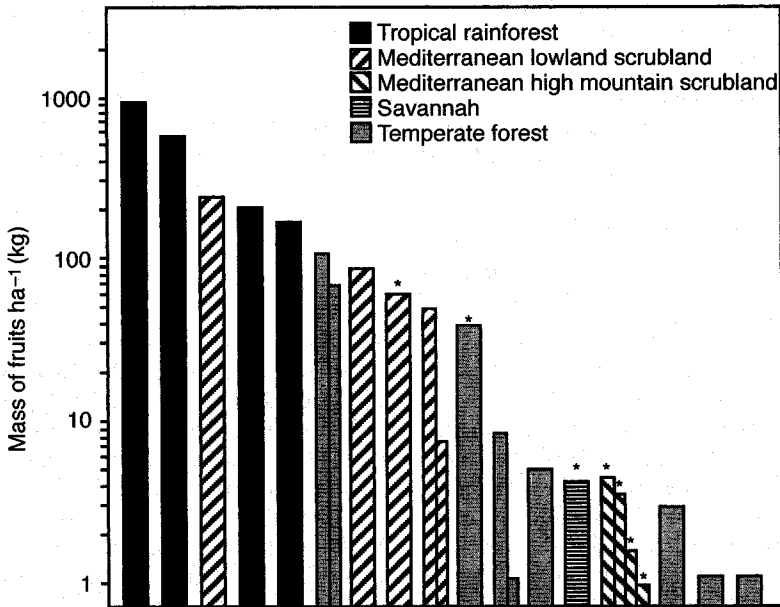


Fig. 6.1. Total production (per unit area) of fleshy fruits in different plant communities (placed in order of decreasing magnitude of production). Bars with asterisks indicate biomass figures as wet mass, all others are dry mass. Double bars indicate data for two localities in a single study. References: Leigh (1975); Johnson and Landers (1978); Baird (1980); Stransky and Halls (1980); Charles-Dominique *et al.* (1981); Hladik (1981); Sorensen (1981); Guitián (1984); Herrera, (1984b, c); Jordano (1984, and unpublished data).

This range of variation is also exemplified when considering between-community variation in production of fleshy fruits, both in numbers and biomass. Overall levels of fruit production in particular habitats are strongly associated with the relative importance of zoochory as an adaptation for the dispersal of seeds (Fig. 6.1), but rigorous estimation of absolute abundance is subject to numerous potential biases (Blake *et al.*, 1990; Chapman *et al.*, 1992b, 1994; Zhang and Wang, 1995). Fruit production in temperate forests of the northern hemisphere is always below 10^5 fruits ha⁻¹, representing less than 10 kg ha⁻¹ (dry mass). Mediterranean scrublands have productions similar to those of some tropical forests, in general around 80 kg (dry mass) ha⁻¹, but fruit density might reach more than 1.4×10^6 fruits ha⁻¹ in good crop years (Herrera, 1984b; Jordano, 1985); however, high-elevation Mediterranean scrublands have productions more similar to

those of temperate forests (Fig. 6.1). Tropical rainforests range widely in production, usually between 180 and approximately 1000 kg ha⁻¹ (dry mass). For additional data, see Blake *et al.* (1990).

Extreme between-year variations in the production of fleshy fruits have been found (e.g. Davies, 1976; Foster, 1982; Jordano, 1985; Herrera, 1988c, 1998), but a direct, causal relationship between these fluctuations and frugivore numbers has rarely been documented. In most instances, studies with long-term data are lacking and inferences about causal associations due to the plant/frugivore interaction are unwarranted or are established without a proper evaluation of the influence of external variables (e.g. climate, food resource levels outside the study area, etc.). Between-year variations in availability of fruits, paralleled or not by variations in frugivore numbers, add an important stochastic component to plant/frugivore interactions, and

long-term data are needed to begin a realistic assessment of their demographic implications (Herrera, 1998).

Seasonality

The overall production figures outlined above illustrate broad patterns of variation in fruit abundance but mask actual availability for frugivores, which frequently face seasonal and annual shortages of this food resource. Figure 6.2 summarizes variation in the phenology of ripe fruit availability in six major community types. In general, fruiting peaks occur during periods of low photosynthetic activity or after periods of high rates of reserve accumulation towards the end of the growing season (French, 1992; see review by Fenner, 1998). Fruiting peaks occur at the end of the dry seasons, matching generalized increases in precipitation, and these trends are evident even without shifting the graphs to compensate for latitudinal differences. Unimodal fruiting peaks of the highly seasonal forests are not replicated in the very humid rainforests, where several peaks of different importance occur as a result of both variations in rainfall intensity within the rainy season and delays in the phenological responses of different growth forms (Frankie *et al.*, 1974a; Croat, 1978; Opler *et al.*, 1980). Several authors point out the absence of significant flowering and fruiting seasonality in certain rainforests of South-East Asia (Koelmeyer, 1959; Putz, 1979) and Colombia (Hilty, 1980). Seasonality in the number of plant species bearing ripe fruits decreases from temperate to tropical forests, largely as a result of the increase in the average duration of the fruiting phenophase (although the seasonal pattern can be strikingly similar in some cases; see Fig. 6.2). Average duration of period of ripe fruit availability for a given species is always less than 1.5 months (mean = 0.6–1.3 months) in temperate forests and always more than 4 months (mean = 4.3–5.8 months) in tropical forests (Herrera, 1984c; see also references in Table 6.2). Lowland Mediterranean scrublands

(Herrera, 1984c; Jordano, 1984) have intermediate averages of 2.2–4.0 months. It would be interesting to know if these consistent patterns of variation reflect similar environmental influences or if, as evidenced for the flowering seasons of temperate forest plants, they are largely attributable to phylogenetic affinities (Kochmer and Handel, 1986; Fenner, 1998).

These differences in the seasonal patterns of fruit availability between the tropics and temperate zones define important differences in frugivory patterns. Temperate frugivory is a strongly seasonal phenomenon among migrant birds (Thompson and Willson, 1978; Stiles, 1980; Herrera, 1982, 1998; Jordano, 1985; Wheelwright, 1986, 1988; Willson, 1986; Snow and Snow, 1988; Noma and Yumoto, 1997; Parrish, 1997) and mammal species, such as carnivores (Debussche and Isenmann, 1989; Herrera, 1989) or warm-temperate pteropodid bats (Funakoshi *et al.*, 1993), which show marked seasonal shifts in diet composition. Tropical frugivores usually exploit fruit food during the whole year, but important seasonal dietary shifts also take place (e.g. Snow, 1962a, b, c; Decoux, 1976; Hilty, 1977; Worthington, 1982; Terborgh, 1983; Leighton and Leighton, 1984; Sourd and Gauthier-Hion, 1986; Fleming, 1988; Erard *et al.*, 1989; Rogers *et al.*, 1990; Williamson *et al.*, 1990; Conklin-Brittain *et al.*, 1998; Wrangham *et al.*, 1998).

Seasonality of fruit availability causes dietary shifts by frugivorous animals, which 'track' the changes in the fruit supply (Loiselle and Blake, 1991). For whole-year resident frugivores, this type of resource tracking involves the sequential consumption of a great variety of fruit species, with a major effect on nutrient dietary balance and nutrient intake (Witmer and van Soest, 1998; Wrangham *et al.*, 1998). Important aspects of the annual cycles of frugivores, such as reproduction, breeding, migratory movements, etc., are associated with seasonal fruiting peaks. However, in most cases, a direct causal link between both cyclic phenomena cannot be established. The long-term studies by

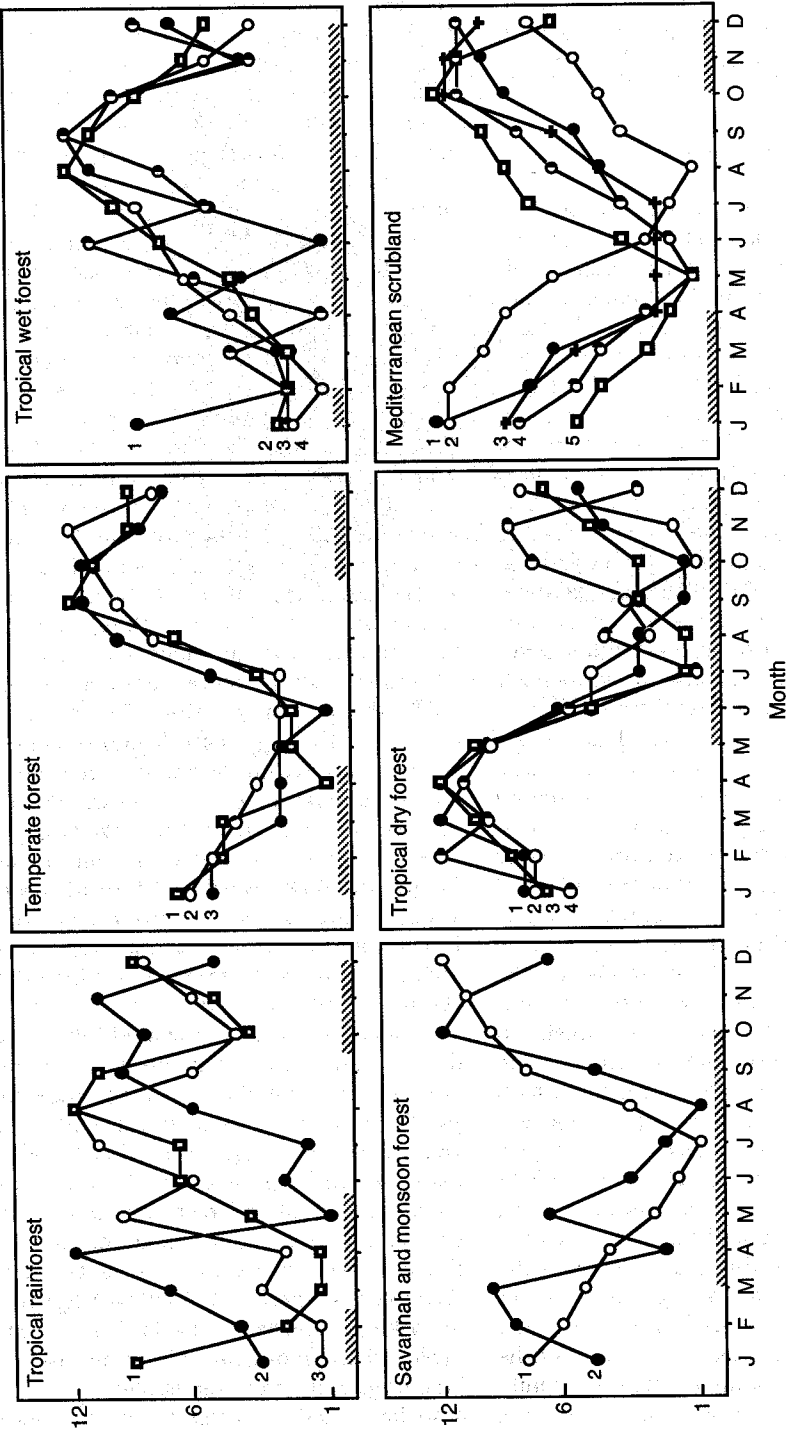


Fig. 6.2. Seasonality patterns in availability of ripe fleshy fruits in several habitat types. Months have been ranked (scores from 1 to 12 in vertical axis) according to proportion of woody species with ripe fruit available. The shaded bars on the abscissa depict the rainy seasons. References: Tropical rainforest, Davis (1945)^{1,3}; Hilly (1980)²; Temperate forest, Halls (1973)¹; Sorensen (1981)²; Cuitián (1984)³; Tropical wet forest, Frankie *et al.* (1974b)¹; Crome (1975)²; Alexandre (1980)³; Medway (1972)⁴; Savannah and monsoon forest, Poupon and Bille (1974)¹; Boofh and Ramakrishnan (1981)²; Tropical dry forest, Daubenmire (1972)¹; Frankie *et al.* (1974a)²; Morel and Morel (1972)³; Lieberman (1982)⁴; Mediterranean scrubland, Herrera (1984c)^{1,3}; Mooney *et al.* (1977), California², Chile⁴; Jordano (1984)⁵.

Crome (1975) and Innis (1989) in the rainforests of Queensland (Australia) clearly show that seasonal patterns of abundance of certain fruit-pigeons are strongly associated with the seasonal patterns of fruit ripening. Similarly, Leighton and Leighton (1984) found a good correlation between local densities of major frugivorous vertebrates (fruit-pigeons, hornbills, primates and ungulates) and fruit abundance in a Bornean rainforest; regional migration, nomadism, exploitation of aseasonal fruit types (e.g. *Ficus*) or alternate food resources were means of escaping seasonal fruit scarcity in time and space (see also Whitney and Smith (1998) for African *Ceratogymna* hornbills). Wheelwright (1983) describes marked shifts in habitat selection by resplendent quetzals, which track the seasonal sequence of ripe fruit availability among *Lauraceae*. Migratory or nomadic movements among Megachiroptera (Marshall, 1983) can be associated with changes in the fruit supply. Also, the annual cycle of frugivorous bird abundance in Mediterranean scrubland has been found to track closely the abundance and biomass cycle of ripe fruits (Jordano, 1985). On the other hand, Reid (1990) showed no clear relation between the seasonal abundance patterns of the mistletoe bird (*Dicaeum hirundinaceum*) and its preferred fruit, *Amyema quadang* (*Loranthaceae*), in Australia. The breeding seasons of certain tropical frugivorous birds (e.g. Snow, 1962a, b; Worthington, 1982), bats (Marshall, 1983; Fleming, 1988) and primates (e.g. Terborgh, 1983) all match local maxima of ripe fruit availability. Loiselle and Blake (1991) found that frugivorous birds bred when the fruit supply was low but, after the breeding season, moved into areas where fruit was more abundant. Seasonal use of fruits as an alternative food resource for temperate passerines is probably the major impelling influence on the evolution of long-distance migratory movements in the Nearctic and Palaearctic (Levey and Stiles, 1992).

The evidence outlined by these studies suggests that seasonal fruiting patterns can have a great effect on the annual cycles of

most frugivores (van Schaik *et al.*, 1993). Frugivorous animals, on the other hand, probably have a negligible effect on shaping the abundance patterns of fleshy fruits in time. Thus, for western European bird-dispersed plants, Fuentes (1992) found parallel seasonal trends in bird abundance and the number and biomass of fruits, but not in the proportion of species with ripe fruit; frugivores might favour the seasonal displacement of fruit availability by positive demographic effects on particular plant species fruiting when birds are most abundant. Major patterns of convergence in community-level fruiting patterns strongly support the findings of previous studies showing: (i) a complex role of climate (alternation of drought and rainfall seasons) in shaping the fruiting curves at a community level in relation to flowering and leafing activity (Janzen, 1967; Borchert, 1983; Gautier-Hion *et al.*, 1985a; Hopkins and Graham, 1989); (ii) a prominent role of germination requirements at the start of the rainy season (Garwood, 1983); (iii) phylogenetic constraints in the timing and duration of the fruiting phenophase (Kochmer and Handel, 1986; Gorchov, 1990); (iv) the effect of physiological constraints derived from the integration of flowering, fruit growth, ripening and seed dispersal phases of the reproductive cycle (Primack, 1987; Fenner, 1998); and (v) potential effects of frugivores in shaping fruit availability patterns but not the fruiting phenophase itself (Debussche and Isenmann, 1992; Fuentes, 1992).

Spatial distribution

Relative to other food resources, such as animal prey (e.g. insects), fruits are extremely aggregated in space, usually in relatively isolated patches, with high local abundance. In addition to the intrinsic spacing patterns of the adult trees, which determine the spacing patterns of the fruits themselves, the spatial distribution of fruits as food resources for foraging animals is constrained by two major factors: (i) successional characteristics of the

patch; and (ii) relative frequency of fruit-bearing trees in the patch. Fruit abundance increases in gaps and secondary growth of temperate forests (Thompson and Willson, 1978; Willson *et al.*, 1982; Martin, 1985), and fruiting individuals of a given species usually bear larger crops when growing in open sites rather than the forest interior (Piper, 1986a; Denslow, 1987). Work in tropical rainforest (De Foresta *et al.*, 1984; Levey, 1988a, b; Murray, 1988; Restrepo and Gómez, 1998) showed that patchiness in fruit availability is predictably associated with tree-fall gaps and other disturbances. Individual plants growing in Costa Rican tree-fall gaps produced more fruit over a longer period of time than conspecifics growing in intact forest understorey; the diversity of fruiting plants also increased in gaps (Levey, 1988b, 1990).

The same pattern exists in temperate forests, where mature stands are dominated by *Quercus*, *Fagus* and *Acer* species, among others, and fleshy-fruited shrubs and treelets are characteristic of early successional stages and forest gaps (Marks, 1974; Smith, 1975; Kollmann and Poschod, 1997). Forest gaps of temperate forest are sites of increased local concentration of fruits (Sherburne, 1972; Sorensen, 1981; Blake and Hoppes, 1986; Martin and Karr, 1986). For example, Blake and Hoppes (1986) found an average fruit abundance at the start of the fruiting season (September) of approximately 50 fruits 80 m^{-2} in Illinois forest gaps versus approximately five fruits 80 m^{-2} in forest interior plots. Among the reasons for these trends in both tropical and temperate forests are: (i) increased abundance of individual plants in gaps; (ii) increased diversity of fleshy-fruit-producing species; and (iii) increased crop sizes among individuals growing in gaps.

In Mediterranean shrubland, however, pioneer, successional species with dry fruits and capsules are progressively substituted by endozoochorous species, which eventually dominate the late successional stands (Bullock, 1978; Houssard *et al.*, 1980; Debussche *et al.*, 1982; Herrera,

1984d). For example, average cover of fleshy-fruited species in southern Spanish Mediterranean, lowland shrubland, mature stands (Jordano, 1984) is 96.88% and it is 62.00% in open, successional stands.

Two additional sources of local patchiness in fruit availability have seldom been considered. First, abundance will be influenced by the frequent association of dioecism with production of fleshy fruits (Givnish, 1980; Donoghue, 1989). In Mediterranean shrubland, the relative cover of female individuals can vary on local patches between 20 and 95%, and increasing local abundance of male, non-fruiting plants is associated with decreased fruit availability (Jordano, 1984). This factor is probably irrelevant as a source of patchiness in fruit abundance in temperate forests, but might prove to be important in tropical habitats, where dioecism is relatively frequent. Secondly, fleshy-fruited plants are frequently associated with particular patches below the closed canopy of taller trees, probably because of increased recruitment in these foci as a result of increased seed rain beneath trees (McDonnell and Stiles, 1983; Tester *et al.*, 1987; Hoppes, 1988; Izhaki *et al.*, 1991; Holl, 1998). Bat roosts, nests of frugivorous birds, fruiting plants where frugivores defend feeding territories, traditional perches for sexual displays and latrines of certain 'carnivore' mammals are among the many types of sites that create recruitment foci, with seed density orders of magnitude greater than in sites elsewhere in the forest (Lieberman and Lieberman, 1980; Stiles and White, 1986; Dinerstein and Wemmer, 1988; Théry and Larpin, 1993; Fragoso, 1997; Kinnaird, 1998). In addition, seed rain of fleshy-fruited species is significantly higher beneath female, fruit-bearing, plants compared with male plants of dioecious species (Herrera *et al.*, 1994), a result of preferential foraging by fruit-seeking frugivores. All these processes generate predictable spatial patterns of fruit availability, which, in turn, influence the pattern of patch use by foraging frugivores.

Fruit characteristics

Fruits are particulate foods, which frugivorous animals usually harvest, handle and swallow as individual items. Relevant traits of fleshy fruits, from the perspective of the foraging animal, include design (e.g. size, number and size of seeds, mass of pulp relative to fruit mass), nutrient content (relative amounts of lipids, protein, carbohydrates and minerals per unit mass of fruit processed) and secondary metabolites (Table 6.1B). These traits influence the overall, intrinsic profitability of fruits, by determining both the total amount of pulp ingested per fruit handled and the nutrient concentration of the ingesta (Herrera, 1981a), but the profitability of a given fruit should be examined in the context of an interaction with a particular frugivore species (Martínez del Río and Restrepo, 1993).

Fruit size and design

The ability to handle, swallow and process a given fruit efficiently depends on fruit size relative to body size of the frugivorous animal, particularly the gape width and mouth size. These types of constraints are similar to those found among gape-limited predators seeking particulate food and, from the plant perspective, they restrict the potential range and diversity of frugivores and dispersers (Pratt and Stiles, 1985; Wheelwright, 1985). Consumption of extremely large-seeded fruits (e.g. family *Lauraceae*, *Palmae*, etc.) by frugivorous birds is largely confined to large-bodied species (toucans, trogons, bellbirds: Wheelwright, 1985; see also Pratt, 1984) or terrestrial species (trumpeter (*Psophia crepitans*): Erard and Sabatier, 1988; cassowary (*Casuarius casuarius*): Pratt, 1983; Stocker and Irvine, 1983). Bonaccorso (1979) reported a significant positive relationship between body-mass variation among individual phyllostomid bats of three species and the mass of individual fruits taken. Extremely large seeds (> 3 cm length) have been reported to be dispersed

exclusively by large mammals (apes and elephants: Tutin *et al.*, 1991; Chapman *et al.*, 1992a).

The maximum and mean diameter of fruit species included in the diets of Costa Rican birds is positively correlated with gape width, and the number of bird species feeding on the fruits of a particular species of *Lauraceae* was inversely correlated with fruit diameter (Wheelwright, 1985). Reduced species richness of avian frugivores visiting large-fruited species was also reported by Green (1993) in subtropical Australian rainforest. Lambert (1989a, b) found that seven species of frugivorous pigeons in Malaysia fed on at least 22 *Ficus* species, and a positive relation exists between body size and mean fig diameter of the species consumed. Fig size choice by different bird species was influenced by body size, in spite of the fact that the structure of the syconium enables exploitation by birds of all sizes (Jordano, 1983; Lambert, 1989a). In turn, gape width strongly limited the size and variety of fruits included in the diet of six warbler species (genus *Sylvia*) in southern Spain (Jordano, 1987b). The average fruit size consumed (calculated by weighting the fruit diameter of each fruit species by the relative consumption) was positively correlated with gape width (Fig. 6.3a; but see Johnson *et al.* (1985) for North American migrant birds). In addition, the average percentage of fruits dropped during short feeding bouts decreased in the larger species with wider gape (Fig. 6.3b), indicating increasingly larger handling costs for smaller species. Snow and Snow (1988) reported a similar decrease in fruit-handling success with fruit diameter/bill width ratios greater than 1.0. Rey and Gutiérrez (1996) reported that blackcaps switch from swallowing whole wild olive fruits to fruit pecking in the olive orchards, where seeds are twice as large; as a result, only 4.9% of faecal samples from orchards contained seeds, but 58.1% of those from the wild contained wild olive seeds. In a more exhaustive set of experiments with several Mediterranean passerine species, Rey *et al.* (1997) showed that fruit size

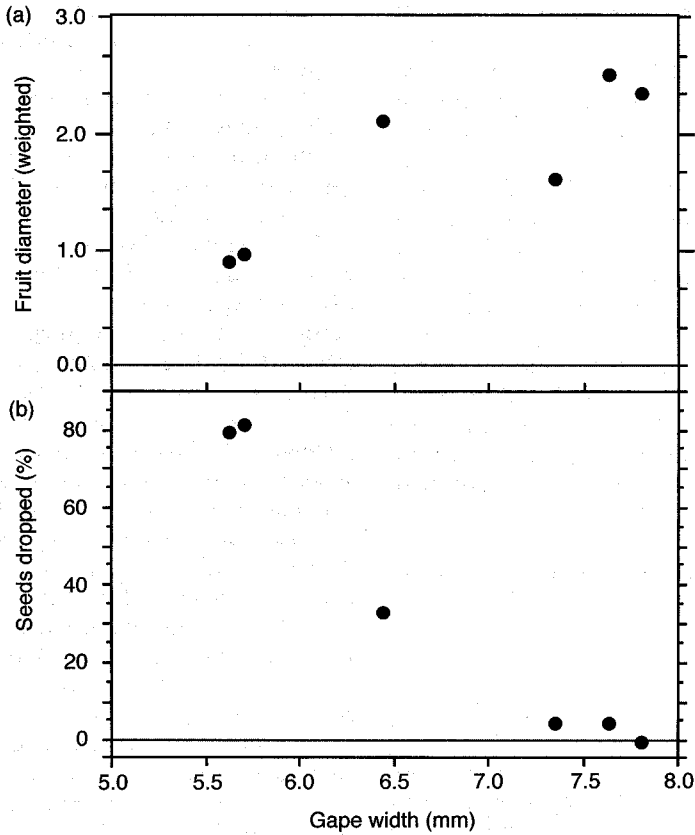


Fig. 6.3. Relationship between mean gape width (width of the bill measured at the commissures) of six species of *Sylvia* warblers and mean fruit size in the diet. (a) fruit size of each plant species consumed weighted by the frequency of consumption and, (b) the mean percentage of fruits which are dropped during feeding sequences at *Prunus mahaleb* trees, a species with average fruit diameter of 8.4 mm. Data from Jordano (1987b), Jordano and Schupp (2000). Dots, in order of increasing gape width, indicate *S. conspicillata*, *S. cantillans*, *S. melanocephala*, *S. atricapilla*, *S. communis* and *S. borin*.

determined a shift from swallowing to pecking, as pecking frequency increased with the enlargement of the fruit size; all the species showed increased fruit-handling failure rate when trying to swallow increasingly large fruits. These trends reflect the increase in handling cost associated with picking, seizing and positioning in the bill of increasingly larger fruits, but the main effect of fruit size on handling success, especially in drupes and other single-seeded fruits, is due to seed size and not to fruit size.

Few studies have concentrated, however, on intraspecific comparisons of fruit removal as related to fruit size variation

among individual plants. Bonaccorso (1979) reported strong selectivity by individual bats of figs of *Ficus insipida* differing in size, which suggests strong fruit size selection limited by aerodynamic constraints on fruit transport on the wing. Howe (1983) reported that an average of 62% of variation in seed removal of *Virola surinamensis* by birds was accounted for by the aril : seed ratio of individual trees; 78% variation in seed size of this species is among individual crops (Howe and Richter, 1982). Significant correlations are frequently obtained between seed dispersal efficiency (the percentage of the seed crop dispersed) and both fruit and seed size,

although the sign most probably varies as a result of the degree of gape limitation of the particular set of frugivores interacting with a plant species (Herrera, 1988a; White and Stiles, 1991; Sallabanks, 1992; Herrera *et al.*, 1994; Jordano, 1995b).

The potential selective pattern on fruit seediness differs with seed size and seed packaging, and complex allocation patterns to flesh, seed endocarp and seed content exist in fleshy fruits (Lee *et al.*, 1991). For multiseeded fruits, the fraction of total fruit mass allocated to seeds increases with seed number, and frugivores are expected to select few-seeded fruits (Herrera, 1981b). In drupes and other single-seeded fruits, seed burden per unit pulp mass increases with increasing fruit size, and frugivores are expected to select small fruits, especially if gape-limited (Snow and Snow, 1988; Jordano, 1995b; Rey *et al.*, 1997). Future studies should bridge the gap in our knowledge of the demographic effect of these types of selective pressures on the plant populations by considering simultaneously the effect of fruit size and seed size on germination and early seedling vigour and survival.

Allocating many small seeds within a given fruit increases the potential diversity of dispersers by allowing small frugivores to ingest pulp pieces and seeds. Levey (1987) found that the percentage of seeds dropped during feeding trials with several tanager (Thraupidae) species in captivity increased as a function of seed size; birds consistently dropped more than 60% of seeds that were greater than 2.0 mm in length. These birds are 'mashers', which crush all fruits in their bills; the largest seeds are worked to the edge of the bill and dropped and the smallest seeds are swallowed along with pulp pieces. In contrast, manakins (Pipridae) are 'gulpers', which swallow the whole fruits and defecate all seeds up to the 10 mm threshold imposed by their gape width; however, the percentage of fruits taken by manakins decreased as seed size increased. See Rey and Gutiérrez (1996) for a similar example of switching between 'gulper' and 'masher' behaviour.

The same trend is also exhibited by other taxonomic groups. The smallest species of African forest frugivorous ungulates of genus *Cephalophus* (*C. monticola*, 4.9 kg) take no fruit above 3 cm diameter and the largest (*C. sylvicultor*) consumes fruit up to 6 cm in diameter (Dubost, 1984). Similar size-related constraints have been found in bats (Fleming, 1986) and primates (Hylander, 1975; Terborgh, 1983; Corlett and Lucas, 1990; Tutin *et al.*, 1996; Kaplin and Moermond, 1998). For example, seed size strongly influences whether seeds are swallowed, spat out or dropped *in situ* by long-tailed macaques (*Macaca fascicularis*); seeds of most species with individual seeds less than 4.0 mm width are swallowed (Corlett and Lucas, 1990; see also Gautier-Hion, 1984). Kaplin and Moermond (1998) report that most seeds > 10 mm are dropped by *Cercopithecus* monkeys, but variability in behaviour as seed predators or legitimate dispersers was observed. In summary, all this evidence indicates that small frugivores are limited in the largest fruit they can efficiently handle and process and, on the other hand, increase in fruit size generally limits the range of potential seed dispersers to the largest frugivores. Both assertions are especially true for drupes or other single-seeded fruits, and have important implications for the resulting seed dispersal pattern, the evolution of fruit and seed shape and their biogeographical patterns (Mack, 1993). Thus, evidence of negative allometry in the development of large-fruited species (e.g. *Lauraceae*) has been interpreted as an adaptation to gape-limited avian frugivores (Mazer and Wheelwright, 1993; but see Herrera, 1992).

As stated by Wheelwright (1985), fruit size alone does not explain the wide variability in the number of frugivore species feeding at different plant species that have fruits of the same size. Studies examining interspecific trends in fruit structural characteristics have also found that overall size provides the main source of functional variation in fruits relative to the types of frugivores consuming them, but additional important traits were the number of seeds

per fruit, the mass of each seed and the mass of pulp per seed (Janson, 1983; Wheelwright *et al.*, 1984; Gautier-Hion *et al.*, 1985b; O'Dowd and Gill, 1986; Debussche *et al.*, 1987; Herrera, 1987; Debussche, 1988). However, only fruit size among another 15 fruit traits examined by Jordano (1995a; see Appendix to this chapter) was associated with a major type of seed disperser when accounting for phylogenetic affinities in a comparative analysis of a large data set of angiosperms.

Nutrient content of the pulp

Comparative studies of the nutrient content of fleshy fruits have revealed that most variation in components can be explained by a few major patterns of covariation that have a major correlate with phylogeny, especially at the family and genus level (Jordano, 1995a). Herrera (1987) found, by means of factor analysis, that 46.5% of the variance in nutrient content among 111 species of the Iberian Peninsula was accounted for by the strong negative correlation between lipid and non-structural carbohydrate (NSC) content; three additional factors accounted for 51.1% of variance. Therefore, rather than the succulence continuum suggested by some authors, pulp composition patterns included: high lipid–low NSC–low fibre; low lipid–high NSC–low fibre; and medium lipid–medium NSC–high fibre. Variation in protein and water content was independent of these pulp types. Similar patterns have been described by other authors (Wheelwright *et al.*, 1984; Gautier-Hion *et al.*, 1985b; Johnson *et al.*, 1985; O'Dowd and Gill, 1986; Debussche *et al.*, 1987; Jordano, 1995a) and are probably caused by the great variation in lipid content among angiosperm fruit pulps relative to other constituents and its strong inverse correlation with carbohydrate content.

The pulp of fruits has been considered repeatedly as deficient in certain nutrients, especially nitrogen and protein (Snow, 1971; Morton, 1973; White, 1974; Berthold, 1977; Thomas, 1984). Relative to other dietary items usually consumed by verte-

brate frugivores (Table 6.3; Appendix to this chapter), the fruit pulp shows the highest concentration of soluble carbohydrates and the lowest relative amount of protein. Lipid content is relatively high but shows extreme interspecific variation. The importance of the mineral fraction is relatively constant among food types, but the content of particular cations is very variable (Nagy and Milton, 1979; Piper, 1986b; Herrera, 1987; Pannell and Koziol, 1987). Fruits are extremely poor in protein in comparison with leaves and insects. However, their energetic value in terms of soluble carbohydrates and lipids exceeds that of any other food type (Table 6.3). Therefore, the combination of traits that best characterizes the fruit pulp nutritive content is the excess of digestible energy relative to protein, the high water content and the extreme deficiency in some compounds relative to others (i.e. imbalance between components).

The Appendix to this chapter summarizes most of the information available at present on the nutrient content of the pulp of the main angiosperm families dispersed by vertebrate frugivores. Detailed reports for local or regional floras include, among others: Hladik *et al.* (1971); Sherburne (1972); White (1974); Crome (1975); Frost (1980); Stiles (1980); Viljoen (1983); Wheelwright *et al.* (1984); Johnson *et al.* (1985); O'Dowd and Gill (1986); Piper (1986b); Debussche *et al.* (1987); Herrera (1987); Fleming (1988); Snow and Snow (1988); Eriksson and Ehrlén (1991); Hughes *et al.* (1993); Corlett (1996); Witmer (1996); Heiduck (1997); Ko *et al.* (1998).

In the case of frugivorous birds, virtually nothing is known about the protein demand in natural conditions, although recent efforts have been made to understand the nutritional limitations of fruits (Sorensen, 1984; Karasov and Levey, 1990; Martínez del Rio and Karasov, 1990; Levey and Grajal, 1991; Levey and Duke, 1992; Witmer, 1996, 1998a; Witmer and van Soest, 1998). Information available, mostly from domestic, granivorous species, indicates that a diet with 4–8% protein (wet mass) is necessary for maintenance (several authors cited in Moermond and Denslow,

Table 6.3. Summary of nutrient contents of different food types consumed by vertebrate frugivores. Figures are mean and range of % of each component relative to dry mass. Data for seeds refer to wet mass.

Food type	Water	Protein	Lipids	Non-structural carbohydrates	Minerals
Insects ¹	63.7 (56.8–70.4)	68.3 (59.9–75.9)	16.8 (9.4–21.2)	14.9 (0.5–20.0)	8.9 (3.1–19.0)
Seeds ²	11 (4–12)	11 (6–14)	4 (0.3–9)	69 (61–73)	2.2 (1.1–5.3)
Neotropical fruits ³	71.3 (38.0–95.2)	7.8 (1.2–24.5)	18.5 (0.7–63.9)	67.8 (5.6–98.3)	5.6 (1.3–19.4)
Mediterranean fruits ⁴	69.9 (36.9–90.1)	6.4 (2.5–27.7)	9.0 (3.7–58.8)	80.1 (33.2–93.7)	4.6 (1.1–13.1)
Mature leaves ⁵	59.4 (46.2–76.2)	12.6 (7.1–26.1)	3.3 (0.7–10.7)	6.9 (1.9–14.7)	4.9 (1.5–11.3)
Young leaves ⁵	71.9 (54.0–82.3)	18.2 (7.8–36.3)	3.2 (0.7–6.3)	15.4 (1.8–32.7)	5.0 (3.4–7.5)

References: ¹, White (1974); ², Jenkins (1969) cited in Moermond and Denslow (1985); ³, see references in Appendix; ⁴, Herrera (1987); ⁵, Hladik (1978); Oates (1978); Oates *et al.* (1980); Waterman *et al.* (1980).

1985), by providing a daily consumption of 0.43 g N kg^{-0.75} day⁻¹ (Robbins, 1983). Considering that the high amount of water in the pulp of fleshy fruits acts as a 'solvent' of the included nutrients, most fruits contain amounts of protein, relative to dry mass of pulp, within the limits adequate for maintenance. Thus, average protein content for a sample of angiosperm fleshy fruits (Appendix to this chapter) is 6.12 ± 4.47% (mean ± SD, *n* = 477 species), ranging between 0.1 and 27.7%.

These nutrient levels are adequate if the fruit supply in nature is not limiting, but this is an infrequent situation (Foster, 1977; Witmer, 1996, 1998a). Dinerstein (1986) found that the protein content of the fruits consumed by frugivorous bats (*Artibeus*, *Sturnira*) in Costa Rican cloud forest (mean = 6.7% protein, dry mass) was apparently sufficient to sustain the protein demands of lactating females; otherwise females could be depending on previously accumulated protein reserves. The data available regarding *Carollia perspicillata* (Herbst, 1986; Fleming, 1988) indicate that dietary mixing of a protein-rich fruit, such as *Piper* spp. (*Piperaceae*) and an energy-rich fruit, such as *Cecropia peltata* (*Cecropiaceae*), adequately balanced the daily net energy and nitrogen requirements. In contrast to these

phyllostomid bats, totally frugivorous pteropodid bats relying on low-quality *Ficus* fruit food (less than 4.0% protein, dry mass) obtain sufficient protein by overingesting energy from fruits, but are unable to supplement this diet with animal prey (Thomas, 1984). In other pteropodids (*Rousettus*), Korine *et al.* (1996) reported a positive nitrogen balance on a totally fruit diet due to exceptionally low nitrogen demands (55% lower than expected from allometry), apparently as an adaptation to periods of low fruit availability. Overingestion of energy to meet the protein needs has been reported for the totally frugivorous oilbird *Steatornis caripensis* (Steatornithidae) (White, 1974). Early findings by Berthold (1976) that lipids and protein in fruits were insufficient for maintenance and migratory fat deposition by warblers (*Sylvia* spp.) have been challenged by the experiments of Simons and Bairlein (1990) demonstrating significant body mass gain by *Sylvia borin* when fed on a totally frugivorous diet, although additional work has confirmed loss of body mass and nitrogen on diets of sugary fruits for some species (Izhaki and Safriel, 1989; Witmer, 1996, 1998a; Witmer and van Soest, 1998). Several studies reveal a positive nitrogen balance of specialized frugivorous birds, such as phainopeplas or

waxwings, when feeding on fruits with a protein content greater than 7.0% dry mass (Walsberg, 1975; Berthold and Moggingen, 1976; Studier *et al.*, 1988; Witmer, 1998a).

Therefore, the poor value of fruits as a unique food largely results from the internal imbalance of major nutritive components relative to others – basically the extreme protein and nitrogen deficiency relative to energy content. Thus, it is paradoxical that certain neotropical fruits, qualified as highly nutritious, had calorie:protein ratios greater than 1500 (Moermond and Denslow, 1985), when others, considered as poor (*Rubiaceae*, *Melastomataceae*), had ratios more similar to those of insects. The main effect of these types of relative deficiencies for frugivorous animals is that the assimilation of a particular nutrient can be limited by the impossibility of processing enough food material to obtain it, and not by the scarcity of the nutrient itself. That is, the effect is due to a digestive bottleneck (Kenward and Sibly, 1977; Sibly, 1981). Consumption of minor amounts of animal prey provides the necessary nitrogen input to escape the constraint imposed by the overingestion of energy, as demonstrated by field studies of phyllostomid bats and frugivorous warblers (Fleming, 1988; Jordano, 1988; see also Bowen *et al.*, 1995).

Direct interaction among different components present in the pulp, such as secondary metabolites, can limit nutrient digestibility and assimilation (Herrera, 1981a; Izhaki and Safriel, 1989; Mack, 1990; Cipollini and Levey, 1992, 1997). The presence of tannins, together with alkaloids and saponins, is particularly frequent among Mediterranean species (Jordano, 1988, and references therein). The presence of tannins in the pulp may cause lower assimilation of proteins and damage the digestive epithelium (Hudson *et al.*, 1971; Swain, 1979). Experiments by Sherburne (1972) demonstrate that other types of secondary compounds, such as glycosides or alkaloids, have a direct effect on frugivore foraging by preventing feeding or drastically reducing the palatability of unripe fruits. However, little is known

about the effects of metabolites that act like tannins and phenols, reducing the assimilation efficiency (Izhaki and Safriel, 1989; Mack, 1990; Cipollini and Levey, 1997).

Finally, the content in the fruit pulp of cations and microelements, such as calcium, phosphorus, iron, manganese and zinc, is frequently below the requirements of frugivorous birds, and situations of negative balance in wild birds have been reported (Studier *et al.*, 1988). These types of effects should be controlled in experiments assessing the nutritional limitation of fruit food for frugivores.

Frugivory

Frugivory appears to be a feeding mode that is open to many types of organisms. No special adaptations, such as deep beaks or special digestive processing of the ingesta, are necessary to consume fruit, but certain morphological, anatomical and physiological characteristics determine an animal's ability to rely extensively on fruit food. The purpose of this section is to review patterns of anatomical and physiological variation associated with exclusive or extensive frugivory.

At least three basic types of frugivory can be defined, relative to their potential consequences for seed dispersal. First, legitimate dispersers swallow whole fruits and defecate or regurgitate seeds intact. Secondly, pulp consumers tear off pulp pieces while the fruit is attached to its peduncle, or they mandibulate the fruits and ingest only the pulp by working the seed(s) out. Finally, seed predators may extract seeds from fruits, discard the pulp, crack the seed and ingest its contents or can swallow whole fruits and digest both pulp and seeds. From the plant's perspective, these categories define a wide gradient of seed dispersal 'quality' (Snow, 1971; McKey, 1975; Howe, 1993; Schupp, 1993), from frugivores that deliver seeds unharmed (dispersers) to those that destroy seeds (granivores), with no clear-cut limits between them (Jordano and Schupp, 2000). Single traits, such as body size, wing form or

bill width, are not satisfactory predictors of frugivory intensity or the type of frugivorous behaviour shown by a species, and simultaneous consideration of a number of traits is needed. Herrera (1984a) found that a multiple discriminant analysis of body mass and six ratios describing bill shape accurately predicted the assignment of Mediterranean scrubland birds to three frugivory types. Seed dispersers showed larger body size and flatter and wider bills than non-frugivores and pulp/seed consumers. Consumers of pulp that discarded the seeds beneath the plants (finches, emberizids and parids) were characterized by smaller size, deeper beaks and narrower gapes. Non-frugivores showed more slender bills than the other two groups. Actually, species of seed dispersers, pulp/seed consumers and non-frugivores occupy a continuum along the discriminant function, emphasizing the absence of clear limits between categories.

Whether a given frugivore behaves as a seed disperser, pulp consumer or seed predator in a particular interaction with plants is not only dependent on frugivore ecomorphology and behaviour, but also on fruit characteristics (especially seed size) of the plants in the specific situation. Detailed descriptions of these categories and associated behavioural patterns are given by, among others: Hladik and Hladik (1967); Hladik (1981); Janzen (1981a, b, c, 1982); Fleming (1982); Herrera (1984c); Moermond and Denslow (1985); Levey (1986, 1987); Bonaccorso and Gush (1987); Snow and Snow (1988); Bodmer (1989a); Corlett and Lucas (1990); Green (1993); Corlett (1998); Jordano and Schupp (2000). It is apparent from these studies that the different types of frugivory are present in all groups of vertebrate frugivores, but in markedly different proportions.

Anatomical characteristics of frugivores

Frugivore size and form

Body mass is a major determinant of intensity of frugivory. The relative importance of

fruit in the diet of Mediterranean passerines is strongly correlated with body mass (Herrera, 1984a, 1995; Jordano, 1984, 1987c). Smaller birds, such as those in genera *Phylloscopus*, *Saxicola*, *Hippolais* and *Acrocephalus*, only sporadically consume fruits. Fruit makes up 30–70% of diet volume among medium-sized *Phoenicurus*, *Luscinia*, the smaller *Sylvia* warblers and *Erithacus* and always more than 80% in the larger species (*Sylvia atricapilla*, *S. borin*, *Turdus* spp., *Cyanopica cyanus* and *Sturnus* spp.). Katusic-Malmborg and Willson (1988) found a similar relationship for eastern North American frugivorous birds, but Willson (1986) found no consistent differences in body size between frugivores and non-frugivores in a number of habitats in this region.

Body size affects frugivory intensity by limiting the maximum number of fruits that can be swallowed or otherwise processed in feeding bouts (e.g. during short visits to plants) and the maximum amount of pulp mass that can be maintained within the gut, since gut capacity is strongly correlated with body mass. Thus, average number of fruits ingested per feeding visit to *Prunus mahaleb* plants is 1.5 for *Phoenicurus ochruros* (16.0 g), 9.0 for *Turdus viscivorus* (107.5 g), and 21.0 for *Columba palumbus* (460.0 g) (Jordano and Schupp, 2000). The number of fruits consumed per visit by frugivorous birds has been found to be strongly correlated with body mass in a number of studies (Fig. 6.4). Therefore, body size alone sets an upper limit to the potential maximum number of seeds that a given frugivore can disperse after a feeding bout. Note that sporadic visits by large frugivores can have a far greater effect on crop removal than consistent visitation by small frugivores, but the net result on seed dispersal also depends on differences in postforaging movements between small and large frugivores (Schupp, 1993).

Body size differs markedly among species showing different types of frugivory, and influences fruit and seed handling prior to ingestion or immediately after it. Usually, small species tend to be

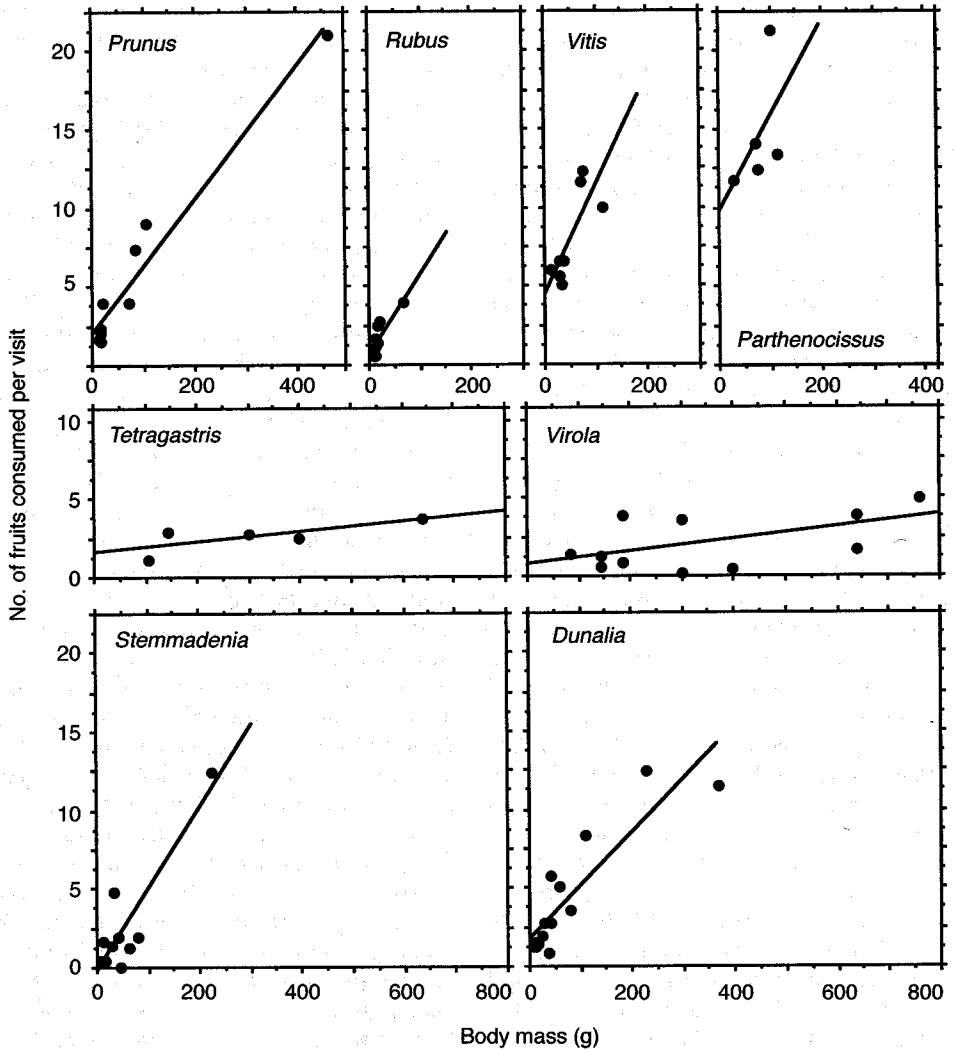


Fig. 6.4. Relationship between number of fruits consumed per visit and body mass of frugivorous birds in different plant species. Data from Jordano (1982) (*Rubus ulmifolius*); Howe and Vande Kerckhove (1981) (*Virola surinamensis*); Howe (1980) (*Tetragastris panamensis*); McDiarmid *et al.* (1977) (*Stemmadenia donnell-smithii*); Cruz (1981) (*Dunalia arborescens*); P. Jordano (unpublished data) (*Prunus mahaleb*) and Katusic-Malmberg and Willson (1988) (*Vitis vulpina* and *Parthenocissus quinquefolia*).

pulp consumers rather than legitimate dispersers, mostly though their inability to handle fruits efficiently and swallow them intact. Thus, fruit and seed swallowing among frugivorous primates is restricted to large hominoids and cebids (Corlett and Lucas, 1990); smaller species either spit out seeds (some cercopithecines; but see Kaplin and Moermond, 1998) or consume

only pulp and discard seeds (Terborgh, 1983), although some small species, such as *Saguinus*, can swallow very large seeds (Garber, 1986).

The use by frugivores of different foraging manoeuvres to reach fruits on plants is constrained by external morphology and body proportions, which can be considered in most cases as preadaptations to other

forms of prey use. Fitzpatrick (1980) showed that fruit use among tyrannid flycatchers is restricted to three groups of genera, with generalist foraging modes and fruit-feeding techniques that reflect the typical insect-foraging manoeuvres. Among Mediterranean frugivorous birds, the relative importance of fruits in the diet is significantly larger for foliage-gleaning species than for those with more specialized or stereotyped means of prey capture, such as sallyers, flycatchers and trunk foragers (Jordano, 1981). Therefore, it is reasonable to conclude that the ecomorphological configuration of a species is a preadaptation limiting feeding on fruit food, especially for those partial frugivores that consume other prey types; functional and behavioural predisposition, rather than specific adaptations, is expected (Herrera, 1984a; but see Moermond and Denslow, 1985).

Differences in fruit capture modes among frugivores show strong ecomorphological correlations, especially with wing morphology, bill form or dental characteristics and locomotory morphology (Hylander, 1975; Karr and James, 1975; Moermond and Denslow, 1985; Moermond *et al.*, 1986; Bonaccorso and Gush, 1987; Levey, 1987; Snow and Snow, 1988; Corlett and Lucas, 1990). Fleming (1988) reported relatively more elongated wings and higher wing loadings (g cm^{-2} of wing surface) among plant-visiting phyllostomid bats, which are more able to perform rapid, straight flights and hovering than insectivorous or carnivorous species. Frugivorous bats are quite conservative in the way they reach fruits, major differences being found in fruit handling and postforaging movements. The ecomorphological patterns that define the patterns of habitat selection among groups of these species (canopy-dwelling stenodermines and ground-storey carollines and glossophagines) strongly influence frugivory patterns, fruit selectivity and fruit-foraging behaviour (Bonaccorso and Gush, 1987; Fleming, 1988; see also Marshall and McWilliam (1982) and Marshall (1983) for information on Old World pteropodids).

Among frugivorous birds, fruits may be taken from a perch or on the wing (Herrera

and Jordano, 1981; Moermond and Denslow, 1985; Foster, 1987; Snow and Snow, 1988; Jordano and Schupp, 2000). Ground-foraging frugivorous birds are larger and rarely use branches (Erard and Sabatier, 1988), but some perching species also forage for fruits on the ground (e.g. *Turdus* spp.; Snow and Snow, 1988). The description that follows relies heavily on detailed accounts and experiments reported by Denslow and Moermond (1982); Levey *et al.* (1984); Santana and Milligan (1984); Moermond and Denslow (1985); Levey (1986, 1987); Moermond *et al.* (1986); Foster (1987); Snow and Snow (1988); Green (1993); and Jordano and Schupp (2000). In addition to reaching from a perch, Moermond and Denslow (1985) describe four distinct flight manoeuvres by which birds pluck fruits: hovering, the method used by manakins, flycatchers and small tanagers; stalling, used by trogons and similar to hovering; and swooping and stalling, involving a continuous movement from perch to perch plucking the fruit on the way, which is the method used by most cotingids; and taking fruit from perches by picking, reaching and hanging. The first two manoeuvres are the two most commonly used, but those species that take most fruit on the wing are unable to reach well from a perch.

From the plant's perspective, the patterns described above have important implications for seed dispersal. These studies demonstrated that consistent choices between fruit species are made by foraging birds, based on accessibility restrictions that set different foraging costs, depending on anatomical characteristics. Consequences for seed dispersal are important, because small changes in accessibility override preferences for particular fruits; hence non-preferred fruits are consumed when accessibility to preferred fruits decreases. Other things being equal, decreasing fruit accessibility to legitimate dispersers would increase fruit retention time on branches and increase the probability of resulting damage or consumption by non-disperser frugivores (Denslow and Moermond, 1982; Jordano, 1987a). The ability to access and

pick fruits of a given species by different frugivores varies, depending on the positions of the fruits within the infructescence or their locations relative to the nearest perch (and the thickness of that perch). In turn, differences in feeding techniques may influence dietary diversity by affecting which specific types of fruit displays are accessible. For example, frugivorous birds that take fruit on the wing show lower diet diversity and are more selective than species that pick fruits from perches (Wheelwright, 1983; Levey *et al.*, 1984; Wheelwright *et al.*, 1984; Moermond *et al.*, 1986). An ecomorphologically diverse array of visitors might result in a more thorough removal of the crop if different species predominantly take fruits from different positions in the canopy differing in accessibility to their foraging mode (Kantak, 1979; Herrera and Jordano, 1981; Santana and Milligan, 1984; Jordano and Schupp, 2000). In addition, if microhabitat selection is related to ecomorphological variation, individual trees differing in their relative position within a given habitat can differ markedly in the particular frugivore assemblage visiting the tree (see, for example, Manasse and Howe, 1983; Traveset, 1994).

Once the fruit is plucked, differences in dental characteristics, mouth size and bill shape among frugivores have important consequences for external seed treatment and seed dispersal. Two basic handling modes, gulping and mashing, originally described for frugivorous birds (Levey, 1987), can probably be expanded to accommodate fruit handling behaviour by most vertebrate frugivores. For example, phyllostomid bats (*Artibeus* spp.) take single bites out of fruits (*Ficus* spp.), slowly masticating the pulp and then pressing the food bolus against the palate with the tongue; thus, they squeeze the juice and expectorate the pulp along with seeds (Morrison, 1980; Bonaccorso and Gush, 1987). In contrast, *Carollia* spp. masticate the pulp and swallow it along with the seeds and discard the fruit skin (Bonaccorso and Gush, 1987; Fleming, 1988). Both behaviours are functionally similar to mashing, but the consequences

for the plant depend on frugivore movement after fruit plucking. Many ungulates swallow whole fruits and defecate seeds (Alexandre, 1978; Merz, 1981; Short, 1981; Lieberman *et al.*, 1987; Dinerstein and Wemmer, 1988; Bodmer, 1989b; Sukumar, 1990; Chapman *et al.*, 1992a; Fragoso, 1997) and others spit out seeds (Janzen, 1981c, 1982). Seed spitting is a common behaviour among primates, especially cercopithecines, which use cheek pouches to store food and later spit out the seeds, but whether a particular seed is defecated, spat out or destroyed is strongly dependent upon seed size and fruit structure (Corlett and Lucas, 1990; Tutin *et al.*, 1996; Kaplin and Moermond, 1998). New World apes (ceboids) and Old World hominoids apparently swallow and defecate most seeds intact (Hladik and Hladik, 1967; Hladik *et al.*, 1971; Hladik, 1981; Garber, 1986; Idani, 1986; Janson *et al.*, 1986; Rogers *et al.*, 1990; Tutin *et al.*, 1991, 1996; Wrangham *et al.*, 1994; Corlett, 1998), but some species mash fruits or tear off pulp pieces and can spit out or destroy seeds (Howe, 1980; Terborgh, 1983). Colobines and some cercopithecines destroy most seeds they consume (McKey *et al.*, 1981; Davies *et al.*, 1988), but at least some *Cercopithecus* can disperse relatively large seeds by dropping or defecating them unharmed (Kaplin and Moermond, 1998).

In summary, frugivore ecomorphology *per se* determines, from the plant perspective, the position of each frugivore species along a gradient ranging between zero and 1.0 survival probability for the seeds after interaction; and the main result of the studies discussed above is that vertebrate frugivore ecomorphologies are not distributed at random over this gradient.

Digestion of fruits

The bizarre digestive structures of some specialized frugivorous birds were documented long ago by ornithologists (Forbes, 1880; Wetmore, 1914; Wood, 1924; Desselberger, 1931; Cadow, 1933; Docters van Leeuwen, 1954; Walsberg, 1975;

Decoux, 1976). Typically, in birds, an oesophagus, which may or may not be dilated into a crop, is continued in a stomach, with a glandular proventriculus and a muscular ventriculus or gizzard. Common traits of modified digestive systems of frugivorous birds (Fig. 6.5; also including *Ducula* and *Ptilinopus* pigeons (Cadow, 1933) are: (i) absence or extreme reduction and simplification of the crop and/or proventriculus; (ii) presence of a thin-walled, non-muscular gizzard; (iii) lateral position of the simplified gizzard as a 'diverticulum' and an almost direct continuation of the oesophagus into the duodenum; and (iv) short intestines relative to body size. Despite the absence of a distinct crop, some specialized frugivorous birds, such as waxwings, can store fruits in the distensible oesophagus (Levey and Duke, 1992). This ability to store fruits oral to the gizzard somewhat offsets the problem of process-rate limitation, by allowing ingestion of two meals of fruit in a single foraging bout. Frugivorous bats also show a

typical stomachal structure, where the oesophagus leads into a cardiac vestibule and the rest of the stomach is an elongated tube, with a conspicuous, large, fundic caecum (Bhide, 1980, and references therein; see also Fleming, 1988).

Extreme diversification is also found in the anatomy of the digestive tract among non-volant, mammalian frugivores (Langer, 1986). Apart from ruminant artiodactyls, which consume fleshy fruits only sporadically (Bodmer, 1990), the digestive processing by non-ruminant frugivores differs chiefly between foregut and hindgut fermenters. To my knowledge, no comparative assessment has been made of the differential consequences for seed survival within the gut between these two types of digestive strategies (but see Bodmer, 1989a) and what fruit or seed traits, if any, are consistently associated with safe seed delivery by these frugivorous mammals. However, it is well known that fore-stomach fermenters usually crack seeds before ingestion (e.g. some colobine monkeys and

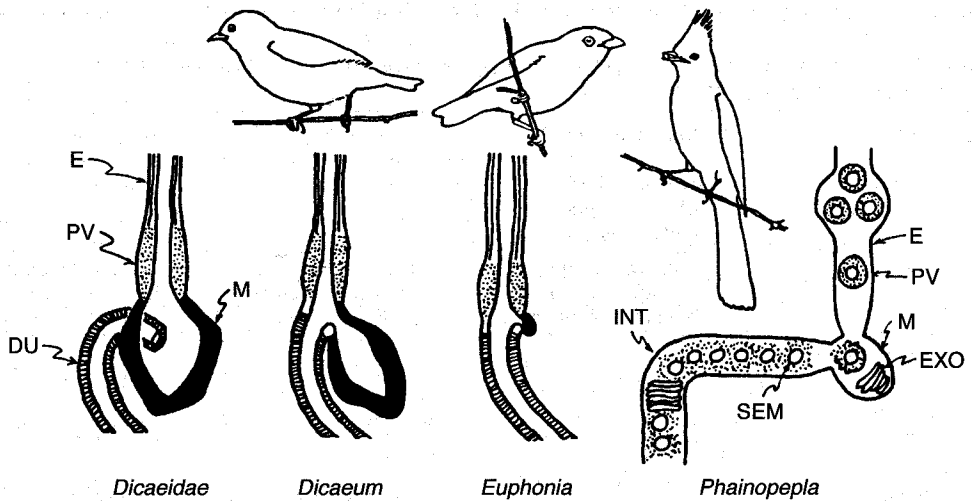


Fig. 6.5. Schematic representation of several types of proventriculus and gizzard configurations in specialized frugivorous birds. Left, arrangement of a relatively differentiated 'normal' muscular gizzard (M) stomach and associated oesophagus (E), proventriculus (PV) and duodenum (DU) in insectivorous Dicaeidae (after Desselberger, 1931). Note the normal approximation of the cardiac and pyloric ends of the stomach similar to most birds. Extreme simplification of the gizzard, with thinner walls and lack of hard epithelium and location of the gizzard as a lateral diverticulum along the oesophagus-duodenum axis is characteristic of frugivorous dicaeids (*Dicaeum*) and *Euphonia* tanagers (Forbes, 1880). Right: arrangement in phainopeplas (*Phainopepla nitens*), with schematic view of ingested fruits, exocarps (EXO) being accumulated in the simplified gizzard and seeds (SEM) passing to the small intestine (INT) (after Walsberg, 1975).

peccaries) and some hindgut fermenters also destroy most seeds they ingest (e.g. tapirs and suids: Janzen, 1981a; Corlett, 1998).

These digestive patterns are perhaps extreme examples of specialization not found in partial frugivores. Pulliainen *et al.* (1981) examined the digestive systems of three European granivorous birds and three seed dispersers and found no difference, except for *Bombycilla garrulus*, which is a specialized frugivore (Berthold and Moggingen, 1976; Voronov and Voronov, 1978), which showed the largest liver mass. Eriksson and Nummi (1982) reported higher liver activity and detoxification ability in *B. garrulus* relative to granivorous and omnivorous species. However, Herrera (1984a) showed no significant differences in relative mass of gizzard, liver and relative intestine length among avian seed dispersers, pulp/seed predators and non-frugivores (for additional data, see Magnan, 1912; Cvitanic, 1970). The largest livers were found among muscicapid warblers and would have preadapted them to frugivory by enabling efficient detoxification

of the secondary metabolites present in the pulp. In addition, a closer examination of variation in frugivory among six *Sylvia* warblers (Jordano, 1987b) revealed that most variation in fruit consumption across species was accountable by considering only external morphology. Functional modulation of gut morphology allowing constant digesta retention and extraction efficiency usually require prolonged time periods and do not seem alternatives open to frugivores, which frequently face local and short-term changes in fruit supply (Karasov, 1996; McWilliams and Karasov, 1998). Therefore, rather than elaborate morphological transformations, one finds more functional compensatory modulations to digest a soft, dilute food with low nutrient density that has a large energy content relative to protein (Herrera, 1984a; Moermond and Denslow, 1985; Karasov and Levey, 1990; Afik and Karasov, 1995; Karasov, 1996).

There are marked functional differences among different diet types from the perspective of the digestion process (Table 6.4). Ruminant diets are characteristically

Table 6.4. Some characteristics of ruminant, carnivore and frugivore diets from the perspective of digestive physiology (modified after Morris and Rogers, 1983).

Characteristics	Ruminant diets	Animal prey	Frugivore diets
Nature of diet	Structural and photosynthetic parts of plants	Animal tissue	Fruit pulp
Digestibility	Cell-wall components are refractory to mammalian enzymes	Readily digested by mammalian and avian enzymes	Readily digested, but presence of indigestible seeds
Food passage through the gut	Very slow	Slow	Very rapid
Organic matter digestibility (%)	Most forages < 65	> 85	c. 60–80
Presence of natural toxins	Generalized	None in species normally eaten	Generalized
Proximate constituents of the diet:			
Lipids	Low	High	Variable–low
Protein	Low (generally)	Very high	Very low
Non-structural carbohydrates	Low	Very low	Very high
Structural carbohydrates	Very high	Absent	Variable–low

high in structural hexose and pentose polymers, which require special pregastric microbial digestion, which, in addition, detoxifies many secondary plant substances (Morris and Rogers, 1983). In contrast with this slow digestion process, the digestive processing of the fruit pulp is much more rapid and more similar to digestion of vegetative plant parts by non-ruminant herbivores. In general, both forage and fruit diets show much lower digestibilities than diets based on animal prey. In addition, a sizeable fraction of the fruit food mass ingested by frugivores (the seeds) is actually indigestible and causes gut displacement (Levey and Grajal, 1991; Witmer, 1998b). Herbivore diets, and fruits are no exception, pose a frequent problem by creating digestive bottlenecks (Kenward and Sibly, 1977), which prevent frugivores from increasing fruit intake to compensate for low fruit quality. The energy requirements can be adequately met, but the food-processing rate is too slow to meet the demand for micronutrients and nitrogen, which are deficient in the fruit pulp, and an alternative source is needed (Foster, 1978; Moermond and Denslow, 1985).

Frugivores, as monogastric herbivores, base their feeding on rapid processing of their poor-quality food and maximization of ingestion rate. They thus appear to be process-rate-limited, because ingestion rate is limited by the processing of the previous meal (Sorensen, 1984; Worthington, 1989; Levey and Grajal, 1991; Levey and Duke, 1992). Throughput rate – the rate of flow of digesta past a specified point in the gut – is a function of both gut capacity (intestine length) and food retention time (Sibly, 1981; Hume, 1989; Levey and Grajal, 1991). Rapid processing of separate pulp and seed fractions, rapid passage of seeds, partial emptying of the rectal contents, rectal antiperistalsis and nutrient uptake in the rectum are all characteristics of the digestive process of frugivores to cope with nutrient-poor fruit pulp (Levey and Duke, 1992). For frugivores that defecate seeds, high throughput rates of indigestible seeds must be achieved, with minimum costs for pulp digestion and assimilation. Karasov

and Levey (1990) have demonstrated that this cost exists as a lower digestive efficiency, due to the absence of compensatory high rates of digestive nutrient transport, among frugivores (but see Witmer, 1998b). In consequence, an important functional adaptation among strong frugivores would be a relatively large gut (e.g. long intestine) and extremely short throughput times; therefore, nutrient assimilation is maximized with high throughput rates. Holding constant the throughput rate, a larger gut allows processing of a greater volume of digesta at the same processing speed.

Among strongly frugivorous vertebrate species, high throughput rates are achieved by extreme shortening of throughput times (e.g. Turcek, 1961; Milton, 1981; Sorensen, 1983; Herrera, 1984a; Levey, 1986, 1987; Jordano, 1987b; Worthington, 1989; Karasov and Levey, 1990; Levey and Grajal, 1991). Seeds are processed much more quickly than pulp, either by rapid regurgitation or by 'selective' processing and defecation (but see Levey and Duke, 1992), indicating that they limit fruit processing by gut displacement and that frugivores void them selectively in order to maximize gut capacity for digestible pulp. Time to regurgitate seeds by frugivorous birds is very rapid, frequently 5–20 min, while throughput times for seed defecation are much longer, usually in the range of 0.3–1.5 h (Levey, 1986; Snow and Snow, 1988; Worthington, 1989; Levey and Grajal, 1991). In some species, such as the phainopeplas (Fig. 6.5), an active mechanism for selective pulp retention is used; but, in most instances, differences in throughput times might be caused by the differences in specific gravity between pulp and seeds.

Relative intestine length is greater among Mediterranean frugivorous *Sylvia* warblers than among non-frugivorous muscicapid warblers (Jordano, 1987b), although gut passage time is shorter in the former. For a sample of Mediterranean scrubland frugivorous passerines, variation across species in the relative importance of fruit in the diet is positively correlated with food throughput rate (Fig. 6.6), indicating that the ability to modulate retention

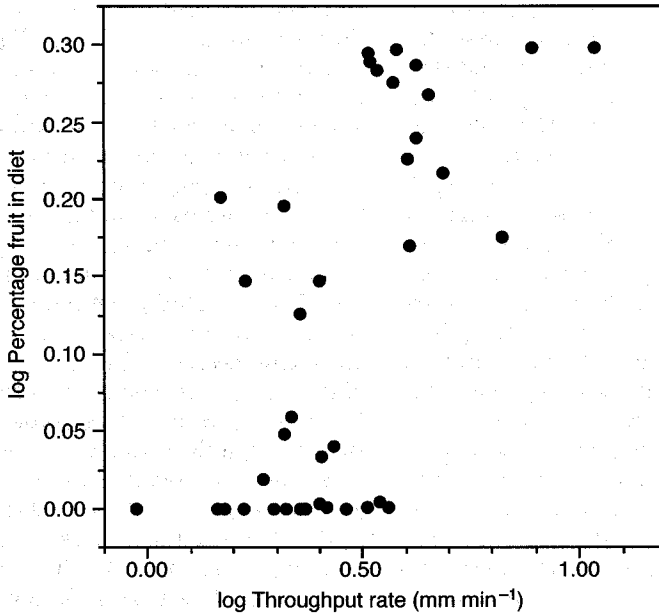


Fig. 6.6. Relationship between relative importance of fruits in the diet of several Mediterranean scrubland passerine birds (as percentage of total diet made up by fruits) and food passage rate (mm min^{-1}), the quotient of intestine length divided by gut passage time. Species ($n = 38$) include *Turdus* spp., *Sylvia* spp., *Phoenicurus phoenicurus*, *Muscicapa striata*, *Ficedula hypoleuca*, *Erithacus rubecula*. Regression fit is $y = 1.539 + 0.041x$ ($r^2 = 0.465$; $F = 8.69$; $P = 0.015$).

time of digesta to achieve a high throughput rate might be important for sustained frugivory. Similarly, McWilliams and Karasov (1998) reported that compensatory modulation of retention time or digesta mixing (and not rate of hydrolysis and absorption) explained the remarkably constant digestive efficiency in waxwings exposed to varied fruit-feeding costs.

Evidence that the size of indigestible seed material limits feeding rates by causing gut displacement and represents an important foraging cost for frugivores mostly comes from observations in captivity (Bonaccorso and Gush, 1987; Levey, 1987; Fleming, 1988; Snow and Snow, 1988; Corlett and Lucas, 1990; Levey and Duke, 1992; but see Witmer, 1998b), which revealed: (i) negative correlations between seed size and the number of seeds ingested per feeding bout; (ii) continuous feeding rates of birds and bats, resulting in at least one ingested seed retained in the gut; (iii) selective throughput times for seeds and pulp; and (iv) immediate consumption of

new fruits after defecation or regurgitation, implying that ingested seeds in the crop limited ingestion of additional fruits. Apparently, however, frugivores might compensate for these costs to achieve adequate intake of basic nutrients (Levey and Duke, 1992; Witmer, 1998b; Witmer and van Soest, 1998). These costs of the internal handling of seed ballast are obviously overcome by frugivorous mashers and spitters, as well as by pulp predators, which manage seeds externally; however, these frugivores have increased handling costs and lower rates of pulp ingestion per fruit handled.

Foraging for fruits and seed transport

Most seed movement away from the parent trees of fleshy-fruited species is a direct consequence of movement patterns by frugivores. Frugivore movements take place on a habitat template with numerous microhabitats, patches, safe sites or other

potential 'targets' for seed delivery. These patches differ in potential 'quality' for plant recruitment, measured as the probabilities for early survival of seeds, germination and seedling establishment (Schupp, 1993). From the plant perspective, the potential evolutionary and demographic relevance of the interaction with a particular disperser depends on the number of seeds it moves and how they are delivered over this habitat template, which includes a non-random distribution of patches of variable probability for the establishment and survival of the plant propagules. Therefore, the two main aspects of frugivory that influence the resulting seed dispersal are the seed-processing behaviour (both external and digestive) and the ranging behaviour of the frugivore (Schupp, 1993; Jordano and Schupp, 2000). The former determines the number of seeds that are transported and delivered unharmed, in conditions adequate for germination; the latter defines the potential range of microsites that will intercept delivered seeds. The aim of this final section is to review how the fruit and frugivore characteristics previously considered interact and result in seed deposition patterns with implications for differential seed and seedling survival.

The spatial pattern of seed fall in zoochorous species, i.e. the seed shadow, is a function of the species of frugivore eating the fruit, its movement rates and its seed throughput rates (Hoppes, 1987; Murray, 1988; see also Willson and Traveset, Chapter 4, this volume). Note that two of the factors, namely the species identity and the seed throughput rates, can be expected to remain more or less invariant in their effect on the seed shadow independently of the particular ecological context (e.g. fruit-handling patterns, defecation rates, fruit-capture behaviours and other characteristics of the frugivore). In contrast, movement rates, which depend on movements between foraging locations and the distances between these locations, are much more 'context sensitive' and dependent on the particular ecological situation.

Fruit processing and seed deposition

Fruit processing by frugivores determines how many seeds are delivered to potential safe sites in an unharmed condition. Two important components of fruit processing are the number of fruits handled and the probability that seeds survive the fruit handling by the frugivore. If the number of safe sites increases with distance from parent plants or if the probability of seed and early seedling survival increases with distance, an important component of seed processing will be how fast seeds are delivered after fruit capture.

A typical feeding bout for most frugivores, especially small-sized temperate and tropical birds and phyllostomid bats, includes consumption of one or a few fruits during discrete visits to individual plants that occur along foraging sequences (Herrera and Jordano, 1981; Fleming, 1988; Snow and Snow, 1988; Green, 1993; Sun and Moermond, 1997; Jordano and Schupp, 2000). The resulting pattern of seed delivery will differ markedly between species that process fruits through the digestive tract and defecate seeds and those that process seeds orally by spitting, regurgitating or mashing prior to ingestion. These two general types of seed-processing behaviours are present in most communities and differ in their immediate consequences for seed delivery. I must emphasize here that they do not represent a dichotomy of frugivore strategies but rather a continuum gradient of seed-processing rate (e.g. the number of viable seeds delivered per unit foraging time). Even the same frugivore species can be ranked in different positions along this gradient when interacting with different plant species.

Rapid processing of seeds by frugivores that mash or spit out seeds involves mastication and slow mandibulation of the fruit to separate the pulp from the seeds prior to ingestion, and this usually results in increased risk of seed damage by cracking of the endocarp, excessive mechanical scarification, etc. (Hylander, 1975; Levey, 1987; Corlett and Lucas, 1990). Short-

distance delivery of seeds, usually below the parent plant, is the likely result of oral fruit processing, resulting in highly clumped seed distributions, irrespective of how many seeds are dispersed. In addition, low mixing of different seed species is expected, since fruits are processed individually. Frugivores that process fruits orally either expectorate seeds while foraging on the same plant for more fruits (e.g. birds that mash fruits, some neotropical primates) or temporarily exit to nearby perches to process the fruit and then return to the same foraging patch. Highly clumped seed distributions have been reported as a result of the activity of phyllostomid bats, which mash fruits (e.g. *Carollia*) or expectorate a food bolus with seeds (e.g. *Artibeus*) (Bonaccorso and Gush, 1987; Fleming, 1988). The same applies to territorial birds that regurgitate seeds within a close range of the feeding plant or display perches (Pratt and Stiles, 1983; Pratt, 1984; Snow and Snow, 1984; Théry and Larpin, 1993; Kinnaird, 1998; Wenny and Levey, 1998) and tapirs and large primates using recurrent movement patterns (Fragoso, 1997; Julliot, 1997). Clumped seed distributions are not caused by a high number of seeds being processed, since the longer times to handle fruits (birds that regurgitate seeds are an exception) result in slower feeding rates, but are caused by the recurrent use of the same perches and sites for fruit handling, resting, defecation, etc.

In contrast, digestive seed processing involves a longer retention time for seeds and increases the probability that the seed will be moved away from the parent plant. This might result in more scattered seed delivery, unless postforaging movements concentrate seeds at traditional roosts, latrines, pathways, etc. Also, the degree of scattering depends on frugivore size. Blackcaps scatter one to three seeds in single droppings at no particular locations in Mediterranean shrubland (Jordano, 1988; Debussche and Isenmann, 1994), but large ungulates and some primates can concentrate hundreds of seeds in single droppings (Dinerstein and Wemmer, 1988; Fragoso,

Julliot, 1997). The longer retention times of seeds within the gut obviously increase the probability of seed delivery to longer distances. Fruit handling prior to ingestion is minimal, but there is a greater risk of digestive seed damage, especially in frugivores with long retention times, such as ungulates, parrots, some pigeons and terrestrial birds and some finches (Janzen, 1981a, 1982; Gautier-Hion, 1984; Erard and Sabatier, 1988; Murray, 1988; Bodmer, 1989a; Lambert, 1989b). Finally, seed clumping in faeces is strongly dependent on frugivore size (Howe, 1989; White and Stiles, 1990) and this has important implications for seed survival, germination and seedling competition. Few studies, however, have documented how these patterns translate into positive net effects of non-random ('directed') seed dispersal by frugivores (Reid, 1989; Ladley and Kelly, 1996; Wenny and Levey, 1998).

Proximate consequences of seed deposition patterns

Frugivory influences on plant fitness and recruitment do not end with seed delivery. For every dispersal episode, it matters how many and where seeds reach the ground and the particular mix of seed species delivered. There are a number of detailed studies on the ranging behaviour of frugivores and I shall not attempt to consider them in detail here (e.g. Gautier-Hion *et al.*, 1981; Hladik, 1981; Terborgh, 1983; Fleming, 1988; Murray, 1988; Chavez-Ramirez and Slack, 1994; Sun *et al.*, 1997). This is probably the aspect of zoochory that is most 'context-sensitive'. Most of the animal-orientated studies of frugivore movements and ranging behaviour have emphasized the patchy nature of the movements and foraging effort and the influences of external factors, such as seasonality, between-year variations in the fruit supply and numbers of other frugivores, habitat structure and abundance of alternative fruit sources and other food resources. These factors influence the 'where' component of seed deposition pat-

terns, but I wish to concentrate on the 'how' component and point out some recent research and promising directions.

The greater probability of seed mixing for internally processed seeds has far-reaching implications for postdispersal seed and seedling survival, which have only recently been considered in detail in explicit relation to frugivore activity. Bullock (1981) showed that aggregated dispersal of several seeds of *Prunus ilicifolia* in coyote faeces increased seedling survival and that seedlings resulting from clumped dispersal in single droppings showed greater above-ground biomass than spaced seedlings. He reported that grafting between roots was commonly observed among seedlings from a cohort, indicating some direct physiological integration among different genets in such a group of seedlings. Studies by Lieberman and Lieberman (1980); Herrera (1984b, c); Jordano (1988); Loiselle (1990); White and Stiles (1990); Théry and Larpin (1993); Fragoso (1997); and Julliot (1997) strongly support the hypothesis that frugivorous animals can have determinant effects on plant community composition by differentially dispersing particular combinations of seed species. Detailed studies are needed to obtain experimental support for this hypothesis.

Observational evidence indicates that combinations of seed species in the faeces of dispersal agents are not the result of a process of random assortment of the available fruits in the diet, but rather indicate the presence of consistent choice patterns. Preliminary correlative evidence comes from studies of hemiparasitic and parasitic plants, which need highly directed dispersal to particular hosts (Herrera, 1988b; Reid, 1989; Ladley and Kelly, 1996), but a similar effect can be important for vines. Additional evidence has been obtained from detailed studies of individual diet variation in frugivore populations (Jordano, 1988; Loiselle, 1990; White and Stiles, 1990) and seed-rain studies (Stiles and White, 1986). Loiselle (1990) has demonstrated experimentally that specific combinations of dispersed seeds in faeces of

tropical frugivorous birds have a direct influence on seed germination and early seedling vigour and survival.

Studies of germination rates in deposited seeds, early seedling survival and variations in seedling biomass, adequately linked with detailed information of frugivory patterns, such as those described above, are the necessary tools for exploring the potential consequences of the fruit/frugivory interface in plant demography.

Concluding remarks: an agenda for the fruit/frugivory interface

Seed dispersal is a central demographic process in plant populations. The interaction of fruits and frugivores determines the net result of the whole predispersal reproductive phase, being its last step. However, events occurring during this fruit-removal, seed-delivery episode have a direct influence on later-occurring demographic processes, such as germination and early seedling establishment and survival. The studies of fruit-frugivore interactions considered in this chapter have documented what could be designated as the largely 'invariant' fruit and frugivory patterns that characterize each interacting species in the particular scenario where the interaction occurs (e.g. fruit and seed size, design, nutrient configuration, fruiting display, etc.; and body size, ecomorphology, fruit-handling behaviour and digestive process of food, etc.). Description of these patterns has enabled us in the last 25 years to elaborate predictions about the outcomes of particular combinations of characteristics and to test them by evaluating the associated costs in terms of seed losses for the plants or foraging costs for the frugivorous animals.

But we need to translate the effects of these interactions into a demographic and evolutionary context in order to assess the relative contributions of the derived selection pressures in shaping the patterns we are observing. In this context, the net outcomes of the interactions may or may not have evolutionary consequences if their effects are 'screened off' by factors external

to the interaction itself. The same can be said for the potential of frugivores to impose 'dispersal limitation' on the recruitment of their food plants (Jordano and Herrera, 1995; Clark *et al.*, 1999). Thus, the outcome of the invariant patterns described above depends, in addition, on 'context-sensitive' effects, which represent a largely stochastic component of the fruit-removal, seed-dispersal phase. Among them, plant spacing patterns, neighbourhood structure, site-specific habitat heterogeneity, density of alternative resources, temporal variations in fruit production and frugivore numbers, etc., produce effects that shape the result of the 'invariant' fruit/frugivore patterns.

A future avenue of research would assess the net demographic outcome of the fruit/frugivory interface by associating probabilities of seed delivery, resulting from a given interaction, with probabilities of seed and seedling survival in different microhabitats (e.g. see Willson and Traveset, Chapter 4, and Crawley, Chapter 7, in this volume). In this way, the relative roles of seed dispersal limitation and recruitment limitation in determining abundance could be gauged (Dalling *et al.*, 1998). The preliminary protocols have been developed (e.g. Heithaus *et al.*, 1982; Herrera, 1988a; Jordano, 1989) for incorporating the consequences of the predispersal events and the deferred consequences for the postdispersal phase (McDonnell and Stiles, 1983; Howe *et al.*, 1985; Fleming, 1988; Katusic-Malmborg and Willson, 1988; Murray, 1988; Schupp, 1988, 1993; Herrera *et al.*, 1994; Jordano and Herrera, 1995; Schupp and Fuentes, 1995; Wenny and Levey, 1998; Clark *et al.*, 1999; Jordano and Schupp, 2000). These studies emphasize the need to estimate the fitness effects of interactions with frugivores for individual plants in natural populations and consider whether the effects of frugivores are offset by events in subsequent stages of recruitment. In addition, it is necessary to

consider how demographic processes (especially seed germination and seedling establishment) are influenced by variation in traits relevant to the plant-frugivore interaction.

In 1591, the Italian painter Giuseppe Arcimboldo finished *Vertumnus*, an oil-painting on wood depicting a portrait of Emperor Rudolf II in a frontal view of head and shoulders. When admired from a distance, this image of Vertumnus, a Roman deity responsible for vegetation and metamorphosis, appears as a neat, brightly coloured and meticulously elaborate picture. On approaching the painting, one discovers that Arcimboldo illustrated at least 34 species of fleshy fruits, which, carefully assembled, served as natural models to produce Vertumnus' image. Grapes, cherries, pears, figs, blackberries, peaches and plums, among many others, serve as the eyes, ears, lips, nose, etc. of this incredible fruit dish. What I admire about this intriguing, funny face is the painter's ability to produce an ordered image from such a chaotic ensemble of fruits and plant parts. I think that the last two decades of research on the fruit-frugivory interface have yielded many fruits, which, like Arcimboldo's model objects, need an elaborate assembly to produce a neat image. The efforts to bridge the consequences of frugivory and seed dispersal with the demographic and evolutionary processes in plant and frugivore populations are a first sketch of that picture.

Acknowledgements

This research was supported by grants PB96-0857 and 1FD97-0743-C03-01 from the Comisión Interministerial de Ciencia y Tecnología (CICYT), the Ministerio de Educación y Ciencia and the European Commission, and also by funds from the Consejería de Educación y Ciencia (Junta de Andalucía).

References

- Abrahamson, W.G. and Abrahamson, C.R. (1989) Nutritional quality of animal dispersed fruits in Florida sandridge habitats. *Bulletin of the Torrey Botanical Club* 116, 215–228.
- Afik, D. and Karasov, W.H. (1995) The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* 76, 2247–2257.
- Alexandre, D.Y. (1978) Le rôle disséminateur des éléphants en forêt de Tai, Côte-d'Ivoire. *La Terre et la Vie* 32, 47–72.
- Alexandre, D.Y. (1980) Caractère saisonnier de la fructification dans une forêt hygrophile de Côte-d'Ivoire. *Revue d'Ecologie (Terre et Vie)* 34, 335–350.
- Atramentowicz, M. (1988) La frugivorie opportuniste de trois marsupiaux didelphidés de Guyane. *Revue d'Ecologie (Terre et Vie)* 43, 47–57.
- Baird, J.W. (1980) The selection and use of fruit by birds in an eastern forest. *Wilson Bulletin* 92, 63–73.
- Barquín, E. and Wildpret, W. (1975) Diseminación de plantas canarias: datos iniciales. *Vieraea* 5, 38–60.
- Beehler, B. (1983) Frugivory and polygamy in birds of paradise. *Auk* 100, 1–12.
- Berthold, P. (1976) Animalische und vegetabilische Ernährung omnivorer Singvogelarten: Nahrungsbevorzugung, Jahresperiodik der Nahrungswahl, physiologische und ökologische Bedeutung. *Journal für Ornithologie* 117, 145–209.
- Berthold, P. (1977) Proteinmangel als Ursache der schädigenden Wirkung rein vegetabilischer Ernährung omnivorer Singvogelarten. *Journal für Ornithologie* 118, 202–205.
- Berthold, P. and Moggingen, S. (1976) Der Seidenschwanz *Bombycilla garrulus* als frugivorer Ernährungsspezialist. *Experientia* 32, 1445.
- Bhida, S.A. (1980) Observations on the stomach of the Indian fruit bat, *Roussetus leschenaulti* (Desmarest). *Mammalia* 44, 571–579.
- Blake, J.G. and Hoppes, W.G. (1986) Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. *Auk* 103, 328–340.
- Blake, J.G., Loisel, B.A., Moermond, T.C., Levey, D.J. and Denslow, J.S. (1990) Quantifying the abundance of fruits for birds in tropical habitats. *Studies in Avian Biology* 13, 73–79.
- Bodmer, R.E. (1989a) Frugivory in Amazonian Artiodactyla: evidence for the evolution of the ruminant stomach. *Journal of Zoology, London* 219, 457–467.
- Bodmer, R.E. (1989b) Ungulate biomass in relation to feeding strategy within Amazonian forests. *Oecologia* 81, 547–550.
- Bodmer, R.E. (1990) Ungulate frugivores and browser-grazer continuum. *Oikos* 57, 319–325.
- Bonaccorso, F.J. (1979) Foraging and reproductive ecology in a Panamanian bat community. *Bulletin of the Florida State Museum* 24, 359–408.
- Bonaccorso, F.J. and Gush, T.J. (1987) Feeding behaviour and foraging strategies of captive phyllostomid fruit bats: an experimental study. *Journal of Animal Ecology* 56, 907–920.
- Boojh, R. and Ramakrishnan, P.S. (1981) Phenology of trees in a sub-tropical evergreen montane forest in North-east India. *Geo-eco-trop* 5, 189–209.
- Borchert, R. (1983) Phenology and control of flowering in tropical trees. *Biotropica* 15, 81–89.
- Bowen, S.H., Lutz, E.V. and Ahlgren, M.O. (1995) Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology* 76, 899–907.
- Bullock, S.H. (1978) Plant abundance and distribution in relation to types of seed dispersal. *Madroño* 25, 104–105.
- Bullock, S.H. (1981) Aggregation of *Prunus ilicifolia* (Rosaceae) during dispersal and its effect on survival and growth. *Madroño* 28, 94–95.
- Burrows, C.J. (1994) Fruits, seeds, birds and the forests of Banks Peninsula. *New Zealand Natural Sciences* 21, 87–108.
- Cadow, A. (1933) Magen und Darm der Fruchtauben. *Journal für Ornithologie* 81, 236–252.
- Chapman, L.J., Chapman, C.J. and Wrangham, R.W. (1992a) *Balanites wilsoniana*: elephant dependent dispersal. *Journal of Tropical Ecology* 8, 275–283.
- Chapman, C.A., Wrangham, R. and Chapman, L.J. (1992b) Estimators of fruit abundance of tropical trees. *Biotropica* 24, 527–531.
- Chapman, C.A., Wrangham, R. and Chapman, L.J. (1994) Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26, 160–171.
- Charles-Dominique, P., Atramentowicz, M., Charles-Dominique, M., Gerard, H., Hladik, A., Hladik, C.M. and Prevost, M.F. (1981) Les mammifères frugivores arboricoles nocturnes d'une forêt Guyanaise: inter-relations plantes-animaux. *Revue d'Ecologie (Terre et Vie)* 35, 341–435.
- Chavez-Ramirez, F. and Slack, R.D. (1994) Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe juniper. *Oikos* 71, 40–46.

- Cipollini, M.L. and Levey, D.J. (1992) Relative risks of microbial rot for fleshy fruits: significance with respect to dispersal and selection for secondary defense. *Advances in Ecological Research* 23, 35–91.
- Cipollini, M.L. and Levey, D.J. (1997) Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *American Naturalist* 150, 346–372.
- Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J. and Wyckoff, P. (1999) Interpreting recruitment limitation in forests. *American Journal of Botany* 86, 1–16.
- Conklin-Brittain, N.L., Wrangham, R.W. and Hunt, K.D. (1998) Dietary responses of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology* 19, 949–970.
- Corlett, R.T. (1996) Characteristics of vertebrate-dispersed fruits in Hong Kong. *Journal of Tropical Ecology* 12, 819–833.
- Corlett, R.T. (1998) Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. *Biological Review* 73, 413–448.
- Corlett, R.T. and Lucas, P.W. (1990) Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia* 82, 166–171.
- Courts, S.E. (1998) Dietary strategies of Old World fruit bats (Megachiroptera, Pteropodidae): how do they obtain sufficient protein? *Mammal Review* 28, 185–194.
- Croat, T.B. (1978) *Flora of Barro Colorado Island*. Stanford University Press, Stanford.
- Crome, F.H.J. (1975) The ecology of fruit pigeons in tropical Northern Queensland. *Australian Wildlife Research* 2, 155–185.
- Cruz, A. (1981) Bird activity and seed dispersal of a montane forest tree (*Dunalia arborescens*) in Jamaica. *Biotropica (Suppl.)* 13, 34–44.
- Cvitanic, A. (1970) The relationships between intestine and body length and nutrition in several bird species. *Larus* 21–22, 181–190.
- Dalling, J.W., Hubbell, S.P. and Silveira, K. (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology* 86, 674–689.
- Daubenmire, R. (1972) Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. *Journal of Ecology* 60, 147–170.
- Davies, A.G., Bennett, E.L. and Waterman, P.G. (1988) Food selection by two south-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biological Journal of the Linnean Society* 34B, 33–56.
- Davies, S.J.J.F. (1976) Studies on the flowering season and fruit production of some arid zone shrubs and trees in Western Australia. *Journal of Ecology* 64, 665–687.
- Davis, D.E. (1945) The annual cycle of plants, mosquitoes, birds, and mammals in two Brazilian forests. *Ecological Monographs* 15, 245–295.
- Debussche, M. (1988) La diversité morphologique des fruits charnus en Languedoc méditerranéen: relations avec les caractéristiques biologiques et la distribution des plantes, et avec les disseminateurs. *Acta Oecologica, Oecologia Plantarum* 9, 37–52.
- Debussche, M. and Isenmann, P. (1989) Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. *Oikos* 56, 327–338.
- Debussche, M. and Isenmann, P. (1992) A Mediterranean bird disperser assemblage: composition and phenology in relation to fruit availability. *Revue d'Ecologie* 47, 411–432.
- Debussche, M. and Isenmann, P. (1994) Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos* 69, 414–426.
- Debussche, M., Escarré, J. and Lepart, J. (1982) Ornithochory and plant succession in Mediterranean abandoned orchards. *Vegetatio* 48, 255–266.
- Debussche, M., Cortez, J. and Rimbault, I. (1987) Variation in fleshy fruit composition in the Mediterranean region: the importance of ripening season, life-form, fruit type, and geographical distribution. *Oikos* 49, 244–252.
- Decoux, J.P. (1976) Régime, comportement alimentaire et régulation écologique du métabolisme chez *Colius striatus*. *La Terre et la Vie* 30, 395–420.
- De Foresta, H., Charles-Dominique, P. and Erard, C. (1984) Zoochorie et premières stades de la régénération naturelle après coupe en forêt guyanaise. *Revue d'Ecologie (Terre et Vie)* 39, 369–400.
- Denslow, J.S. (1987) Fruit removal rates from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. *Canadian Journal of Botany* 65, 1229–1235.
- Denslow, J.S. and Moermond, T.C. (1982) The effect of fruit accessibility on rates of fruit removal from tropical shrubs: an experimental study. *Oecologia* 54, 170–176.
- Desselberger, H. (1931) Der Verdauungskanal der Dicaeiden nach Gestalt und Funktion. *Journal für Ornithologie* 79, 353–374.
- Dinerstein, E. (1986) Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. *Biotropica* 18, 307–318.

- Dinerstein, E. and Wemmer, C.M. (1988) Fruits rhinoceros eat: dispersal of *Trewia nudiflora* (Euphorbiaceae) in lowland Nepal. *Ecology* 69, 1768–1774.
- Docters van Leeuwen, W.M. (1954) On the biology of some Loranthaceae and the role birds play in their life-history. *Beaufortia* 4, 105–208.
- Donoghue, M.J. (1989) Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. *Evolution* 43, 1137–1156.
- Dowsett-Lemaire, F. (1988) Fruit choice and seed dissemination by birds and mammals in the evergreen forests of upland Malawi. *Revue d'Ecologie (Terre et Vie)* 43, 251–286.
- Dubost, G. (1984) Comparison of the diets of frugivorous forest ruminants of Gabon. *Journal of Mammalogy* 65, 298–316.
- Erard, C. and Sabatier, D. (1988) Rôle des oiseaux frugivores terrestres dans la dynamique forestière en Guyane française. In: Ouellet, H. (ed.) *Acta XIX Congressus Internationalis Ornithologici*. University of Ottawa Press, Ottawa, Canada, pp. 803–815.
- Erard, C., Thery, M. and Sabatier, D. (1989) Régime alimentaire de *Rupicola rupicola* (Cotingidae) en Guyane française. Relations avec la frugivorie et la zoochorie. *Revue d'Ecologie (Terre et Vie)* 44, 47–74.
- Eriksson, K. and Nummi, H. (1982) Alcohol accumulation from ingested berries and alcohol metabolism in passerine birds. *Ornis Fennica* 60, 2–9.
- Eriksson, O. and Ehrlén, J. (1991) Phenological variation in fruit characteristics in vertebrate-dispersed plants. *Oecologia* 86, 463–470.
- Estrada, A. and Fleming, T.H. (eds) (1986) *Frugivores and Seed Dispersal*. Junk, Dordrecht.
- Estrada, A., Coates-Estrada, R. and Vázquez-Yanes, C. (1984) Observations on fruiting and dispersers of *Cecropia obtusifolia* at Los Tuxtlas, Mexico. *Biotropica* 16, 315–318.
- Fenner, M. (1998) The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics* 1, 78–91.
- Fitzpatrick, J.W. (1980) Foraging behavior of neotropical tyrant flycatchers. *Condor* 82, 43–57.
- Fleming, T.H. (1982) Foraging strategies of plant-visiting bats. In: Kunz, T.H. (ed.) *Ecology of Bats*. Plenum Press, New York, pp. 287–325.
- Fleming, T.H. (1986) Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. In: Estrada, A. and Fleming, T.H. (eds) *Frugivores and Seed Dispersal*. Junk, Dordrecht, pp. 105–118.
- Fleming, T.H. (1988) *The Short-tailed Fruit Bat: a Study in Plant-Animal Interactions*. University of Chicago Press, Chicago.
- Forbes, W.A. (1880) Contributions to the anatomy of passerine birds. Part I. On the structure of the stomach in certain genera of tanagers. *Proceedings of the Zoological Society, London* 188, 143–147.
- Foster, M.S. (1977) Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58, 73–85.
- Foster, M.S. (1978) Total frugivory in tropical passerines: a reappraisal. *Tropical Ecology* 19, 131–154.
- Foster, M.S. (1987) Feeding methods and efficiencies of selected frugivorous birds. *Condor* 89, 566–580.
- Foster, M.S. and McDiarmid, R.W. (1983) Nutritional value of the aril of *Trichilia cuneata*, a bird-dispersed fruit. *Biotropica* 15, 26–31.
- Foster, R.B. (1982) Famine on Barro Colorado Island. In: Leigh, E.G., Rand, E.S. and Windsor, D. (eds) *The Ecology of a Tropical Forest*. Smithsonian Institution Press, Washington, DC, pp. 201–212.
- Fragoso, J.M.V. (1997) Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology* 85, 519–529.
- Frankie, G.W., Baker, H.G. and Opler, P.A. (1974a) Comparative phenological studies in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 62, 881–919.
- Frankie, G.W., Baker, H.G. and Opler, P.A. (1974b) Tropical plant phenology: applications for studies in community ecology. In: Lieth, H. (ed.) *Phenology and Seasonality Modelling*. Ecological Studies, Vol. 8, Springer Verlag, Berlin, pp. 287–296.
- Franklin, J.F., Maeda, T., Ohsumi, Y., Matsui, M., Yagi, H. and Hawk, G.M. (1979) Subalpine coniferous forests of central Houshu, Japan. *Ecological Monographs* 49, 311–334.
- French, K. (1992) Phenology of fleshy fruits in a wet sclerophyll forest in Southeastern Australia: are birds an important influence? *Oecologia* 90, 366–373.
- Frost, P.G.H. (1980) Fruit–frugivore interactions in a South African coastal dune forest. In: Noring, R. (ed.), *Acta XVII Congressus Internationalis Ornithologici*. Deutsche Ornithologen Gesellschaft, Berlin, pp. 1179–1184.
- Fuentes, M. (1992) Latitudinal and elevational variation in fruiting phenology among western European bird-dispersed plants. *Ecography* 15, 177–183.
- Funakoshi, K., Watanabe, H. and Kunisaki, T. (1993) Feeding ecology of the northern Ryukyu fruit bat, *Pteropus dasymallus dasymallus*, in a warm-temperate region. *Journal of Zoology* 230, 221–230.

- Garber, P.A. (1986) The ecology of seed dispersal in two species of callitrichid primates (*Sanguinus mystax* and *Sanguinus fuscicollis*). *American Journal of Primatology* 10, 155–170.
- Gardner, A.L. (1977) Feeding habits. In: Baker, R.J., Knox-Jones, J. and Carter, D.C. (eds) *Biology of Bats in the New World Family Phyllostomatidae*, Part II. Special Publication, Museum Texas Technical University No.13, Austin, Texas, pp. 295–328.
- Garwood, N.C. (1983) Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs* 53, 159–181.
- Gautier-Hion, A. (1984) La dissémination des graines par les cercopithecidés forestiers africains. *Revue d'Ecologie (Terre et Vie)* 39, 159–165.
- Gautier-Hion, A., Gautier, J.P. and Quris, R. (1981) Forest structure and fruit availability as complementary factors influencing habitat use of monkeys (*Cercopithecus cephus*). *Revue d'Ecologie (Terre et Vie)* 35, 511–536.
- Gautier-Hion, A., Duplantier, J.M., Emmons, L., Feer, F., Heckestweiler, P., Mougazi, A., Quris, R. and Sourd, C. (1985a) Coadaptation entre rythmes de fructification et frugivorie en forêt tropicale humide du Gabon: mythe ou réalité? *Revue d'Ecologie (Terre et Vie)* 40, 405–434.
- Gautier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J.P., Dubost, G., Emmons, L., Erard, C. and Heckestweiler, P. (1985b) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65, 324–337.
- Gentry, A.H. (1982) Patterns of neotropical plant species diversity. In: Hecht, M.K., Wallace, B. and Prance, G.T. (eds) *Evolutionary Biology*, Vol. 15. Plenum Press, New York, pp. 1–84.
- Givnish, T.J. (1980) Ecological constraints on the evolution of breeding systems in seed plants: dioecy and dispersal in gymnosperms. *Evolution* 34, 959–972.
- Gorchov, D.L. (1990) Pattern, adaptation, and constraint in fruiting synchrony within vertebrate-dispersed woody plants. *Oikos* 58, 169–180.
- Green, R.J. (1993) Avian seed dispersal in and near subtropical rainforests. *Wildlife Research* 20, 535–537.
- Gutián, J. (1984) Ecología de una comunidad de Passeriformes en un bosque montano de la Cordillera Cantábrica Occidental. Unpublished PhD thesis, Universidad de Santiago, Santiago.
- Halls, L.K. (1973) *Flowering and Fruiting of Southern Browse Species*. Forest Service Research Paper SO-90, US Department of Agriculture, Washington, DC, 10 pp.
- Harding, R.S.O. (1981) An order of omnivores: nonhuman primate diets in the wild. In: Harding, R.S.O. and Teleki, G. (eds) *Omnivorous Primates: Gathering and Hunting in Human Evolution*. Columbia University Press, New York, pp. 191–214.
- Heiduck, S. (1997) Food choice in masked titi monkeys (*Callicebus personatus melanochir*): selectivity or opportunism? *International Journal of Primatology* 18, 487–502.
- Heithaus, E.R., Stashko, E. and Anderson, P.K. (1982) Cumulative effects of plant–animal interactions on seed production by *Bauhinia unguolata*, a neotropical legume. *Ecology* 63, 1294–1302.
- Herbst, L.H. (1986) The role of nitrogen from the fruit pulp in the nutrition of the frugivorous bat *Carollia perspicillata*. *Biotropica* 18, 39–44.
- Herrera, C.M. (1981a) Are tropical fruits more rewarding to dispersers than temperate ones? *American Naturalist* 118, 896–907.
- Herrera, C.M. (1981b) Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos* 36, 51–58.
- 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) Adaptation to frugivory of Mediterranean avian seed dispersers. *Ecology* 65, 609–617.
- Herrera, C.M. (1984b) Habitat–consumer interactions in frugivorous birds. In: Cody, M.L. (ed.) *Habitat Selection in Birds*. Academic Press, New York, pp. 341–365.
- Herrera, C.M. (1984c) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs* 54, 1–23.
- Herrera, C.M. (1984d) Tipos morfológicos y funcionales en plantas del matorral mediterráneo del sur de España. *Studia Oecologica* 5, 7–34.
- Herrera, C.M. (1987) Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecological Monographs* 57, 305–331.
- Herrera, C.M. (1988a) The fruiting ecology of *Osyris quadripartita*: individual variation and evolutionary potential. *Ecology* 69, 233–249.
- Herrera, C.M. (1988b) Plant size, spacing patterns, and host-plant selection in *Osyris quadripartita*, a hemiparasitic dioecious shrub. *Journal of Ecology* 76, 995–1006.
- Herrera, C.M. (1988c) Variaciones anuales en las poblaciones de pájaros frugívoros y su relación con la abundancia de frutos. *Ardeola* 35, 135–142.
- Herrera, C.M. (1989) Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. *Oikos* 55, 250–262.

- Herrera, C.M. (1992) Interspecific variation in fruit shape: allometry, phylogeny, and adaptation to dispersal agents. *Ecology* 73, 1832–1841.
- Herrera, C.M. (1995) Plant–vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics* 26, 705–727.
- Herrera, C.M. (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* 68, 511–538.
- Herrera, C.M. and Jordano, P. (1981) *Prunus mahaleb* and birds: the high efficiency seed dispersal system of a temperate fruiting tree. *Ecological Monographs* 51, 203–221.
- Herrera, C.M., Jordano, P., López Soria, L. and Amat, J.A. (1994) Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs* 64, 315–344.
- Hilty, S.L. (1977) Food supply in a tropical frugivorous bird community. Unpublished PhD thesis, University of Arizona.
- Hilty, S.L. (1980) Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. *Biotropica* 12, 292–306.
- Hladik, A. (1978) Phenology of leaf production in rainforest of Gabon: distribution and composition of food for folivores. In: Montgomery, G.G. (ed.) *The Ecology of Arboreal Folivores*. Smithsonian Institution Press, Washington, DC, pp. 51–71.
- Hladik, C.M. (1981) Diet and the evolution of feeding strategies among forest primates. In: Harding, R.S.O. and Teleki, G. (eds) *Omnivorous Primates*. Columbia University Press, New York, pp. 215–254.
- Hladik, C.M. and Hladik, A. (1967) Observations sur le rôle des primates dans la dissémination des végétaux de la forêt gabonaise. *Biologia Gabonica* 3, 43–58.
- Hladik, C.M., Hladik, A., Bousset, J., Valdebouze, P., Viroben, G. and Delrot-Laval, J. (1971) Le régime alimentaire des primates de l'île de Barro-Colorado (Panama). *Folia Primatologica* 16, 85–122.
- Hoffmann, A.J. and Armesto, J.J. (1995) Modes of seed dispersal in the Mediterranean regions in Chile, California, and Australia. In: Arroyo, M.T.K., Zedler, P.H. and Fox, M.D. (eds) *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia*. Springer-Verlag, New York, USA, pp. 289–310.
- Holl, K.D. (1998) Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? *Restoration Ecology* 6, 253–261.
- Hopkins, M.S. and Graham, A.W. (1989) Community phenological patterns of a lowland tropical rainforest in north-eastern Australia. *Australian Journal of Ecology* 14, 399–413.
- Hoppes, W.G. (1987) Pre- and post-foraging movements of frugivorous birds in an eastern deciduous forest woodland, USA. *Oikos* 49, 281–290.
- Hoppes, W.G. (1988) Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology* 69, 320–329.
- Houssard, C., Escarré, J. and Romane, F. (1980) Development of species diversity in some Mediterranean plant communities. *Vegetatio* 43, 59–72.
- Howe, H.F. (1980) Monkey dispersal and waste of a neotropical fruit. *Ecology* 61, 944–959.
- Howe, H.F. (1981) Dispersal of neotropical nutmeg (*Viola sebifera*) by birds. *Auk* 98, 88–98.
- Howe, H.F. (1983) Annual variation in a neotropical seed-dispersal system. In: Sutton, S.L., Whitmore, T.C. and Chadwick, A.C. (eds) *Tropical Rainforest: Ecology and Management*. Blackwell Scientific Publications, London, pp. 211–227.
- Howe, H.F. (1984) Constraints on the evolution of mutualisms. *American Naturalist* 123, 764–777.
- Howe, H.F. (1986) Seed dispersal by fruit-eating birds and mammals. In: Murray, D.R. (ed.) *Seed Dispersal*. Academic Press, Sydney, Australia, pp. 123–190.
- Howe, H.F. (1989) Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79, 417–426.
- Howe, H.F. (1993) Specialized and generalized dispersal systems: where does 'the paradigm' stand? In: Fleming, T.H. and Estrada, A. (eds) *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 3–13.
- Howe, H.F. and Estabrook, G.F. (1977) On intraspecific competition for avian dispersers in tropical trees. *American Naturalist* 111, 817–832.
- Howe, H.F. and Richter, W.M. (1982) Effects of seed size on seedling size in *Viola surinamensis*: a within and between tree analysis. *Oecologia* 53, 347–351.
- Howe, H.F. and Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13, 201–228.
- Howe, H.F. and Vande Kerckhove, G.A. (1981) Removal of wild nutmeg (*Viola surinamensis*) crops by birds. *Ecology* 62, 1093–1106.
- Howe, H.F., Schupp, E.W. and Westley, L.C. (1985) Early consequences of seed dispersal for a neotropical tree (*Viola surinamensis*). *Ecology* 66, 781–791.
- Hudson, D.A., Levin, R.J. and Smith, D.H. (1971) Absorption from the alimentary tract. In: Bell, D.J. and Freeman, B.M. (eds) *Physiology and Biochemistry of the Domestic Fowl*, Vol. I. Academic Press, London, pp. 51–71.

- Hughes, L., Westoby, M. and Johnson, A.D. (1993) Nutrient costs of vertebrate-dispersed and ant-dispersed fruits. *Functional Ecology* 7, 54–62.
- Hume, I.D. (1989) Optimal digestive strategies in mammalian herbivores. *Physiological Zoology* 62, 1145–1163.
- Hylander, W.L. (1975) Incisor size and diet in anthropoids with special reference to Cercopithecidae. *Science* 189, 1095–1098.
- Idani, G. (1986) Seed dispersal by pygmy chimpanzees (*Pan paniscus*): a preliminary report. *Primates* 27, 441–447.
- Innis, G.J. (1989) Feeding ecology of fruit pigeons in subtropical rainforests of south-eastern Queensland. *Australian Wildlife Research* 16, 365–394.
- Izhaki, I. and Safriel, U.N. (1989) Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos* 54, 23–32.
- Izhaki, I., Walton, P.B. and Safriel, U.N. (1991) Seed shadows generated by frugivorous birds in an eastern mediterranean scrub. *Journal of Ecology* 79, 575–590.
- Janson, C.H. (1983) Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* 219, 187–189.
- Janson, C.H., Stiles, E.W. and White, D.W. (1986) Selection on plant fruiting traits by brown capuchin monkeys: a multivariate approach. In: Estrada, A. and Fleming, T.H. (eds) *Frugivores and Seed Dispersal*. Junk, Dordrecht, pp. 83–92.
- Janzen, D.H. (1967) Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* 21, 620–637.
- Janzen, D.H. (1981a) Digestive seed predation by a Costa Rican Baird's tapir. *Biotropica* (Suppl.) 13, 59–63.
- Janzen, D.H. (1981b) Guanacaste tree seed-swallowing by Costa Rican range horses. *Ecology* 62, 587–592.
- Janzen, D.H. (1981c) *Enterolobium cyclocarpum* seed passage rate and survival in horses, Costa Rican Pleistocene seed dispersal agents. *Ecology* 62, 593–601.
- Janzen, D.H. (1982) Differential seed survival and passage rates in cows and horses, surrogate pleistocene dispersal agents. *Oikos* 38, 150–156.
- Janzen, D.H. (1983) Dispersal of seeds by vertebrate guts. In: Futuyma, D.J. and Slatkin, M. (eds) *Coevolution*. Sinauer Associates, Sunderland, Massachusetts, pp. 232–262.
- Janzen, D.H., Miller, G.A., Hackforth-Jones, J., Pond, C.M., Hooper, K. and Janos, D.P. (1976) Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). *Ecology* 57, 1068–1075.
- Johnson, A.S. and Landers, J.L. (1978) Fruit production in slash pine plantations in Georgia. *Journal of Wildlife Management* 42, 606–613.
- Johnson, R.A., Willson, M.F., Thompson, J.N. and Bertin, R.I. (1985) Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology* 66, 819–827.
- Jordano, P. (1981) Alimentación y relaciones tróficas entre los passeriformes en paso otoñal por una localidad de Andalucía central. *Doñana Acta Vertebrata* 8, 103–124.
- Jordano, P. (1982) Migrant birds are the main seed dispersers of blackberries in southern Spain. *Oikos* 38, 183–193.
- Jordano, P. (1983) Fig-seed predation and dispersal by birds. *Biotropica* 15, 38–41.
- Jordano, P. (1984) Relaciones entre plantas y aves frugívoras en el matorral mediterráneo del área de Doñana. PhD thesis, Universidad de Sevilla, Sevilla.
- Jordano, P. (1985) El ciclo anual de los passeriformes frugívoros en el matorral mediterráneo del sur de España: importancia de su invernada y variaciones interanuales. *Ardeola* 32, 69–94.
- Jordano, P. (1987a) Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology* 68, 1711–1723.
- Jordano, P. (1987b) Frugivory, external morphology and digestive system in Mediterranean sylviid warblers *Sylvia* spp. *Ibis* 129, 175–189.
- Jordano, P. (1987c) Notas sobre la dieta no-insectívora de algunos Muscicapidae. *Ardeola* 34, 89–98.
- Jordano, P. (1988) Diet, fruit choice and variation in body condition of frugivorous warblers in Mediterranean scrubland. *Ardea* 76, 193–209.
- Jordano, P. (1989) Pre-dispersal biology of *Pistacia lentiscus* (Anacardiaceae): cumulative effects on seed removal by birds. *Oikos* 55, 375–386.
- Jordano, P. (1995a) Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *American Naturalist* 145, 163–191.
- Jordano, P. (1995b) Frugivore-mediated selection on fruit and seed size: birds and St Lucie's cherry, *Prunus mahaleb*. *Ecology* 76, 2627–2639.
- Jordano, P. and Herrera, C.M. (1995) Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience* 2, 230–237.
- Jordano, P. and Schupp, E.W. (2000) Determinants of seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70.

- Julliot, C. (1997) Impact of seed dispersal of red howler monkeys *Alouatta seniculus* on the seedling population in the understorey of tropical rain forest. *Journal of Ecology* 85, 431–440.
- Kantak, G.E. (1979) Observations on some fruit-eating birds in Mexico. *Auk* 96, 183–186.
- Kaplin, B.A. and Moermond, T.C. (1998) Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology* 45, 83–101.
- Karasov, W.H. (1996) Digestive plasticity in avian energetics and feeding ecology. In: Carey, C. (ed.) *Avian Energetics and Nutritional Ecology*. Chapman and Hall, New York, pp. 61–84.
- Karasov, W.H. and Levey, D.J. (1990) Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiological Zoology* 63, 1248–1270.
- Karr, J.R. and James, F.C. (1975) Eco-morphological configurations and convergent evolution in species and communities. In: Cody, M.L. and Diamond, J.M. (eds) *Ecology and Evolution of Communities*. Belknap Press, Cambridge, Massachusetts, pp. 258–291.
- Katusic-Malmberg, P. and Willson, M.F. (1988) Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois woodlot. *Condor* 90, 173–186.
- Kenward, R.E. and Sibly, R.M. (1977) A woodpigeon (*Columba palumbus*) feeding preference explained by a digestive bottle-neck. *Journal of Applied Ecology* 14, 815–826.
- Kinnaird, M.F. (1998) Evidence for effective seed dispersal by the Sulawesi red-knobbed hornbill, *Aceros cassidix*. *Biotropica* 30, 50–55.
- Ko, I.W.P., Corlett, R.T. and Xu, R.J. (1998) Sugar composition of wild fruits in Hong Kong, China. *Journal of Tropical Ecology* 14, 381–387.
- Kochmer, J.P. and Handel, S.N. (1986) Constraints and competition in the evolution of flowering phenology. *Ecological Monographs* 56, 303–325.
- Koelmeyer, K.O. (1959) The periodicity of leaf change and flowering in the principal forest communities of Ceylon. *Ceylon Forester* 4, 157–189.
- Kollmann, J. and Poschod, P. (1997) Population processes at the grassland–scrub interface. *Phytocoenologia* 27, 235–256.
- Korine, C., Arad, Z. and Arieli, A. (1996) Nitrogen and energy balance of the fruit bat *Rousettus aegyptiacus* on natural fruit diets. *Physiological Zoology* 69, 618–634.
- Kunz, T.H. and Diaz, C.A. (1995) Folivory in fruit-eating bats, with new evidence from *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica* 27, 106–120.
- Ladley, J.J. and Kelly, D. (1996) Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): dependence on birds. *New Zealand Journal of Ecology* 20, 69–79.
- Lambert, F. (1989a) Fig-eating by birds in a Malaysian lowland rain forest. *Journal of Tropical Ecology* 5, 401–412.
- Lambert, F. (1989b) Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. *Ibis* 131, 521–527.
- Langer, P. (1986) Large mammalian herbivores in tropical forests with either hindgut- or forestomach-fermentation. *Zeitschrift für Säugetierkunde* 51, 173–187.
- Lee, W.G., Grubb, P.J. and Wilson, J.B. (1991) Patterns of resource allocation in fleshy fruits of nine European tall-shrub species. *Oikos* 61, 307–315.
- Leigh, E.G., Jr (1975) Structure and climate in tropical rain forest. *Annual Review of Ecology and Systematics* 6, 67–86.
- Leighton, M. and Leighton, D.R. (1984) Vertebrate responses to fruiting seasonality within a Bornean rainforest. In: Sutton, S.L., Whitmore, T.C. and Chadwick, A.C. (eds) *Tropical Rainforests: Ecology and Management*. Blackwell Scientific Publications, Oxford, pp. 181–209.
- Levey, D.J. (1986) Methods of seed processing by birds and seed deposition patterns. In: Estrada, A. and Fleming, T.H. (eds) *Frugivores and Seed Dispersal*. Junk, Dordrecht, pp. 147–158.
- Levey, D.J. (1987) Seed size and fruit-handling techniques of avian frugivores. *American Naturalist* 129, 471–485.
- Levey, D.J. (1988a) Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58, 251–269.
- Levey, D.J. (1988b) Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69, 1076–1089.
- Levey, D.J. (1990) Habitat-dependent fruiting behaviour of an understory tree, *Miconia centrodresma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology* 6, 409–420.
- Levey, D.J. and Duke, G.E. (1992) How do frugivores process fruit: gastrointestinal transit and glucose absorption in cedar waxwings (*Bombycilla cedrorum*). *Auk* 109, 722–730.
- Levey, D.J. and Grajal, A. (1991) Evolutionary implications of fruit-processing limitations in cedar waxwings. *American Naturalist* 138, 171–189.
- Levey, D.J. and Stiles, F.G. (1992) Evolutionary precursors of long-distance migration: resource availability and movement patterns in neotropical landbirds. *American Naturalist* 140, 447–476.
- Levey, D.J., Moermond, T.C. and Denslow, J.S. (1984) Fruit choice in neotropical birds: the effect of distance between fruits on preference patterns. *Ecology* 65, 844–850.

- Lieberman, D. (1982) Seasonality and phenology in a dry tropical forest in Ghana. *Journal of Ecology* 70, 791–806.
- Lieberman, D., Lieberman, M. and Martin, C. (1987) Notes on seeds in elephant dung from Bia National Park, Ghana. *Biotropica* 19, 365–369.
- Lieberman, M. and Lieberman, D. (1980) The origin of gardening as an extension of infra-human seed dispersal. *Biotropica* 12, 316.
- Loiselle, B.A. (1990) Seeds in droppings of tropical fruit-eating birds: importance of considering seed composition. *Oecologia* 82, 494–500.
- Loiselle, B.A. and Blake, J.G. (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72, 180–193.
- Losos, J.B. and Greene, H.W. (1988) Ecological and evolutionary implications of diet in monitor lizards. *Biological Journal of the Linnean Society* 35, 379–407.
- McDiarmid, R.W., Ricklefs, R.E. and Foster, M.S. (1977) Dispersal of *Stemmadennia donnell-smithii* (Apocyanaceae) by birds. *Biotropica* 9, 9–25.
- McDonnell, M.J. and Stiles, E.W. (1983) The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56, 109–116.
- McKey, D. (1975) The ecology of coevolved seed dispersal systems. In: Gilbert, L.E. and Raven, P.H. (eds) *Coevolution of Animals and Plants*. University of Texas Press, Austin, pp. 159–191.
- McKey, D.B., Gartlan, J.S., Waterman, P.G. and Choo, G.M. (1981) Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biological Journal of the Linnean Society* 16, 115–146.
- McWilliams, S.R. and Karasov, W.H. (1998) Test of a digestion optimization model: effects of costs of feeding on digestive parameters. *Physiological Zoology* 71, 168–178.
- Mack, A.L. (1990) Is frugivory limited by secondary compounds in fruits? *Oikos* 57, 135–138.
- Mack, A.L. (1993) The sizes of vertebrate-dispersed fruits: a neotropical–paleotropical comparison. *American Naturalist* 142, 840–856.
- Magnan, A. (1912) Essai de morphologie stomacal en fonction du régime alimentaire chez les oiseaux. *Annales des Sciences Naturelles, Zoologie, 9e Série* 15, 1–41.
- Manasse, R.S. and Howe, H.F. (1983) Competition for dispersal agents among tropical trees: influences of neighbors. *Oecologia* 59, 185–190.
- Marks, P.L. (1974) The role of pin cherry (*Prunus pennsylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecological Monographs* 44, 73–88.
- Marks, P.L. and Harcombe, P.A. (1981) Forest vegetation of the Big Thicket, Southeast Texas. *Ecological Monographs* 51, 287–305.
- Marshall, A.G. (1983) Bats, flowers and fruit: evolutionary relationships in the Old World. *Biological Journal of the Linnean Society* 20, 115–135.
- Marshall, A.G. and McWilliam, A.N. (1982) Ecological observations on Epomorphorinae fruit-bats (Megachiroptera) in West African savannah woodland. *Journal of Zoology, London* 198, 53–67.
- Martin, T.E. (1985) Selection of second-growth woodlands by frugivorous migrating birds in Panama: an effect of fruit size and plant density? *Journal of Tropical Ecology* 1, 157–170.
- Martin, T.E. and Karr, J.R. (1986) Temporal dynamics of neotropical birds with special reference to frugivores in second-growth woods. *Wilson Bulletin* 98, 38–60.
- Martínez del Río, C. and Karasov, W.H. (1990) Digestion strategies in nectar- and fruit-eating birds and the sugar composition of plant rewards. *American Naturalist* 136, 618–637.
- Martínez del Río, C. and Restrepo, C. (1993) Ecological and behavioral consequences of digestion in frugivorous animals. In: Fleming, T.H. and Estrada, A. (eds) *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects*. Kluwer Academic Publisher, Dordrecht, The Netherlands, pp. 205–216.
- Mazer, S.J. and Wheelwright, N.T. (1993) Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. *Evolutionary Ecology* 7, 556–575.
- Medway, L. (1972) Phenology of a tropical rain forest in Malaya. *Biological Journal of the Linnean Society* 4, 117–146.
- Merz, G. (1981) Recherches sur la biologie de nutrition et les habitats préférés de l'éléphant de forêt, *Loxodonta africana cyclotis* Matschie. *Mammalia* 45, 299–312.
- Milewski, A.V. (1982) The occurrence of seeds and fruits taken by ants versus birds in Mediterranean Australia and Southern Africa, in relation to the availability of soil potassium. *Journal of Biogeography* 9, 505–516.
- Milewski, A.V. and Bond, W.J. (1982) Convergence in myrmecochory in Mediterranean Australia and South Africa. In: Buckley, R.C. (ed.) *Ant-Plant Interactions in Australia*. Junk, Dordrecht, pp. 89–98.
- Milton, K.L. (1981) Food choice and digestive strategies of two sympatric primate species. *American Naturalist* 117, 496–505.
- Moermond, T.C. and Denslow, J.S. (1985) Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. In: Buckley, P.A., Foster, M.S.,

- Morton, E.S., Ridgely, R.S. and Buckley, F.G. (eds) *Neotropical Ornithology*. Ornithological Monographs No. 36, American Ornithologist Union, Washington, pp. 865–897.
- Moermond, T.C., Denslow, J.S., Levey, D.J. and Santana, E. (1986) The influence of morphology on fruit choice in neotropical birds. In: Estrada, A. and Fleming, T.H. (eds) *Frugivores and Seed Dispersal*. Junk, Dordrecht, pp. 137–146.
- Mooney, H.A., Kummerov, J., Johnson, A.W., Parsons, D.J., Keeley, S.A., Hoffmann, A., Hays, R.I., Gilberto, J. and Chu, C. (1977) The producers – their resources and adaptive responses. In: Mooney, H.A. (ed.) *Convergent Evolution in Chile and California*. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp. 85–143.
- Morel, G. and Morel, M.Y. (1972) Recherches écologiques sur une savane sahéenne du Ferlo septentrional, Sénégal: l'avifaune et son cycle annuel. *La Terre et la Vie* 26, 410–439.
- Morris, J.G. and Rogers, Q.R. (1983) Nutritionally related metabolic adaptations of carnivores and ruminants. In: Margaris, N.S., Arianoutsou-Faraggitaki, M. and Reiter, R.J. (eds) *Plant, Animal and Microbial Adaptations to Terrestrial Environment*. Plenum, New York, pp. 165–180.
- Morrison, D.W. (1980) Efficiency of food utilization by fruit bats. *Oecologia* 45, 270–273.
- Morton, E.S. (1973) On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *American Naturalist* 107, 8–22.
- Murray, K.G. (1988) Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs* 58, 271–298.
- Nagy, K.A. and Milton, K. (1979) Aspects of dietary quality, nutrient assimilation and water balance in wild howler monkeys (*Alouatta palliata*). *Oecologia* 39, 249–258.
- Noma, N. and Yumoto, T. (1997) Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. *Ecological Research* 12, 119–129.
- Oates, J.F. (1978) Water-plant and soil consumption by guereza monkeys (*Colobus guereza*): a relationship with minerals and toxins in the diet? *Biotropica* 10, 241–253.
- Oates, J.F., Waterman, P.G. and Choo, G.M. (1980) Food selection by the South Indian leaf-monkey, *Presbytis johnii*, in relation to food chemistry. *Oecologia* 45, 45–56.
- O'Dowd, D.J. and Gill, A.M. (1986) Seed dispersal syndromes in Australian *Acacia*. In: Murray, D.R. (ed.) *Seed Dispersal*. Academic Press, Sydney, Australia, pp. 87–121.
- Opler, P.A., Frankie, G.W. and Baker, H.G. (1980) Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 68, 167–188.
- Pannell, C.M. and Koziol, M.J. (1987) Ecological and phytochemical diversity of arillate seeds in *Aglaia* (Meliaceae): a study of vertebrate dispersal in tropical trees. *Philosophical Transactions of the Royal Society, London, Series B* 316, 303–333.
- Parrish, J.D. (1997) Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. *Condor* 99, 681–697.
- Piper, J.K. (1986a) Effects of habitat and size of fruit display on removal of *Smilacina stellata* (Liliaceae) fruits. *Canadian Journal of Botany* 64, 1050–1054.
- Piper, J.K. (1986b) Seasonality of fruit characters and seed removal by birds. *Oikos* 46, 303–310.
- Poupon, H. and Bille, J.C. (1974) Recherches écologiques sur une savane sahéenne du Ferlo septentrional, Sénégal: influence de la sécheresse de l'année 1972–1973 sur la strate ligneuse. *La Terre et la Vie* 28, 49–75.
- Pratt, T.K. (1983) Diet of the dwarf cassowary *Casuarus bennetti picticollis* at Wau, Papua New Guinea. *Emu* 82, 283–285.
- Pratt, T.K. (1984) Examples of tropical frugivores defending fruit-bearing plants. *Condor* 86, 123–129.
- Pratt, T.K. and Stiles, E.W. (1983) How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. *American Naturalist* 122, 797–805.
- Pratt, T.K. and Stiles, E.W. (1985) The influence of fruit size and structure on composition of frugivore assemblages in New Guinea. *Biotropica* 17, 314–321.
- Primack, R.B. (1987) Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* 18, 409–430.
- Pulliaian, E., Helle, P. and Tunkkari, P. (1981) Adaptive radiation of the digestive system, heart and wings of *Turdus pilaris*, *Bombycilla garrulus*, *Sturnus vulgaris*, *Pyrrhula pyrrhula*, *Pinicola enucleator* and *Loxia pytyopsittacus*. *Ornis Fennica* 58, 21–28.
- Putz, F.E. (1979) Aseasonality in Malaysian tree phenology. *Malaysian Forester* 42, 1–24.
- Reid, N. (1989) Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. *Ecology* 70, 137–145.
- Reid, N. (1990) Mutualistic interdependence between mistletoes (*Amyema quandang*), and spiny-cheeked honeyeaters and mistletoebirds in an arid woodland. *Australian Journal of Ecology* 15, 175–190.
- Restrepo, C. and Gómez, N. (1998) Responses of understory birds to anthropogenic edges in a neotropical montane forest. *Ecological Applications* 8, 170–183.

- Rey, P.J. and Gutiérrez, J.E. (1996) Pecking of olives by frugivorous birds: a shift in feeding behaviour to overcome gape limitation. *Journal of Avian Biology* 27, 327–333.
- Rey, P.J., Gutiérrez, J.E., Alcántara, J. and Valera, F. (1997) Fruit size in wild olives: implications for avian seed dispersal. *Functional Ecology* 11, 611–618.
- Robbins, C.T. (1983) *Wildlife Feeding and Nutrition*, Academic Press, New York.
- Rogers, M.E., Maisels, F., Williamson, E.A., Fernández, M. and Tutin, C.E.G. (1990) Gorilla diet in the Lopé Reserve, Gabon: a nutritional analysis. *Oecologia* 84, 326–339.
- Sallabanks, R. (1992) Fruit fate, frugivory, and fruit characteristics: a study of the hawthorn, *Crataegus monogyna* (Rosaceae). *Oecologia* 91, 296–304.
- Santana, E. and Milligan, B.G. (1984) Behavior of toucanets, bellbirds, and quetzals feeding on lauraceous fruits. *Biotropica* 16, 152–154.
- Schlesinger, W.H. (1978) Community structure, dynamics and nutrient cycling in the Okefenokee Cypress swamp forest. *Ecological Monographs* 48, 43–65.
- Schupp, E.W. (1988) Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51, 71–78.
- Schupp, E.W. (1993) Quantity, quality, and the effectiveness of seed dispersal by animals. In: Fleming, T.H. and Estrada, A. (eds) *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 15–29.
- Schupp, E.W. and Fuentes, M. (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2, 267–275.
- Sherburne, J.A. (1972) Effects of seasonal changes in the abundance and chemistry of the fleshy fruits of northern woody shrubs on patterns of exploitation by frugivorous birds. Unpublished PhD thesis, Cornell University.
- Short, J. (1981) Diet and feeding behaviour of the forest elephant. *Mammalia* 45, 177–185.
- Sibly, R.M. (1981) Strategies of digestion and defecation. In: Townsend, C.R. and Calow, P. (eds) *Physiological Ecology: an Evolutionary Approach to Resource Use*. Blackwell Scientific Publications, London, pp. 109–138.
- Simons, D. and Bairlein, F. (1990) The significance of seasonal frugivory in migratory garden warblers *Sylvia borin*. *Journal für Ornithologie* 131, 381–401.
- Smith, A.J. (1975) Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. *Ecology* 56, 19–34.
- Snow, B.K. (1979) The oilbirds of Los Tayos. *Wilson Bulletin* 91, 457–461.
- Snow, B.K. and Snow, D.W. (1984) Long-term defence of fruit by mistle thrushes *Turdus viscivorus*. *Ibis* 126, 39–49.
- Snow, B.K. and Snow, D.W. (1988) *Birds and Berries*. T. & A.D. Poyser, Calton, UK.
- Snow, D.W. (1962a) A field study of the black and white manakin, *Manacus manacus*, in Trinidad. *Zoologica* 47, 65–109.
- Snow, D.W. (1962b) A field study of the golden-headed manakin, *Pipra erythrocephala*, in Trinidad, W.I. *Zoologica* 47, 183–198.
- Snow, D.W. (1962c) The natural history of the oilbird, *Steatornis caripensis*, in Trinidad, W.I. Part 2. Population, breeding ecology and food. *Zoologica* 47, 199–221.
- Snow, D.W. (1971) Evolutionary aspects of fruit-eating by birds. *Ibis* 113, 194–202.
- Snow, D.W. (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13, 1–14.
- Sorensen, A.E. (1981) Interactions between birds and fruit in a temperate woodland. *Oecologia* 50, 242–249.
- Sorensen, A.E. (1983) Taste aversion and frugivore preference. *Oecologia* 56, 117–120.
- Sorensen, A.E. (1984) Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). *Journal of Animal Ecology* 53, 545–557.
- Sourd, C. and Gauthier-Hion, A. (1986) Fruit selection by a forest guenon. *Journal of Animal Ecology* 55, 235–244.
- Stiles, E.W. (1980) Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *American Naturalist* 116, 670–688.
- Stiles, E.W. and White, D.W. (1986) Seed deposition patterns: influence of season, nutrients, and vegetation structure. In: Estrada, A. and Fleming, T.H. (eds) *Frugivores and Seed Dispersal*. Junk, Dordrecht, pp. 45–54.
- Stocker, G.C. and Irvine, A.K. (1983) Seed dispersal by cassowaries (*Casuarius casuarius*) in North Queensland's rainforests. *Biotropica* 15, 170–176.
- Stransky, J.J. and Halls, L.K. (1980) Fruiting of woody plants affected by site preparation and prior land use. *Journal of Wildlife Management* 44, 258–263.
- Studier, E.H., Szuch, E.J., Thompkins, T.M. and Cope, V.M. (1988) Nutritional budgets in free flying birds: cedar waxwings (*Bombycilla cedrorum*) feeding on Washington hawthorn fruit (*Crataegus phaenopyrum*). *Comparative Biochemistry and Physiology* 89A, 471–474.

- Sukumar, R. (1990) Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. *Journal of Tropical Ecology* 6, 33–53.
- Sun, C. and Moermond, T.C. (1997) Foraging ecology of three sympatric turacos in a montane forest in Rwanda. *Auk* 114, 396–404.
- Sun, C., Ives, A.R., Kraeuter, H.J. and Moermond, T.C. (1997) Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia* 112, 94–103.
- Swain, T. (1979) Tannins and lignins. In: Rosenthal, G.A. and Janzen, D.H. (eds) *Herbivores: Their Interaction with Secondary Plant Metabolites*. Academic Press, New York, pp. 657–682.
- Tanner, E.V.J. (1982) Species diversity and reproductive mechanisms in Jamaican trees. *Biological Journal of the Linnean Society* 18, 263–278.
- Terborgh, J. (1983) *Five New World Primates. A Study in Comparative Ecology*, Princeton University Press, Princeton, New Jersey.
- Tester, M., Paton, D., Reid, N. and Lange, R.T. (1987) Seed dispersal by birds and densities of shrubs under trees in arid south Australia. *Transactions of the Royal Society of South Australia* 111, 1–5.
- Théry, M. and Larpin, D. (1993) Seed dispersal and vegetation dynamics at a cock-of-the-rock's lek in the tropical forest of French-Guiana. *Journal of Tropical Ecology* 9, 109–116.
- Thomas, D.W. (1984) Fruit intake and energy budgets of frugivorous bats. *Physiological Zoology* 57, 457–467.
- Thompson, J.N. and Willson, M.F. (1978) Disturbance and the dispersal of fleshy fruits. *Science* 200, 1161–1163.
- Traveset, A. (1994) Influence of type of avian frugivory on the fitness of *Pistacia terebinthus*. *Evolutionary Ecology* 8, 618–627.
- Turcek, F.J. (1961) *Ökologische Beziehungen der Vögel und Gehölze*. Slowakische Akademie der Wissenschaften, Bratislava.
- Tutin, C.E.G., Williamson, E.A., Rogers, M.E. and Fernandez, M. (1991) A case study of a plant–animal relationship: *Cola lizae* and lowland gorillas in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 7, 181–199.
- Tutin, C.E.G., Parnell, R.J. and White, F. (1996) Protecting seeds from primates: examples from *Diospyros* spp. in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 12, 371–384.
- van Schaik, C.P., Terborgh, J.W. and Wright, S.J. (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24, 353–377.
- Viljoen, S. (1983) Feeding habits and comparative feeding rates of three Southern African arboreal squirrels. *South African Journal of Zoology* 18, 378–387.
- Voronov, H.R. and Voronov, P.H. (1978) [Morphometric study of the digestive system of the Waxwing (*Bombycilla garrulus* L.) (Aves, Bombycillidae)]. *Vestnyk Zoology* 5, 28–31.
- Walsberg, G.E. (1975) Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. *Condor* 77, 169–174.
- Waterman, P.G., Mbi, C.N., McKey, D.B. and Gartlan, J.S. (1980) African rainforest vegetation and rumen microbes: phenolic compounds and nutrients as correlates of digestibility. *Oecologia* 47, 22–33.
- Wenny, D.G. and Levey, D.J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences USA* 95, 6204–6207.
- Wetmore, A. (1914) The development of stomach in the euphonias. *Auk* 31, 458–461.
- Wheelwright, N.T. (1983) Fruits and the ecology of resplendent quetzals. *Auk* 100, 286–301.
- Wheelwright, N.T. (1985) Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66, 808–818.
- Wheelwright, N.T. (1986) The diet of American robins: an analysis of US Biological Survey records. *Auk* 103, 710–725.
- Wheelwright, N.T. (1988) Seasonal changes in food preferences of American robins in captivity. *Auk* 105, 374–378.
- Wheelwright, N.T., Haber, W.A., Murray, K.G. and Guindon, C. (1984) Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16, 173–192.
- White, D.W. and Stiles, E.W. (1990) Co-occurrences of foods in stomachs and feces of fruit-eating birds. *Condor* 92, 291–303.
- White, D.W. and Stiles, E.W. (1991) Fruit harvesting by American robins: influence of fruit size. *Wilson Bulletin* 103, 690–692.
- White, S.C. (1974) Ecological aspects of growth and nutrition in tropical fruit-eating birds. Unpublished PhD thesis, University of Pennsylvania.
- Whitney, K.D. and Smith, T.B. (1998) Habitat use and resource tracking by African *Ceratogymna* hornbills: implications for seed dispersal and forest conservation. *Animal Conservation* 1, 107–117.

- Williamson, E.A., Tutin, C.E.G., Rogers, M.E. and Fernandez, M. (1990) Composition of the diet of lowland gorillas at Lopé in Gabon. *American Journal of Primatology* 21, 265–277.
- Willson, M.F. (1986) Avian frugivory and seed dispersal in eastern North America. In: Johnston, R.F. (ed.) *Current Ornithology*, Vol. 3. Plenum, New York, pp. 223–279.
- Willson, M.F. (1988) Spatial heterogeneity of post-dispersal survivorship of Queensland rainforest seeds. *Australian Journal of Ecology* 13, 137–145.
- Willson, M.F., Porter, E.A. and Condit, R.S. (1982) Avian frugivore activity in relation to forest light gaps. *Caribbean Journal of Science* 18, 1–4.
- Willson, M.F., Irvine, A.K. and Walsh, N.G. (1989) Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica* 21, 133–147.
- Witmer, M.C. (1996) Annual diet of cedar waxwings based on US Biological Survey records (1885–1950) compared to diet of American robins: contrasts in dietary patterns and natural history. *Auk* 113, 414–430.
- Witmer, M.C. (1998a) Ecological and evolutionary implications of energy and protein requirements of avian frugivores eating sugary diets. *Physiological Zoology* 71, 599–610.
- Witmer, M.C. (1998b) Do seeds hinder digestive processing of fruit pulp? Implications for plant/frugivore mutualisms. *Auk* 115, 319–326.
- Witmer, M.C. and van Soest, P.J. (1998) Contrasting digestive strategies of fruit-eating birds. *Functional Ecology* 12, 728–741.
- Wood, C.A. (1924) The Polynesian fruit pigeon, *Globicera pacifica*, its food and digestive apparatus. *Auk* 41, 433–438.
- Worthington, A.H. (1982) Population sizes and breeding rhythms of two species of manakins in relation to food supply. In: Leigh, E.G., Rand, A.S. and Windsor, D.M. (eds) *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Smithsonian Institution Press, Washington, DC, pp. 213–225.
- Worthington, A.H. (1989) Adaptations for avian frugivory: assimilation efficiency and gut transit time of *Manacus vitellinus* and *Pipra mentalis*. *Oecologia* 80, 381–389.
- Wrangham, R.W., Chapman, C.A. and Chapman, L.J. (1994) Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* 10, 355–368.
- Wrangham, R.W., Conklin-Brittain, N.L. and Hunt, K.D. (1998) Dietary responses of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology* 19, 949–970.
- Zhang, S.Y. and Wang, L.X. (1995) Comparison of three fruit census methods in French Guiana. *Journal of Tropical Ecology* 11, 281–294.

Appendix

Summary statistics (sample size, mean and SE of the mean for each family and variable) of fruit characteristics and pulp constituents of vertebrate-dispersed plants, by families.

Family	Fruit diameter (mm)	Pulp dry mass (g)	Seed dry mass (g)	Relative yield	kcal g ⁻¹ dry mass	kcal fruit ⁻¹	% Water	Lipids	Protein	Carbo-hydrates	Ash
<i>Anacardiaceae</i> (n = 12)											
	5	6	5	6	10	5	9	10	10	10	7
	7.6	0.047	0.117	21.25	5.410	0.122	57.12	0.240	0.054	0.638	0.033
	2.3	0.029	0.093	6.90	0.473	0.051	7.69	0.080	0.005	0.090	0.007
<i>Annonaceae</i> (n = 11)											
	3	5	3	4	5	3	7	8	9	7	5
	15.1	0.374	0.405	16.28	3.043	1.458	71.67	0.114	0.042	0.636	0.022
	1.8	0.156	0.233	4.28	0.629	1.181	6.53	0.039	0.009	0.093	0.008
<i>Apocynaceae</i> (n = 10)											
	2	3	3	3	8	2	7	9	9	9	6
	6.1	0.313	0.147	15.80	4.734	2.026	79.09	0.143	0.047	0.762	0.032
	2.4	0.290	0.099	6.05	0.412	1.904	3.47	0.069	0.014	0.094	0.011
<i>Caprifoliaceae</i> (n = 26)											
	16	17	16	17	21	14	25	17	21	17	15
	6.6	0.088	0.127	15.97	4.175	0.426	71.60	0.057	0.060	0.756	0.060
	0.4	0.057	0.104	1.80	0.086	0.284	3.27	0.016	0.010	0.049	0.007
<i>Ericaceae</i> (n = 10)											
	8	8	8	8	6	4	10	6	6	6	6
	9.9	0.199	0.026	17.25	4.200	1.275	78.61	0.047	0.034	0.899	0.024
	1.4	0.129	0.007	2.70	0.029	1.091	2.85	0.006	0.002	0.012	0.006
<i>Lauraceae</i> (n = 46)											
	36	39	26	39	27	21	41	39	40	28	4
	15.6	0.510	0.680	14.32	4.337	1.956	68.03	0.271	0.061	0.274	0.032
	0.9	0.089	0.134	0.93	0.360	0.396	2.05	0.021	0.007	0.044	0.004
<i>Liliaceae</i> (n = 13)											
	11	13	12	13	8	8	13	8	8	8	10
	9.3	0.055	0.091	14.18	4.056	0.243	69.06	0.030	0.046	0.782	0.061
	0.6	0.008	0.022	1.94	0.078	0.049	2.88	0.008	0.006	0.067	0.008
<i>Melastomataceae</i> (n = 7)											
	2	3	3	3	6	2	7	4	6	6	3
	4.9	0.035	0.009	22.03	3.407	0.202	75.11	0.044	0.035	0.738	0.057
	0.4	0.027	0.006	8.30	0.386	0.176	4.85	0.016	0.009	0.080	0.012
<i>Meliaceae</i> (n = 19)											
	4	7	4	7	15	4	9	17	18	15	8
	12.4	0.237	0.120	20.96	5.627	1.232	53.88	0.305	0.075	0.588	0.032
	2.7	0.052	0.015	4.19	0.346	0.283	7.16	0.059	0.016	0.071	0.008
<i>Moraceae</i> (n = 39)											
	14	8	7	7	20	6	18	19	25	18	12
	13.4	0.588	0.286	10.77	3.462	2.997	79.67	0.044	0.055	0.653	0.071
	2.0	0.254	0.177	1.19	0.238	1.378	1.50	0.008	0.007	0.057	0.008
<i>Myrsinaceae</i> (n = 4)											
	3	4	3	4	3	3	4	4	4	3	2
	8.9	0.029	0.030	11.98	3.376	0.126	82.45	0.062	0.041	0.629	0.066
	2.4	0.009	0.013	1.39	0.942	0.052	2.94	0.021	0.019	0.165	0.013
<i>Myrtaceae</i> (n = 18)											
	8	8	4	8	11	3	14	14	16	12	9
	15.5	0.730	0.477	10.86	3.265	0.805	82.29	0.022	0.040	0.722	0.037
	3.1	0.433	0.313	1.85	0.347	0.374	2.02	0.004	0.003	0.077	0.005

Family	Fruit diameter (mm)	Pulp dry mass (g)	Seed dry mass (g)	Relative yield	kcal dry mass g ⁻¹	kcal fruit ⁻¹	% Water	Lipids	Protein	Carbo-hydrates	Ash
<i>Oleaceae</i> (n = 9)											
	7	6	5	6	8	5	6	8	9	7	7
	7.4	0.123	0.072	15.62	4.254	0.207	62.98	0.079	0.046	0.796	0.029
	0.7	0.084	0.038	1.13	0.334	0.094	4.79	0.049	0.005	0.060	0.005
<i>Palmae</i> (n = 17)											
	6	7	6	7	13	3	11	14	14	13	6
	13.7	0.582	1.436	12.34	4.356	5.396	54.30	0.181	0.061	0.592	0.079
	1.2	0.412	1.015	4.35	0.361	3.999	9.00	0.048	0.012	0.069	0.021
<i>Piperaceae</i> (n = 11)											
	1	2	1	2	10	1	11	11	11	10	1
	5.1	0.118	0.170	13.55	2.468	0.964	83.27	0.057	0.074	0.389	0.125
	-	0.103	-	5.75	0.285	-	2.24	0.014	0.007	0.044	-
<i>Rhamnaceae</i> (n = 13)											
	7	7	7	7	10	6	11	10	11	10	7
	8.2	0.110	0.090	16.20	3.785	0.494	66.50	0.014	0.053	0.839	0.051
	1.2	0.084	0.044	3.12	0.120	0.389	3.44	0.004	0.011	0.031	0.013
<i>Rosaceae</i> (n = 47)											
	37	34	31	34	36	26	40	31	38	30	26
	12.3	0.390	0.120	21.83	3.928	1.757	66.78	0.023	0.044	0.787	0.044
	0.9	0.116	0.025	1.75	0.109	0.594	2.08	0.002	0.004	0.045	0.004
<i>Rubiaceae</i> (n = 23)											
	8	15	9	15	10	5	19	10	16	10	7
	7.8	0.019	0.013	11.31	3.875	0.035	81.99	0.047	0.045	0.728	0.043
	1.6	0.006	0.005	2.22	0.171	0.007	2.82	0.016	0.011	0.052	0.010
<i>Rutaceae</i> (n = 6)											
	3	3	2	3	4	2	3	5	4	4	4
	16.5	0.503	0.862	4.29	4.285	2.178	72.50	0.104	0.100	0.650	0.066
	6.8	0.276	0.826	4.47	0.371	1.931	8.88	0.030	0.007	0.043	0.011
<i>Sapotaceae</i> (n = 10)											
	2	4	3	4	7	2	6	9	9	8	7
	16.2	0.477	0.145	21.13	3.761	1.327	74.08	0.073	0.063	0.742	0.045
	4.4	0.228	0.065	3.64	0.309	0.902	3.59	0.016	0.013	0.066	0.011
<i>Smilacaceae</i> (n = 4)											
	3	4	2	4	4	4	4	4	4	4	2
	7.4	0.036	0.051	12.55	4.215	0.153	77.45	0.011	0.050	0.488	0.069
	0.1	0.005	0.012	0.62	0.214	0.026	3.67	0.004	0.006	0.215	0.019
<i>Solanaceae</i> (n = 25)											
	13	13	10	13	19	8	24	21	22	19	7
	11.2	0.099	0.085	10.54	3.019	0.522	81.33	0.044	0.093	0.487	0.056
	0.8	0.021	0.021	1.04	0.345	0.123	1.43	0.022	0.009	0.063	0.012
<i>Tiliaceae</i> (n = 6)											
	0	0	0	0	6	0	0	6	6	6	6
	-	-	-	-	2.945	-	-	0.010	0.064	0.650	0.039
	-	-	-	-	0.249	-	-	0.003	0.012	0.054	0.006
<i>Ulmaceae</i> (n = 5)											
	3	3	2	3	5	3	3	4	5	4	3
	8.9	0.118	0.068	33.67	5.044	0.494	44.87	0.241	0.084	0.380	0.082
	0.5	0.063	0.066	5.02	0.628	0.243	11.20	0.136	0.027	0.183	0.017
<i>Viscaceae</i> (n = 9)											
	6	7	4	6	6	3	7	6	7	5	3
	5.6	0.041	0.010	15.55	4.847	0.161	74.13	0.163	0.084	0.671	0.040
	0.5	0.021	0.003	3.08	0.430	0.049	5.12	0.075	0.023	0.081	0.003

Family	Fruit diameter (mm)	Pulp dry mass (g)	Seed dry mass (g)	Relative yield	kcal dry mass g^{-1}	kcal fruit ⁻¹	% Water	Lipids	Protein	Carbo-hydrates	Ash
<i>Vitaceae</i> (<i>n</i> = 8)	6	5	2	5	5	3	7	5	5	4	2
	9.2	0.071	0.050	13.72	4.528	0.279	81.86	0.138	0.041	0.509	0.016
	0.5	0.022	0.000	2.20	0.286	0.127	3.16	0.060	0.017	0.227	0.010

Only families with more than four species sampled have been included. For each family, numbers above the mean of each variable indicate the number of species with data available for that variable. Figures for pulp constituents are proportions relative to pulp dry mass.

Data from Snow (1962c); Sherburne (1972); White (1974); Crome (1975); McDiarmid *et al.* (1977); Nagy and Milton (1979); Snow (1979); Frost (1980); Morrison (1980); Howe (1981); Howe and Vande Kerckhove (1981); Beehler (1983); Foster and McDiarmid (1983); Jordano (1983); Viljoen (1983); Estrada *et al.* (1984); Wheelwright *et al.* (1984); Johnson *et al.* (1985); Moermond and Denslow (1985); Dinerstein (1986); Piper (1986b); Sourd and Gauthier-Hion (1986); Debussche *et al.* (1987); Herrera (1987); Pannell and Koziol (1987); Atramentowicz (1988); Dowsett-Lemaire (1988); Abrahamson and Abrahamson (1989); Izhaki and Safriel (1989); Worthington (1989); F.H.J. Crome, personal communication; C.M. Herrera and P. Jordano, unpublished data.

n, Number of species sampled per family.

CABI Publishing is a division of CAB International

CABI Publishing
CAB International
Wallingford
Oxon OX10 8DE
UK

Tel: +44 (0)1491 832111
Fax: +44 (0)1491 833508
Email: cabi@cabi.org
Web site: <http://www.cabi.org>

CABI Publishing
10 E 40th Street
Suite 3203
New York, NY 10016
USA

Tel: +1 212 481 7018
Fax: +1 212 686 7993
Email: cabi-nao@cabi.org

© CAB International 2000. All rights reserved. No part of this publication may be reproduced in any form or by any means, electronically, mechanically, by photocopying, recording or otherwise, without the prior permission of the copyright owners.

A catalogue record for this book is available from the British Library,
London, UK.

Library of Congress Cataloging-in-Publication Data

Seeds : the ecology of regeneration in plant communities / edited by M. Fenner.-- 2nd ed.

p. cm.

Includes bibliographical references.

ISBN 0-85199-432-6 (alk. paper)

1. Seeds--Ecology. 2. Plants--Reproduction. I. Fenner, Michael, 1949-

QK661 .S428 2000

575.6'8--dc21

00-041388

ISBN 0 85199 432 6

Typeset by Columns Design Ltd, Reading.
Printed and bound in the UK by Biddles Ltd, Guildford and King's Lynn.