2 Fruits and Frugivory

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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 and fish, which are able to obtain energy and nutrients from it (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 animal-mediated seed dispersal.

Early conceptual contributions to the study of frugivory emphasized dichotomies in frugivory patterns and fruit characteristics that presumably had been originated by co-evolved interactions (Snow, 1971; McKey, 1975; Howe and Estabrook, 1977; van der Pijl, 1982). 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 three decades has centred around these seminal ideas and there is a bulk 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 (see Estrada and Fleming, 1986; Fleming and Estrada, 1993; Corlett, 1998; Levey *et al.*, 2002; Dennis *et al.*, 2007, for reviews). Frugivory and dispersal influence the evolution of plant traits through effects on population processes, but notably absent are predictive frameworks that link frugivory patterns, associated differences in seed/seedling mortality and differential reproductive success, and demographic patterns in natural plant populations (Howe, 1989). 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,

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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 p~~redictive 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).

For most frugivores, fleshy fruits are a non-exclusive food resource that is supplemented with animal prey, vegetative plant parts, seeds, etc. (Hladik, 1981; Moermond and Denslow, 1985; Fleming, 1986; Howe, 1986; Willson, 1986; Corlett, 1998, 2011). Very few vertebrates rely totally on fruit food but many species are 'partial' frugivores that consume other prey together with various amounts of fruit; dietary habits among these species range between sporadic fruit consumption to almost totally frugivorous diets. For example, only 17 families of birds (15.6%) can be considered as strictly frugivorous, yet 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; Muscarella and Fleming, 2007; Kunz *et al.*, 2011), 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; Lambert and Garber, 1998; Lambert, 2011) 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, turtles, 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; Olesen and Valido, 2004). Fish are extremely important frugivores in some habitats, such as Amazonian várzea forest or the Pantanal, subject to periodic inundation (Horn *et al.*, 2011).

Frugivorous animals, relying sporadically or obligately on fruits for food have a central role in demography, population genetics 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 (Jordano and Herrera, 1995; Nathan and Muller-Landau, 2000; Wang and Smith, 2002); (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-Malmborg 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', that must be searched, handled and efficiently processed, and the ability of frugivores to perform these tasks with consequences for the plants themselves (Martin, 1985a). 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 2.1) include those that define their spatial distribution and the temporal patterns of availability, both seasonally and between years, and their food value as prey, which must be processed as discrete items. Availability characteristics influence overall abundance of frugivores in particular habitat patches, their foraging movements, and important aspects of the 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 between 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 2.2). Mediterranean scrubland and some tropical dry and humid forests and woodlands usually range between 50–70%; temperate coniferous and broad-leaved forests vary within 30–40% of woody species animal dispersed. 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.

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. 2.1), but the 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 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

Table 2.1. Summary of major characteristics of fleshy fruits as food resources for frugivorous vertebrates.

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

Table 2.2. 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)	43.9 (31.7–64.3)	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).
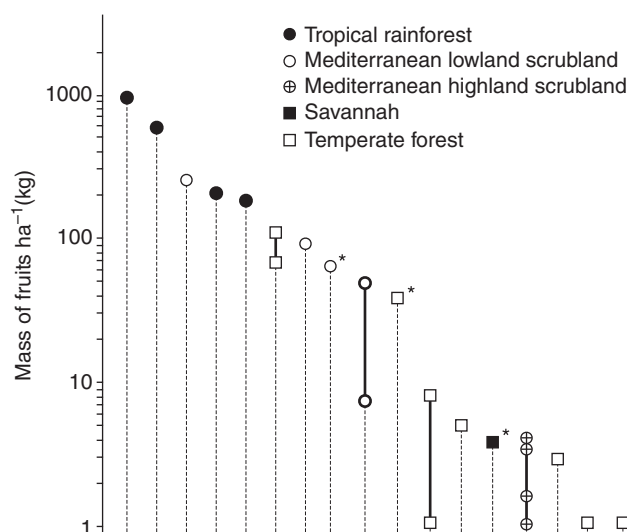
Fig. 2.1. Total production (per unit area) of fleshy fruits in different plant communities (placed in order of decreasing magnitude of production). Symbols with asterisks indicate biomass figures as wet mass, all others are dry mass. Thick lines join values for several localities. References: Leigh (1975); Johnson and Landers (1978); Baird (1980); Stransky and Halls (1980); Sorensen (1981); Charles-Dominique *et al.* (1981); Hladik (1981); Guitián (1984); Herrera (1984b,c); Jordano (1984, 1985, 1988, 1993).

more similar to those of temperate forests (Fig. 2.1). Tropical rainforests range widely in production, usually between 180 and approximately 1000 kg ha⁻¹ (dry mass). For additonal data, see Blake *et al.* (1990).

Extreme between-year variations in production of fleshy fruits have been found (Davies, 1976; Foster, 1982; Jordano, 1985, 1993; Levey, 1988a; Herrera 1998, among others) but a direct, causal, relation between

these fluctuations and frugivore numbers has been rarely 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.
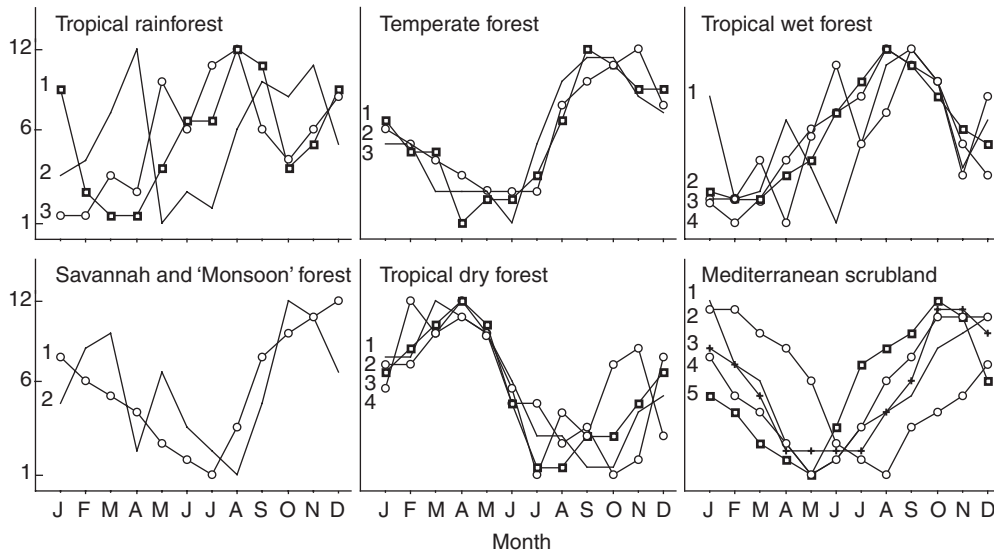
Seasonality

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 2.2 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), Colombia (Hilty, 1980), and South-East Brazil (Morellato *et al.*,

2000). 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. 2.2). 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 2.2). 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; Staggemeier *et al.*, 2010).

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; 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 (Snow, 1962a,b,c; Decoux, 1976; Hilty, 1977; Worthington, 1982; Terborgh, 1983; Leighton and Leighton, 1984; Sourd and Gautier-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

Fig. 2.2. Seasonal 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]; Hilty (1980)[2]. Temperate forest, Halls (1973)[1]; Sorensen (1981)[2]; Guitián (1984)[3]. Tropical wet forest, Frankie *et al.* (1974)[1]; Crome (1975)[2]; Alexandre (1980)[3]; Medway (1972)[4]. Savannah and Monsoon forest, Poupon and Bille (1974)[1]; Boojh and Ramakrishnan (1981)[2]. Tropical dry forest, Daubenmire (1972)[1]; Frankie *et al.* (1974)[2]; Morel and Morel (1972)[3]; Lieberman (1982)[4]. Mediterranean scrubland, Herrera (1984c)[1, 3]; Mooney *et al.* (1977), California[2], Chile[4]; Jordano (1984)[5].

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 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 alternative 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 that 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 to areas where fruit was more abundant. Seasonal use of fruits as an alternative food resource for temperate passerines is probably the major impelling influence in 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 in 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/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; Staggemeier *et al.*, 2010); (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 like 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 that 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, 1985b), 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 treefall gaps produced more fruit over a longer period of time than conspecifics growing in intact forest understory; 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* spp., *Fagus* spp., *Acer* spp., among others, and fleshy-fruited shrubs and treelets are characteristics of early successional stages and forest gaps (Marks, 1974; Smith, 1975; Kollmann and Poschlod, 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 average fruit abundance at the start of the fruiting season (September) of approximately 50 fruits 80 m^{-2} in Illinois forest gaps versus approximately 5 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 avaialbility (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-fruiting 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; Clark *et al.*, 2004). 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 densities orders of magnitude greater than 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.

Using a spatially explicit approach García *et al.* (2011) dissected the predictable spatial patterns of bird abundance and seed predation rate at three hierarchical spatial scales (broad, intermediate and fine). Scale-specific spatial distributions were explained by the response of animals to plant resource availability and habitat structure, with a hierarchically nested response of frugivores to the scales of fruit availability. Birds tracked fruits at large spatial scales and, within some systems, even across consecutive scales. Seed predation distribution was more responsive to habitat features than to resource availability. This suggests that consistent responses of frugivory patterns within and across spatial scales (García and Ortiz-Pulido, 2004) may condition the redundancy of seed dispersal as an ecosystem function.

Fruit Characteristics

Fruits are particulate foods that 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 2.1B; van der Pijl, 1982). 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 (Martin, 1985a; Martínez del Rio 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 (toucans, trogons, bellbirds; Wheelwright, 1985; also see 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 (also see Kalko *et al.*, 1996). Extremely large seeds (>3 cm length) have been reported to be dispersed exclusively by large mammals (apes, rhinos and elephants: Tutin *et al.*, 1991; Chapman *et al.*, 1992a). Most oversized fruit species in the paleotropics and neotropics, however, are most likely characteristic of the 'megafauna' syndrome, i.e. adaptations to animal frugivores extinct during the late Pleistocene (Janzen and Martin, 1982; Guimarães *et al.*, 2008).

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). Snow and Snow (1988) reported a decrease in fruit handling success (percent fruits dropped or rejected) with fruit diameter/bill width ratios greater than 1.0 (Fig. 2.3a). 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) (Fig. 2.3b,c). 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 (however 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 (Fig. 2.3c), indicating increasingly larger handling costs for smaller species (Snow and Snow, 1988). 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 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.
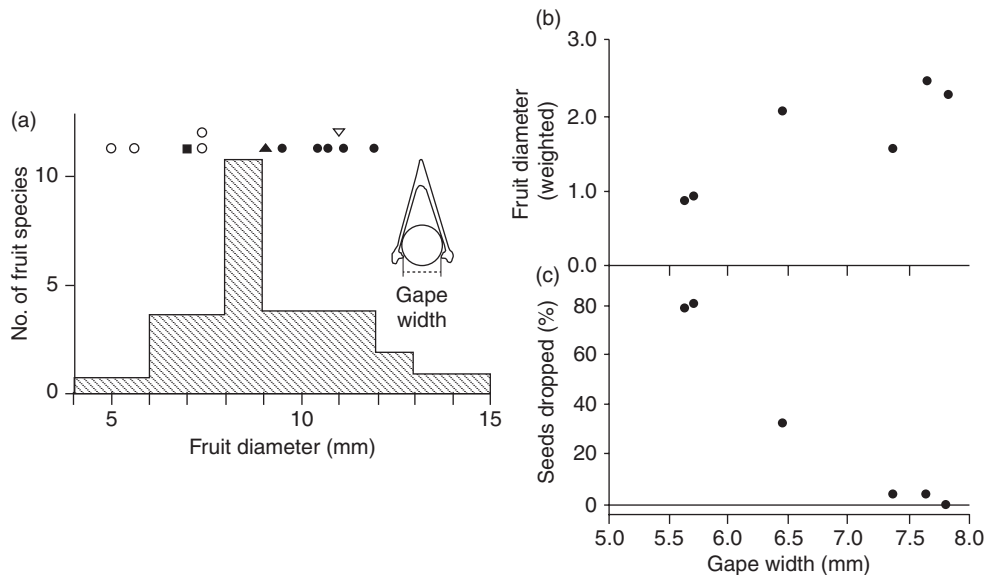
Fig. 2.3. (a) Frequency distribution of fruit diameter for bird-dispersed plants in southern England, and gape-widths (width of the bill measured at the commissures) of the main seed dispersers (Snow and Snow, 1988). Filled circles, *Turdus* spp.; open circles, warblers; square, *Erithacus rubecula*; filled triangle, *Sturnus unicolor*; open triangle, *Bombycilla garrulus*. (b) Relationship between mean gape width of six species of *Sylvia* warblers and mean fruit size in the diet; fruit size of each plant species weighted by the frequency of consumption. (c) The mean percentage of fruits which are dropped during feeding sequences at *Prunus mahaleb*, a tree species with average fruit diameter of 8.4 mm. Data from Jordano (1987b), Jordano and Schupp (2000). Circles, in order of increasing gape width, indicate *S. conspicillata, S. cantillans, S. melanocephala, S. atricapilla, S. communis* and *S. borin*.

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 suggest strong fruit size selection limited by aerodynamic constraints on fruit transport on the wing. These results have been validated more recently for the whole bat community, where small bats preferentially ate small-fruited and strangler figs while large bats consumed mostly large-fruited and free-standing figs (Kalko *et al.*, 1996; Wendeln *et al.*, 2000). 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% of the variation in seed size of this species is among individual crops (Howe and Richter,

1982). Intraspecific variation in fruit and seed size is thus sufficient for selective animal frugivores to exert strong phenotypic selection on fruit and seed size (Wheelwright, 1993; Jordano, 1995a). 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 (Jordano, 1987b, 1995a; Snow and Snow 1988; Rey *et al.*, 1997). However, small-bodied frugivores might cause strong negative selection pressures on fruit and seed size by differentially dispersing the more accessible smaller seeds (Jordano, 1995a). 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 and the potential for evolutionary shifts mediated by frugivores.

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 function of seed size; birds consistently dropped more than 60% of seeds which 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 or 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; however 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 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; Kitamura *et al.*, 2002; Traveset *et al.*, 2004; Galetti *et al.*, 2011) 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 vertebrate frugivores (Table 2.3), 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 any other food type (Table 2.3). Therefore, the combination of traits that best characterizes the fruit

Table 2.3. 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).

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 nutrient content of the pulp of the main angiosperm families dispersed by vertebrate frugivores (Jordano, 1995b). Detailed reports for local or regional floras include: 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); Kitamura *et al.*, 2002; Traveset *et al.*, 2004; and Galetti *et al.* (2011), among others.

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, 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 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 positive nitrogen balance of specialized frugivorous birds, such as phainopeplas or waxwings, when feeding on fruits with 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; Izhaki, 2002). 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 organism. 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 mandibulate fruits and ingest only 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; Schupp *et al.*, 2010), 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 predators. Consumers of pulp that discarded the seeds beneath 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 predators 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 predator 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, 2011); 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; 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. 2.4). 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 pulp consumers rather than legitimate dispersers, mostly by 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) or consume only pulp and discard seeds (Terborgh, 1983), although some
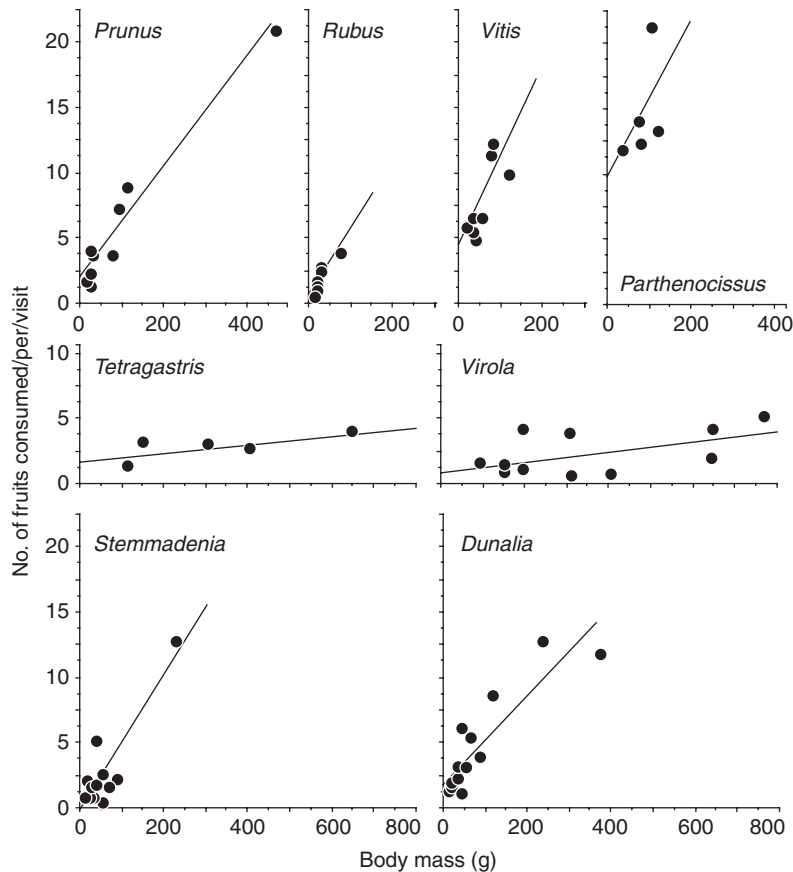
Fig. 2.4. Relationship between number of fruits consumed per visit and body mass of frugivorous birds in different plant species. Data from Jordano (1982) (*Rubus ulmifolius*); Howe and Vande Kerckhove (1981) (*Virola surinamensis*); Howe (1980) (*Tetragastris panamensis*); McDiarmid *et al.* (1977) (*Stemmadenia donnell-smithii*); Cruz (1981) (*Dunalia arborescens*); Jordano and Schupp (2000) (*Prunus mahaleb*) and Katusic-Malmborg and Willson (1988) (*Vitis vulpina* and *Parthenocissus quinquefolia*).

small species such as *Saguinus* can swallow very large seeds (Garber, 1986). Among Mediterranean mammal species the range of frugivory types generates a broad gradient between the extremes of antagonism (most seeds ingested are destroyed) and mutualism as outcomes of the interactions (Fig. 2.5; Perea *et al.*, 2013).

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
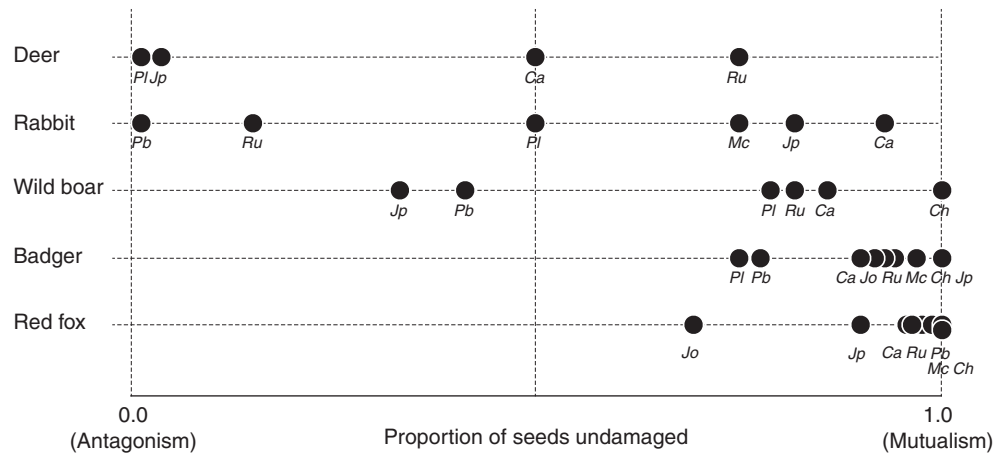
Fig. 2.5. Variation in the proportion of seeds dispersed undamaged by different species of Mediterranean mammal frugivores. Each dot represents the fraction of seeds undamaged recovered from scats of each animal species, corresponding to several plant species in their diets: Pl, *Pistacia lentiscus*; Jp, *Juniuperus phoenicea*; Ca, *Corema album*; Ru, *Rubus ulmifolius*; Pb, *Pyrus bourgaeana*; Mc, *Myrtus communis*; Ch, Chamaerops humilis; and Jo, J. *oxycedrus*. Modified from Perea *et al.* (2013).

prey types; functional and behavioural predisposition, rather than specific adaptations, are expected (Herrera, 1984; however 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; 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 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; Carlo and Morales, 2008).

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* species 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 that 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; Perea *et al.*, 2013). New World apes (ceboids) and Old World hominoids apparently swallow and defecate intact most seeds (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;

Lambert and Garber, 1998; Lambert, 2011) 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 (Fig. 2.5); and the main result of the studies discussed above is that vertebrate frugivore ecomorphologies are not distributed at random over this gradient. Our task is to search for these patterns and measure their consequences in plant–frugivore interactions.

Digestion of fruits

The bizarre digestive structures of some specialized frugivorous birds have been 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. 2.6, 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.
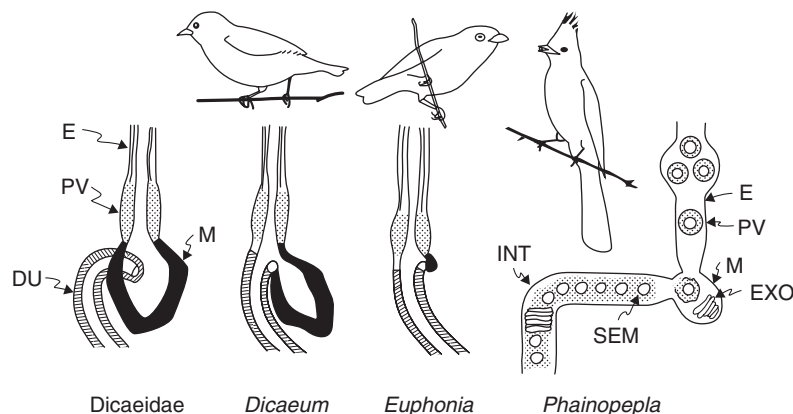
Fig. 2.6. Schematic representation of several types of proventriculus and gizzard configurations in specialized frugivorous birds. Left, arrangement of a relatively differentiated 'normal' muscular gizzard (M) stomach and associated oesophagus (E), proventriculus (PV) and duodenum in insectivorous Dicaeidae (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).

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 and 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). Aside 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 (however see Bodmer, 1989a,b) 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 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) and 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 and liver and relative intestine length among avian seed dispersers and pulp/seed consumers 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 requires prolonged time periods and does not seem an alternative 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 adaptations to digest a soft, dilute food with low nutrient density that has a great caloric 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 2.4). Ruminant diets are characteristically high in structural hexose and pentose polymers requiring 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 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 or nitrogen, which are deficient in the fruit pulp, and an alternative source is needed (Foster, 1978; Moermond and Denslow, 1985).

Table 2.4. 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	~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	–	Variable–low

Frugivores, as monogastric herbivores, base their feeding on rapid processing of their poor-quality food and maximization of the 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 (i.e. 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 this indigestible material 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 (however 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 (however 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 0.3–1.5 h (Levey, 1986; Snow and Snow, 1988; Worthington, 1989; Levey and Grajal, 1991). Levey (1986) also showed that pulp throughput times are longer than seed retention times. In some species, such as the phainopeplas (Fig. 2.6), 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 was positively correlated with food throughput rate (r^2 = 0.465; F = 8.69; P = 0.015; n = 38 species including *Turdus* spp., *Sylvia* spp., *Erithacus rubecula*, and several other muscicapids; Jordano, pers. obs.). This indicates that the ability to modulate retention 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. Rapid fruit handling and processing thus appear to be very limiting for sustained frugivory.

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; however 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 internal handling of seed ballast are obviously overcome by frugivorous mashers and spitters, as well as by pulp consumers, 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. The interaction of frugivore movement patterns and complex landscapes creates the template on which plant regeneration occurs, an ecological process that links movement ecology with plant dispersal patterns (Nathan *et al.*, 2008). When adequately integrated, these aspects of movement and landscape can be useful to model animal-mediated seed dispersal and predict long-distance dispersal events (Levey *et al.*, 2008). 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; Schupp *et al.*, 2010). 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 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 (Nathan *et al.*, 2008; Schupp *et al.*, 2010). 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 (i.e. the seed shadow) is a function of the species of frugivore eating the fruit, its movement rates, and seed throughput rates (Hoppes, 1987; Murray, 1988; Chapman and Russo, 2005; Russo *et al.*, 2006). 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 that 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, then 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; Russo *et al.*, 2006). 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 inmediate 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 (e.g. Fig. 2.5) 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 coat, 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 that mash fruits (e.g. *Carollia*) or expectorate

a food bolus with seeds (*Artibeus*), and territorial birds that regurgitate seeds within a close range of the feeding plant or display perches (Pratt and Stiles, 1983; Snow and Snow, 1984; Pratt, 1984; 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 for fruit handling, resting, 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 1–3 seeds in single droppings at no particular locations in Mediterranean shrubland (Jordano, 1988; Debussche and Isenmann, 1994), but large ungulates concentrate hundreds of seeds in single droppings (Dinerstein and Wemmer, 1988; Howe, 1989; Fragoso, 1997; Julliot, 1997; Bueno *et al.*, 2013). 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; Lambert, 2011). Finally, seed clumping in faeces is strongly dependent on frugivore size (Howe, 1989; White and Stiles, 1990; Bueno *et al.*, 2013)

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 up with seed delivery. For every dispersal episode, it matters how many and where seeds reach the ground and the particular mixing of seed species delivered. There are a number of detailed studies on the ranging behaviour of frugivores and I will not attempt to consider them in detail here (Gautier-Hion *et al.*, 1981; Hladik, 1981; Terborgh, 1983; Fleming, 1988; Murray, 1988, among others). 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 patterns 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 that have only recently been considered in detail in explicit relation to frugivore activity. Studies by Lieberman and Lieberman (1980), Herrera (1984b, c), Jordano (1988), Loiselle (1990), White and Stiles (1990), Théry and Larpin (1993) 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, but recent analyses (Clark *et al.*, 2004; Chapman and Russo, 2005; Carlo and Morales, 2008; Damschen *et al.*, 2008) show compelling evidence for large-scale effects of dissemination by frugivores.

Observational evidence indicates that particular combinations of seed species in 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 that need highly directed dispersal to particular hosts (Herrera, 1988; 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 fall studies (Stiles and White, 1986; Clark *et al.*, 2004; Carlo and Morales, 2008). Loiselle (1990) has demonstrated experimentally that specific combinations of dispersed seeds in faeces of tropical frugivorous birds have 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. The main influences arise from limitation of the two processes that determine animal-mediated seed dispersal: arrival of seeds to dissemination sites and postdispersal survival and establishment. These limitation effects have several components that can be directly linked to the activity of the frugivorous animals (Fig. 2.7; Nathan and Muller-Landau, 2000). While reproductive output – directly related to reproductive success after flowering – limits the amount of seeds available for dispersal (source limitation), multiple influences determine whether or not frugivore activity limits recruitment (Fig. 2.7) through the combined effects of quantity and quality components of effectiveness (Schupp *et al.*, 2010).

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 transition have a direct influence on later-occurring stages such as germination and early seedling establishment. The studies of fruit–frugivore interactions considered in this chapter have documented what could be designated as largely 'invariant' fruit and frugivory patterns that characterize each interacting species in a particular scenario where the interaction occurs (e.g. fruit and seed size, design, nutrient configuration, fruiting display; and body size, ecomorphology, fruit handling behaviour and digestive processing of food, etc.). Description of these patterns has enabled us in the last 35 years to elaborate predictions about the outcomes of particular combinations of characteristics and test them by evaluating the associated costs in terms of seed losses for the plants or as foraging costs for the frugivorous animals.

But we need to translate the effects of these interactions into a demographic and evolutionary context 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 (Fig. 2.7; Jordano and Herrera, 1995; Clark *et al.*, 1999; Nathan and Muller-Landau, 2000). Thus, the outcome of the invariant
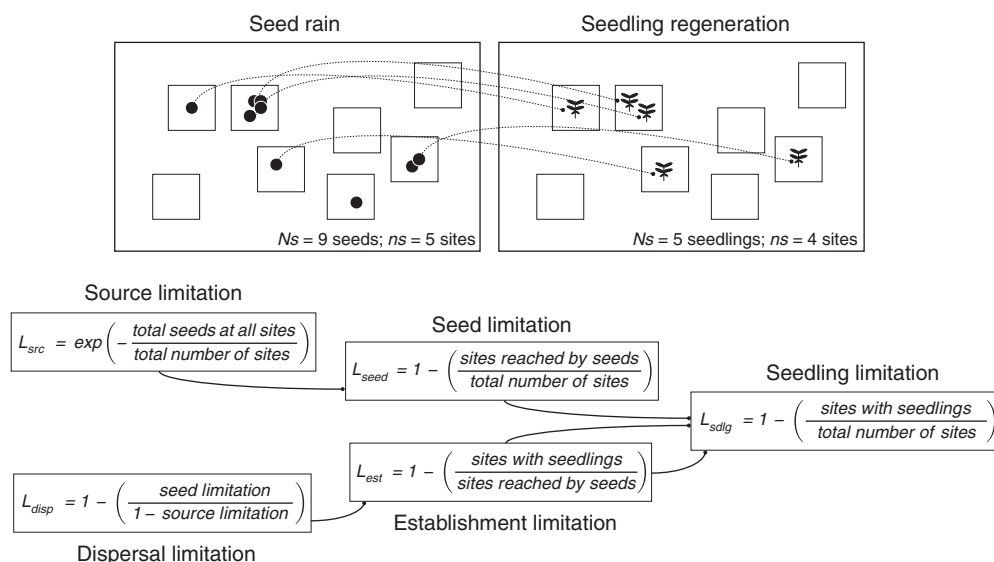
Fig. 2.7. Decomposing recruitment limitation (Nathan and Muller-Landau, 2000). Total failure to recruit at a given site or recruitment at less than maximum density can be the result of failure of seeds to arrive and/or the lack of suitable conditions for seedling and sapling establishment. Indices of dispersal and recruitment limitation can be estimated from seed trap data (seed rain) and seedling recruitment plots, from basic data on number of seeds sampled, number of sites (traps) with at least one seed, number of seedlings emerging, and number of sites (plots) with at least one seedling recruited. These indices indicate the influence of dispersal (arrival) and recruitment (survival) factors by calculating how many sites would be won if that factor were not limiting, but all other limitations were still present and thus the proportion of those sites lost because it is limiting.

patterns described above depends in addition on 'context-sensitive' effects that 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 Chapters 3 and 4 in this volume). This is central to assessing the role of frugivore activity in limiting colonization and, potentially, the success of vegetation restoration efforts (García *et al.*,

2010). In this way, the relative roles of seed dispersal limitation and recruitment limitation in determining abundance and genetic structure could be gauged (Dalling *et al.*, 1998; García and Grivet, 2011). The preliminary protocols have been developed (e.g. Heithaus *et al.*, 1982; 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 for measures of the net outcome 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, 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 elaborated 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 three decades of research on the fruit–frugivory interface have yielded many fruits that, 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 demographic and evolutionary processes in plant and frugivore populations are a first sketch of that picture.

Acknowledgements

Appendix

Summary statistics (sample size, mean and standard error of the mean for each family and variable) of fruit characteristics and pulp constituents of vertebrate-dispersed plants, by families. The FRUBASE dataset (Jordano, 1995a) is accessible at the DRYAD Digital Repository: doi:10.5061/dryad.9tb73.

Family	Fruit diameter (mm)	Pulp dry mass (g)	Seed dry mass (g)	Relative yield	Kcal/g dry mass	Kcal/ fruit	Percent water	Lipids	Protein	Carbo-hydrates	Ash
Anacardiaceae 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
Annonaceae 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
Apocynaceae 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
Caprifoliaceae 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
Ericaceae 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
Lauraceae 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
Liliaceae 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
Melastomataceae 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
Meliaceae 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
Moraceae 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

Continued

Continued.

Family	Fruit diameter (mm)	Pulp dry mass (g)	Seed dry mass (g)	Relative yield	Kcal/g dry mass	Kcal/ fruit	Percent water	Lipids	Protein	Carbo-hydrates	Ash
Myrsinaceae 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
Myrtaceae 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
Oleaceae 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
Palmae 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
Piperaceae 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	–
Rhamnaceae 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
Rosaceae 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
Rubiaceae 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
Rutaceae 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
Sapotaceae 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
Smilacaceae 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
Solanaceae 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

Continued

Continued.

Family	Fruit diameter (mm)	Pulp dry mass (g)	Seed dry mass (g)	Relative yield	Kcal/g dry mass	Kcal/ fruit	Percent water	Lipids	Protein	Carbo-hydrates	Ash
Tiliaceae 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
Ulmaceae 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
Viscaceae 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
Vitaceae N=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 >4 species sampled have been included. Figures for pulp constituents are proportions relative to pulp dry mass.

References used: 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, 1995a); Viljoen (1983); Estrada *et al.* (1984); Wheelwright *et al.* (1984); Johnson *et al.* (1985); Moermond and Denslow (1985); Dinerstein (1986); Piper (1986b); Sourd and Gautier-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.

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