[**2**](#PageMark1)[**Fruits**](#PageMark1)[**and**](#PageMark1)[**Frugivory**](#PageMark1)

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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 regur- gitate, 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 fruit- ing 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 characteris- tics 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 interact- ing with specialized frugivores providing high-quality dispersal; fruits with succu- lent, watery, carbohydrate-rich pulps occupy the other extreme by having their numerous small seeds dispersed by oppor- tunist 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 character- istics, 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). However, studies of frugivory have rarely been linked con- ceptually 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 evolu- tionary context, where fitness differentials in plant populations are measured and associated with individual variation in dispersal-related traits. Predictive frame- works that link frugivory patterns, associated

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differences in seed/seedling mortality and differential reproductive success with demographic patterns in natural plant pop- ulations 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 sup- plemented 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 mate- rial 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 ungu- lates such as brocket deer (*Mazama* spp.) and African cephalophines (*Cephalophus* spp.) can include up to 85% of fruit mate- rial in their diet (Dubost, 1984; Bodmer, 1989a, 1990). However, partially frugivo- rous mammals include opossums, phalan- gers, 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 sporadi- cally 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 dis- tribution of the seeds, i.e., the ‘seed shadow’ (Janzen *et al.*, 1976), they provide a template over which future spacing pat- terns of adult plants will build up; and

(iii) seed deposition patterns by frugivores directly affect patterns of early seed sur- vival 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 con- sequences for the plants themselves (Martin, 1985a). Throughout the chapter, any men- tion of fruits will be with reference to fleshy fruits, loosely defined to include any struc- ture enclosing seeds surrounded by a fleshy, edible, pulp layer (Howe and Smallwood, 1982). Most references to frugivorous ani- mals 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 charac- teristics, temporal and spatial patterns of availability, and intrinsic traits such as

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design and nutritive value. The second part reviews frugivore traits that influence fruit choice, fruit and seed processing, and forag- ing movements that have implications for seed deposition patterns.

**Fruit Production and Availability**

Fleshy fruits are, for the organisms consum- ing them, discrete food items available in an extremely diverse array of spatial and tem- poral configurations. The various character- istics (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 habi- tat 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 ulti- mately influence seed deposition patterns, because they determine the movement pat- terns of frugivores foraging for fruits in rela- tion to the mosaic of habitat patches.

**Production and abundance of fruits**

Variation between communities in the fre- quency 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 and 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 exempli- fied 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 temper- ate forests of the northern hemisphere is always below 105 fruits ha−1, representing less than 10 kg ha−1 (dry mass). Medi-

terranean scrublands have productions similar to some tropical forests, in general around 80 kg (dry mass) ha−1, but fruit den- sity might reach more than 1.4 × 106 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

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**Table 2.2.** Percentages of woody species adapted for endozoochorous seed dispersal by vertebrates in different vegetation types.

Vegetation type Mean (Range) Referencesa

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

aReferences: 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).

Tropical rainforest

Mediterranean lowland scrubland

1000

100

10

1

Mediterranean highland scrubland Savannah

Temperate forest

**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); Charles-Dominique *et al.* (1981); Hladik (1981); Sorensen (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

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these fluctuations and frugivore numbers has been rarely documented. In most instances, studies with long-term data are lacking and inferences about causal associ- ations due to the plant–frugivore interac- tion are unwarranted or are established without a proper evaluation of the influ- ence 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 sto- chastic component to plant–frugivore inter- actions and long-term data are needed to begin a realistic assessment of their demo- graphic implications.

**Seasonality**

The overall production figures outlined above illustrate broad patterns of variation in fruit abundance but mask actual avail- ability 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 precipi- tation and these trends are evident even without shifting the graphs to compensate for latitudinal differences. Unimodal fruit- ing 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 rain- fall intensity within the rainy season and delays in the phenological responses of dif- ferent 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 dura- tion of the fruiting phenophase (although the seasonal pattern can be strikingly similar in some cases; see Fig. 2.2). Average dura- tion of period of ripe fruit availability for agiven 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 pat- terns of variation reflect similar environ- mental 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 pat- terns of fruit availability between the trop- ics and temperate zones define important differences in frugivory patterns. Temperate frugivory is a strongly seasonal phenome- non 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) 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 sup- ply (Loiselle and Blake, 1991). For whole- year resident frugivores, this type of

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Tropical rainforest Temperate forest Tropical wet forest

12

6

1

1

2

3

1 2 3

1

2 3 4

12

Savannah and ‘monsoon’ forest Tropical dry forest

1

2

Mediterranean scrubland

6

1

1

2

1 2 3 4

3 4 5

J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D

Month

**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. 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.* (1974a)2; Morel and Morel (1972)3; Lieberman (1982)4. Mediterranean scrubland, Herrera (1984c)1, 3; Mooney *et al.* (1977), California2, Chile4; Jordano (1984)5.

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 rain- forests of Queensland (Australia) clearly show that seasonal patterns of abundance of certain fruit pigeons are strongly associ- ated with the seasonal patterns of fruit rip- ening. Similarly, Leighton and Leighton (1984) found a good correlation between local densities of major frugivorous verte- brates (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 avail- ability 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 abun- dance 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 sea- sonal abundance patterns of the mistletoe bird (*Dicaeum hirundinaceum*) and its preferred fruit, *Amyema* *quadang*

(Loranthaceae) in Australia. The breeding

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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 sup- ply was low but, after the breeding season, moved to areas where fruit was more abun- dant. Seasonal use of fruits as an alterna- tive 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 par- allel 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 sea- sonal 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 ger- mination requirements at the start of the rainy season (Garwood, 1983); (iii) phylo- genetic constraints in the timing and dura- tion 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 fruit- ing 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 characteris- tics 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 succes- sional 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

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in forest interior plots. Among the reasons for these trends in both tropical and temperate forests are: (i) increased abundance of indi- vidual plants in gaps; (ii) increased diver- sity 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 substi- tuted 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 patchi- ness in fruit availability have seldom been considered. First, abundance will be influ- enced by the frequent association of dioec- ism 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 increas- ing local abundance of male, non-fruiting plants is associated with decreased fruit availability (Jordano, 1984). This factor is probably irrelevant as a source of patchi- ness in fruit abundance in temperate for- ests, but might prove to be important in tropical habitats where dioecism is rela- tively frequent. Secondly, fleshy-fruiting plants are frequently associated with par- ticular 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 signifi- cantly higher beneath female, fruit-bearing plants compared with male plants of dioec- ious species (Herrera *et al.*, 1994), a result of preferential foraging by fruit-seeking frugi- vores. All these processes generate predict- able 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 predict- able 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 spa- tial 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 swal- low as individual items. Relevant traits of fleshy fruits, from the perspective of the for- aging animal, include design (e.g. size, number and size of seeds, mass of pulp rela- tive to fruit mass), nutrient content (relative amounts of lipids, protein, carbohydrates and minerals per unit mass of fruit pro- cessed) 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

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given fruit should be examined in the con- text 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 frugi- vores 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 casu- arius*): Pratt, 1983; Stocker and Irvine, 1983). Bonaccorso (1979) reported a signifi- cant positive relationship between body mass variation among individual phyllos- tomid 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, how- ever, 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 rain- forest. Lambert (1989a,b) found that seven species of frugivorous pigeons in Malaysia fed on at least 22 *Ficus* species, and a posi- tive 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 swal- lowing 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 swal- low increasingly large fruits. These trends reflect the increase in handling cost associ- ated with picking, seizing and positioning in the bill of increasingly larger fruits, but the main effect of fruit size on handling suc- cess, especially in drupes and other single- seeded fruits, is due to seed size and not to fruit size.

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(b) 3.0

(a)

10

5

Gape

width

(c)

2.0 1.0 0.0

80

60

0

5

10

Fruit diameter (mm)

15

40

20

0

5.0 5.5 6.0 6.5 7.0 7.5 8.0

Gape width (mm)

**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 that 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, how- ever, 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 selec- tion 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 stran- gler 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 surina- mensis* 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 ani- mal 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, 1988; 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

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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 a 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 spe- cies 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 effi- ciently handle and process and, on the other hand, increase in fruit size generally limits the range of potential seed dispers- ers to the largest frugivores. Both asser- tions are especially true for drupes or other single-seeded fruits, and have important implications for the resulting seed disper- sal 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 vari- ability 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 over- all size provides the main source of func- tional variation in fruits relative to the types of frugivores consuming them, but additional important traits were the num- ber 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

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major type of seed disperser when account- ing for phylogenetic affinities in a com- parative 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 varia- tion in components can be explained by a few major patterns of covariation that have a major correlate with phylogeny, espe- cially 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 corre- lation between lipid and non-structural carbohydrate (NSC) content; three addi- tional factors accounted for 51.1% of vari- ance. 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 correla- tion 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 diet- ary items usually consumed by vertebrate frugivores (Table 2.3), the fruit pulp shows the highest concentration of soluble carbo- hydrates and the lowest relative amount of protein. Lipid content is relatively high but shows extreme interspecific variation. The importance of the mineral fraction is rela- tively 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 carbohy- drates 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.

Non-structural

Food type Water Protein Lipids carbohydrates Minerals

Insects1

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)

Seeds2

11

(4–12)

11

(6–14)

4

(0.3–9)

69

(61–73)

2.2

(1.1–5.3)

Neotropical fruits3

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 fruits4

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 leaves5

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 leaves5

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).

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pulp nutritive content is the excess of digestible energy relative to protein, the high water content, and the extreme defi- ciency in some compounds relative to oth- ers (i.e. imbalance between components).

The Appendix to this chapter summa- rizes 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 nutri- tional 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, granivo- rous species, indicates that a diet with 4–8%

protein (wet mass) is necessary for mainte- nance (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, rela- tive 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 con- sumed by frugivorous bats (*Artibeus, Sturnira*) in Costa Rican cloud forest (mean = 6.7% protein, dry mass) was apparently suf- ficient to sustain the protein demands of lactating females; otherwise females could be depending on previously accumulated protein reserves. The data available regard- ing *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), ade- quately balanced the daily net energy and nitrogen requirements. In contrast to these phyllostomid bats, totally frugivorous pter- opodid 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 supple- ment 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 pro- tein 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

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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 particu- lar nutrient can be limited by the impossibil- ity of processing enough food material to obtain it, and not by the scarcity of the nutri- ent itself. That is, the effect is due to a diges- tive bottleneck (Kenward and Sibly, 1977; Sibly, 1981). Consumption of minor amounts of animal prey provides the necessary nitro- gen input to escape the constraint imposed by the overingestion of energy, as demon- strated by field studies of phyllostomid bats and frugivorous warblers (Fleming, 1988; Jordano, 1988; see also Bowen *et al.*, 1995).

Direct interaction among different com- ponents present in the pulp, such as sec- ondary 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 gly- cosides 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 assimila- tion efficiency (Izhaki and Safriel, 1989; Mack, 1990; Cipollini and Levey, 1997).

Finally, the content in the fruit pulp of cations and microelements, such as cal- cium, phosphorus, iron, manganese, and zinc, is frequently below the requirements

of frugivorous birds, and situations of nega- tive balance in wild birds have been reported (Studier *et al.*, 1988). These types of effects should be controlled in experi- ments 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 spe- cial adaptations, such as deep beaks or spe- cial digestive processing of the ingesta, are necessary to consume fruit, but certain mor- phological, anatomical and physiological characteristics determine an animal’s abil- ity 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, legiti- mate 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 man- dibulate fruits and ingest only pulp by work- ing 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 perspec- tive, 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 satisfac- tory 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

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frugivory types. Seed dispersers showed larger body size and flatter and wider bills than non-frugivores and pulp-seed preda- tors. 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 preda- tor in a particular interaction with plants is not only dependent on frugivore ecomor- phology and behaviour, but also on fruit characteristics (especially seed size) of the plants in the specific situation. Detailed descriptions of these categories and associ- ated 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 differ- ent types of frugivory are present in all groups of vertebrate frugivores, but in mark- edly different proportions.

**Anatomical Characteristics**

**of Frugivores**

**Frugivore size and form**

Body mass is a major determinant of inten- sity 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 vol- ume 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 differ- ences 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 spe- cies 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 pri- mates is restricted to large hominoids and cebids (Corlett and Lucas, 1990); smaller species either spit out seeds (some cerco- pithecines) or consume only pulp and dis- card seeds (Terborgh, 1983), although some

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20 15 10

5

*Prunus*

*Rubus*

*Vitis*

0

10 5 0

0

200 400

*Tetragastris*

0

200

0

*Virola*

200

0

*Parthenocissus*

200 400

20 15 10

5

0

0

*Stemmadenia*

200 400 600 800

0

*Dunalia*

200 400 600 800

Body mass (g)

**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 mutual- ism as outcomes of the interactions (Fig. 2.5; Perea *et al.*, 2013).

The use by frugivores of different for- aging manoeuvres to reach fruits on plants is constrained by external morphology and body proportions, which can be con- sidered 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 rela- tive importance of fruits in the diet is sig- nificantly larger for foliage-gleaning species than for those with more specialized or ste- reotyped means of prey capture, such as sallyers, flycatchers and trunk foragers (Jordano, 1981). Therefore, it is reasonable to conclude that the ecomorphological con- figuration of a species is a preadaptation limiting feeding on fruit food, especially for those partial frugivores that consume other

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Deer

*Pl Jp* *Ca* *Ru*

Rabbit

*Pb* *Ru* *Pl* *Mc* *Jp* *Ca*

Wild boar

*Jp* *Pb* *Pl Ru Ca* *Ch*

Badger

*Pl Pb* *Ca Jo Ru Mc Ch Jp*

Red fox

*Jo* *Jp Ca Ru Pb*

*Mc Ch*

0.0

(Antagonism)

Proportion of seeds undamaged

1.0

(Mutualism)

**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, *Juniperus 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 adapta- tions, are expected (Herrera, 1984a; however see Moermond and Denslow, 1985).

Differences in fruit capture modes among frugivores show strong ecomorpho- logical correlations, especially with wing morphology, bill form or dental characteris- tics, 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 carnivo- rous species. Frugivorous bats are quite conservative in the way they reach fruits, major differences being found in fruit hand- ling and postforaging movements. The eco- morphological patterns that define the patterns of habitat selection among groups of these species (canopy-dwelling steno- dermines 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 for- age for fruits on the ground (e.g. *Turdus* spp., Snow and Snow, 1988). The descrip- tion 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 simi- lar to hovering; swooping and stalling,

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involving a continuous movement from perch to perch plucking the fruit on the way, which is the method used by most cot- ingids; and taking fruit from perches by picking, reaching and hanging. The first two manoeuvres are the two most com- monly 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 pat- terns described above have important impli- cations 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 acces- sibility to preferred fruits decreases. Other things being equal, decreasing fruit accessi- bility 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, differ- ences 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 ecomorphologi- cally diverse array of visitors might result in a more thorough removal of the crop if dif- ferent species predominantly take fruits from different positions in the canopy dif- fering 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 exam- ple, 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 accom- modate fruit handling behaviour by most vertebrate frugivores. For example, phyllos- tomid 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 func- tionally similar to mashing, but the conse- quences for the plant depend on frugivore movement after fruit plucking. Many ungu- lates 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 par- ticular 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 homi- noids 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;

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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 sur- vival 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 ran- dom over this gradient. Our task is to search for these patterns and measure their conse- quences 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 diges- tive 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 ‘diver- ticulum’ 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 wax- wings, 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.

E

PV

E

DU

M

INT

PV

M

EXO

Dicaeidae

*Dicaeum*

*Euphonia*

SEM

*Phainopepla*

**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). (From Walsberg, 1975.)

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Frugivorous bats also show a typical stom- achal structure where the oesophagus leads into a cardiac vestibule and the rest of the stomach is an elongated tube with a con- spicuous 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 sporadi- cally (Bodmer, 1990), the digestive process- ing by non-ruminant frugivores differs chiefly between foregut and hindgut fer- menters. To my knowledge, no comparative assessment has been made of the differen- tial 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 con- sistently associated with safe seed delivery by these frugivorous mammals. However, it is well known that fore-stomach ferment- ers usually crack seeds before ingestion (e.g. some colobine monkeys, and pecca- ries) 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 signif- icant differences in relative mass of gizzard and liver and relative intestine length among avian seed dispersers and pulp/seed con- sumers 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 detoxifica- tion 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 spe- cies was accountable by considering only external morphology. Functional modula- tion 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 morpho- logical transformations one finds more functional adaptations to digest a soft, dilute food with low nutrient density that has a great caloric content relative to pro- tein (Herrera, 1984a; Moermond and Denslow, 1985; Karasov and Levey, 1990; Afik and Karasov, 1995; Karasov, 1996).

There are marked functional differ- ences among different diet types from the perspective of the digestion process

(Table 2.4). Ruminant diets are characteris- tically high in structural hexose and pen- tose 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 veg- etative plant parts by non-ruminant herbi- vores. In general, both forage and fruit diets show much lower digestibilities than diets based on animal prey. In addition, a size- able fraction of the fruit food mass ingested by frugivores (the seeds) is actually indi- gestible and causes gut displacement (Levey and Grajal, 1991; Witmer, 1998b). Herbivore diets, and fruits are no exception, pose a fre- quent problem by creating digestive bottle- necks (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).

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**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 frac- tions, rapid passage of seeds, partial empty- ing 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 adap- tation 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 process- ing 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), indi- cating that they limit fruit processing by gut displacement and that frugivores void them selectively in order to maximize gut capa- city for digestible pulp. Time to regurgitate seeds by frugivorous birds is very rapid,

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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 dif- ferences 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 mus- cicapid warblers (Jordano, 1987b), although gut passage time is shorter in the former. For a sample of Mediterranean scrubland frugiv- orous passerines, variation across species in the relative importance of fruit in the diet was positively correlated with food through- put 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 indi- cates that the ability to modulate retention time of digesta to achieve a high through- put rate might be important for sustained frugivory. Similarly, McWilliams and Karasov (1998) reported that compensatory modula- tion of retention time or digesta mixing (and not rate of hydrolysis and absorption) explained the remarkably constant diges- tive efficiency in waxwings exposed to var- ied fruit-feeding costs. Rapid fruit handling and processing thus appear to be very limit- ing for sustained frugivory.

Evidence that the size of indigestible seed material limits feeding rates by causing gut displacement and represents an impor- tant 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 regurgita- tion, implying that ingested seeds in the crop limited ingestion of additional fruits. Apparently, however, frugivores might compensate for these costs to achieve ade- quate intake of basic nutrients (Levey and Duke, 1992; Witmer, 1998b; Witmer and van Soest, 1998). These costs of internal hand- ling 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 land- scapes 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 evolu- tionary 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 habi- tat template, which includes a non-random distribution of patches of variable probabil- ity for establishment and survival of the plant propagules. Therefore, the two main aspects of frugivory that influence the

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resulting seed dispersal are the seed pro-

A typical feeding bout for most frugi-

cessing behaviour (both external and diges- tive) 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 ade- quate for germination; the latter defines the potential range of microsites that will inter- cept delivered seeds. The aim of this final section is to review how the fruit and frugi- vore characteristics previously considered interact and result in seed deposition pat- terns 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 characteris- tics 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 hand- ling 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 pro- cessing will be how fast seeds are delivered after fruit capture.

vores, 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 pat- tern 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 communi- ties and differ in their immediate conse- quences for seed delivery. I must emphasize here that they do not represent a dichotomy of frugivore strategies but rather, a contin- uum gradient of seed processing rate (e.g. the number of viable seeds delivered per unit foraging time). Even the same frugivore spe- cies can be ranked in different positions along this gradient (e.g. Fig. 2.5) when inter- acting with different plant species.

Rapid processing of seeds by frugivores that mash or spit out seeds involves mastica- tion 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, result- ing in highly clumped seed distributions irrespective of how many seeds are dis- persed. In addition, low mixing of different seed species is expected since fruits are pro- cessed 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

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a food bolus with seeds (*Artibeus*), and ter- ritorial 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 drop- pings at no particular locations in Medi- terranean 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 reten- tion 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 terres- trial 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 frugi- vores 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 move- ments 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 fac- tors influence the ‘where’ component of seed deposition patterns but I wish to con- centrate 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

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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 indi- cate the presence of consistent choice pat- terns. 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 var- iation 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 demon- strated experimentally that specific combi- nations of dispersed seeds in faeces of tropical frugivorous birds have direct influ- ence on seed germination and early seed- ling vigour and survival.

Studies of germination rates in depos- ited seeds, early seedling survival and vari- ations 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 sur- vival 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 limi- tation), 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 interac- tion of fruits and frugivores determines the net result of the whole predispersal repro- ductive phase, being its last step. However, events occurring during this fruit removal– seed delivery transition have a direct influ- ence on later-occurring stages such as germination and early seedling establish- ment. The studies of fruit–frugivore interac- tions considered in this chapter have documented what could be designated as largely ‘invariant’ fruit and frugivory pat- terns that characterize each interacting spe- cies in a particular scenario where the interaction occurs (e.g. fruit and seed size, design, nutrient configuration, fruiting dis- play; 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 elabor- ate predictions about the outcomes of par- ticular 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 pres- sures in shaping the patterns we are observing. In this context, the net outcomes of the inter- actions 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

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Seed rain Seedling regeneration

*Ns* = 9 seeds; *ns* = 5 sites *Ns* = 5 seedlings; *ns* = 4 sites

Source limitation

*Lsrc = exp − total seeds at all sites*

*total number of sites*

Seed limitation

*sites reached by seeds Lseed = 1 −*

*total number of sites*

Seedling limitation

*Lsdlg = 1 −*

*sites with seedlings total number of sites*

*Ldisp = 1 −*

*seed limitation*

*1 − source limitation*

*sites with seedlings*

*Lest = 1 −*

*sites reached by seeds*

Establishment limitation

Dispersal limitation

**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 addi- tion on ‘context-sensitive’ effects that repre- sent a largely stochastic component of the fruit removal–seed dispersal phase. Among them, plant spacing patterns, neighbour- hood structure, site-specific habitat hetero- geneity, 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 coloni- zation and, potentially, the success of vegetation restoration efforts (García *et al.*,

2010). In this way, the relative roles of seed dispersal limitation and recruitment limita- tion in determining abundance and genetic structure could be gauged (Dalling *et al.*, 1998; García and Grivet, 2011). The pre- liminary protocols have been developed (e.g. Heithaus *et al.*, 1982; Jordano, 1989) for incorporating the consequences of the predispersal events and the deferred con- sequences 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 frugi- vores for individual plants in natural popu- lations and consider whether the effects of frugivores are offset by events in subsequent

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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 dis- tance, this image of Vertumnus, a Roman deity responsible for vegetation and meta- morphosis, appears as a neat, brightly col- oured and meticulously elaborated picture. On approaching the painting, one discov- ers that Arcimboldo illustrated at least

34 species of fleshy fruits, which, carefully assembled, served as natural models to produce Vertumnus’ image. Grapes, cher- ries, 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 intri- guing funny face is the painter’s ability to produce an ordered image from such a cha- otic 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 elab- orate assembly to produce a neat image. The efforts to bridge the consequences of frugivory and seed dispersal with demo- graphic and evolutionary processes in plant and frugivore populations are a first sketch of that picture.

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**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*

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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*

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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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