Plant–Animal Interactions

An Evolutionary Approach

Edited by

Carlos M. Herrera

Estación Biológica de Doñana
Consejo Superior de Investigaciones Científicas
E-41013 Sevilla
Spain

Olle Pellmyr

Department of Biology
Vanderbilt University
Nashville, TN 37235
USA

2002

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Chapter 7 Seed dispersal by vertebrates

Carlos M. Herrera

7.1 Introduction

Aside from the profound physiological differences derived from the ability of plants to build carbon-based organic molecules out of light, water and atmospheric carbon dioxide, the major macroscopic difference between plants and animals possibly lies in the very limited mobility of adult plants in comparison to adult animals. Adult plants remain fixed in space for their whole lives, anchored to their indispensable source of water and minerals. In the long run some adult plants may move by clonal growth but, in comparison with animals, the distances involved are negligible.

The absence of movement of adult plants entails decisive limitations at two critical stages in their reproductive cycles, namely sexual reproduction and offspring dispersal. These two processes require the movement of some reproductive structure across space. Sexual reproduction requires that pollen grains travel a variable distance from their place of origin to meet the female gametophytes, and dispersal of seeds involves their movement away from the maternal parent. Given this need for 'movement' inherently associated with the reproductive process, and provided that animals have such a quality in abundance, it should not surprise us that plants have developed a countless variety of mechanisms to use animals as the vectors of their pollen and seeds. This enormous diversity in the exploitation of animal movement for pollen and seed dispersal was once deemed one of the decisive factors responsible for the tremendous diversification and ecological success of angiosperms. More recent studies, however, are either inconsistent with that earlier view or only partly support it. Furthermore, dispersal of seeds by animals was not a functional novelty brought in by the angiosperms (Fig. 7.1). The habit is widespread among extant gymnosperms and, most likely, occurred in many extinct lineages as well, whose seeds were embedded in, or closely associated with, well-developed fleshy structures (see Chapter 2). In fact, seed dispersal by animals is proportionally much more frequent among extant gymnosperm than angiosperm lineages (64% vs. 27% of extant families respectively; Herrera 1989a).

In comparison to other aspects of plant reproduction, the study of plant–animal seed-dispersal systems from an explicitly evolutionary viewpoint is relatively recent. Darwin pioneered evolutionary studies of plant reproduction, and devoted considerable attention to studying the adaptation of plants to pollinators and the evolution of plant-breeding systems. In contrast, he paid only sporadic and cursory attention to seed dispersal in his writings. The recent emphasis on the evolutionary aspects involved in seed dispersal by animals may be traced back to a few influential studies published in the seventies (e.g. Snow 1971; McKey 1975). More recent overviews of the evolutionary ecology of plant–animal interactions for seed dispersal are provided by Janzen (1983a), Herrera (1985a, 1986) and Jordano (1992).

7.2 Seed dispersal: a summary of concepts

Dispersal is the process by which individuals move from the immediate environment of their parents to settle in a more or less distant area. Although it is not exclusive to plants, plant dispersal differs from animal dispersal in one important respect. While in animals the dispersing individual generally depends on their own locomotive powers, offspring dispersal in plants is always of a passive nature, as the seed has no control of either the dispersal process in itself or where it will eventually end up. This means that animal parents can play little or no role in determining the course of dispersal of their autonomous offspring, whereas dispersal of plant offspring will most often be determined by the traits of its maternal parent rather than by their own traits.

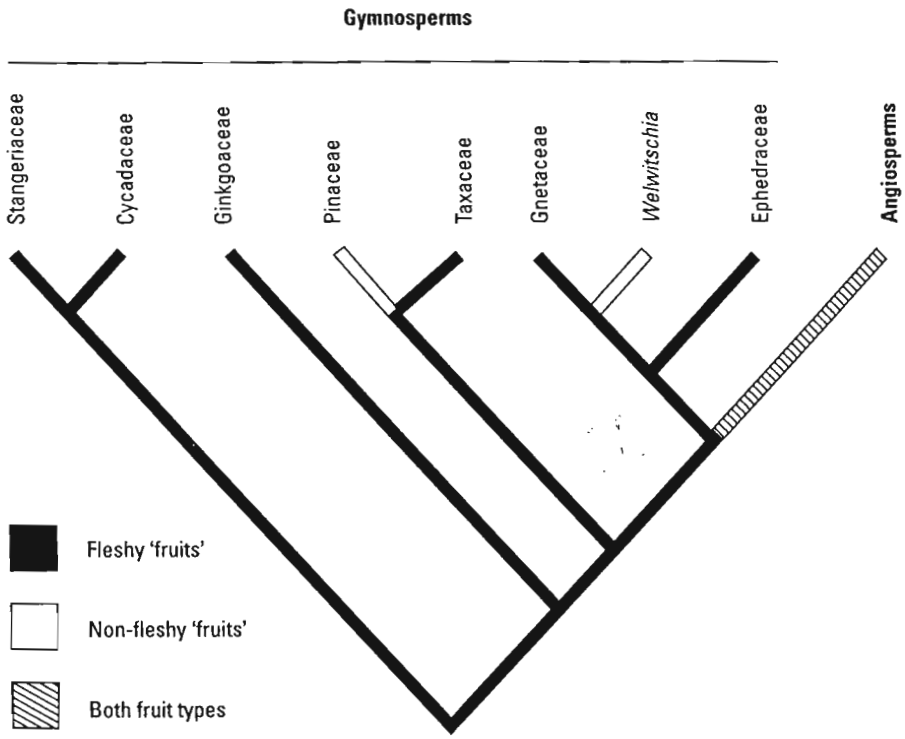


Figure 7.1 Distribution of fleshy 'fruits' (i.e. packages made up of seeds plus the accessory nutritious tissues that are used as food by animals) over the major lineages of extant seed plants. The phylogenetic arrangement shown follows the so-called 'anthophyte hypothesis' (e.g. Loconte & Stevenson 1990), whereby the Gnetales (= Gnetaceae + Ephedraceae + *Welwitschia* in the graph) are considered a sister group to angiosperms.

Seed dispersal may have different benefits to plants. These benefits may be classified in two major categories depending on whether they are related to circumstances of the 'departure' (i.e. the mere act of seeds leaving the parent) or the 'arrival' (i.e. the specific end-point of dispersal, or where the seeds eventually end up). This distinction makes sense in the light of theoretical models which have established that dispersal can provide a variety of fitness benefits even when a more favourable environment is not eventually reached by the dispersing organism (Johnson & Gaines 1990). But it can also help to explain some general evolutionary patterns exhibited by plant–vertebrate seed-dispersal systems, as shown in Section 7.8.2 later in this chapter.

7.2.1 Departure-related benefits

Merely leaving the immediate vicinity of the maternal parent may be advantageous to seeds. Escaping from the area of 'chemical influence' of the parent plant, for example, might result in increased seed germination and survival. Plants frequently produce chemicals that, after becoming incorporated to the soil, inhibit the germination not only of the seeds of other species ('allelopathy'), but of their own seeds as well ('autoallelopathy'; Solomon 1983). In most instances, however, departure-related benefits are not so straightforward, and depend in complex ways on the advantages derived from increasing the distance from the parent plant and of leaving a high-density concentration of competing siblings. As distance from the parent and seed/seedling density are usually correlated, the effects of these two factors are difficult to separate in the field without careful experimental manipulation. Seed density usually decreases away from the parent plant, hence seed dispersal may be advantageous simply because of improved survival prospects as a consequence of declining seedling competition with neighbours. In addition, some natural enemies of seeds

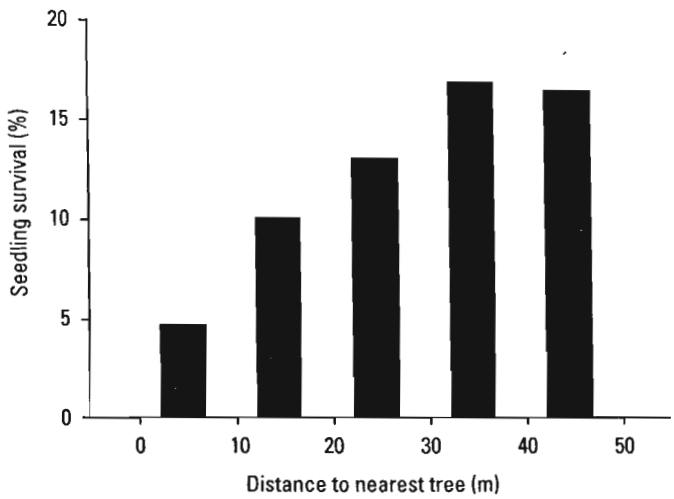


Figure 7.2 Seed/seedling survival over a 6-week period as a consequence of distance to the nearest conspecific in the tropical forest tree *Virola surinamensis*. Survival increases steadily with increasing distance to the nearest conspecific, reaching a plateau around 30–50 m. Distance-dependent herbivory and seed predation by insects and vertebrates were responsible for the observed pattern. (Drawn from data in Howe et al. 1985.)

and seedlings (e.g. pathogens, herbivores, seed-predators) respond to density and distance from the parent. In the tropical forest tree *Virola surinamensis*, for example, seed and seedling survival increase steadily with increasing distance from the nearest conspecific plant (Fig. 7.2). In this and many other investigations, the impact of fungal pathogens and animal seed-predators is greatest closest to the parent plants, which gives rise to a decline in seed and seedling mortality with increasing distance from adults (e.g. Augspurger 1984).

7.2.2 Arrival-related benefits

Seed dispersal may also be advantageous because of some particular characteristics of the point of arrival of seeds. For example, seed dispersal will be advantageous whenever it allows the quick occupation of vacant habitats or microhabitats. This is illustrated by the prevalence of species with well-developed seed dispersal mechanisms in the colonization of new volcanic islands (Whittaker & Jones 1994); by the rapid northward recolonization by forest plants of recently deglaciated territories during successive Pleistocene interglacials (Johnson & Webb 1989); and by the ability of plant species to migrate latitudinally in response to long-term climatic modifications (Huntley & Webb 1989).

Some species may have special requirements for seed germination or seedling establishment. In some mistletoes, for example, seedling establishment is optimal in a narrow range of host twig diameter (Sargent 1995). For these species with special requirements, seed dispersal may be highly advantageous if it predictably enhances the probability of seeds reaching such favourable microsites. This was termed 'directed dispersal' by Howe and Smallwood (1982), and it has been frequently suggested in relation to seed dispersal by animals. There are, however, very few well-documented examples, which probably reflects both the rarity of the phenomenon in nature and the difficulties faced by researchers when trying to objectively identify 'favourable' microsites from the viewpoint of plants. One of these few examples involves the ant-dispersed herb *Corydalis aurea*. In this species, directed dispersal of seeds to ant nests effectively increases the population growth rate because of a significant increase in the survival of seeds to reproduction (Hanzawa et al. 1988). Another well-documented instance of directed dispersal is provided by the tropical forest tree *Ocotea endresiana* and its major seed dispersers, the bellbirds (*Procnias tricarunculata*) (Fig. 7.3). The seeds dispersed by birds of this species predominantly land at microsites characterized by lower incidence of fungal pathogens and increased seedling survival rates. This directed dispersal to favourable microsites eventually results in increased seedling survival rates (Wenny & Levey 1998).

7.3 Seed dispersal by vertebrates

Seed dispersal by animals is an intrinsically heterogeneous phenomenon that involves an astounding diversity of animal and plant lineages, proximate mechanisms, and plant–animal functional, ecological and evolutionary relationships. Natural history and botanical details illustrating this enormous diversity may be found in the classical treatises of Ridley (1930) and van der Pijl (1969), and in more recent reviews focusing on the ecological and evolutionary implications of plant–animal dispersal relationships (Janzen 1983a; Sorensen 1986; Jordano 1992). With the outstanding exception of ants (see Chapter 8), invertebrates play only an anecdotal role as seed-dispersers, and this chapter will be concerned exclusively with the dispersal of seeds by vertebrates.

The diverse modalities of seed dispersal by vertebrates may be classified into one of three main *functional* categories. This will depend on whether dispersal is a casual

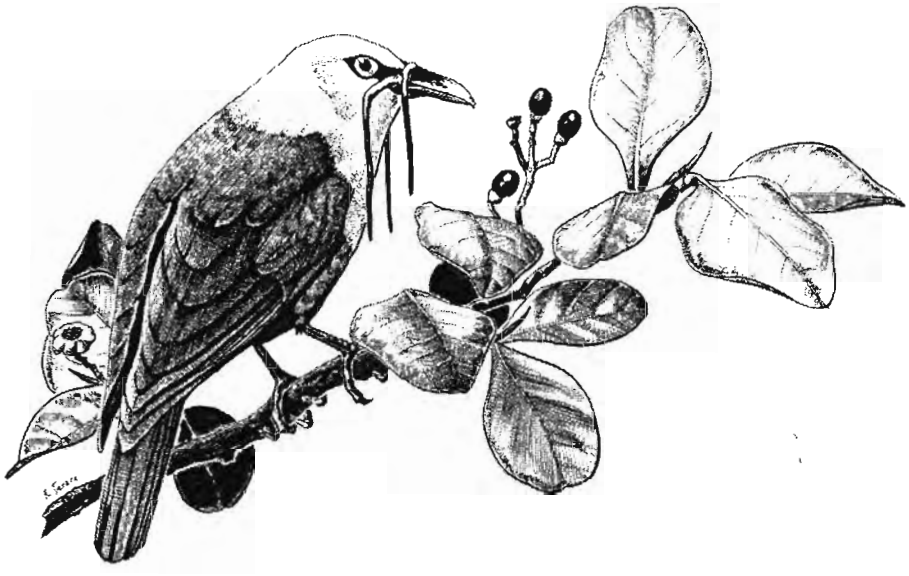


Figure 7.3 Seeds of the Neotropical forest tree *Ocotea endresiana* (Lauraceae) that are dispersed by frugivorous bellbirds (*Procnias tricarunculata*; Cotingidae) tend to land predominantly at forest microsites that are characterized by the lower incidence of fungal pathogens (Wenny & Levey 1998). (Drawing by Rodrigo Tavera.)

consequence of deliberate seed-harvesting by seed-predators or a result of incidental picking up of seeds. In the latter case, it will also depend on whether seed transport takes place internally or externally (Box 7.1). Rather than highlighting structural particularities, this classification emphasizes unifying functional features. As with any biological classification, however, some exceptions occur that do not fit easily. This applies, for example, to some tropical dispersal systems where vertebrates participate as primary dispersers and ants then act as secondary dispersers of vertebrate-dispersed seeds (Levey & Byrne 1993). Another exception occurs in situations where wind is the primary disperser and vertebrates then perform further dispersal of wind-dispersed seeds (Vander Wall 1992). These binary or 'two-stage' seed-dispersal systems have been little studied so far, but future studies may eventually prove that their frequency in nature is much higher than hitherto recognized.

Each of the three major categories of animal seed dispersal recognized in Box 7.1 has its own set of physical constraints, ecological requirements and life-history consequences. Harvest-based dispersal systems, for example, are associated with extensive seed mortality (see Chapter 5). Dispersal by external adhesion is constrained by seed size, as heavy seeds can hardly remain attached to animal fur or feathers for little more than a short time. Dispersal in animal interiors requires the evolution of some rewarding bait to entice animals and make them become internally 'contaminated' with inadvertently ingested seeds. This means that the three major modalities of animal seed dispersal are ecologically and evolutionarily so disparate as to be treated separately. Animal seed dispersal based on imperfect harvesting was dealt with in Chapter 5 on granivory, because it is closer to a variant of seed-predation from both the plants' and animals' viewpoint. Dispersal by contamination of animal exteriors is not considered in this book, as it does not qualify as a plant–animal interaction. In a functional sense, it does not differ greatly from wind dispersal, in that both wind and animal agents pick up seeds incidentally and passively, with no opportunity of interaction between the plant and its animate or inanimate disperser. Seed dispersal in animal interiors will be the subject of the rest of this chapter, and the expression 'vertebrate seed dispersal' will be used hereafter to refer exclusively to this dispersal mode.

7.4 Dispersal in animal interiors

7.4.1 The mutualism: exchanging food for movement

Plants dispersed by vertebrates have evolved edible seed appendages or coverings that are ingested and digested by animals that later eject the seeds in conditions suitable for germination. The package made up of seeds plus the accessory nutritious tissues that are used as food by animals may be termed 'fruit', although it does not always originate from an ovary (the true 'fruit' in a botanical sense). The fleshy portion may originate from the seed coat (as in

Box 7.1 Main functional categories of seed dispersal by vertebrates

Seed dispersal by vertebrates comprises a mixture of heterogeneous phenomena involving a broad variety of animal lineages, proximate mechanisms, and plant–animal functional, ecological and evolutionary relationships. All that variety, however, boils down to three major categories that differ in the essential mechanisms involved.

1 Imperfect harvesting Animals that forage for the seeds themselves (granivores) take them away from the parent plant to be eaten (and thus killed) some time later. As a consequence of this delay from harvesting to consumption, a certain proportion of harvested seeds accidentally escape destruction, thus fortuitously converting genuine harvesters into occasional seed-dispersers. Seed dispersal based on imperfect harvesting is typically associated with situations where animals intensively harvest temporarily superabundant seed crops and store the excess food in caches for future use.

Granivorous birds and mammals are most often involved in this dispersal system (see Chapter 5). Well-known examples from temperate latitudes include dispersal of pine seeds by nutcrackers, acorn dispersal by jays and small-mammal dispersal of many forest trees. This dispersal system may be much more common in tropical forests that hitherto recognized, with rodents playing a prominent role (Forget 1993).

2 Collection of seeds Animals do not actively seek seeds for food but perform dispersal as a consequence of becoming 'contaminated' with mature seeds. Seeds are picked up from the maternal plant (primary dispersal) or elsewhere (secondary dispersal), and then discarded some distance away in conditions suitable for germination. Both external (by adhesion following simple physical contact) and internal (by ingesting seed-'contaminated' food), picking up may occur, which leads to the following two major sub-categories.

2.1 Dispersal on animal exteriors Mature seeds become accidentally attached to the animals' surface after fortuitous contact with the maternal plant, and are then dislodged some distance away. Characteristic examples include the dispersal of hooked or viscid seeds of terrestrial plants entangled in mammalian fur or, less often, birds' feathers (Sorensen 1986), but also the seeds of both terrestrial and aquatic plants dispersed in the muddy feet of animals.

2.2 Dispersal via animal interiors Seeds accidentally enter the digestive system of animals, generally when they ingest plant structures closely associated with seeds. These are subsequently spat out, regurgitated or defecated in conditions suitable for germination. This category includes the dispersal of 'fleshy-fruited' plants (i.e. those producing berries, drupes or functionally analogous structures) by frugivorous vertebrates, undoubtedly the most widespread, and ecologically and evolutionarily diverse, plant–animal seed dispersal system. Birds and mammals are the organisms playing the most prominent roles by far in this mode of seed dispersal, but other vertebrates, like fishes, tortoises or lizards, may also be important dispersers for some species or in some particular habitats (Milton 1992; Souza-Stevaux et al. 1994; Valido & Nogales 1994).

species with arillate seeds) or from ancillary floral structures like bracts or the floral receptacle itself (see Plate 7.1 facing p. 84). This great variety of morphological and anatomical origins of the nutritious portion of fruits contrasts sharply with the homogeneity of its function. Such functional convergence suggests that (i) there have been consistent selective pressures on plants favouring the evolution of plant traits enhancing seed dispersal in animal interiors based on food rewards; and (ii) the modification of pre-existing anatomical structures to turn them into food rewards for frugivorous animals has been relatively simple to evolve, and has not involved many genetic changes. In plants, intra- and interspecific variation in important morphological and architectural traits, including many flower and fruit characteristics, are often governed by just one or two genes. This means that important phenotypic changes may be brought about with only minimal genetic reorganization (Gottlieb 1984).

The relationship between animal-dispersed plants and their dispersers is generally of a mutualistic nature, as both partners derive some benefit from their participation. The food reward provided by the plants is 'exchanged' for a service, namely the movement of seeds provided by the animals. Nevertheless, the outcome of ecological interactions is often quite context-dependent, and the mutualistic nature of the relationship between plants and the vertebrates feeding on their fruits must be corroborated in each particular instance. A given disperser may have a mutualistic relationship with some plant species but not with others. In northern temperate habitats, titmice (Paridae) predominantly behave as fruit-predators that feed on fruit pulp or the seeds themselves without performing seed dispersal, but as mutualists of a few species whose seeds they disperse successfully (Snow & Snow 1988). In some tropical frugivorous birds with lek mating systems, males probably play predominantly

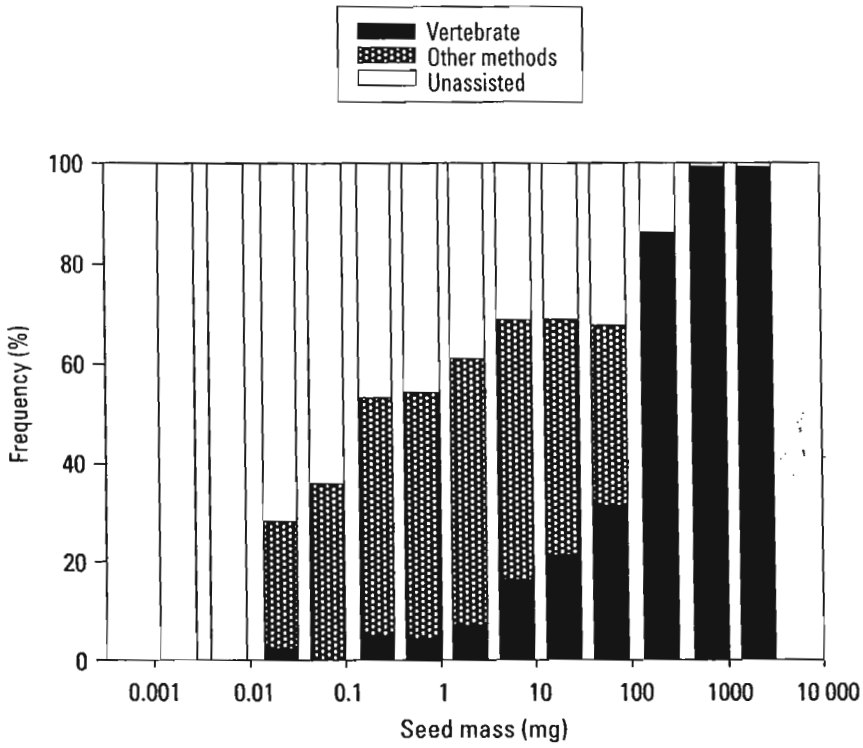


Figure 7.4 The proportion of species with different seed-dispersal methods (vertical axis) varies with seed size (horizontal axis, note the logarithmic scale). The majority of the smallest-seeded species lack special dispersal mechanisms, while vertebrate seed dispersal typically prevails among the largest-seeded species. Other seed-dispersal methods (including ant, wind, adhesive and ballistic dispersal) tend to occur most often among species with intermediate-sized seeds. (Modified from data in Hughes et al. 1994.)

non-mutualistic relationships with their food plants by generating high-density concentrations of dispersed seeds at lek sites, while females of the same species will disseminate seeds more widely and thus behave as mutualists (Krijger et al. 1997).

7.4.2 Taxonomic and ecological distribution: plants

Vertebrate dispersal occurs, and has occurred, in many and disparate seed-plant lineages, both extant and extinct (see Chapter 2 and Fig. 7.1). Starting with seed ferns (pteridosperms) in the early Carboniferous, it has evolved independently on innumerable occasions and ecological scenarios. Among extant taxa, vertebrate dispersal may characterize whole orders (e.g. Cycadales in the gymnosperms), but it occurs more often in subsets of families within orders, subsets of genera within families, or even small groups of species within large genera (e.g. species of *Hypericum* in the Hypericaceae and *Galium* in the Rubiaceae). Vertebrate dispersal also occurs sporadically in some very large families that are almost homogeneously characterized by other seed-dispersal methods, like Asteraceae (*Clibadium*, *Chrysanthemoides*) and Poaceae (*Lasiacis*, *Olmeca*). This extremely patchy distribution of vertebrate seed dispersal among and within levels of the taxonomic hierarchy, along with the variety of anatomical origins of the nutritious portion of fruits noted earlier, indicates that its evolution has been not subject to consistent morphological and ontogenetic constraints, and that it has been selectively advantageous many times and in many ecological scenarios (Herrera 1989a). There is evidence, however, that the fleshy fruit-producing habit is most frequent among basal (i.e. most primitive) angiosperm lineages (e.g. Magnoliales, Laurales), which is consistent with suggestions that the earliest angiosperms had fleshy fruits (Donoghue & Doyle 1989).

Seed dispersal by vertebrates is predictably associated with plant growth form, seed size, habitat type and geographical location. It is generally associated with a large seed size. In four British and Australian temperate floras, for example, almost all species with seeds heavier than ≈ 100 mg are dispersed by vertebrates (Fig. 7.4). The proportion of species that are dispersed by vertebrates is generally highest among trees or shrubs and lowest among herbs. In the regional flora of the north-western Iberian Peninsula, for example, 46% of woody species (shrubs and trees combined) are dispersed by vertebrates, but only 8% of herbaceous species (Buide et al. 1998). In a Brazilian tropical dry forest, proportions of woody and herbaceous species dispersed by vertebrates were 52% and 22% respectively (Gottsberger & Silberbauer-

Gottsberger 1983). As a consequence of this correlation between growth form and dispersal mode, the relative importance of vertebrate-dispersed plants differs among types of plant community, decreasing from forests to scrublands to herbaceous formations (Fig. 7.5).

Within each growth form, the frequency of vertebrate dispersal decreases with increasing latitude, altitude and aridity, and with decreasing soil fertility (Willson et al. 1990; Westoby et al. 1990). Considering woody taxa alone, for example, vertebrate-dispersed species account for ≈ 35–44% of local species in temperate forests and Mediterranean scrublands, but their importance increases to 75–90% of species in humid tropical forests (Fig. 7.6).

Availability of dispersers does not provide a general explanation of geographical differences in the frequency of vertebrate dispersal (Hughes et al. 1994). For example, frugivorous vertebrates are rather scarce in the southern hemisphere temperate rainforests of Chile, yet the frequency of vertebrate seed dispersal in these habitats is roughly comparable to that found in tropical forest communities harbouring abundant and diverse frugivorous vertebrates (Armesto & Rozzi 1989). Variation in

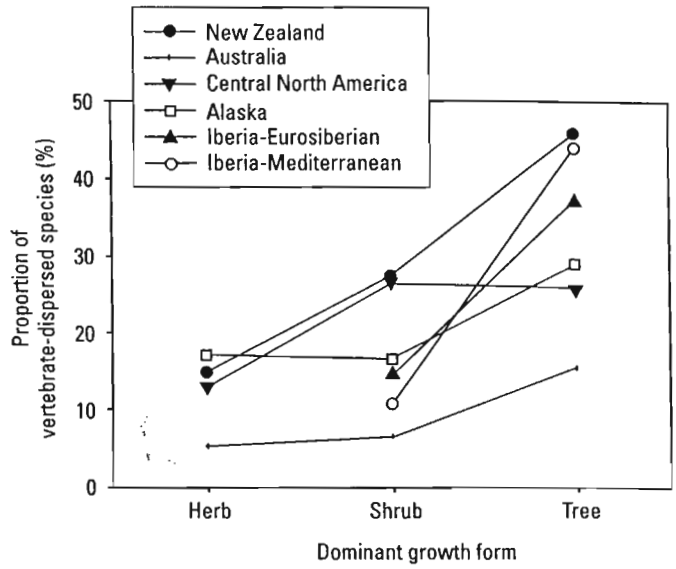


Figure 7.5 Variation among major plant-community categories from several non-tropical regions in the average proportion of plant species whose seeds are dispersed by vertebrates. In all regions considered, there is a consistent trend for the relative importance of vertebrate-dispersed species to increase from herb- through shrub- to tree-dominated plant communities. Each symbol represents the average value for a number of plant communities. (From data in Willson et al. 1990 and Guitián & Sánchez 1992.)

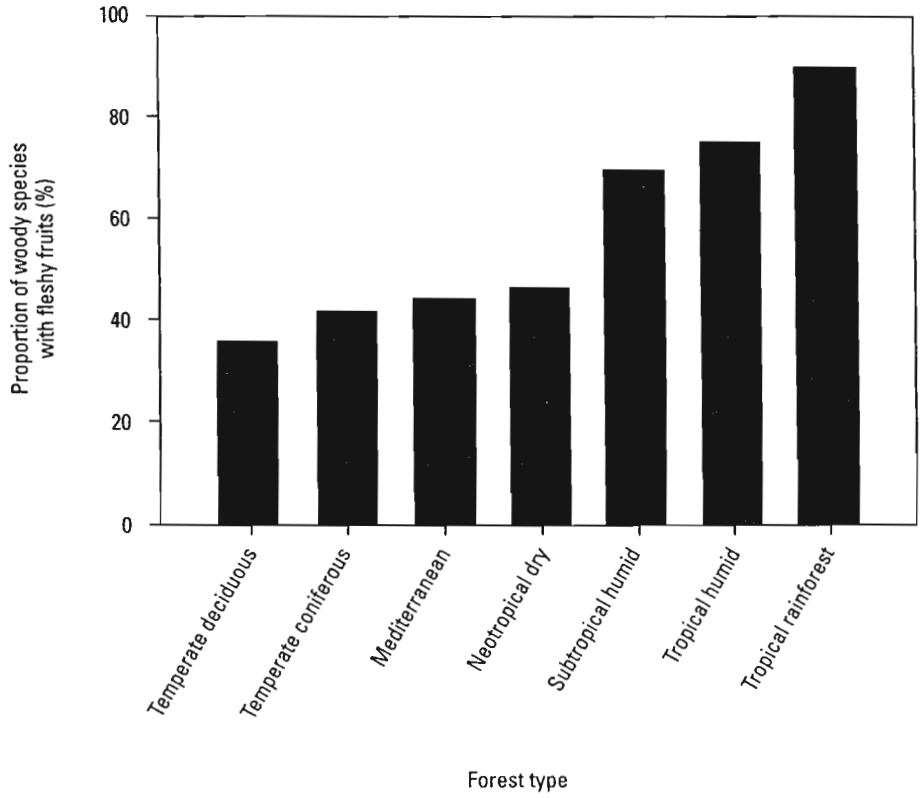


Figure 7.6 Proportion of woody species producing fleshy fruits in different forest types. (Modified from Jordano 1992.)

abiotic factors provides a parsimonious explanation for differences among plant communities in the importance of vertebrate dispersal. Variation in moisture availability and soil fertility determine differences in vegetation structure and in the relative importance of different growth forms. This will ultimately mould seed size distributions (because seed size is related to growth form) and consequently affect the proportion of different dispersal modes in plant communities (Hughes et al. 1994). The large percentage of woody plants in tropical moist forests that have vertebrate-dispersed seeds thus most likely results from strong selection for large seed size, rather than from particularities of the relationships with vertebrate dispersers (Westoby et al. 1990).

7.4.3 Taxonomic and ecological distribution: frugivores

All major lineages of vertebrates take part in fruit consumption and seed dispersal, but their importance as dispersal agents is very unequal. Birds and mammals are the only or main dispersers of the vast majority of vertebrate-dispersed plants, and an important fraction of lineages in these two major vertebrate groups maintains some links with plants related to seed dispersal. About 36% of 135 extant families of terrestrial birds, and 20% of 107 families of non-marine mammals, are partly or predominantly frugivorous (Fleming 1991). Examples of avian seed-dispersers include thrushes, waxwings and warblers in temperate habitats, and hornbills, bulbuls, toucans and manakins in tropical forests. Seed-dispersing mammals include such disparate groups as bats, lemurs, gorillas, foxes, rhinoceros and elephants. This extraordinary diversity of avian and mammalian frugivores indicates that frugivory, and associated seed dispersal, has evolved on many occasions in the vertebrate phylogeny. Fish are important seed dispersers for some tropical plants (Souza-Stevaux et al. 1994), but their quantitative importance in riparian and seasonally inundated tropical habitats is still poorly known. Tortoises and lizards are prominent seed-dispersers only in arid and insular environments (Milton 1992; Valido & Nogales 1994). There is at least one reported instance of seed dispersal by a tropical tree-frog (Da Silva et al. 1989), but dispersal by amphibians is unlikely to represent little more than a biological anecdote.

Frugivorous vertebrates are no exception to overall latitudinal trends in species diversity, and most families of frugivorous birds and mammals occur in the tropics (Fleming et al. 1987). This tropical concentration of frugivorous taxa apparently stimulated the earlier notion that the interaction between fleshy fruit-producing plants and their dispersers was 'a quintessential tropical phenomenon' (Fleming et al. 1987), and led to the 'calumnious claim [that] the ecology of plant-animal interactions in the temperate zone is downright uninteresting' (Willson 1986). Nevertheless, a more balanced picture has emerged as recent studies have increasingly shown that vertebrate frugivory is quantitatively and qualitatively important in non-tropical regions too. Autumn bird communities of central and north-eastern North America, for example, have a greater proportion of frugivorous species than pristine Amazonian tropical forests (Terborgh et al. 1990; Willson 1991), and Mediterranean forests and scrublands are characterized by very dense populations of frugivorous birds in autumn and winter (Herrera 1995). Fruits may also be more important than hitherto recognized in the nutrition of a large proportion of the terrestrial avian community in Arctic forest-tundra habitats. Many species of Arctic birds feed heavily on fleshy fruits during the autumn migration (Guitián et al. 1994), but also during the breeding season, as fruits produced during the previous summer are preserved in good condition beneath the snow (Norment & Fuller 1997).

The earlier notion that 'specialized' frugivores relying heavily on fruit for food are a distinguishing feature of tropical habitats has also been challenged recently. On one hand, supposedly specialized tropical frugivorous birds, like some species of trogons, toucans, manakins or touracos, actually are not as extensively frugivorous as previously thought, and regularly include significant amounts of animal food in their diets (Remsen et al. 1993; Sun & Moermond 1997). And on the other hand, many non-tropical frugivores depend almost exclusively on fruits for food for extended periods. These include sylviid warblers, thrushes and waxwings among birds (Herrera 1995; Witmer 1996a), and several families of mammals in the order Carnivora (Herrera 1989b; Willson 1993). In the Mediterranean region, for example, fruits regularly contribute >90% of the diet of several species of sylviid warblers during the autumn–winter period (Herrera 1995). These and other studies have contributed to the demise of the earlier myth of plant–frugivore interactions as an essentially tropical phenomenon. It must be emphasized that the strength of the relationship of frugivores with

plants can only be evaluated by detailed studies of the actual nutritional importance of fruit food. As quantitative information of this sort is still remarkably sparse for the majority of frugivores, generalizations on the taxonomic and ecological correlates of the extent of frugivory by vertebrates should be made with caution.

7.5 Plant adaptations

One central issue in the study of plant–disperser interactions from an evolutionary perspective is the degree to which selection pressures of plants on frugivores, and of frugivores on plants, have influenced morphological, physiological and behavioural traits in each group of organisms. In the case of plants, the fitness advantages derived from seed dispersal by vertebrates have selected for fruit and fruiting-related traits enhancing fruit consumption by seed dispersers. These include the timing of fruit presentation, fruit traits enhancing discovery by dispersers, and fruit size and nutritional composition, as detailed in the following sections. Plant–disperser interactions, however, do not take place in an ecological vacuum, and fruit and fruiting-related traits are also susceptible to selective forces imposed by abiotic factors and non-mutualistic organisms like seed- and fruit-predators. The possible influence of selective pressures other than those exerted by dispersal agents on dispersal-related plant traits also needs to be taken into consideration.

7.5.1 Fruiting phenology

Selection from dispersers may lead to either clumped or staggered fruiting seasons of locally coexisting plants. These two contrasting possibilities may occur in the same habitat. In central Panama, bird-dispersed species of *Psychotria* have clumped, and those of *Miconia* staggered fruiting seasons (Poulin et al. 1999). The staggering of fruiting seasons was formerly interpreted as a response to selection for decreasing competition among plants for dispersers, but subsequent studies have provided little support for this hypothesis (Wheelwright 1985a; van Schaik et al. 1993). In the case of the *Miconia* and *Psychotria* species mentioned above, their respective phenological patterns can hardly be due to selection from current dispersers, as these are roughly the same for the two plant genera.

Clumped fruiting seasons generally lead to well-defined seasonal peaks in fruit abundance. In northern temperate habitats, for example, most vertebrate-dispersed plants ripen their fruits in late summer and autumn, while in Mediterranean forests and shrublands fruit ripening peaks in autumn–winter (Herrera 1995; Noma & Yumoto 1997). Although less marked than in temperate habitats, fruiting seasonality is also a salient feature of tropical and subtropical forests (van Schaik et al. 1993). Synchronous fruiting by plants sharing the same dispersers may enhance each other's dispersal by mutually attracting more dispersers than each would alone.

Local peaks of fruit availability often coincide with peaks of disperser abundance, which have frequently been interpreted as evidence of disperser selection on the time of fruit ripening (Herrera 1985b; Noma & Yumoto 1997). It is difficult, however, to distinguish this scenario from the converse, that dispersers may respond numerically to, or time their seasonal displacements to coincide with, fruiting peaks (Levey 1988; van Schaik et al. 1993). In general, there is little current support for the once-favoured notion that disperser availability has been the main selective agent shaping the time of fruit ripening in vertebrate-dispersed plants. In wet sclerophyll forests of south-eastern Australia, peak fruiting occurs during autumn, but fruit-eating birds are equally abundant from spring through autumn (French 1992). Among western European bird-dispersed plants, available evidence is contrary to the notion of phenological adjustments by individual species to the marked latitudinal and elevational variations in seasonal patterns of disperser abundance. Local fruiting peaks match disperser abundance peaks because species that fruit at times of greatest disperser abundance are locally dominant, but not because of adjustments by component species (Fuentes 1992). In the predominantly bird-dispersed *Crataegus monogyna*, for example, the more northerly European populations do not fruit significantly earlier than southern populations, as would be expected if local populations had adjusted fruiting seasons to match peaks in disperser abundance (Guitián 1998).

Abiotic factors and organisms other than dispersal agents seem to have played prominent roles in the evolution of fruiting phenologies of vertebrate-dispersed plants. Seasonality in temperature and water availability sets limits on the time of fruit development and maturation. This holds even for the weakly seasonal tropics, where the influence of insolation and water availability on the phenology of woody plants has been more pervasive than the influence of biotic factors like dispersers (van

Schaik et al. 1993). In western Europe, latitudinal shifts in the ripening season of bird-dispersed plants mainly reflect climatic constraints rather than selective pressures from dispersers (Debussche & Isenmann 1992). Microbes, invertebrates and vertebrate seed- and fruit-predators often destroy large numbers of ripe fruits and seeds before they are dispersed, thus they may also influence the evolution of ripening seasons. In central Sweden, for example, around 99% of the fruits of the bird-dispersed shrub *Viburnum opulus* are eaten by bullfinches (*Pyrrhula pyrrhula*) and bank voles (*Clethrionomys glareolus*), which are seed-predators and do not disperse seeds, while fewer than 1% of fruits are eaten by legitimate seed-dispersers (Englund 1993). Since the abundance and/or activity of fruit-damaging microbes and animals varies seasonally, then selection for escaping from these destructive agents has probably contributed decisively to drive ripening seasons closer to those times of the year when the risk is at its lowest (Herrera 1982b).

7.5.2 Advertisement

Those food resources whose fitness is reduced by vertebrate consumption (e.g. insects, seeds) have evolved adaptations that reduce detectability by harmful consumers. Fruit consumption by vertebrate dispersers, in contrast, by being advantageous to plants, has selected for fruit traits that enhance detectability by frugivores. The ripe fruits of vertebrate-dispersed plants are characterized by distinctive odours, conspicuous coloration or some combination of these.

7.5.2.1 Chemical signals

The ecological correlates of chemical signalling by wild ripe fruits remain virtually unknown, in contrast with the extensive attention received by visual signalling (see below). Evidence based on human perception suggests that wild fruits differ widely in the amount and nature of emitted volatiles, and that fruits scented to the human nose seem to be significantly associated with dispersal by nocturnal mammals (van der Pijl 1969; Herrera 1989b). Nevertheless, this may just reflect our own biased mammalian perception. Fruits that are unscented to humans may still produce volatile compounds detectable by analytical procedures and by other organisms (Scarpati et al. 1993). Fruit volatiles may mediate the relationship of fruits not only with dispersers, but also with fruit- and seed-predators, and its study deserves more attention than it has received so far.

7.5.2.2 Visual signals

In the spectrum visible to humans, ripe fruits vary in colour from reds, blacks and blues to greens and browns. Although exceptions abound, fruits that are green or otherwise dull-coloured when ripe tend to be associated with seed dispersal by mammals, whereas fruits dispersed by birds tend to be brightly pigmented. The partial dichotomy between 'bright' and 'dull' ripe fruits has probably been selected for by the contrasting sensory capacities of birds and mammals (Janson 1983). Red and black fruits predominate among bird-dispersed plants in both tropical and temperate regions, and there is only minor geographical variation in colour spectra (Fig. 7.7). The visual conspicuousness of fruits may be further enhanced by the juxtaposition of two or more bright colours. This juxtaposition may occur in the infructescence itself, as frequently found in species where the contrasting colours of ripe and unripe fruits produce conspicuous bicoloured displays (Willson & Thompson 1982). In some species, it is the contrast between the ripe fruits and the adjacent leaves which enhances visual conspicuousness, and this kind of bicoloured fruit advertisement method was named 'foliar flag' by Stiles (1982). Ripe fruits of many bird-dispersed plants reflect ultraviolet light. This may also have evolved to enhance the visual signals of these fruits, since the colour vision of many bird species extends to the near UV (Willson & Whelan 1989).

The bright fruit colours of bird-dispersed plants represent adaptations for promoting avian frugivory. This has been proved by carefully controlled experiments showing that fruiting displays differing in coloration differ in the probability of being discovered and/or consumed by avian frugivores in the field. Frugivorous birds generally discriminate among fruits on the basis of colour and often exhibit consistent colour preferences. In the colour-polymorphic *Rubus spectabilis*, frugivorous birds select fruits on the basis of colour, and consistently favour red over orange fruits on both local and regional scales in western North America (Gervais et al. 1999). The observations that bicoloured fruit displays occur more often among species with small fruits, and among those fruiting at times of year when dispersers are relatively scarce, provide further support to the adaptive value of fruit conspicuousness (Willson & Thompson 1982; Herrera 1987).

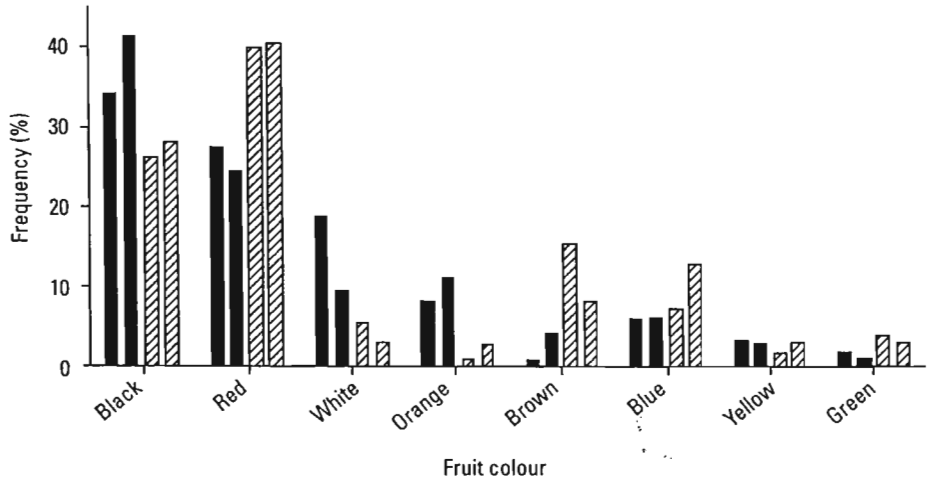


Figure 7.7 Frequencies of bird-dispersed plant species producing ripe fruits of various colours in two Neotropical (Peru and Costa Rica, N= 134 and 252 species respectively; filled bars) and European (central Europe and Spain, N= 137 and 111 species respectively; hatched bars) regions. (From data in Wheelwright & Janson 1985 and C.M. Herrera, unpublished.)

Nevertheless, factors unrelated to consumption by dispersers may also have influenced the evolution of fruit colour in bird-dispersed plants. Fruit colours may be adaptive in defending fruit against consumers that damage the fruit, either because of the deterrent properties of the pigments themselves (e.g. antifungal phenolic pigments) or because certain damaging agents cannot perceive certain colours (e.g. red fruits 'inconspicuous' to frugivorous arthropods) (Willson & Whelan 1990). Fruit colour may also be an evolutionary by-product of selection acting on some correlated character. In the Australian shrub *Rhagodia parabolica*, seed germination behaviour is correlated with fruit colour, and selection acting on seed germination, rather than selection by dispersers acting directly on fruit colour, may explain fruit colour in this species (Willson & O'Dowd 1989). Physiological factors may also sometimes be involved in the evolution of fruit colour. Plants with large or otherwise costly fruits may have green ripe fruits because photosynthesis may compensate for respiratory costs (Cipollini & Levey 1991).

7.5.3 Fruit size

Size is an important attribute of fruits, because it sets limits to ingestion by relatively small-sized dispersers that swallow them whole, like birds. Fruit size is probably less important in relation to consumption by large vertebrates with wide gapes, or by small frugivores that mandibulate or chew up fruits to pieces. Fruits eaten by mammals tend to be larger than those eaten by birds (Janson 1983; Herrera 1989b). Among bird-dispersed plants, interspecific differences in fruit size explain differences in the species composition of dispersers, and the mean size of ingested fruits tends to be correlated with gape width among frugivorous birds (Wheelwright 1985b; Jordano 1987a).

Geographical patterns in fruit size are related to variation in dispersers' body size. Tropical forests include considerably larger fruits than temperate-zone forests and, within the tropics, Palaeotropical fruits tend to be larger than Neotropical ones (Mack 1993). These differences are related to the greater size range spanned by tropical frugivores relative to temperate-zone counterparts, and by the relative scarcity of large frugivores in the Neotropics. In western Europe, the mean fruit diameter of bird-dispersed plants is closely correlated across habitats with the mean gape width of disperser species (Fig. 7.8).

It is difficult to assess whether all these patterns actually reflect plant adaptations to variable disperser-size distributions. The correlation across habitats between the sizes of dispersers and fruits may mean that differences in fruit size have evolved to match variations in the local disperser-size distribution, but also that local disperser assemblages differing in size distributions are built up in response to regional variations in fruit size. Like other fruit traits, fruit size is correlated with plant phylogeny (Jordano 1995), and differences in the taxonomic

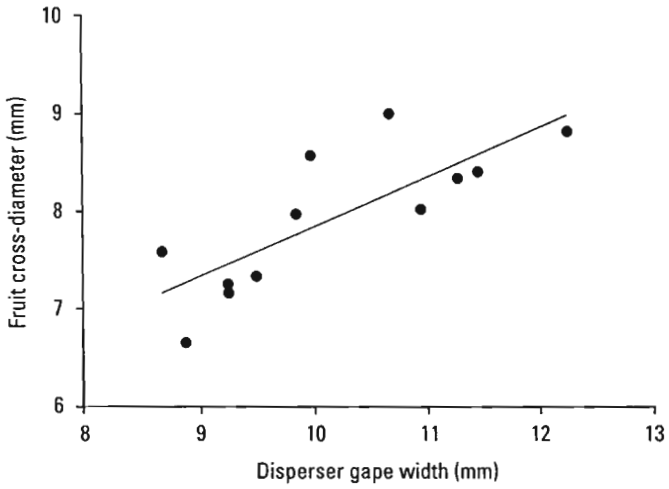


Figure 7.8 In western Europe, the average fruit cross-diameter of bird-dispersed plants is significantly related to, and slightly smaller than, the average gape width of local bird dispersers. Points in the graph represent average values for 12 localities from different habitat types. (Modified from Herrera 1985b.)

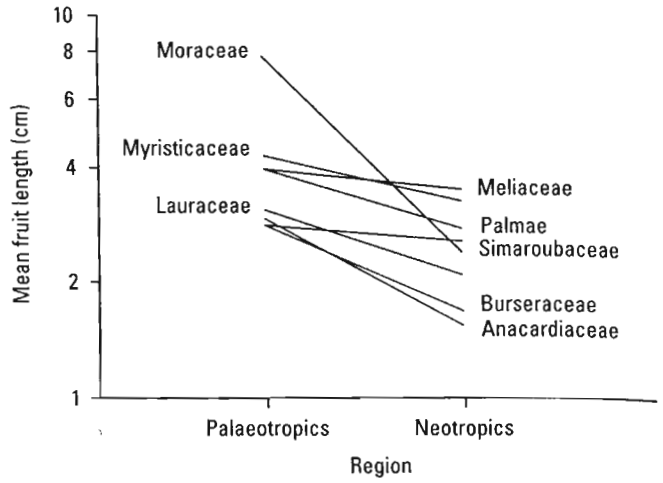


Figure 7.9 Palaeotropical fruits tend to be larger, on average, than Neotropical fruits, which is in accordance with the relative scarcity of large-sized vertebrate frugivores in the New World. As illustrated in this graph, the difference holds also within the 8 plant families represented in both the Palaeotropics and the Neotropics. The transcontinental difference thus most likely has some adaptive basis, and is not the exclusive consequence of phylogenetic correlates of fruit size and variation in the composition of fruiting plant assemblages. (From data in Mack 1993.)

composition of fruiting plants at different sites might account in part for patterns of variation in mean fruit size. An adaptive component does seem to exist, however, at least in the case of the fruit-size differences between the Neotropical and Palaeotropical fruits mentioned above, as geographical differences persist after accounting for phylogenetic correlations of fruit size (Fig. 7.9).

There is also unequivocal field and laboratory evidence indicating that fruit size may frequently be subject to selection by dispersers, at least among bird-dispersed species. Fruit choice, the handling mode and the foraging efficiency of frugivorous birds is strongly influenced by fruit size (Rey et al. 1997). As a consequence of size-based fruit preferences of frugivores, differences among individual plants in the size of fruits frequently result in differential seed-dispersal success, which provides a proximate mechanism for natural selection to operate on fruit size (Sallabanks 1993; Wheelwright 1993).

7.5.4 Pulp composition

7.5.4.1 Nutrients

Fruit pulp is the reward offered by plants to dispersers, and its nutritional value is a critical element in the plant–disperser interaction. Compared to other biological materials, fruit pulp is characterized, on average, by high water and carbohydrate content, and low protein and lipid content. There is, however, considerable interspecific variability in major nutrient composition, and this variability is in itself one distinctive feature of fruit pulp as a food resource for animals. In a set of 111 bird- and mammal-dispersed species from the Iberian Peninsula, lipid contents ranged between 0.2 and 59%, protein between 1 and 28%, and soluble carbohydrates between 26 and 93% of pulp dry mass (Fig. 7.10). Equivalent levels of variability have been found in all vertebrate-dispersed floras that have been studied so far from the viewpoint of the nutritional value of fruits (e.g. Wheelwright et al. 1984; French 1991). Fruit pulp also generally contains vitamins, carotenoids, amino acids and minerals that may play significant roles in the nutritional ecology of frugivores (Izhaki 1988; Jordano 1988). Little is known about the patterns of occurrence of these minor pulp constituents in wild fruits and their nutritional effects on consumers, but the fact that they occur at low concentrations does not necessarily mean that they are nutritionally irrelevant to frugivores. In cedar waxwings (*Bombycilla cedrorum*), for example, carotenoid pigments from ingested fruits are responsible for feather coloration (Witmer 1996b).

Earlier hypotheses on the evolution of plant–disperser interactions conferred great significance on the nutrition-

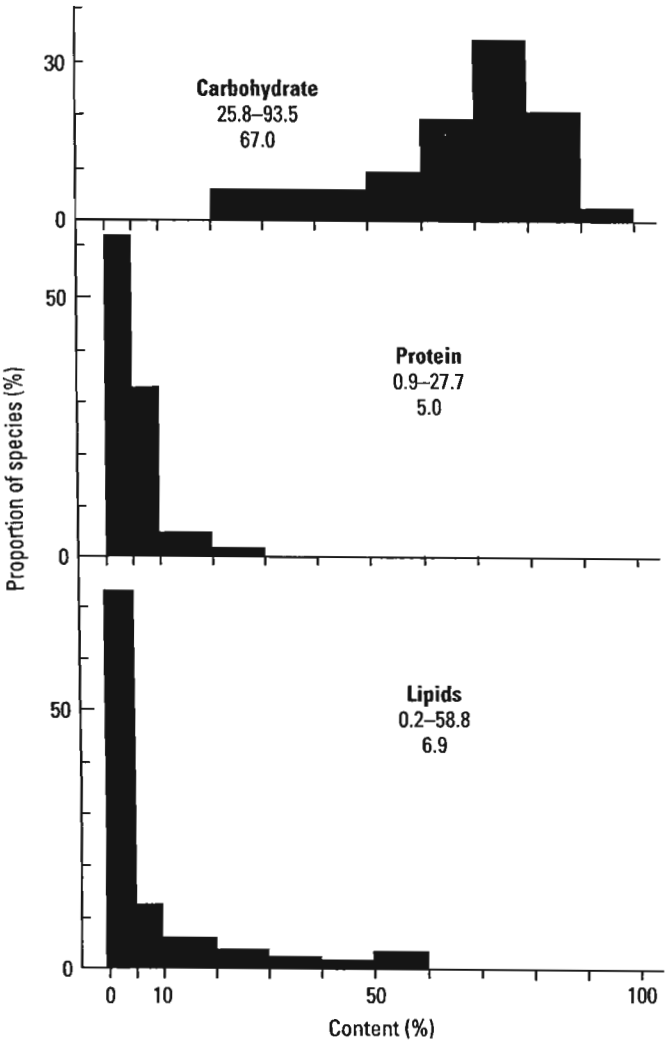


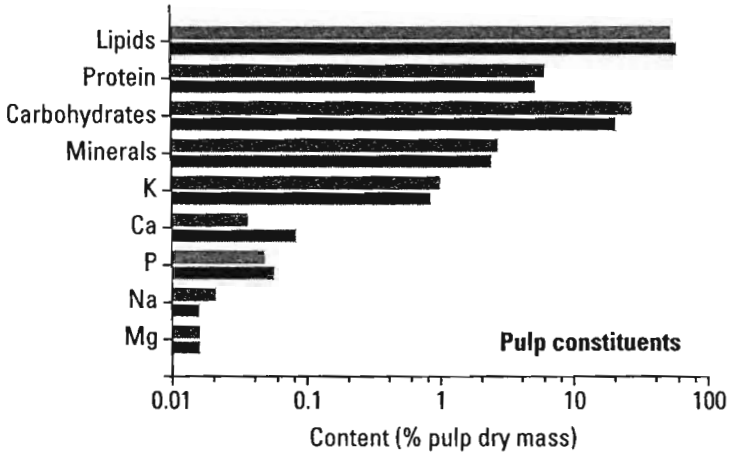
Figure 7.10 Frequency distributions of contents (as percentage of dry pulp mass) of non-structural carbohydrate, protein and lipids, in fruit pulp of vertebrate-dispersed plants from the Iberian Peninsula (N= 111 species). Ranges and means are shown for each constituent. (From Herrera 1987.)

al features of fruit pulp, as indicative of plants' adaptations to dispersers and the 'specialization' of the mutualism. Three main lines of evidence have subsequently de-emphasized the importance of fruit pulp quality as a trait reflecting plants' adaptations to dispersers. First, frugivores frequently do not discriminate on the basis of pulp nutritional quality, or their selection is inconsistent in time and/or space (Borowicz 1988; Whelan & Willson 1994). Second, there is often no relationship between the nutritional value of fruit pulp and seed-dispersal success, either within or among plant species (Herrera 1984a; Jordano 1989). And third, the nutritional composition of fruit pulp is strongly correlated with plant phylogeny, with a substantial part of interspecific variance in nutrient concentration being attributable to taxonomic affiliation at the genus level and above (Herrera 1987; Jordano 1995). The nutritional characteristics of fruits seem relatively 'resistant' to evolutionary modification, as exemplified by the similarity in pulp characteristics of closely related species living in ecologically disparate scenarios and having their seeds dispersed by quite different agents (Fig. 7.11).

The nutritional characteristics of fruits are often related to the season of ripening, and seasonal variation sometimes matches dispersers' requirements. In Mediterranean habitats, for example, the mean water content of pulp is highest among species ripening during the dry summer, and lipid content is highest among winter-ripening ones, which may reflect plant adaptations to dispersers (Herrera 1995). Recent investigations, however, suggest that seasonality in fruit composition reflects the different fruiting phenologies of taxonomic groups that differ intrinsically in fruit composition (Eriksson & Ehrlén 1991; Herrera 1995). Similar explanations probably apply also to community-wide elevational and geographical patterns of variation in pulp composition (Herrera 1985b; French 1991). Given the close correlation between pulp composition and phylogeny, differences in the taxonomic composition of fruiting plant assemblages may explain much of the observed regional, elevational or seasonal variation in the average composition of fruits. For example, the greater average lipid content of the pulp of fruits in tropical habitats (Herrera 1981) may be explained by the greater representation there of species from plant families which produce characteristically lipid-rich fruits regardless of their geographical location. Further studies explicitly addressing the effects of phylogenetic correlations are still needed to elucidate the extent to which patterns of fruit nutritional composition actually reflect plant adaptations to dispersers (Jordano 1995; Eriksson & Ehrlén 1998).

7.5.4.2 Secondary metabolites

In addition to nutrients, fruits often contain secondary metabolites. Their concentration generally declines during ripening, but ripe fruits of many species still contain important amounts of phenolics, alkaloids, saponins, or cyanogenic glycosides in the pulp (Herrera 1982b). In some species, the concentration of secondary metabolites in ripe fruits may reach potentially lethal levels. Tropane alkaloids are so abundant in the fruits of deadly night-



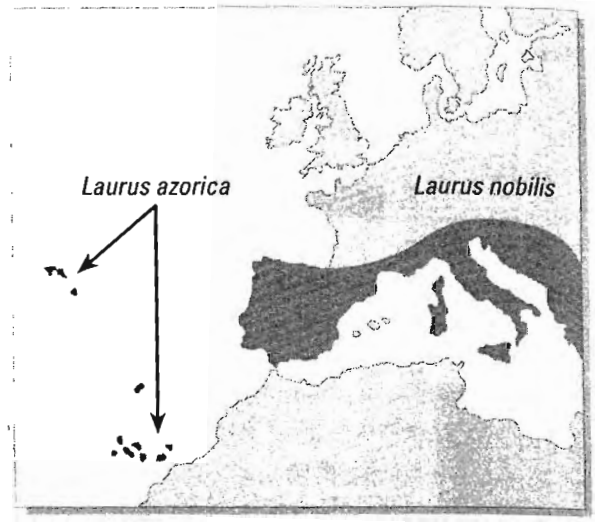


Figure 7.11 Nutritional composition of fruit pulp is closely correlated with phylogeny and may experience negligible changes over very long periods, as illustrated here by a comparison of the two extant species of *Laurus* (Lauraceae). The species derive from a common ancestor and have been geographically isolated since the Pliocene. They differ in morphological features, chromosome numbers, habitat type and seed-dispersers, but their fruits are virtually identical with respect to major pulp constituents. (Drawn from data in Herrera 1986.)

shade (*Atropa belladonna*) that their consumption often produces serious poisoning in humans and livestock. Given the mutualistic nature of the relationship between plants and their dispersers, the widespread occurrence of potentially toxic compounds in the pulp of ripe fruits is a biological paradox demanding some adaptive explanation. Secondary metabolites in the pulp of ripe fleshy fruits may inhibit seed germination, induce frugivores to leave fruiting plants early in a foraging bout, and modify the passage rate of seeds through dispersers' guts (Cipollini & Levey 1997a). Their primary function, however, is probably one of defence against microbial pathogens and invertebrate pests that may consume fruit pulp without dispersing seeds. Because of the negative incidence of such organisms in the dispersal process, the occurrence of secondary metabolites within ripe pulp presumably represents a tradeoff with respect to defence from damaging agents and palatability for dispersers. According to this hypothesis, fruiting plants that are at greater risk of attack by pests or pathogens (for example, because a low consumption rate by dispersers leads to prolonged exposure to damaging agents), should be under greater selection pressure for fruit defence than are plants with low risk of pest or pathogen attack (Herrera 1982b; Cipollini & Levey 1997a).

A number of studies provide unequivocal support for the 'palatability–defence tradeoff hypothesis'. In eastern North America, for example, the autumn-ripening, long-lasting fruits of *Vaccinium macrocarpon* are better defended against fungal fruit rot agents than the summer-ripening, quickly-removed fruits of *Vaccinium corymbosum* (Cipollini & Stiles 1993). On the other hand, fruit defence from pathogens has a measurable cost to plants in terms of reduced seed-dispersal prospects, because defensive chemical compounds in fruit pulp act to reduce the acceptability of fruits to dispersers (Cipollini & Levey 1997b; Levey & Cipollini 1998). There remains much still to be learned about the identity, ecological distribution and evolutionary significance of secondary metabolites in ripe fruits. As aptly stressed by Cipollini and Levey (1997a), secondary metabolites may eventually prove more important than other fruit attributes in understanding patterns of fruit use by dispersers.

7.5.5 Fruit 'syndromes'

Some particular combinations of fruit traits involving, for example, colour, smell, size and type of presentation, occur disproportionately more frequently in nature than other combinations. Such combinations of fruit traits have sometimes been intepreted as defining so-called 'fruit syndromes', and it often happens that suites of correlated fruit characters are related to consumption by particular groups of dispersers. In a Peruvian tropical

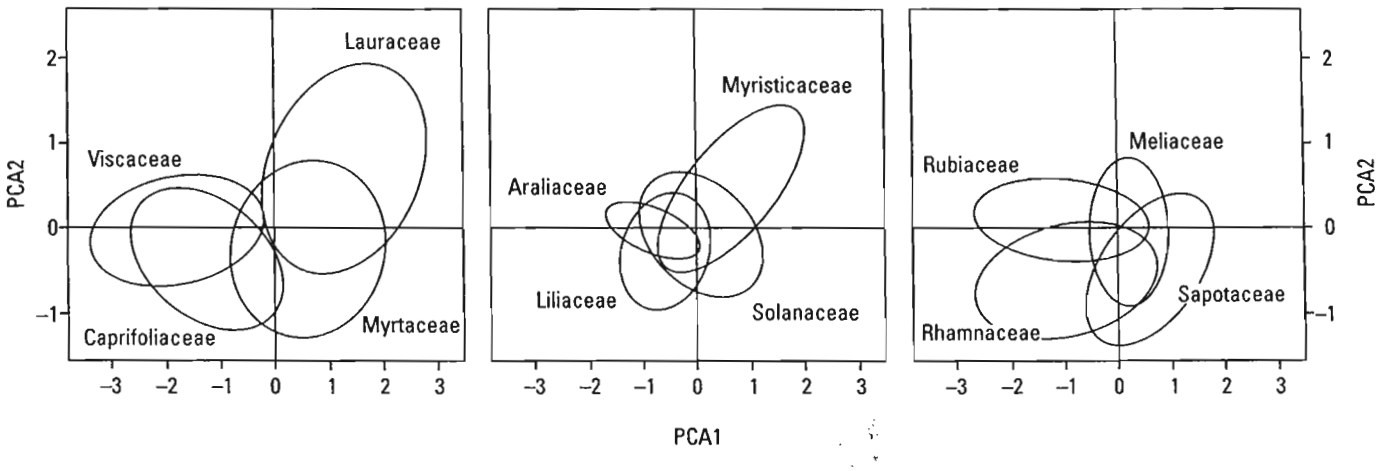


Figure 7.12 Angiosperm families inherently differ in the characteristics of their fleshy fruits. This graph depicts the relative location of a number of families on the plane defined by the first two principal components of fleshy fruit characteristics (PCA1 and PCA2). Each family is represented by its 90% equal frequency ellipse, that is, the contour line encompassing 90% of species for each family. The two principal components summarize variation in fruit mensural (e.g. size, mass), structural (e.g. number of seeds, pulp/seed ratio) and nutritional (e.g. lipids, protein) characteristics. (Modified from Jordano 1995.)

rainforest, for example, most fruits belong to one of two classes: large, dull-coloured fruits with a protective husk, or small brightly-coloured fruits without a husk. The characteristics of these two fruit classes match the size and visual ability of mammals and birds respectively, and the animals also prefer to eat one class of fruits (Janson 1983). In Mediterranean forests and scrublands, bright fruit colours tend to be associated with small size, lack of a perceptible smell and the persistence of fruits on the plants after ripening. Large fruits tend to be dull in colour, scented to the human nose, and to fall to the ground after ripening. Fruits in the former group are eaten exclusively by birds, while those in the second group are eaten by both birds and terrestrial mammals (Herrera 1989b). Similar non-random combinations of fruit traits into *statistically* distinguishable suites, and the frequent association of such suites with particular groups of fruit consumers, have been reported from other plant and frugivore assemblages from all over the world.

Do fruit 'syndromes', and their association with major groups of frugivorous vertebrates, actually reflect plant adaptations to different kinds of dispersers? This hypothesis was first critically examined by Fischer and Chapman (1993), who found that fruit character complexes are rare in nature, and that the results of analyses of covariation among fruit characters are extremely sensitive to the investigator's choice of sampling unit. In their study, no significant trait associations existed when plant genera were used as sampling units, but they did occur when species were the units chosen. Jordano (1995), in a thorough investigation, found that dispersal syndromes are only minimally attributable to plant adaptations to dispersers, but rather they largely reflect the great influence of plant phylogeny on fruit traits (Fig. 7.12). After plant phylogeny is accounted for, there is a conspicuous lack of evolutionary correlation between the seed-dispersal agent (bird, mammal or mixed dispersal) and the vast majority of mensural, structural and nutritional fruit traits. Of all fruit traits considered by Jordano, only fruit dimensions were found to be significantly related to dispersal type after accounting for phylogenetic effects, and he concluded that 'correlated evolution [of fruit traits] with type of seed disperser is, at best, only evident for fruit diameter'.

7.6 Animal adaptations

It has been sometimes suggested that, compared with other food habits like herbivory, carnivory or nectarivory, frugivory does not require drastic morphological and physiological modifications on the part of animals (Fleming 1991). This certainly holds true for occasional frugivory, as it is a common observation that most terrestrial vertebrates are able to ingest some fruits sporadically. Nevertheless, fruits represent a substantial fraction of the diet for only a relatively small subset of terrestrial vertebrates. These 'heavy frugivores' are those most directly

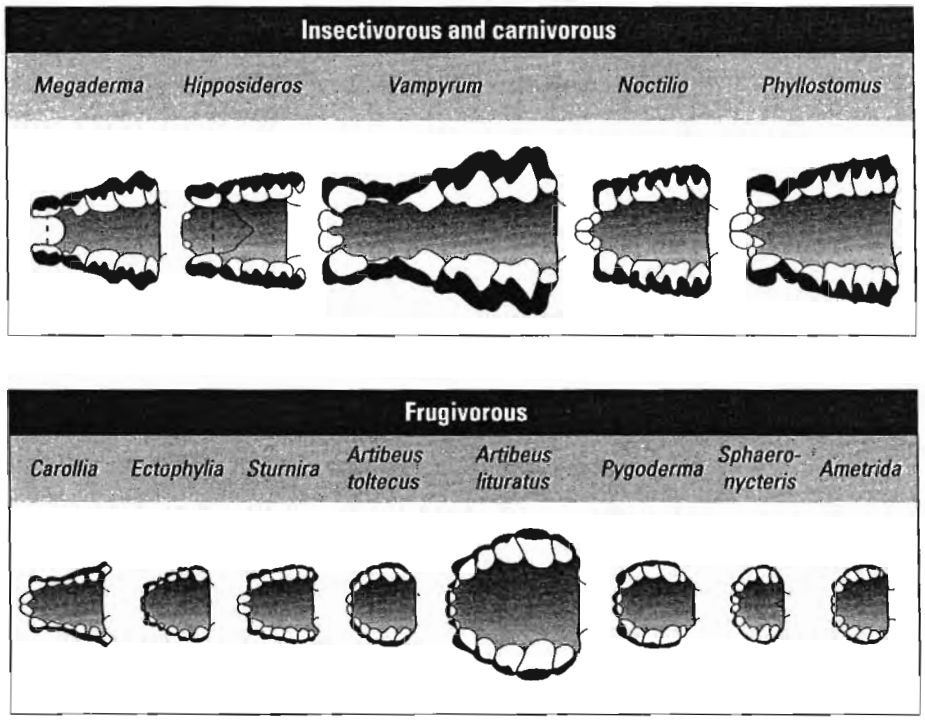


Figure 7.13 Frugivorous animals often differ from non-frugivorous relatives in the morphology of their trophic structures. Shown in this figure are ventral views of palates of insectivorous and carnivorous (upper row) and frugivorous (lower row) New World bats, drawn to the same scale. The two groups of species differ in craneal morphology, with frugivorous species having proportionally shorter and wider palates than non-frugivorous ones. (From Freeman 1988.)

relevant from the viewpoint of the evolution of plant–disperser interactions, and will be the ones considered in this section. Extensive frugivory is made possible in these species by a distinct suite of morphological, physiological and behavioural adaptations that enable them to exploit efficiently a food resource characterized by its poor food value, strong nutritional imbalance, extremely variable chemical composition and marked unpredictability in time and space.

7.6.1 External and internal morphology

Highly frugivorous passerine birds tend to have shorter, broader and flatter bills, and wider gapes, than do those that never eat fruit or do so only infrequently (Herrera 1984b). Distinct morphological trends also exist in frugivorous mammals. Among New World bats, fruit-eating species are characterized by short canines and palates that are broader than they are long, in comparison to the longer canines and palates longer than they are wide of insectivorous and carnivorous species (Fig. 7.13). The smaller tooth area of frugivorous bats is also related to their diet of juicy, soft fruit. Unlike carnivorous species, which have enlarged lower molars that occlude with the upper teeth, the premolars of frugivorous bats engage before the molars, which points to the importance of anterior dentition (incisors, canines and premolars) in biting through the skin of fruits (Freeman 1988). In the case of frugivorous bats, these morphological patterns most likely reflect adaptations actually evolved to exploit fruits more efficiently. In the case of some frugivorous passerines, however, differential bill morphology probably represents a pre-adaptation enabling them to become efficient frugivores, rather than a direct adaptation to frugivory (Herrera 1984b).

The digestive system of some frugivorous birds has noticeable peculiarities that were already noted by zoologists nearly a century ago. In some species that feed heavily on fruits for most or all of the year, the gizzard tends to be smaller and less muscular, the liver larger, and the intestine shorter than in less frugivorous relatives (Pulliainen et al. 1981; Richardson & Wooller 1988). Shortening of the intestine allows for the rapid processing of fruits, while the reduction of gizzard musculature is a response to a reduced need for crushing hard food. Increased liver size may be a response to an increased demand for detoxifying capacity, derived from the frequent presence of toxins in ripe fruits noted above (Herrera 1984b). The simplification of the digestive tract reaches its extreme in the case of mistletoe birds (Dicaeidae) and other passerines feeding extensively on mistletoe fruits (Fig. 7.14). Simplification of the digestive tract, however, is only one of the array of

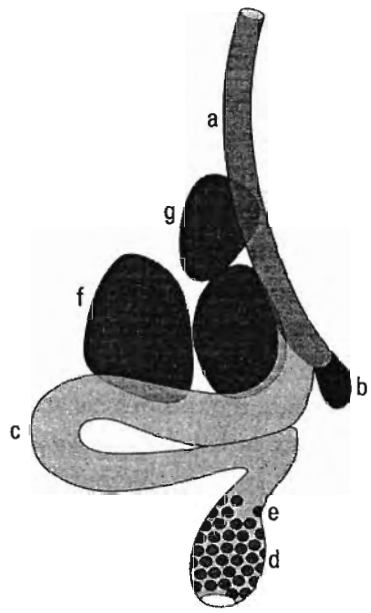


Figure 7.14 Birds feeding heavily on fruits throughout the year tend to have reduced gizzards and shorter intestines. This reduction reaches its extreme in mistletoe birds (Dicaeidae) and other passerines feeding extensively on mistletoe berries. The graph shows a ventral view of the alimentary tract of the Australian mistletoe bird (*Dicaeum hirundinaceum*) lying in its natural position (a, oesophagus; b, gizzard; c, small intestine; d, large intestine; e, caecum; f, liver; g, heart; scale line is 7.5 mm). (From Richardson & Wooller 1988.)

'macroscopical' digestive adaptations exhibited by frugivorous animals. In fruit pigeons of the Australasian region, for example, a distinct arrangement of connective tissue and muscle layers leads to increased elasticity of the oesophagus and glandular stomach, which is clearly advantageous in allowing larger fruits to pass through (Landolt 1987).

Shortening of the intestine, although frequently emphasized in older accounts of vertebrate frugivory, is probably not the most common adaptation evolved by frugivores for the rapid processing of many fruits. As described in Section 7.6.2 below, frugivores have evolved a variety of ways of shortening food-retention time without modification of the length of the digestive tract. In fact, increased frugivory is quite often associated with increased intestine length, as an adaptive response for increasing intestinal absorption of the water-diluted nutrients in fruit juice. Old World fruit bats (Pteropodidae) have relatively longer intestines than their insectivorous counterparts, and the intestine may be up to nine times their body length (Kunz & Ingalls 1994). The importance of increased intestine length for frugivory is further exemplified by the fact that, among birds, diets differing in the amount of fruit may induce changes in intestine length. In the heavily frugivorous bulbul, *Pycnonotus leucogenys*, intestine length fluctuates seasonally, being longer at times of year when the birds are most strongly frugivorous (Al-Dabbagh et al. 1987). In pine warblers (*Dendroica pinus*) experimentally fed on either insect-based, fruit-based or seed-based diets for nearly two months, intestine length and mass at the end of the experimental period were greatest in the group of experimental birds that had been feeding on the fruit-based diet (Levey et al. 1999).

Gross modifications of the digestive tract are not apparent in species that feed heavily on fruits during only part of the year, like migratory frugivorous birds from temperate latitudes (Herrera 1984b). In these cases, adaptations favouring sustained frugivory during extended periods consist of more subtle functional modifications of the digestive system, like those described in the next section.

7.6.2 Digestive physiology

As noted above, the rewarding portion of fruits is generally characterized by high-water, high-sugar and very low-protein content. In addition, the nutritional reward obtainable by frugivores is further diluted by the presence of indigestible seeds and, often, secondary metabolites in fruit pulp. Digestive adaptations to cope with nutrient dilution, nutritional imbalance and secondary compounds are thus essential for sustained frugivory.

7.6.2.1 Coping with nutrient dilution

Seeds occupy space in the digestive tract that could otherwise accomodate nutritious material. Selection has thus favoured digestive adaptations that overcome this 'gut limitation' and act to rapidly evacuate ingested seeds. In manakins, small seeds pass through the gut in only 12–15 min, while larger seeds are regurgitated within 7–9 min of ingestion (Worthington 1989). Among southern Spanish frugivorous passerines, species that rely heavily on fruits for food have shorter gut-retention times relative to body mass than occasional frugivores (Fig. 7.15), and this ability for rapidly processing fruits seems essential for their extensive and sustained frugivory (Jordano 1987a). Avian frugivores have the ability to modulate retention times in response to variations in diet composition. In

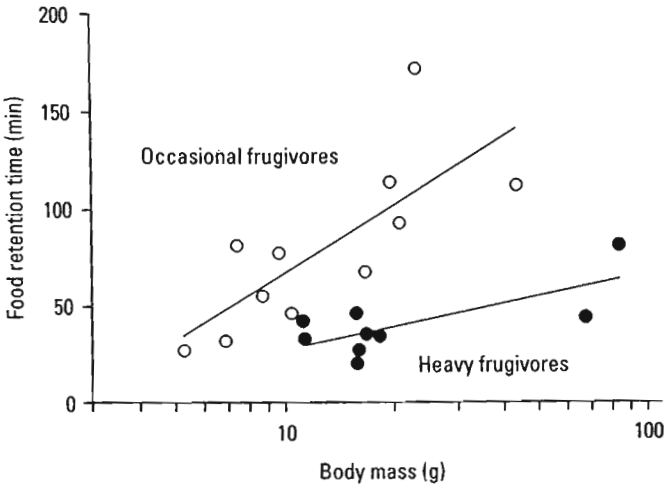


Figure 7.15 For a given body mass, food passes more rapidly through the digestive tract of 'strong' than of 'occasional' frugivores in species of southern Spanish frugivorous birds. Occasional frugivores are species feeding infrequently on fruits that do not usually perform seed dispersal, while strong frugivores are species depending heavily on fruits for food for extended periods and behaving as legitimate seed dispersers. (From Herrera 1984b.)

yellow-rumped warblers (*Dendroica coronata*) acclimatized to different diets, retention times decrease from seed-through insect- to fruit-based diets (Afik & Karasov 1995). Rapid digestive processing is not exempt from costs, however, and a tradeoff may arise between the rate and efficiency of digestive processing. The faster food is processed, the lower the nutrient extraction efficiency, and yellow-rumped warblers on diets associated with shorter retention times extracted less of the nutrients (Afik & Karasov 1995).

The ability of frugivores to adjust enzymatic activity in the gut as a function of the composition of the diet is probably one further adaptive trait allowing them to feed on relatively diluted food. Among the experimental pine warblers (*Dendroica pinus*) mentioned above that were fed on insect-, fruit- and seed-based diets, birds fed on fruit (i.e. carbohydrate-rich food) exhibited the highest intestinal activity of enzymes related to the transformation and assimilation of carbohydrates (amylase, maltase and sucrase) (Levey et al. 1999).

7.6.2.2 Coping with nutritional imbalance and secondary compounds

Most fruits are very deficient in nitrogen, which perhaps represents the most important nutritional constraint that frugivorous animals must cope with. Regular ingestion of small amounts of animal food seems to be the commonest way of complementing the poor protein intake associated with frugivory. Old and New World frugivorous bats regularly supplement their diets by hunting insects even when fruits are abundantly available (Courts 1998), and heavily frugivorous tropical birds like toucans and quetzals frequently include insects and small vertebrates in their diets (Wheelwright 1983; Remsen et al. 1993). An intrinsically low protein requirement is one further trait that facilitates the subsistence of frugivores on a diet of sugar-dominated fruits, as found by Worthington (1989) for manakins and Witmer (1998) for cedar waxwings (*Bombycilla cedrorum*). In manakins, a short-term positive nitrogen balance was achieved at very low nitrogen concentrations in a fruit diet, only about 1.3% N in dry pulp.

With very few exceptions, individuals of most species of frugivores usually ingest fruit of several species over very short periods of time. The vast majority of faecal samples of frugivorous passerines contain remains of more than one fruit species, sometimes up to 8 species (Herrera 1984a; Loiselle 1990). Given the short seed-retention times of these species, this indicates that the birds had been feeding on that many species during the short time immediately preceding capture. Varied fruit diets probably exemplify an adaptive response to overcome the nutritional imbalance of fruits and the frequent presence of secondary metabolites (Jordano 1988). By feeding simultaneously on fruits of different species with contrasting nutrient compositions, frugivores may achieve nutritional complementarity and a more balanced diet than if they relied on the fruits of a single species. Furthermore, when fruits that contain potentially harmful secondary metabolites are consumed in mixtures, the toxicity experienced by a forager due to any particular diet item can be ameliorated or diluted. This may explain the frequent observation that captive frugivorous birds fed on single-fruit diets quickly lose weight and their body condition deteriorates (Izhaki & Safriel 1989). In a set of species of frugivorous birds from southern Spanish scrublands, the extent of frugivory in the different species was positively correlated with the short-term diversity of the fruit mixtures consumed, suggesting that sustained frugivory is strongly dependent on the capacity to construct varied diets in the short term (Herrera 1984a). By means of a series of elegant field experiments, Whelan et al. (1998) have convinc-

Figure 7.16 In Mediterranean scrublands, frugivorous birds that feed only occasionally on fruits tend to avoid completely species whose ripe fruits contain potentially toxic metabolites. The proportion of toxic fruit species in the diet rises disproportionately as the degree of frugivory increases. Points in the graph represent average values for 17 passerine species from three different habitats. (Plotted from data in Herrera 1985c.)

ingly demonstrated that North American migrant frugivorous birds effectively treat different fruit species as complementary resources.

Extensive frugivory is frequently associated with the capacity to exploit fruits containing secondary metabolites in the pulp, including poisonous substances or potentially harmful digestion inhibitors (Fig. 7.16). This ability of many frugivores to exploit poisonous fruits can be explained only by the greater detoxifying capacity of their guts. There is evidence suggesting that heavily frugivorous birds tolerate potentially harmful compounds found in fruits better than occasional frugivores or non-frugivores. In northern Europe, the heavily frugivorous waxwings (*Bombycilla garrulus*) metabolize ethanol, which frequently occurs in over-ripe berries, at a much faster rate ($900\,mg\,kg^{-1}\,h^{-1}$) than either occasional frugivores like starlings (*Sturnus vulgaris*, $270\,mg\,kg^{-1}\,h^{-1}$) or granivores like greenfinches (*Carduelis chloris*, $130\,mg\,kg^{-1}\,h^{-1}$) (Eriksson & Nummi 1982). Frugivorous birds also seem to have better detoxification abilities than frugivorous or omnivorous mammals. The lethal dose of the alkaloid atropine, found in the berries of *Atropa belladonna*, is nearly a thousand times higher for European blackbirds (*Turdus merula*) than for humans (Seuter, 1970).

7.6.3 Behaviour

Fruits are probably more unevenly distributed in time and space than other kinds of food exploited by animals. Abundance of fruits varies markedly among years and seasons, and within as well as between habitats, which generally leads to patchy and unpredictable distributions in time and space (Levey 1988; Herrera 1998). A distinct suite of behavioural and physiological traits allow frugivores to withstand or escape from temporary situations of fruit scarcity and efficiently locate unpredictable fruit sources.

Seasonal migration and habitat shifts are the two most generalized responses of frugivores to fluctuations in fruit availability. Resplendent quetzals (*Pharomacrus moccino*) resident in Costa Rican cloud forest sequentially occupy different habitat types while closely tracking the local abundance of their highly preferred lauraceous fruits (Wheelwright 1983), and Australian fruit pigeons regularly undertake migrations across lowland rainforest in response to local variations in fruit supply (Crome 1975). The nomadic behaviour frequently exhibited by frugivorous birds, in the tropics and elsewhere, is a further behavioural trait that allows them to discover and exploit unpredictable patches of locally abundant fruits. In southern Spain, overwintering populations of blackcap warblers (*Sylvia atricapilla*) closely track fruit over large-scale mosaics of fruit abundance (Rey 1995). In African and Asian tropical forests, species of hornbills (Bucerotidae) wander over quite large areas while closely following broad-scale geographical variations in fruit availability (Kinnaird et al. 1996).

Among less mobile vertebrates, the ability to shift diet in response to occasional fruit scarcity is essential for long-term frugivory. Frugivorous primates in Amazonian tropical forest turn to feed more on nectar, leaves, insects or seeds at times when fruit become less abundant (van Schaik et al. 1993). Adjusting the time of reproduction to periods of high fruit abundance is another adaptive response of frugivores to cope with the marked temporal variability of their food supply. Birth peaks in New World frugivorous primates coincide with fruiting peaks, as do the breeding seasons of many tropical frugivorous birds and bats (Fleming 1992). In a Costa Rican cloud forest, the timing of lactation in frugivorous bats closely matches peaks in local fruit abundance (Fig. 7.17).

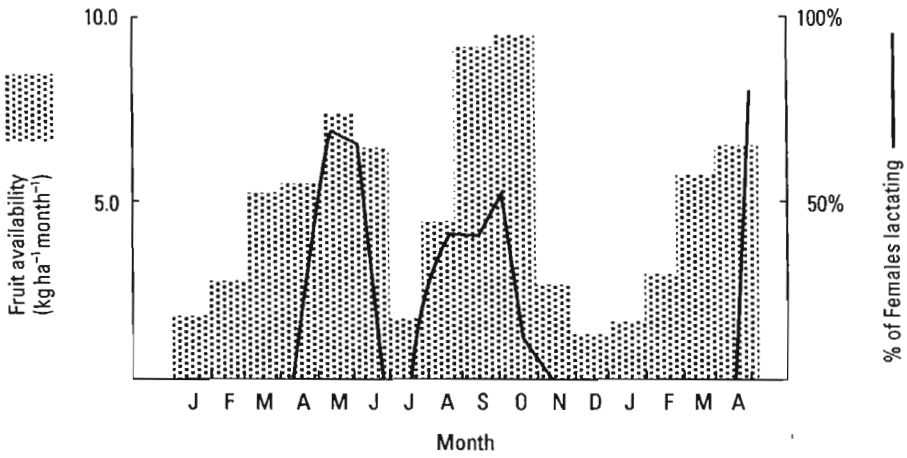


Figure 7.17 Some frugivores adjust the time of reproduction to periods of high fruit availability. In a Costa Rican tropical cloud forest, the two annual lactation periods of the frugivorous bat *Artibeus toltecus* are closely coincident with local peaks in fruit availability. (From Dinerstein 1986.)

7.7 Patterns of mutual dependence

There are no known instances of obligate plant–disperser mutualisms. For example, no animal-dispersed plant is known to depend strictly on dispersal agents for the germination of their seeds and the perpetuation of their populations. Seeds of animal-dispersed plants often germinate more easily after passing through the gut of their dispersal agents, and this observation has sometimes been construed as indicative of the dependence of plants on their dispersal agents. Nevertheless, among more than 200 species dispersed by birds, mammals and reptiles that have been tested so far, passage through the dispersers' digestive tracts had some significant effect on seed germination in only 50% of instances, and in these cases the effect could be either enhancement or inhibition (Traveset 1998). The earlier intriguing hypothesis that the endemic tree *Calvaria major* was nearly extinct in the island of Mauritius because its seeds required a passage through the digestive tract of the now extinct dodo (*Raphus cucullatus*) has been dismissed by subsequent investigations (Witmer & Cheke 1991).

Plant–vertebrate seed-dispersal systems are characterized not only by the absence of obligate partnerships, but also by weak mutual dependence between species of plants and animals, and by the prevalence of unspecific relationships. Most species of animal-dispersed plants depend on arrays of frugivorous species for dispersing their seeds, arrays often composed by species belonging to different major groups. Each species of frugivore, in turn, consumes the fruits and disperses the seeds of a number of taxonomically unrelated plant species. In a community of eight diurnal primates in the Lopé Reserve in Gabon, individual species feed on the fruits of between 20 (black colobus, *Colobus satanas*) and 114 (chimpanzee, *Pan troglodytes*) different plant species (Tutin et al. 1997). In a Costa Rican lower montane forest, each species of frugivorous bird feeds on an average of 10.1 fruit species, while each plant species has its fruits eaten by an average of 4.5 bird species, and these figures are most likely rough underestimates (Wheelwright et al. 1984). Furthermore, the vast majority of pair-wise interactions between plant and disperser species correspond to situations in which the relative dependence of the plant on the disperser, and of the disperser on the plant, are both minimal (Fig. 7.18). A few examples are known of plant species that apparently depend on only one or perhaps a few species of animal dispersers. In tropical Africa, for example, elephants seem to be the only current dispersers of the large-seeded tree *Balanites wilsoniana*, and European robins (*Erithacus rubecula*) are the almost exclusive dispersers of *Viburnum tinus* in the western Mediterranean Basin (Chapman et al. 1992; Herrera 1995). In these and other situations of heavily dependent plants, however, the relationship is quite asymmetrical, since the single species of animal disperser of a given plant acts as the disperser of many other plants as well (Jordano 1987b).

Mutual specificity is significantly lower in plant–disperser than in plant–pollinator systems. For a habitat with m species of animal-dispersed plants and n species of frugivorous animals, the 'connectance' of the mutualistic system may be defined as the number of plant–animal pair-wise interactions actually observed divided by the maximum possible (i.e. $m \times n$). Thus defined, lower

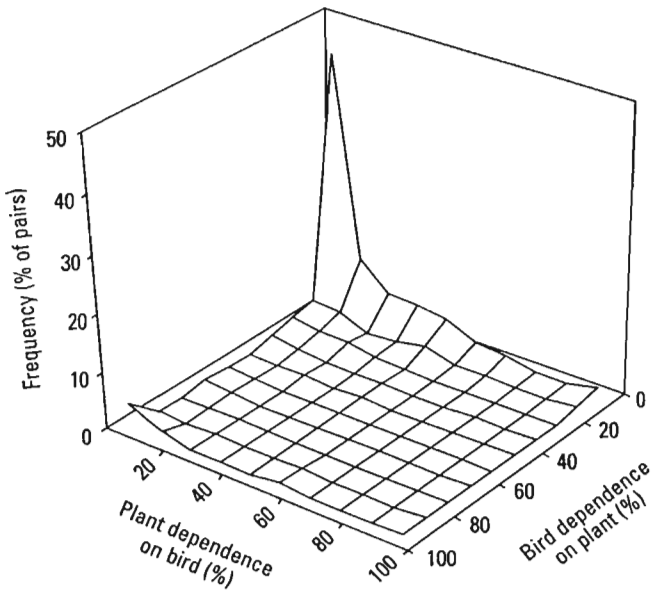


Figure 7.18 In plant–bird seed-dispersal systems, most plant–bird species pairs exemplify situations in which the dependence of the bird on the plant, and of the plant on the bird, are both negligible. For each bird–plant species pair, bird dependence on the plant was measured by the proportion of fruit food contributed by the plant, and plant dependence on the bird was assessed using the proportion of seeds dispersed. (Drawn from data in Jordano 1987b.)

connectance denotes higher average specificity, and vice versa. Jordano (1987b) found that mean specificity in both plant–pollinator and plant–disperser system increased with the increasing number of species involved, but that the increase in specificity was steeper in plant–pollinator systems. This indicates that, for any given number of plants and animals involved, the mutual specificity between plants and animals is smaller in seed dispersal than in pollination systems.

7.8 Factors hindering reciprocal specialization

The preceding sections have shown that, compared with other kinds of plant–animal interactions covered in this book, plant–vertebrate seed-dispersal systems are those for which the evidence of reciprocal specialization—or mutual adaptation—between animal and plant counterparts is the weakest. No examples of obligate partnerships exist, and the general picture is one of loose interdependence between species of plants and species of dispersers. This contrasts with earlier models and formulations of the evolution of plant–disperser systems, which were characterized by expectations of coevolution and mutual adaptations. Plant–disperser interactions have been thoroughly studied during the last two decades, so the notion of weak reciprocal adaptation is unlikely to stem from imperfect knowledge and is not expected to be modified substantially in future as more and more detailed studies accumulate. What, then, are the ecological and evolutionary peculiarities of animal seed dispersal that have limited the extent of mutual specialization between plants and dispersers?

7.8.1 The genetic consequences of animal seed dispersal

The main genetic consequence associated with seed dispersal by frugivorous animals appears to be preventing, or greatly reducing, the local genetic differentiation of plant populations. A small-scale, local genetic structure was traditionally hypothesized to be particularly common in plants because they are immobile as adults, and gene dispersal via pollen and seeds was often thought to be spatially restricted. Nevertheless, the distribution of dispersal distances of animal-dispersed plants frequently has very long tails. Although the vast majority of seeds are dispersed over short to medium distances, a small but ecologically and evolutionarily highly significant number of seeds are transported to very long distances (Portnoy & Willson 1993). Enhanced gene flow and increased genetic homogeneity of populations are thus expected under these circumstances, with local genetic structuring being less intense and/or frequent among animal-dispersed plants. This expectation has been confirmed by most studies that have investigated the spatial structure of vertebrate-dispersed plants using genetic markers. In a Florida population of the bird-dispersed shrub *Psychotria nervosa*, Dewey and Heywood (1988) found no evidence of spatial structuring of allele frequencies for either of the polymorphic enzyme loci studied. In the bird- and mammal-dispersed pioneer tree *Cecropia obtusifolia*, Alvarez-Buylla and Garay (1994) found high levels of gene flow and negligible population differentiation in a Mexican rainforest.

The spatial distribution of genetic variability within populations may influence significantly the evolutionary dynamics of the population, and population structure may provide the substrate for local selective forces to promote adaptive evolution, and may be a first step towards speciation. If animal seed dispersal generally enhances gene flow and persistently smoothes out spatial genetic

Table 7.1 Some of the most significant differences between seed and pollen dispersal by animals. (Based on Wheelwright & Orians 1982.)

	Pollen dispersal	Seed dispersal
Suitable site for arrival ('target')	Stigma of conspecific flower	Site appropriate for germination and establishment
Characteristics of target	Distinctive (colour, shape) and spatially predictable, often apparent at a distance	Spatially unpredictable, many subtle factors involved
Temporal availability of target	Synchronous with pollen dispersal	Unpredictable, often independent of habitat type or phenology of conspecific plants
Ability of plant to direct animal vectors to target	High, incentives (nectar, pollen) provided at target site	Low, no incentive to disperser at target site

patterns of plant populations at large spatial scales, then animal-dispersed plants will be characterized by a low probability of local or regional differentiation, including the evolution of adaptations to local dispersal agents.

7.8.2 Factors limiting plant specialization

Earlier expectations of mutual adaptation and coevolution between fleshy-fruited plants and their vertebrate dispersers were in part motivated by the superficial resemblance between pollen and seed dispersal by animals. As mutual adaptations between animal-pollinated plants and their pollinators had been known since Darwin's time, concepts from the well-established field of pollination biology were uncritically exported to the younger field of plant–disperser interactions (Wheelwright & Orians 1982). Nevertheless, pollen and seed dispersal by animals are fundamentally dissimilar (Table 7.1), and their differences have manifold evolutionary implications. The two most important distinctions are (i) that a definite target exists for dispersing pollen grains (the conspecific stigma) but not for dispersing seeds; and (ii) that the plant can control pollinators' movements by providing incentives at the target site (nectar, pollen), but there are no similar incentives for seed dispersers to drop seeds in appropriate places. These differences are best framed in terms of the departure-related versus arrival-related advantages of dispersal described in Section 7.2 earlier in this chapter.

In pollen dispersal, the existence of a definite target for pollen grains has made possible the evolution of 'payment upon delivery'. This, in turn, has promoted the evolution of complex morphological and functional floral traits 'manipulating' the behaviour of pollinators and enhancing the arrival-related component of pollen dispersal. In contrast, plants do not have a definite 'target' for their seeds, because favourable germination sites frequently do not exist when seeds are dispersed, and plants can hardly 'know' in advance where and when will they appear. Arrival-related advantages are unpredictable in time and space, and thus largely out of the control of the parent plant and hardly susceptible to natural selection. This has constrained vertebrate seed-dispersal systems to function on the basis of 'advance payment' alone. Advance payment has hampered the evolution of traits enhancing arrival-related benefits of dispersal (i.e. the quality of the germination microsites reached by dispersed seeds). But, on the other hand, the departure-related advantages of dispersal are quite predictable and straightforward, and under the control of the parent plant, which has strongly favoured the evolution of traits enhancing departure-related benefits (i.e. consumption by seed-dispersers) like fruit conspicuousness and nutritional reward. Departure-enhancing traits are easy to evolve, as shown by the wide distribution of the fleshy-fruit habit in the phylogeny of seed plants, and the morphological convergence of anatomically disparate structures into functional fleshy fruits, as noted earlier in this chapter.

There are innumerable options available to plants to restrict the range of animals visiting their flowers and to evolve adaptations to particular pollinators, as exemplified by the amazing diversity of flower colours, internal and external morphologies, and the amount and type of reward evolved by animal-pollinated angiosperms. By contrast, there are only a few rather coarse ways available to plants to restrict the range of vertebrate species that feed

on their fruits, and thus few morphological options for the diversification of fleshy fruits. Fruit structure, size and colour, and the chemical composition of the pulp, all play proximate roles in restricting the assemblage of frugivores that interact with any given plant species, but only up to a certain threshold. Beyond this, the nature of the reward on which the plant–disperser interaction is based precludes further filtering based on morphological modifications and, consequently, sets limits on the possibilities of plants to specialize on the most effective or beneficial disperser(s) (Herrera 1985a; Jordano 1987b). That there are few morphological opportunities for evolutionary diversification inherently associated with animal seed dispersal is exemplified by the low frequency with which seed and fruit traits are useful to taxonomists to differentiate higher-level plant taxa. In a dichotomous key to the European flora, for example, fruit-related traits are used in only 2.9% and 21.3% of dichotomies that differentiate plant families and genera respectively. Flower-related characters, in contrast, are used in 63.4% and 54.4% of familial and generic dichotomies respectively.

7.8.3 Factors limiting frugivore specialization

Temporal inconsistency—in both the short and the long term—in the patterns of plant–disperser relationships is one important factor limiting the possibilities of frugivore specialization on plants. Although there are some notorious examples of vertebrate-dispersed plants that ripen fruit over the whole year, like some tropical fig trees or the Mediterranean hemiparasitic shrub *Osyris quadripartita* (Milton et al. 1982; Herrera 1988b), the vast majority of species have distinct fruiting seasons. Vertebrate frugivores are relatively long-lived, so the fruits of most species they feed on represent ephemeral resources that are available only during relatively short periods of the annual cycle. Specialization on the fruits of particular species is hardly possible under these circumstances.

Long-term inconstancy in the species composition of the fruit supply further contributes to limit the specialization of frugivores on particular plant species. Crop sizes of vertebrate-dispersed plants tend to fluctuate less among years than those of species with other seed-dispersal methods, but important annual fluctuations commonly occur in most species (Herrera et al. 1998). Few long-term studies have investigated in sufficient detail the consequences of this variation, but the limited evidence available suggests that plant–vertebrate seed-disperser interactions are representative of non-equilibrial ecological systems (DeAngelis & Waterhouse 1987). A 12-yr study of the interaction between bird-dispersed plants and their main dispersers in a south-eastern Spanish Mediterranean montane scrubland has revealed loose patterns of mutual interdependence among species of plants and birds, important temporal fluctuations, the predominance of abiotic over biotic driving factors, and virtually complete decoupling of the temporal dynamics of the plant and bird species (Herrera 1998). Non-equilibrial relationships between plants and dispersal agents will lead to temporal inconsistencies in selection pressures associated with the interaction, which will generally operate against mutual adaptations of interacting species. In the 12-yr study mentioned earlier, annual variation in the species composition of the fruit diet of the two major bird dispersers (*Erithacus rubecula* and *Sylvia atricapilla*) involved drastic changes in the identity of the plant species that predominated in their diets. Similar long-term variability in the diet composition of frugivores has invariably been found whenever studies have encompassed a sufficient number of years (e.g. Loiselle & Blake 1994).

7.9 Pending issues

This chapter has summarized the main topics emerging from the numerous studies that have addressed plant–disperser interactions from an evolutionary viewpoint in the last 25 years. There are, however, a number of equally relevant topics that have not been covered because available information is scarce, inconclusive or simply non-existent. Some of these missing aspects are critical to a proper understanding of the evolution of plant–disperser interactions. It is worth highlighting some of these here, to provide both a rough guide to pending issues in the field and a list of possibilities available for the interested student.

Despite efforts to achieve a balanced treatment, the picture presented in this chapter mainly reflects current knowledge of vertebrate frugivory and seed dispersal as delineated by studies on frugivorous birds and bird-dispersed plants. Birds are doubtless prominent frugivores that deserve considerable attention, but their predominance in this chapter reflects in part the distinct 'avian bias' that has characterized recent studies of the evolutionary ecology of frugivory and seed dispersal. More studies are needed, contributing to a broader and more balanced picture of the ecology and evolution of frugivory

and seed dispersal by non-avian vertebrates, particularly mammals and reptiles. Little is known, for example, on the quantitative role played by terrestrial 'carnivorous' mammals (e.g. mustelids, canids) as seed-dispersal agents in those relatively undisturbed habitats where they have not been extirpated, and on the digestive and behavioural adaptations that allow them to shift seasonally between carnivorous and frugivorous diets. Given the tremendous differences in mobility, trophic apparatus and sensory abilities among major groups of vertebrates, it seems safe to predict that a picture of plant–disperser interactions based on a more balanced knowledge of different groups of dispersal agents will be considerably richer than the one presented here.

The genetic consequences of seed dispersal by vertebrates are still very poorly understood. For example, comparative studies are needed to address the effect on the genetic structure of plant populations of seed dispersal by animals that differ in mobility and foraging patterns, like birds, bats and non-flying mammals. Dissecting the relative contribution of seed and pollen dispersal to the genetic structuring of plant populations may also help us to understand some of the evolutionary contrasts between plant–pollinator and plant–disperser systems outlined above.

Methodological problems have so far precluded attempts at connecting the departure and arrival stages of seed dispersal for maternal progenies. Much is known on the factors influencing the departure-related component of dispersal success, but virtually nothing is known on whether maternal fruit and fruiting traits translate into differential arrival-related success of vertebrate-dispersed seeds. The development of methods allowing the tracking of seed crops from the parent plant through the arrival sites has perhaps been one of the most vexing issues in the study of plant–disperser interactions. Such methods would allow, for instance, assessing the shape of the distribution of seed-dispersal distances from parent plants, particularly the reach of dispersal tails. Theoretical models predict that spatial genetic patterns will be smoothed out by gene flow at a rate which depends only on the variance of the distance between parent and offspring. The genetic consequences of seed dispersal will thus depend more closely on the variance of dispersal distances than on the modal or average distances travelled by seeds. Such variance cannot be estimated unless effective methods are developed for constructing whole distributions of dispersal distances.

Very few studies so far have examined patterns of spatial and temporal variation of the mutual relationships between species of animal-dispersed plants and their vertebrate counterparts. These investigations suggest, for example, that there is little spatial congruence between the geographical ranges of plants and the vertebrates with which they interact for seed dispersal (Jordano 1993), and that the long-term dynamics of plants and frugivores may run independently of each other (Herrera 1998). Patterns of spatial and temporal variation in plant–disperser interactions, in combination with information on the genetic structure of plant populations, are essential to evaluate mutual adaptations between plants and seed-dispersers at local or regional scales in the context of the recent 'geographic mosaic' theory of coevolution (Thompson 1994).