

Chapter 11

Habitat–Consumer Interactions in Frugivorous Birds

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I. INTRODUCTION

Berrylike, fleshy fruits (“fruits” hereafter) are fed upon by a substantial fraction of the avifauna in many regions and habitat types (e.g., Rowan, 1970; Lein, 1972; Pearson, 1977). Geographical variation in the relative contribution of frugivores to local avifaunas is related to the proportional significance of fruit-producing species in the plant community. Frugivorous birds usually are absent or unimportant in grasslands, deserts, or scrublands on very nutrient-poor soils,

where the production of fleshy fruits tends to be uncommon among plants (Ellner and Shmida, 1981; Milewski and Bond, 1982; Herrera, 1984c). They acquire the greatest prominence in forested ecosystems or scrublands on fertile soils, where fruit-producing plants are widespread (Howe and Smallwood, 1982). The steep latitudinal gradient in fruit production rates from north temperate forests through Mediterranean scrublands to tropical forests (Table I) runs parallel to a pronounced variation in the relative contribution of frugivores to local or regional avifaunas (Lein, 1972; Morse, 1975; Pearson, 1977; Thompson and Willson, 1979; Herrera, 1984a). Karr (1971) estimates that 10–20% of the increased number of tropical-zone breeding bird species over temperate-zone birds in similar habitats is due to a substantially greater fruit availability. Variation among tropical forests in the abundance and diversity of frugivorous birds, particularly their relative scarcity in southeastern Asian dipterocarp forests, is also to be

TABLE I

Yearly Production of Fleshy Fruits in Several Regions and Habitat Types^a

Source	Fruits/ha ($\times 10^3$)	Wet mass (kg/ha)	Dry mass (kg/ha)	Reference
Red maple forest (New Jersey)	16.3	2.7	1.3	Baird (1980)
Oak–hickory forest (New Jersey)	12.2	2.6	1.3	Baird (1980)
Floodplain forest (New Jersey)	74.0	22.6	7.4	Baird (1980)
Old pine plantation (Georgia)	—	32.9	—	Johnson and Landers (1978)
Mixed deciduous woodland (England)	14.9	1.8	0.5	Sorensen (1981)
Mixed deciduous forest (northern Spain)	45.2	10.5	2.1	J. Guitián (unpublished)
Mediterranean montane scrub (southern Spain)	65.6–433.2	11.9–104.5	6.1–40.1	Herrera (1984a)
Mediterranean lowland scrub (southern Spain)	1400.0	223.7	97.7	Herrera (1984a)
Pine forest (Texas)	—	—	64.4–129.9	Stransky and Halls (1980)
Tropical rainforest (Panama)	—	—	983.3	Leigh (1975)
Tropical wet forest (location unreported)	—	—	500	Hladik and Chivers, in Fleming (1979)
Old second growth forest (Guyana)	397.5	—	180.4	Charles Dominique <i>et al.</i> (1981)

^a Figures obtained in most cases after recalculation of original data.

related to geographical variation in the significance of fruit-producing plants in the habitat (Fogden, 1972; Pearson, 1977; Karr, 1980).

Virtually any bird species, including raptors, ducks, gulls, or shrikes, may occasionally indulge in frugivory (e.g., Turček, 1961; Tutman, 1969; Ogawa, 1977; Thiollay, 1978; Grant, 1979; Lemke, 1979). It is, however, for those species that fruits play an important energetic or nutritional role that ecological implications of frugivory are most apparent. Detailed field studies assessing quantitatively the importance of fruit food for individual bird species are surprisingly scarce, but accumulating evidence is revealing that substantial frugivory may eventually prove to be more common than expected, particularly in non-tropical habitats (see, e.g., Brensing, 1977; Salomonson and Balda, 1977; Walsberg, 1977; Herrera and Jordano, 1981; Jordano and Herrera, 1981; Jordano, 1982; Debussche and Isenmann, 1983). Although frugivory tends to be most intense in some tropical and subtropical bird families (e.g., Coliidae, Pipridae, Dicaeidae, Trogonidae, Rhamphastidae, Cotingidae; Snow, 1981), there are also strongly frugivorous temperate representatives in the Mimidae, Turdidae, Sylviidae, and Bombycillidae (Putnam, 1949; Arvey, 1951; Havlin, 1977; Moore, 1978; Herrera, 1981d; Jordano and Herrera, 1981). This broad group of "strong" frugivores will be in the focus of the present contribution. It is beyond its scope to examine either the selective pressures involved in the evolution of avian frugivory or the set of adaptations enabling birds to subsist on fruit food (see, e.g., Snow, 1971, 1981; Morton, 1973; McKey, 1975; Foster, 1978; Herrera, 1984b, for an entry to the literature).

Relative to other well-studied groups such as insectivores or granivores, frugivorous birds have been much less frequently the subject of ecological studies. As a result, we know very little about their ecology, including the factors involved in their selection of habitat, and this will become apparent in the sections to follow. The aims of this chapter are to suggest a variety of factors which are presumably important in the choice of habitat by frugivorous birds and to highlight the peculiar mutualism-mediated relationship existing between seed-dispersing frugivores and the fruit-producing plant assemblage that enables these birds to promote, in part, the perpetuation and expansion of their preferred habitats.

II. FRUIT ABUNDANCE

Fruit supply is subject to strong spatiotemporal patterning. This is not, of course, a unique feature of this food type, but fruit conspicuousness renders these patterns much more readily discernible than those exhibited by cryptic avian food types such as foliage invertebrates or small seeds. On the other hand, the extremely patchy and erratic nature of fruit as a food supply for birds and the broad

range of spatiotemporal scales on which fruit clumps occur have been repeatedly emphasized in the literature (e.g., Fogden, 1972; Karr, 1976; Bullock, 1978; Fleming, 1979), and there are reasons to suggest that fruit supply is much more unevenly distributed in time and space than other avian food types. This is presumably responsible for the broad within- and between-habitat utilization patterns ordinarily exhibited by species of frugivores (e.g., Rowan, 1967; Snow, 1962a; Brosset, 1981), as discussed in the following section.

A. Patterns in Time

A seasonal alternation of scarcity and superabundance seems to be an outstanding feature of fruit food in both tropical (Smythe, 1970; Foster, 1974; Frankie *et al.*, 1974; Crome, 1975; Alexandre, 1980; Lieberman, 1982) and nontropical (Sherburne, 1972; Thompson and Willson, 1979; Sorensen, 1981; Herrera, 1984a) habitats. Local fluctuations are least pronounced in tropical forests and increase in amplitude with increasing latitude.

Responses of tropical frugivores to seasonal fruit shortages range from temporal changes in food selection (Foster, 1977) to habitat shifts. The magnitude of the latter depends on the size of the spatial scale on which heterogeneity in seasonal fruit abundance patterns occurs. Resplendent Quetzals (*Pharomacrus moccino*) resident in Costa Rican cloud forest sequentially occupy four contiguous habitat types while closely tracking local abundance of their highly preferred lauraceous fruits (Wheelwright, 1983). *Dicaeus hirundinaceus* seasonally occupy all major Australian forest types, migrating in response to variations in the abundance of mistletoe berries, their main food (Keast, 1958). Long distance intratropical migration of *Vireo flavoviridis* and *Legatus leucophaius* in the Neotropics seems to have been selected for by seasonal changes in fruit abundance (Morton, 1977), and several species of Australian fruit pigeons regularly undertake migrations across lowland rainforest in response to local variations in fruit supply (Crome, 1975).

Increasing local seasonality in flowering and fruiting as one moves away from the tropics gives rise to long periods of extreme fruit scarcity occurring simultaneously over vast areas. This fact, by precluding the possibility of short-range habitat shifts, is responsible for the almost general absence of year-round frugivory among temperate birds. Most nontropical frugivores feed on insects at times of fruit shortage (e.g., Morton, 1973; Havlin, 1977), but habitat shifts in response to fruit supply may also occur. Altitudinal zonation of vegetation in the Guadalquivir Valley, southern Spain, provides an almost uninterrupted sequence of abundant fruit availability periods from early summer through late winter. *Sylvia atricapilla*, one of the most significant regional frugivores (Jordano and Herrera, 1981), tends to occupy at each season the altitudinal belts where fruits are most abundant (Fig. 1). This species inhabits in the course of a year virtually

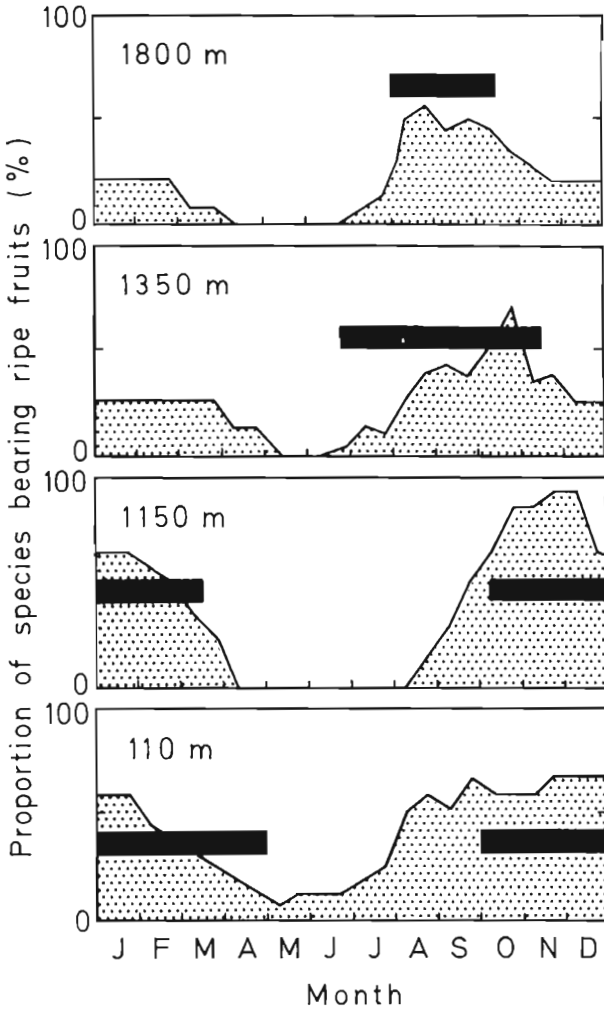


Fig. 1. Seasonal habitat occupancy (black bars) by *Sylvia atricapilla*, a strong frugivore, of four southern Spanish habitats occurring at different elevations and differing in fruiting phenology. Habitat occupancy during the period in which the bird is mainly insectivorous (April–May) is not shown, although it occurs at 1350- and 1150-m sites. From high to low elevation, habitats considered are pine (*Pinus nigra*) forest, pine forest–montane scrub ecotone, cool-climate montane scrub, and warm-climate lowland scrub.

all vegetational formations of the region, including habitats as disparate as successional deciduous scrub in mountains, highland pine forests, open juniper woodlands, and a variety of dense sclerophyllous scrublands (see also Bairlein, 1983).

Strong supra-annual variation in fruit abundance often occurs in montane and high-latitude plant communities (Laine, 1978; Herrera, 1984a). In contrast to periodical habitat shifts or regular migrations promoted by predictable seasonal rhythms, supra-annual fruiting patterns promote irregular displacements of frugivores over vast areas. *Turdus pilaris* and *Bombycilla garrulus* some years exhibit irruptive movements in northern and central Europe, apparently determined by extensive failure of *Sorbus* trees, their critical autumn–winter food (Ulfstrand, 1963). Provided some fruits are available, these irruptive birds may be found in any major habitat type (Bezzel, 1966; Tyrväinen, 1970, 1975; Kolunen and Vikberg, 1978).

Available information suggests that (1) species of frugivorous birds are often very catholic in their choice of major habitat types, (2) their ability to exploit fruits in a variety of habitats seems essential to the maintenance of frugivory, given the intense temporal fluctuations experienced by their food resource, and (3) gross habitat type selection is very often determined by fruit availability alone. I examine in subsequent sections the significance of other variables.

B. Patterns in Space

Horizontal distribution of fruit-producing plants, as well as their relative cover and species richness in the plant community, determine the patterns of spatial distribution of fruits within habitats. If differences in successional stages of contiguous vegetation patches exist, they can produce important horizontal heterogeneity in food supply for frugivores.

Fruit-bearing plants in temperate forests mostly are earlier successional shrubs whose fruit production intensity is very sensitive to shading (Halls, 1973; Baird, 1980). Fruits accordingly are concentrated in clearings and forest edges, and become scarce in the interior of mature forest stands dominated by nut- or cone-producing trees (e.g., Auclair and Cottam, 1971; Sherburne, 1972; Marks, 1974; A. J. Smith, 1975). Species of avian frugivores preferentially select these light gaps, relative to the forest interior (Willson *et al.*, 1982).

In Mediterranean scrublands, in contrast, fruit-bearing plants replace earlier successional non-fruit-producing shrubs and eventually dominate the vegetation in mature scrublands (Houssard *et al.*, 1980; Herrera, 1984c). This produces a very small scale patchiness in fruit distribution in late successional formations, where distribution of fruits becomes virtually continuous at times of peak availability (Herrera, 1984a). Small-sized frugivorous birds characteristic of these scrublands (*Erithacus rubecula*, *Sylvia atricapilla*, *S. melanocephala*) avoid ear-

ly successional scrub and disturbed patches in favor of dense mature stands (Fernández, 1982).

Fruit abundance is predictably associated with light gaps in a Costa Rican lowland rainforest understory, and abundance of frugivorous birds (mostly manakins, tyrant flycatchers, and tanagers) parallels fruit supply (Fig. 2). This pattern, however, does not seem to be general to all tropical rainforests. Understory frugivores in a Panamanian forest are not more abundant in treefall gaps than in nearby forest interior (Willson *et al.*, 1982), and no frugivorous species shows a preference for gaps (Schemske and Brokaw, 1981). Light gaps in these forests do not seem to produce more fruits than closed forest understory (Schemske and Brokaw, 1981). Further studies in tropical forests are needed to assess the generality of frugivores' responses to gap-related fruit abundance patterns.

The limited evidence available suggests that patchiness in successional stages of vegetation has important habitat implications for frugivorous birds. However, differences among plant community types in the distribution of the fruit-producing habit along the successional gradient (see, e.g., Opler *et al.*, 1980, Howe and Smallwood, 1982, Herrera, 1984a) preclude broad generalizations on the responses of frugivores to patchy habitats generated by asynchronous disturbances of the vegetation (White, 1979).

Patterns of habitat use by frugivores, particularly their daily displacements between distantly spaced fruit sources, are very poorly known. Both the isolation of fruiting patches and the food value of individual patches presumably have important effects on the time and energy budget of avian frugivores. One expects that the ability to exploit (on a daily basis) widely spaced and/or individually

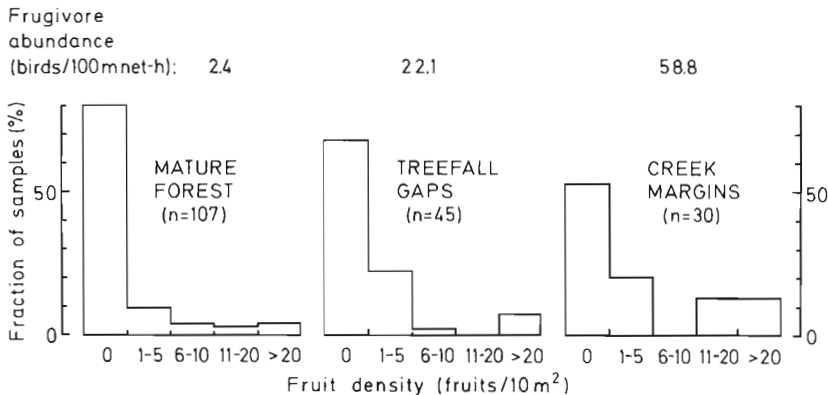


Fig. 2. Variation in fruit and frugivore abundance in the understory of a Costa Rican lowland rainforest (Finca La Selva, February 1980). Fruits were counted within 10 m² rectangular quadrat samples (*n*, number of samples examined in each habitat category). Frugivore abundance estimated by mist-net captures per netting effort. (Based on information supplied by F. G. Stiles.)

low-reward fruiting patches increases with body size, and the scanty field evidence available supports this expectation (Snow, 1962c; Walsberg, 1977; Davies, 1978; Davison, 1981). Interhabitat differences in average spacing and food value of fruiting patches shown previously will presumably affect differentially the selection of habitat by frugivores having different body sizes, but no field data are available to test this possibility.

Although isolated fruiting plants or widely spaced patches dominated by fruit-producing species often represent very dense concentrations of food for frugivores, territorial defense of these clumped resources is uncommon. As stated by Buskirk (1976): "Fruit cannot be banked over time and a suitable series of sequentially ripening fruit trees usually does not occur on a tract of land small enough to be defended by permanent territorial behavior. Defense of a superabundant fruit crop against trespassers would be energy consuming without yielding a realizable savings of food for future use." The few documented cases of feeding territories among frugivores (e.g., *Ilex*, *Juniperus*; Lederer, 1977a; Salomonson and Balda, 1977; Moore, 1978; Snow and Snow, 1984) involve plants having large crops of long-lasting fruits. This suggests that the temporary nature of most fruits actually renders its defense unprofitable. The importance of fruit crop size in determining territorial behavior has been shown by Lederer (1977b, 1981) for *Myadestes townsendi* feeding on juniper fruit. (See Buskirk, 1976; Karr, 1976; Walsberg, 1977; Moore, 1977, for further discussion on social systems of frugivores as they relate to the distribution in space of fruit supply).

III. FRUIT CHARACTERISTICS

Fruits are made up of seeds and pulp, and frugivorous birds handle them in a variety of ways. Some species feed on seeds alone, discarding the pulp (e.g., some finches, Newton, 1972). Others ingest the pulp and seeds together, cracking the latter in the bill or the gizzard (e.g., parrots, finches, gamebirds; Turček, 1961; Newton, 1972; Janzen, 1981), while some others feed only on the pulp and ignore the seeds (e.g., titmice, Sorensen, 1981). There is finally a fourth group, that of species ingesting whole fruits and later defecating or regurgitating the seeds intact (Snow, 1971). All these groups have often been pooled under the single denomination of "frugivores," but they greatly differ in important aspects of their feeding ecology (Snow, 1971, Herrera, 1984b). In particular, nutrient and energy yield should vary substantially according to the part(s) of fruit actually being used as food, since seeds are far more nutritious than fruit pulp for most species. Little is known about the food value of fruits to avian frugivores that digest seeds, and I concentrate for the remainder of the chapter on species ingesting whole fruits and using pulp alone as food. These are the most genuine frugivores, for they maintain a mutualistic relationship with their food plants and

have been ultimately responsible for the evolution and maintenance of the fruit-producing habitat among plants (Snow, 1971; McKey, 1975).

A. Fruit Size

For birds that ingest whole fruits, gape width imposes an upper limit on the maximum size of fruit that can be ingested. Field observations confirm this intuitive assessment. Larger birds are able to ingest larger fruits. Small fruits are generally fed upon by more species than large ones, which can be handled effectively only by the limited subset of larger frugivores (Terborgh and Diamond, 1970; Leck, 1971; Diamond, 1973; Katak, 1979; Herrera, 1981a). To the extent that average fruit cross diameter varies among habitat types, one should expect this variable to influence habitat selection by frugivores that ingest whole fruits.

The average fruit cross diameters of local fruit-producing species vary significantly with elevation in the Guadalquivir Valley, southern Spain. Plant species of Mediterranean scrublands tend to have smaller fruits than those of highland pine forests, and this elevational gradient is closely paralleled by variation in average gape width of local frugivorous species (Fig. 3). Scrubland frugivores

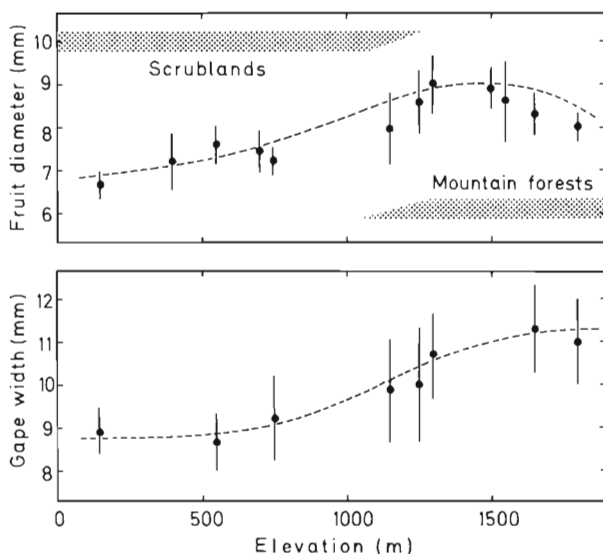


Fig. 3. Local averages for cross diameter of fruit species and gape width of frugivorous bird species experience parallel increases with elevation in the Guadalquivir Valley, southern Spain. Dominant frugivores in lower elevation scrublands are several small-sized (12–20 gm body weight) species, while larger-sized *Turdus* species (60–110 gm) predominate in highland forests. Vertical segments extend over ± 1 SE of the mean.

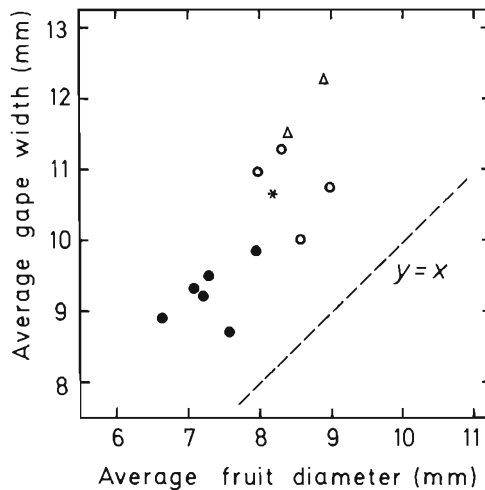


Fig. 4. Average gape width of avian frugivorous species is significantly related ($r = 0.801$, $p < 0.001$) to, and is about 2 mm larger than, average fruit cross diameter of local fruit-producing species in a sample of temperate, Mediterranean, and tropical habitats. Each symbol denotes a single locality: circles, southern Spanish habitats (filled circles, lowland scrub; open circles, highland pine forests); triangles, European temperate forests; asterisk, a Costa Rican highland locality (Cerro de la Muerte, 3100 m elevation). [Based on data in Sorensen (1981), information supplied by J. Guitián and P. Jordano, and author's unpublished data.]

are mostly small birds in the genera *Sylvia* and *Erithacus*, while large frugivores in the genus *Turdus* predominate numerically in highland forests (Jordano, 1982; C. M. Herrera, 1984a, unpublished data).

A plot of average fruit diameter against mean bird gape width reveals a significant linear relation between the two variables for southern Spanish locations (Fig. 4). Additional data from two temperate forests and a Neotropical highland locality fit remarkably well to the same general relation. Regardless of region and habitat type, therefore, the average gape width of local frugivores (feeding on whole fruits) runs roughly parallel to the average diameter of local fruit species, the two magnitudes differing by only 1–2.5 mm in the sample of localities considered (Fig. 4). Further data are needed to assess the generality of this relation, but the preliminary evidence presented strongly points to a significant role of fruit size alone in determining the composition of local assemblages of avian frugivores and, therefore, influencing habitat selection.

B. Fruit Quality

In marked contrast with other avian foods, the specific energetic and nutritional values of fruits vary dramatically among plant species, both among and

within habitats. Lipid content of (dry) pulp may fall somewhere between 1 and 67%, protein between 1 and 25%, and minerals between 1 and 14% (White, 1974; Crome, 1975; Foster, 1978; Frost, 1980; C. M. Herrera, 1981a, unpublished data). Many ripe fruits contain toxic compounds or digestion inhibitors in the pulp whose nature and concentration vary greatly among species (Kear, 1958; Herrera, 1982b). Furthermore, the proportion of edible fruit pulp relative to seeds (which are not digested) is also very variable (Herrera, 1981a, 1982b), contributing to amplify interspecific variation in nutritional and energetic value of fruits to consumers. Interhabitat variation in the composition of fruiting plant assemblages leads to substantial variation in the nutritional configuration of food resources found by avian frugivores. Along the Guadalquivir Valley, local plant communities differ appreciably in the frequency distributions of protein and lipid content of fruit pulp (Fig. 5). Sclerophyllous scrublands under 1200 m elevation are characterized by the presence at each locality of several species having lipid content in excess of 20% dry weight of pulp, whereas high energy fruits are absent from highland pine forests. Although other factors are also involved (e.g., accessibility, secondary compounds in the pulp, palatability, pulp–seed weight ratio; Howe and Vande Kerckhove, 1980; Herrera, 1981c; Moermond and Denslow, 1983; Sorensen, 1983), nutrient and energy content of pulp are important in fruit choice by at least some species (Graber and Powers, 1981; Herrera, 1981b, 1984a), and one should expect interhabitat differences in the nutritional configuration of fruit resources to influence habitat selection by frugivores.

Small birds have higher metabolic rates and energy requirements relative to body weight than larger ones (Kendeigh *et al.*, 1977, Walsberg, 1980), a difference which is accentuated under low temperatures (Kendeigh, 1970). One should therefore expect to find in autumn–winter, when climatic conditions are most severe, a negative relation between body size and the proportional importance of energy-rich fruits in the diet. This relation does exist for southern Spanish frugivores (Fig. 6). Heavy fruit consumption by small birds in autumn–winter could be possible if an adequate supply of energy-rich fruits is available. In contrast, the lower relative energy requirements of large frugivores would enable them to subsist more easily on comparatively low-energy fruits. The size-related, differential reliance of these birds on energy-rich fruits (Fig. 6) could be adduced to explain their differential prominence in habitats at different elevations (Figs. 3 and 6), since the frequency of lipid-rich fruits varies with elevation in the region (Fig. 5).

High-energy fruits are produced by a minority of plant species in both tropical and nontropical habitats, and some frugivores relying on them for subsistence seem to be particularly sensitive to interhabitat variation in species composition of fruit supply. Geographical distribution and habitat type utilization of the African Palm-nut Vulture (*Gypohierax angolensis*), having a great dependence on the very oil-rich fruits of the palm *Elaeis guineensis* (Thiollay, 1978), are

apparently dictated by the presence of this plant (Thomson and Moreau, 1957; Winterbottom, 1978). A close association exists also in the western Mediterranean Basin between *Sylvia melanocephala* and *Pistacia lentiscus*, whose very nutritious fruits are the basis of the bird's autumn–winter diet; the bird inhabits a variety of plant communities, greatly differing in physiognomy and composition, but presence of *P. lentiscus* seems indispensable in order to *S. melanocephala* to occupy a habitat in that season (C. M. Herrera 1984a, unpublished data). The association of Bellbirds (*Procnias*) with montane habitats in Central and South America has been interpreted as a consequence, in part, of their reliance on lauraceous fruits that are numerically more important in montane than lowland habitats (Snow, 1973).

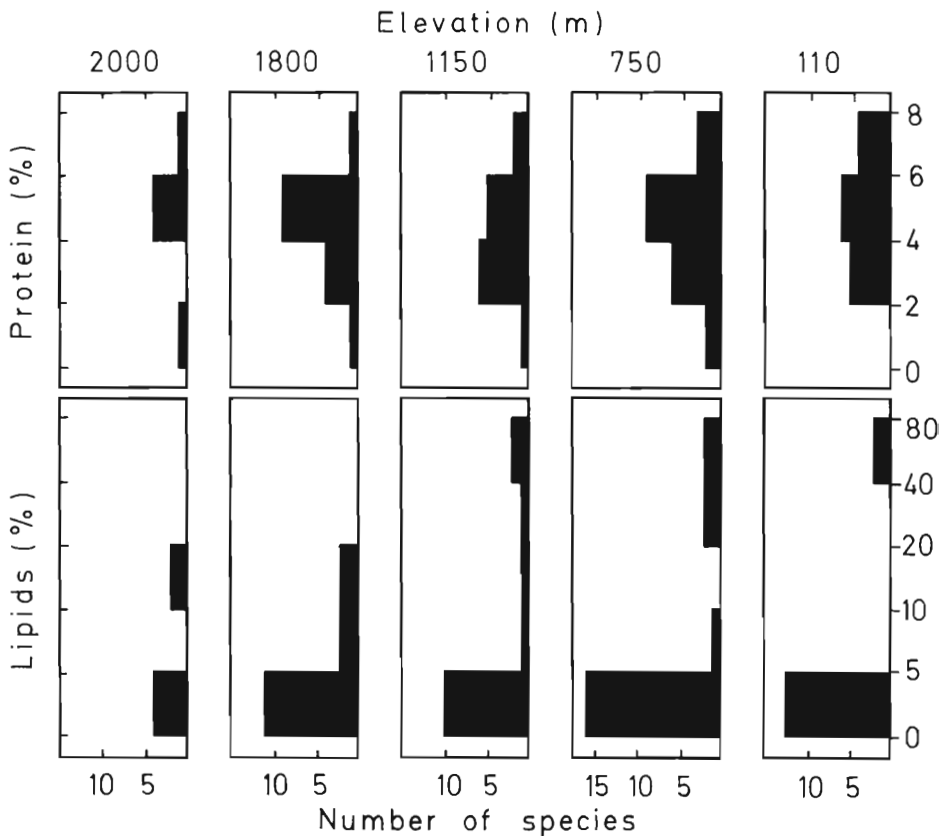


Fig. 5. Nutritional configuration of fruit species assemblages found by avian frugivores (as assessed by protein and lipid content of dry fruit pulp) varies markedly among plant communities occurring at various elevations in the Guadalquivir Valley, southern Spain. Note logarithmic scale used in the graphs for lipid content.

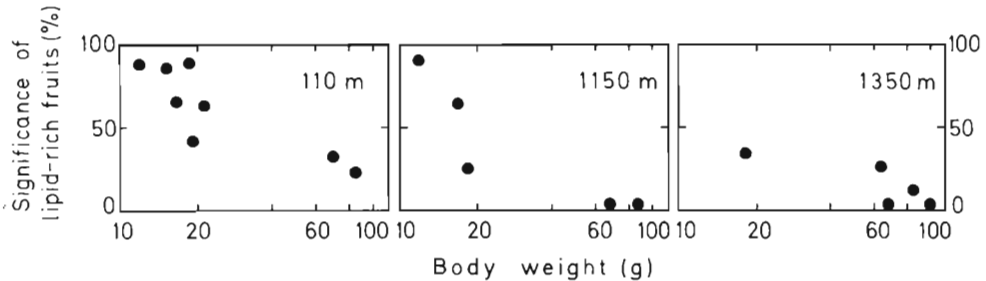


Fig. 6. In autumn-winter, the relative contribution (percentage of total fruits ingested) of lipid-rich fruits (lipid content of dry pulp greater than 20%) to the diet of southern Spanish avian frugivores declines with increasing body weight in three different habitat types (varying in vegetational composition and frequency of lipid-rich fruits; see Fig. 5). Dots represent individual bird species. [Based on data in Herrera (1984a and unpublished).]

Virtually nothing is known about the nutritional requirements of avian frugivores, but the limited information available seems to suggest that the strong nutritional imbalance characterizing the pulp of most fruit species forces many frugivores to have mixed-species diets in order to get a balanced input of energy, protein, vitamins, and minerals (Foster, 1978; Herrera, 1982a, 1984a). In southern Spain, single fecal samples of *Sylvia atricapilla* contain remains of up to nine fruit species, even though the birds face at times a virtually unlimited supply of highly energetic fruits. Other frugivores in the region and elsewhere behave similarly, ingesting a variety of fruit species over short time periods (Snow, 1977; Wheelwright, 1983; Herrera, 1984a). Although they are very poorly understood, nutritional constraints allow one to envisage subtle effects of interhabitat differences in nutritional configuration of fruit supply on habitat choice by frugivores.

We know next to nothing about the influence of secondary compounds in the pulp of ripe fruits on food selection by frugivores, but these do have some influence (Kear, 1958; Sherburne, 1972; Herrera, 1982a; Sorensen, 1983). The relative abundance of fruits defended (against fruit pests) chemically, by means of either digestion inhibitors like tannins or poisons like alkaloids, varies regionally and between habitat types (C. M. Herrera, unpublished data). Presumably, so does the chemical configuration of secondary compounds in fruits in different vegetation formations. It seems reasonable to expect these factors to have some significance in determining habitat choice by frugivores. Thus, the responses to habitat-specific chemical configuration of fruits presumably will differ among bird species as a function of somewhat species-specific attributes such as detoxification capacity (see Walker, 1983) and overall reliance on fruit for food. Blackbirds (*Turdus merula*) overwintering in southern Spanish montane pine forests strongly prefer the fruits of *Crataegus monogyna* over those of *Rosa*

canina, apparently because of the much higher tannin concentration found in the pulp of the latter; the two species are virtually identical with regard to other pulp constituents (Herrera, 1985b). As a consequence, these birds tend to avoid *Rosa*-dominated forest understories in favor of *Crataegus*-dominated ones (C. M. Herrera, unpublished data).

IV. HABITAT–CONSUMER INTERACTION

A. Frugivores as Modifiers of Habitats

I have been considering so far the influence of habitats on frugivorous birds, but the influence of these consumers on their habitats deserves consideration also.

Through selectively dispersing the seeds of different plant genotypes in relation to their preferences, seed-dispersing frugivorous birds are able to exert directional selective pressures on fruit-producing plants. Since the birds and their food plants interact mutualistically, these pressures will result in the evolution of fruit traits that are favorable to the birds (e.g., conspicuousness, abundance). This, coupled with a similar selective potential by plants on their dispersal agents, forms the basis of plant–disperser coevolutionary processes as initially envisaged by Snow (1971) and McKey (1975). Subsequent studies have elaborated further on the notion of plant–disperser coevolution, and I omit here a more detailed presentation of these widely held coevolutionary notions (see Howe and Smallwood, 1982; Janzen, 1983, Herrera, 1985a, for reviews). It must be noted that, in addition to changes in individual plant species, plant–disperser coevolution may produce over the long-term an “improvement” of habitats for frugivores. The regular staggering of the fruiting seasons of coexisting plants as a way of alleviating competition for seed vectors has as a consequence an extended period of fruit availability (Snow, 1965; Smythe, 1970), with obvious benefits to birds.

In addition to bird–plant interactions taking place on an evolutionary time scale, other types of mutual influences occur between frugivorous birds and their food plants on an ecological time scale. To some degree, seed-dispersing birds potentially have an ability to shape their own habitats, an aspect which to date has not received more than anecdotal attention in avian ecological studies, although it is a unique feature of this group of birds. Plant ecologists have long recognized, however, the importance of avian seed dispersers in the dynamics of plant communities (Auclair and Cottam, 1971; Livingston, 1972; Marks, 1974; A. J. Smith, 1975; Harper, 1977).

In the Colorado Desert, berries of the mistletoe *Phoradendron californicum* are the Phainopepla’s (*Phainopepla nitens*) major food during several months.