

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Mixed deciduous forest (northern Spain)	45.2	10.5	2.1	J. Guitián (unpublished)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

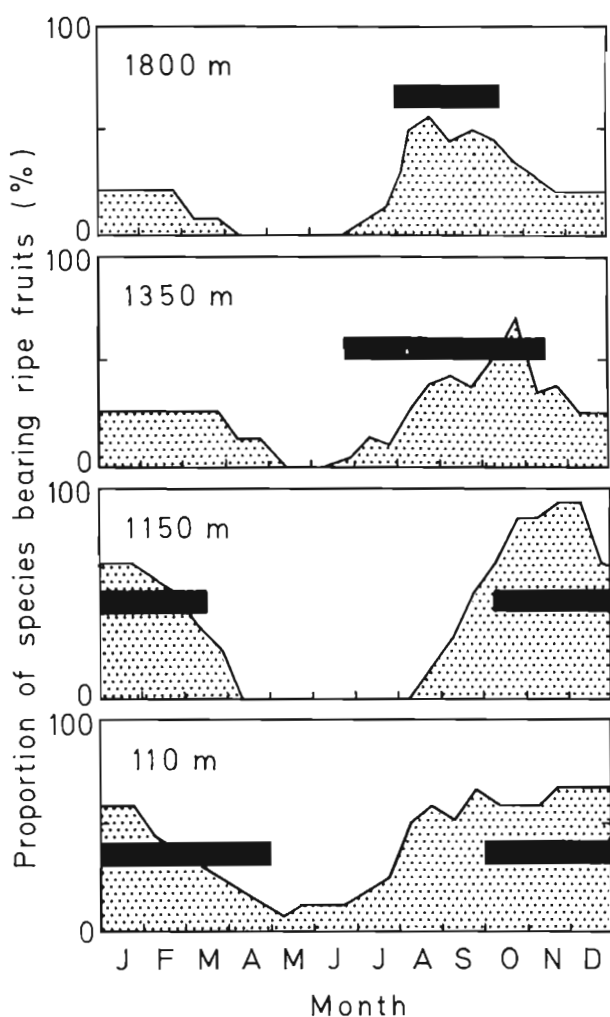


Fig. 1. Seasonal habitat occupancy (black bars) by *Sylvia atricapilla*, a strong frugivore, of four southern Spanish habitats occurring at different elevations and differing in fruiting phenology. Habitat occupancy during the period in which the bird is mainly insectivorous (April-May) is not shown, 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

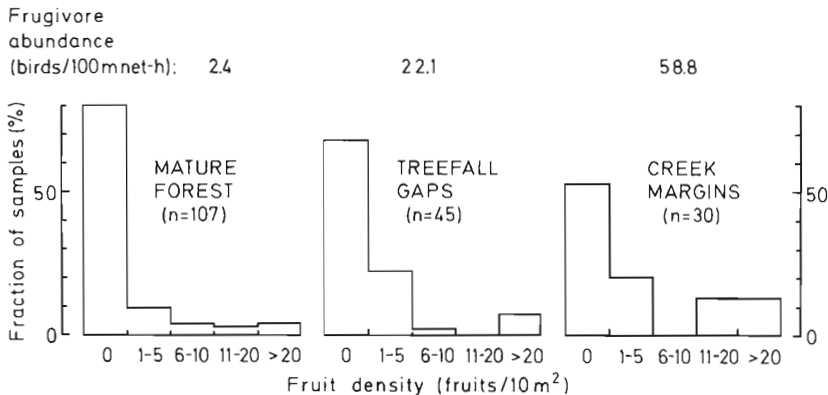


Fig. 2. Variation in fruit and frugivore abundance in the understory of a Costa Rican lowland rainforest (Finca La Selva, February 1980). Fruits were counted within 10 m² rectangular quadrat samples (*n*, number of samples examined in each habitat category). Frugivore abundance estimated by mist-net 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; Kantak, 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

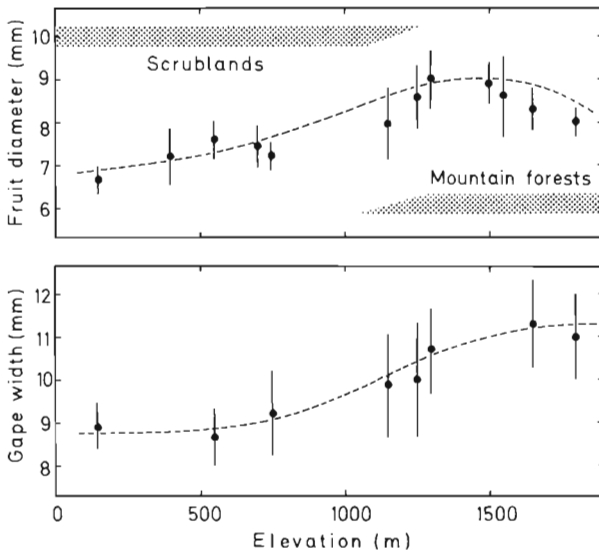


Fig. 3. Local averages for cross diameter of fruit species and gape width of frugivorous bird species experience parallel increases with elevation in the Guadalquivir Valley, southern Spain. Dominant frugivores in lower elevation scrublands are several small-sized (12–20 gm body weight) species, while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

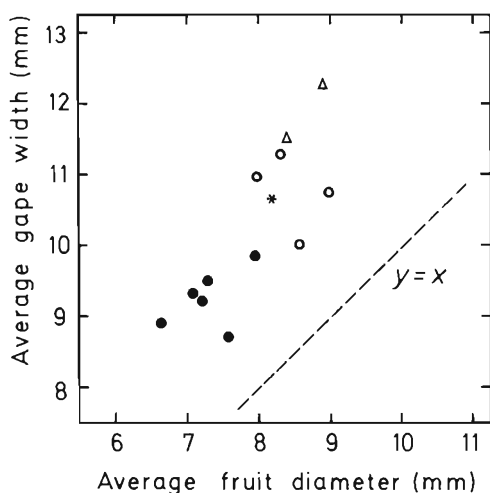


Fig. 4. Average gape width of avian frugivorous species is significantly related ($r = 0.801$, $p < 0.001$) to, and is about 2 mm larger than, average fruit cross diameter of local fruit-producing species in a sample of temperate, Mediterranean, and tropical habitats. Each symbol denotes a single locality: 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 Den-slow, 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).

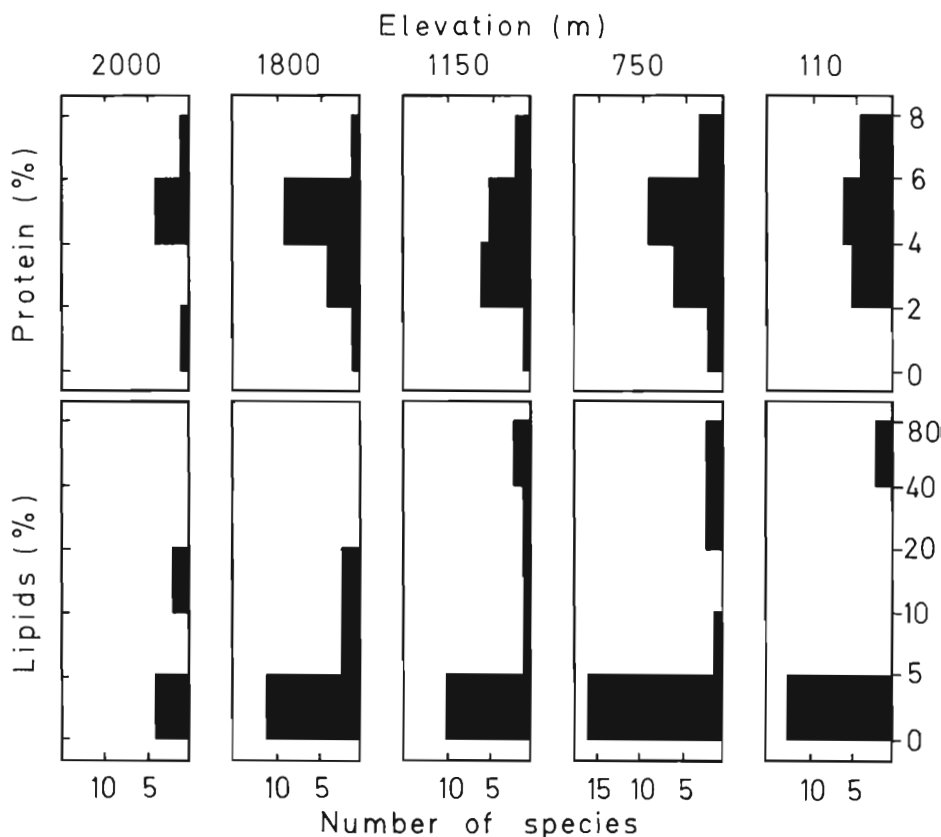


Fig. 5. Nutritional configuration of fruit species assemblages found by avian frugivores (as assessed by protein and lipid content of dry fruit pulp) varies markedly among plant communities occurring at various elevations in the Guadalquivir Valley, southern Spain. Note logarithmic scale used in the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

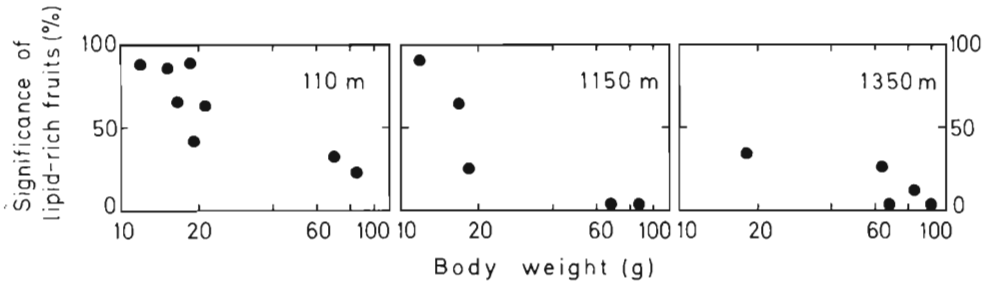


Fig. 6. In autumn–winter, the relative contribution (percentage of total fruits ingested) of lipid-rich fruits (lipid content of dry pulp greater than 20%) to the diet of southern Spanish avian frugivores declines with increasing body weight in three different habitat types (varying in vegetational composition 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.

Resident birds are always associated with mistletoe, and local population densities usually reflect the local abundance of mistletoe berries (Walsberg, 1977). The *Phainopeplas* help in the distribution of the mistletoe, for they eat the berries and the seeds pass through the digestive tract and cling to the branches below, where they germinate (Crouch, 1943; Walsberg, 1975). High densities of mistletoe clumps are indicative of an extended residence of *Phainopeplas* in an area (Crouch, 1943). A similar relation presumably exists in Australia and south-eastern Asia between some *Dicaeidae* and tropical mistletoes. These birds are heavily dependent on mistletoe berries for food, and they disseminate the seeds of their food plants (Docters van Leeuwen, 1954; Keast, 1958). The ability of some *Dicaeidae* to increase the carrying capacity of their environment and enhance favorable habitat attributes goes further than just spreading the seeds of their food plants; some species are pollinators of the same mistletoes which will later supply them with fruits (Docters van Leeuwen, 1954), and this pollinating activity obviously enhances fruit production to the birds' benefit. To the extent that mistletoes are a critical resource determining habitat selection by *Phainopepla* and *Dicaeidae*, the birds themselves are shaping their own habitats by introducing and spreading their critical food resource. In other words, birds are ultimately responsible for a habitat feature that promotes its utilization by the birds themselves.

The interaction between seed-dispersing frugivores and their habitats is vastly more complex than suggested by the previous simple examples. Most frugivores disperse the seeds of many plant species in the course of a season or over much shorter periods (Snow, 1962a, 1962b; Snow 1970, 1972; Snow and Snow, 1971; Frost, 1980; Cruz, 1981; Greenberg, 1981; Herrera, 1981b; Jordano and Herrera, 1981; Wheelwright, 1983), promoting simultaneously the recruitment of a broad plant assemblage rather than that of one or a few species. Birds "assemble" multispecies sets of seeds within themselves, thus in some sense restore sections of their habitats (in seed stage) in their guts and later in feces or regurgitations spread over their foraging areas. Nevertheless, many factors interact to determine the density, dispersion patterns, and composition of plant communities, and seed dispersal is only the first step in this process (Harper, 1977; Howe and Smallwood, 1982).

Regardless of these complications, however, the overall effects of multispecies seed dispersal by birds will generally be (1) an enhancement of the fruit-producing component of habitats and (2) a trend toward some "improvement" of habitat quality from the viewpoint of frugivores. Early successional shrubs of northern temperate forests occupy transient habitat patches created by treefall gaps and other disturbances and are later eliminated as succession proceeds (Auclair and Cottam, 1971; Marks, 1974; A. J. Smith, 1975). The preference of some frugivores for forest edges and clearings facilitates immigration of successional scrub seeds into newly opened patches; a few years later, the patch will

become an important fruit source to birds, which will tend to select preferentially these spots over surrounding forest (Thompson and Willson, 1978; Willson *et al.*, 1982; McDonnell and Stiles, 1983). The species composition of seeds brought into the newly created gap by birds will be a function of the species composition of the fruit supply found by the birds in other gaps in the area but also of the differential preference of birds for the various fruit species (McDonnell and Stiles, 1983). Seeds of preferred species will be proportionally over-represented in the incoming flux. It is likely that, other things being equal, these species will also tend to be overrepresented in the plant community that eventually dominates the patch and supplies further fruit to birds. The conclusion emerging from this example is that, to the extent that current species composition (and hence energetic, nutritional and chemical configuration of fruit supply) of fruiting patches in temperate forests has been shaped by specific fruit preferences of past frugivores, current habitat selection by these same seed-dispersing frugivores cannot be interpreted conventionally. Such frugivores play a far from passive role with respect to vegetation composition and structure.

The positive feedback which takes place between bird-dispersed plants and seed-dispersing birds on both ecological and evolutionary time scales raises the question: Are birds found where they are because the habitat attributes match their preferences, or do habitat attributes match birds' preferences to some degree because the birds have been there long enough to promote these attributes?

B. Southern Spanish Frugivores: A Case Example

As mentioned earlier, species of large-sized frugivores in the genus *Turdus* (mainly *T. torquatus*, *T. viscivorus*, *T. iliacus*, and *T. merula*) are predominant in undisturbed habitats in southern Spanish highlands in autumn–winter. The most extreme case is exemplified by Ring Ouzels (*T. torquatus*), which are largely confined to elevations above 1600 m where they feed almost entirely on the berries of Dwarf Junipers (*Juniperus communis nana*) (R. Zamora, unpublished data). In the highlands, plant communities are characterized by a dearth of lipid-rich fruits and the predominance of relatively large fruits. In contrast, small-sized frugivores predominate in lowland habitats, where average fruits are smaller and have higher lipid content. To what extent do differently sized frugivores select different habitats because of differences in the size and nutritional quality of fruits, as implied in earlier sections (the conventional look at habitat selection), and to what extent do size and quality of fruits differ among habitats because of differences over the long-term in the average body size of their complement of frugivorous species? This is the kind of circular reasoning that often emerges from analysis of coevolutionary processes and can be solved only by consideration of variables external to the plant–bird system (C. C. Smith, 1975).

Regardless of feeding habits, the proportional contribution of small species to bird communities tends to decline with increasing elevation (Affre, 1980; Thiollay, 1980; Lebreton and Broyer, 1981), probably as a consequence of size-related differential ability to cope with adverse thermal environments. This indicates, therefore, that the altitudinal segregation of differently sized frugivores in southern Spain is not necessarily a response to variation in some habitat attributes affecting its suitability to birds (fruit size and quality), as the correlative evidence alone would suggest. Independently of the plant-seed disperser interaction, fruiting plants living at different elevations have faced different size structures of avian disperser assemblages. Selection of small birds against large-fruited plants presumably has favored a decrease in fruit size in lowlands (Herrera, 1984a). In plant genera with species pairs whose members segregate altitudinally (e.g., *Pistacia*, *Daphne*, *Phillyrea*, *Lonicera*) the lowland species invariably has smaller fruits than its highland counterpart.

An analogous explanation may be adduced in relation to elevational variation in fruit quality. First, the small lowland frugivores have probably selected for increased energy content of fruits in their habitats more strongly than have large highland birds (Fig. 6, and Herrera, 1984a). Second, mild winters and evergreenness of plants have made possible the evolution in the lowlands of energy-rich winter fruits in response to selection by birds but not in the highlands, where greater climatic severity produces more deciduous plant species. Plant species having the most lipid-rich fruits in highland habitats are all evergreen.

Evolutionary processes do not seem to have contributed to the habitat-consumer matching in the case of Blackbirds (*Turdus merula*) overwintering in southern Spanish pine forests mentioned earlier. These birds prefer *Crataegus* fruits to those of *Rosa* and occupy preferentially forest understories dominated by the former species. They do, however, regularly ingest small numbers of *Rosa* fruits even where *Crataegus* is superabundant, apparently because these provide vitamins to the birds. As a result, birds tend to concentrate the few *Rosa* seeds they disperse under their preferred *Crataegus* plants, promoting a very close spatial association of both species permitted by the climbing habit of *Rosa* (Herrera, 1985b). It is relatively frequent to find pine forest understories having *Rosa* alone (avoided by *T. merula*), but habitats having *Crataegus* alone are extremely rare. It thus seems as if birds' behavior serves to add a *Rosa* component to *Crataegus*-dominated habitats. This has the consequence of birds finding their minor, albeit important, fruit food spatially close to their staple food species. The savings in locomotion costs lead perhaps to the observed preference for this habitat type (see Herrera, 1985b for further details on this complex interaction). To summarize, seed-dispersing birds have the ability to assemble in their guts the food species they like in the proportions they like, and some bird generations later, what they prefer may be found assembled again (in the way they like) in the form of adult, fruit-producing plants in bird-generated preferred habitats.

V. CONCLUDING REMARKS

In addition to illustrating the scant knowledge we have about frugivorous birds and their habitats, this chapter should have made apparent to the reader that, because of their mutualistic interaction with food resources, frugivores that disperse seeds are unique among birds in their relation with their habitats.

Frugivores are commonly less numerous in terms of species but often more abundant in terms of individuals than insectivores in bird communities (Snow and Snow, 1971; Karr, 1976; Brosset, 1981; Herrera, 1984a). This should be related to the fact that fruits can be abundant and tend to be conspicuous, but the number of ways they can be exploited efficiently is limited, thus affording little opportunity for specialization; the reverse is true of insects. These differences stem from the contrasting ecological relations fruits and insects maintain with their consumers (mutualism versus predation; Snow, 1971). Furthermore, as discussed earlier, strong spatiotemporal patterning of fruits will generally select against specialized habitat use. On the other hand, interspecific competition, a factor which has played a central role in the evolution of precise habitat selection among insectivores (Svärdson, 1949; Lack, 1971; Cody, 1978), is relatively unimportant in frugivorous species assemblages which most often exploit temporarily superabundant food (Fleming, 1979). And finally, seed-dispersing frugivores have a potential ability to make their habitats become, in ecological and evolutionary time scales, better "adjusted" to their preferences (although the extent to which this ability is realized in nature remains to be ascertained by future studies). For all these reasons, I contend that habitat selection by frugivores should not be analyzed using the usual ecological approaches that have proved useful with other birds maintaining nonmutualistic relations with their food resources. Some factors which may be relevant in studies of habitat selection by frugivores have been outlined previously. On the other hand, owing to their conspicuousness, properties of fruits are readily measurable (size, nutritional value, abundance) as compared to cryptic avian foods. Accordingly, the ultimate factors (see Hildén, 1965) determining habitat selection may be more easily assessed for frugivores than for other groups in which evidence based on quantification of proximate factors is the usual basis for habitat selection studies (e.g., Cody, 1968, 1978; James, 1971; Anderson and Shugart, 1974).

The implications of the habitat-shaping ability of avian seed dispersers transcend those related to the subject of habitat selection. One essential requirement for coevolutionary processes to take place is a reasonable degree of spatiotemporal coincidence of interacting counterparts, as nicely illustrated by highly coevolved host-parasite systems (Brooks, 1979; Waage, 1979). Coincidence will reinforce reciprocal selective pressures, hence promoting mutual adaptation. Despite the recent interest in plant-disperser coevolution (McKey, 1975; Howe and Estabrook, 1977), the implications of the ability of seed dispersers to shape

their habitats in function of their preferences have been generally neglected in favor of the consideration of evolutionary processes occurring on longer time scales. The nonevolutionary component of the interaction between avian seed dispersers and their habitats may be seen as the first step toward coevolution. By differentially disseminating plant species with contrasting fruiting-related traits, birds are potentially able to shape plant communities which best meet their preferences; this has as a consequence a progressive reinforcement of their association with these habitats and an increase in the scope of evolutionary interactions through increased opportunities of spatial coincidence of species. Analogously, by differentially disseminating plant genotypes with different fruiting-related traits, birds are able to shape food species evolutionarily according to their preferences. This latter process has received the most attention from investigators, but I suspect that the nonevolutionary process of habitat–consumer interaction will eventually prove much more significant than expected and that some observed patterns of close plant–bird mutualistic congruency could be explained in these terms without invoking coevolution. Ecological and evolutionary interactions between seed dispersers and fruit plants occur simultaneously, and both processes tend naturally to produce patterns of mutual adjustment, so it may be difficult in practice to separate their effects. For this reason at least, nonevolutionary aspects should be considered in addition to evolutionary ones in studies of plant–disperser interaction at the community level.

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REFERENCES

- Affre, G. (1980). Distribution altitudinale des oiseaux dans l'est des Pyrénées françaises. *L'Oiseau et R.F.O.* **50**, 1–22.
- Alexandre, D. Y. (1980). Caractère saisonnier de la fructification dans une forêt hygrophile de Côte-d'Ivoire. *Terre et Vie* **34**, 335–359.
- Anderson, S. H., and Shugart, H. H. (1974). Habitat selection of breeding birds in an East Tennessee deciduous forest. *Ecology* **55**, 828–837.
- Arvey, M. D. (1951). Phylogeny of the waxwings and allied birds. *Univ. Kans. Publ. Mus. Nat. Hist.* **3**, 473–530.

- Auclair, A. N., and Cottam, G. (1971). Dynamics of black cherry (*Prunus serotina* Ehrh.) in southern Wisconsin oak forests. *Ecol. Monogr.* **41**, 153–177.
- Baird, J. W. (1980). The selection and use of fruit by birds in an eastern forest. *Wilson Bill.* **92**, 63–73.
- Bairlein, F. (1983). Habitat selection and associations of species in European Passerine birds during southward, post-breeding migrations. *Ornis Scand.* **14**, 239–245.
- Bezzel, E. (1966). Die Invasion des Seidenschwanzes (*Bombicilla garrulus*) 1965/1966 in Bayern. *Anz. Ornithol. Ges. Bayern* **7**, 847–854.
- Brensing, D. (1977). Nahrungsökologische Untersuchungen an Zugvögeln in einem südwestdeutschen Durchzugsgebiet während des Wegzuges. *Vogelwarte* **29**, 44–56.
- Brooks, D. R. (1979). Testing the context and extent of host–parasite coevolution. *Syst. Zool.* **28**, 299–307.
- Brosset, A. (1981). Evolution divergente des comportements chez deux bulbuls sympatriques (Pycnonotidae). *Alauda* **49**, 94–111.
- Bullock, S. H. (1978). Plant abundance and distribution in relation to types of seed dispersal in chaparral. *Madroño* **25**, 104–105.
- Buskirk, W. H. (1976). Social systems in a tropical forest avifauna. *Am. Nat.* **110**, 293–310.
- Charles-Dominique, P., Atramentowicz, M., Charles-Dominique, M., Gerard, H., Hladik, H., Hladik, C. M., and Prevost, M. F. (1981). Les Mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: Inter-relations plantes-animaux. *Terre et Vie* **35**, 341–435.
- Cody, M. L. (1968). On the methods of resource division in grassland bird communities. *Am. Nat.* **102**, 107–147.
- Cody, M. L. (1978). Habitat selection and interspecific territoriality among the sylviid warblers of England and Sweden. *Ecol. Monogr.* **48**, 351–396.
- Crome, F. H. J. (1975). The ecology of fruit pigeons in tropical Northern Queensland. *Aust. Wildl. Res.* **2**, 155–185.
- Crouch, J. E. (1943). Distribution and habitat relationships of the Phainopepla. *Auk* **60**, 319–333.
- Cruz, A. (1981). Bird activity and seed dispersal of a montane forest tree (*Dunalia arborescens*) in Jamaica. *Biotropica* **13**, 34–44.
- Davies, S. J. J. F. (1978). The food of emus. *Aust. J. Ecol.* **3**, 411–422.
- Davison, G. W. H. (1981). Diet and dispersion of the great argus *Argusianus argus*. *Ibis* **123**, 485–494.
- Debussche, M., and Isenmann, P. (1983). La consommation des fruits chez quelques fauvettes méditerranéennes (*Sylvia melanocephala*, *S. cantillans*, *S. hortensis* et *S. undata*) dans la région de Montpellier (France). *Alauda* **51**, 302–308.
- Diamond, J. M. (1973). Distributional ecology of New Guinea birds. *Science* **179**, 759–769.
- Docters van Leeuwen, W. M. (1954). On the biology of some Javanese Loranthaceae and the role birds play in their life-history. *Beaufortia* **4**, 105–207.
- Ellner, S., and Shmida, A. (1981). Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* **51**, 133–144.
- Fernández, V. (1982). Relaciones entre la estructura de la vegetación y las comunidades de pájaros en las Sierras de Algeciras. MS. thesis, Univ. Seville, Seville.
- Fleming, T. H. (1979). Do tropical frugivores compete for food? *Am. Zool.* **19**, 1157–1172.
- Fogden, M. P. L. (1972). The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* **114**, 307–343.
- Foster, M. S. (1977). Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* **58**, 73–85.
- Foster, M. S. (1978). Total frugivory in tropical passerines: A reappraisal. *J. Trop. Ecol.* **19**, 131–154.

- Foster, R. B. (1974). Seasonality of fruit production and seed fall in a tropical forest ecosystem in Panama. Ph.D. thesis, Univ. Microfilms Int., Univ. of Michigan, Ann Arbor, Michigan.
- Frankie, G. W., Baker, H. G., and Opler, P. A. (1974). Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* **62**, 881–919.
- Frost, P. G. H. (1980). Fruit-frugivore interactions in a South African coastal dune forest. In “Acta XVII Congressus Internationalis Ornithologici” (R. Nohring, ed.), pp. 1179–1184. Deuts. Orn. Ges., Berlin.
- Graber, J. W., and Powers, P. M. (1981). Dwarf sumac as winter bird food. *Am. Midl. Nat.* **105**, 410–412.
- Grant, G. S. (1979). Ring-billed Gulls feeding on date fruits. *Condor* **81**, 432–433.
- Greenberg, R. (1981). Frugivory in some migrant tropical forest wood warblers. *Biotropica* **13**, 215–223.
- Halls, L. K. (1973). Flowering and fruiting of southern browse species. *U.S. For. Serv. Res. Pap.* SO–90, 1–10.
- Harper, J. L. (1977). “The Population Biology of Plants.” Academic Press, London and New York.
- Havlin, J. (1977). Ein Vergleich der Nahrung des Stars und der Amsel. *Folia Zool.* **26**, 45–56.
- Herrera, C. M. (1981a). Are tropical fruits more rewarding to dispersers than temperate ones? *Am. Nat.* **118**, 896–907.
- Herrera, C. M. (1981b). Fruit food of Robins wintering in southern Spanish mediterranean scrubland. *Bird Study* **28**, 115–122.
- Herrera, C. M. (1981c). Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos* **36**, 51–58.
- Herrera, C. M. (1981d). Datos sobre la dieta frugívora del Mirlo (*Turdus merula*) en dos localidades del Sur de España. *Doñana Acta Vert.* **8**, 306–310.
- Herrera, C. M. (1982a). Defense of ripe fruits from pests: Its significance in relation to plant–disperser interactions. *Am. Nat.* **120**, 218–241.
- Herrera, C. M. (1982b). Seasonal variation on the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* **63**, 773–785.
- Herrera, C. M. (1984a). A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecol. Monogr.* **54**, 1–23.
- Herrera, C. M. (1984b). Adaptation to frugivory of Mediterranean avian seed dispersers. *Ecology* **65**, 609–617.
- Herrera, C. M. (1984c). Tipos morfológicos y funcionales en plantas del matorral mediterráneo del sur de España. *Studia Oecologica*, (in press).
- Herrera, C. M. (1985a). Determinants of plant–animal coevolution: The case of mutualistic vertebrate seed dispersal systems. *Oikos* **44** (in press).
- Herrera, C. M. (1985b). Seed dispersal and fitness determinants in wild rose: Effects of hawthorn, birds, mice, and browsing ungulates. *Oecologia* **63** (in press).
- Herrera, C. M., and Jordano, P. (1981). *Prunus mahaleb* and birds: The high-efficiency seed dispersal system of a temperate fruiting tree. *Ecol. Monogr.* **51**, 203–218.
- Hildén, O. (1965). Habitat selection in birds. A review. *Ann. Zool. Fenn.* **2**, 53–75.
- Houssard, C., Escarré, J., and Romane, F. (1980). Development of species diversity in some mediterranean plant communities. *Vegetatio* **43**, 59–72.
- Howe, H. F., and Estabrook, G. F. (1977). On intraspecific competition for avian dispersers in tropical trees. *Am. Nat.* **111**, 817–832.
- Howe, H. F., and Smallwood, J. (1982). Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* **13**, 201–228.
- Howe, H. F., and Vande Kerckhove, G. A. (1980). Nutmeg dispersal by tropical birds. *Science* **210**, 925–927.

- James, F. C. (1971). Ordinations of habitat relationships among breeding birds. *Wilson Bull.* **83**, 215–236.
- Janzen, D. H. (1981). *Ficus ovalis* seed predation by an orange-chinned parakeet (*Brotogetis jugularis*) in Costa Rica. *Auk* **98**, 841–844.
- Janzen, D. H. (1983). Dispersal of seeds by vertebrate guts. In "Coevolution" (D. J. Futuyma and M. Slatkin, eds.), pp. 232–262. Sinauer, Sunderland, Massachusetts.
- Johnson, A. S., and Landers, J. L. (1978). Fruit production in slash pine plantations in Georgia. *J. Wildl. Manage.* **42**, 606–613.
- Jordano, P. (1982). Migrant birds are the main seed dispersers of blackberries in southern Spain. *Oikos* **38**, 183–193.
- Jordano, P., and Herrera, C. M. (1981). The frugivorous diet of blackcap populations *Sylvia atricapilla* wintering in southern Spain. *Ibis* **123**, 502–507.
- Kantak, G. E. (1979). Observations on some fruit-eating birds in Mexico. *Auk* **96**, 183–186.
- Karr, J. R. (1971). Structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr.* **41**, 207–233.
- Karr, J. R. (1976). Seasonality, resource availability, and community diversity in tropical bird communities. *Am. Nat.* **110**, 973–994.
- Karr, J. R. (1980). Geographical variation in the avifaunas of tropical forest undergrowth. *Auk* **97**, 283–298.
- Kear, J. (1958). Plant poisons in the diet of wild birds. *Bull. Br. Ornithol. Club.* **88**, 98–102.
- Keast, A. (1958). The influence of ecology on variation in the Mistletoebird (*Dicaeum hirsutinaceum*). *Emu* **58**, 195–206.
- Kendeigh, S. C. (1970). Energy requirements for existence in relation to size of bird. *Condor* **72**, 60–65.
- Kendeigh, S. C., Dol'nik, V. R., and Gavrilov, V. M. (1977). Avian energetics. In "Granivorous Birds in Ecosystems" (J. Pinowski and S. C. Kendeigh, eds.), pp. 127–204. Cambridge Univ. Press, London and New York.
- Kolunen, H., and Vikberg, P. (1978). Irruptions of the waxwing *Bombicilla garrulus* in S. Finland. *Ornis Fenn.* **55**, 126–131. (In Finnish, with English summary).
- Lack, D. (1971). "Ecological Isolation in Birds." Blackwell, Oxford.
- Laine, K. (1978). Aspects of annual variation in the numbers of flowers, berries and seeds in the Kilpisjärvi area. *Kilpisjärvi Notes* **2**, 12–16. (In Finnish, with English summary).
- Lebreton, P., and Broyer, J. (1981). Contribution à l'étude des relations avifaune/altitude. I. Au niveau de la région Rhône-Alpes. *L'Oiseau et R.F.O.* **51**, 265–285.
- Leck, C. F. (1971). Overlap in the diet of some neotropical birds. *Living Bird* **10**, 89–106.
- Lederer, R. J. (1977a). Winter territoriality and foraging behavior of the Townsend's Solitaire. *Am. Midl. Nat.* **97**, 101–109.
- Lederer, R. J. (1977b). Winter feeding territories in the Townsend's Solitaire. *Bird Banding* **48**, 11–18.
- Lederer, R. J. (1981). Facultative territoriality in Townsend's Solitaire (*Myadestes townsendi*). *Southwest. Nat.* **25**, 461–467.
- Leigh, E. G. (1975). Structure and climate in tropical rain forest. *Annu. Rev. Ecol. Syst.* **6**, 67–86.
- Lein, M. R. (1972). A trophic comparison of avifaunas. *Syst. Zool.* **21**, 135–150.
- Lemke, T. O. (1979). Fruit-eating behavior of Swallow-tailed Kites (*Elanoides forficatus*) in Colombia. *Condor* **81**, 207–208.
- Lieberman, D. (1982). Seasonality and phenology in a dry tropical forest in Ghana. *J. Ecol.* **70**, 791–806.
- Livingston, R. B. (1972). Influence of birds, stones and soil on the establishment of pasture juniper, *Juniperus communis*, and red cedar, *J. virginiana* in New England pastures. *Ecology* **53**, 1141–1147.

- McDonnell, M. J., and Stiles, E. W. (1983). The structural complexity of old vegetation and the recruitment of bird-dispersed plant species. *Oecologia* **56**, 109–116.
- McKey, D. (1975). The ecology of coevolved seed dispersal systems. In "Coevolution of Animals and Plants" (L. E. Gilbert and P. H. Raven, eds.), pp. 159–191. Univ. of Texas Press, Austin.
- Marks, P. L. (1974). The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Monogr.* **44**, 73–88.
- Milewski, A. V., and Bond, W. J. (1982). Convergence of myrmecochory in mediterranean Australia and South Africa. In "Ant–Plant Interactions in Australia" (R. C. Buckley, ed.), pp. 89–98. Junk, The Hague.
- Moermond, T. C., and Denslow, J. S. (1983). Fruit choice in neotropical birds: Effects of fruit type and accessibility on selectivity. *J. Anim. Ecol.* **52**, 407–420.
- Moore, F. R. (1977). Flocking behaviour and territorial competitors. *Anim. Behav.* **25**, 1063–1065.
- Moore, F. R. (1978). Interspecific aggression: Toward whom should a mockingbird be aggressive? *Behav. Ecol. Sociobiol.* **3**, 173–176.
- Morse, D. H. (1975). Ecological aspects of adaptive radiation in birds. *Biol. Rev.* **50**, 167–214.
- Morton, E. S. (1973). On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *Am. Nat.* **107**, 8–22.
- Morton, E. S. (1977). Intrapopulation migration in the yellow-green vireo and piratic flycatcher. *Auk* **94**, 97–106.
- Newton, I. (1972). "Finches." Collins, London.
- Ogawa, I. (1977). Pellet analysis of the bull-headed shrike *Lanius bucephalus* and the seasonal change of food habits. *Tori* **26**, 63–75. (In Japanese, with English summary).
- Opler, P. A., Baker, H. G., and Frankie, G. W. (1980). Plant reproductive characteristics during secondary succession in neotropical lowland forest ecosystems. *Biotropica* **12**, 40–46.
- Pearson, D. L. (1977). A pantropical comparison of bird community structure on six lowland forest sites. *Condor* **79**, 232–244.
- Putnam, L. S. (1949). The life history of the Cedar Waxwing. *Wilson Bull.* **61**, 141–182.
- Rowan, M. K. (1967). A study of the colies of southern Africa. *Ostrich* **38**, 63–115.
- Rowan, M. K. (1970). The foods of South African birds. *Ostrich* **8**, Suppl., 343–356.
- Salomonson, M. G., and Balda, R. P. (1977). Winter territoriality of Townsend's Solitaires (*Myadestes townsendi*) in a piñon–juniper–ponderosa pine ecotone. *Condor* **79**, 148–161.
- Schemske, D. W., and N. Brokaw (1981). Treefalls and the distribution of understory birds in a tropical forest. *Ecology* **62**, 938–945.
- Sherburne, J. A. (1972). Effects of seasonal changes in the abundance and chemistry of the fleshy fruits of northeastern woody shrubs on patterns of exploitation by frugivorous birds. Ph.D. thesis, Univ. Microfilms Int., Ann Arbor, Michigan.
- Smith, A. J. (1975). Invasion and ecesis of bird-disseminated woody plants in temperate forest sere. *Ecology* **56**, 19–34.
- Smith, C. C. (1975). The coevolution of plants and seed predators. In "Coevolution of Animals and Plants" (L. E. Gilbert and P. H. Raven, eds.), pp. 51–77. Univ. of Texas Press, Austin.
- Smythe, N. (1970). Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *Am. Nat.* **104**, 25–35.
- Snow, B. K. (1970). A field study of the bearded bellbird in Trinidad. *Ibis* **112**, 299–329.
- Snow, B. K. (1972). A field study of the calfbird *Perissocephalus tricolor*. *Ibis* **114**, 139–162.
- Snow, B. K. (1977). Territorial behavior and courtship of the male three-wattled bellbird. *Auk* **94**, 623–645.
- Snow, B. K., and Snow, D. W. (1971). The feeding ecology of tanagers and honeycreepers in Trinidad. *Auk* **88**, 291–322.

- Snow, B. K., and Snow, D. W. (1984). Long-term defence of fruit by mistle thrushes. *Ibis* **126**, 39–49.
- Snow, D. W. (1962a). A field study of the black and white manakin, *Manacus manacus*, in Trinidad. *Zoologica N.Y.* **47**, 65–104.
- Snow, D. W. (1962b). A field study of the golden-headed manakin, *Pipra erythrocephala*, in Trinidad. W. I. *Zoologica N.Y.* **47**, 183–198.
- Snow, D. W. (1962c). The natural history of the oilbird, *Steatornis caripensis*, in Trinidad, W. I. Part 2. Population, breeding ecology and food. *Zoologica N.Y.* **47**, 199–221.
- Snow, D. W. (1965). A possible selective factor in the evolution of fruiting seasons in tropical forest. *Oikos* **15**, 274–281.
- Snow, D. W. (1971). Evolutionary aspects of fruit-eating by birds. *Ibis* **113**, 194–202.
- Snow, D. W. (1973). Distribution, ecology and evolution of the bellbirds (*Procnias*, Cotingidae). *Bull. Br. Mus. (Nat. Hist.), Zool.* **25**, 369–391.
- Snow, D. W. (1981). Tropical frugivorous birds and their food plants: A world survey. *Biotropica* **13**, 1–14.
- Sorensen, A. (1981). Interactions between birds and fruits in a British woodland. *Oecologia* **50**, 242–249.
- Sorensen, A. (1983). Taste aversion and frugivore preference. *Oecologia* **56**, 117–120.
- Stransky, J. J., and Halls, L. K. (1980). Fruiting of woody plants affected by site preparation and prior land use. *J. Wildl. Manage.* **44**, 258–263.
- Svärdson, G. (1949). Competition and habitat selection in birds. *Oikos* **1**, 157–174.
- Terborgh, J., and Diamond, J. M. (1970). Niche overlap in feeding assemblages of New Guinea birds. *Wilson Bull.* **82**, 29–52.
- Thiollay, J. M. (1978). Les rapaces d'une zone de contact savane-forêt en Côte-d'Ivoire: Spécialisations alimentaires. *Alauda* **47**, 147–170.
- Thiollay, J. M. (1980). L'évolution des peuplements d'oiseaux le long d'un gradient altitudinal dans l'Himalaya central. *Terre et Vie* **34**, 199–269.
- Thompson, J. N., and Willson, M. F. (1978). Disturbance and the dispersal of fleshy fruits. *Science* **200**, 1161–1163.
- Thompson, J. N., and Willson, M. F. (1979). Evolution of temperate fruit/bird interactions: Phenological strategies. *Evolution* **33**, 973–982.
- Thomson, A. L., and Moreau, R. E. (1957). Feeding habits of the palm-nut vulture *Gypohierax*. *Ibis* **99**, 608–613.
- Turček, F. (1961). "Okologické Beziehungen der Vögel und Gehölze." Slovak. Akad. Wissensch., Bratislava.
- Tutman, I. (1969). Beobachtungen an olivenfressenden Vögeln. *Vogelwelt* **90**, 1–8.
- Tyrväinen, H. (1970). The mass occurrence of the fieldfare (*Turdus pilaris* L.) in the winter of 1964/65 in Finland. *Ann. Zool. Fenn.* **7**, 349–357.
- Tyrväinen, H. (1975). The winter irruption of the fieldfare *Turdus pilaris* and the supply of rowan-berries. *Ornis Fenn.* **52**, 23–31.
- Ulfstrand, S. (1963). Ecological aspects of irruptive bird migration in northwestern Europe. *Proc. Int. Ornithol. Congr. 13th*, pp. 780–794.
- Waage, J. K. (1979). The evolution of insect/vertebrate associations. *Biol. J. Linn. Soc.* **12**, 187–224.
- Walker, C. H. (1983). Pesticides and birds-mechanisms of selective toxicity. *Agric. Ecosys. Environ.* **9**, 211–226.
- Walsberg, G. E. (1975). Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. *Condor* **77**, 169–174.
- Walsberg, G. E. (1977). Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilonotidae). *Univ. Calif. Publ. Zool.* **108**, 1–63.

- Walsberg, G. E. (1980). Energy expenditure in free-living birds: Patterns and diversity. In "Acta XVII Congressus Internationalis Ornithologici" (R. Nohring, ed.), pp. 300-305. Deuts. Orn. Ges., Berlin.
- Wheelwright, N. T. (1983). Fruits and the ecology of Resplendent Quetzals. *Auk* **100**, 286-301.
- White, P. S. (1979). Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* **45**, 229-299.
- White, S. C. (1974). Ecological aspects of growth and nutrition in tropical fruit-eating birds. Ph.D. thesis, Univ. Microfilms Int., Ann Arbor, Michigan.
- Willson, M. F., Porter, E. A., and Condit, R. S. (1982). Avian frugivore activity in relation to forest light gaps. *Caribb. J. Sci.* **18**, 1-6.
- Winterbottom, J. M. (1978). Birds. In "Biogeography and Ecology of Southern Africa" (M. J. A. Werger, ed.), Vol. 2, pp. 949-979. Junk, The Hague.