

A STUDY OF AVIAN FRUGIVORES, BIRD-DISPERSED PLANTS, AND THEIR INTERACTION IN MEDITERRANEAN SCRUBLANDS¹

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Abstract. Fruit production and patterns of seed dispersal by birds were studied at two elevations in the mediterranean scrublands of southern Spain. Fleshy-fruit-producing species represent a very prominent fraction of woody plants in terms of cover (57-76%) and species number (49-66%). Fruit production occurs year round in the lowland site but is confined to August-February upslope. Ripe fruits are most abundant (>10⁵ ripe fruits/ha) in November-December. Fruit abundance fluctuates widely between years at the highland locality but only slightly in the lowlands. In both communities, the dominant species ripen fruits in autumn-winter, display the highest within-plant fruit densities, and tend to have the most lipid-rich fruits. Fruits differ in pulp nutritive value, seediness, and relative amount of pulp among species but are remarkably uniform in size (mostly 5-10 mm transverse diameter).

Two-thirds of the passerine species at each site eat some fruit. Of these species, 69% (highland) and 26% (lowland) are resident "fruit predators," feeding on either pulp or seeds alone, and damaging the seeds when eating pulp and seeds together. The rest are overwintering or migratory seed dispersers that ingest whole fruits without damaging seeds. Seed dispersers are most common in late autumn-winter, coincident with the peak in fruit abundance and the predominance of lipid-rich fruits. A few small (12-18 g body mass) disperser species (*Erithacus rubecula*, *Sylvia atricapilla*, *Sylvia melanocephala*) account for most of the frugivory at each site and disperse the majority of seeds. Fruit predators either are relatively scarce or eat fruits infrequently, or fruits represent a negligible fraction of their diets.

Fruit removal was very high (89-100% of crops) among species with fruits smaller than the gape width of the abundant small-sized dispersers, and very low among species with fruits larger than gape width. Removal success was negatively correlated with fruit size among species having fruits smaller than dominant dispersers' gape width. No relation has been found between removal success and fruit quality, fruiting time, ripening rate, or within-plant fruit density. The principal dispersers at each site ate mainly the most nutritious fruits, although not to the exclusion of less nutritious fruits. Substantial pairwise plant-bird reciprocity is not common. (The avian species disperses a substantial fraction of a plant's seeds, which in turn provide the bulk of the bird's energy supply.)

Current bird-plant seed dispersal interactions are the result of evolutionary, climatic, and geographical factors in the Mediterranean. Mutualistic congruency largely is, in these cases, an epiphenomenon of these factors, not resulting necessarily from mutual adaptations (coevolution). It is suggested that actual coevolution involving a smaller set of bird and plant species may facilitate the persistence of noncoevolving (or very slowly coevolving) plant species, thus favoring the existence of a chronic "anachronism load" (with regard to dispersal) in the plant community.

Key words: *avian frugivory; coevolution; Erithacus rubecula; flowering phenology; fruiting phenology; mediterranean habitats; plant ecology; scrublands; seed dispersal; Spain; Sylvia atricapilla; Sylvia melanocephala.*

INTRODUCTION

Many plants have their seeds dispersed by frugivorous birds (Howe and Smallwood 1982). Fleshy fruits (which may be viewed as packages containing seeds plus surrounding nutritive material, termed fruits hereafter) are eaten by birds, which obtain a reward as a result of digesting the pulp and take the seeds away from the parent plant to be later discarded in conditions suitable for germination. While avian frugivory and seed dispersal have been studied much earlier (Ridley 1930, Schuster 1930), the evolutionary implications for the participants in this mutualistic system have been recognized only recently (Snow 1971, McKey 1975). Every interacting participant may exert

selective pressure on the other part, and some phenotypic traits of both plants and avian seed dispersers may evolve in response to these pressures (Howe and Smallwood 1982). Plant-bird seed dispersal systems constitute particularly favorable examples with which to study coevolutionary processes, i.e., birds and plants evolutionarily changing in a stepwise manner (Snow 1971, McKey 1975, Howe and Estabrook 1977, Herrera 1982b).

Recent field examinations of earlier models and predictions on seed dispersal by vertebrates (Snow 1971, McKey 1975, Howe and Estabrook 1977, Howe 1979) have been conducted mostly in the tropics or have concentrated on the dispersal of individual plant species by arrays of specific dispersers (e.g., Howe 1977, 1980, 1981, McDiarmid et al. 1977, Howe and De Steven 1979, Howe and Vande Kerckhove 1980, 1981, Her-

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ra and Jordano 1981, Jordano 1982). These studies have promoted an empirical basis for understanding the dispersal ecology of some species and have provided the elements for recognition of a variety of dispersal ecologies among endozoochorous plants, particularly in tropical habitats (Howe and Smallwood 1982, Howe 1982).

Comprehensive studies of plant–bird seed dispersal interactions have not been undertaken in tropical areas (but see Greenberg 1981), and only a few regional overviews have been assembled elsewhere (Thompson and Willson 1979, Stiles 1980, Herrera 1982*b*). Studies dealing with one or a few plant species miss significant factors in the evolution of plant–disperser interactions. Avian dispersers associated with any single plant species not only feed on its fruits (and disperse its seeds), but also ordinarily eat other fruit species or food types simultaneously available. The importance of the bird-to-plant and plant-to-bird selective pressures for any given species pair will probably depend on the degree of relative mutual dependence. The statistical properties of the frequency distribution of pairwise reciprocal dependence values at the local community level will ultimately determine the strength and nature of selective forces driving any possible plant–bird coadaptive process.

The principal objective of this study was the examination of local patterns of fruit production and avian seed dispersal at the community level. The study was conducted in two mediterranean scrublands in southern Spain. Results will also be used to test the generality of some coevolutionary patterns suggested previously, based largely on results in tropical habitats (Snow 1971, 1981, McKey 1975, Howe and Estabrook 1977, Howe and Smallwood 1982), namely (1) fruits eaten by specialized frugivores are typically large seeded and have a pulp high in fats and protein; (2) fruits eaten by unspecialized frugivores are small seeded and have a less nutritious pericarp; (3) plants dispersed by specialized frugivores have more extended and constant periods of fruit availability (slower ripening rates) than species dispersed by opportunistic frugivores; (4) “low-investment” plants producing superabundant low-quality fruits should have lower dispersal success than “high-investment” plants producing fewer, high-quality fruits.

STUDY SITES

Cazorla: the highland site

Cazorla (hereafter referred to as the highland site) is in the Sierra del Pozo range (Serranía de Cazorla-Segura, Jaén province), a limestone mountain system in the Guadalquivir River drainage. The site (37°59'N, 2°54'W) is in the Arroyo de las Truchas valley, a 2500-ha drainage in which much of the natural vegetation is preserved. This montane scrubland is dominated by *Quercus*, *Phillyrea*, and *Arbutus*.

A plot (4 ha) in dense sclerophyllous scrub (3–4.5

m tall) was chosen on an east-facing slope of the valley at 1150 m elevation. Dominant woody species are *Quercus ilex*, *Phillyrea latifolia*, *Viburnum tinus*, and *Arbutus unedo*; *Pinus halepensis* and *P. pinaster* form negligible cover in much of the plot. Recent disturbances are restricted to two trails and scattered patches of planted pines. There is no record of fire in the area for the last 60 yr (J. Cuadros, *personal communication*).

The Serranía de Cazorla-Segura mountain range is one of the few enclaves in southern Spain with a diverse and relatively unaltered vertebrate fauna. There is no record to my knowledge of recent local avian extinctions.

Mean annual rainfall is 673 mm, with 65.8% falling in autumn–winter and 23.7% in spring. Average temperatures of the coldest and hottest months are 3.3° and 23.2°C, respectively (Montero and González 1974). Frosts commonly occur throughout the winter, and light snowfalls occur sporadically. Two seasons limit plant growth: a winter 4-mo (cold-limiting) and a summer 2.5-mo (drought-limiting) period (Montero and González 1974).

El Viso: the lowland site

The lowland site (3.5 ha) is on nearly level terrain near El Viso del Alcor (Sevilla province), at 100 m elevation, and is surrounded by arable land and citrus and olive tree groves. Natural vegetation on the fertile alluvial soils of the lowlands of the Guadalquivir River valley was virtually extirpated by man several centuries ago, although the site has remained mostly undisturbed for at least the last 50 yr. Vegetation is dominated by *Pistacia lentiscus*, *Quercus coccifera*, *Smilax aspera*, *Genista hirsuta*, and *Myrtus communis*, which forms an impenetrable scrub up to 2–2.5 m tall with scattered old *Arbutus unedo* “emergents” (up to 5 m tall). *Pinus pinea* is scattered over most of the plot, probably planted ≈50 yr ago.

Mean annual rainfall is 580 mm, with 63% falling in autumn–winter and 33% in spring. Average temperatures of the coldest and hottest months are 9.3° and 27.0° (Ministerio de Agricultura 1975). Winter is extremely mild, with an average of 5 d with frost (Linés Escardó 1970). The dry summer is the only limiting period to plant growth, lasting for ≈4 mo (Montero and González 1974). In the cold-stress vs. drought-stress gradient proposed by Mitrakos (1980) for mediterranean vegetation, El Viso site is close to the predominantly drought-stressed extreme, while Cazorla is nearer the predominantly cold-stressed one.

Many vertebrate species have been eliminated from this site through very long-term disturbance. Large birds (raptors, corvids, gamebirds) are totally absent. Abundance and diversity of small- and medium-sized passerines are, however, comparable to those found in extensive scrublands in the northern fringe of the Guadalquivir valley (C. M. Herrera, *personal observation*). The less restrictive habitat size requirements

of these birds, along with the great areal extent of olive tree groves, must have contributed to the maintenance of a rich passerine avifauna, particularly in the case of frugivores (Muñoz-Cobo and Purroy 1979, Santos 1981, Suárez and Muñoz-Cobo, *in press*). The assemblage of small avian frugivores inhabiting El Viso site is most likely the same as in the past on similar habitats (Herrera 1982*d*).

METHODS

Bird populations

The dense vegetation at the two study scrublands precluded censuses and direct observations on foraging behavior or fruit feeding without serious biases. Instead I relied on capturing birds with mist nets to study the bird component of the plant-frugivore system.

Nets were operated periodically at both study sites from October 1978 through February 1982. During the first study year, nets (standard 12.2-m black nets) were erected 2–5 d/mo at every site, except for May, July, and September in Cazorla. In subsequent years, netting was conducted more irregularly, but in all years, I trapped birds at both sites in the period October–December, the time of greatest fruit availability. Record was kept of the trapping effort (net-hours) in each netting session. Total effort over the entire study period was 2967 and 1804 net-hours, and nets were operated on a total of 43 and 40 d, in Cazorla and El Viso, respectively.

Trapped birds were kept in individual clean cloth bags until manipulation. Feces were obtained from many individuals by administration of 1% sodium chloride water solution (Moody 1970) and combined with previously produced samples in the bags. The resulting sample was collected on filter paper and air dried at ambient temperature. They were examined following the procedures described by Herrera (1981*b*) and Herrera and Jordano (1981). The relative contributions in volume made up by animal and vegetable matter were estimated to the nearest 10%. Among vegetable remains, fleshy fruits received special attention, and the percentage in volume made up by fruit remains other than seeds (usually fruit skins) was also estimated. Seeds and skins were identified to species by comparison with reference collections. For each plant species identified in the sample, the minimum number (or fraction) of fruits represented was estimated from the number of seeds (when present) and the amount of fruit skin, the largest figure being taken as representative for the sample. Potential limitations of these methods have been pointed out elsewhere (Herrera and Jordano 1981, Jordano and Herrera 1981).

Plant populations

Coverage of woody perennials was determined by line interception on 10 (Cazorla) and 15 (El Viso) 20-

m linear transects. The phenology of flowering and fruiting was recorded for all fruit-producing species at each site from October 1978 through February 1982. For El Viso, I had supplementary information starting on October 1977. The interval between visits to study sites was variable in Cazorla, ranging from 1 to 3 mo, while in El Viso it was usually <2 wk. Fruit abundance and its variation were studied in greater detail during the period October 1978–October 1979. Fruit availability during the abundance peak (October–December) was also determined in the highland site in all subsequent study years.

Fruit abundance was estimated by different methods at the two sites. In Cazorla, the vegetation is quite homogeneous and the important fruit-producing species have high dominance. Accurate estimates of fruit abundance could be obtained by sampling a relatively small area. The infrequency of visits to this site precluded a close monitoring of fruiting based on counts of marked plants. I assessed fruit abundance by counting all fruits borne on plants within 10 permanent rectangular plots (20 × 1.25 m). Counts were conducted monthly during the period October 1978–April 1979, bimonthly from October 1981 to April 1982, and in November 1979 and 1980.

Individuals from the seven most important fruit-producing species were marked (10–20 per species) at El Viso at the start of the study. Among dioecious species only female plants were chosen. Height and the area covered were determined for all marked shrubs. Within each marked plant, stems were marked, and the fraction of the whole plant volume they represented collectively was estimated. From October 1978 through October 1979, I counted (biweekly or more often) ripe and unripe fruits on marked stems of all tagged individuals. Damaged fruits were counted, as well as any fallen fruit beneath marked stems.

By combining information on within-species seasonal patterns of fruit abundance derived from the counts, relative dominance, within-plant fruit density (=fruits/shrub vertical projection area), and the frequency of fruit-bearing individuals in the population, I was able to produce estimates of the density of ripe fruits for any time in the season for the seven most important fruit-producing species in El Viso. Within-shrub density of ripe fruits was measured in Cazorla for six species, including the most abundant ones. In El Viso, supplementary information from four species was obtained in addition to that from the seven regularly counted ones.

Ripe fruits were collected to prepare pulp samples for chemical analyses and to determine fruit characteristics (fruit transversal diameter, wet mass of whole fruit, percent water content, dry mass of seeds and pulp, and number of seeds per fruit). Methods used and descriptive variables considered have been discussed in detail elsewhere (Herrera 1981*a, b, c*). Results of chemical analyses of pulp included ash, lipid, protein (total nitrogen × 6.25), and fiber content.

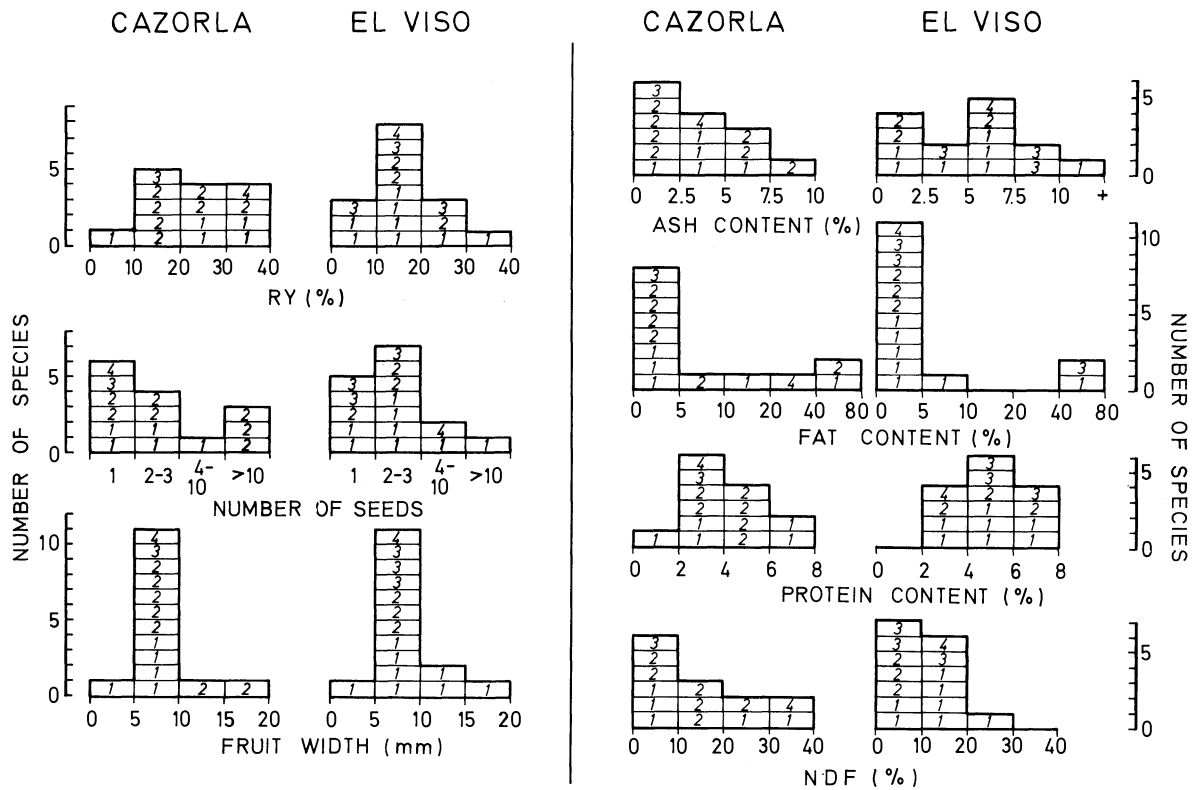


FIG. 1. Frequency distributions of characteristics of ripe fruits at the two study sites. Each individual box represents a single species, and the enclosed number denotes its average density in the habitat at its availability peak (in the period October 1978–September 1979), coded as follows: 1, <0.1 fruits/m²; 2, 0.1–1 fruits/m²; 3, 2–10 fruits/m²; 4, >10 fruits/m². All percentages are on a dry-mass basis (note geometrical scale in fat content frequency distributions). Fruit width refers to transverse diameter, NDF denotes neutral-detergent fiber, and RY is relative dry matter yield (=dry mass of pulp per fruit/fresh mass of whole fruit).

THE PLANTS

Fruit-producing plant assemblages

Fruit-producing species represent a very prominent fraction of woody plants in the study scrublands in terms of cover (76.5 and 56.6% of total in Cazorla and El Viso, respectively) and number of species (65.5 and 48.6% of woody species). Most of these rely entirely on birds for seed dispersal (63.2 and 76.5%); very few either depend exclusively on mammals (10.5 and 5.9%) or have both groups as seed vectors. Eight of the 19 fruit-producing species at the highland site are deciduous, whereas all but 1 of the 17 species at the lowland locality are evergreen. Fruit-producing plants are mainly shrubs and small trees. Herbs are scarce, and the single species in this group (*Tamus communis*) is rare in both localities. Species dispersed exclusively by mammals and three uncommon bird-dispersed species (*Asparagus acutifolius*, *Crataegus monogyna*, and *Tamus communis* at Cazorla) will not be considered hereafter (see Table 1 for lists of species at both sites).

Most species produce typical berries or drupes; *Ru-*

bus ulmifolius (polydrupe) and *Rosa canina* (pseudocarp resulting from the enlarged hypanthium) are exceptions. There are no appreciable differences between the two study sites in the overall fruit characteristics of bird-dispersed species assemblages (Fig. 1). Most fruits are small (5–10 mm across), one or few seeded, and display a broad range (9–38%) of relative dry-matter yield (RY, dry mass of pulp potentially obtainable per mass unit of fresh whole fruit [Herrera 1981a, 1982b]). Substantial interspecies variation exists at both sites with regard to the chemical features of the pulp. Ash content ranges between 1 and 13% (dry-mass basis), with a fairly homogeneous distribution of species over this range. The fruit pulp of most species has a low lipid content (<5%), although several species show remarkably higher figures (up to 58%). *Pistacia lentiscus*, *Pistacia terebinthus*, *Viburnum tinus*, and *Olea europaea* produce fruit with lipid content of the pulp >20%. At least two of these species coexist locally at both study sites (Table 1). Protein content of the fruit pulp is low (2–8%). Neutral-detergent fiber is usually below 20%, although several species show much higher values. Pulp constituents (ash, lipids, protein, fiber)

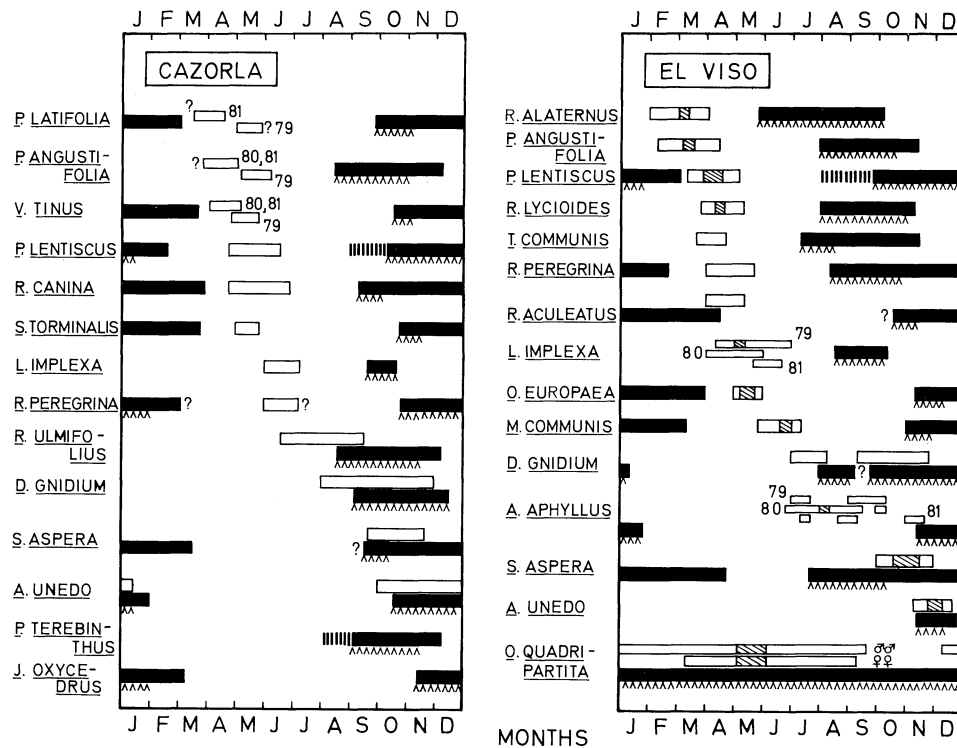


FIG. 2. Flowering and fruiting phenology of the most significant bird-dispersed plant species at the two study sites, 1978–1982. Unfilled bars refer to the flowering season ($\geq 10\%$ of plants in flower; hatched portions in the graph for El Viso denote distinct blooming peaks, $\geq 75\%$ of plants in flower). Filled bars indicate the period during which some ripe, apparently undamaged fruits may be found on the plants. Carets (^^^) mark the ripening period (unripe and ripe fruits coexisting in the population). Several bars have been drawn for a species in the few cases where appreciable variation between sexes or years occurred. Otherwise, bars extend over the most frequently observed periods (1978–1982). For *Smilax aspera* and *Arbutus unedo*, which take nearly 1 yr to mature fruits after flowering, the fruiting periods depicted would correspond to the maturation of the previous year's crop. Fruits of the two *Pistacia* species having hard-coated seeds are consumed by frugivores well before complete pericarp maturity; hence, the broken bars to the left of the actual ripening period. No accurate flowering dates are available for *J. oxycedrus* and *P. terebinthus*.

tend to be randomly intermixed across species. No significant correlation was found for any pair of them, either taking the two sets of locally coexisting species separately, or for the combined species sample.

Phenology of bird-dispersed plants

Most species flower in spring and bear ripe fruits in summer, autumn, or winter (Figs. 2 and 3). Flowering and fruit maturation periods overlap in five species. In three of these (*Osyris quadripartita*, *Smilax aspera*, and *Arbutus unedo*), fruits ripening during the flowering period are the product of the previous year's flowers. The interval between flowering and fruiting seasons thus varies widely among species, ranging from 1 to 12 mo. Except for *O. quadripartita*, which has a fruiting period encompassing the entire year, all species have definite periods of fruit availability ranging from 1 to 9 mo. On the whole, periods of availability of ripe fruits do not closely match ripening seasons, since persistence of ripe fruits on the plants after maturation

varies greatly among species. No substantial changes in overall phenological patterns were observed during the 4-yr study period.

Ripening periods are much more clumped than flowering seasons (Figs. 2 and 3), and most species tend to mature their fruits in autumn and late summer, regardless of flowering time. As a consequence, flowering and fruiting overlap in most species that flower in late summer and autumn. This pattern suggests that the possibilities for temporal staggering of fruiting have been more restricted than for flowering in the habitats studied.

Fruits are unavailable from April to August at the highland locality, while they are available in the lowland site year round. The proportion of species having ripe fruits available per half-month period is much less variable in the lowlands ($\bar{x} = 41.9\%$, $cv = 51.6\%$) than in the highlands ($\bar{x} = 36.3\%$, $cv = 95.9\%$). This differential seasonality persists when only the periods of active fruit maturation are considered (Fig. 3). The

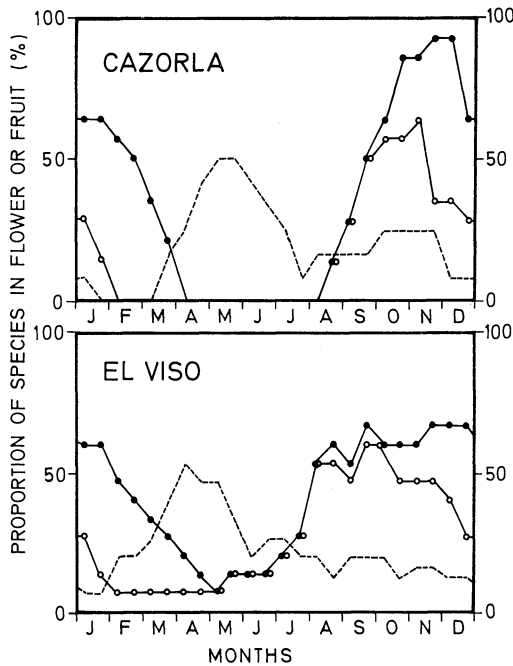


FIG. 3. Seasonality in flowering (broken line) and fruiting (unbroken line) of bird-dispersed plant assemblages at the two mediterranean scrublands. The percent of major species (those in Fig. 2) flowering, ripening fruits (○), and bearing undamaged ripe fruits (●), per half-month period are represented.

absence from the highland site of spring- and early-summer-fruiting species contributes to its greater seasonality, but there is also there an independent trend towards greater interspecific fruiting synchrony. Considering only the seven shared species, the two sites still differ in the seasonality of fruit diversity ($cv = 79.0$ and 105.1% for El Viso and Cazorla, respectively).

Dominant species mature fruits during the local peak

of diversity in fruit production, while those fruiting early in the season, well before the peak, are generally sparse or rare species. *Arbutus unedo*, *Phillyrea latifolia*, and *Viburnum tinus*, accounting for 70.0% of fruit-producing plant cover in Cazorla, mature fruits in the middle of the local peak season. The three earliest-maturing species (*Phillyrea angustifolia*, *Rubus ulmifolius*, *Daphne gnidium*) together account for only 13.2% of fruit-producing plant cover. In El Viso, the fruiting periods of the three commonest species (*Pistacia lentiscus*, *Myrtus communis*, *Smilax aspera*), totalling 62.9% of fruit-producing cover, spread over the longer peak season. The three earliest-maturing species (*Rhamnus alaternus*, *Tamus communis*, *D. gnidium*) account together for <2% of fruit-producing plant cover.

Patterns of fruit production

Temporal pattern of fruit ripening was investigated in seven species at El Viso on the basis of fruit counts on marked plants. Fruiting seasons of these species extend over most of the year; thus, they are adequate for examining possible variations in ripening patterns associated with time of fruit maturation. Results are summarized in Fig. 4. The slope of curves is indicative of the degree of interindividual synchrony in fruit production; steeper curves denote greater synchrony levels. Horizontal separation of the 25 and 75% percentile curves is related to the rate of fruit maturation, which is faster the closer the lines are. Curves are based on data from 61 individual plants and ≈ 8400 fruits. Sample sizes were initially much larger, but data from many marked individuals had to be eventually discarded owing to vandalism of the marked stems and the plastic tags, or because the marked plants did not fruit in the study period.

A broad range of ripening rates and interindividual synchrony levels is represented in the fairly restricted species sample studied. Except for *Myrtus communis*, ripening seasons are fairly long for all species. Both

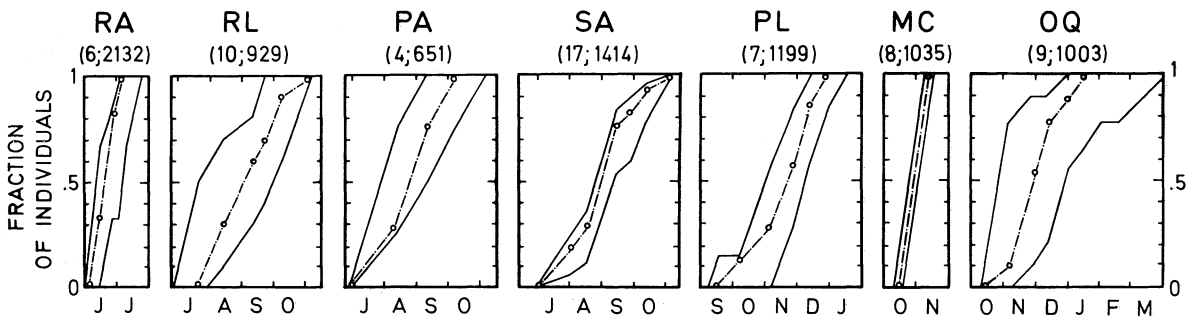


FIG. 4. Ripening patterns of seven selected species at El Viso in the period October 1978–October 1979. Plotted for each species are the fraction of individuals which have matured 25 (left continuous line), 50 (central, broken line), and 75% (right continuous line) of their crops. Figures in parentheses are sample sizes on which the curves are based (number of individuals; number of fruits): RA, *Rhamnus alaternus*; RL, *Rhamnus lycioides*; PA, *Phillyrea angustifolia*; SA, *Smilax aspera*; PL, *Pistacia lentiscus*; MC, *Myrtus communis*; OQ, *Osyris quadripartita*.

TABLE 1. Mean number of ripe fruits/m² each month in the standing crops at the two study sites from October 1978 to September 1979. Excluded are data for species with <0.1 and <0.2 ripe fruits/m² in all months at Cazorla and El Viso, respectively.

Site	Plant species†	% cover	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Cazorla														
	<i>Arbutus unedo</i>	15.9		0.03	0.20									
	<i>Daphne gnidium</i>	1.3	0.02	0.10									...‡	...‡
	<i>Lonicera implexa</i>	0.9	0.22	0.02										...‡
	<i>Phillyrea angustifolia</i>	1.1	0.34	0.18	0.12									...‡
	<i>Phillyrea latifolia</i>	19.1	1.34	1.13	0.46	0.02								
	<i>Pistacia lentiscus</i>	2.3	0.18	0.25	0.18	0.12	0.01							
	<i>Rubia peregrina</i>	2.1		0.06	0.47	0.12	0.02	...‡						
	<i>Rubus ulmifolius</i>	7.7	0.60	0.16									...‡	...‡
	<i>Rosa canina</i>	0.8		0.26	0.06	0.04	0.04	...‡						
	<i>Smilax aspera</i>	4.0	0.34	0.67	0.36	0.35	0.31	...‡						...‡
	<i>Viburnum tinus</i>	18.5	1.97	10.84	9.54	3.84	0.01							
	Total		5.01	13.70	11.39	4.49	0.39	...‡					...‡	...‡
El Viso														
	<i>Myrtus communis</i>	8.2		10.52	9.29	4.25	1.53							
	<i>Osyris quadripartita</i>	6.1	0.87	2.16	2.40	1.67	0.61	0.28	0.23	0.70	0.34	0.09	0.20	0.38
	<i>Phillyrea angustifolia</i>	6.1	0.13	0.03								0.03	0.11	0.47
	<i>Pistacia lentiscus</i> §	18.0												
	Black fruit type		0.47	4.10	4.87	0.33	0.07							0.08
	Red fruit type		52.20	29.76	15.66	7.16	1.08	0.44	0.13			13.61	43.53	79.81
	<i>Rhamnus alaternus</i>	0.5	0.01							0.01	0.23	0.06	0.01	0.01
	<i>Rhamnus lycioides</i>	1.7	0.31	0.16	0.07							0.19	0.20	0.20
	<i>Smilax aspera</i>	9.4	3.62	3.10	2.49	1.98	1.38	0.45	0.04			0.32	0.97	2.91
	Total													
	Ripe fruits		5.41	20.07	19.12	8.23	3.59	0.73	0.27	0.71	0.57	0.69	1.49	4.05
	Including "red-type" fruits of <i>Pistacia lentiscus</i>		57.61	49.83	34.78	15.39	4.67	1.17	0.40	0.71	0.57	14.30	45.02	83.86

† Additional fruit-producing species (percent cover in parentheses; species dispersed by mammals marked with asterisk); Cazorla: *Asparagus acutifolius* (<0.1), *Crataegus monogyna* (<0.1), *Juniperus oxycedrus* (0.8), *Malus sylvestris** (<0.1), *Pistacia terebinthus* (2.0), *Sorbus domestica** (<0.1), *Sorbus tominalis* (<0.1), *Tamus communis* (<0.1). El Viso: *Arbutus unedo* (0.7), *Asparagus acutifolius* (<0.1), *Asparagus aphyllus* (0.9), *Chamaerops humilis** (1.4), *Daphne gnidium* (0.5), *Lonicera implexa* (0.4), *Olea europaea* var. *syvestris* (2.5), *Rubia peregrina* (0.1), *Ruscus aculeatus* (<0.1), *Tamus communis* (<0.1).

‡ ... indicates some ripe fruits present, not quantified.

§ Immature, red-colored fruits are ordinarily eaten by frugivores.

the early-summer-fruiting *Rhamnus alaternus* and the autumn-fruiting *Myrtus communis* ripen fruits quickly and synchronously. The other species display moderate levels of interindividual synchrony, regardless of the location of their ripening seasons on the seasonal gradient. Maturation rates are also apparently unrelated to fruiting time. No obvious relationship exists between fruiting time and fruit production patterns in these species.

Abundance of fruits

Fruit abundance reached remarkably high levels at both sites (Table 1). At Cazorla, average fruit density ranged between 4.5 and 13.7 ripe fruits/m² (rf/m² hereafter) in the period October 1978–January 1979, declining to 0.4 rf/m² in late February 1979, all species combined. Figures for El Viso in the same period ranged between 3.6 and 20.1 rf/m². Over the entire year, average fruit density at this site ranged from 0.4 (April) to 20.1 rf/m² (November). These estimates rep-

resent average densities for the habitat, not within-plant densities, and lead to projected figures of nearly 137 000 and 201 000 ripe fruits/ha available at a given time during the seasonal peaks of abundance in Cazorla and El Viso, respectively. If "unripe" red fruits of *P. lentiscus* (which are also eaten by frugivores) are considered, the projected figure for El Viso rises to ≈840 000 fruits/ha. These estimates are for standing crops of fruits and are well below actual production figures (standing crops equal production minus consumption by frugivores).

Fruit abundance fluctuates seasonally much more strongly than fruit species richness. Species fruiting at the local diversity peak tend to be relatively more abundant in the plant community than those fruiting outside the peak, as stated previously. On the other hand, a significant positive correlation exists between species dominance and average within-plant density of ripe fruits (evaluated at the species' peak of availability; $r_s = 0.777$, $N = 11$ species, $P < .01$; $r_s =$

0.942, $N = 6$ species, $P < .01$; El Viso and Cazorla, respectively). The relation also apparently holds within species across sites; *Smilax aspera*, *Arbutus unedo* and *Pistacia lentiscus* bear more fruits per unit basal area in the locality where they have greater relative cover. This suggests that the relative success of a species at a site (percent cover) and its fruit production intensity are closely linked.

Important year-to-year variation in fruit abundance occurs in the highland site. Fruit counts in November, the month of maximum fruit abundance, yielded densities of 12.5 (1978), 5.6 (1979), 42.5 (1980), and 27.2 (1981) rf/m², all species combined, hence an eightfold variation. Some of the most significant species displayed substantial variation in fruit abundance from 1978 through 1981: *Viburnum tinus* (10.2, 0, 40.5, and 0.6 rf/m²), *Phillyrea latifolia* (0.8, 0, 0, and 24.0 rf/m²), *Pistacia lentiscus* (0.2, 4.9, 0.6, and 1.4 rf/m²). Absence of fruit crops of the two former species in some years was due to substantially reduced or absent flowering. Supra-annual patterns of this magnitude did not occur in El Viso, where all species fruited every year with only minor variations in overall fruit abundance. At this site these variations involved species having low overall significance in the plant community (e.g., *Rhamnus alaternus*).

No consistent, overall relationship exists between fruit abundance and fruit characteristics (Fig. 1). Each site supports one species with lipid content of pulp >20% and a fruit density >1 rf/m² sometime in the year (*V. tinus*, 21.6% lipids, and *P. lentiscus*, 58.8%, in Cazorla and El Viso, respectively). These species are in the upper local extremes of both abundance and quality (measured by lipid content). Commonest fruits in the lowlands have pulps richer in protein and minerals, and lower in fiber, than commonest fruits in the highlands (Fig. 1). These data suggest that the lowlands provide a more predictable food supply, and that the average fruit is also more nutritious and presumably more digestible than in the highland habitat.

Correlates of pulp and fruit quality

Correlations were run between variables characterizing pulp quality on one side (ash, protein, and lipid content) and variables relating to nonchemical fruit features (seed mass per fruit, individual seed mass, mass of pulp per fruit) and fruit-ripening patterns (ripening rate, degree of interindividual ripening synchrony, and crop size/plant basal area) on the other side. Ripening rate was inversely measured by the time taken by all marked individuals to mature their crops (Fig. 4). Interindividual synchrony was measured by the interval between the times in which the earliest and latest individuals have matured 50% of their crops. Crop size was the total number of ripe fruits produced by an individual plant over the entire ripening period. The latter three variables were available only for El Viso species in Fig. 4.

All the correlation coefficients obtained ($N = 18$) were statistically nonsignificant ($P > .05$), and 8 of them had an associated $P \geq .80$. The probability of obtaining by chance alone as many or more coefficients with $P \geq .80$ is 0.02 (binomial test). Results thus firmly point to the conclusion that fruit quality and the other features considered covary randomly in the sample of species studied.

Seasonal patterns in fruit quality documented previously on a regional scale by Herrera (1982b) also occur locally in both Cazorla and El Viso. Average lipid content of pulp increases from summer- through winter-ripening species, and water content follows the opposite trend. Protein content of pulp does not vary significantly among species ripening fruit at different times, and average dry-matter yield (RY) increases significantly from summer- through winter-fruited species. The highest lipid profitabilities (= RY \times lipid content of pulp, dry-mass basis [Herrera 1982b]) are found among autumn- (*Pistacia terebinthus*) and, principally, winter-fruited (*Viburnum tinus*, *Olea europaea*, *Pistacia lentiscus*) species, although many autumn- and winter-fruited species have lipid profitability values as low as those of summer-fruited ones.

THE BIRDS

Only passerine species will be considered throughout. They have provided the bulk of captures (99.6 and 96.7% of total in Cazorla and El Viso, respectively), and previous studies in the region have failed to detect any role of nonpasserines in avian frugivorous assemblages (Herrera and Jordano 1981, Jordano 1982, C. M. Herrera, *personal observation*).

Frequency and types of frugivory

In all, 1014 passerine birds were trapped and 795 fecal collections were analyzed for Cazorla, and 1700 birds and 1096 fecal samples for El Viso, in the period October 1978–February 1982 (see Appendix).

The percentage of fecal samples containing fruit remains was calculated for the period of fruit availability in the habitats (August–April in Cazorla, the entire year in El Viso). These figures indicate the frequency with which fruits are fed upon ("frequency of frugivory," FF hereafter). The proportion of "frugivorous" species (FF > 0) is similarly high at both sites (66.7 and 65.5% of total species in Cazorla and El Viso, respectively).

The broad range of FF values shown by frugivorous species (Table 2) reveals the existence of a continuum in the degree of frugivory rather than a sharp distinction between frugivores and "nonfrugivores" (FF = 0). FF values tend to be higher in Cazorla than in El Viso, but the difference is not significant ($P = .18$, Mann-Whitney U test). The species displaying the greatest degrees of frugivory (as estimated with FF) are *Erithacus rubecula* (90.0 and 83.9%, Cazorla and El Viso, respectively), *Sylvia atricapilla* (100 and

TABLE 2. Residency status and frequency of frugivory (based on percent occurrence of fruit in fecal samples) for fruit predators and seed dispersers. Frequency of frugivory (FF) values are computed only for the period when fruits are available (August–April at Cazorla, the entire year at El Viso). Sample sizes are shown in the Appendix.

	Cazorla		El Viso	
	FF	Residency status*	FF	Residency status*
Fruit predators†				
<i>Aegithalos caudatus</i> (P)	54.3	R		
<i>Carduelis chloris</i> (S)	60.0	R	33.3	R
<i>Coccothraustes coccothraustes</i> (S)	50.0	W		
<i>Fringilla coelebs</i> (S)	71.4	R		
<i>Parus ater</i> (S, P)	18.2	R		
<i>Parus caeruleus</i> (P)	58.2	R	16.7	R
<i>Parus cristatus</i> (P)	64.5	R		
<i>Parus major</i> (S, P)	43.5	R	33.3	R
<i>Phylloscopus collybita</i> (P)			2.1	W
<i>Prunella modularis</i> (S, P)	30.0	W	16.7	W
<i>Pyrrhula pyrrhula</i> (S, P)	100.	W		
<i>Regulus ignicapillus</i> (P)	6.9	R		
Seed dispersers				
<i>Erithacus rubecula</i>	90.0	(R), W	83.9	W
<i>Ficedula hypoleuca</i>			35.7	FM
<i>Hippolais polyglotta</i>			7.1	SM, FM
<i>Luscinia megarhynchos</i>			8.3	SM, (B), FM
<i>Phoenicurus ochruros</i>			50.0	W
<i>Phoenicurus phoenicurus</i>			73.3	SM, FM
<i>Saxicola torquata</i>			50.0	W
<i>Sylvia atricapilla</i>	100.	(R), W	98.7	(SM), (FM), W
<i>Sylvia borin</i>			88.9	(SM), FM
<i>Sylvia cantillans</i>			25.0	SM, FM
<i>Sylvia communis</i>			88.2	(SM), FM
<i>Sylvia melanocephala</i>	82.4	R, W	79.1	(R), W
<i>Turdus merula</i>	100.	R	86.0	R, (W)
<i>Turdus philomelos</i>	100.	W	66.7	W

* B, breeding season immigrant; W, overwintering; SM, spring migrant; FM, fall migrant; R, year-round resident. Species that have several populations differing in residency status coexisting locally have been included in more than one category (the less significant ones are shown in parentheses).

† Part of fruit eaten by fruit predators: S, seeds; P, pulp.

98.7%), *Sylvia melanocephala* (82.4 and 79.1%), *Sylvia borin* (88.9%, El Viso), *Sylvia communis* (88.2%, El Viso) and *Turdus merula* (100 and 86.0%) (Table 2). These birds include fruits almost continuously in their diets while inhabiting the scrublands.

Avian frugivores fall into two neatly defined categories, namely "legitimate seed dispersers" and "fruit predators" (e.g., Snow 1971). The former ingest whole fruits and either regurgitate or defecate the seeds intact. "Fruit predators" feed on either pulp or seeds alone, and when eating pulp and seeds together damage the latter either in the gut or prior to swallowing. Frugivores at both study sites were classed into one or another of these categories on the basis of information derived from the examination of fecal samples or observations on fruit-feeding behavior (Table 2). Although a sharp distinction generally exists between these groups in the study habitats, a few species are legitimate dispersers of some plants and fruit predators of others (e.g., some *Parus* spp.). These were assigned by considering the predominant role they play in their interaction with the array of fruit-producing species in the habitat.

Seed dispersers (eight genera in the Muscicapidae) are taxonomically much less diverse at the familial level than are predators (nine genera, five families). With the exception of *Phylloscopus collybita*, all species of fruit predators present in El Viso occur also in Cazorla, while the reverse situation holds for dispersers, for which the Cazorla assemblage is a very impoverished version of that occurring in El Viso (Table 2). Most fruit predators are resident (66%), while dispersers are mostly migrant or overwintering species (80%). Spring and fall migrant frugivores are entirely absent from the highland locality, whereas they are prominent in the lowland site (Table 2).

Fruit predators represent 68.8% of species in Cazorla, but only 26.3% in El Viso (Table 2). Local assemblages of avian frugivores are thus dominated by species of dispersers in El Viso and fruit predators in Cazorla. Furthermore, fruit predators as a whole tend to eat fruit more often in Cazorla than in El Viso ($P < .05$, Mann-Whitney U test). The four species that are shared by both sites also eat fruits most often in Cazorla when considered individually. Predators thus play a more prominent role in the highland habitat, where

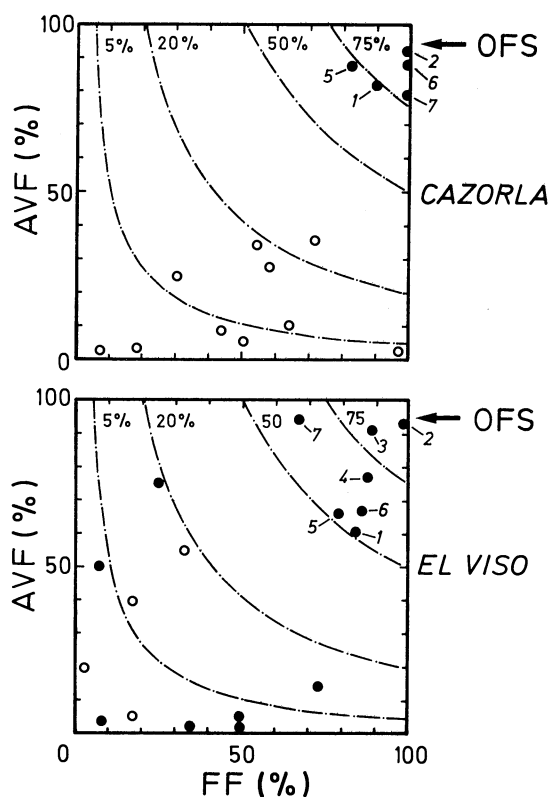


FIG. 5. Incidence of fruits in the diet of frugivorous birds at both study sites. Average volume represented in feces by fruit remains (AVF) is plotted against the frequency of occurrence of fruit in fecal samples (FF). Each symbol refers to a single species (\circ = fruit predators; \bullet = seed dispersers). AVF could not be reliably determined for the feces of *Carduelis chloris*, and this fruit predator has been excluded. Isolines have been drawn for various levels of overall fruit significance (OFS) in the diet (the product $AVF \times FF$, see text). The most significant frugivores are coded as follows: 1, *Erithacus rubecula*; 2, *Sylvia atricapilla*; 3, *Sylvia borin*; 4, *Sylvia communis*; 5, *Sylvia melanocephala*; 6, *Turdus merula*; 7, *Turdus philomelos*.

they are most numerous and most assiduous at frugivory.

Patterns of differential dependence on fruit

Average volume represented by fruit remains (other than seeds) in samples with fruit present (AVF hereafter) was computed for all frugivorous species (Fig. 5). This variable probably underestimates the importance of fruit in relation to that of insects (Jordano and Herrera 1981) but is appropriate for comparative purposes (Herrera and Jordano 1981, Jordano 1981).

At both sites, there is a distinct group of species that simultaneously display very high AVF and FF values, indicating that they feed on fruit almost continuously and that this food type is also dominant in their diets. All of these species are legitimate seed

dispersers and, except for *Sylvia borin* and *S. communis* (migrants restricted to El Viso), are shared by both localities (*Sylvia atricapilla*, *S. melanocephala*, *Erithacus rubecula*, *Turdus merula*, *T. philomelos*). In Cazorla all dispersers fall into this "extreme frugivory" group, but in El Viso there is a loose group of disperser species which have either low AVF, or low FF, or both, indicative of a low overall significance of fruit in the diet. These include *Ficedula hypoleuca*, *Phoenicurus phoenicurus*, *Luscinia megarhynchos*, and *Saxicola torquata*. Fruit predators at both sites tend to display low AVF values, regardless of their frequency of frugivory (FF), suggesting that even on occasions in which they eat fruit, the latter never is an important element in the diet.

The product $AVF \times FF$ for an individual species should be considered as a rough estimate of the overall fruit significance in the diet at the population level (OFS hereafter). Frugivorous species fall into two neatly differentiated groups with regard to this variable: a reduced set of major frugivores, with $OFS > 50\%$, all of which are seed dispersers, and a larger group of minor frugivores (both dispersers and predators) displaying OFS values $< 20\%$ (Fig. 5).

Patterns of bird abundance

Total bird abundance, as estimated with mist net captures, is about three times higher in the lowland site (Fig. 6). There are no reasons to suspect that the capture efficiency of nets or the behavior of birds with respect to them were unequal at the two localities; hence, differences in mist nest yield should be attributed to differences in local bird abundance. Monthly variation of total abundance is similar at both sites, with a marked peak in November–December and a minimum in spring and early summer.

In absolute terms, numbers of individuals of non-frugivorous species are greatest in spring and summer, while those of frugivorous species reach their maximum in autumn–winter. Seed dispersers and fruit predators are similar in their seasonal patterns of abundance. *Erithacus rubecula* and *Sylvia atricapilla* are most directly responsible for the distinct winter peak in capture rates at both sites. These two dispersers are the locally most abundant birds from mid-October through early March. In El Viso, the abundance of dispersers in August–October is mainly due to fall migrants (mainly *Sylvia borin* and *S. communis*).

Frugivorous species comprise the vast majority of captures at both sites, but they are proportionally most important in El Viso. Dispersers largely outnumber fruit predators at the lowland scrub, and the two groups have roughly similar abundance in Cazorla (Fig. 6).

Autumn–winter bird abundance fluctuated at both sites over the years (Table 3). Interannual variation was roughly similar at both sites for nonfrugivores and fruit predators, but in the case of dispersers it was

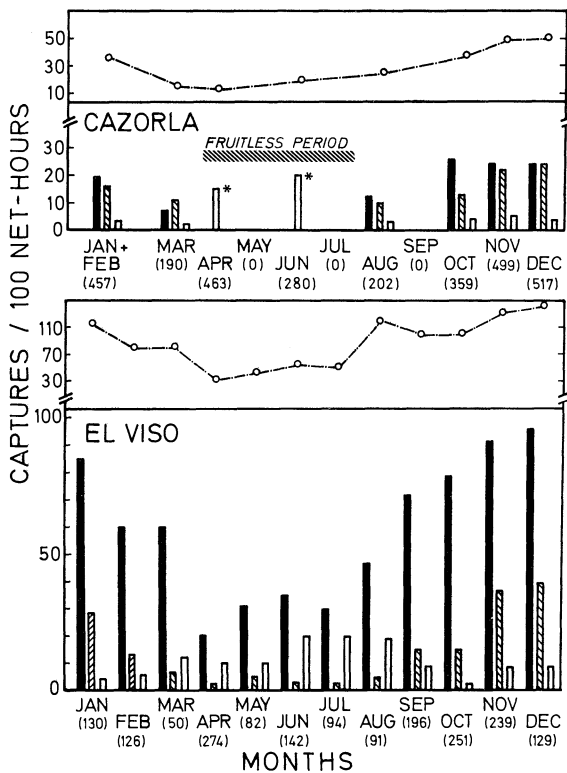


FIG. 6. Monthly variation in the abundance of passerine birds at the two study sites, as estimated by mist-net captures, based on combined data for the period October–February 1982. Figures in parentheses indicate the total netting effort for every month (net-hours). Upper graphs for each locality (—○—) represent the variation in total captures (note different vertical scales for Cazorla and El Viso). Bar graphs illustrate monthly variation in the abundance of legitimate seed dispersers (filled bars), fruit predators (hatched bars), and nonfrugivorous species (open bars). The extent of the local fruitless season in Cazorla has been indicated; during this period, all captures have been combined into a single class (bars marked with asterisks), regardless of the frugivory categories the various species belong to.

substantially lower in El Viso. In Cazorla, the seed-disperser group had the highest year-to-year variability in abundance, while in El Viso it was the least variable one.

Local patterns of frugivory pressure

The frugivory pressure exerted by a single bird species on the local assemblage of fruit-producing plants is proportional to the product of its local abundance times its particular OFS value. I computed for each species the product of its OFS value (= AVF × FF) and the percent of total captures the species represented. The resulting figure was then expressed as a percentage of the total sum for all locally coexisting frugivorous species and used as an arbitrary index of relative frugivory pressure.

At both sites a reduced nucleus of species accounts

TABLE 3. Interannual variation in bird abundance (as estimated with mist-net yields) during the period October–February, the period with highest fruit availability (Table 1). Relative variation = difference between the smallest and largest values expressed as a percentage of the latter.

Site	Season	Captures/100 net-hours		
		Non-frugivores	Fruit predators	Seed dispersers
Cazorla	1978–1979	3.4	18.4	11.3
	1979–1980	3.3	20.8	15.8
	1980–1981	5.9	32.7	32.7
	1981–1982	2.2	13.2	47.1
	Relative variation	62.7	59.6	76.0
El Viso	1978–1979	7.5	21.5	81.7
	1979–1980	3.6	12.4	65.0
	1980–1981	3.1	26.5	114.3
	1981–1982	1.9	30.8	80.8
	Relative variation	74.7	59.7	43.1

for the vast majority of frugivory pressure, whereas the bulk of species contribute little to total frugivory. Three species account collectively for 85 and 84% of the total frugivory pressure in El Viso (*Sylvia atricapilla*, *S. melanocephala*, *Erithacus rubecula*, mentioned in decreasing order of frugivory pressure) and Cazorla (*Erithacus rubecula*, *Sylvia atricapilla*, *Turdus merula*), respectively. Species contributing the greatest frugivory occur in both habitats and are legitimate dispersers. Fruit predators exert a weak frugivory pressure (<10%) at both sites.

SEED DISPERSAL

Fruit removal success

Virtually the entire crops (>80% of fruits) of most large-sized fruit species remained undispersed by birds in all study seasons (*Ruscus aculeatus*, *Juniperus oxycedrus*, *Rosa canina*, *Sorbus torminalis*; average fruit transverse diameter, 11.9, 9.7, 9.5 and 9.8 mm, respectively). All these species have fruit diameters larger than the gape width of principal dispersers (range 7.1–8.6 mm, *Sylvia melanocephala* and *borin*, respectively). Exceptions to this pattern are *Arbutus unedo* (17.1 mm average cross diameter), whose very soft ripe fruits are invariably handled by pecking at the pulp, and *Rubus ulmifolius* (14.6 mm), whose large polydrupes are seen by birds as a composite of small fruitlets (Jordano 1982). Gape width of dispersers thus seems to set a rigid limit on the upper size of fruits that they can ingest whole, and plant species with fruits larger than the local modal class of disperser gape width are at considerable disadvantage.

Estimates of fruit removal success were obtained for the seven most important species in El Viso during the season 1978–1979 on the basis of fruit counts. All

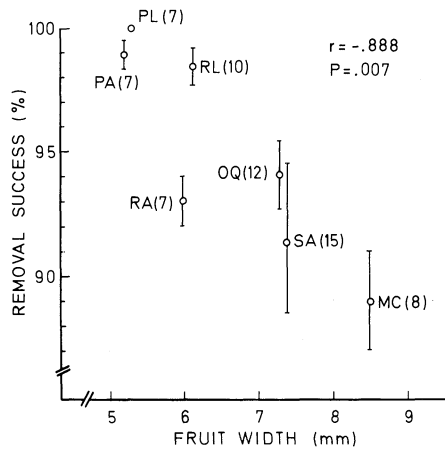


FIG. 7. Decline of average fruit removal success (fraction of total ripe fruits removed) with increasing fruit transverse diameter in a sample of species from El Viso, 1978–1979. Vertical bars extend over ± 1 SE around the mean, and sample sizes (number of plants) are shown in parentheses. Species are coded as follows: MC, *Myrtus communis*; OQ, *Osyris quadripartita*; PA, *Phillyrea angustifolia*; PL, *Pistacia lentiscus*; RL, *Rhamnus lycioides*; RA, *Rhamnus alaternus*; SA, *Smilax aspera*.

species considered had extremely high average removal rates, falling within a narrow range (89–100% of fruits produced, Fig. 7). The percentage of fruit crop removed by birds declines significantly with increasing fruit diameter (Fig. 7). Small variations in fruit width thus lead to measurable interspecific differences in dispersal success even among those plants having fruits below the upper size limit acceptable to dispersers in function of gape width.

I failed to detect any unequivocal relation between removal success and either fruit quality, fruiting time, ripening rate, or within-plant fruit density at the peak of availability.

Fruit consumption patterns of seed dispersers

In this and the next section I deal with legitimate seed dispersers accounting for most frugivory pressure at each site. Four species are treated for Cazorla (*Erithacus rubecula*, *Sylvia atricapilla*, *Sylvia melanocephala*, *Turdus merula*; 87.4% frugivory pressure altogether) and six for El Viso (the same plus *Sylvia borin* and *Sylvia communis*; 98.1%).

El Viso.—Preliminary analyses failed to reveal significant interannual variation in the composition of fruit food of the six species considered; thus, data from all years have been combined (Table 4). Only plant species present in the study plot have been considered. Fruits from four additional species growing on disturbed areas nearby appeared sometimes in the feces, but their overall importance was usually negligible. Fruits of *Ruscus aculeatus* were never detected in fecal sam-

ples. Dispersers of this plant, if any, are as yet unknown to me.

Interspecific differences in composition and diversity of fruit food are partly due to the birds' different seasonal patterns of habitat occupancy. Fall migrants (*S. borin*, *S. communis*), present from late August to early October, rely most heavily on fruits of *Phillyrea angustifolia*, *Pistacia lentiscus*, *Rhamnus lycioides*, and *Smilax aspera*, and their diets display high overall diversity (Table 4). The pattern for *Turdus merula* is closely similar; this resident species is most abundant in late summer and early autumn. Hence Table 4 mainly reflects its diet during that period. Overwintering species (*E. rubecula*, *S. atricapilla*), along with the resident *S. melanocephala* (most abundant and frugivorous in autumn–winter), concentrate on *P. lentiscus* fruits, and diversity of their diets is low. These data indicate that when the nutritive value (lipids) and relative fruit abundance differ less markedly among plant species (summer and early autumn), bird populations tend to show more equitable fruit diets. When differences in food value and fruit abundance of the various species become most pronounced (late autumn, winter), dispersers concentrate on the most abundant and rewarding *P. lentiscus* fruits.

Individuals of most species usually ingest the fruit of several species over very short time periods (Fig. 8). Up to eight species have been recorded in a single fecal sample of *S. atricapilla*. Number of fruit species recorded in fecal samples is a conservative estimate of the actual variety of fruits taken by individuals over a period of, say, several hours, since gut passage times of these species are in the order of 30–50 min (C. M. Herrera, *personal observation*). The three larger-bodied *Sylvia* species (*S. atricapilla*, *S. borin*, and *S. communis*) have the “instantaneously” most varied diets, while *S. melanocephala*, *E. rubecula*, and *T. merula* display much lower within-sample heterogeneity. The former group corresponds to the most strongly frugivorous species (OFS = 68–92%), while the latter are species relying less heavily on fruit for food (OFS = 51–58%). A significant positive correlation exists across species between OFS and average number of fruit species per sample ($r_s = 0.89$, $P < .05$). The most strongly frugivorous dispersers ingest a broader variety of fruit types over short time periods, while more insectivorous ones include in their diets a more restricted complement of fruit species on each occasion.

An index of heterogeneity among individuals (samples) was obtained by dividing overall population fruit diversity by a measure of expected within-sample diversity ($-\sum_i \log f_i$, f_i = frequency of occurrence of fruit species i in feces [Herrera 1976]). Species differ greatly in interindividual constancy in fruit diet composition; *E. rubecula*, *S. atricapilla*, and *S. melanocephala* are remarkably constant, while *S. borin*, *S. communis*, and *T. merula* display low interindividual constancy in diet composition.

TABLE 4. Species composition of the fruit taken by the major avian seed dispersers at El Viso during 1978–1982. Data are percentages in respect to the total number of fruits ingested (N), as estimated from minimum numbers (or fractions thereof) present in the feces examined (p_i); data in parentheses are frequencies of occurrence of fruit species in feces (f_i). See Appendix for sample sizes. Cases in which the fruiting season of a plant and the local residency period of a bird are largely nonoverlapping, are denoted by an asterisk. *Erithacus rubecula* and *Sylvia atricapilla* are overwintering species, *Sylvia borin* and *Sylvia communis* are autumn migrants, and *Sylvia melanocephala* and *Turdus merula* are local residents, which are most abundant and/or frugivorous in autumn–winter and summer–early autumn, respectively. Fruits of *Ruscus aculeatus* were never detected in avian fecal samples; hence, this species has been omitted from the list.

Plant species	Bird species (number of fruits)					
	<i>Erithacus rubecula</i> (N = 133)	<i>Sylvia atricapilla</i> (N = 865)	<i>Sylvia borin</i> (N = 63)	<i>Sylvia communis</i> (N = 83)	<i>Sylvia melanocephala</i> (N = 381)	<i>Turdus merula</i> (N = 104)
	Percent of number of fruits ingested					
<i>Arbutus unedo</i>	0.1 (0.8)	0.1 (1.0)	*	*		
<i>Asparagus aphyllus</i>		0.4 (1.6)	*	*	0.8 (3.1)	
<i>Daphne gnidium</i>		0.5 (2.6)		0.2 (3.3)	1.0 (2.0)	
<i>Lonicera implexa</i>		0.1 (0.3)	1.3 (3.1)		0.3 (0.8)	
<i>Myrtus communis</i>	4.1 (7.5)	2.9 (17.0)	*	*	1.6 (9.8)	7.7 (17.1)
<i>Olea europaea</i>	0.4 (10.8)	3.2 (31.2)	0.1 (3.1)	*	0.4 (10.5)	1.4 (14.3)
<i>Osyris quadripartita</i>	0.4 (5.0)	13.3 (37.3)	18.6 (31.3)	6.2 (16.7)	0.8 (3.9)	31.8 (31.4)
<i>Phillyrea angustifolia</i>	3.7 (4.2)	5.0 (9.6)	32.0 (37.5)	34.0 (56.7)	3.8 (8.6)	35.2 (14.3)
<i>Pistacia lentiscus</i>	88.8 (89.2)	59.9 (62.7)	20.5 (21.9)	36.2 (50.0)	63.0 (61.3)	21.9 (17.1)
<i>Rhamnus alaternus</i>	*	*	4.2 (12.5)		6.2 (8.2)	
<i>Rhamnus lycioides</i>	0.8 (7.5)	1.0 (2.3)	1.6 (3.1)	20.3 (13.3)	19.3 (16.4)	
<i>Rubia peregrina</i>		2.5 (5.5)			1.1 (2.7)	
<i>Smilax aspera</i>	1.7 (0.8)	11.1 (27.7)	21.7 (25.0)	3.0 (10.0)	1.7 (3.5)	2.0 (5.7)
<i>Tamus communis</i>	*	0.1 (0.6)		0.1 (3.3)		
Overall fruit species diversity (1/∑ p _i ²)	1.26	2.54	4.38	3.42	2.27	3.58
Interindividual heterogeneity estimate†	0.12	0.15	0.57	0.56	0.15	0.72

† Computed as $[(-\sum \log_{10} f_i) (\sum p_i^2)]^{-1}$. See text for further details.

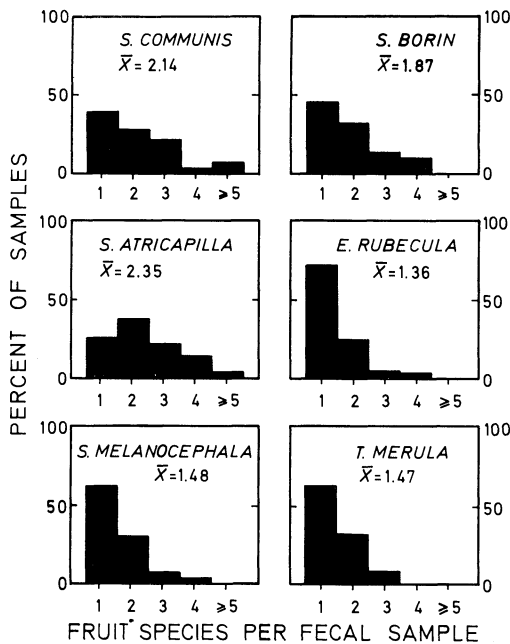


FIG. 8. Frequency distributions of the number of plant species recorded per individual fecal sample of the principal avian seed dispersers at El Viso. Sample sizes are shown in the Appendix.

Cazorla.—Fruit supply varied strongly among years, and the diet of the two major dispersers (*E. rubecula*, *S. atricapilla*) changed accordingly (Table 5). Data for *S. melanocephala* and *T. merula* were insufficient for separate consideration of the four study seasons. *Phillyrea latifolia*, *P. lentiscus*, and *Viburnum tinus* displayed strongest interannual fluctuations in availability, and their variations in abundance are tracked by their importance in the fruit diet of principal dispersers. The fruits of these fluctuating species are most important in the diet of major dispersers, and their changing abundances produce variation over the years in the identity of the dominant fruit food of these birds.

Data correspond to the same period of year for all species, and differences in diet composition (Table 5) must be attributed to differential fruit selection. Among the three most strongly fluctuating plant species, *P. lentiscus* and *V. tinus* produce high-reward, very lipid-rich fruits, while *P. latifolia* has low-reward fruits. *E. rubecula* feeds predominantly on either of the former species, or on both, but never on *P. latifolia* alone. *S. atricapilla*, in contrast, relies very slightly on lipid-rich *V. tinus* fruits even in crop years, while it ingests large proportions of the low-reward *P. latifolia* fruits. In fact, its diet was made almost entirely of this species in 1981–1982, when lipid-rich fruits were extremely

TABLE 5. Species composition of the fruit taken by the principal avian seed dispersers at Cazorla during October–February of years 1978–1982. Data are percentages in respect to the total number of fruits ingested (N), as estimated from minimum numbers (or fractions thereof) present in the feces examined; data in parentheses are frequencies of occurrence of fruit species in fecal samples. See Appendix for sample sizes. Fruit supply varied strongly among years at this site and data for the four study seasons are presented separately for species with sufficient data.

Plant species	Bird species (number of fruits)									
	<i>Erithacus rubecula</i>				<i>Sylvia atricapilla</i>				<i>Sylvia melanocephala</i>	<i>Turdus merula</i>
	1978–1979 ($N = 100$)	1979–1980 ($N = 24$)	1980–1981 ($N = 37$)	1981–1982 ($N = 326$)	1978–1979 ($N = 105$)	1979–1980 ($N = 33$)	1980–1981 ($N = 32$)	1981–1982 ($N = 202$)	($N = 27$)	($N = 26$)
	Percent of number of fruits ingested									
<i>Arbutus unedo</i>	5.8 (50.9)	5.1 (68.8)	2.7 (72.4)	1.5 (41.2)	3.4 (74.1)	2.4 (71.4)	6.0 (100)	1.3 (42.6)	1.7 (28.6)	54.6 (87.0)
<i>Daphne gnidium</i>	1.8 (3.5)						6.3 (5.9)			
<i>Juniperus oxycedrus</i>	0.1 (1.8)	0.1 (6.3)		0.6 (1.5)		1.5 (14.3)				7.0 (21.7)
<i>Lonicera implexa</i>	0.2 (1.8)				7.8 (18.5)				1.5 (7.1)	1.1 (4.3)
<i>Phillyrea angustifolia</i>	3.6 (7.0)			0.2 (0.7)	5.7 (14.8)	3.0 (14.3)				
<i>Phillyrea latifolia</i>	16.5 (47.4)			41.2 (90.4)	50.2 (77.8)	8.4 (28.6)		81.1 (94.4)	2.6 (7.1)	26.6 (26.1)
<i>Pistacia lentiscus</i>	22.1 (33.3)	90.8 (93.8)	28.3 (58.6)	48.9 (72.8)	10.5 (11.1)	82.1 (100.)	28.3 (29.4)	15.4 (27.8)	89.8 (78.6)	
<i>Pistacia terebinthus</i>					0.7 (3.7)					
<i>Rosa canina</i>					0.1 (3.7)					
<i>Rubia peregrina</i>	1.1 (3.5)	2.7 (12.5)	5.6 (20.7)	0.1 (0.7)	9.6 (22.2)	2.6 (28.6)	32.7 (52.9)	0.3 (5.6)		
<i>Rubus ulmifolius</i>	1.5 (29.8)			0.1 (3.7)	0.4 (18.5)		0.8 (5.9)	1.5 (14.8)	3.3 (28.6)	9.0 (13.0)
<i>Smilax aspera</i>	1.1 (7.0)		0.3 (3.4)		4.0 (14.8)		9.4 (41.2)	0.4 (3.7)	0.2 (7.1)	
<i>Sorbus torminalis</i>										1.5 (4.3)
<i>Tamus communis</i>									0.9 (7.1)	
<i>Viburnum tinus</i>	46.2 (61.4)	1.3 (6.3)	63.1 (89.7)	7.4 (19.9)	7.6 (11.1)		16.5 (17.6)			
Overall fruit species diversity*	3.39	1.21	2.07	2.41	3.45	1.46	4.33	1.47	1.24	2.62
Interindividual heterogeneity*	0.32	0.35	0.81	0.27	0.39	0.50	0.98	0.33	0.21	0.53
Average number of species per fecal sample	2.54	1.94	2.45	2.31	2.70	2.57	2.53	1.91	1.64	1.57

* Computed as detailed in Table 4.

scarce. *Sylvia melanocephala* mostly feeds on the rich fruits of *P. lentiscus*, while *T. merula* largely ingests low-reward species (*Arbutus unedo*, *P. latifolia*). There is a gradient of decreasing significance of high-reward fruits in the direction *S. melanocephala* → *E. rubecula* → *S. atricapilla* → *T. merula*.

In crop years, *P. lentiscus* fruits were always much less abundant than those of *V. tinus* or *P. latifolia*, but the amount of *P. lentiscus* in the diet of most species was comparable to the amounts of the other two fruit species when these were available. This preference for *P. lentiscus* fruits is attributable to its much greater food value in terms of lipids and protein, particularly with respect to *P. latifolia*. The preference was strongest in *E. rubecula* and *S. melanocephala*, much less marked in *S. atricapilla*, and nonexistent in *T. merula*, which apparently did not consume *P. lentiscus* fruits at all. Differential reliance of dispersers on high-reward fruit species is not associated apparently with differing levels of frugivory (OFS = 68.8, 90.5, 69.8, and 75.8% for *E. rubecula*, *S. atricapilla*, *S. melanocephala*, and *T. merula*, respectively, all years combined), but rather with differences in body size (average body mass = 16.8, 18.3, 11.4, and 85.1 g, respectively). Significance of high-reward fruits in diet is negatively correlated with body mass in these species ($r_s = -1.00$, $P < .05$).

Fruit diet diversity at the population level fluctuates

strongly between years in *E. rubecula* and *S. atricapilla*. Averaged over years, diversity values for these two species are comparable to that for *T. merula* and appreciably higher than that for *S. melanocephala*. The strong dependence of the latter species on *P. lentiscus* is responsible for its low fruit diet diversity.

Average numbers of plant species present per fecal sample are shown in Table 5. Frequency distributions for individual bird species do not differ substantially from those found in El Viso (Fig. 8) and have been omitted. *E. rubecula* and *S. atricapilla* show minor interannual variations in within-sample diversity, and their averages over the years (2.31 and 2.43 species per sample, respectively) are well above the figures for *S. melanocephala* and *T. merula* (1.64 and 1.57 species per sample, respectively). Interannual constancy in within-sample diversity exhibited by principal dispersers suggests that frugivores actively buffered "instantaneous" fruit diversity against fluctuations in fruit availability. This is further supported by the constancy shown by most species in within-sample diversity at the two study sites.

Interindividual variation in diet composition changed among years for *E. rubecula* and *S. atricapilla* (Table 5). Average figures for these species (0.44 and 0.55, respectively) are comparable to that for *T. merula* (0.53) and substantially higher than the corresponding value for *S. melanocephala* (0.21).

*Plant-disperser reciprocal
dependence patterns*

Methods.—Differential dependence of plants on bird species may be estimated by the proportion of total dispersed seeds removed by the various seed vectors (e.g., Howe 1977, Herrera and Jordano 1981), although this procedure ignores the potentially different survival prospects of seeds removed by different dispersers. Assuming that proportions of disperser species in mist-net catches are equivalent to those in the field, and that relative representation of fruit species in fecal samples accurately describes the specific composition of total fruits being removed by a bird species population at a given time, estimates were obtained for every plant species of the proportion of seeds dispersed by each bird species. After correcting for differences in monthly trapping effort, the number of seeds of every plant being transported by every bird species was inferred from fruit-equivalents in feces for every month of year in which the bird species actually was present. An annual figure was then obtained for every bird-plant species pair by summing partial monthly figures. The percent of total estimated number of seeds being dispersed contributed by every bird species was finally computed for every plant, and these figures were used as estimates of differential reliance for dispersal.

None of a variety of factors (e.g., food biomass, energy, protein, minerals) may be taken singly as the currency for measuring the proportional significance of a particular fruit to a disperser in a generally applicable way. Mixed fruit diets, along with the ordinarily poor and imbalanced composition of fruit pulp with regard to principal nutrients (Herrera 1982a), suggest that a balanced diet requires simultaneous feeding on diverse fruit sources, and that actual dietary significance of fruit types consumed frequently but in small quantities probably is not proportional to their contribution in biomass. In absence of adequate information on nutritional requirements and dietary selection by frugivores, estimates of relative energy contributions will be used to assess the relative dependence of bird species on the various fruit species. For every disperser species I calculated the following product for each food plant: (fraction of total estimated number of fruits in the diet) \times (average dry mass of pulp per individual fruit) \times (energy content of dry pulp [Herrera 1982c]) \times (1 - fiber content of pulp). Resulting figures were summed over plant species and expressed as percentages of this total. To facilitate comparisons between species, these percentages were multiplied by the corresponding OFS value for the bird species and the resulting figures used as indices of relative dependence.

Plant species that have a substantial fraction of their seeds dispersed by mammals (*Juniperus oxycedrus*, *Rubus ulmifolius*) or that were very infrequently consumed (*Pistacia terebinthus*, *Rosa canina*, *Ruscus aculeatus*, *Sorbus torminalis*, *Tamus communis*) were

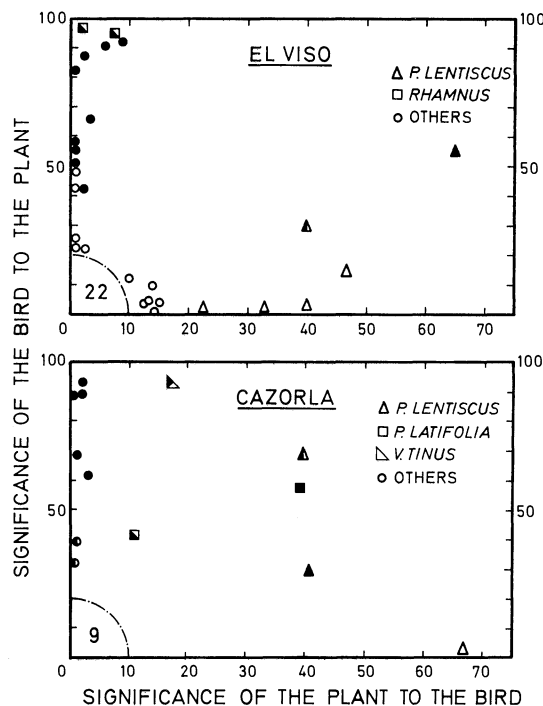


FIG. 9. Patterns of reciprocal dependence between bird-dispersed plants and avian dispersers at the two study sites. Relative significance of a bird to a plant was measured as the estimated percent of seeds which are dispersed by that particular bird species. The index of relative significance of a plant to a bird was obtained by multiplying OFS by the estimated percentage of total dietary energy furnished by fruits which are provided by that particular plant species (see text for details). Each symbol denotes a bird-plant species pair. Points lying near the lower-left extreme have been omitted for clarity, and the number of points is shown in that place. Bird species are coded as follows: filled symbols at both sites are used for *Sylvia atricapilla*; half-filled symbols are used for *Sylvia melanocephala* in El Viso and for *Erithacus rubecula* in Cazorla. Open symbols represent the remaining bird species at every site.

omitted from the analyses. *Arbutus unedo* was similarly excluded; although birds disperse many seeds of this species, I suspect that this represents a secondary phenomenon brought about by the extinction of the large mammals to which their large, soft, scented, small-seeded, ground-falling fruits are presumably adapted. The destructive ways dispersers handle these fruits supports the idea that *A. unedo* has not evolved as a proper bird-dispersed plant.

Results.—Differential abundance and frugivory of bird species, the greater diversity of the plant assemblage relative to that of effective dispersers, and the general concentration of the fruit portion of the dispersers' diet in a few kinds of fruits, all combine to produce a definite pattern of reciprocal plant-bird reliance at the community level (Fig. 9). There is a size-

able fraction of bird-plant species pairs in which the relationship is similarly weak from both the plant's and bird's viewpoints. This effect is most pronounced in El Viso, because of the greater species diversity there of both dispersers and effectively bird-dispersed plants. An important fraction of total bird-plant pairs denote situations of intense asymmetry in which the plants rely extensively for seed dispersal on bird species for which these plants are relatively unimportant. There are finally a few bird-plant species pairs in which the dependence is similarly intense from both the plant's and bird's viewpoints and still fewer in which the bird relies extensively on a plant for which it is unimportant. Correlations between the respective significance of the interaction to the plant and to the bird are non-significant at both sites ($r = -0.023$, $P = .88$; $r = 0.037$, $P = .87$; El Viso and Cazorla, respectively), demonstrating the absence of plant-bird reciprocity as a general phenomenon at the community level.

In El Viso, *P. lentiscus* shows by far the greatest significance to all dispersers. Two of these (*S. atricapilla*, *S. melanocephala*), in turn, are of special relevance to the plant, accounting together for an estimated 84% of total bird-dispersed *P. lentiscus* seeds. The strongest bond is found in the pair *S. atricapilla*-*P. lentiscus* (55.2% of plant's seeds/65.2% of bird's energy). *S. atricapilla* and *S. melanocephala* are especially relevant dispersers for some plants that have little significance for them. In fact, most plants rely on these birds for the dispersal of most of their seeds, including all moderately abundant plants producing low-reward fruits; these plants have most of their seeds dispersed by *S. atricapilla*, but each of them is an unimportant energy source to the bird.

In Cazorla, substantial plant-bird reciprocity is exemplified by the pairs *S. atricapilla*-*P. latifolia* (57.5% seeds/38.9% energy), *S. atricapilla*-*P. lentiscus* (29.4%/40.5%), *E. rubecula*-*P. lentiscus* (69.2%/39.5%), and *E. rubecula*-*V. tinus* (92.5%/16.6%). These figures represent averages over the four study seasons, and in a particular winter each of these birds is strongly dependent on the plant(s) with good crop that year; hence, actual dependence values in a particular season are usually much higher than reflected by average values. As in El Viso, there is a broad array of low-reward plant species which have little significance to *S. atricapilla* but which are strongly dependent on this species for seed dispersal (e.g., *Lonicera implexa*, *Rubia peregrina*, *Smilax aspera*).

While in the lowland habitat the only reciprocity relationship involves the nonfluctuating, ever-dominating *P. lentiscus* fruits, plant-bird reciprocity in the highland site involves species which have asynchronously fluctuating crop sizes. These plants reciprocate with the same two disperser species, but their reciprocity relationships are not actually coincident in time but rather tend to occur on separate years because of the supra-annual pattern in fruit abundance.

DISCUSSION

Peculiarities of mediterranean scrub

Values for annual fruit dry biomass production in these scrublands (98 kg/ha, El Viso; 22, 6, 40, and 39 kg/ha, Cazorla 1978-1981) are intermediate between values for tropical (180-980 kg/ha [Leigh 1975, Fleming 1979, Charles-Dominique et al. 1981]) and mid-latitude temperate forests (0.5-7 kg/ha [Johnson and Landers 1978, Baird 1980, Sorensen 1981, J. Guitián, *personal communication*]). On the basis of per habitat volume unit, biomass production is remarkably similar in scrublands and tropical forests. Scrublands are also intermediate between temperate and tropical forests in the proportion of woody species producing fleshy fruits (Howe and Smallwood 1982). Nevertheless, the much higher fruit production of scrublands relative to midlatitude forests cannot be explained by the slightly greater incidence of fruit-producing species, but rather by the contrasting horizontal distribution of fruiting patches. In temperate forests, fruit-producing plants characteristically reach high cover values in forest edges, gaps, river banks, and early successional stages but decrease greatly in importance and become very patchily distributed in mature forests dominated by non-fruit-producing trees. Within-patch fruit density is often comparable in temperate forests and mediterranean scrub (J. Guitián, *personal communication*), but patches are much more sparse in the former, resulting in lower average production for the habitat as a whole. In contrast, mediterranean fruit-producing plants replace earlier successional non-fruit-producing shrubs and eventually dominate the vegetation in mature scrublands. This produces a very small-scale patchiness in fruit distribution in late successional formations, where fruits become virtually continuously distributed over vast extensions of habitat.

In north temperate forests the greatest abundance and diversity of fruits occurs in summer-early autumn (Halls 1973, Thompson and Willson 1979, Baird 1980, Stiles 1980, Sorensen 1981). In the scrublands studied maximum abundance takes place in late autumn-winter. Evergreenness and rainy, mild winters make possible the abundant autumn-winter fruit production in scrublands (Herrera 1982b), apparently precluded in more northern habitats by severe winters and dominance of deciduous plants.

Ripening periods of individual species in the scrublands are, on average, longer ($\bar{x} = 2.2$ and 3.5 mo) than in northern temperate forests (0.6-1.3 mo [Sherburne 1972, Halls 1973, Thompson and Willson 1979, Sorensen 1981]) and shorter than in tropical forests (4.3-5.8 mo [Crome 1975, Decoux 1976, Hilty 1980, Charles-Dominique et al. 1981]). The range of ripening-season lengths found in El Viso (1-12 mo) is identical to that found in some of these tropical forests, while the range in montane scrubland (0.7-3.5 mo) is much closer to that of temperate forests. Length of ripening period of

individual species has been related to seed dispersal strategy in relation to disperser abundance and the risk of fruit damage (Howe and Estabrook 1977, Thompson and Willson 1979, Herrera 1982a). Without denying the importance of these factors, other aspects unrelated to the dispersal process seem more important to explain variation across communities in the length of ripening seasons, as suggested by the strong linear relationship existing between mean length of ripening season (ML) and average temperature of the coldest month of year (TCM) ($ML = 1.27 + 0.18 TCM$, $r^2 = 0.945$, $P = .00001$; $N = 10$ temperate, mediterranean and tropical localities in Sherburne [1972], Halls [1973], Crome [1975], Decoux [1976], Thompson and Willson [1979], Hilty [1980], Charles-Dominique et al. [1981], Sorensen [1981], and the present study). As the potential vegetative period increases, more time may be allocated by plants to each of their primary functions, and progressively longer ripening seasons will be incorporated into the plant community. This explanation is supported by the fact that both the lower and upper range limits of local ripening-season lengths are correlated with TCM ($r = 0.818$, $P = .01$ and $r = 0.908$, $P = .001$, respectively), but the regression slope is much greater for the upper limit (0.45 vs. 0.05).

Peculiarities of scrubland frugivores

Avian disperser assemblages found in the scrublands are characterized by a dearth of large-bodied species and the dominance of small birds in the range 12–18 g body mass. This contrasts with the patterns in north temperate forests, where dominant dispersers are species in the range 40–100 g body mass (Livingston 1972, Sherburne 1972, Simms 1978, Stiles 1980, Rybczynski and Riker 1981). The scarcity of large frugivores in the scrublands could be attributed in the case of the lowland plot to its small extension and disturbed surroundings, but their absence also from Cazorla makes this an unlikely explanation. In Cazorla, four *Turdus* species are abundant in open pine-juniper woodlands nearby, yet they are very rare in my plot. This should be attributed to many factors. (1) The density of the vegetation presumably renders fruit foraging difficult to these large birds, and the permanent attachment of ripe fruits to plants prevents their acquisition by means of ground foraging; this is supported by the central role of ground-falling *Arbutus unedo* fruits to *T. merula* in Cazorla. (2) The fruiting displays of most species, which produce fruits on thin vertical stems and erect or pendant infructescences, most likely render fruits difficult to obtain by heavy birds lacking good maneuverability.

Small birds have higher metabolic rates and energy requirements relative to body mass than do larger ones (Kendeigh et al. 1977, Walsberg 1980), a difference that is accentuated under low temperatures (Kendeigh 1970). Persistence of small frugivores in autumn-winter

would be possible only in mild climates with an abundant supply of energy-rich fruits as found in southern Spanish scrublands. The small-scale patchiness of fruit distribution in the habitat reduces foraging costs to birds, thus further improving their energy balance. The lower energy requirements of large frugivores relative to small ones permit subsistence chiefly on low-energy fruits, as illustrated by the fruit choice of *T. merula* in the scrublands and the frugivorous winter diet of *Turdus* species in more northern European habitats (Tyrväinen 1970, Simms 1978, Sorensen 1981, Guitián, *in press*). They can also afford the costs incurred in the exploitation of the patchy supply of fruits characteristic of temperate habitat, either through itinerant and opportunistic exploitation of widely spaced patches (Bezzel 1966, Tyrväinen 1970) or by means of territorial defense of fruit clumps in winter when conditions become most critical (Snow and Snow, *in press*; see also Salomonson and Balda [1977] and Moore [1978] for North America).

The proportion of fruit predators relative to total avian frugivores and the resulting level of frugivory are comparable in the scrublands and northern temperate habitats (Moore 1978, Pulliainen 1978, Salomonson 1978, Baird 1980, Stapanian 1980, Sorensen 1981). It is remarkable that large crops of lipid-rich fruits found in autumn-winter in the scrublands did not promote the appearance of a large assemblage of fruit predators. The exploitation of the pulp of these nutritious but small fruits may be unprofitable to fruit predators, or there is sufficient alternative, readily exploitable food available, as suggested by the much greater incidence of winter fruit predation in Cazorla, the site having the most adverse climate.

Scrubland seed dispersal ecology

Results of the present investigation strongly contradict expectations from earlier coevolutionary models (see Introduction). No consistent relation has been found among crop size, fruit quality (lipids and protein), ripening rate and seed size, either among themselves or with removal success. *Viburnum tinus* and *Pistacia lentiscus* ("primary" species hereafter, Cazorla and El Viso, respectively) have very lipid-rich fruits, large crop sizes, high within-plant fruit density, and fruits that ripen during the local peak time of fruit diversity and abundance. These features (crop size, fruit quality, fruiting time) covary independently in the other species, and virtually every possible combination of states of these variables may be found. Removal success of primary species was similar to that of other small-fruited species producing low-reward fruits. The suggested gradient of plant dispersal strategies (high- vs. low-investment [Snow 1971, 1981, McKey 1975, Howe and Estabrook 1977]) and its presumed relationship with fruit removal rates do not exist therefore in the scrublands.

All attributes favorable to plants are found associ-

ated in a small group of primary frugivores (*S. atricapilla*, *S. melanocephala*, *E. rubecula*). These primary frugivores are abundant, and they eat fruit almost continuously; fruits are the main food for a substantial part of year. These species ingest whole fruits without damaging the seeds. The remaining bird species lack one or several of the attributes of primary species; characteristics relevant to seed dispersal mentioned above co-occur in an apparently disorderly fashion. Primary dispersers are "specialized" dispersers (see also Herrera 1984), successfully performing the dispersal of a plant assemblage with diverse fruit or fruiting characteristics. The only common trait among these plants is the production of fruits smaller than disperser gape width. This pattern is again in sharp contrast with earlier generalizations based on tropical examples (see Introduction).

Actual reciprocity occurs only in a few bird-plant species pairs at every site, while in the majority of cases plants are much less important to dispersers than dispersers are to plants. Intense reciprocity only occurs between primary plant and bird species; hence, the plant-bird interaction is mutually strong only in these cases (e.g., *Pistacia lentiscus*-*Sylvia atricapilla*, *Viburnum tinus*-*Erithacus rubecula*). I submit that the whole local bird-plant dispersal system during autumn-winter is maintained by these few pairs of strong bird-plant interaction. Local primary plants indirectly favor seed dispersal of lower-ranking coexisting plants. The prolonged autumn-winter presence of abundant dispersers is made possible by the existence of an abundant supply of highly nutritious fruits provided by primary plants; low-reward or rare species would be unable by themselves alone to attract and maintain as abundant and reliable a supply of dispersers as primary species do. (Abundant populations of overwintering frugivores are found only in habitats with high-reward fruit plants [Muñoz-Cobo and Purroy 1979, Costa 1982, Fernández 1982].)

The maintenance of this relationship is dependent upon the varied diets consistently exhibited by dispersers even when high-reward fruits are abundantly available. The regular inclusion of fruits from low-reward species makes possible the dispersal of these species. Varied diets and the inverse correlation existing between "instantaneous" fruit diet diversity and the relative contribution of insect food (see also Jordano and Herrera 1981) strongly suggest the following. (1) The fruit of no one species provides a balanced or complete diet if taken singly. This observation applies even to *P. lentiscus* (7.9% protein, 58.8% lipids in the pulp), a high-quality species comparable to the most nutritious fruits reported so far from tropical areas (White 1974, Frost 1980). (2) Species with largely frugivorous diets require the fruits of a diversity of taxa, as also seen in tropical frugivores (Snow 1977, Wheelwright 1983). Accordingly, avian frugivores such as *Sylvia atricapilla*, relying most heavily on fruit for food

are more likely to be reliable dispersers for many fruit-bearing species than are less strongly frugivorous species. Such reliability of fruit dispersal also depends on the overall community pattern of fruit abundance and diversity prevailing locally at particular times of year; response of frugivores to a particular fruit type depends on the configuration of the multispecies fruit supply at the community level, not just on species-specific features.

Summer-early-autumn frugivory at El Viso has weak relative significance for the habitat as a whole. Summer-fruiting plants are sparse and have generally small fruit crops. No bird-plant reciprocity relation involves any summer-fruiting species, since summer frugivores do not depend heavily on any single plant for fruit food. There appears to be a much looser relationship between plants and dispersers during that period (Herrera 1982b), but fruit removal success still remains very high among these plants (Fig. 7).

Mutualistic congruency and its evolution

The present study has revealed a seed dispersal system where most seeds are dispersed with a negligible waste to predators and pests, as a result of close congruency between plants and birds. Most plants have fruit sizes below the maximum size acceptable to dominant, small-sized frugivores. Very nutritious fruits are produced in abundance when energy demands of dispersers are highest (Herrera 1982b). The greatest abundance of fruits occurs through production by the most abundant plants when dispersers are most abundant and require most food. Overwintering species build up important fat reserves from lipid-rich fruits (Herrera 1982d) and tend to return to the same localities in successive years, thereby constituting a reliable source of dispersal each year (Herrera and Rodríguez 1979, Benvenuti and Ioale 1980, Finlayson 1980). To what extent are strong reciprocal interdependence (shown above) and mutualistic congruency the result of mutual adaptations between plants and birds? The possible origins of these mutualistic patterns fall under three headings.

History and climate.—Mediterranean climate first appeared in the late Pliocene (Axelrod 1973), and the vegetation found today in the mediterranean-climate areas of Europe is of relatively recent origin (Moreau 1955, Frenzel 1968, Axelrod 1973, Pignatti 1978). The woody members of this flora are, however, "survivors of a richer, tropical-margin vegetation that developed . . . through the Tertiary" (Raven 1973). Most extant avian species arose during the Quaternary (Lambrecht 1933, Brodkorb 1971). The woody species most likely antedated their current dispersers in the Mediterranean region, and their interaction has a relatively recent origin. *Pistacia lentiscus* is thought to have existed since the early Tertiary (Zohary 1952). Some plant traits we observe today in scrublands are unlikely to have evolved in connection with present-day disper-

sers. The atypical year-round fruiting of *Osyris quadripartita* is similar to that of the South African congeneric *O. compressa* (Rowan 1967). The unusual shape, color, and smell (as well as the size) of the fruits and seeds of *Myrtus communis* are virtually identical to those of the similarly shrub-sized *Ugni montana* (Myrtaceae) of neotropical highlands, and the fruits and infructescences of *Smilax aspera* are identical to those of an unidentified Neotropical species in the same genus (C. M. Herrera, *personal observation*). These examples (along with the cases of *Ruscus aculeatus* and *Arbutus unedo* reported above) suggest an "anachronism load" in these plant communities as seen elsewhere (Janzen 1979, Janzen and Martin 1982).

The mild winters of the Mediterranean Basin have favored the establishment of an abundant wintering avifauna that, irrespective of feeding habits, commonly outnumber residents in winter (Herrera and Sorriquer 1977, Finlayson 1981, Costa 1982, Fernández 1982). Overwintering species are mostly small (as most far-migrating European passerines are [Moreau 1972]), and birds of this size are particularly well suited for dwelling in dense vegetation, as revealed by the noticeable association of small-sized *Sylvia* warblers with Mediterranean scrub (Williamson 1968, Cody and Walter 1976). The recurrence of dispersers in their winter residences is not probably a response to a predictable winter fruit supply, since recurrence rates are analogous to those of insectivores or granivores (C. M. Herrera, *personal observation*) and should perhaps be attributed to local climatic predictability.

Mutual adaptations.—The absence of a summer-early-autumn fruiting period in the highland site may be an evolutionary response to the scarcity of autumn migrants. The eastern half of Andalusia, including Cazorla, is characterized by an extreme scarcity of autumn migrants in comparison to western Andalusia (El Viso). Such scarcity is the regional manifestation of a broader geographical pattern of autumn migratory pathways in the Iberian Peninsula, the origins of which remain obscure (Bernis 1962). Autumn migrant frugivores are not only absent from the Cazorla scrubland plot, but are also remarkably scarce in other habitats at higher and lower elevations where some fruits may be locally abundant.

Predominant autumn-winter fruiting may be interpreted as the result of the greater availability of potential dispersers, but also of the low levels of pests on ripe fruits during that period (Herrera 1982a). In addition, evergreenness, autumn-winter rains, and mild temperatures may also favor such a fruiting phenology. Contrasting flowering and fruiting patterns tend to suggest however that disperser pressures may have selected for the narrow range of ripening times observed.

Regardless of whether rich fruits actually evolved *de novo* in response to selection by birds (probably the case of *V. tinus*, whose congeneric European non-

mediterranean species seem to have less lipid-rich fruits) or rather birds selected against the disappearance of a pre-existing habit by countering the alternative selection in plants for conservation of energy and nutrients, the abundant occurrence of winter lipid-rich fruits should be considered a trait evolved in response to dispersers (Herrera 1982b). The close agreement between fruit size and disperser gape width observed most likely has also resulted from selection by birds against large fruits. Concentration of dispersers on lipid-rich fruits and differential removal success of species differing in fruit size support these hypotheses.

Apart from some digestive adaptations common to all seed dispersers (Herrera 1984), behavioral adaptations to autumn-winter frugivory vary in intensity among primary dispersers. The most extreme manifestation is seen in *Sylvia atricapilla*, which possesses an endogenous rhythm controlling food preferences (Berthold 1976), making of it an obligate winter frugivore. *Sylvia melanocephala* is so commonly associated with *Pistacia lentiscus* that it is unusual to find this bird in a site without *Pistacia* (C. M. Herrera, *personal observation*). *Erithacus rubecula*, which does not have any endogenous rhythm of food preferences and always prefers insects to fruits (Berthold 1976), is not an obligate winter frugivore and occupies a variety of habitat types including those without fruits (Herrera 1977).

In these communities there appears to be, within both the bird and plant species assemblages, a steep gradient of increasing adaptation to its interacting counterpart. These two gradients converge in the sense that a few species interact strongly, depend reciprocally on each other to a considerable extent, and most likely have achieved the present status through actual coadaptation. Actual coevolution has thus probably occurred only to a very limited extent.

CONCLUSION

Historical, climatic, and geographical factors may be overwhelmingly important in shaping bird-plant seed dispersal patterns, and mutualistic congruency may to a large extent be an epiphenomenon of these factors, thus not resulting necessarily from bird-plant coevolution. Actual coevolution involving a small group of bird and plant species may facilitate the successful seed dispersal of many other plant species that have not coevolved (or slightly coevolved) with dispersal agents, thus favoring the persistence of a chronic "anachronism load" (with regard to dispersal). In evolutionary time, undifferentiated species in the anachronistic pool may become a material subject to adaptive changes if environment changes. Results of this study strongly support Howe's (1981) view that "McKey strategic dichotomy (of dispersal strategies) is not a sufficient conceptual framework" and "interactions between birds and fruiting trees appear more diverse than the framework predicts."

As suggested by the results of this study, interhabitat differences in plant and bird community structure most likely will determine differences in the distribution of interaction strengths among bird-plant species pairs. Species diversities of avian and plant assemblages should determine the shape of the frequency distribution of interaction strengths, and species-poor assemblages are most likely to give rise to some strong plant-bird reciprocal dependence, as seen in insular situations (Barquín and de la Torre 1975, Temple 1977).

Plant species interact passively via "diet-sharing." Low-reward species may be successfully dispersed by birds which concentrate on rich fruits but not to the exclusion of less nutritious ones. This fact makes apparent that the specific configuration of fruit resources in a habitat may largely determine the dispersal success of a given plant, and the corollaries follow that (1) the interpretation of the dispersal ecology of a single species requires a consideration of the set of species with which it is sharing the disperser assemblage, and (2) coevolution may be envisaged among disperser-sharing plants. Varied diets may be interpreted in the sense that the nutritional configuration of "blocks" of species ordinarily sharing the same habitats and the same dispersers is such that nutrients are found "overdispersed" among species (as found in scrublands), and that disperser-mediated coevolution has occurred among plants, in turn resulting in a manipulation of disperser feeding behavior. Regardless of its actual evolutionary origin, findings above indicate that scrub plants are functionally (for dispersal) interdependent, thus constituting a "dispersal guild" in which individual species benefit from coexistence with other species, a situation conceptually analogous to that of "defense guilds" (Atsatt and O'Dowd 1976).

Passive interactions among plant species and weak adaptedness of old taxa may help to explain the often limited success of simple coevolutionary models (e.g., Frost 1980, Fleming 1981, Herrera 1981a, Herrera and Jordano 1981, Howe and Smallwood 1982, Jordano 1982, Wheelwright 1983, and the present study) and cast doubts on their validity (see also Howe and Smallwood 1982). The anacardiaceous shrub *Pistacia lentiscus* fits most theoretical expectations for a "coevolved" plant, yet all individuals produce every year thousands of fruits containing just empty shells (due to parthenocarpy and intense seed abortion [Grundwag 1975, C. M. Herrera, *personal observation*]); this example further highlights the need for a reconsideration of coevolutionary postulates.

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APPENDIX

Summary of mist-net captures at Cazorla and El Viso study sites in the period October 1978–February 1982, and occurrence of fruit remains in feces.

Species	Type of frugivory*	Cazorla				El Viso	
		Fruitless season (May–July)		Fruiting season (August–April)		Total captures	No. fecal samples analyzed (no. with fruit)†
		Total captures	No. fecal samples analyzed (no. with fruit)	Total captures	No. fecal samples analyzed (no. with fruit)†		
<i>Aegithalos caudatus</i>	P	5	0	79	46 (25)		
<i>Carduelis carduelis</i>	NF					50	0; 15 (0)
<i>Carduelis chloris</i>	P			9	5 (3)	188	21 (7)
<i>Certhia brachydactyla</i>	NF	1	1 (0)	37	22 (0)	1	0
<i>Cisticola juncidis</i>	NF					4	1 (0); 2 (0)
<i>Coccothraustes coccothraustes</i>	P			2	2 (1)		
<i>Emberiza cia</i>	NF	1	0	7	6 (0); 6 (0)		
<i>Erithacus rubecula</i>	D	32	18 (0)	284	269 (242)	165	143 (120)
<i>Ficedula hypoleuca</i>	D	1	1 (0)			15	14 (5)
<i>Fringilla coelebs</i>	P	9	4 (0)	28	21 (15)		
<i>Garrulus glandarius</i>	NF	1	1 (0)	6	4 (0)		
<i>Hippolais polyglotta</i>	D					18	14 (1)
<i>Lanius excubitor</i>	NF	1	1 (0)			1	0
<i>Lanius senator</i>	NF					47	2 (0); 5 (0)
<i>Locustella naevia</i>	NF					2	1 (0)
<i>Luscinia megarhynchos</i>	D					25	24 (2)
<i>Motacilla alba</i>	NF					2	2 (0); 17 (0)
<i>Muscicapa striata</i>	NF	1	1 (0)			2	1 (0)
<i>Parus ater</i>	P	6	0	13	11 (2)		
<i>Parus caeruleus</i>	P	9	2 (0)	126	98 (57)	10	6 (1)
<i>Parus cristatus</i>	P	17	4 (0)	35	31 (20)		
<i>Parus major</i>	P	1	0	27	23 (10)	20	18 (6)
<i>Phoenicurus ochruros</i>	D			1	1 (0)	5	4 (2)
<i>Phoenicurus phoenicurus</i>	D					31	30 (22)
<i>Phylloscopus bonelli</i>	NF	6	3 (0)			9	1 (0); 10 (0)
<i>Phylloscopus collybita</i>	P			7	2 (0)	182	47 (1)
<i>Phylloscopus trochilus</i>	NF	4	0			12	1 (0); 15 (0)
<i>Prunella modularis</i>	P			11	10 (3)	11	6 (1)
<i>Pyrrhula pyrrhula</i>	P			2	2 (2)		
<i>Regulus ignicapillus</i>	P	3	1 (0)	45	29 (2)	2	0
<i>Saxicola torquata</i>	D					7	4 (2)
<i>Sitta europaea</i>	NF			2	1 (0); 1 (0)		
<i>Serinus serinus</i>	NF					54	0; 17 (0)
<i>Sylvia atricapilla</i>	D	14	13 (0)	105	105 (105)	335	316 (312)
<i>Sylvia borin</i>	D					38	36 (32)
<i>Sylvia cantillans</i>	D	6	5 (0)	4	3 (0)	4	4 (1)
<i>Sylvia communis</i>	D					36	34 (30)
<i>Sylvia melanocephala</i>	D	3	3 (0)	18	17 (14)	356	320 (253)
<i>Troglodytes troglodytes</i>	NF	1	0	2	0; 3 (0)		
<i>Turdus merula</i>	D	6	3 (0)	32	23 (23)	59	43 (37)
<i>Turdus philomelos</i>	D			3	3 (3)	5	3 (2)

* NF, nonfrugivores; D, seed dispersers; P, fruit predators.

† For nonfrugivores with few fecal samples collected, assignment to this category is supported by the examination of a number of gizzards (data in italics) (C. M. Herrera, *personal observation*).