

SEASONAL VARIATION IN THE QUALITY OF FRUITS AND DIFFUSE COEVOLUTION BETWEEN PLANTS AND AVIAN DISPERSERS¹

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Abstract. The hypothesis is formulated that, among vertebrate-dispersed plants, species ripening fruits at different times of year should differ in the nutritional properties of their fruits in such a way as to match the seasonally changing demands of their major dispersers. This was tested for a sample of 62 species of southern Spanish bird-dispersed plants, and results fully conform to expectations. Species ripening fruits during the dry mediterranean summer, when water demands of dispersers are highest, have the most watery fruits. Species producing fruits in winter, when energy needs of avian frugivores are at a maximum, possess fruits with the highest lipid content. No marked seasonal trend in protein yield of fruits was found, which is consistent with the fact that protein demands of avian dispersers appear to be fairly constant during the summer-through-winter period considered. Coupling between fruit quality and frugivores' needs is shown to be most likely related to coevolution between plants and birds, and not to fortuitous coincidence over time of fruit quality and disperser needs. The significance of highly rewarding winter fruits for the evolution of some physiological and behavioral traits among overwintering dispersers points to the existence of a closely coevolved system involving the latter and the assemblage of winter-ripening mediterranean evergreens. It is concluded that the seasonal gradient in plant-bird coevolutionary adjustment has been concurrently brought about by (1) seasonally changing demands of dispersers, and (2) the differential coevolutionary potentials open to the plant-bird system through changing spatio-temporal asymmetry in relationships between vegetation and avifauna.

Key words: *avian frugivores; fruit quality; lipids; mediterranean plants; plant-bird coevolution; protein; Spain.*

INTRODUCTION

Endozoochorous seed dispersal by birds is based on the provision of food by the plant (van der Pijl 1972). Discrete packages produced by plants containing some seeds plus a certain amount of pulp are usually termed "fruits," although they do not always develop from an enlarged ovary. True dispersers ingest the whole fruit, either regurgitate or defecate the seeds in condition suitable for germination, and obtain a nutritious reward as a consequence of digesting the pulp (Snow 1971, McKey 1975). The benefits obtained by the plant in having their seeds dispersed are difficult to express quantitatively, but they relate to increased gene flow (Levin and Kerster 1974), escape from predators (Janzen 1970) and colonizing new habitat patches (Livingston 1972, Smith 1975). The advantage gained by the birds is of much more immediate nature and may easily be measured in terms of the energy or specific nutrients obtained. Potential disadvantages to the plant originate from the allocation of extra energy and nutrients to the pulp; disadvantages to the birds derive from the ingestion of nutritionally irrelevant seeds.

It has been suggested that frugivorous birds and bird-dispersed plants are involved in a coevolutionary race in which each tends to obtain the most reward in

return for the least expenditure (e.g., Snow 1971, Herrera 1981a). Since the two groups involved have conflicting interests, compromise situations will necessarily evolve for the system to persist. The equilibrium point will be displaced closer to either plant's or bird's optimum depending on environmental circumstances (e.g., Howe and Estabrook 1977, Herrera 1981a). Diverse features of the dispersal performed by the birds have been related to the nutritional reward offered by the plant in the pulp (e.g., Snow 1971, McKey 1975, Howe and Estabrook 1977, Frost 1980, Howe and Vande Kerckhove 1980). Detailed studies on the ecological correlates of nutritionally relevant features of fruits are, however, still lacking, despite the obvious significance they have for the understanding of the bird-side advantage in the bird-plant mutualistic system, as well as for evaluating the degree of coevolutionary adjustment existing between birds and plants (Herrera 1981d). In this paper I formulate a hypothesis relating nutritive features of fruits to the changing nutritional demands of their dispersers in seasonal habitats, and provide a test of it based on the analysis of the phenological correlates of fruit quality among southern Spanish bird-dispersed plants. The hypothesis to be tested is that the nutritional features of bird-dispersed fruits vary seasonally to match the seasonal demands of their major dispersers. This was first suggested by Snow (1971), but it has remained untested to date despite its potential significance to the under-

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standing of plant-disperser coevolution. Although the concept of coevolution implies the existence of evolutionary changes affecting the two parts involved in the process (plants and avian dispersers in this case; Janzen 1980), I will concentrate in this paper on the analysis of plants' features presumably evolved in response to selective pressures from the birds.

Nutritional elements in fruit pulp which may be relevant to birds include carbohydrates, minerals, lipids, and protein. The latter two have been the ones most frequently dealt with in the literature (e.g., Snow 1971, Morton 1973, White 1975, Foster 1977), and are most likely among the most valuable ones to frugivores. In arid habitats or seasons water contained in fruit pulp may possess particular relevance to the birds (Walsberg 1975), and I will consider it below along with lipids and protein.

STUDY AREA AND METHODS

Sampling sites

Field work was conducted from October 1978 to November 1980 at six study sites located in Andalusia, the southernmost Spanish region. Study localities were chosen to represent common natural vegetational formations in the area. They include two lowland and four highland stations of relatively undisturbed vegetation. Lowland sites are in the lower Guadalquivir River valley, and the highland ones in the Sierra de Cazorla, a rugged mountain range in the uppermost course of the same valley (see Polunin and Smythies 1973:83–89 for a description). The two groups of localities are nearly 250 km apart and encompass a broad range of elevations, with corresponding variation in species composition of plant communities, ranging from lowland sclerophyllous scrub to mountain coniferous forest (Table 1).

The climate of the region is typically mediterranean, characterized by rainy mild winters and dry hot summers (Aschmann 1973). Absolute values of rainfall and temperature vary among sites as a consequence of elevational differences, with lowland sites warmer and drier than highland ones. Overall patterns of seasonality are, however, identical at all sites, with a marked succession of dry and wet seasons in the course of the year (Fig. 1).

The number and identity of bird-dispersed species were recorded at each site. Species were classed as dispersed by birds mainly on the basis of previous studies on the feeding ecology of frugivorous birds in the area (Herrera 1981a, b, c, Herrera and Jordano 1981, Jordano and Herrera 1981, Jordano 1981) and, for a few uncommon species, because features of their fruits unequivocally matched the ornithophilous syndrome described by van der Pijl (1972). The total number of bird-dispersed species per site varies between 17 and 25 and many species are shared by contiguous stations along the elevational gradient (Table 1).

Observations on fruiting phenology

Time of ripening of fruits was determined on the basis of field observations and/or fruit counts of marked plants conducted at study sites. For the purpose of this paper, all plant species present in any site were assigned to one of three phenological classes depending on the time of ripening of their fruits. Categories used were June–August, September–October and November–February ("summer," "autumn," and "winter" hereafter). I assigned species to the phenological classes on the basis of the time when most ripe fruits were present. This time was usually coincidental with the end of the ripening period.

Considering only the peak of fruit abundance as a phenological criterion, instead of the whole period of

TABLE 1. Relevant features of study sites.

Site	Location	Elevation (m)	Dominant woody species	No. of bird-dispersed species	No. of species shared with preceding site
Viso	37°26'N, 5°45'W	100	<i>Pistacia lentiscus</i> , <i>Phillyrea angustifolia</i> , <i>Olea europaea</i>	18	...
Gelves	37°22'N, 6°3'W	100	<i>Pistacia lentiscus</i> , <i>Olea europaea</i> , <i>Ceratonia siliqua</i>	17	12
Borosa	38°N, 2°51'W	750	<i>Quercus ilex</i> , <i>Pinus halepensis</i> , <i>Phillyrea latifolia</i>	25*	12
El Cantalar	37°59'N, 2°54'W	1150	<i>Quercus ilex</i> , <i>Arbutus unedo</i> , <i>Phillyrea latifolia</i> , <i>Viburnum tinus</i>	17*	15
Roblehondo	37°57'N, 2°52'W	1350	<i>Pinus nigra</i> , <i>Quercus ilex</i> , <i>Juniperus oxycedrus</i>	18*	6
Cabañas	37°49'N, 2°57'W	1700	<i>Pinus nigra</i> , <i>Juniperus communis</i> , <i>Berberis hispanica</i>	21*	10

* Species in the genus *Rosa* are often difficult to separate, and hybrids frequently occur; thus they have all been treated as a single morphospecies.

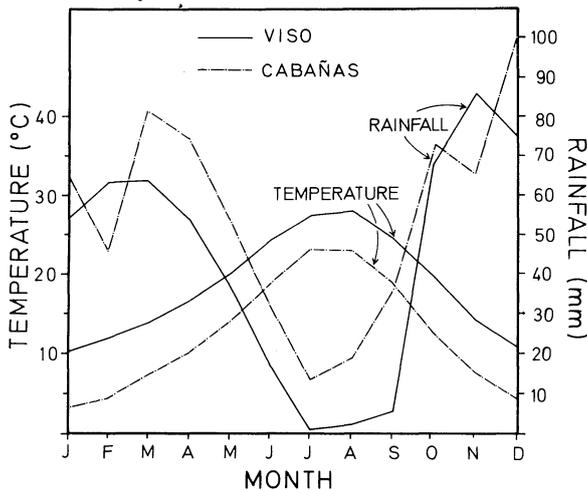


FIG. 1. Seasonal patterns of rainfall and mean monthly temperature at the two most climatically extreme study sites (see Table 1 for details of localities). Data were taken from the nearest meteorological stations, reported in Montero and González (1974).

fruit availability, emphasizes the time of fruit production, as opposed to that of fruit consumption, which normally extends over the whole period of fruit availability. Time of retention of ripe fruits on the plants varied according to season and, to a lesser degree, species. Seasonal patterns in fruit quality could thus disappear from the point of view of frugivores if fruits of earlier maturing species remain available during later periods. This was not the case at my study sites, where, with a few minor exceptions, average persistence time of ripe fruits on the plants was shortest for summer-fruiting (<1 mo), longest for winter-fruiting (>1.5 mo), and intermediate for autumn-fruiting species.

Slight among-site variation in ripening dates occurred in some species. In most of these instances variation was not large enough to spread over more than a single phenological class. In the remaining few instances in which two classes were involved, the rule of thumb used was to assign the species to the class to which it belongs in the site where it is most abundant.

Observations on flowering phenology of fruit-producing plants were also carried out at the same sites. Species were classed into six flowering phenology categories, each encompassing 2 mo (from January–February through November–December). Criteria used were similar to those described for fruiting, species being assigned on the basis of the time when most open flowers were present.

Fruit characteristics

For every plant species, relevant features of ripe fruits were individually recorded in a sample usually consisting of 20–30 fruits coming from as many indi-

vidual plants as possible. These included fresh mass of the whole fruit, percent water content of pulp alone (*WP*), dry mass of both pulp and seeds per fruit, and number of seeds per fruit (all masses recorded to nearest 0.1 mg). Average figures resulting from the individual fruits in the sample were taken as representative for the species. Although some between-site variation in fruit features may occur in some species (Herrera 1981a), I did not account for this fact, and a single set of descriptive data was used per species. Accurate values of *WP* were usually very difficult to determine directly owing to the watery nature of most fruits. For 30 species, it was obtained indirectly by arithmetically combining data on percent water content of the whole fruit (*WF*), percent water content of seeds, and relative proportion in mass made up by seeds in the fresh fruit. A strong correlation was found between *WP* and *WF* values in this group of species ($r = .927$, $N = 30$, $P \leq .001$), and *WF* values were subsequently used for all species as approximate estimates of *WP*.

Samples of dry pulp were prepared for as many species as possible by carefully separating pulp and seeds of fruits previously dried at 40°C to constant mass. Chemical determinations of crude lipid and crude protein (mass of N \times 6.25) were carried out by standard analytical procedures (details are obtainable from B. García Criado, Centro de Edafología y Biología Aplicada, Salamanca, Spain).

Data used in the analyses

Relevant features of plant communities which have provided the data for this study are summarized in Table 2. Sites are virtually identical with respect to the relative contributions of the various growth forms to the whole of the bird-dispersed species, with shrubs contributing the largest number of species at all sites. Localities are also statistically indistinguishable with respect to overall patterns of fruiting phenology, despite the broad range of elevations they encompass.

Since the main objective of this paper is to compare fruit features of plant species differing in fruiting phenology, and since sites do not differ in phenological trends, I have combined all species present in any site to obtain a single sample. This procedure does not introduce any apparent bias, while it has the advantage of conveniently increasing sample sizes for the purpose of statistical comparisons. Nine further species not recorded in any study site but present in nearby areas, and for which data on phenology and fruit features were available, were added to the sample. The 62-species resulting sample has provided the raw data for the analyses to follow (see the Appendix for a list of species).

The sample used represents >80% of total native, and virtually 100% of abundant and/or widespread, bird-dispersed species in Andalusia. I am thus confident that this sample is extensive enough to avoid sys-

TABLE 2. Compositional features of local assemblages of bird-dispersed plant species which have provided the data for this study. See Table 1 for the other site features and the Appendix for a list of species.

Site	Ripening season			Number of species				
	Summer	Autumn	Winter	Growth habit				
				Trees	Large shrubs	Small shrubs	Vines	Herbs
Viso	8	3	7	3	5	5	2	3
Gelves	7	5	5	3	4	6	2	2
Borosa	9	9	7	7	9	3	4	2
El Cantalar	5	7	5	6	5	2	2	2
Roblehondo	8	7	3	6	6	2	3	1
Cabañas	7	8	6	6	8	5	1	(1)*
Difference among sites:								
C-statistic		5.15				11.53		
P		>.85				>.90		

* Refers to a single mistletoe species.

tematic bias derived from disproportionate representation of particular taxonomic or ecological groups.

RESULTS

For a disperser which has to ingest whole fruits and process useless seeds in order to obtain a nutritive reward, the net profitability in some valuable substance inherent to a given kind of fruit is directly related to the product of two factors: (1) a "chemical" component, related to the richness of dry pulp in that substance, and (2) a "design" or "aspect" component which basically depends on seed/pulp mass ratio and water content of pulp (Herrera 1981d). The overall profitability of the fruit for substance *i* (OP_i) may be expressed as

$$OP_i = \frac{(1 - WP)P}{P + S} d_i \quad (1)$$

where *S* = wet mass of seeds in fruit, *P* = wet mass of pulp (*P* + *S* equals fresh mass of whole fruit), *WP* = water content of pulp, and *d_i* = percent mass of dry pulp made up by substance *i*. The first factor in Eq. 1 is the above-mentioned "design" component (relative yield, *RY* hereafter) of overall fruit profitability in substance *i* (OP_i), and *d_i* is the "chemical" component. OP_i may be expressed in terms of mass of substance *i* obtainable per mass unit of fresh whole fruit ingested (Herrera 1981d).

Overall profitability for crude lipid and crude protein were computed for fruits of 50 species according to Eq. 1 (see Appendix). They represent estimates of the maximum amount of these nutrients obtainable by a bird after ingesting and processing fruits.

There is a significant trend of progressive increase in both protein and lipid profitability from summer-through winter-ripening species, to reach maximum figures in the latter group (Table 3). The trend is particularly noticeable for lipids, with species ripening fruits in winter displaying average profitabilities 12

times higher than the mean figure for summer-ripening ones. In the case of protein, the change is only about 2-fold from summer to winter. These changes are brought about by concurrent variation in chemical profitability of pulp and design profitability of fruit.

RY significantly increases from summer through winter, although the absolute amount of the change is fairly small (1.5-fold). Increase in *RY* is related to a decrease in water content of pulp (as estimated by *WF*) from summer to winter, since the average fruit mass and the amount of dry pulp per fruit experience only slight, nonsignificant seasonal changes (Table 3). Lipid content of dry pulp significantly increases from an average value of 2.5% among summer-fruiting species up to 19.7% among winter-fruiting ones, a nearly 8-fold increase. Protein content does not experience any significant change, and pulps have on average ≈4.5% protein at all seasons. Water content of whole fruits decreases from 67.9% among summer-ripening species to 52.0% among winter-fruiting ones.

It is clear from the above that the strong seasonal increase in lipid profitability of bird-dispersed fruits as the season progresses is mainly dependent on the important increase in relative lipid richness of pulp, and only secondarily on the slight increase in relative richness of fruits in dry mass of nutritive matter (Fig. 2). The moderate though significant increase in protein profitability, on the other hand, depends exclusively on the latter. These results indicate that, for a frugivorous bird, the potential energetic reward contained in a fruit from an average plant species increases from summer through winter. This implies greater absolute costs to the plant (in terms of energy necessary to synthesize pulp constituents) for producing the "reward section" of an average individual fruit. These increased costs are not, however, associated with the placement of either larger or more seeds in the fruits. Total mass of seeds per fruit, mean mass of individual seeds, and number of seeds per fruit

TABLE 3. Seasonal variation of fruit features related to profitability to dispersers among southern Spanish bird-dispersed plant species. Means \pm 1 SD are shown. Symbols refer to Eq. 1 in the text.

Variable	Equivalent in Eq. 1	Ripening season			F value†
		Summer	Autumn	Winter	
“Design” profitability (%)	$RY = (1 - WP)P/(P + S)$	16.3 \pm 6.2	20.9 \pm 7.6	23.5 \pm 8.1	5.8**
Water content of whole fruit (%)‡	—	67.9 \pm 9.3	60.0 \pm 9.2	52.0 \pm 16.4	9.6***
Dry mass of pulp per fruit (mg)	$(1 - WP)P$	52.9 \pm 56.7	97.2 \pm 86.9	122.8 \pm 245.6	1.2NS
Mass of fresh whole fruit (mg)	$(P + S)$	324.1 \pm 340.6	414.9 \pm 296.7	468.0 \pm 738.8	0.5NS
N (number of species)		25	19	18	
“Chemical” profitability					
Lipid content of pulp (%)	d_1	2.5 \pm 1.2	7.4 \pm 13.7	19.7 \pm 18.7	10.1***
Protein content of pulp (%)	d_2	4.3 \pm 1.7	4.3 \pm 1.8	5.0 \pm 1.4	1.0NS
N (number of species)		18	17	15	
Overall profitability					
Lipids (%)	OP				
Protein (%)	$RY \cdot d_1$	0.38 \pm 0.21	1.55 \pm 2.96	4.73 \pm 4.64	13.2***
N (number of species)	$RY \cdot d_2$	0.69 \pm 0.29	0.85 \pm 0.34	1.12 \pm 0.38	6.8**
		18	17	15	

† F values were computed after arcsin transformation in the case of percentage data. *** $P < .001$; ** $P < .01$; NS, not significant.

‡ Used as an indirect estimate of water content of pulp alone (WP in Eq. 1); see Methods.

do not vary significantly with time of ripening (Table 4). The investment made by the plants in terms of costly lipid and protein mass, per either individual seed or unit of seed mass, thus increases noticeably from summer to winter. In other words, it seems that plants “pay” more to dispersers in winter for performing the dispersal of the same mass of seeds.

Distribution of plant species among flowering phenology classes was found to be similar in summer-, autumn- and winter-fruited species ($G = 2.68$, $df = 2$, $P > .25$), with the vast majority of species flowering during periods II and III (see Appendix). There are thus substantial differences among fruiting phenology classes in the average time elapsed from flowering to fruiting. I did not find, however, any significant correlation between either lipid or protein profitability and flowering-to-fruiting interval of individual plant species, both within fruiting phenology classes and for all classes combined. These results indicate that fruit quality is largely independent of the length of time the plant takes to mature them, apparently being associated most strongly with the time of ripening.

DISCUSSION

General aspects

Seed dispersal is but one of the events in the life cycle of plants, and making fruits attractive to dispersers only one of the goals to achieve a successful reproduction. On the other hand, reproduction shares time, energy, and nutrients with growth and maintenance, and a delicate balance usually exists between all these activities (Stebbins 1971, Harper 1977). Fruiting phenology and fruit features are therefore shaped over evolutionary time not only by plant-disperser interactions, but also by many other selective forces not directly related to the dispersal process. Accordingly, predictions derived from a hypothesis based solely on the consideration of the plant-disperser interaction would only apply if the whole set of environmental

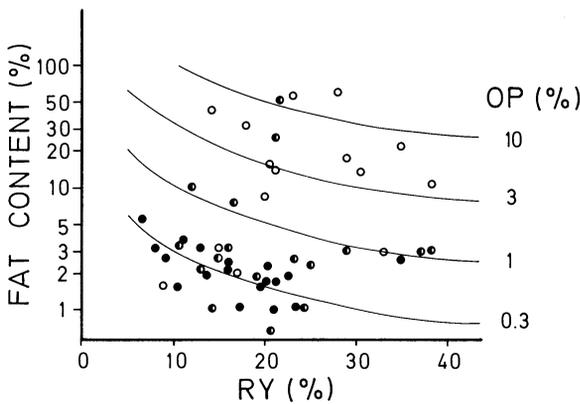


FIG. 2. Distribution of plant species over the plane defined by “chemical” (with respect to lipid content, d_1) and “design” profitability (relative yield, RY) of their fruits (see text for a definition of these concepts). Summer-, autumn- and winter-fruited species are represented by filled, half-filled and open dots, respectively. Isolines of overall profitability (OP) have been drawn to show the substantial increase in this measure from summer- to winter-ripening species (note the logarithmic scale on the vertical axis). Seasonal increase in overall profitability is basically brought about by changes in d_1 , and only marginally by variation of “design” profitability RY (see text for further details).

TABLE 4. Seasonal variation of fruit features related to seed content among southern Spanish bird-dispersed plant species. Mean \pm 1 SD; sample sizes (number of species) in parentheses.

	Ripening season			F value
	Summer (25)	Autumn (19)	Winter (18)	
Number of seeds per fruit	3.5 \pm 5.6	2.1 \pm 2.3	2.8 \pm 3.2	0.6†
Dry mass of an individual seed (mg)	31.0 \pm 50.7	50.7 \pm 45.8	74.4 \pm 163.5	1.0†
Dry mass of seeds per fruit (mg)	47.0 \pm 48.7	73.1 \pm 64.6	90.3 \pm 159.1	1.0†

† Not significant.

limitations shaping a plant's life history allows for the development of the particular fruit features being predicted. In mediterranean habitats of southern Spain fruiting has apparently been possible for plants during most of the year, and avian frugivory has thus had the opportunity to develop during an extended period, involving resident, migratory, and overwintering species (Herrera 1981a, b, c, Herrera and Jordano 1981, Jordano 1981, Jordano and Herrera 1981). These regional conditions have provided an useful background for testing the hypothesis relating fruit quality to variation in dispersers' demands.

The hypothesis examined in this paper implicitly originates from the belief that frugivorous birds are able to become selective agents of plants by favoring those species and/or genotypes which provide them with the fruits best matching their requirements. There is some circumstantial evidence supporting this contention (Howe and Vande Kerckhove 1980, Herrera 1981a), although further studies are needed to prove its generality. The hypothesis also relies on the assumption that avian frugivores use nutritional features of fruits as a selective criterion when constructing their diets. Food selection by herbivores is not, however, solely affected by purely nutritional attributes of plant food (Freeland and Janzen 1974, Westoby 1974). Among nectar-feeding birds and foliage-eating mammals, food selection has been shown to depend, among others, on specific taste preferences, concentration and identity of secondary components, and digestibility (e.g., Freeland and Janzen 1974, Stiles 1976, McKey et al. 1978, Milton 1979, Oates et al. 1980, Schwartz et al. 1980). Nevertheless, food choice has always been found related to feeding value in terms of both energy and nutrient content (e.g., Moss 1968, Gardarsson and Moss 1970, Hainsworth and Wolf 1976, Stiles 1976, Milton 1979). Undigestible fiber and a variety of toxic compounds accompany nutritive substances in fruit pulp (e.g., Kear 1968, Janzen 1978, Gartlan et al. 1980), just as in plant foliage (Freeland and Janzen 1974) and, often, in floral nectar too (Baker 1977). Although no studies have been conducted so far on the food choice of avian frugivores, there is no a priori reason to expect a response to nutrients and secondary substances essentially different from that displayed by other vertebrate herbivores when feeding

on plant food. Therefore, although other varied factors will surely affect fruit selection, the significance of nutritional value justifies the approach followed in this paper.

Seasonally changing demands of avian dispersers in southern Spanish habitats

Bird-dispersed plants in southern Spain are chiefly dispersed by a relatively small group of species in the passerine families Sylviidae, Turdidae, Muscicapidae, and Corvidae, mentioned in decreasing order of importance. Although the relative significance of dispersers with differing residency status may vary slightly among localities, a simplified, yet general picture common to all my study sites may be put forward based on information in Herrera (1974), Ferns (1975), Herrera and Soriguer (1977), Cónsul and Alvarez (1978), Thomas (1979), Torres and León (1979), Herrera (1981a, b, c), Herrera and Jordano (1981), Jordano (1981) and Jordano and Herrera (1981). From June to August, seed dispersal is accomplished by juveniles and postbreeding adults of a few resident species. In September and October, large numbers of migrants from the north largely outnumber resident frugivores. During this period most dispersal is performed by these migrants. From November through March, several overwintering species are common in most habitat types, and they consistently perform most seed dispersal during this long period. Spring migrants and breeding residents disperse few seeds due to a general scarcity of fruits during the spring. The identity of avian dispersers varies similarly in other regions (see, e.g., Livingston 1972, Thompson and Willson 1979, Baird 1980, Stiles 1980, for North America).

Nutritional demands of birds presumably vary according to season, residency status, and availability of alternative insect food. The abundance of insects for birds in some mediterranean habitats of southern Spain has been shown to be highest in April–May, steadily decreasing afterwards to a minimum in December–January (Herrera 1977a). This pattern of variation in insect abundance, showing a pronounced decrease starting in the late rainy season and continuing from summer to winter, appears to be shared by all mediterranean-climate habitats of the world (Swan 1952, Blondel 1969, Cody 1974, Atkins 1977).

Protein requirements of dispersers are probably highest in summer. At this time they are resident species whose populations are made up of adult birds actively molting plumage along with recently fledged juveniles which are probably still growing, with the associated increase in protein requirements these activities imply (Fisher 1972, Payne 1972). Protein needs are surely much lower for both autumn migrants and winter residents, neither of which group is involved in any growth process. Energy requirements, on the other hand, almost certainly increase from summer to autumn-winter, mainly owing to substantially increased thermoregulatory costs derived from a steady decrease in ambient temperature (Calder and King 1974) and to fat deposition usually taking place among autumn migrants and overwintering birds (King 1972, Blem 1976, Herrera 1977b, 1981c). It is difficult to generalize about the energy requirements of autumn migrants relative to overwintering birds. While the former require large quantities of fuel for long flights, actual fattening may occur either at southern Spanish stopover sites or elsewhere in the north (Herrera 1974, Thomas 1979). Deposition of migratory fat by locally resting lean birds appears to be strongly related to hyperphagia, rather than to shifts in food selection (Berthold 1975, Blem 1976). Although lean individuals are only a fraction of birds temporarily resting at stopover sites (Herrera 1974, Rappole and Warner 1976), energy demands must usually be very high among these birds. In contrast to overwintering birds subject to heavy nocturnal mass losses, energy is probably not essential to short-term, day-to-day survival of migrants, but rather to future survival elsewhere during the course of active migration.

In southern Spain, summer drought is usually long and severe enough to dry up virtually all streams and small rivers. Drinking water for birds becomes very scarce, and they tend to congregate near watering points until rains begin in early autumn (Herrera 1977a; see also Williams and Koenig 1980). On the other hand, increased evaporative water loss in summer resulting from very high temperatures and behavioral thermoregulatory mechanisms based on enhancement of evaporative cooling, certainly will increase water requirements of resident birds relative to autumn and winter. The most significant avian dispersers are small birds in the mass range 12–90 g, among which water losses are most pronounced (Bartholomew and Cade 1963). Furthermore, water loss of migrants crossing southern Spain during late summer and early autumn is probably greatly increased by the high local temperatures (Berger and Hart 1974), and it has been suggested that dehydration may often be critical among trans-Mediterranean migrants (Fogden 1972, Langslow 1976).

Combining information above on disperser requirements and availability of alternative sources, it appears that while protein needs most likely parallel the

abundance of alternative insect sources, water and energy needs vary in opposite ways to availability of alternative sources. This indicates that the "requirements/alternative sources" ratio, roughly equaling the potential demands placed on fruits by dispersers, will show much more noticeable changes for water and energy than for protein. Specifically, water demands will decrease, and energy demands increase, from summer through winter, while a much less definite pattern is to be expected for protein demands. According to the hypothesis stated earlier in this paper, this leads to the following predictions. (1) Southern Spanish plant species ripening their fruits during autumn-winter should produce fruits with higher energy rewards (lipids) than those ripening in summer. (2) Seasonal variation in protein reward will show an ill-defined pattern. (3) There should be a well-defined pattern in water content of pulp, with a decreasing trend from summer- through winter-ripening species. Results fully support these predictions.

Coevolution or fortuitousness?

The finding that fruit food value matches frugivores' needs is not sufficient to support the notion of bird-plant coevolution. The system could well have evolved fortuitously if there were some sort of complementarity between birds' and plants' requirements for energy, water, and nutrients owing to concurrent variation of relevant (but independent) environmental factors to both groups of organisms (Janzen 1980).

With an array of plant species as varied as that dealt with in this paper, it is difficult to generalize about the possible environmental limitations on fruit quality. There are, however, several general aspects which must be accounted for. The summer dry season characteristic of mediterranean-type climates represents an adverse season to all plants. Soil water deficit coupled with high temperatures impose serious limitations on plant life, and these factors have been responsible for the evolution of some characteristic features of mediterranean plant communities (e.g., Mooney and Dunn 1970a, Mooney et al. 1974, Cody and Mooney 1978). Deep-rooted species, as most fruit-producing plants are, can utilize soil moisture which in summer is deep in the soil to maintain a positive carbon gain even during this adverse period (Larcher 1961, Mooney and Dunn 1970b, Mooney et al. 1974). The cold winter temperatures may at times generate some stress to plants (Mitrakos 1980), but they are generally not cold enough to promote cessation of photosynthetic activity in evergreen (winter-ripening) plants.

Two facts support the notion of fruit features having evolved to meet disperser demands. (1) The production of the most watery fruits precisely during the dry summer, when water is scarcest to the plant, could hardly be reconciled with any suggestion of fortuitous coincidence between fruit features and disperser needs. (2) Assuming that energy and nutrients are

TABLE 5. Relative importance (percent cover) of plant species differing in fruiting phenology at two study sites (see Tables 1 and 2). Importance values computed in relation to the total cover represented by fruit-producing species only.

	Percent cover					
	Viso			El Cantalar		
	Summer-fruiting	Autumn-fruiting	Winter-fruiting	Summer-fruiting	Autumn-fruiting	Winter-fruiting
Total cover	17.1	17.3	65.6	14.3	36.6	49.1
Average cover of individual species	2.1	5.8	9.4	2.9	5.2	9.8

valuable commodities to plants and waste of these commodities will receive a severe evolutionary "penalty," then if plants "pay" more in winter for dispersing the same amount (in terms of both mass and number) of seeds, and this increase in expenditure matches an increase in disperser requirements, it may be concluded that dispersers have driven the system towards the production of high-yield fruits, apparently indispensable for their successful winter survival (Herrera 1981c, Jordano and Herrera 1981).

Production by plants of more costly fruits in winter has probably been allowed over evolutionary time by the peculiar features of mediterranean climate, favoring evergreenness and making possible autumn-winter photosynthetic activity. Release of plants in autumn-winter from the previous summer water stress probably results in greater photosynthate availability to evergreens. Nevertheless, greater photosynthate availability occurring when fruits happen to be richer does not necessarily support the "fortuitous coincidence" view of the evolution of the system. Plants could well continue producing summer-type, relatively low-cost fruits through autumn and winter, thus saving energy and nutrients which could profitably be used for growth, maintenance, or future reproduction. On the other hand, in the most unlikely case of an extraordinary surplus of energy and nutrients in winter to plants, it would be difficult to explain why this excess manifests itself only in the lipid fraction of the pulp, and not at all in the protein fraction. I therefore conclude that nutritional correlates of fruiting phenology and the matching of fruit quality and birds' needs are not mere incidental consequences of plants and birds responding to the same environmental factors.

In addition to the "null hypothesis" of fortuitous coincidence, further alternative interpretations of the results presented in this paper could be suggested. Features of winter fruits might have evolved independently of dispersers, simply to decrease the risk of damage by low temperatures. Although the fatty, water-poor nature of winter fruits may actually confer some protection against frost, this explanation seems most unlikely. Winter climate of the Guadalquivir Valley is extremely mild (mean January temperature mostly $>8^{\circ}\text{C}$; Linés Escardó 1970) and costly adaptations to infrequent risks should be unlikely. On the

other hand, winter fatty fruits are often damaged by heavy frosts in exceptionally cold winters (C. M. Herrera, *personal observation*). Furthermore, had fatty pulps mainly evolved as a frost defense, fatty fruits should be most frequent in northern latitudes, a trend strongly contradicted by facts (Snow 1971, White 1975).

Water content may be higher in the summer because this is an energetically inexpensive way to make fruits appear larger, and perhaps improve attractiveness to birds. The size of fruits does not vary seasonally in the sample of species analyzed (average diameter 7.3, 8.2 and 8.2 mm for summer-, autumn- and winter-fruiting species, respectively; $F = 1.09$, $P > .30$); thus this explanation must be rejected.

*Close diffuse coevolution : winter-fruiting
mediterranean flora and associated
overwintering avifauna*

The study of species-specific fruit features as done in this paper is a first step in the analysis of plant-community-specific fruit features, in which each species should be weighted by a factor relating to its abundance. To birds, plant systematics are not of interest, but rather the relative abundances of fruits that vary in quality. In southern Spanish mediterranean scrub, dominant species are precisely winter-ripening ones with high lipid profitability (Table 5). Relative importance, in terms of vegetative cover, of fruit-producing species increases from summer- through winter-fruiting species, and this applies both to species considered individually and to the overall importance of whole phenological classes. Since spacing of fruiting plants most likely will influence foraging costs to dispersers, data in Table 5 suggest not only that winter-fruiting species provide the most rewarding fruits to birds, but also that the costs of movement between plants are reduced at that season.

It has been shown elsewhere (Herrera 1981b, c, Jordano and Herrera 1981) that the principal overwintering dispersers rely most heavily on the most rewarding species of winter fruits for subsistence, while feeding only marginally on relatively poorer fruits simultaneously available. This provides a strong selective pressure favoring plant species with the richest fruits, which is a necessary factor to drive any coevolution-

ary process underlying nutritional correlates of fruiting phenology. On the other hand, the western Mediterranean Basin provides most important winter quarters for many fruit-eating birds, including species of warblers, thrushes, and starlings (e.g., Bernis 1960, Hope Jones 1961, Blondel 1969, Klein et al. 1973, Langslow 1979). As I have suggested elsewhere (Herrera 1981c), these migratory habits have most likely evolved in response to the increased survival opportunities provided by the production of high-quality fruits during the winter season by dominant plants of mediterranean scrub. The latter fact must actually favor the development of the circummediterranean wintering habit among some species "preadapted" to frugivory. In addition to this overall pattern, particular bird species appear to have developed specific adaptations to winter frugivory. The most striking case is that of *Sylvia atricapilla*, perhaps the most significant disperser for the majority of southern Spanish winter-fruiting species (Jordano and Herrera 1981). This species experiences a circannual endogenous rhythm controlling food preferences, with fruits being preferred to insects during winter (Berthold 1976). Obviously, this singular adaptation would not have developed in the absence of highly rewarding fruits in the wintering grounds of the species. Year-to-year wintering site constancy shown by individuals of this and other frugivorous species (Herrera and Rodríguez 1979, Benvenuti and Ioale 1980), probably constitutes a further adaptation to predictable and rich winter fruit supply.

Increase in winter fruit quality in response to greater nutritional demands of dispersers has thus most likely in turn originated specific physiological and behavioral traits in disperser populations. This situation represents a clear instance of "diffuse" coevolution on a regional scale, as Janzen (1980) has termed the process in which two arrays of species populations interact between themselves and generate reciprocal selective pressures on a group-to-group, rather than species-to-species, basis.

To provide satisfactory explanation of the much higher investment per dispersed seed in that season in the light of current coevolutionary models (Snow 1971, McKey 1975, Howe and Estabrook 1977), it is necessary to suggest the possible advantages to plants of having their seeds dispersed in winter rather than in either summer or autumn. These advantages are not immediately clear. The vast majority of winter-fruiting species have seed dormancy mechanisms delaying germination until at least 1 yr after seed production (Catalán 1978, C. M. Herrera, *personal observation*). Thus the first explanation that comes to mind: that dispersal is coincidental with winter rains to ensure adequate water supply for germination and early seedling growth, must be rejected. Alternative hypotheses could be suggested that relate winter-fruiting advantages to the reduction of seed predation or fruit des-

iccation, but adequate information for supporting any of these suggestions is lacking.

Southern Spanish winter frugivores mainly originate from central and northern Europe (e.g., Bernis 1960, Hope Jones 1961, Blondel 1969, Klein et al. 1973, Langslow 1979). Other populations of *Sylvia atricapilla* winter in Africa south of the Sahara (Moreau 1972). The advantages derived to wintering frugivores by participating in the coevolutionary process with rich-fruit-producing plants must be related to the presumably much lower mortality risks involved in the shorter migratory journey leading them to the western Mediterranean Basin instead of the long migratory flight over the inhospitable Sahara to arrive at tropical winter quarters.

Spatial and temporal asymmetry in bird-plant interactions and the potential for diffuse coevolution

Seed dispersal by frugivores is an intrinsically mutualistic process in which both birds and plants get some benefit. In a specified regional context the mutualistic bird-plant system may ideally be located at different points on the seasonal dimension, and diverse temporal options are potentially open to plants and birds (Snow 1965, Thompson and Willson 1979, Stiles 1980). Options providing the best possible balance to both plants and birds are most likely ultimately to be favored by natural selection. Nevertheless, situations of asymmetry inherent to the bird-plant interaction probably modify the potential for coevolution by introducing constraints on the evolution of some traits.

Regardless of the implications to plants derived from fruiting at different times which are unrelated to dispersal itself (e.g., pollinator availability, physiological limitations), different temporal options imply the utilization by the plant of different disperser assemblages. The latter differ in nutritional requirements as stressed in this paper, but also probably with regard to other so far unexplored features related to dispersal quality. It must be noted, however, that the nature and identity of these seasonally changing assemblages may often be largely independent of the fruiting process itself. The abundance of transient migratory populations in autumn is a predictable, recurrent event which has its origin in distant northern regions, and is completely independent of the production of fruits by local plants. Similarly, the *presence* of resident birds in a habitat is in most instances unrelated to the production of fruits. In contrast, overwintering birds in southern Spain have probably evolved their winter residency status on the basis of the availability of rich fruits as discussed above. These circumstances provide different starting points for the bird-plant diffuse coevolutionary system to develop. Since in summer and autumn the presence of the birds is largely unre-

lated to the production of fruits, it may be suggested that summer- and autumn-ripening plants have had a starting "advantage" in the game they are playing with birds, thus having an opportunity to drive the system towards the production of relatively poor fruits, since their supply of dispersers does not depend to a large degree on the provision of costly, highly rewarding pulps. Most likely the potential for close interdependence has been relatively restricted in these instances, since there does not exist the necessity among plants to "catch" dispersers and/or the possibility of retaining them longer "at hand." They will be available regardless of the quality of the "bait," although some "bait" will obviously be necessary to attract them to the plants. Furthermore, they place relatively low nutritional demands on plants, thus favoring a loose dependency. On the other hand, since winter dispersers will no longer remain available to plants if the latter do not provide them with nutritive rewards adequate for survival (birds would otherwise die or migrate), birds have driven the winter system towards the production of rich fruits. This has also had a high potential for the evolution of close interdependence, with plants investing more per seed dispersed and birds developing particular, at times sophisticated behavioral traits, as discussed above.

I therefore conclude that the seasonal gradient in fruit quality reflects a gradient of (diffuse) coevolutionary closeness between plants and birds whose evolution has been concurrently brought about by the seasonally changing demands of dispersers and the differential coevolutionary potentials open through changing benefit asymmetries in vegetation-avifauna relationships, the origin of the latter being largely independent of both the birds and the plants.

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APPENDIX

Plant species and relevant fruit features analyzed in this paper. Nomenclature follows Tutin et al. (1964 to 1980).

Species	Family	Fruiting season*	Flowering season†	WF‡ (%)	Overall profitability (OP) (%)	
					Lipids	Protein
<i>Amelanchier ovalis</i>	Rosaceae	S	II	59.6	0.88	0.67
<i>Arbutus unedo</i>	Ericaceae	W	VI	65.2	0.96	1.23
<i>Arum italicum</i>	Araceae	S	III	65.1	0.29	0.88
<i>Asparagus acutifolius</i>	Liliaceae	W	IV	38.2
<i>Asparagus albus</i> §	Liliaceae	W	V	61.3
<i>Asparagus aphyllus</i>	Liliaceae	W	IV	56.1
<i>Berberis hispanica</i>	Berberidaceae	S	III	64.4	0.91	1.08
<i>Corema album</i> §	Empetraceae	S	II	74.6	0.38	0.15
<i>Cornus sanguinea</i>	Cornaceae	A	III	52.0	5.30	1.37
<i>Cotoneaster granatensis</i>	Rosaceae	A	...	58.6	0.42	1.04
<i>Cotoneaster integerrimus</i>	Rosaceae	A	II	50.4
<i>Crataegus monogyna</i>	Rosaceae	A	III	56.4	0.58	0.63
<i>Crataegus laciniata</i>	Rosaceae	A	III	54.4	0.35	0.74
<i>Daphne gnidium</i>	Thymelaeaceae	S	IV	81.9	0.24	0.73
<i>Daphne laureola</i>	Thymelaeaceae	S	II	78.8	0.16	0.55
<i>Frangula alnus</i>	Rhamnaceae	S	...	67.4
<i>Hedera helix</i>	Araliaceae	W	V	70.0	5.87	0.92
<i>Ilex aquifolium</i>	Aquifoliaceae	W	III	49.8	0.47	0.73
<i>Iris foetidissima</i>	Iridaceae	A	...	48.2
<i>Jasminum fruticans</i>	Oleaceae	A	III	70.0	1.22	0.79
<i>Juniperus communis</i>	Cupressaceae	W	III	51.5	4.79	1.20
<i>Juniperus oxycedrus</i>	Cupressaceae	W	III	29.0	4.00	1.00
<i>Juniperus phoenicea</i>	Cupressaceae	W	II	36.4	2.95	0.99
<i>Juniperus sabina</i>	Cupressaceae	W	II	53.6	4.02	2.04
<i>Laurus nobilis</i> §	Lauraceae	W	II	20.6	12.45	1.42
<i>Ligustrum vulgare</i>	Oleaceae	A	III	74.0	0.36	0.65
<i>Lonicera arborea</i>	Caprifoliaceae	A	III	73.2	0.61	0.63
<i>Lonicera etrusca</i>	Caprifoliaceae	S	III	69.2	0.47	0.72
<i>Lonicera implexa</i>	Caprifoliaceae	S	III	54.3	0.43	0.74
<i>Lonicera periclymenum</i> §	Caprifoliaceae	S	IV	70.6
<i>Lonicera splendida</i>	Caprifoliaceae	S	III	70.4	0.36	0.71
<i>Myrtus communis</i>	Myrtaceae	W	III	72.4	0.35	0.64
<i>Olea europaea</i>	Oleaceae	W	II	49.7	6.12	1.15
<i>Osyris alba</i>	Santalaceae	S	II	60.1	0.29	1.06
<i>Osyris quadripartita</i>	Santalaceae	W	III	57.8	0.14	0.59
<i>Phillyrea angustifolia</i>	Oleaceae	S	I	47.8	0.37	0.47
<i>Phillyrea latifolia</i>	Oleaceae	A	II	63.0	0.50	0.38
<i>Pistacia lentiscus</i>	Anacardiaceae	W	II	46.8	16.64	1.56
<i>Pistacia terebinthus</i>	Anacardiaceae	A	III	51.2	12.07	1.65
<i>Prunus mahaleb</i>	Rosaceae	S	II	63.8	0.41	0.36
<i>Prunus prostrata</i>	Rosaceae	S	III	67.2	0.38	0.56
<i>Prunus ramburii</i> §	Rosaceae	A	...	50.7	0.26	0.76
<i>Prunus spinosa</i>	Rosaceae	S	II	68.9	0.35	0.66
<i>Rhamnus alaternus</i>	Rhamnaceae	S	I	55.8	0.15	1.14
<i>Rhamnus lycioides</i>	Rhamnaceae	S	II	53.2	0.21	1.19
<i>Ribes alpinum</i>	Grossulariaceae	S	III	78.3
<i>Rosa sp. (canina group)</i>	Rosaceae	A	III	55.2	0.81	1.25
<i>Rubia peregriana</i>	Rubiaceae	A	III	76.9	1.20	0.63
<i>Rubus ulmifolius</i>	Rosaceae	S	IV	74.4
<i>Ruscus aculeatus</i>	Liliaceae	A	II	61.2	0.13	0.80
<i>Sambucus ebulus</i> §	Caprifoliaceae	S	III	77.0
<i>Sambucus nigra</i> §	Caprifoliaceae	S	III	81.6
<i>Smilax aspera</i>	Liliaceae	A	V	66.8	0.28	0.69
<i>Sorbus aria</i>	Rosaceae	A	III	53.2	1.04	1.15
<i>Sorbus torminalis</i>	Rosaceae	A	III	54.8	1.11	0.73
<i>Tamus communis</i>	Dioscoreaceae	S	II	79.8	0.36	0.33
<i>Taxus baccata</i>	Taxaceae	A	...	70.1	0.04	0.48
<i>Viburnum lantana</i>	Caprifoliaceae	S	III	62.7
<i>Viburnum tinus</i>	Caprifoliaceae	W	II	29.5	7.50	1.28
<i>Viscum album</i>	Loranthaceae	W	II	76.9	1.69	0.81
<i>Viscum cruciatum</i> §	Loranthaceae	W	II	71.5	3.02	1.24
<i>Vitis vinifera</i>	Vitaceae	S	III	71.4	0.35	0.50

* S, A, W: summer-, autumn- and winter-ripening, respectively (see Methods).

† I to VI, 2-mo periods from January–February through November–December.

‡ Water content of the whole fruit, used as an indirect estimate of water content of pulp alone (see Methods).

§ Species not recorded at any study site (Table 1) but present in nearby areas.

|| Species in the genus *Pistacia* display a complex pattern of fruit ripening, with various colors of "ripe" fruits occurring in succession (C. M. Herrera, *personal observation*). Data presented here refer to "black-type" and "bluish-green-type," for