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ADAPTATION TO FRUGIVORY OF MEDITERRANEAN AVIAN SEED DISPERSERS[1]

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Abstract. Morphological and digestive correlates of seed dispersal were investigated in 41 bird species of mediterranean scrublands of southern Spain. Seed dispersers (feeding on whole fruits and voiding seeds unharmed) are indistinguishable from nonfrugivores and fruit predators (feeding on pulp or seeds and not performing dispersal) in the ratio of gizzard mass, liver mass, and intestine length to body mass, but differ significantly in bill morphology and average gut passage time (GPT). Seed dispersers tend to be flatter and broader billed than other groups, and have a wider mouth relative to bill width. GPT of seed dispersers is significantly shorter than that of other groups. Morphological correlates of seed dispersers suggest that adaptations for insectivory serve as preadaptations for feeding on whole fruits. Shorter GPT's, in contrast, appear to be an adaptation indispensable to sustained, intense frugivory. Seasonal frugivory imposes limits on commitments to permanent structural modifications, and more subtle functional adaptations are to be expected. In the context of plant-disperser coevolution, unapparent adaptations of seed dispersers to plants are as relevant as the more conspicuous structural adaptations reported for year-round frugivores. In mediterranean scrublands they suffice to maintain a high-efficiency seed dispersal system.

Key words: avian ecology; coevolution; digestive adaptations; food passage rate; frugivory; mediterranean scrublands; morphology; seed dispersal.

INTRODUCTION

Plants producing fleshy fruits ("fruits" hereafter) are dispersed by frugivorous vertebrates (Ridley 1930, van der Pijl 1972). This relationship is mutualistic, and reciprocal adaptations to reinforce it are likely to exist (Snow 1971, McKey 1975, Howe and Smallwood 1982). Recent studies on the evolutionary ecology of plant-disperser interactions have emphasized plant adaptations for efficient seed dispersal (e.g., Howe and Estabrook 1977, Salomonson 1978, Howe and Vande Kerckhove 1979, 1980, Thompson and Willson 1979, Fleming 1981, Herrera 1981*c*, 1982*a*, Denslow and Moermond 1982, Stiles 1982, Willson and Thompson 1982). In contrast, structural and functional adaptations of vertebrate dispersers for frugivory have received little attention (but see Snow 1973, McKey 1975, Walsberg 1975, Morrison 1980, Milton 1981). The objectives of this paper are: (1) to identify unique morphological and digestive features of avian seed dispersers, using coexisting nonfrugivores and nondisperser frugivores as "control" groups; and (2) to determine if these features are adaptations for frugivory. Results of these analyses are also used to examine whether the much greater reliance of seed dispersers (plants' mutualists) on fruit food relative to nondisperser frugivores (nonmutualists) (Herrera, *in press*) may be interpreted in terms of their adaptations to fruit food and, therefore, if these adaptations are indicative of plant-disperser coevolution in scrublands (Herrera 1982*a*).

METHODS

Information on avian frugivory was gathered from 1978 to 1982 in two areas of sclerophyllous scrublands in southern Spain. A detailed account of field methods, vegetation of study sites, and bird-plant relationships is presented elsewhere (Herrera, *in press*). In this paper I concentrate on morphological and digestive features of scrubland birds in relation to frugivory. The species considered include all those recorded at the sites in the 4-yr study, excluding the rarest species (those yielding single captures in mist nets).

Mist-netted birds were weighed and the following measurements taken: bill length from feathers to tip, width and depth of the bill at the posterior edge of nostrils, and gape width (distance between the commissural points). This last measure was taken by inserting the pointed tips of vernier calipers into the bird's open mouth and slowly separating them until a gentle pressure was exerted on the mouth commissures.

To obtain estimates of food passage time through the gut many birds were given a small amount (0.1–0.5 mL, depending on bird size) of barium sulfate in water suspension (1:1 in volume) containing "fast green," an innocuous stain. The suspension was placed in the gizzard by an orally inserted plastic catheter (1.5 mm external diameter) connected to a graduated syringe. Birds were then held in cloth bags and examined frequently. The time between administration and first appearance of feces containing the stained barium sulfate was noted. This time was used to assess interspecies variation in gut passage time (GPT). The barium treatment was not applied to all birds netted in the study areas, and some GPT's were obtained (using the

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same technique) for birds at other sites to increase sample sizes of some species.

The general relation between barium-determined and actual food passage times is unknown, and hence my GPT's may differ from actual times. In the case of several of the frugivores in my study, barium-determined times are often longer than actual fruit passage times (Sorensen, *in press*, C. M. Herrera, *personal observation*). The barium method has some obvious advantages, however: (1) it is possible to obtain data from many individuals and species in the field; (2) it is applicable to species differing strongly in feeding habits; (3) it can be standardized; and (4) by using an inert marker, the method emphasizes inherent digestive properties by reducing or eliminating effects arising from the nature of the food on intestinal passage (e.g., laxative effects of fruits, as shown later).

Specimens of as many species as possible were dissected to examine certain features of their digestive tracts. Since I had to minimize disturbances to my study populations, birds were not collected on the study plots. Except for a few birds which died accidentally during mist-netting, specimens came from other sources (road kills, hunters, personal collections), but all were from southern Spain. Information recorded for dissected birds included: length of intestine from gizzard to cloaca, liver mass (wet), and gizzard mass (wet), after removal of food. This last measurement was for the muscular gizzard, disregarding the proventriculus. These organs have been shown to change seasonally in some species (e.g., Spitzer 1972, Pendergast and Boag 1973, Silverin 1981). The data presented here are representative of seasons when the species are present (migrants) or are most abundant (residents) in the scrublands studied (see Herrera, *in press*, for detailed data on the seasonal status of species studied).

RESULTS

Scrubland passerines have been divided into three groups according to diet and fruit handling techniques (see Herrera, *in press*, for diet composition data supporting species assignments): "Nonfrugivores," species which do not eat fruit (even when abundantly available); "Seed dispersers," frugivores which ingest the fruits whole and defecate or regurgitate the seeds unharmed; "Fruit predators," frugivores which handle fruits in a destructive way, in feeding on the pulp ("pulp predators") or the seeds ("seed predators") alone, without effecting seed dispersal. Seed predators characteristically extract the seed(s) from ripe fruits, discard the pulp, and eat the kernel after husking the seed(s). Pulp predators peck at the pericarp, ingesting pieces of pulp and neglecting the seed(s). Nonfrugivores (9 families, 15 species) are much more diverse at the familial level than frugivores (5 families, 26 species). Among frugivores, all seed dispersers (14 species) are in the Muscicapidae (warblers, flycatchers, thrushes), all seed predators (4 species) belong to the Fringillidae (finches), and pulp predators (8 species) are distributed among four families (Prunellidae, Muscicapidae, Aegithalidae, Paridae) (Table 1).

TABLE 1. Distribution of passerine species of mediterranean scrublands of southern Spain according to family and frugivory class. Family nomenclature follows Storer (1971*a*). See Results for definitions of categories and Appendix for a complete list of species.

Family	Frugivory class			
	Nonfrugivores	Seed dispersers	Fruit predators	
			Pulp	Seeds
	Number of species			
Laniidae	2			
Motacillidae	1			
Troglodytidae	1			
Prunellidae			1	
Muscicapidae	5	14	2	
Aegithalidae			1	
Certhiidae	1			
Sittidae	1			
Paridae			4	
Corvidae	1			
Fringillidae	2			4
Emberizidae	1			

It must be emphasized that the three major species groups considered here are associated in the scrubland habitat with different levels of frugivory. Fruit predators consume fruits with variable frequency, but this food type always represents a minor fraction of total food biomass. Seed dispersers ingest fruits very often and these represent a substantial fraction of the diet for most species (Herrera, *in press*). This paper is concerned with identifying unique features of strong frugivores that disperse seeds, rather than with a detailed examination of the correlates of fruit handling methods. Pulp and seed predators (occasional frugivores) are therefore treated together in most analyses below, even though they feed on different fruit parts. From the viewpoint of their relation with foodplants both groups have similarly detrimental effects on seed dispersal and thus are functionally equivalent.

Morphological correlates of frugivory

Each species was characterized by mean body mass (log transformed) and six ratios describing bill dimensions and shape: bill length, width, and depth divided by cube root of body mass; bill width and depth divided by bill length; and bill width divided by gape width. Through emphasizing shape-related aspects, morphological ratios have the advantage over original measures of minimizing size-mediated intercorrelation between variables which could obscure the results of multivariate analyses.

A stepwise multiple discriminant analysis (MDA) revealed significant differences among the three groups (Table 2). Variables relating to body mass, bill shape, and relative gape width (D, E, F, G in Table 2) con-

TABLE 2. Results of multiple stepwise discriminant analysis of morphological features of nonfrugivorous, fruit-predatory and seed-dispersing birds of mediterranean scrublands of southern Spain. N = number of species in each group.

Morphological variables*	Overall mean	Group means: Nonfrugivores ($N = 15$)	Group means: Fruit predators ($N = 12$)	Group means: Dispersers ($N = 14$)	Canonical coefficients†: CV I	Canonical coefficients†: CV II	F‡	P
A. Bill length/(body mass)$^{1/3}$	4.29	4.75	3.92	4.12	···	···	0.99	.38
B. Bill width/(body mass)$^{1/3}$	2.05	2.01	2.28	1.89	···	···	0.52	.60
C. Bill depth/(body mass)$^{1/3}$	1.76	1.81	2.14	1.39	···	···	0.23	.80
D. Log_{10} body mass	1.22	1.24	1.14	1.28	−2.11	0.72	3.73	.03
E. (Bill width/gape width) × 100	65.12	64.70	73.49	58.39	0.09	0.02	3.88	.03
F. (Bill width/bill length) × 100	49.02	44.05	58.36	46.36	−0.13	−0.16	8.09	.001
G. (Bill depth/bill length) × 100	42.30	39.98	54.80	34.06	0.11	0.06	6.42	.004

* Linear measurements in millimetres, masses in grams.

† Only those for variables contributing significantly to discriminant functions are shown.

‡ Evaluated after the last step adding a significant variable to the discriminant functions.

tributed significantly to discrimination among groups. Neither variable describing bill size (length, width, depth) in relation to body mass (A, B, C) contributed significantly to discriminant functions. Mouth width relative to bill width was the first variable entering the discriminant functions, and was the single most significant variable in group differentiation ($F = 9.18$, $P = .0006$).

All pairwise comparisons between groups were statistically significant (Fig. 1). Size and position of confidence ellipses in the canonical plane indicated that seed dispersers were the most distinct and homogeneous group. Nonfrugivores and fruit predators were the two most similar groups, and both were fairly homogeneous. Nonfrugivores occupied an intermediate position between seed dispersers and fruit predators. This morphological pattern corresponded closely to the pattern of within- and among-group taxonomic heterogeneity in Table 1.

Seed dispersers tended to be larger bodied, and to have flatter and broader bills than the other groups. They also tended to have a wider gape relative to bill width. Fruit predators, on the other hand, tended to be smaller and to have relatively deeper bills and narrower gapes. Nonfrugivores tended to have bills that were relatively more slender and weaker at the base than those of the other two groups (Table 2). A principal components analysis (PCA) of the same morphological data revealed identical intergroup differences. This further supports the existence of different morphological patterns, since segregation on the morphological plane in PCA does not rely on a priori grouping of species as in MDA.

The morphological segregation of seed dispersers from the other two groups was not a simple consequence of the exclusive participation of Muscicapidae in this group (Table 1), however. Average (±SD) scores on the first canonical axis (CV I) for seed dispersing (−1.30 ± 0.53), nonfrugivorous (−0.21 ± 0.62), and fruit predatory (+0.05 ± 0.60) muscicapid species differed significantly ($F = 10.35$, $P = .001$), and their relative magnitudes were similar to those of the entire species set.

Dispersers and predators did not overlap on CV I, the most significant axis of segregation among frugivores (Fig. 2). Seed predators were clumped on the positive extreme, showing minimal overlap with pulp predators. A pattern of essentially continuous variation in the proportions of the trophic apparatus was therefore associated with an abruptly discontinuous pattern of avian fruit utilization techniques: from swallowing whole fruits, through pecking at the pulp, to feeding on enclosed seeds.

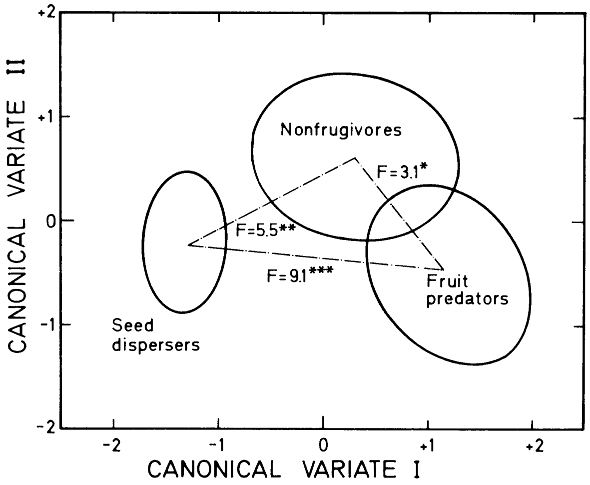

FIG. 1. Distribution of seed disperser, nonfrugivorous, and fruit predatory species over the plane defined by the two canonical variates (Table 2). Ninety-five percent confidence ellipses are shown for every group. F values shown beside lines connecting ellipse centers refer to the difference between the groups concerned after the last step in discriminant analysis that added a significant variable to discriminant functions. * $P < .05$; ** $P < .01$; *** $P < .001$. See Table 2 for numerical results of analysis.

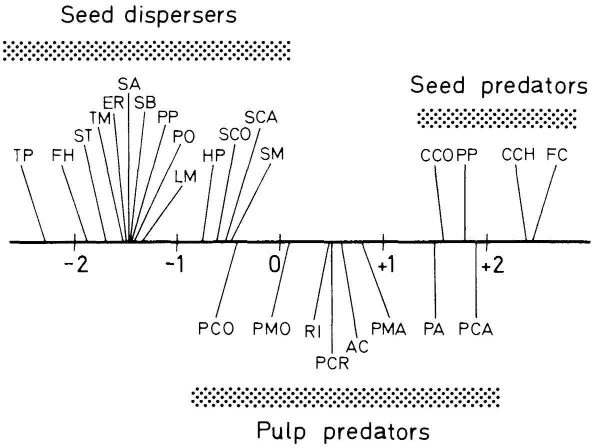

FIG. 2. Position of frugivorous species along the first canonical axis of discriminant analysis on morphology (Table 2). Species are symbolized by the initials of generic and specific names; the second letter of the species name is added when necessary to avoid ambiguity. (See Appendix for complete species names.)

Digestive system

Data on the size of digestive organs were obtained for 25 species (see Appendix). Comparisons between species groups were performed using averages for the ratios of gizzard and liver mass to body mass, and the ratio of intestine length to the cube root of body mass. (Intestine length increases across species in proportion to body mass cube root; McLelland 1979.) There were no significant differences among groups in the length of intestine ($F = 0.63$, $P = .54$), or mass of gizzard ($F = 0.23$, $P = .80$) and liver ($F = 2.60$, $P = .09$) relative to body mass. However, seed dispersers showed a significantly larger ratio of liver mass to body mass than did the combined nonfrugivores and fruit predators groups ($F = 5.17$, $P = .037$). To determine whether greater liver size was statistically dependent on the habit of feeding on whole fruits or was a taxonomic artifact, I performed a similar comparison for muscicapid species alone. The liver comprised on the average 3.96 ± 0.55% of body mass in the nonfrugivorous and fruit predatory muscicapids. This was virtually identical to the value for seed dispersers (4.03 ± 0.67%) ($F = 0.04$, $P = .85$), all of which belong to this family. The liver constituted a significantly larger fraction of body mass in the Muscicapidae (4.01 ± 0.59%) than in other species combined (2.97 ± 0.82%) ($F = 13.48$, $P = .0016$). Thus, the greater relative liver size of seed dispersers is due to their affiliation in the Muscicapidae, and not to the type of frugivory they exhibit.

Gut passage time

Average gut passage times (GPT) were obtained for 30 species (see Appendix). GPT increases linearly with log body mass within the three species groups, but regression lines were much steeper for nonfrugivores and fruit predators than for seed dispersers (Fig. 3). For a given body mass, seed dispersers had shorter GPT than did other groups, and the difference became more pronounced as body mass increased. For comparison, GPT of an 80-g disperser was similar to that of a 9-g nondisperser, and for species of ≈15 g body mass, GPT of nondispersers was ≈2.5 times that of dispersers. Covariance analysis revealed a significant overall heterogeneity of the three regressions ($F = 9.78$, $P = .0007$). The regressions of fruit predators and nonfrugivores were indistinguishable ($F = 0.001$, $P = .98$). When these two groups were combined, comparison with seed dispersers revealed a highly significant heterogeneity in the regressions ($F = 20.31$, $P = .0001$). These results demonstrate that seed dispersers are a distinct group with regard to GPT.

The difference in GPT between seed dispersers and the other groups persisted after the analysis was restricted to the Muscicapidae. Average values (±SD) of GPT/log body mass ratio were significantly smaller ($F = 16.82$, $P = .001$) for muscicapids that are seed dispersers (29.9 ± 8.5) than for those that are not (64.0 ± 22.9). I therefore conclude that shorter GPT's of seed dispersers are not a fortuitous consequence of taxonomic relationships.

Fruits often have laxative effects, and the shorter GPT's of seed dispersers might be a short-term effect of sustained fruit ingestion in the hours or days immediately preceding capture. The alternative hypoth-

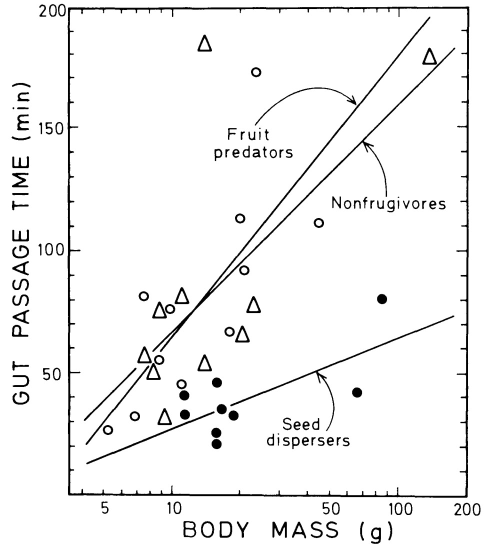

FIG. 3. Variation of gut passage time with body mass. Symbols represent average values for individual species (see Appendix): nonfrugivores, triangles; fruit predators, open dots; seed dispersers, filled dots (see Results for definitions of these categories). Least squares regression lines are shown (note logarithmic scale on horizontal axis).

TABLE 3. Seasonal differences in average (±SD) gut passage time (GPT) of some frugivorous species. Sample sizes (number of GPT determinations) are shown in parentheses.

	Insectivorous (spring–summer)	Frugivorous (autumn–winter)	*F*	*P*
	Gut passage time (min)			
Seed dispersers				
Erithacus rubecula	32.5 ± 32.2 (35)	36.3 ± 25.8 (104)	0.50	.48
Sylvia atricapilla	24.3 ± 17.3 (20)	36.6 ± 24.6 (79)	4.49	.04
Pulp predators				
Aegithalos caudatus	22.9 ± 15.7 (16)	63.0 ± 53.8 (5)	7.59	.001
Parus ater	49.7 ± 35.4 (13)	65.0 ± 51.9 (7)	0.62	.44
Parus major	69.4 ± 32.7 (45)	54.3 ± 40.6 (9)	1.46	.23

esis is that GPT (as measured with barium sulfate) is a species-specific feature, independent of the food currently being consumed. Within-species comparisons of GPT for individuals with and without fruit in their current diets should help to decide between these two hypotheses. Fruits are not available in spring and early summer in one of my study scrublands, yet some resident frugivores are present, relying entirely on insects for food at these times (Herrera, *in press*). Sufficient data for seasonal comparisons of GPT are available for two seed dispersers and three pulp predators (Table 3) which are entirely insectivorous in spring–early summer, and consistently frugivorous in autumn–winter (Herrera, *in press*). Only two species exhibited significant seasonal variation in GPT, and in both instances GPT was longer when they were frugivorous. Both dispersers and pulp predators ingest fruit pulp, where any potentially laxative substance should be found. Hence, these results falsify the first hypothesis above and favor the view that the shorter GPT of seed dispersers is an inherent feature. Results of the seasonal comparisons should not be taken, however, as ruling out fruit laxative effects; these may exist, and seasonal constancy of GPT may only indicate that the barium sulfate method is insensitive to them.

As shown above, intestine length relative to body size is similar in all groups; hence GPT variation results from variation in the passage rate of ingesta (length units of digestive tract per time unit).

DISCUSSION

Digestive system

Previous studies have shown that either the gizzard is smaller, the liver larger, or the intestine shorter, in frugivorous birds, and have interpreted these differences as adaptations to improve digestive efficiency and/or food processing rate (Wetmore 1914, Wood 1924, Desselberger 1931, Walsberg 1975, Pulliainen et al. 1981). The species examined were strongly frugivorous for most or all of their lives (*Bombycilla, Dicaeus, Euphonia, Phainopepla, Ducula*). My analysis has not detected significant differences between scrubland seed dispersers and other birds in the relative size of digestive organs. Most of these birds are strongly frugivorous from summer through fall and winter, but are largely insectivorous for the remainder of the year. Major structural adaptations to a frugivorous diet may have been precluded by the conflicting demands of a seasonally shifting diet, or perhaps the frugivorous habit is too recent to have promoted significant structural adaptations (see Concluding discussion). At any rate, most seed dispersers are able to subsist for long periods on a fruit-dominated diet, either in the mediterranean scrublands or in their African winter quarters (Moreau 1972, Herrera 1981*b* and *in press,* Jordano 1981, Jordano and Herrera 1981), even without major structural adaptations. Adaptations in the fine structure of the digestive tract cannot, however, be ruled out (see Balla and Ziswiler 1979).

Large livers relative to body size are shown by birds with protein-rich diets (McLelland 1979). The fact that the Muscicapidae, which include many seed dispersers, have the largest livers of the groups examined here suggests that this familial trait, presumably associated with its originally insectivorous, protein-rich diet (see below), has "preadapted" (sensu Bock 1980) it to frugivory. The well-known detoxification capacity of the avian liver (Brattsten 1979) is important because of the frequent presence of toxins in the pulp of ripe fruits (Herrera 1982*b*), and probably increases with liver size (see Jaksić et al. 1979, Pulliainen et al. 1981, and references therein).

Morphology

Morphological correlates of avian frugivory have often been suggested which relate to trophic and/or locomotory structures (see e.g., Storer 1971*b,* Snow 1973, Karr and James 1975, Ricklefs 1977, Rybczynski and Riker 1981, Traylor and Fitzpatrick 1982). Quantitative studies usually have treated frugivores as a single group (Karr and James 1975, Ricklefs 1977, Rybczynski and Riker 1981), thus failing to recognize the remarkable heterogeneity in fruit-handling techniques that they exhibit (e.g., Howe 1977, McDiarmid et al. 1977, Herrera and Jordano 1981, Janzen 1981, Jordano 1983). Variation in fruit-handling behavior has been shown here to relate to structure of the bill, suggesting that pooling species with different feeding methods may hide important relationships. This may account for Karr and James' (1975: Table 5) failure to find significant canonical correlations between frugivory and morphology.

Among scrubland frugivores, those that swallow whole fruits and feed most heavily on fruit (seed dispersers) are most distinct in morphology. Fruit predators, for whom fruit is a minor food, are similar to nonfrugivores in morphology. Is the morphology of dispersers an adaptation to feeding on whole fruits, or is ingestion of whole fruits largely a consequence of morphological preadaptation? Answering this is difficult (Bock 1980, Jaksić 1981), but some evidence supports the second possibility.

Seed and pulp predators are but occasional frugivores, feeding mostly on seeds (Fringillidae) and insects (Aegithalidae, Muscicapidae, Paridae) and having bill morphologies adapted to these foods (Newton 1967, Partridge 1976). These two groups, along with the strongly frugivorous seed dispersers, are distributed uninterruptedly along the morphological gradient defined by the first canonical variate (Fig. 2). The Muscicapidae, to which all dispersers belong, is a large family of primarily insectivorous species that prey on small- to medium-sized arthropods taken from vegetation (Sylviinae), ground (Turdinae), or air (Muscicapinae). These insectivorous habits are probably responsible for the relatively homogeneous bill morphology of family members. This family is split into several smaller ones by some authors (van Tyne and Berger 1976) and may eventually prove to be polyphyletic (Sibley and Ahlquist 1980). Insectivory on mobile insect prey requires, among other things, (1) strength at the bill tip to subdue prey, (2) an ability to hold mobile prey between the jaws prior to swallowing, and (3) in the case of flycatchers, a relatively broad gape (Lederer 1980). Bill morphology of the "generalized insectivorous" type of (muscicapid) seed dispersers fulfills these requirements (see e.g., Beecher 1951, Bock 1966, Storer 1971*b*, Lederer 1975, 1980, Greenberg 1981). Regardless of locomotory aspects, which are not treated here, feeding on whole fruits requires an ability to detach the fruit from the plant and hold it firmly in the jaws (most fruits are nearly spherical). It also necessitates broad gape to allow fruit passage. These requirements are well served by adaptations 1, 2, and 3 above, as illustrated not only by muscicapid frugivores but also by New World tyrannids, another essentially insectivorous group with many frugivorous members (17 out of 88 genera; Fitzpatrick 1980, Traylor and Fitzpatrick 1982). It should be noted that those muscicapids which usually hunt insects by sallying flights from perches invariably use the same technique when feeding on fruits (Herrera and Jordano 1981, Jordano 1982). It is therefore reasonable to consider the bill morphology of seed dispersers as the cause (preadaptation), not the (evolutionary) consequence, of their feeding on whole fruits.

Gut passage time

Fruits enclose one or several seeds, which are not digested by seed dispersers but occupy a space in their digestive tracts that could otherwise accommodate nutritious material. The pulp of most fruits, on the other hand, is high in water (up to 90%) and, on a dry mass basis, contains much digestible carbohydrate, some lipids, but very little protein (Hulme 1970, White 1974). As a consequence, the dry mass of nutritious material obtainable by seed dispersers per mass unit of fresh whole fruit ingested is very low (Herrera 1981*a*). The low nutritive value of individual fruits is offset by great seasonal abundance in many habitats, particularly in the temperate zone (Johnson and Landers 1978, Thompson and Willson 1979, Baird 1980, Sorensen 1981). In the mediterranean scrublands of southern Spain, instantaneous density often is near one million fruits/ha (Herrera, *in press*). It is therefore the ability to process fruits rapidly that enables birds to exploit these virtually unlimited, but individually minimally rewarding items.

For seed dispersers, fruit processing has two separate components, evacuation of useless seeds and digestion of pulp. Scrubland dispersers either regurgitate or defecate seeds, mostly within 5–30 min of fruit ingestion (Sorensen, *in press*, C. M. Herrera, *personal observation*). Rapid seed processing alone increases ingestion rate and enhances potential assimilation rate. Its actual significance in improving assimilation rate depends on the food value of the material replacing the evacuated seeds. I suggest that the greater the food value of the pulp, the greater the advantage of rapid seed processing; with decreasing food value of the pulp, speeding the process of pulp digestion should become more important. The watery and almost fiberless nature of most fruit pulps favors rapid digestion and absorption of nutrients, facilitating the evolution of rapid pulp passage rates (Morrison 1980, Milton 1981, Sibly 1981, and references therein). In contrast, long retention times are advantageous when low digestibility (as opposed to nutrient dilution) is responsible for the low food value of abundant forage (Milton 1981, Sibly 1981).

Significantly shorter GPT's of scrubland seed dispersers should be interpreted as an indispensable feature for sustained subsistence on a strongly frugivorous diet. In addition, this characteristic is an adaptive evolutionary response to fruit-feeding. The Muscicapidae are homogeneous in the size of digestive organs, yet seed dispersers in this family have substantially shorter GPT's than nondispersers. Similar differences exist within each of the two subfamilies (Sylviinae, Muscicapinae) that have both dispersers and nondispersers in the sample of species studied here. An advantageous trait is thus possessed by seed dispersers which is not exhibited by related nondisperser taxa, and actual adaptation to frugivory is therefore most likely responsible for the difference.

The seasonal constancy of GPT (as measured with barium sulfate) among dispersers may be due to (1) the fact that short GPT's are not particularly disadvantageous when insect prey are abundant (spring–early summer) and ingestion rates are not limiting, and (2) physiological constraints that preclude substantial seasonal alteration in GPT, the autumn–winter advantages of short GPT outweighing disadvantages at other times. Hard insects, especially beetles, are often recovered intact from feces of seed dispersers, but this never occurs among nondisperser muscicapids. This suggests that rapid processing actually impairs assimilation of food items less digestible than fruit pulp. Further studies are needed to elucidate the digestive trade-offs faced by seasonally frugivorous birds.

Concluding discussion

From the viewpoint of the mutualistic interaction of plants with seed dispersers, it is important to consider if differential reliance on fruit food exhibited by fruit predators and seed dispersers is related to their morphological and digestive differences. The preadapted morphology of dispersers enables feeding on whole fruits (a necessary condition for legitimate frugivory), but it is their functional digestive adaptation that most likely allows sustained and heavy frugivory. Among pulp predators, their long GPT's probably render unprofitable a diet based chiefly on low-quality, albeit highly digestible food. Among seed predators that strip the pulp and crack seeds, long fruit-handling times resulting from poorly suited bill morphology (C. M. Herrera, *personal observation*) most likely lower the place of fruits in their ranking of preferences due to decreased energy intake rate (Willson 1971, Willson and Harmeson 1973). Adaptations of dispersers enabling them to consume fruits in greater quantities will ultimately increase the fitness of fruit-bearing plants and should be seen as a step in the process of plant-disperser diffuse coevolution in scrublands (Herrera 1982*a*). The absence of these adaptations among nonmutualistic fruit predators similarly points to a coevolutionary component in the patterns revealed by this study.

The interaction between seed dispersers and plants in southern Spanish scrublands is of relatively recent origin (Herrera, *in press*). Given enough evolutionary time, morphological and structural digestive adaptations could perhaps evolve among avian dispersers. Seasonal frugivory imposes limits on commitments to permanent structural modifications, however, and potentially flexible, more subtle functional adaptations should be expected. The adaptation in GPT (see also Berthold 1976, Herrera, *in press*) is of this kind, and is much less apparent than the structural adaptations of year-round frugivores (e.g., Wetmore 1914, Wood 1924, Desselberger 1931, Walsberg 1975). In the context of plant-disperser coevolution, however, unapparent adaptations can be as relevant as conspicuous structural ones in reinforcing the mutualistic interaction. In mediterranean scrublands these adaptations maintain a plant-bird seed dispersal system with high levels of mutualistic congruency and reciprocal benefit (Herrera, *in press*).

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APPENDIX

Morphological and digestive data used in the present study (average figures). *N* = number of individuals examined.

		Morphology						Gut passage time		Digestive system			
Species	Type of frugivory*	*N*	Body mass (g)	Bill length (mm)	Bill width (mm)	Bill depth (mm)	Mouth width (mm)	(min)	*N*	*N*	Gizzard mass (g)	Intestine length (mm)	Liver mass (g)
Aegithalos caudatus	FP(P)	33	6.9	5.2	3.3	3.1	5.3	32	(21)				
Carduelis carduelis	NF	23	14.7	12.2	5.3	6.6	6.5	185	(3)	3	0.332	173	0.424
Carduelis chloris	FP(S)	35	23.8	12.5	8.8	9.7	10.8	171	(4)	5	0.359	217	0.683
Certhia brachydactyla	NF	23	8.3	15.0	3.0	2.8	5.9	51	(5)				
Cisticola juncidis	NF	10	8.5	9.4	3.7	3.2	6.6						
Coccothraustes coccothraustes	FP(S)	9	44.5	19.0	14.8	14.7	16.3	111	(7)	3	1.038	373	0.858
Emberiza cia	NF	33	23.0	11.2	6.2	5.8	8.0	79	(34)				
Erithacus rubecula	SD	33	16.8	9.7	4.7	3.3	8.0	35	(139)	21	0.724	175	0.781
Ficedula hypoleuca	SD	13	15.5	8.5	5.2	3.3	7.9			3	0.554	150	0.451
Fringilla coelebs	FP(S)	33	21.1	11.5	6.6	7.1	8.0	92	(25)	5	0.646	226	0.903
Garrulus glandarius	NF	11	139.6	27.3	14.5	12.4	18.8	179	(11)	3	5.712	455	3.112
Hippolais polyglotta	SD	9	11.3	11.3	5.0	3.1	7.7	42	(5)				
Lanius excubitor	NF	8	63.2	17.3	7.8	9.1	14.6						
Lanius senator	NF	34	30.9	12.9	7.1	6.9	12.5			2	0.744	217	0.897
Locustella naevia	NF	4	13.0	10.3	3.7	3.4	6.9						
Luscinia megarhynchos	SD	15	20.9	12.1	5.1	3.9	9.2						
Motacilla alba	NF	18	21.3	11.7	4.1	3.5	7.0			2	0.653	145	0.714
Muscicapa striata	NF	9	14.1	12.0	6.2	3.8	9.5	54	(11)				
Parus ater	FP(P)	76	8.8	8.5	3.7	3.4	5.3	55	(20)				
Parus caeruleus	FP(P)	87	9.8	6.7	4.1	3.9	5.2	77	(25)	18	0.129	133	0.386
Parus cristatus	FP(P)	68	10.9	8.3	3.9	3.5	6.1	43	(19)				
Parus major	FP(P)	48	16.8	10.1	5.3	4.8	7.3	67	(54)	7	0.384	142	0.533
Phoenicurus ochruros	SD	11	16.0	10.4	4.7	3.3	8.4	25	(3)	7	0.552	159	0.563
Phoenicurus phoenicurus	SD	33	15.8	10.1	4.7	3.5	8.6	22	(3)	2	0.565	142	0.627
Phylloscopus bonelli	NF	17	7.5	9.0	4.1	2.9	6.1	57	(18)				
Phylloscopus collybita	FP(P)	71	7.5	7.8	3.4	2.3	5.6	81	(15)	4	0.240	106	0.342
Phylloscopus trochilus	NF	14	9.0	8.4	3.7	2.6	5.5	76	(28)	4	0.185	116	0.358
Prunella modularis	FP(P)	16	19.9	10.5	5.2	3.9	6.8	113	(8)	5	1.408	226	0.729
Pyrrhula pyrrhula	FP(S)	9	21.4	8.8	8.3	8.6	10.2			2	0.721	195	0.403
Regulus ignicapillus	FP(P)	21	5.3	7.9	3.2	2.3	5.1	27	(8)	2	0.130	66	0.220
Saxicola torquata	SD	23	15.8	10.6	4.8	3.5	9.3	46	(4)				
Serinus serinus	NF	19	10.9	7.3	5.3	5.6	6.3	80	(3)				
Sitta europaea	NF	19	20.5	16.9	5.5	4.7	8.3	65	(20)				
Sylvia atricapilla	SD	75	18.3	10.1	5.1	3.6	8.5	34	(99)	23	0.542	146	0.839
Sylvia borin	SD	30	19.0	9.9	5.2	3.8	8.6			7	0.412	150	0.813
Sylvia cantillans	SD	13	9.7	8.3	3.9	2.8	6.3						
Sylvia communis	SD	33	16.7	10.0	4.6	3.6	7.5			2	0.404	135	0.722
Sylvia melanocephala	SD	56	11.4	10.0	4.3	3.1	7.1	33	(39)	11	0.465	128	0.502
Troglodytes troglodytes	NF	9	9.3	10.5	3.4	2.9	6.2	32	(4)	3	0.279	107	0.348
Turdus merula	SD	79	85.1	21.6	7.7	7.1	13.4	80	(39)	6	2.329	266	3.999
Turdus philomelos	SD	19	68.2	16.4	6.6	6.0	13.7	43	(2)	13	1.882	357	2.020

* NF, nonfrugivores; SD, seed dispersers; FP, fruit predators (parenthetical S and P indicate seed and pulp predators, respectively).