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BREEDING SYSTEMS AND DISPERSAL-RELATED MATERNAL REPRODUCTIVE EFFORT OF SOUTHERN SPANISH BIRD-DISPERSED PLANTS

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Dioecious plants, characterized by the occurrence of separate male and female individuals, represent a relatively unimportant fraction of the total world's flora (Bawa, 1980). Nevertheless, owing to the nonrandom distribution of the dioecious habit among life forms, successional stages and habitat types, dioecy may become a prominent feature of some regional or taxonomic plant assemblages (Ashton, 1969; Bawa, 1974; Bawa and Opler, 1975; Bawa, 1980; Conn et al., 1980; Freeman et al., 1980; Givnish, 1980). The dioecious condition has been found to be relatively overrepresented in later successional stages of tropical vegetation (Opler et al., 1980) and among trees and shrubs (Bawa, 1980; Conn et al., 1980; Freeman et al., 1980), vertebrate-dispersed plants (Bawa, 1980; Givnish, 1980), small-flowered tropical species (Bawa and Opler, 1975; Opler et al., 1975), wind-pollinated temperate plants (Freeman et al., 1980), and tropical species pollinated by small opportunistic insects (Opler et al., 1975; Bawa, 1980).

Although promoting outcrossing has been traditionally suggested as the principal selective pressure underlying the evolution of dioecy (see recent reviews by Willson, 1979; Bawa, 1980; Givnish, 1980), some of the ecological correlates of the dioecious habit have recently served to suggest alternative and/or complementary explanations to its evolution (Freeman et al., 1976; Willson, 1979; Bawa, 1980; Freeman et al., 1980; Givnish, 1980; Cox, 1981). In particular, the strong association found between dioecy and seed dispersal by vertebrates has lent support to the notion of this breeding system having evolved among these plants in response to disperser-mediated, intrasexual competition pressures favoring a disequilibrium in the allocation of resources to male and female functions (Bawa, 1980; Givnish, 1980; but see Thomson and Barrett, 1981). It was assumed by the last-mentioned authors that vertebrate dispersers will select for higher dispersal-related maternal expenditure, thus ultimately favoring the spread of dioecy. In this context, it is of interest to compare female investment in disperser-attracting structures shown by dioecious and nondioecious vertebrate-dispersed plants.

Increased "returns" in fitness with increasing maternal absolute reproductive effort were considered by Bawa (1980) and Givnish (1980) in relation to the size of fruit crops only, assuming that plants with larger fruit crops have greater attractiveness to dispersers (Howe and Estabrook, 1977; Howe and Vande Kerckhove, 1979; Howe, 1980). Nevertheless, crop size is just a single component of the total female reproductive investment associated with vertebrate-dispersal. The amount of flesh (the food reward which attracts dispersers to fruits; Snow, 1971; McKey, 1975) per fruit, and the energy and nutrients per weight unit of flesh, are two further important aspects of a plant's fruiting pattern which influence fruit consumption by frugivores and hence, presumably, the fitness of the plant. At an intraspecific level, frugivores have been shown to favor plant phenotypes with a higher flesh content per fruit (Howe and Vande Kerckhove, 1980) and, among species, dispersers seem to prefer those with the most nutritious fruits and/or those with higher flesh/seed ratios (Herrera, 1981*a*, 1981*b*; Jordano and Herrera, 1981). Plants might therefore obtain increased "returns" in fitness to their maternal investment by increasing either the quality or the quantity of fruits, or both. I compare in this paper dioecious and nondioecious species with regard to both fruit quality and crop size.

METHODS

The species sample analyzed in this paper comprises 73 southern Spanish bird-dispersed (see below) species representing more than 85% of the total native bird-dispersed flora of Andalusia, the southernmost Spanish mainland region lying in the range of latitudes 36°–38°30′N and longitudes 2°–7°W. Species are representative of vegetational formations ranging from lowland mediterranean sclerophyllous scrub to mountain coniferous forest. Details of study sites and vegetation types sampled have been given elsewhere (Herrera, 1982*a*). Sites fall neatly into two distinct groups, namely those with nutrient-rich, deep alluvial soils in the lowlands of the Guadalquivir River valley, and those with shallow, nutrient-poor rocky soils in limestone mountains of the upper course of the same valley (e.g., Anonymous, 1962, 1971). Climate of the region is typically mediterranean, with cool rainy winters and hot dry summers (Linés Escardó, 1970). Lowlands are slightly warmer and drier than highlands (Herrera, 1982*a*).

I have deliberately restricted my analysis to species known (or presumed, see below) to be exclusively or largely dispersed by birds to avoid any bias derived from including species dispersed by other vertebrates which may have evolved different fruit features or fruiting patterns. Species were classed as bird-dispersed mainly on the basis of previous studies on the diet of southern Spanish avian frugivores (Herrera, 1981*b*, in press; Herrera and Jordano, 1981; Jordano and Herrera, 1981; Jordano, in press *a*) and, in a few instances, because the fruits unequivocally matched the ornithophilous syndrome described by van der Pijl (1972). A list of plant species used in the analyses is shown in the Appendix. Although some of these may locally have moderately diverse assemblages of avian dispersers (Jordano, 1982) and a distinct seasonal pattern in the composition of disperser assemblages takes place in southern Spanish habitats (Herrera, 1982*a*), the vast majority of plant species considered in this paper have to rely for seed dispersal, regardless of habitat type, on a fairly reduced group of widespread and abundant passerines belonging to a few related genera (*Sylvia, Turdus, Phoenicurus, Erithacus*) (Herrera, 1981*a*, 1981*b*, in press; Herrera and Jordano, 1981; Jordano, 1982; in press *a*; Jordano and Herrera, 1981).

For every plant species, information was recorded in relation to growth form, breeding system, crop size, and fruit quality. With respect to growth form, species were classed as either herbs, woody vines, small shrubs (height < 0.75 m), large shrubs (0.75–3 m) or trees (> 3 m).

Breeding System.—Species were classed as either dioecious, monoecious or hermaphroditic, mainly based on information presented by Tutin et al. (1964–1980). For five species, my own field observations on plants growing in southern Spain (Herrera, unpubl.) did not agree with these authors (e.g., in the case of some functionally dioecious species with apparently hermaphroditic flowers) and in these instances species were classed according to my own records (see the Appendix for species affected by this procedure).

Crop Size.—Crop size was considered to be the total number of ripe fruits produced by an individual plant over an entire fruiting season. This magnitude often varied markedly between individuals and, in some species, also between years, sometimes spreading over a wide range of values for any given species. It was thus often difficult to obtain a single meaningful figure representative for a species. To overcome this problem partly, I instead assigned species to one of five mutually exclusive categories of crop size roughly representing an increasing geometric series on the basis of field observations conducted in southern Spain from late 1978 through early 1981. For assigning species to classes I used the modal class of crop size, that is, the most frequently observed range of number of fruits produced per individual plants at my Andalusian study sites. For species of *Juniperus,* in which fruit maturation takes two years or more after anthesis (Ceballos and Ruiz, 1971), I considered this long period as the fruiting season of individual plants. For some species with individuals displaying substantial interannual variation in crop size (e.g., *Rhamnus alaternus, Viburnum tinus, Phillyrea latifolia*), figures corresponding to years of higher fruit production were used.

The number of individual plants on which data on crop size are based varies between species, from counts of only 5–10 individuals for the rarest species to data from more than 50 individuals for the commonest ones. Although the degree of accuracy in the determination of crop sizes thus presumably varies between species, I am confident that results have been not affected seriously for this reason since, among species with extensive data, the range of interindividual variation in crop size most often did not exceed the limits of a single class of crop size.

Fruit Quality.—Two separate components of individual fruit quality were considered, namely quality of the flesh (caloric and mineral content) and relative amount of flesh per fruit.

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 weight. Chemical determinations of crude lipid, crude protein (total $N \times 6.25$), fiber and ash were carried out by standard analytical procedures. The proportion of "soluble" carbohydrates was obtained by difference. Estimates of gross caloric content of dry pulp were then obtained using conversion factors of 9.45, 5.65 and 4.10 kcal/g for lipid, protein and carbohydrates, respectively (Paine, 1971). Partial data referring to chemical analyses of fruit pulps of most species used here have been presented elsewhere (Herrera, 1981*c,* 1982*a*).

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 individual plants as possible. For the purpose of this paper, I considered (1) number of seeds per fruit; (2) total dry weight of seeds per fruit; and (3) dry weight of pulp per fruit (all weights to nearest 0.1 mg). Average figures resulting from the individual fruits in the sample were taken as representative for the species and are shown in the Appendix. Although some between-site variation in fruit features may occur in some species (Herrera, 1981*a*), I did not account for this fact, and a single set of descriptive data was used per species.

Nonparametrical statistical tests (Siegel, 1956) will be used throughout.

RESULTS

Occurrence of Dioecy

Of the 73 species considered, 25 (34.3%) are dioecious, four (5.5%) monoecious and the remaining 44 (60.2%) hermaphroditic. Owing to the minor contribution of monoecious species, they will be combined hereafter with hermaphroditic species in a single category ("nondioecious" species). Dioecious species represent a very prominent fraction of southern Spanish bird-dispersed plants, which is consistent with previous findings by other authors (Bawa, 1980; Givnish, 1980). These figures are strikingly similar to those reported by Bawa (1980 Table 4) for two neotropical regional floras, where dioecious species represented 33.3% and 22.9% of all animal-dispersed species.

I have been unable to locate adequate floristic information to compare the relative incidence of dioecy in my sample of bird-dispersed plants with the frequency of occurrence among other species differing in seed dispersal methods living in the same general region. Detailed information regarding the specific composition of woody vegetation of two 3.5-ha intensively surveyed plots of lowland and montane mediterranean scrub (Viso and El Cantalar sites; Herrera, 1982*a*) is however available. At these two sites, dioecious species represent 56.3% and 38.9% of ver-

TABLE 1. *Relative importance of dioecious and nondioecious (hermaphroditic and monoecious) taxa among woody plants growing at two southern Spanish 3.5-ha plots of mediterranean sclerophyllous scrub (see Herrera, 1982a for site descriptions).*

	Percent of species		
	Dioecious	Non-dioecious	Significance[a]
Lowland site			
Vertebrate-dispersed (N = 16 spp.)	56.3	43.7	P = .002
Other (N = 18 spp.)	5.6	94.4	
Montane site			
Vertebrate-dispersed (N = 18 spp.)	38.9	61.1	P = .027
Other (N = 10 spp.)	0	100	

[a] Fisher exact probability test.

tebrate-dispersed (endozoochorous) woody species, but only 5.6% and 0% of woody species with other dispersal methods. Differences are highly significant at both sites (Table 1).

Of the species considered in this paper, 60 (82.2%) are largely confined to either of the two major substrate types mentioned earlier (fertile alluvial and nutrient-poor rocky soils in lowlands and highlands, respectively), and the remaining 13 species are found on both lowland and highland sites. Dioecious species represent 43.5% of species restricted to lowland fertile-soil habitats, and 27.0% of those limited to highland, poor-soil sites, but this difference does not reach statistical significance (G = 1.71, $d.f.$ = 1, P = .19). If the species simultaneously occurring on lowlands and highlands are also considered, dioecious and nondioecious species still continue to be similarly represented across the three categories (G = 1.83, $d.f.$ = 2, P = .40).

Crop Size

Since plants differing in size will tend to produce (other things being equal) differently-sized fruit crops, the effect of growth form must be accounted for when comparing dioecious and nondioecious species with regard to crop size. A three-way test of independence among growth form, breeding system and crop size (Table 2) reveals that there is a strong overall dependence among these variables in the sample of species studied. Of the three pairwise independence tests, only that relating to variation of crop size with growth form is significant, indicating that crop size is strongly dependent on growth form, as expected. Nonsignificance of the interaction term suggests that variation of crop size with growth form is similar within the dioecious and nondioecious species groups.

There is no significant relationship between breeding system and growth form in the sample studied (P = .76), indicating that the various growth forms are quite similar with regard to the frequency of occurrence of dioecious taxa. The analysis also reveals that there is no significant association between breeding system and crop size when the effects of growth form are held constant. This is further illustrated in Figure 1, where frequency distributions of modal crop sizes for dioecious and nondioecious taxa are compared. Although there seems to be a trend towards less interspecific variation in crop size within the group of dioecious species, the two distributions do not differ statistically (D = .21, P = .23, Kolmogorov-Smirnov two-sample test), hence in the species sample studied dioecious and nondioecious species are similar with regard to the component of maternal expenditure relating to the number of fruit produced per individual and season.

Fruit Quality

Average values for dioecious and nondioecious taxa of variables characterizing dispersal-related maternal expenditure re-

TABLE 2. *Three-way test of independence (Sokal and Rohlf, 1969) among crop size (CS), growth form (GF) and breeding system (BS) in a sample of 73 southern Spanish bird-dispersed plant species.*

Hypothesis tested	Degrees of freedom	*G*-statistic	*P*
GF × CS independence	16	53.42	<.0001
GF × BS independence	4	1.86	.76
CS × BS independence	4	6.36	.17
GF × CS × BS interaction	16	21.26	.17
GS × CS × BS independence	40	82.80	<.0001

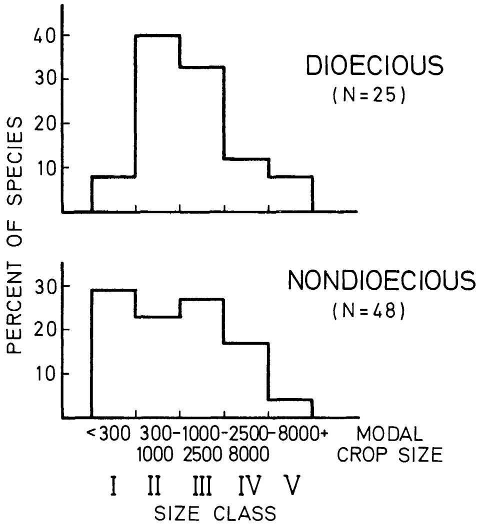

FIG. 1. Frequency distributions of crop size for dioecious and nondioecious (hermaphroditic and monoecious, see text) species (*N* = number of species in each group). "Modal crop size" refers to the most frequently observed range of number of ripe fruits produced by individuals of a species over an entire fruiting season (see Methods).

lated to fruit quality are presented in Table 3, all growth forms combined. Two distinct components have been considered: (1) amount of pulp, both absolute (per individual fruit) and relative (per number and weight of seeds); and (2) quality of the pulp with regard to energy and nutrient content. These two components were later combined to obtain various absolute and relative overall estimates of maternal investment in each individual fruit.

Dioecious and nondioecious species do not differ significantly with regard to either dry weight of pulp placed in each fruit, pulp/seed ratio, or weight of pulp produced per individual seed. The two groups of species do differ, however, in the quality of the pulp, with dioecious species having fruits with pulps significantly higher in energy (kcal/g), and lower in mineral (% ash) content, than those of nondioecious species. Nevertheless, overall estimates of fruit cost to the plant as measured by the energy placed in pulp per either individual fruit, individual seed, or seed weight unit, do not differ significantly for dioecious and nondioecious species. Differences in overall mineral costs approach statistical significance in two comparisons, with nondioecious species tending to place more minerals per individual fruit and seed weight unit than dioecious ones. These results demonstrate that, on the whole, there are only very slight, nonsignificant differences between dioecious and nondioecious species with regard to the overall energy and mineral costs of individual fruits, both in absolute (per fruit) and relative (per seed weight and number) terms. Marginally significant differences tend to suggest greater mineral expenditure in the fruits of nondioecious species.

Comparisons of fruit costs within growth forms were possible for trees, large shrubs and small shrubs. For herbs and woody vines sample sizes were too small to conduct separate analyses. A summary of dioecious-nondioecious comparisons is presented in Table 4. Within every growth form, the direction of differences is generally coincident with those obtained in the comparisons of all growth forms combined. Twenty-eight out of 33 comparisons in Table 4 are in the directions revealed in Table 3. This tends to suggest that the various growth forms conform to the general pattern of differences when considered individually. Only four comparisons were statistically significant. All of these were in the class of large shrubs, and in the four instances reflected greater costs of individual fruits to nondioecious

TABLE 3. *Energy and nutrients in the pulp of southern Spanish bird-dispersed plants, all growth forms combined. Mean values ± 1 standard deviation are shown, sample sizes in parentheses.*

Maternal investment in fruit pulp	Dioecious species	Nondioecious[a] species	Difference[b]
(1) "Quantity" Component			
Dry weight of pulp per fruit (mg)	64.9 ± 67.7 (25)	88.0 ± 114.7 (48)	n.s.
Pulp/seed dry weight ratio	1.33 ± 1.10 (25)	1.43 ± 1.40 (48)	n.s.
Dry weight of pulp per individual seed (mg)	47.1 ± 63.0 (25)	40.5 ± 54.7 (48)	n.s.
(2) "Quality" Component			
Energy content of pulp (Kcal/g dry weight)	4.66 ± 1.04 (22)	4.29 ± 0.54 (38)	$P = .04$
Mineral content of pulp (% ash, dry weight)	4.30 ± 2.91 (24)	4.98 ± 2.27 (43)	$P = .01$
(3) Overall costs			
(a) Energy			
Total energy in pulp per fruit (kcal)	0.34 ± 0.43 (22)	0.41 ± 0.50 (38)	n.s.
Energy in pulp per individual seed (kcal)	0.26 ± 0.42 (22)	0.20 ± 0.25 (38)	n.s.
Energy in pulp per seed weight unit (kcal/g)	6.35 ± 5.12 (22)	6.39 ± 6.25 (38)	n.s.
(b) Minerals			
Total minerals in pulp per fruit (mg)	2.36 ± 2.15 (24)	4.73 ± 6.73 (43)	$P = .06$
Minerals in pulp per individual seed (mg)	1.53 ± 1.60 (24)	2.20 ± 2.98 (43)	n.s.
Minerals in pulp per seed weight unit (mg/g)	50.8 ± 43.8 (24)	69.1 ± 63.2 (43)	$P = .07$

[a] Includes hermaphroditic and monoecious species.

[b] Tested with Mann-Whitney U-test for large samples using the z-transform of U (Siegel, 1956). Levels of significance determined according to the area under the normal curve (one-tailed). n.s., nonsignificant ($P > .20$ in all cases).

species in terms of minerals and amount of pulp per fruit. These results indicate that, within growth forms, there are no or very slight differences between breeding systems with regard to the maternal expenditure in the pulp of individual fruits, and that observed trends point to greater costs among nondioecious taxa.

It has been shown so far that dioecious and nondioecious species do not differ significantly in dispersal-related maternal effort with regard to the number of fruit produced (crop sizes), and that the cost of individual fruits is also roughly similar. Nevertheless, differences could perhaps still exist between the two groups if there were some significant relationship between crop size and fruit quality across species, and the nature of this relationship were different in dioecious and nondioecious species. To explore this possibility I related crop size to total energy and min-

TABLE 4. *Summary of within-growth form comparisons of maternal expenditure in fruit pulp by dioecious (D) and nondioecious (ND) taxa, showing the direction of differences. Only those comparisons marked with asterisks are statistically significant (* P < .05; ** P < .01). Direction of differences was evaluated by comparing the appropriate average values. Significance was tested with Mann-Whitney test.*

	Small shrubs	Large shrubs	Trees
Dry weight of pulp per fruit	D < ND	D < ND*	D < ND
Pulp/seed dry weight ratio	D < ND	D < ND	D < ND
Dry weight of pulp per individual seed	D > ND	D < ND	D > ND
Energy content of pulp	D > ND	D > ND	D > ND
Mineral content of pulp	D < ND	D < ND*	D < ND
Total energy in pulp per fruit	D < ND	D < ND	D > ND
Energy in pulp per individual seed	D > ND	D < ND	D > ND
Energy in pulp per seed weight unit	D > ND	D < ND	D < ND
Total minerals in pulp per fruit	D < ND	D < ND**	D < ND
Minerals in pulp per individual seed	D < ND	D < ND	D < ND
Minerals in pulp per seed weight unit	D > ND	D < ND**	D < ND

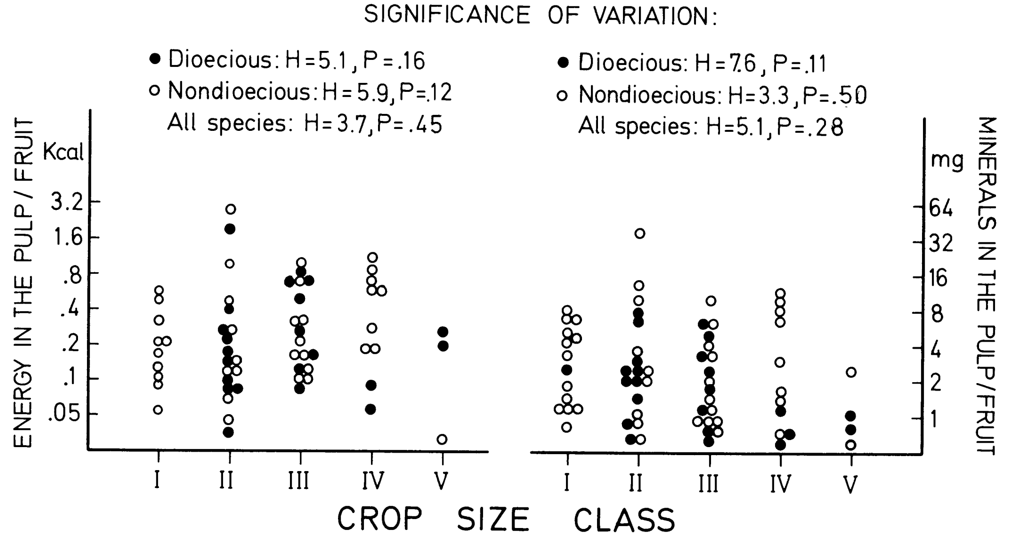

FIG. 2. Variation of fruit quality (total energy and nutrients contained in the pulp of a single fruit) with crop size. Crop size classes as defined in Figure 1. Significance of variation tested by means of Kruskal-Wallis one-way analysis of variance (Siegel, 1956).

eral content in the pulp of individual fruits (Fig. 2). There is no clear pattern of variation relating fruit quality to crop size for either dioecious, nondioecious, or all species combined, and observed variation is statistically nonsignificant in all instances.

DISCUSSION

Givnish's (1980) model for the evolution of dioecy among animal-dispersed plants represents an explanation of the differential occurrence of dioecy *among* species assemblages with different seed dispersal methods. Based on the empirical observation that dioecy is proportionally overrepresented among animal-dispersed taxa (see also Bawa, 1980), Givnish proposed a model for the *within*-species evolution of this breeding system. The core of his model could thus perhaps be properly tested only by studying within-species variation in maternal dispersal-related expenditure, through comparisons of resource allocation patterns by individuals differing in breeding system. Apart from the practical difficulties associated with selecting the appropriate study subject, such *within*-species test would probably be only indirectly relevant to the pattern under study (the differential occurrence of dioecy *across* species assemblages), unless it were performed for many species belonging to both animal-dispersed and non-animal-dispersed categories. For different reasons, Thomson and Barrett (1981) have also pointed out the difficulties involved in testing Givnish's model. Even though they do not emanate immediately from the original model, somewhat less restrictive tests may be envisaged which are based on comparisons between species.

According to Bawa (1980) and Givnish (1980), the critical factor in the evolution of dioecy among vertebrate-dispersed plants is not that dispersal by frugivores is more expensive than other dispersal methods, but rather the disproportionate gains in fitness derived to these plants from an increase in absolute maternal reproductive investment specifically directed to improve attractiveness to seed dispersers. A testable prediction arising indirectly from this explanation to the high incidence of dioecy among vertebrate-dispersed plants is that, other things being equal, dioecious species should tend to show a greater absolute female investment in disperser-attracting structures than their nondioecious counterparts. If within species the dioecious state actually results from an increase in maternal effort, species which have already acquired this state should tend to show greater maternal effort than those which still did not, all else being equal. Results presented in this paper demonstrate that the absolute dispersal-related maternal reproductive expenditure, measured in terms of energy and nutrients, does not differ significantly for dioecious and nondioecious bird-dispersed species. Nondioecious taxa are able to produce as many and as good fruits as dioecious ones and still retain the male reproductive function. This finding is inconsistent with the prediction stated earlier. Two kinds of reasons may be advanced to account for this disagreement: (1) inadequacies of the comparisons performed, as a test of the model; and (2) inadequacies in the model being tested.

Depending on species-specific average values of absolute maternal effort, any value on the x-axis of Figure 1 in Givnish (1980) may fall on either side of the various critical threshold points separating the hermaphroditic and dioecious conditions for several species. In other words, since the value of absolute effort at the critical point of theoretical disequilibrium between paternal and maternal expenditures almost certainly varies among species, interspecific comparisons of observed dispersal-related maternal expenditure could be considered a reasonably valid test of Givnish's model only if the major sources of interspecific variation in absolute effort are accounted for. Although further factors may be suggested, one should expect plant size (growth form) and growing conditions (soil fertility, climate) to be among the most important factors explaining interspecies variation of absolute effort in large and heterogeneous species sets such as that used in this paper. Accordingly, two related kinds of comparisons of dispersal-related maternal effort between dioecious and nondioecious taxa may be performed which one may reasonably expect to serve as an indirect test of Givnish's model: (1) between species in a relatively narrow range of plant sizes (e.g., within the same growth form); and (2) for all growth forms combined, provided that dioecious and nondioecious species sets are similar with regard to their distribution across growth forms and growing conditions. Comparisons presented in this paper are of these two kinds, and the raw data used have been shown to meet the latter requirements.

It has been found that the two breeding systems do not differ significantly with regard to their relative distribution across growth forms and growing conditions in the sample of species studied. Inasmuch as growth form, climate and soil fertility are the factors responsible for most interspecies variation in absolute maternal effort in my species sample, comparisons performed in this paper should be regarded as reasonable tests of Givnish's model. Further factors not accounted for here could influence observed maternal effort (e.g., competition, herbivory, habitat disturbances). These neglected variables would invalidate comparisons only if the nature of their effects on maternal expenditure vary with breeding system and its significance in explaining interspecific variation in maternal effort are greater than that of the variables I have accounted for (growth form and growing conditions). Although this seems unlikely, no information is available in this regard; hence the possibility that observed results are due to inadequacies of the test cannot be ruled out entirely.

Some limitations inherent to Givnish's model can be suggested which could help to interpret the observed pattern of similar maternal expenditure in dioecious and nondioecious species. Although between-species comparisons performed in this paper are subject to the limitations pointed out above, considerations to follow mainly refer to the within-species context in which the model was originally devised, and thus are largely independent of the potential weakness of my comparative approach. I do not intend to mean that inadequacies in the within-species context are directly responsible for the between-species patterns shown above, but rather to stress that serious reasons exist to question some of model's assumptions, and hence that apparently anomalous results may not be due to inappropriateness of my test but rather to actual incorrectness of the model.

Resource Allocation

Like other models (e.g., Charnov et al., 1976; Maynard Smith, 1978), Givnish's is based on the assumption that male and female functions share energy and nutrients. Although this must be generally true for maternal and paternal floral expenditures, it may not apply generally to the case of the dispersal-related fraction of maternal reproductive effort owing to two reasons: (1) fruits contribute partially to their own production costs; and (2) there is virtually no temporal overlap in resource use between male and dispersal-related female functions.

As pointed out by Thompson and Stewart (1981), ". . . for the principle of allocation to be useful, there must be a limited pool of the resource and this pool must not be increased in size by the very act of allocation". Owing to their photosynthetic activity, most developing fruits contribute a substantial amount of their own costs of production in both perennial and annual plants (Bazzaz and Carlson, 1979; Bazzaz et al., 1979). For some vertebrate-dispersed perennial species, Bazzaz et al. (1979) reported contributions to total carbon balance around 20%. As expected from the consideration of surface/volume ratios, the proportional contribution of developing fruits tends to be greater for smaller fruits. Fruit dry weight at maturity and percent contribution to total carbon balance are significantly correlated in the data presented by Bazzaz et al. (1979 Table 1) ($r_s = -.450$, $P < .05$). Bird-dispersed fruits dealt with in this paper have total dry weights falling in the lower range of fruit sizes considered by Bazzaz et al. (1979), thus probably contribute significantly to their own production costs and, accordingly, competition with male reproductive function should be greatly reduced. This applies only to the energy and carbon requirements for fruit production, but not to the mineral-related costs (Thompson and Stewart, 1981). For these, fruits must rely on the general mineral supply of the plant and, in this regard, they could compete with male function. Nevertheless, this must be mitigated by temporal staggering of nutrient demands for flowers and fruits, as discussed below.

Temporal segregation of sexual functions may often make unreasonable the assumption of maleness and vertebrate-dispersal being two metabolic sinks competing extensively, unless both functions depend exclusively on previously stored metabolites. This latter possibility would particularly apply to species which do not reproduce sexually every year (e.g., Sohn and Policansky, 1977; Janzen, 1978; Silvertown, 1980; Davis, 1981; Udovic, 1981), but not to the most ordinary case of adult perennial plants reproducing every year, for which current energy and nutrient availability seems to determine seed and/or fruit numbers (Janzen, 1971, 1976; Halls, 1973; Rockwood, 1973; Coombe, 1976; Stephenson, 1980; Willson and Price, 1980; Myers, 1981). The agricultural literature provides many examples of developing tree fruits that predominantly utilize metabolites produced by current photosynthesis and therefore unavailable to the plant at the time of flower production (Bollard, 1971; Nitsch, 1971; Coombe, 1976). The contribution to fruit development from current photosynthesis of nearby leaves has been shown for both wild (Janzen, 1971; Stephenson, 1980) and cultivated (Coombe, 1976) trees. It has also been shown for some cultivated trees that the rates of photosynthesis in leaves increase to high levels at the time when accumulation in the fruit is greatest (Coombe, 1976).

It is clear from the studies mentioned above that paternal and dispersal-related maternal reproductive investment do not extensively share the same resources. Furthermore, if vertebrate-dispersed plants maximize their maternal fitness during one reproductive season by adjusting the amount of maternal investment to the resources available at several sequential stages (Lloyd, 1980; Lloyd et al., 1980; Stephenson, 1980), then the relationship between male effort and the eventual dispersal-related female effort should be very loose.

It must be noted that the preceding reasoning is not intended to mean that fruit production by perennial plants does not compete for energy and/or nutrients with other plant functions (e.g., growth; Nitsch, 1971; Harper, 1977; Coombe, 1976). It rather emphasizes the fact that the principle of allocation may often be an unwarranted assumption when male and dispersal-related female functions are involved.

Dispersal Success and Maternal Effort

A further aspect to be considered, which is central to Givnish's model (see also Bawa, 1980) is the assumption that a steep increase in plant fitness follows from a linear increase in absolute dispersal-related maternal effort. This was made explicit for crop size (not for fruit quality), based on the assumption of increased attractiveness of larger fruit crops to frugivores. Nevertheless, increased number of visits by frugivores to plants with larger fruit crops (e.g., Howe and De Steven, 1979; Howe and Vande Kerckhove, 1979; Howe, 1980) does not always result in greater dispersal success (percent of seeds produced which are actually dispersed). Among long-lived perennials, as most vertebrate-dispersed species are, seasonal reproductive output summed over the entire lifetime of the individual is what natural selection will tend to maximize. Since energy and nutrient availability often limit the actual absolute reproductive output per season (e.g., Halls, 1973; Rockwood, 1973; Janzen, 1976; Stephenson, 1980; Willson and Price, 1980), high seed (plus pulp) waste rates per season (low dispersal success) occurring frequently over a plant's lifetime would represent an evolutionary disadvantage. Seed dispersal success should thus tend to be maximized among polycarpic plants as a way of saving energy and nutrients which could be reallocated to other functions. It thus seems reasonable to consider the variation of seed dispersal success with dispersal-related maternal investment rather than, or in addition to, total number of seeds dispersed as considered by Givnish.

At an intraspecific level, Howe and Estabrook (1977) and Howe (1979) have dealt with the expected shape of curves relating dispersal success to crop size. In some cases, predicted curves present a critical threshold level of crop size beyond which further increases in crop size do not improve, or even impair, dispersal success (e.g., through the attraction of seed-damaging frugivores). Howe and Vande Kerckhove (1979) have shown that particularly small and large individuals of the tree *Casearia corymbosa* disperse smaller proportions of seeds than those of intermediate fecundity. They showed that a quadratic equation was the best fitted to the relationship between crop size and dispersal success. For *Tetragastris panamensis,* Howe (1980) has similarly shown that trees producing the largest and smallest crops tend to waste proportionally more seeds than trees with intermediate crops. This suggests that, at least for some species, an increase of maternal effort actually results in greater seed dispersal success only below some critical level of crop size, but that returns in fitness (as measured by dispersal success) to maternal investment decrease beyond that threshold. On the other hand, no significant relationship has been found between seed dispersal success and crop size in several other tropical species (Howe and De Steven, 1979; Howe and Vande Kerckhove, 1981; Howe, in press). These studies further indicate that within-species variation in dispersal success is not straightforwardly related to dispersal-related maternal effort as measured by crop size.

In interspecific comparisons, it is also unclear that species with greater crop sizes consistently disperse a larger proportion of seeds, since variation in fruit quality plays an important role. Species with small crops of highly rewarding fruits may actually disperse a greater proportion of seeds than those producing much larger crops of less rewarding fruits (e.g., Bonaccorso et al., 1980; Howe, 1981; Howe, in press; Jordano, in press *b*). Total maternal investment per tree is similar in *Tetragastris panamensis,* with large crops of inexpensive fruits, and *Virola surinamensis,* producing few highly-rewarding fruits, but the latter species has a greater dispersal success (Howe, in press). These observations do not imply, however, that species offering low-quality fruits to dispersers invariably have a low dispersal success. High seed dispersal success has been demonstrated for species producing large numbers of fruits possessing extremely low nutritive profitability (Herrera and Jordano, 1981; Jordano, 1982).

In addition to seed output, another potentially important component of plant fitness is the probability that the seeds dispersed will arrive at an appropriate germination site. An individual plant having all its seeds removed by "dispersers" which later take them to places where seedling establishment and growth are extremely unlikely (e.g., Snow 1962; Vázquez-Yanes et al., 1975), will not have higher fitness than a conspecific with lower dispersal success but whose seeds arrive at favorable germination sites. Patterns of postdispersal seed survival among vertebrate-dispersed plants are still very poorly understood, but it has been well established so far that (1) not all seeds taken away from a parent plant are later deposited in microhabitats of comparable survival value (Howe and Primack, 1975; Smith, 1975; Janzen et al., 1976; Vander Kloet, 1976; Salomonson, 1978; Glyphis et al., 1981; Herrera and Jordano, 1981); and (2) location of seed shadows may vary among conspecific individuals depending on varied factors, often unrelated to either crop size or seed dispersal success (Janzen et al., 1976; Heithaus and Fleming, 1978; Fleming and Heithaus, 1981; Glyphis et al., 1981; Herrera and Jordano, 1981), which are not under the control of the plant (see Wheelwright and Orians, 1982).

I do not intend to mean that dispersers lack the ability to become strong selective agents on their resource plants, but rather to emphasize that pressures originating from dispersers are far more subtle, complex and variable than just those tending to favor an increase in absolute maternal reproductive expenditure (via crop size and/or fruit quality). In temperate habitats, for instance, factors such as the presence of secondary compounds in fruit flesh, availability of alternate fruit sources, time of year, within-plant fruiting patterns, and risk of damage to ripe fruits by non-disperser vertebrates, pathogens and invertebrates, all combine intricately to modify both the nature and strength of the selective pressures posed by dispersers on single plant traits such as crop size (Thompson and Willson, 1978; 1979; Herrera, 1981*a*; 1982*a*; 1982*b*; Sorensen, 1981). The high variance which seems to be a characteristic feature of the interactions between plants and seed dispersers (Hubbell, 1980) is difficult to reconcile with the rather high predictability of success for a particular genotype which is inherent in Givnish's model (Thomson and Barrett, 1981).

SUMMARY

Dispersal-related maternal reproductive investment has been studied in a sample of 73 southern Spanish bird-dispersed plant species. Maternal effort directed to attract dispersers was considered in relation to (1) the number of fruits produced per individual plant, and (2) the cost of individual fruits in terms of energy and nutrients in the pulp. Dioecious and nondioecious species have similar maternal investment associated with seed dispersal by vertebrates. This result is inconsistent with the expectation, indirectly derived from Givnish's (1980) pollination-dispersal model, of greater absolute maternal investment associated with seed dispersal among dioecious species. The validity, as a test of the model, of the comparisons per-

formed is discussed. On the other hand, it is shown that some assumptions of the Givnish model either are not fully supported by facts or do not apply generally to fruiting plants. In particular, (1) one should expect male and dispersal-related female efforts not to rely extensively on the same energy and nutrients, and thus correlations between them should be greatly obscured; (2) there is not a straightforward relationship between seed dispersal success and maternal effort as measured by crop size. Owing to the large variances characterizing plant-disperser interactions in nature, one should not expect a neat relationship between crop size (or, in general, any measure of absolute dispersal-related maternal expenditure) and returns in fitness to the parent plant.

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APPENDIX. Crop size, growth form and fruit features of southern Spanish bird-dispersed plants considered in this paper. Nomenclature follows Tutin et al. (1964–1980).

Species	Growth[a] form	Crop size[b] class	Dry weight of pulp per fruit (mg)	Dry weight of seeds per fruit (mg)	Number of seeds per fruit	Ash content of pulp (% dry weight)	Energy content of pulp (Kcal/g dry weight)
Dioecious							
Asparagus acutifolius	SS	I	46.7	44.1	1.1	6.0	—
Asparagus aphyllus	SS	I	40.1	58.7	1.5	—	—
Bryonia dioica	H	II	21.8	36.1	3.3	9.3	4.40
Corema album	SS	II	10.5	29.6	3.0	3.7	4.29
Ilex aquifolium	T	II	43.8	103.0	3.2	4.7	4.15
Juniperus communis	LS	III	32.3	31.3	2.8	2.3	4.95
Juniperus oxycedrus	T	III	180.1	86.8	1.4	2.9	4.58
Juniperus sabina	LS	III	51.0	27.0	2.5	2.4	4.80
Juniperus thurifera	T	III	166.7	69.2	3.1	3.7	4.19
Laurus nobilis	T	II	282.7	697.7	1	2.6	6.99
Osyrus alba	SS	II	95.8	99.4	1	3.2	4.13
Osyrus quadripartita	LS	III	23.1	80.3	1	8.2	3.94
Phillyrea angustifolia[c]	LS	IV	13.0	29.2	1	1.1	4.22
Pistacia lentiscus	LS	V	29.0	25.4	1	2.5	7.23
Pistacia terebinthus	T	V	39.4	49.3	1	2.5	7.09
Rhamnus alaternus[c]	T	IV	22.9	35.9	3.0	5.1	4.04
Rhamnus lycioides[c]	SS	III	30.8	30.9	2.5	1.2	4.18
Rhus coriaria	LS	IV	10.5	8.8	1	3.0	—
Ribes alpinum	SS	II	18.8	11.2	3.3	4.7	4.11
Smilax aspera	WV	II	25.1	38.6	1.5	8.7	3.94
Tamus communis	H	II	57.9	87.0	4.5	13.1	3.80
Taxus baccata	T	III	158.3	69.9	1	1.4	4.09
Viscum album[c]	SS	II	58.0	11.4	1	3.9	4.46
Viscum cruciatum[c]	SS	II	31.8	11.2	1	4.6	4.77
Vitis vinifera sylvestris	WV	III	132.8	49.6	1.8	2.5	4.13
Nondioecious (Hermaphroditic and monoecious)							
Amelancher ovalis	LS	II	68.6	22.1	7.3	3.8	4.11
Arum italicum[d]	H	I	51.6	83.5	2.2	6.7	4.05
Asparagus albus	SS	I	28.9	28.4	1.1	6.4	3.98
Berberis hispanica	SS	III	29.3	21.4	1.5	2.9	4.29
Berberis vulgaris	SS	III	25.6	20.3	1.6	3.3	4.38
Celtis australis	T	IV	222.4	134.0	1	5.0	4.00
Cornus sanguinea	LS	IV	36.9	52.6	1	4.6	5.34
Cotoneaster granatensis	LS	III	25.0	49.9	2.0	8.4	4.01
Cotoneaster integerrimus	LS	II	16.4	37.7	2.0	—	—
Crataegus monogyna	T	IV	171.0	123.7	1	4.3	4.09
Crataegus laciniata	T	IV	168.3	227.9	2.4	4.9	4.05
Daphne gnidium	SS	II	9.5	9.0	1	3.5	4.22
Daphne laureola	SS	I	21.7	22.3	1	6.1	4.01
Frangula alnus	LS	III	18.8	41.6	2.6	—	—
Hedera helix	WV	IV	51.9	36.4	2.2	0.5	5.86
Iris foetidissima	H	I	43.1	56.5	1	2.9	—
Jasmium fruticans	SS	I	39.2	32.1	1.2	3.9	4.41
Juniperus phoenicea[d]	T	III	45.4	34.9	7.4	2.6	4.85
Ligustrum vulgare	SS	II	18.0	24.4	1.1	4.7	4.18
Lonicera arborea	LS	III	66.3	22.2	2.2	7.4	3.98
Lonicera etrusca	WV	II	39.3	27.0	3.0	9.3	3.90
Lonicera implexa	WV	II	36.7	37.7	2.7	5.5	4.03
Lonicera periclymenum	WV	II	30.4	22.5	3.9	3.5	4.40
Lonicera splendida	WV	I	82.3	25.4	3.6	9.6	3.85
Myrtus communis	LS	III	67.4	39.7	7.5	5.2	4.05
Olea europaea	T	IV	90.3	221.0	1	1.6	6.40
Phillyrea latifolia	T	III	41.6	54.3	1	2.2	4.21

APPENDIX. Continued.

Species	Growth[a] form	Crop size[b] class	Dry weight of pulp per fruit (mg)	Dry weight of seeds per fruit (mg)	Number of seeds per fruit	Ash content of pulp (% dry weight)	Energy content of pulp (Kcal/g dry weight)
Polygonatum odoratum	H	I	52.0	72.9	4.1	8.2	—
Prunus mahaleb	T	IV	48.4	79.5	1	6.3	4.06
Prunus prostrata	SS	I	23.2	35.1	1	4.8	4.17
Prunus ramburii	LS	II	105.6	110.1	1	9.8	3.81
Prunus spinosa	LS	II	260.8	241.9	1	5.0	4.08
Rosa canina	LS	III	189.1	103.3	11.0	5.1	4.11
Rosa sp. 1	SS	I	122.2	100.8	8.6	5.9	4.01
Rosa sp. 2	SS	I	156.3	80.7	5.9	2.6	—
Rosa sp. 3	LS	II	690.5	661.2	31.7	6.0	4.02
Rubia peregrina	WV	I	12.3	11.1	1.2	5.9	4.47
Rubus ulmifolius	LS	V	131.2	55.2	28.8	2.1	—
Ruscus aculeatus[d]	SS	I	142.3	243.4	1.4	5.3	4.02
Ruscus hypophyllum[d]	SS	I	54.8	240.1	1.6	9.6	3.96
Sambucus ebulus	H	III	22.9	9.3	3.0	—	—
Sambucus nigra	LS	V	4.5	3.5	2.6	5.5	4.33
Solanum nigrum	H	II	9.1	39.3	40.2	—	—
Solanum dulcamara	H	I	43.1	40.9	27.6	—	—
Sorbus aria	T	III	255.3	30.4	3.8	2.4	4.20
Sorbus torminalis	T	IV	293.0	51.7	2.5	4.1	4.12
Viburnum lantana	LS	III	26.9	32.1	1	2.4	—
Viburnum tinus	LS	III	36.4	37.6	1	4.3	5.14

[a] H, herb; SS, small shrub; LS, large shrub; WV, woody vine; T, tree.
[b] I, <300 fruits; II, 300–1000; III, 1000–2500; IV, 2500–8000; V, >8000.
[c] Species not considered by Tutin et al. (1964–1980) as dioecious but included in this group on the basis of own observations (Herrera, unpubl).
[d] Monoecious species.