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ANGIOSPERM FLESHY FRUITS AND SEED DISPERSERS:  
A COMPARATIVE ANALYSIS OF ADAPTATION AND  
CONSTRAINTS IN PLANT-ANIMAL INTERACTIONS

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*Abstract.*—Variation in phenotypic traits of angiosperm fleshy fruits has been explained as the result of adaptations to their mutualistic seed dispersers. By analyzing the information available on fleshy fruit characteristics of 910 angiosperm species, I assess the hypothesis of evolutionary association between fruit phenotypic traits and type of seed disperser (birds, mammals, and mixed dispersers) and address explicitly and quantitatively alternative null hypotheses about phylogenetic effects. Phylogenetic affinity among plant taxa is accounted for by comparative methods including nested ANOVA, phylogenetic autocorrelation, and independent contrasts. Averaging over the 16 fruit traits examined, phylogenetic effects down to genus level explain 61% of total variance. Phylogenetic autocorrelations are strong among close relatives, reaching significance for 11 of the 16 fruit traits examined. When assessed by independent contrast methods, correlated evolution between type of disperser and fruit traits is confined to fruit diameter. Differences among dispersal syndromes in other traits vanish after accounting for phylogenetic effects. These analyses reveal that seed dispersal syndromes are not entirely interpretable as current adaptations to seed dispersers. Their status as exaptations can be assessed by combining experimental studies of natural selection on fruit size and rigorous comparative and cladistic tests of adaptational hypotheses.

Plant adaptations to one or a few seed dispersers are rare in nature, but relatively invariant, integrated sets of fruit morphologies known as syndromes (Ridley 1930; van der Pijl 1982; Janson 1983) have been identified and interpreted as reflecting broad adaptations to the “disperser/dispersal environment” (Howe 1986; Fleming et al. 1993). Central to this adaptationist interpretation is the assumption that a mutual benefit accrues to both parts, and this benefit is the main factor impelling the coevolution of the interaction. Recent studies challenge this view by discovering limitations to plant-seed disperser coevolution. Genetic constraints (Howe 1984), phylogeny and history (Herrera 1986, 1992*a*; Janson 1992), diversity and asymmetry of the interactions (Jordano 1987*c*), and extensive variation in the outcome of the interactions themselves (Howe 1983; Wheelwright 1988) have been identified as the main obstacles for the evolution of tight, co-evolved relationships. A central issue relevant to this question is therefore the estimation of the relative magnitudes of “constraints” (McKittrick 1993) and “specific adaptations” in the evolution of plant-frugivore mutualisms.

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Previous studies have suggested that phylogenetic constraints are important in plants (see, e.g., Lechowicz 1984; Hodgson and Mackey 1986; Kochmer and Handel 1986; Herrera 1987, 1992*b*; Baldwin and Schultz 1988; Michaels et al. 1988; Donoghue 1989; Stratton 1989; Willson et al. 1989; Gorchoy 1990; Mazer 1990; Willson and Whelan 1990; Chazdon 1991; Lee et al. 1991; Schupp and Feener 1991; Bremer and Eriksson 1992; Fischer and Chapman 1993), but few have attempted to consider their effects explicitly and quantitatively (but see Janson 1992). A comparative approach (Pagel and Harvey 1988) is indispensable for distinguishing similarity that is attributable to common ancestry from similarity attributable to parallel and convergent evolutionary change. The latter is expected among plants sharing the same major seed dispersers if evolutionary change in fruit traits is attributable to coevolved selective pressures by frugivores. Note that both types of effects are not necessarily mutually exclusive, as phylogenetic effects do not prevent natural selection acting on phenotypic traits but set limits to its action by imposing a rigid pattern of covariation among characters. A whole set of recently developed comparative methods (Felsenstein 1985; Pagel and Harvey 1988, 1989; Grafen 1989; Harvey and Pagel 1991; Harvey and Purvis 1991; Martins and Garland 1991; Garland et al. 1992, 1993) can be used for assessing the evolutionary association among quantitative characters but, as far as I know, have never been used with plant data. Here I adopt an explicitly comparative approach to test for evolutionary associations between fruit traits and seed disperser types.

My objective in this article is to answer the following questions. First, what fraction of total phenotypic variance in angiosperm fleshy fruits can be explained by shared ancestry? Residual variation is likely the result of selective forces (adaptations, *sensu stricto*) (Gould and Vrba 1982) and certainly one of the potential major forces is that exerted by frugivores. Second, are fleshy fruit characteristics such as fruit design and particular nutrient combinations in the pulp predictably associated with seed dispersal by particular frugivore groups when phylogenetic affinity among plant taxa is accounted for? If phylogenetic affinity explains a large fraction of total phenotypic variance in fruit traits, we might expect severe constraints for evolutionary modification of fruit structure as suggested by Herrera (1986, 1992*a*) and Wheelwright (1988). Both the broad set of plant data considered and the general categories of disperser types imposed by the available information set limitations to this analysis. However, its validity stems in identifying general trends (and robust methods to assess them) that bear on the important question of the evolutionary, clade-wide association between angiosperm fleshy fruit characters and seed disperser types.

#### ADAPTIVE HYPOTHESES AND PREDICTIONS

The last two decades of studies on the dispersal ecology of animal-dispersed plants have centered in adaptive explanations of the enormous morphological variation in fruit types and frugivore behaviors (see reviews in Howe 1986; Jordano 1992). A strictly adaptationist hypothesis states that fleshy fruit phenotypic variation is exclusively the result of a plant's adaptation to its seed dispersers

(Snow 1971; McKey 1975; Janson 1983). The earlier surveys of Ridley (1930), Turcek (1961, 1967), and van der Pijl (1982), providing correlative evidence for the hypothesis, have been largely supported by more exhaustive studies (Snow 1981; Janson 1983; Wheelwright et al. 1984; Gauthier-Hion et al. 1985; O'Dowd and Gill 1986; Debussche et al. 1987; Herrera 1987, 1989; Debussche 1988; Debussche and Isenmann 1989; Willson 1991, 1993).

Ideally, support for the adaptive hypothesis would come from detailed measures of natural selection on fruit traits in the field. Both experimental studies in captivity and field observations have found positive correlations between gape width of frugivorous birds and maximum diameter of the fruits ingested (Wheelwright 1985; Piper 1986; Jordano 1987*b*; Debussche and Isenmann 1989; Lambert 1989; also see Fleming 1988), which suggests that individual plants may differentially disperse seeds on the basis of fruit, seed size, or seed load variation (Howe and Vande Kerckhove 1980, 1981; Herrera 1981, 1984; Howe 1981; Piper 1986; Jordano 1987*a*; Obeso 1988; Wheelwright 1993; but see Fleming et al. 1985; Foster 1990). Field evidence for differential fruit removal from individual crops mediated by differences in pulp nutrient quality is, however, scanty (Manasse and Howe 1983; Piper 1986; Jordano 1987*a*, 1989; Herrera 1988; Foster 1990). In addition, most of these studies have shown that the selective patterns by frugivores were subject to extreme spatial and temporal variation, which added inconsistency in their strength, direction, and persistence.

To the extent that birds, bats, nonflying mammals, and so forth, differ in preference patterns for different fruit traits, the above selection pressures might translate into the differences between syndromes found in correlative studies across species (see Howe 1986, pp. 150–155; Fleming et al. 1993). The following can thus be predicted under the presence (or great influence) of dispersal/disperser selective effects:

1. Species in different disperser/dispersal categories should differ in overall fruit morphology or particular traits when phylogenetic effects are controlled for. The variance explained by disperser type will not show significant reductions after controlling for phylogenetic effects. This, together with nonsignificant results for phylogenetic effects when estimated by adequate comparative methods (autocorrelation, independent contrasts), will suggest the absence of phylogenetic constraints in fruit morphology and pulp composition, which would add support to the adaptive hypothesis.

2. Consider a gradient of variation in the composition of the disperser assemblage among a set of species, from those dispersed exclusively, or predominantly, by birds, through those showing a similar importance of birds and mammals (mixed dispersal), and then, at the other extreme, those dispersed exclusively, or predominantly, by mammals. Ideally each species would fall somewhere along the gradient depending on the relative importance of birds and mammals in, say, number of visits to the plants, total fruit removal, or number of established seedlings recruited from seed dispersed by them. The adaptive hypothesis predicts particular trends of variation for fruit traits along this gradient that can be summarized as follows: overall fruit size, seed number, relative yield of pulp, nonstructural carbohydrates, and fiber would tend to increase from "bird" to "mixed" to

“mammal” disperser types. Individual seed size, energy content per gram of pulp, lipids, and protein, would show a decrease along this gradient.

#### METHODS

##### *Data*

Quantitative information on traits of angiosperm fleshy fruits (910 species in 392 genera and 94 families) was compiled from both published and unpublished sources including data on 42% of the angiosperm families with this fruit type. Unpublished material comes from collections (C. M. Herrera and P. Jordano, unpublished data) for 42 species in Costa Rica and several Mediterranean species not included in Herrera's published study (1987). The data include 92 North American species, 46 North European, 86 Mediterranean (Europe), 277 Neotropical, and 409 Paleotropical (244 African, 165 Indo-Malayan-Australian). Copies of the data set are available from me upon request (also see Jordano 1992). Fruit size (length and diameter), fresh fruit mass, dry mass of seed(s) per fruit, dry mass of pulp per fruit, individual seed dry mass, number of seeds per fruit, and relative content of dry pulp with respect to fresh mass of the whole fruit (relative yield) were considered “design traits.” Proportion of water, proportions of lipids, soluble carbohydrates, protein, minerals, and acid-detergent fiber with respect to dry mass of pulp, as well as the energy content per gram of dry mass of pulp, and the total energy content/fruit were considered “nutrient content” traits. Figures for relative yield of pulp, total energy per fruit, and total energy per gram of pulp were computed when necessary for estimating these variables from raw data.

Although the analytical methods used in the articles surveyed were obviously varied, most authors followed the methods outlined by the Association of Official Analytical Chemists (1975). Lipids were obtained in most cases with microsoxhlet extraction and protein content by micro-Kjeldahl analysis. When studies reported total nitrogen (N), I used  $N \times 6.25$  as an estimate of crude protein content. Studies reporting analyses of the whole fruit (i.e., including seeds) were excluded.

Ideally, each species should be characterized by the relative proportions of total visits or fruits removed by each major frugivore group, corrected by their effectiveness in terms of seedlings recruited from the seeds removed (Murray 1988; Schupp 1993). This type of information is lacking for most species, and I attempted to assign them to three broad categories along a gradient between species totally, or mostly, dispersed by birds to species typically dispersed by mammals alone. Disperser type categories used as classificatory criteria were dispersal predominantly by birds, mixed (birds and mammals), and mammals (primates, bats, ungulates). Previous studies have emphasized differences among these broad categories (Ridley 1930; Janson 1983; Howe 1986; Fischer and Chapman 1993), and I used them in the analyses. These general categories pose obvious limitations to the present analysis but, on the other hand, solve the potential shortcomings of establishing finer “ad hoc” syndromes when appropriate information is lacking for most taxa (see table 1 in Fischer and Chapman 1993). Species were assigned to the three categories on the basis of published information in the

original articles, general treatments (Ridley 1930; Turcek 1961, 1967; Croat 1978; van Roosmalen 1985; Snow and Snow 1988; Willson 1991, 1993), personal comments of the authors, and personal observations (C. M. Herrera and P. Jordano, unpublished data) for Mediterranean and European species and some Central American taxa. Assignments were based mostly on qualitative assessments of the frequency of feeding records, importance of fruits in the diet, and frequency of references with positive records of feeding by different frugivore types. Information about congeneric species together with fruit morphology (see Janson 1983, 1992) was used in a few cases. The robustness of these criteria varied obviously according with the quality of the background information we presently have for different plant-disperser systems. The categories therefore are rough, and future analyses might show they have to be reassigned for some taxa, but I am confident that the general conclusions of the present analysis will hold. Thus, preliminary analyses with data subsets with greater resolution of disperser types (Mediterranean, North American, and some Neotropical sets) did not reveal that partitioning the dispersal types into additional categories (i.e., large and small birds, bats and nonflying mammals) would alter the main conclusions.

#### *Use of Taxonomic Information*

I performed the analysis using the classification system of Cronquist (1981) and estimated phylogenetic effects and relatedness using the taxonomic relationship among the 910 species in the data set. The important caveat must be made that a more explicitly phylogenetic arrangement is to be preferred for future reanalyses of this data set. More local analyses, now possible with the phylogenetic information for certain taxa, have a great potential for increasing the power of comparative tests (see, e.g., Eriksson and Bremer 1991; Bremer and Eriksson 1992) if combined with greater resolution of the disperser types, and they will be the goal of subsequent articles.

A phylogenetic classification system (Sporne 1956) is an estimate of a phylogeny that can be used to allow analyses with available information. But the conclusions drawn need to be reassessed when more refined phylogenetic information becomes available. Miles and Dunham (1993) provide an updated discussion of the problems inherent in choosing a well-supported phylogeny in comparative studies and the potential weaknesses inherent when using taxonomies instead of phylogenetic trees (also see de Querioz and Gauthier 1992; Garland et al. 1992).

#### *Statistical Analyses*

*Nested ANOVA and autocorrelation methods.*—Analyses were performed on transformed variables (natural logs for weights and linear dimensions and angular transformations for proportions). The variance components, as a percentage of total variance for each taxonomic level, were estimated with NESTED and VARCOMP procedures (SAS Institute 1988) and are used as a description of the *patterns* of variance partitioning and their consistency among traits. Taxonomic levels (class, subclass, order, family, and genus) were specified as nested random effects within each higher level, with class effect being fixed (Bell 1989). However, I did not estimate significance levels for these effects, as the nominal de-

degrees of freedom are lacking because of nonindependence of the data, and the nested ANOVA is heavily unbalanced.

The phylogenetic autocorrelation method (Cheverud and Dow 1985; Cheverud et al. 1985; Gittleman and Kot 1990) partitions the total phenotypic variance of a trait across a number of species into a component attributable to their phylogenetic relationships and a specific component not attributable to phylogenetic inheritance. Autocorrelation coefficients and proportional variance accounted for by phylogeny were estimated by a network autocorrelation model,  $y = \rho \mathbf{W}y + e$ , using the method described in detail by Gittleman and Kot (1990).

The phylogenetic autocorrelation  $\rho$ , measuring the extent to which the phenotypic trait values ( $y$ ) correlate throughout the phylogeny, is estimated by  $\mathbf{W}y$ , representing a linear combination of the total variation in a trait  $y$  among species weighed by their phylogenetic or taxonomic relatedness (matrix  $\mathbf{W}$ ). A maximum likelihood procedure was used to estimate  $\rho$  and  $R^2$ , the variance explained by the model. Higher  $\rho$  values indicate that the more related species tend to be more similar. I used Moran's  $I$  statistic (Moran 1950) to estimate autocorrelation; at any level,  $I$  compared the phenotypic trait of a species with a weighted average of the trait over a set of neighbors. The weights ( $w_{ij}$ ) are functions of the taxonomic relatedness of the species included in the analysis to each other. I used a hierarchical distance (one for congeneric species, two for confamilial species, and so on up to five for species in the same class). To improve model fit I used the grid search procedure for a maximum likelihood estimator described by Gittleman and Kot (1990) to derive  $w_{ij}$  values:  $w_{ij} = 1/d_{ij}^\alpha$ , where  $d_{ij}$  is the distance between species  $i$  and  $j$ , and  $\alpha$  is a variable-weighting index obtained by maximum likelihood estimation. By this method, the form of the decreasing function of phylogenetic connectivity values ( $w_{ij}$ ) when increasing phylogenetic distance need not be assumed a priori, as in the Cheverud et al. (1985) method. All data were standardized to mean zero and unit variance prior to the analysis. Residuals from the autoregressive model were tested for independence following Gittleman and Kot (1990).

*Independent contrasts methods.*—I addressed the hypothesis of functional association (correlated evolution) between fruit characters and dispersal syndrome by using independent contrasts methods (Felsenstein 1985; Burt 1989). I used the Comparative Analysis by Independent Contrasts (CAIC) package, version 1.2, developed by A. Purvis (1991), Oxford University, which implements a variety of methods for continuous and discrete variables (Garland et al. 1992). I report here the results obtained with the punctuational change assumption (equal, fixed branch lengths), because analyses with the gradualistic assumption (variable branch lengths) were highly consistent. The evolutionary correlation between two characters is tested by assessing the relationship between contrasts on the  $X$  predictor variable (e.g., disperser type) and contrasts on the  $Y$ -dependent variable (e.g., fruit diameter) (Harvey and Pagel 1991). If a positive relationship between the two traits exists, it will show up, when the contrasts are plotted, as a positive slope across taxa. I tested this relationship by ordinary least squares regression through the origin, with contrasts standardized using branch lengths of the phylogenetic tree. In addition, I used a binomial test to assess the probability of getting

a given proportion of positive contrasts; an equal number of positive and negative contrasts are expected under the hypothesis of no evolutionary relationship between the traits examined. Harvey and Pagel (1991) and Pagel and Harvey (1992) give details for the calculation of the contrasts and address the problem of unresolved nodes, an issue for which there is no optimal solution yet. The method used to resolve polytomies at multiple nodes uses values of the  $X$  variable to split the taxa (congeners) into two groups, above and below the mean of  $X$ , yielding two subnodes for the multiple node. The linear contrast is computed as the difference between values of these recomputed subnodes (Purvis 1991).

I coded disperser type as a categorical variable with three levels: birds, value of one; mixed, two; and mammals, three. I then interpret the output for the relationships between contrasts on the continuous traits (e.g., fruit diameter or lipid content of the pulp) and contrasts on this variable as a difference in proportions of each disperser category associated with differences in the continuous trait. The rationale for this procedure follows logic developed by Fleming et al. (1993). Suppose each species is located along an ideal gradient of disperser types between an extreme with species totally, or predominantly, dispersed by birds, and another one with species totally, or predominantly, dispersed by mammals. Species with mixed seed dispersal would be closer to one or the other extreme depending on their relative reliance on birds and mammals for fruit removal and seed dispersal. Thus, positive and linear relationships between, say, fruit size contrasts and disperser type contrasts would mean that evolutionary increases in fruit size are associated with evolutionary changes to a greater proportion of mammalian dispersal that might be illustrated by a greater proportion of mammal species in the disperser coterie of the taxa involved in the contrast or by a greater total proportion of seeds dispersed by mammals (Pagel and Harvey 1988; Harvey and Pagel 1991).

Summary statistics are given as mean and 1 SD, unless otherwise stated. Probability levels were fixed at .05. However, in most instances I used a Bonferroni-corrected  $P$  level of .0031, since most comparisons across groups are tablewise and involve separate univariate tests for the 16 fruit traits considered here ( $P = .05/16$ ) (Rice 1989).

## RESULTS

### *General Trends of Variation*

A factor analysis of the correlation matrix (across species) between fruit traits reveals that five significant components account for 77.3% of total variation, which indicates a distinct pattern of covariation among traits (table 1). Families show largely nonoverlapping distributions of species values on the space defined by this component structure (fig. 1), and family effects accounted for a 27.49% of total variation on principal component (PC) 1 and 8.48% for PC 2. Note that conventional parametric tests (ANOVA, MANOVA) for these differences would yield invalid  $P$  values and biased parameter estimates, because species are not phylogenetically independent, and the nominal degrees of freedom would be



TABLE 1

RESULTS OF A FACTOR ANALYSIS OF ANGIOSPERM FLESHY FRUIT TRAITS BASED ON THE CORRELATION MATRICES OF BOTH ORIGINAL VARIABLES AND INDEPENDENT CONTRASTS

Fruit Trait	PC 1	PC 2	PC 3	PC 4	PC 5
Fruit length	.4227	...	...	...	...
	<i>.8952</i>	...	...	...	...
Fruit diameter	.4110	...	...	...	...
	<i>.8506</i>	...	...	...	...
Fruit fresh mass	.4379	...	...	...	...
	<i>.9320</i>	...	...	...	...
Pulp dry mass	.4018	...	...	...	...
	<i>.8776</i>	...	...	...	...
Seed(s) dry mass/fruit	.3662	...	...	...	...
	<i>.8043</i>	...	...	...	...
Number of seeds/fruit	...	...	...	...	.7328
	...	...	...	<i>.9170</i>	...
Seed dry mass	...	...	...	...	-.6140
	<i>.4554</i>	...	...	<i>-.7066</i>	<i>.3024</i>
Relative yield of pulp	...	...	.5878	...	...
	...	...	<i>.6608</i>	...	<i>-.3888</i>
Energy content/g pulp	...	-.2983	...	...	...
	...	<i>.7603</i>	...	...	<i>.4579</i>
Energy content/fruit	.3619	...	.2581	...	...
	<i>.8764</i>	...	<i>.3223</i>	...	...
Water in pulp (%)	...	...	-.4858	...	...
	...	...	<i>-.7645</i>	...	...
Lipids	...	.2674	...	...	...
	...	...	...	...	<i>.8710</i>
Protein	...	...	...	-.6427	...
	...	...	...	...	...
Nonstructural carbohydrates	...	-.8118	...	...	...
	...	<i>.8216</i>	...	...	...
Minerals	...	...	...	-.6088	...
	...	...	...	...	...
Fiber	...	.3747	.4571	-.3563	...
	...	...	<i>.5968</i>	...	...
Eigenvalues	5.31	2.74	1.61	1.41	1.29
	<i>4.93</i>	<i>2.20</i>	<i>1.71</i>	<i>1.56</i>	<i>1.20</i>
% Variance	33.22	17.11	10.09	8.82	8.05
	<i>30.83</i>	<i>13.75</i>	<i>10.66</i>	<i>9.77</i>	<i>7.49</i>

NOTE.—Varimax rotation method with principal component extraction was used on both the correlation matrix for all species in the sample with pairwise deletion of missing values (original variables, values not in italic) and the correlation matrix for independent contrasts in each variable (values in italic). Figures show correlations of each variable with each principal component (PC 1–PC 5). Only these five components, with eigenvalues >1.0, were considered significant (Legendre and Legendre 1979). Loadings <|0.25| are omitted.

incorrect. Therefore, I repeated the principal components analysis (PCA) on the correlation matrix obtained for the independent contrasts. Results were highly consistent with the pattern obtained from the previous analysis (table 1), as expected from the significant consistency between the two matrices ( $r = 0.8057$ ,  $t = 7.24$ ,  $P \ll .0001$ ; Mantel test with randomization,  $n = 1,000$ ) (Legendre and Legendre 1979).

Because of the strong covariation among all size variables, taxa with either

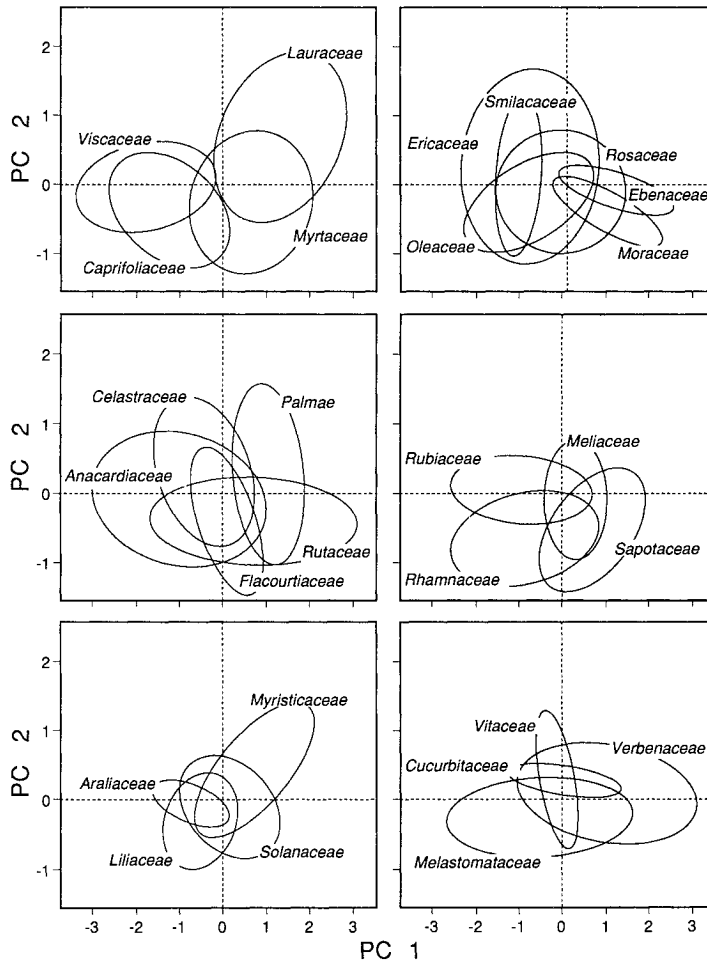


FIG. 1.—Relative locations of angiosperm species, by families, on the first two principal components of fleshy fruit characteristics. Equal frequency ellipses ( $P = .900$ ) are plotted for each family. These ellipses are the contour lines encompassing 90% of the data points (species) for each family. Fruit-size-related variables have high positive loads on PC 1, both lipid content and fiber show high positive loads on PC 2, and nonstructural carbohydrates and energy content per gram of pulp have negative loads on it (table 1). Both axes account for 50.3% of total variance.

large, multiseeded fruits (e.g., Moraceae) or large, drupaceous, or few-seeded fruits (e.g., Lauraceae, Rutaceae, Sapotaceae, some Rosaceae) score high on a first component associated with overall fruit size (fig. 1). Small-fruited taxa, notably Caprifoliaceae (*Sambucus*), Loranthaceae (*Cladocolea*), Viscaceae (*Dendrophthora*), Thymelaeaceae (*Daphne*), Melastomataceae (*Miconia*), and some Rubiaceae (*Nertera*, *Putoria*, *Relbunium*) score low on it. Only the first and fifth

components, which depict the trade-off between individual seed mass and seed number per fruit, involve large loads of "morphological" traits. The components 2, 3, and 4 involve pulp "nutritional" traits (table 1). Thus, PC 2 is interpretable by the strong dissociation between lipids and nonstructural carbohydrates. Taxa with lipid-rich and relatively fibrous pulp score high on it (most *Palmae*, *Lauraceae*, *Myristicaceae*, some *Anacardiaceae*, and *Celastraceae*). Fruits rich in soluble carbohydrates, such as *Mimusops*, *Sideroxylon* (*Sapotaceae*), *Pancovia*, *Paullinia* (*Sapindaceae*), *Dictyophleba*, *Lacmellea* (*Apocynaceae*), and most *Melastomataceae*, *Rhamnaceae*, *Flacourtiaceae*, *Rosaceae*, *Myrtaceae*, and *Capri-foliaceae* show negative scores on PC 2 (fig. 1).

The third component (PC 3) illustrates the inverse relationship across species between relative yield of pulp, energy content per fruit and fiber, on one hand, and pulp water content on the other (table 1). The watery, succulent fruits of *Liliaceae* (*Clintonia*, *Dianella*, *Paris*), *Ranunculaceae* (*Actaea*), some *Rubiaceae* (*Coprosma*, *Coussarea*), and *Empetraceae* (*Empetrum*) species score negatively on this axis. These species have relatively large fruits rich in minerals. Taxa with relatively dry, fibrous, and pulpy fruits typically yield a high amount of energy per fruit, irrespective of the major organic component, and show high positive scores on this PC 3; they include *Crataegus*, *Hesperomeles*, *Sorbus* and *Pyrus* (*Rosaceae*), *Arbutus* and *Arctostaphylos* (*Ericaceae*), *Elaeocarpus* and *Muntingia* (*Elaeocarpaceae*), *Ziziphus* (*Rhamnaceae*), and some *Annonaceae*.

Finally, species with high protein and mineral contents show negative scores on PC 4 (*Ekebergia* and some *Trichilia*, *Meliaceae*; *Ximenia*, *Olacaceae*; *Zingiberaceae*, and most *Piperaceae*). In addition, taxa that typically show high content of nonprotein nitrogen in the pulp score negatively on this axis, and these include *Ruscus*, *Ripogonum* (*Liliaceae*); *Bryonia*, *Citrullus*, *Coccinia* (*Cucurbitaceae*); *Tamus* (*Dioscoreaceae*); and *Mandragora* (*Solanaceae*).

#### *Phylogenetic and Adaptive Effects in Fruit Phenotypic Variance*

*Phylogenetic variance components.*—Partitioning of phenotypic variation among higher categories in the Linnean hierarchy (fig. 2) suggests high similarity in fruit traits among close phylogenetic relatives. On the average, phylogenetic effects down to genus level explain 61% of total phenotypic variance in the traits examined. All the tests revealed large effects of the nested taxonomic hierarchy on the 16 fruit traits, with explained variances ranging from 26.1% (relative yield of pulp) to 89.2% (number of seeds per fruit). For 13 of 16 traits, the variance explained by the nested model accounted for more than 30.0% of total variance. The intraclass correlation coefficients up to the ordinal level were generally less than 0.15, which indicates that a negligible fraction of total variance was accounted for by class, subclass, and order effects in this sample. Only seed(s) dry mass/fruit, individual seed dry mass, and minerals showed relatively large subclass and order effects, with intraclass correlations between 0.20 and 0.30 (fig. 2).

Family intraclass correlations were large for most form and design traits (fig. 2), especially fruit, pulp, and seed(s) masses, individual seed mass, and seed number per fruit. This pattern contrasts with the smaller familial effects and

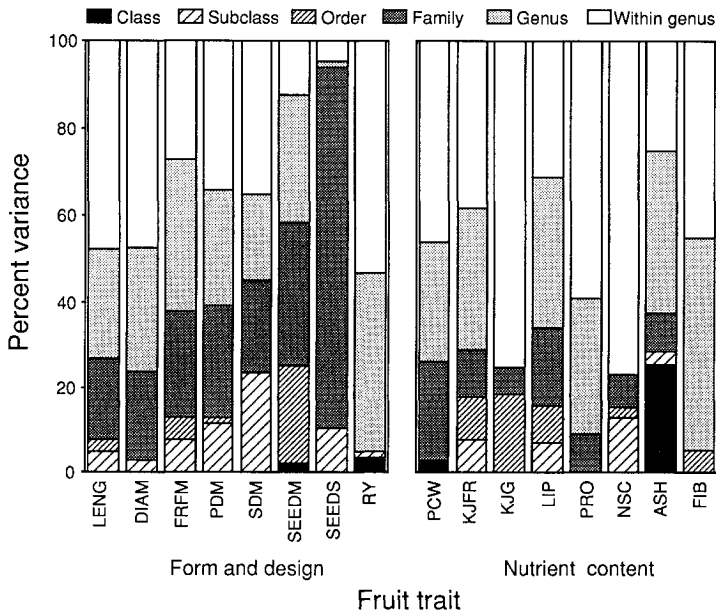


FIG. 2.—Percentages of total trait variance accounted for by taxonomic levels (class to genus) of Cronquist (1981) phylogenetic classification system in a nested ANOVA of angiosperm fleshy fruit characteristics. Fruit traits are grouped in “form and design,” or structural, and nutrient content characteristics. Abbreviations for traits are LENG, fruit length; DIAM, fruit diameter; FRFM, fruit fresh mass; PDM, pulp dry mass; SDM, dry mass of seed(s) per fruit; SEEDM, dry mass of individual seed; SEEDS, number of seeds per fruit; RY, relative yield of pulp ( $100 \cdot \text{PDM}/\text{FRFM}$ ); PCW, percentage water content; KJFR, energy content (kJ) per fruit; KJG, energy content per gram of dry pulp. Nutrient contents are given as proportions relative to pulp dry mass: LIP, lipids; PRO, protein; NSC, nonstructural carbohydrates; ASH, minerals; FIB, fiber.

greater generic effects exhibited by nutrient traits (fig. 2). Excluding the constructed variates RY, KJFR, and KJG, average intraclass correlations for family among form and design traits (0.459) are significantly higher than those for nutrient content traits (0.209;  $t = 2.27, P = .04$ ). Including all taxonomic levels down to genus, the differences between the two groups of traits are only marginally significant (average intraclass correlations for genus, 0.697 and 0.523, respectively;  $t = 1.77, P = .105$ ). Therefore, the two groups of traits differ in the types of phylogenetic effects but only marginally in the overall magnitude of these effects.

*Phylogenetic and specific components: an autocorrelation model.*—By fitting the autoregressive model, significant autocorrelations were obtained for 11 of the 16 fruit traits examined (table 2). This indicates a general effect of phylogeny on most phenotypic variation of angiosperm fleshy fruits. As estimated by  $R^2$ , sizable significant fractions of total variance in fruit and seed masses, fruit seediness, energy reward/fruit, and lipid content can be accounted for by phylogeny (table 2). Fruit dimensions, pulp water content, and protein show significant phyloge-

TABLE 2  
PHYLOGENETIC AUTOCORRELATION COEFFICIENTS ( $\rho$ ), ASSOCIATED SE,  $R^2$ , AND SAMPLE SIZE, FOR  
ANGIOSPERM FLESHY FRUIT TRAITS

Fruit Trait	$n$	$\alpha$	$\rho$	$P$	SE( $r$ )	$R^2$
Fruit length	504	1.00	.24	*	.043	7.65
Fruit diameter	597	3.30	.24	*	.043	8.29
Fruit fresh mass	428	1.00	.46	*	.041	29.68
Pulp dry mass	376	1.40	.42	*	.045	25.67
Seed(s) dry mass/fruit	263	1.00	.38	*	.055	21.76
Number of seeds/fruit	320	1.30	.34	*	.051	16.80
Seed dry mass	194	3.00	.44	*	.059	31.56
Relative yield of pulp	370	7.00	.10	NS	.052	2.16
Energy content/g pulp	453	.10	.16	NS	.046	3.46
Energy content/fruit	233	1.10	.37	*	.058	21.67
Water in pulp (%)	506	4.00	.21	*	.043	7.12
Lipids	495	1.20	.41	*	.039	23.12
Protein	561	8.00	.14	*	.042	4.03
Nonstructural carbohydrates	462	.001	.15	NS	.046	3.04
Minerals	264	.20	.06	NS	.062	.55
Fiber	232	7.00	.03	NS	.066	.14

NOTE.—Variable  $n$ , number of species;  $P$ , probability level; NS, nonsignificant. Coefficient  $\alpha$  is a maximum likelihood estimate of the variable weighting index used to obtain phylogenetic distances (see text);  $R^2$  is the total amount of variation (%) explained by the phylogeny. Asterisks mark significant values for the Bonferroni-corrected probability level  $P < .05/16 = .003$ .

netic components, but these account for much lower fractions of total phenotypic variance. Finally, relative yield of pulp, mass-specific energy content, soluble carbohydrates, minerals, and fiber show negligible phylogenetic effects (table 2).

Figure 3 shows the taxonomic correlograms for fruit traits computed according to Gittleman and Kot (1990). These values of Moran's  $I$  depict the correlations between trait values and weighted averages of these values over sets of taxonomic neighbors. The correlograms locate where the taxonomic effects show up and, more importantly, if the way phylogenetic autocorrelations change with taxonomic distance is consistent across traits. A pattern that emerges from figure 3 is that most fruit traits show decaying correlograms, with strong autocorrelations between close taxonomic relatives that decrease when one proceeds up the Linnean hierarchy. The decaying of  $I$  values is steeper for design traits than for nutrient traits, which adds support to the results reported above from nested ANOVA.

#### *Evolutionary Associations between Fruit Phenotypic Variation and Type of Seed Disperser*

*Patterns of variation associated with seed dispersal syndromes.*—A central issue in this study is whether differences between seed dispersal syndromes are supported when the phylogenetic relationships between species are controlled for. To an unknown degree, these differences may arise from the association between phylogeny and fruit characteristics, because individual species are not independent data points.

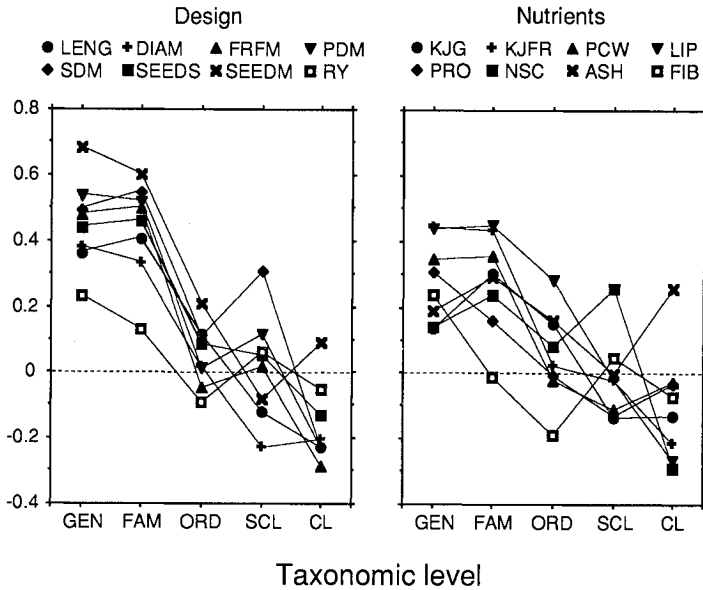


FIG. 3.—Phylogenetic correlograms for design and nutrient content traits (abbreviations as in fig. 2) of angiosperm fleshy fruits. Values of Moran's  $I$  statistic at various nested taxonomic levels (genus, family, order, subclass, and class, along the abscissa) are plotted for each fruit trait. Moran's  $I$  values were rescaled by maximum  $I$  values ( $I_{max}$ ) for comparison across traits (Gittleman and Kot 1990). Correlograms show how phylogenetic correlations change along the nested taxonomic hierarchy.

Ignoring phylogenetic similarity, species whose fruits are consumed and seeds dispersed by different types of vertebrate frugivores differ in most fruit traits examined (tables 3 and 4), and the general trends of variation observable confirm those found in previous studies with smaller data sets. First, average fruit size, estimated either by the length, diameter, or fresh mass of the fruit, increases from bird-dispersed species to mammal-dispersed species, with intermediate values for taxa with mixed dispersal. Second, the total energy reward per fruit increases, in a parallel trend, from bird- to mammal-dispersed species, a result of the strong correlation across species between fruit size and dry mass of pulp per fruit. Third, bird-dispersed species show higher lipid and mass-specific energy contents than mixed- and mammal-dispersed species.

*Controlling phylogenetic variation.*—Comparisons across species in fruit traits have been routinely used to infer evolutionary associations between trait values and type of seed disperser. This type of comparison is illustrated in table 3, and the statistical significance of the ANOVA tests among seed disperser groups is summarized in table 4. Groups of species differing in type of seed disperser differ significantly in nine of the 16 fruit traits examined. However, this effect accounts for less than 20% of variance of any trait (table 4).

If these differences are mainly the result of the phylogenetic affinities among species, then they would vanish when controlling for the influence of shared

TABLE 3  
SUMMARY STATISTICS FOR FRUIT TRAITS OF ANGIOSPERM SPECIES DISPERSED BY DIFFERENT TYPES OF  
VERTEBRATE FRUGIVORES

FRUIT TRAIT	BIRDS			MIXED*			MAMMALS		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
Fruit length	11.88	7.22	266	14.70	7.96	192	29.28	22.75	46
Fruit diameter	10.21	5.37	332	13.20	7.32	217	23.56	18.56	48
Fruit fresh mass	1.485	4.792	264	1.881	3.469	134	5.611	15.898	30
Pulp dry mass	.144	.303	238	.274	.465	119	.637	.842	19
Seed(s) dry mass/fruit	.185	.406	172	.163	.227	76	.310	.428	15
Number of seeds/fruit	8.9	32.5	203	106.9	494.1	93	8.3	20.1	24
Seed dry mass	0.1097	.4753	123	.0803	.1655	58	.5532	14.738	13
Relative yield of pulp	13.65	6.84	234	16.68	8.70	117	20.04	12.05	19
Energy content/g									
pulp	17.87	5.70	221	15.38	5.56	173	14.64	5.13	59
Energy content/fruit	2.18	4.49	159	4.02	6.04	63	16.99	16.35	11
Water in pulp (%)	71.82	16.02	259	73.57	14.46	203	72.29	16.30	44
Lipids	.149	.171	228	.070	.125	207	.082	.138	60
Protein	.063	.046	264	.057	.041	231	.051	.035	66
Nonstructural									
carbohydrates	.540	.270	204	.565	.273	197	.597	.251	61
Minerals	.055	.038	121	.047	.028	111	.047	.036	32
Fiber	.130	.099	98	.170	.110	103	.150	.127	31

NOTE.—Lengths are given in millimeters masses in grams, energy contents in kilojoules, and values for lipids to fiber are proportions relative to dry mass of pulp.

\* Seeds dispersed by birds and mammals.

ancestry. In this situation, I would also expect large reductions in  $R^2$  values when phylogenetic effects are subtracted. It is possible to perform such tests with the autoregressive model, by testing the differences between dispersal syndromes on the specific values,  $S$ , which represent residual variation. The main assumption is that this residual depicts the independent evolution of each species. Thus,

$$S = T - \rho W y,$$

where  $T$  is the total phenotypic value, represented by the  $y$  vector (Cheverud and Dow 1985; Cheverud et al. 1985). I ran the ANOVA tests for each trait again on these  $S$  values in order to test for differences between seed disperser types controlling for phylogenetic effects. Table 4 shows that the number of traits with significant differences decreased from nine to six. In addition,  $R^2$  values were reduced, on the average, 32% of the initial values explained when using total phenotypic variation. Traits still showing significant differences between types of seed disperser when controlling for phylogenetic effects were fruit length and diameter, fruit and pulp masses, energy content/fruit, and lipids. The variance accounted for by this model was extremely low for lipids (4.8%), fresh fruit mass (3.2%), and pulp dry mass (6.8%), which indicates that sizable variation attributable to major seed dispersers is really present only in fruit size and total energetic content/fruit (largely a correlate of fruit size).

TABLE 4

SIGNIFICANCE OF THE DIFFERENCES IN FRUIT TRAITS AMONG SPECIES PREDOMINANTLY DISPERSED BY BIRDS (B), MAMMALS (Mm—BATS, UNGULATES, PRIMATES), AND WITH MIXED SEED DISPERSAL BY BOTH GROUPS OF FRUGIVOROUS VERTEBRATES (Mx)

FRUIT TRAITS (df)	TOTAL PHENOTYPIC VARIATION					PHYLOGENETIC VARIATION CONTROLLED				
	F	R <sup>2</sup>	B	Mx	Mm	F	R <sup>2</sup>	B	Mx	Mm
Fruit length (2, 503)	44.61*	15.1	A	B	C	39.33*	13.6	A	B	C
Fruit diameter (2, 596)	49.61*	14.3	A	B	C	41.40*	12.3	A	B	C
Fruit fresh mass (2, 429)	19.83*	8.5	A	B	C	6.98 <sup>NS</sup>	3.2	A	AB	B
Relative yield of pulp (2, 371)	6.94*	3.6	A	B	B	4.94 <sup>NS</sup>	2.6	A	B	AB
Pulp dry mass (2, 377)	25.18*	11.9	A	B	B	13.67*	6.8	A	B	B
Seed(s) dry mass/fruit (2, 264)	3.63 <sup>NS</sup>	2.7	A	A	A	2.77 <sup>NS</sup>	2.1	A	A	A
Number of seeds/fruit (2, 322)	8.71*	5.2	A	B	A	2.35 <sup>NS</sup>	1.4	A	A	A
Seed dry mass (2, 193)	1.98 <sup>NS</sup>	2.0	A	A	A	1.06 <sup>NS</sup>	1.1	A	A	A
Energy content/g pulp (2, 455)	10.80*	4.6	A	B	AB	6.91 <sup>NS</sup>	2.9	A	B	AB
Energy content/fruit (2, 234)	27.67*	19.4	A	B	C	19.83*	14.6	A	A	B
Water in pulp (%) (2, 508)	.62 <sup>NS</sup>	.2	A	A	A	.33 <sup>NS</sup>	.1	A	A	A
Lipids (2, 497)	21.16*	7.9	A	B	B	12.62*	4.8	A	B	B
Protein (2, 563)	2.62 <sup>NS</sup>	.9	A	A	A	1.33 <sup>NS</sup>	.5	A	A	A
Nonstructural carbohydrates (2, 464)	1.13 <sup>NS</sup>	.5	A	A	A	1.36 <sup>NS</sup>	.6	A	A	A
Minerals (2, 263)	1.76 <sup>NS</sup>	1.3	A	A	A	2.22 <sup>NS</sup>	1.7	A	A	A
Fiber (2, 231)	3.39 <sup>NS</sup>	2.9	A	B	B	3.14 <sup>NS</sup>	2.7	A	A	A

NOTE.—Separate ANOVA tests were carried out on the total phenotypic variance and on residual variance after controlling for phylogenetic effects by means of an autocorrelation method (see text). R<sup>2</sup> is the percentage of variation explained by the model (disperser categories). Entries with different letters indicate significant differences (Scheffé a posteriori test, P < .05) between the means of each trait variable. NS, Not significant.

\* P < .003, Bonferroni-corrected significance level (P = .05/16 = .003).

*Independent contrasts analysis.*—The angiosperm phylogenetic classification of Cronquist (1981) provides a total of 541 nodes for the 910 species in the data set, 59.5% of the maximum possible resolution with a bifurcating phylogeny of 909 nodes. The number of nodes available for a given trait is reduced, however, because of missing values and by the fact that variation for type of seed disperser is absent at a number of nodes (contrasts with value zero), especially generic nodes. Most congeners share the same type of seed dispersal agent, as expected by the conservative fruit morphology and pulp composition shown at this taxonomic level (fig. 2).

Table 5 summarizes the results of both regression through the origin and sign tests on the contrasts comparisons, and the latter are plotted in figure 4. Each point in this figure indicates an independent comparison of the type of seed disperser in a given taxon plotted against the independent comparison in trait value for that taxon. Contrasts in type of seed disperser (independent variable) are forced to be positive, and their values along the X-axis are interpretable as an increasing importance of mammals in the dispersal of each taxon (see Methods).



TABLE 5

SUMMARY OF THE ANALYSIS OF THE RELATIONSHIPS BETWEEN DISPERSER-TYPE CONTRASTS AND FRUIT TRAIT CONTRASTS FOR ANGIOSPERM SPECIES

FRUIT TRAIT	df	SLOPE	NUMBER OF CONTRASTS		BINOMIAL <i>P</i>
			Positive	Negative	
Fruit length	164	.1278*	92	67	.075
Fruit diameter	183	.1183*	107	71	.01
Fruit fresh mass	50	.2145 <sup>NS</sup>	86	64	NS
Pulp dry mass	138	.3124*	73	65	NS
Seed(s) dry mass/fruit	104	.1361 <sup>NS</sup>	60	42	NS
Seed dry mass	83	.3144 <sup>NS</sup>	47	35	NS
Number of seeds/fruit	114	-.9248 <sup>NS</sup>	35	38	NS
Relative yield of pulp	137	.0545 <sup>NS</sup>	73	64	NS
Energy content/fruit	100	.3553*	59	41	NS
Energy content/g pulp	154	-.0464 <sup>NS</sup>	68	86	NS
Water in pulp (%)	165	.0348 <sup>NS</sup>	84	80	NS
Lipids	163	-.0727*	68	95	.10
Protein	174	-.0124 <sup>NS</sup>	92	78	NS
Nonstructural carbohydrates	157	.0207 <sup>NS</sup>	85	71	NS
Minerals	114	-.0162 <sup>NS</sup>	54	55	NS
Fiber	99	.0019 <sup>NS</sup>	45	49	NS

NOTE.—For each trait, separate regressions through the origin were calculated between disperser-type contrasts and fruit trait contrasts. NS, Not significant. Bonferroni-corrected significance levels are given for slopes. Binomial probabilities are the *P* levels for the binomial test on an equal number of positive and negative contrasts for each trait. Contrasts equal to zero for the type of seed disperser were excluded from calculation of the regression slopes and binomial *P*.

\*  $P < .05/16 = .0031$ .

I omitted those taxa that were internally homogeneous with regard to type of seed disperser. Independent contrasts for the trait values (*Y* variable) can be zero, positive, or negative. Each pair of positive *X-Y* values therefore indicates an independent evolutionary instance in which a change for mixed or mammal dispersal (i.e., an increase in the relative importance of mammals as dispersers of a taxon) has been associated with a positive change in the trait value (i.e., an increase in fruit or seed size, pulp mass, or amount of a given nutrient).

Results of the independent contrasts analyses (table 5) are consistent with those obtained using the autoregressive methods (table 4). The prevailing pattern illustrated by figure 4 is that evolutionary changes in fruit characteristics and type of seed disperser have been largely independent. Among fruit form and design variables only fruit length, diameter, and dry mass of pulp showed a significant trend to increase along the bird-mixed-mammal continuum of syndromes (fig. 4A). Among nutrient content traits, only energy content per fruit and lipid content showed significant trends (table 5; fig. 4B), but the correlation for lipids was negative. The correlation of energy content/fruit is a side effect of the strong covariation between this derived variable and fruit size. Obviously, larger fruits, with a greater amount of pulp, also yield a greater amount of energy per fruit. Thus, the partial correlation between disperser type contrasts and energy content/fruit contrasts is only 0.001 after fruit size effects are removed (by partialing out

fruit diameter). Therefore, the only evolutionary correlations evidenced by the independent contrast analysis involve fruit size and lipid content.

The negative correlation between lipid content contrasts and disperser type contrasts (table 5; fig. 4B) indicates that high lipid content is evolutionarily associated with avian seed dispersal and decreases among taxa with mammal dispersal. However,  $R^2$  is very small for this trait (5.6%), and the correlation vanishes when controlling the influence of three outliers (the three bottom data points in the panel for lipids, fig. 4B). These contrasts correspond to the genus *Aglaia* (Meliaceae), and families Anacardiaceae and Apocynaceae, which show relatively large amounts of lipids in the pulp but with extreme variation among species differing in disperser type. Among Apocynaceae, species with mixed dispersal show much higher lipid content ( $0.34 \pm 0.09$ ,  $n = 3$ ; genera *Stemmadenia* and *Tabernaemontana*) than those dispersed by mammals (e.g., genera *Lacmellea*, *Thevetia*, *Landolphia*;  $0.044 \pm 0.063$ ,  $n = 6$ ). The same trend occurs in Anacardiaceae, where bird-dispersed *Pistacia*, *Rhus*, and *Harpephyllum* show average proportions of lipids ( $0.378 \pm 0.07$ ,  $n = 6$ ) well above species with mixed dispersers such as in genera *Spondias*, *Pseudospondias*, *Tapirira*, *Trichoscypha*, and *Sclerocarya* ( $0.025 \pm 0.07$ ,  $n = 6$ ). Finally, the same extreme trend exists among *Aglaia*, with lipid content of  $0.492 \pm 0.09$ ,  $n = 3$ , in bird- and mixed-dispersed taxa and  $0.089 \pm 0.059$ ,  $n = 3$ , among mammal-dispersed species.

As indicated by the binomial tests (table 5), there is evidence only for taxa with greater proportions of mammal-dispersed species to show larger fruits; the sign tests are significant only for fruit diameter and, marginally, for fruit length. The results therefore indicate that correlated evolution between type of seed disperser and fleshy fruit phenotypic characteristics is largely confined to fruit size, especially the external dimensions.

*Pairwise comparisons among congeners.*—I carried out a further test to see if the trends shown in tables 4 and 5 and figure 4 hold when closely related species differing in type of seed disperser are compared. I selected those genera in the data set for which several species differ in type of seed disperser. For each genus, I averaged trait values across species sharing the type of seed disperser and compared these means among disperser categories (Wanntorp 1983). I tallied the number of genera showing increases or decreases in average trait values when congeners dispersed by birds are compared with those dispersed by birds and mammals (mixed dispersal) and/or those that are mammal dispersed. Each comparison within a genus adds an independent observation to a sign test under the null hypothesis that equal number of within-genus comparisons should go in the same direction.

The pairwise comparisons (table 6) reveal only a significant trend for larger fruits (greater diameter and, marginally, greater length) to occur among mixed- or mammal-dispersed species (sign tests,  $P = .053$  and  $P = .115$ , respectively). For the other traits that showed significant, or marginally significant, results in the autocorrelation and contrasts analyses, no significant trend is evident in the within-genus pairwise comparisons (table 6). To sum up, only fruit size (fruit diameter and, marginally, fruit length) show correlated evolution with type of seed disperser when phylogenetic effects are controlled for.

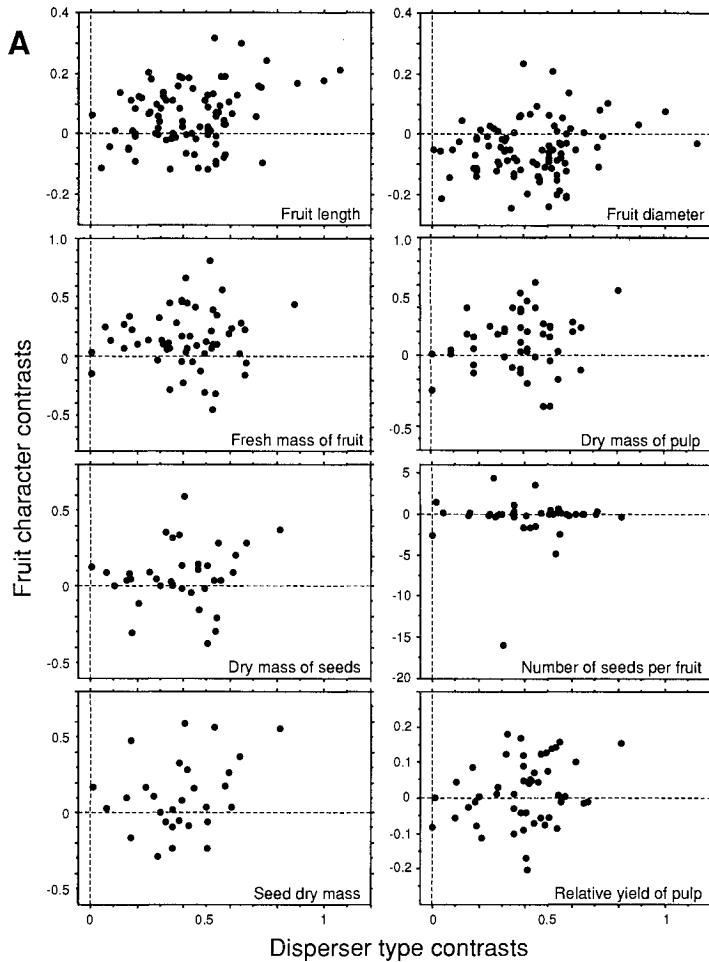
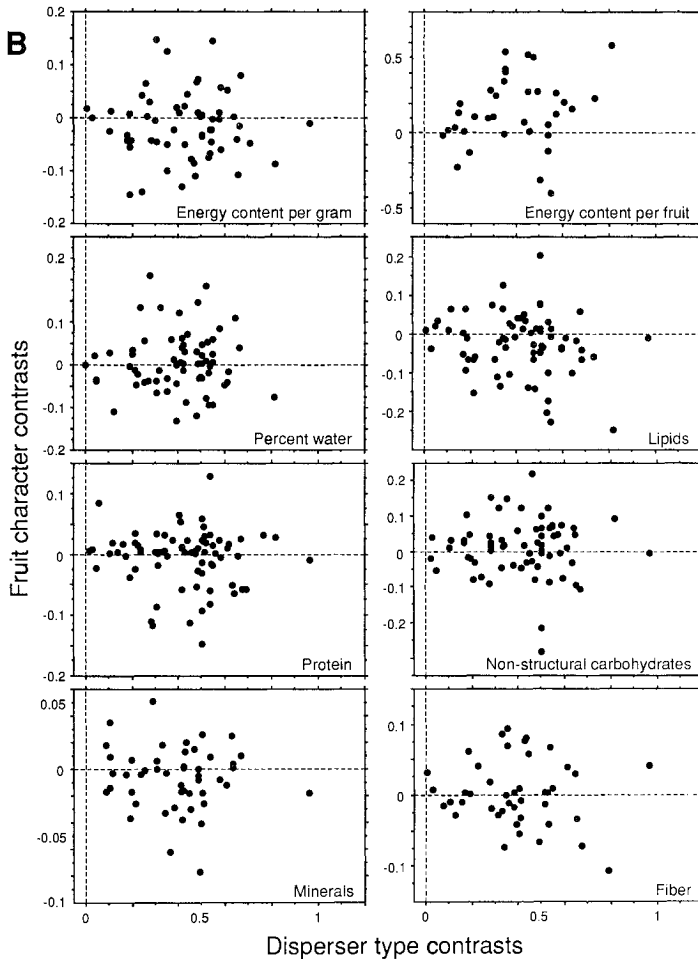


FIG. 4.—Plots of the contrasts for comparisons on seed disperser type against the comparisons on fruit trait values for angiosperm species and the phylogenetic classification of Cronquist (1981). A, Morphological and design traits; B, pulp water content and nutrient traits. Data points represent a comparison among different taxa within each higher node of the taxonomic tree according to the arrangement of Cronquist (1981; assumed to be a phylogenetic tree). Each of these nodes contributes a linear contrast of differences in disperser type and trait values among taxa at the node.

#### DISCUSSION

##### *General Patterns of Fleshy Fruit Phenotypic Variation*

Only three major patterns of covariation among fleshy fruit traits explain the morphological variation in the large data set studied here. Almost 60% of total phenotypic variation can be reduced to three major gradients of design: fruit size, including both external dimensions and mass; a marked negative covariation between nonstructural carbohydrates and lipids and fiber; and a “succulence”



gradient, with extremes defined, on one side, by highly fibrous fruits, yielding both a large amount of pulp and energy and, on the other, fruits with watery pulps. To a large extent, morphological and design traits (size, pulp allocation, and seediness) show independent patterns of covariation relative to nutritional traits (water, major organic components, fiber, and minerals).

If fruit morphology results from selection by seed dispersers not subject to constraints, clusters at particular zones of the total morphometric space of fruit variation should not be expected; rather, the range of morphological variation among species would span most of this space. The opposite trend was found, and different families and genera tended to cluster at particular combinations of PC values, showing highly significant differences in these variates (also see Gauthier-Hion et al. 1985; Herrera 1987). A similar result concerning flowering time and phenological variation was obtained by Kochmer and Handel (1986). This outcome therefore suggests that fruit morphological variation is largely an

TABLE 6

NUMBER OF GENERA THAT SHOW A GIVEN TREND OF VARIATION IN FRUIT CHARACTERISTICS WHEN CONGENERIC SPECIES DISPERSED BY DIFFERENT TYPES OF FRUGIVORES ARE CONTRASTED IN THE SEQUENTIAL COMPARISON BIRDS-MIXED-MAMMAL DISPERSAL

TRAIT	TRAIT VALUES INCREASE		TRAIT VALUES DECREASE		BINOMIAL P
	n	Genera	n	Genera	
LENG	16	<i>Astrocaryum</i> , <i>Canthium</i> , <i>Cryptocarya</i> , <i>Ficus</i> , <i>Homalanthus</i> , <i>Mouriri</i> , <i>Ochna</i> , <i>Ocotea</i> , <i>Olea</i> , <i>Parinari</i> , <i>Prunus</i> , <i>Rutidea</i> , <i>Sapium</i> , <i>Solanum</i> , <i>Sorbus</i> , <i>Syzygium</i>	9	<i>Celtis</i> , <i>Chionanthus</i> , <i>Crataegus</i> , <i>Diospyros</i> , <i>Garcinia</i> , <i>Polyscias</i> , <i>Protium</i> , <i>Simarouba</i> , <i>Virola</i>	.10
DIAM	19	<i>Astrocaryum</i> , <i>Canthium</i> , <i>Celtis</i> , <i>Crataegus</i> , <i>Cryptocarya</i> , <i>Ficus</i> , <i>Garcinia</i> , <i>Homalanthus</i> , <i>Mouriri</i> , <i>Ochna</i> , <i>Ocotea</i> , <i>Prunus</i> , <i>Rutidea</i> , <i>Sapium</i> , <i>Simarouba</i> , <i>Solanum</i> , <i>Sorbus</i> , <i>Syzygium</i> , <i>Citharexylum</i>	8	<i>Chionanthus</i> , <i>Diospyros</i> , <i>Olea</i> , <i>Parinari</i> , <i>Polyscias</i> , <i>Protium</i> , <i>Virola</i> , <i>Ribes</i>	.05
FRFM	3	<i>Crataegus</i> , <i>Prunus</i> , <i>Sorbus</i>	5	<i>Citharexylum</i> , <i>Ribes</i> , <i>Chamaedorea</i> , <i>Coprosma</i> , <i>Planchonella</i>	NS
LIP	5	<i>Citharexylum</i> , <i>Chamaedorea</i> , <i>Aglaia</i> , <i>Dacryodes</i> , <i>Uapaca</i>	8	<i>Crataegus</i> , <i>Prunus</i> , <i>Sorbus</i> , <i>Virola</i> , <i>Ribes</i> , <i>Beilschmiedia</i> , <i>Cissus</i> , <i>Heisteria</i>	NS
PDM	3	<i>Crataegus</i> , <i>Prunus</i> , <i>Sorbus</i>	4	<i>Virola</i> , <i>Ribes</i> , <i>Chamaedorea</i> , <i>Coprosma</i>	NS
KJFR	2	<i>Prunus</i> , <i>Vitis</i>	5	<i>Crataegus</i> , <i>Sorbus</i> , <i>Virola</i> , <i>Ribes</i> , <i>Chamaedorea</i>	NS

NOTE.—Trait values were averaged for congeneric species sharing dispersal agents and contrasted. Table entries indicate the number (n) and identity of the genera that show each type of trend in the comparison between birds, mixed, and mammals. Thus, 16 genera show a trend for an increase in average fruit length from bird- to mixed or mammal-dispersed congeners, while nine genera show the opposite trend. Only genera with enough data available for intrageneric contrasts are included for each trait. Only those traits that resulted in significant or marginally significant trends in the independent contrasts analysis or autocorrelation analysis are included. Binomial probabilities are the P levels for the binomial test on equal number of genera showing each trend of variation. NS, Not significant. Abbreviations for fruit traits are as in fig. 2.

intrinsic and relatively stable property of higher taxonomic levels (family, in this case).

The analysis revealed a marked decoupling of fruit "form" and "design" characteristics and nutrient content characteristics, a pattern evident also when analyzing the correlation matrix on contrasts. In fact, the only pattern of covariation among design and nutrient traits was that fibrous fruits tend to yield a greater relative amount of pulp per fruit. Otherwise, variation in these two main components of fruit morphology is independent. Figure 1 shows that some families spanned great variation along PC 1 while showing a narrow range of scores on PC 2 (confidence ellipses oriented horizontally, e.g., Melastomataceae, Rutaceae, Rubiaceae, Ebenaceae, Rhamnaceae). Others show the opposite trend (confidence ellipses oriented vertically, e.g., Lauraceae, Smilacaceae, Ericaceae, Palmae, Flacourtiaceae, Meliaceae, Vitaceae). The fact that these two gradients (size and lipid-soluble carbohydrate content) explain one-half of total variation in fleshy fruit characteristics means that they are two major lines of familial diversification and reveals that variation in fruit form and pulp composition within higher taxa is bounded by constraints.

The preceding result is not unexpected. Studies by Sporne (1956, 1976) and Stebbins (1951), for example, indicate that characteristics of angiosperm reproductive structures co-vary within higher taxa, since floral, carpel, seed, and fruit traits are ultimately associated and connected along an ontogenetic path (Primack 1987). Constraints on fruit size and internal design most likely arise from developmental limitations imposed by the particular arrangement of floral parts, especially the structure of the gynoecium. On the other hand, PCA loadings for the organic constituents of the pulp suggest that conservative expression of nutrient composition within higher taxa might be attributable to allocation patterns among major biosynthetic pathways. In addition, certain combinations of major compounds (e.g., high water and lipid content, or low water and high soluble-carbohydrate content) might be simply incompatible from a metabolic or physiological perspective. That different parts of the flower and fruit are highly integrated and show correlated evolution was proposed by Vavilov (1922) and then established more formally by Sporne (1956). These are relevant points to a rigorous analysis of fruit and flower evolution in relation to seed dispersers and pollinators. A highly structured pattern of covariation among different parts of the phenotype does not prevent the action of natural selection among coevolving partners, but it imposes limits on the resulting evolutionary change.

#### *Phylogenetic Constraints on Seed Dispersal Syndromes*

Previous work on comparative fruit morphology and seed dispersal agents largely ignored alternatives to the adaptationist hypothesis or, if the potential effect of alternative sources of variation was acknowledged (Herrera 1986; Debussche et al. 1987; Willson et al. 1989; French 1991; Lee et al. 1991), no explicit quantification of its significance was attempted. How important is adaptation to seed dispersers in explaining fruit variation not accounted for by phylogeny or random effects?

The nested ANOVA analysis showed that an average of 61% of total pheno-

typic variation in any angiosperm fleshy fruit trait can be accounted for by taxonomic affiliation down to genus. Seed size and seed number per fruit showed the highest phylogenetic variance component values, as expected from their close relation to flower and carpellar structure. Family effects were large for most design traits and smaller for pulp nutrient traits. These, in contrast, showed greater generic variance component values, which thus adds evidence to the finding of this study (also see Herrera 1987) of a decoupling of the two groups of traits. Janson (1992) reported a strong invariance in the kinds of dispersal syndromes evolved within higher taxa (genera and families), apparently a result of relatively fixed developmental and ontogenetic programs or low adaptive value of transitional, intermediate forms, between syndromes. To some extent, phylogenetic variance components estimate the relative size of "plesiomorphic" components of the phenotype. Little variation is therefore available for species-specific responses to selection by seed dispersers, since the potential for diversification within a given higher taxa (e.g., genus) is "nested" within this large component of descent. Thus, interactions with seed dispersers were probably relevant in shaping the major lines of diversification for angiosperm families and genera, but we might expect very low evolutionary response among congeneric species to these mutualists. More local analyses, with a taxonomic scope narrower than the one used here, can obtain greater resolution for the definition of disperser types, hence more power to test adaptive trends within a rigorous phylogenetic framework.

The phylogenetic autocorrelograms of the 16 traits examined here describe a decaying function of phenotypic similarity with ascending taxonomic hierarchy. They further indicate a highly structured pattern of variation related to phylogenetic affinity. There is a much steeper gradient of decreasing autocorrelation with increasing taxonomic level for design traits than for pulp nutrient content traits. Since phylogenetic effects are expected to be relevant in complex anatomical structures or physiological processes that evolve as integrated suites of traits (Stebbins 1974), these will show up more clearly in fruit form and structure, considered characteristic attributes of families (Cronquist 1981). The autoregressive pattern is stronger in fruit design than in pulp nutrient content, and the former group of traits shows more homogeneous correlograms (fig. 3), which supports this view.

Phylogenetic autocorrelation coefficients were highly significant for 11 of the 16 phenotypic traits examined, which indicates that a sizable fraction of phenotypic variance can be accounted for when considering *simultaneously* all phylogenetic relatedness among species. Phylogenetic effects are important for two main groups of traits, namely fruit and seed mass and fruit seediness among design traits and energy content per fruit and lipids among nutrient content traits. Other traits showed significant autocorrelations but lower  $R^2$  values (e.g., fruit dimensions, pulp water content, protein). Future studies should therefore pay attention to other effects not examined here (growth form, fruit accessibility, and color), but some analyses suggest a sizable phylogenetic component in them (see, e.g., Hodgson and Mackey 1986; Willson and Whelan 1990; Chazdon 1991; Fischer and Chapman 1993). When using original data, significant differences between

syndromes were obtained for nine of the 16 traits. Differences between syndromes in fruit length and diameter, pulp dry mass, energy content/fruit, and lipids remained, and the coefficients of determination for lipids and pulp mass were approximately halved when phylogenetic relatedness was accounted for. Therefore, the first prediction addressed in this study (i.e., differences among syndromes should remain after controlling for phylogenetic effects) is supported only in part for a minority of the traits examined. However, the fraction of strict sense "adaptive" variation exhibited by these traits was extremely small ( $\leq 15\%$ ).

#### *Dispersal Syndromes Revisited*

Present-day functional associations between fruit traits and major seed dispersers do not necessarily imply their coevolution as a causal process. All the above analyses strongly indicate that dispersal syndromes are not interpretable only in terms of current adaptation to seed dispersers and demonstrate a significant historic component in present-day phenotypic variation among angiosperm fleshy fruits (also see Bremen and Eriksson 1992; Herrera 1992a; Fischer and Chapman 1993). Phenotypic variance accounted for by higher nodes was "subtracted" in the previous analyses and considered nonadaptive because it illustrates the plesiomorphic load of the traits. However, fleshy fruit plesiomorphies are probably a result of adaptations to past mutualistic interactions and should be incorporated in a comparative analysis.

The analysis by independent contrasts revealed two strong patterns. First, a lack of evolutionary correlation between seed dispersal type and most fleshy fruit traits; in fact, only fruit diameter and, marginally, fruit length and pulp lipid content showed a trend for covariation with type of seed disperser. The results were therefore highly consistent with and supported those of the two previous analyses. Second, fruit dimensions, especially diameter, showed a significant association with type of disperser, tending to increase with increasing participation of mammals among the dispersal agents. This supports earlier findings of cross-species studies showing the same trend (Janson 1983; Gauthier-Hion et al. 1985; Dowsett-Lemaire 1988; Debussche and Isenmann 1989; Herrera 1989; Willson 1993). This result is not incompatible with the finding of significant phylogenetic effects in fruit dimensions. The point is that the possibilities for evolutionary change in these traits are tightly bounded by the *bauplan* inherited by each species.

The evidence from the analysis of contrasts and the pairwise comparisons demonstrated that evolutionary increases in fruit size (diameter and, marginally, length) are significantly associated with mixed and mammal dispersal. Studies showing a potential selective effect of frugivores on fruit size are numerous, but few have addressed both the necessary and sufficient conditions to demonstrate the operation of natural selection (Schupp 1993; Wheelwright 1993). In contrast to other fruit traits, frugivore selection on fruit size has immediate implications on key aspects of plant demography, because of the association among fruit size, seed size, and seedling vigor; germination probability; and successful seedling establishment. I would expect that the effects of present-day selective pressures and phylogenetic or developmental constraints as contributing causal processes to plant-disperser coevolution could be dissected more finely in future studies on



particular species groups (e.g., diversified taxa such as *Solanum*, or Rubiaceae) in which comparative data and well-established phylogenies can be combined with detailed ecological experiments (Bremer and Eriksson 1992). In addition, general trends such as those described in the present study for the whole angiosperm clade could be tested in smaller subsets of the clade (E. Martins, personal communication). Future studies should address the shortcomings imposed by the characteristics of the large data base used here and take advantage of the new comparative methods and availability of well-established phylogenies, combined with rigorous field studies of frugivore activity.

All the fruit traits examined show important phylogenetic effects and extremely low potential for coevolutionary species-specific adaptation to seed dispersers, probably because of constraints imposed by development and integration with predispersal reproductive structures. A recent model for the evolution of specialized seed dispersal among vertebrate-dispersed plants predicted a central role of phylogenetic conservatism and rapid punctuated evolution in fruit traits (Fleming et al. 1993), and the results of the present analysis strongly support this view. But this is a complicated situation. The hypothesis that fruit traits evolved as adaptations to seed dispersers but are now maintained by something other than selection is hard to falsify (Howe 1985), but it is probably correct for most individual fruit traits. The idea of phylogenetic inertia and/or developmental constraints implicitly recognizes that the origin and maintenance of adaptations to seed dispersers are decoupled, which makes the hypothesis difficult to test (Coddington 1988; McKittrick 1993). The present analysis suggests that natural selection might not be involved in maintaining adaptations to seed dispersers, at least for most fruit phenotypic traits, and that correlated evolution with type of seed disperser is, at best, only evident for fruit diameter. To the extent that the patterns of covariation between fruit traits and disperser type are epiphenomena of other selective pressures, such as flower design, pollinator-derived effects, or physiological constraints on fruit design (Cipollini and Levey 1991; Herrera 1992*b*), fleshy fruit characteristics are to be considered as exaptations (Gould and Vrba 1982) to their present-day seed dispersers.

The present study and other recent analyses (Bremer and Eriksson 1992; Herrera 1992*a*, 1992*b*; Janson 1992; Fischer and Chapman 1993) demonstrate the need to address the historic component of plant-disperser interactions by using both rigorous comparative methods and sound experimental evidence for ecological effects. Although these are key aspects for understanding the mechanisms of plant-seed disperser (also pollinator) coevolution above the species level, they would be difficult to integrate. Recent evidence of multiple types of constraints on coevolution (Wheelwright and Orians 1982; Howe 1984; Herrera 1986; Jordano 1987*c*; Wheelwright 1988; Janson 1992; present study) argue against a single formulation to represent all contributing causal factors adequately. This is a general issue in evolutionary biology today, not specific to the study of plant-disperser coevolution. A major problem is the lack of a common currency to measure the effects of contributing causal processes, and probably the only alternative will be a piecemeal approach to integration (Mitchell 1992). This explicitly recognizes the plurality of causal processes (present-day selection, phylogenetic effects, on-

togenetic constraints, and random variation) and the singularity of the particular combination of effects and their significance in each particular situation.

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