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INTERSPECIFIC VARIATION IN FRUIT SHAPE: ALLOMETRY, PHYLOGENY, AND ADAPTATION TO DISPERSAL AGENTS[1]

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Abstract. Investigations on fruit and fruiting characteristics of animal-dispersed, fleshy-fruited plants have been generally interpreted in terms of adaptations by plants to dispersal agents. Most often, these studies did not formulate non-adaptive, alternative null hypotheses, and the potential influence of phylogenetic effects on observed patterns was not assessed either. This paper presents an analysis of interspecific variation in fruit shape (as assessed by length and width) among vertebrate-dispersed plants of the Iberian Peninsula. Tests of predictions from both adaptive (to dispersal agents) and null (based on allometry) hypotheses are presented and the influence of phylogenetic effects is also accounted for. Interspecific variation in fruit shape was unrelated to seed dispersal mode ("bird dispersed" vs. "bird plus mammal dispersed"), and predictions from adaptive hypotheses were not supported. Variation in fruit shape did not depart significantly from that predicted by the allometry-based, null hypothesis. Deviations of individual species from the predicted allometric relationship were unrelated to dispersal mode, and originated from genus- and species-specific variation in fruit shape. There exists a considerable influence of phylogeny on fruit shape variation, and nearly half of total variance is attributable to variation among genera within families. After accounting for phylogenetic effects, the null hypothesis still held within taxonomic categories above the species level. Observed constancy in the relative variation of fruit length and width, despite variation in dispersal mode and morphological type, is interpreted in terms of shared morphogenetic and physical constraints independent of dispersal. The implications of substantial phylogenetic effects on interspecific patterns of variation in fruit and fruiting traits are discussed.

Key words: allometry; bird dispersal; comparative method; fruit characteristics; fruit shape; Iberian Peninsula; mammal dispersal; phylogenetic effects; regression methods.

INTRODUCTION

Owing to the potentially coevolutionary nature of their relationship with seed vectors (Snow 1971, McKey 1975, Howe and Estabrook 1977, Janzen 1983), the fruit and fruiting characteristics of endozoochorously dispersed plants have frequently been examined from an adaptationist perspective. Variation in traits like fruiting phenology, fruit size and color, nutritional composition of the pulp, and type of fruiting display, among others, has been often studied in recent years (e.g., Stiles 1980, Herrera 1982, 1987, Willson and Thompson 1982, Janson 1983, Johnson et al. 1985, Wheelwright and Janson 1985, Piper 1986, Debussche et al. 1987, Debussche and Isenmann 1989, Willson and Whelan 1990). These investigations generally attempted to interpret observed interspecific patterns in terms of adaptations of plants to their animal seed dispersers. Irrespective of their success in verifying adaptationist expectations, most previous analyses aiming to seek adaptive explanations for observed variation in dispersal-related plant features have faced at least two potentially important methodological problems.

Firstly, studies testing adaptationist hypotheses related to variation in fruit and fruiting traits generally have not formulated alternative, non-adaptive hypotheses that could play the role of "null hypotheses" (sensu Strong 1980). This fact must probably be attributed, in part, to the influence of adaptationist traditions in recent evolutionary ecology (Gould and Lewontin 1979, Herrera 1986), but also to the formidable practical difficulties involved in formulating biologically reasonable null hypotheses when complex traits, like most fruit and fruiting features, are involved. And secondly, most investigations were conducted in interspecific contexts and, therefore, used species as the "units" for analyses and comparisons. Species, however, are not statistically independent entities, as they are all related among themselves to a variable degree and belong to a common, hierarchically organized phylogeny (Felsenstein 1985). Similarity between species may be due to parallel and convergent evolutionary change in response to similar selective pressures (the implicit assumption in most studies using species as the units for analyses), but also to common inheritance (Felsenstein 1985, Pagel and Harvey

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1988*b*). The use of species as statistically independent units tends to overestimate degrees of freedom in statistical analyses and, therefore, to overemphasize the extent of convergence or parallel evolutionary change (Pagel and Harvey 1988*b*, Burt 1989). Spurious interspecific patterns, or "taxonomic artifacts," may thus emerge simply as a consequence of "phylogenetic effects" if one does not account for the non-independence of the taxonomic entities used in the analyses. The influence of phylogenetic effects on interspecific patterns of fruit and fruiting traits has received little attention to date, but even the few preliminary studies available suggest that it may often be substantial (Herrera 1986, 1987, Gorchov 1990). For other reproductive plant traits not related to dispersal, the importance of phylogenetic effects as explanations for interspecific patterns has been demonstrated whenever specific attention has been paid to them (Hodgson and MacKey 1986, Kochmer and Handel 1986, Mazer 1989, 1990, Stratton 1989).

I present in this paper an analysis of interspecific variation in a single fruit trait, namely fruit shape. (Throughout, I use "fruits" in its ecological, not botanical sense, to denote "functional fruits," i.e., packages made up of seeds plus accessory tissues used as food by vertebrate dispersers, irrespective of their anatomical origin.) Rather surprisingly, this character has never been examined in detail before despite its evident simplicity and potential ecological significance (see *Hypotheses and predictions* below). It is a common observation that, with a few noticeable exceptions from tropical habitats (e.g., *Cecropia, Piper*), the ripe fleshy fruits of animal-dispersed plants typically are roughly spherical or ellipsoidal in shape. This usually holds not only for "true" fruits originating from a single ovary like berries or drupes, but also for fruits of varied anatomical origins (consider, e.g., *Juniperus* strobili, *Ficus* syconia, and *Fragaria* pseudocarps). This general uniformity in fruit shape would perhaps suggest the existence of selective pressures from the animals that eat them and disperse the enclosed seeds, leading to convergence. Variations occurring within the general spherical-ellipsoidal fruit template might also be explained as adaptations to dispersers. Alternatively, patterns of variation in fruit shape might reflect allometric constraints and/or phylogenetic effects.

Fruit shape has some advantages in relation to other, more complex fruit traits, for conducting a rigorous examination of adaptive hypotheses. Although an accurate description of fruit shape would obviously require further measurements, it may conveniently be summarized by its two dominant linear dimensions, namely fruit length and fruit width (transversal diameter). These variables describe the fruit's "aspect ratio," and roughly define its shape from side view (throughout this paper "fruit shape" will be used in this restricted context). Furthermore, one straightforward null hypothesis may be formulated based on allometric considerations. My objective here is to test both adaptive and null hypotheses related to variation in fruit shape among animal-dispersed plants from the Iberian Peninsula, dissecting the relative importance of allometry, phylogenetic effects, and adaptation to dispersers, as explanations for observed patterns of variation. This is the first investigation of these characteristics conducted on a dispersal-related trait of fleshy-fruited plants.

Hypotheses and predictions

(1) Null hypothesis.—From simple scaling considerations, and assuming that fruit density remains roughly constant (see *Applicability of hypotheses* in this section), variation of fruit length (L) and fruit width (W) with fresh fruit mass (M) would be described by the power equations

$$L = k_l M^{1/3}, \quad \text{and} \quad W = k_d M^{1/3}, \tag{1}$$

where k_l and k_d are constants. The ordinary allometric equations are obtained by taking logarithms:

$$\log L = (1/3)\log M + \log k_l;$$
$$\log W = (1/3)\log M + \log k_d. \tag{2}$$

Solving for the log M term and rearranging, the expected allometric relationship between L and W becomes

$$\log W = \log L + \log k_d - \log k_l. \tag{3}$$

As $\log k_l$ and $\log k_d$ are constants, the relation may be written as either

$$\log W = \log L + a \tag{4}$$

or

$$\log L = \log W - a, \tag{5}$$

where a stands for $\log(k_d/k_l)$.

Allometry thus provides a simple null hypothesis against which to test observed variation in fruit shape. If variation in shape depends mainly on allometric constraints ("null hypothesis" hereafter), the prediction may be advanced that the slope of the regression line between log fruit length and log fruit width should equal unity (from Eqs. 4 and 5). Departures from this prediction would reveal shape variation that cannot be accounted for by allometry alone.

(2) Adaptive hypotheses.—Gape width of vertebrate dispersal agents sets a fairly rigid upper limit to the size of fruits that can be grasped and swallowed. Among comparatively small vertebrates that swallow fruits whole, like most frugivorous birds, interspecific correlations between gape width and mean size of ingested fruits have been often reported (Wheelwright 1985, Jordano 1987*b*, Debussche and Isenmann 1989, Lambert 1989), and size is also often an important determinant of fruit choice by frugivorous birds in experimental conditions (McPherson 1988). Furthermore, interspecific differences in the composition of the dis-

perser assemblages of bird-dispersed plants are related to variation in fruit size (Kantak 1979, Pratt and Stiles 1985, Lambert 1989), and differences between species in relative seed dispersal success are sometimes related to variation in fruit size (Herrera 1984, Piper 1986).

Fruits are usually swallowed lengthwise by birds, hence fruit width, rather than fruit length, is probably the dimension most directly influencing whether a fruit can be ingested by a given disperser or not (Wheelwright 1985). In some bird-dispersed species, mean fruit width of individual plants is correlated with fruit crop removal rates (Piper 1986, Jordano 1987*a*, Herrera 1988, Obeso 1988). One would thus expect that selective pressures for keeping fruit size within the "swallowable" range, if any, would be stronger on fruit width than on fruit length. At this regard, Obeso (1988) found that individual variation in fruit width, but not in fruit length, was related to variation in fruit crop removal rate in a southern Spanish bird-dispersed plant. It may then be predicted that, among species dispersed by small- to medium-sized frugivorous birds that swallow the fruits whole, fruit width should tend to increase proportionally slower than fruit length with increasing fruit mass (i.e., comparatively large fruits should tend to be proportionally more elongated than small ones). This prediction would be supported if the regression slope in Eq. 4 were significantly smaller than unity.

In contrast, fruit size is probably less important in setting limits to ingestion by comparatively large vertebrates that have wide gapes, like most non-flying mammalian frugivores (Debussche and Isenmann 1989, Herrera 1989). In this case, selective pressures on fruit size, if any, would be expected to have similar effects on fruit width and fruit length. The prediction may thus be advanced that groups of plants having dispersal agents with contrasting body sizes and fruit handling capabilities (e.g., birds vs. mammals) would exhibit different fruit length–width relationships, yielding contrasting regression slopes for Eq. 4.

(3) Applicability of hypotheses.—The null and adaptive hypotheses described above are designed specifically for Iberian plants and frugivores and, although they will probably hold for other plant–frugivore systems as well, they should not be uncritically applied without re-evaluating their assumptions. At least two of these may not hold elsewhere. Among Iberian plants, water content of most fruit species falls within relatively narrow limits (Herrera 1987: Fig. 6), thus supporting the assumption of rough constancy in fruit density required by the null hypothesis. In tropical habitats, in contrast, fruit density may be more variable (Snow 1971, McKey 1975). Another assumption that will not hold universally is that gape width of frugivorous birds sets a rigid limit to the size of fruits that can be ingested. In the Neotropics, for instance, at least two major groups of frugivorous birds (tanagers and emberizid finches) handle fruits by crushing them in the bill (Levey 1987). Because these birds do not swallow fruits whole, they are much less gape limited in the sizes of fruits they can take, and the adaptive hypotheses would need to be re-evaluated for those dispersal systems where these birds participate.

Methods

Data set

I used the comprehensive data base for fleshy fruits from the Iberian Peninsula described in detail by Herrera (1987), with minor additions (six species). A total of 117 species, in 35 families and 64 genera, were included in the analyses, representing nearly 95% of families, 90% of genera, and 60% of species with fleshy fruits that occur on the Iberian Peninsula. Most taxa not included in the sample were either narrow endemics or belonged to species complexes, including microspecies in the genera *Rosa* and *Rubus*, which accounted for 55% of "missing" species (Herrera 1987). The species sample was dominated by shrubs (53.0% of species). Trees represented 24.8%, herbs 15.4%, and woody vines 6.8%. Taxonomically, the sample was dominated by the families Rosaceae (27 species), Caprifoliaceae (13), Liliaceae (10), Rhamnaceae (7), and Solanaceae (7). Information on geographical provenance and sampling methods, and a list of species, may be found in Herrera (1987).

The information available for each species included length and width (measured with calipers to the nearest 0.05 mm) from at least 20 fully mature, individual fruits collected from several (usually 5–10) plants of a single population. In a few cases (three species), only average values for fruit length and width were available, and these species were dropped from some analyses requiring detailed information from individual fruits.

In the Iberian Peninsula, seed dispersal of fleshy-fruited plants is performed by birds and terrestrial mammals (Herrera 1987, 1989). Bird dispersal is mainly accomplished by small- (body mass 12–18 g) to medium- (80–100 g) sized species in the genera *Turdus*, *Sylvia*, *Erithacus*, and *Phoenicurus*, all of which swallow the fruits whole (Guitián 1984, Herrera 1984, 1985, Jordano 1984, 1987*b*, 1988, Fuentes 1990). There are no instances of avian dispersers handling fruits by crushing them in the bill prior to swallowing ("mashers" sensu Levey 1987). With minor exceptions (e.g., participation of rabbits, *Oryctolagus cuniculus*, in the dispersal of some species; R. C. Soriguer, *personal communication*), mammalian dispersal is performed by carnivorous mammals in the families Canidae (*Vulpes*, *Canis*), Ursidae (*Ursus*), Mustelidae (*Martes*, *Meles*), and Viverridae (*Genetta*) (Herrera 1989, and referenced therein). Species in the sample were categorized for the analyses into two broad groups according to its known seed dispersal agents, namely "bird dispersed" ($N = 73$ species) and "bird plus mammal dispersed" (44 species). Assignment of species to groups was mainly based on published information (Herrera 1989, and

references therein), but I also used my own unpublished records for some species. Exclusive mammalian dispersal has been not proven to date for any Iberian fleshy-fruited plant. If it at all occurs, it will certainly involve a negligible proportion of species.

Regression analyses

Testing the predictions formulated above requires the evaluation of regression coefficients. Three statistical techniques are usually employed to estimate regression slopes: least squares regression (LSR hereafter; the familiar Model I linear regression method); reduced major axis regression (RMAR; also sometimes termed "geometric mean regression," or "standard major axis regression"); and major axis regression (MAR). The three methods are derived from the same general structural relation model by making different assumptions about the nature of error variability in the variables involved (Kuhry and Marcus 1977, Seim and Sæther 1983, Rayner 1985). The accuracy of the slope estimate provided by a particular method will depend on the extent to which its assumptions hold in the actual data, and inappropriate selection of the method may lead to erroneous inferences (Pagel and Harvey 1988*a*). Although LSR has been the most widely used method in allometry and ecological studies (e.g., Peters 1983), it is also probably the least appropriate, as their assumptions will only rarely be met. The relevant assumptions of the three methods, using Eq. 4 above for notational reference, are briefly summarized below. For further details, see Kuhry and Marcus (1977), Sokal and Rohlf (1981), Seim and Sæther (1983), Rayner (1985), and McArdle (1988).

Regression slope estimates from LSR assume that log W, but not log L, is measured with error, and a particular causation direction is also involved (the "predictor" or "independent" variable is used to infer the value of the "criterion" or "dependent" one). In contrast, both RMAR and MAR methods allow for error in both variates, and do not distinguish predictor from criterion variables. In RMAR, the regression slope is estimated on the assumption that the ratio of the error variances of the two variables equals the ratio of their actual variances, and it is computed as the ratio of the standard deviation of log W to the standard deviation of log L. MAR assumes equality of the error variances of the two variates, and the slope relating log W and log L is an estimate of the slope of the major axis of the equal frequency bivariate ellipse of paired log W and log L values.

In interspecific comparisons, estimates of species means depart from their true values because of measurement error and sampling error. As noted above, the determination of the magnitude of error for the variables under study is essential for a correct selection of the slope determination method. In the case of fruit length and width, measurement error will probably be negligible, and almost all variability will be due to sampling error. Pagel and Harvey (1988*a*) proposed that calculation of within-species variances for each species can provide estimates of error variances in interspecific comparative studies, thus helping to select the most appropriate regression method for interspecific comparisons (see also Seim and Sæther 1983). This method will be used here.

Intraspecific variation

Although the main emphasis of the present study is on interspecific patterns, intraspecific variation in L and W will also be examined because of its relevance to the interpretation of interspecific variation in fruit shape. We would tend to recognize a given interspecific pattern as a truly adaptive one when it is inconsistent with the prevailing patterns of variation within species. For this reason, the null hypothesis based on allometry (which, obviously, applies also intraspecifically) will be separately tested for individual species. In this way, supplementary information will be obtained for interpreting the results of interspecific analyses. It is important to note, however, that including intraspecific analyses here should not be taken as an indication that the same logic about selective forces on fruit shape (see *Introduction: Hypotheses and predictions* and *Adaptive hypotheses*) applies equally inter- and intraspecifically. Intraspecific analyses are merely used for determining whether within-species variation in fruit shape conforms or not to expectations derived from allometry.

In intraspecific studies, sampling variability could be estimated by obtaining, for individual species, within-population variances of L and W for a sufficiently large number of populations. I do not have these data, and estimates of within-species sampling variability that could help to decide on the most suitable slope estimation method are thus not possible. For this reason, the three slope estimation methods will simultaneously be used for each species. If results are consistent, confidence may be placed on conclusions even in absence of precise information on the applicability of the underlying assumptions.

Interspecific variation and phylogenetic effects

A variety of methods have been described in recent years to assess the influence of phylogeny on interspecific patterns (e.g., Felsenstein 1985, Pagel and Harvey 1988*b*, Bell 1989, Burt 1989, Grafen 1989, Gittleman and Kot 1990). Some of them require a detailed knowledge of the phylogeny of the species involved (or, at least, a plausible phylogenetic hypothesis), and their application to a taxonomically very heterogeneous sample, such as the one used here, is impractical. Methods that infer phylogeny from the taxonomic hierarchy and are based on the use of nested analysis of variance and covariance are more appropriate in the present instance, and will be those used here (following Pagel and Harvey 1988*b*, and, particularly, Bell 1989 where methodological details and justification may be found).

TABLE 1. Summary of intraspecific regressions of log fruit diameter on log fruit length using three different methods of estimating the regression slope (b) for the same data. N = 93 species. SD = standard deviation.

Estimation method	% significant departures from $b = 1.0$	Estimated slope, b (Mean ± 1 SD)
Least squares	10.8	0.8338 ± 0.2813
Reduced major axis	9.7	1.1335 ± 0.3443
Major axis	11.8	0.9816 ± 0.4507

* For a given estimation method, "% significant departures" denotes the proportion of species examined ($N = 93$) for which b differed significantly ($P < .05$) from unity, the value predicted from the null hypothesis.

The taxonomic hierarchy may be used as a nesting hierarchy, with individual observations nested within species, species nested within genera, and so on. When a single continuous character is under consideration, nested analysis of variance (ANOVA) provides estimates of the proportion of its total variance that is attributable to a particular taxonomic level, independent of other levels. Assuming that the taxonomic hierarchy reasonably reflects phylogeny, nested ANOVA allows for an estimation of the effects of common descent (at various levels of the taxonomic hierarchy) on observed patterns of variation. If one ecological categorizing variable (e.g., seed dispersal mode) is added as a further nesting level, the relative contribution of phylogenetic effects and ecological factors to total variation may be assessed. When two continuous variables are involved, as in the present instance (fruit length and width), nested analysis of covariance (ANCOVA) further allows for an estimation of phylogenetic effects on patterns of covariation. In particular, nested ANCOVA will be used to obtain taxonomy-independent regression slopes for the variation of fruit length and width (Bell 1989).

Significance tests

For LSR and RMAR estimation methods, comparisons of regression slopes with the expected value from the null hypothesis were performed with ordinary two-tailed t tests using standard errors of slope estimates. In RMAR, the standard error of the slope estimate was considered equal to the standard error of the LSR regression coefficient (Sokal and Rohlf 1981, McArdle 1988). In the MAR method, significance of departure from the predicted regression slope was tested by determining the 95% confidence interval for the calculated slope value using the method in Sokal and Rohlf (1981), and determining whether this range encompassed the predicted value.

In the batteries of simultaneous tests involved in intraspecific comparisons, the nominal significance level of .05 was adjusted using the Bonferroni method (dividing by the number of tests being performed simultaneously). Throughout this paper, means are shown ±1 SD, and N denotes sample size. All logarithmic transformations used logarithms to base 10.

RESULTS

Intraspecific variation

The null hypothesis was intraspecifically tested in 114 species (see *Methods: Intraspecific variation* for justification). In 21 of these, LSR regressions obtained were not statistically significant (F tests, $P > .05$), probably because sample sizes were not adequate to reveal variation patterns in species exhibiting reduced fruit variability. A summary of regression results for the remaining 93 species is shown in Table 1. Slopes yielded by the three estimation methods differed significantly ($H = 38.92$, df = 2, $P < .0001$; Kruskal-Wallis analysis of variance), with LSR consistently yielding the shallowest, and RMAR the steepest, slopes.

In the vast majority of species, intraspecific variation in fruit shape did not depart from that expected from allometry. Irrespective of estimation method, the slope of the log W – log L regression did not depart significantly from unity in nearly 90% of the species examined, hence the null hypothesis was generally upheld. The three estimation methods did not differ significantly with regard to their outcomes for particular species (i.e., significant or nonsignificant departure from the prediction; $T = 0.316$, df = 2, $P = .85$; Cochran's test for related observations, Conover 1980). Species exhibiting significant departures were irregularly scattered among families and genera, and no evident taxonomic pattern was discernible.

Interspecific variation

To decide on the suitability of the different slope estimation methods in interspecific comparisons, estimates of the error variance associated with log L and log W were obtained by computing for each species the sample standard deviations of these magnitudes. The averages of individual species' standard deviations were 0.04119 ± 0.01881 and 0.04332 ± 0.01813 for log L and log W, respectively (N = 114 species). Estimates of the actual variances, obtained by computing the variances of species means for these magnitudes, were 0.02909 and 0.02843 for log L and log W, respectively. The ratio of log L to log W estimated error variances (0.90) is smaller than the ratio of estimated actual variances (1.02). The ratio of the log L to log W mean standard deviations is close to unity (0.951), and its 95% confidence interval (obtained using a bootstrap procedure and 1000 replications) was 0.848–1.061, thus encompassing unity. These results indicate that the assumption of the LSR method is not met in the data, as there is substantial error variability in both variables. Although the data probably are also suited for

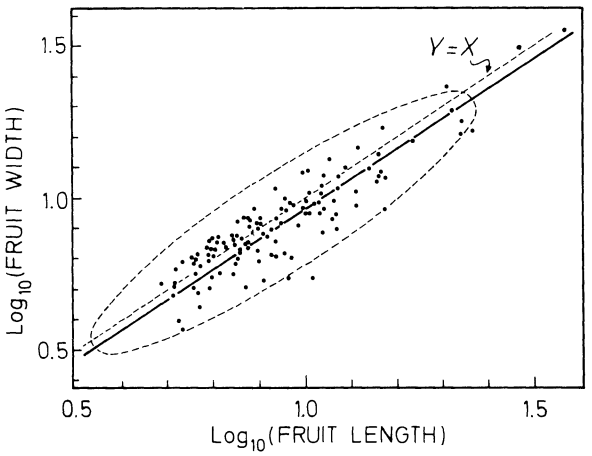

FIG. 1. Variation of $\log_{10}$(mean fruit width) with $\log_{10}$(mean fruit length) (both measured in millimetres) in a sample of 117 species of Iberian animal-dispersed, fleshy-fruited plant species. Regression line (——) was fitted using the major axis estimation method (equation: $\log W' = 0.9873 \log L - 0.0190$). Shown also are the 95% bivariate equal-frequency ellipse and, for reference, the line $Y = X$ (both – – –).

RMAR, the similarity in error variabilities associated with log L and log W' provides more justification for using MAR, and this method will be used in the remainder of this paper for estimating regression slopes.

Mean W' and L were computed for each species, and the regression equation was obtained after logarithmic transformation of species means (Fig. 1). The equation obtained for the functional relation between log W' and log L (measured in millimetres) among species was $\log W' = 0.9873 \log L - 0.0190$. The 95% confidence interval for the slope (0.9034–1.0789) encompasses unity, hence interspecific variation of fruit shape is in accordance with the prediction from the null hypotheses.

Nested analysis of covariance (ANCOVA) was used to determine if this pattern continues to hold after accounting for the considerable taxonomic heterogeneity represented in the sample, and to assess if the null hypothesis also holds for variation in fruit shape taking place among higher taxonomic entities. For this analysis, L and W' of individual fruits were log transformed, and each individual fruit was classified according to species, genus, and family. Individual fruits represented replicates within species (error term), species were nested within genera, and genera within families. Number of species in the data set was too small for expanding the taxonomic hierarchy beyond the family level.

In the species set studied, differences among genera within families accounted for most of the variation in fruit dimensions (Table 2) (48.9 and 45.0% of total variance for log W' and log L, respectively). Variation among families (19.1 and 20.0%), and among species within genera (23.6 and 27.4%), accounted for a smaller proportion of total variance. The largest covariance component also occurred at the genus level. After accounting for taxonomic effects, the overall, intrinsic regression slope was 0.989, which did not differ significantly from 1 (Table 2). Intrinsic regressions at every taxonomic level likewise yielded slopes not differing from 1. The null hypothesis is thus also supported after accounting for potential phylogenetic effects derived from the taxonomical heterogeneity of the sample and the statistical non-independence of species due to shared ancestry.

In addition to providing a convenient null hypothesis, allometry may also be used as a subtraction criterion. The scatter of species around the log W'–log L regression in Fig. 1 reflects the influence of factors other than allometry, including dispersal mode and phylogenetic effects. Examination of the regression residuals may thus provide further insight into the potential influence of ecological and phylogenetic factors on fruit shape after statistically removing purely allometric effects. The influence of dispersal mode (bird dispersal vs. bird plus mammal dispersal) and phylogenetic effects (as inferred from taxonomic affiliation) on regression residuals was examined simultaneously using a random effects nested ANOVA (Table 3). The effect of dispersal mode on regression residuals was not sig-

TABLE 2. Nested analysis of variance and covariance of log fruit width (W') and log fruit length (L) for Iberian vertebrate-dispersed plants.*

		Mean squares			Variance components			Intrinsic major axis slope
Level	df	Log W'	Log L	Mean product	Log W' (%)	Log L (%)	Covariance	b (95% CLS)
Family	35	1.08259	1.06197	0.96453	0.00537 (19.1)	0.00553 (20.0)	0.00512	1.016 (0.853, 1.211)
Genus	27	0.68343	0.64982	0.58744	0.01378 (48.9)	0.01245 (45.0)	0.01180	0.945 (0.718, 1.238)
Species	51	0.14395	0.16333	0.12549	0.00665 (23.6)	0.00757 (27.4)	0.00582	1.082 (0.828, 1.424)
Error†	2427	0.00238	0.00211	0.00160	0.00238 (8.4)	0.00210 (7.6)	0.00160	
Total	2540	0.02734	0.02766	0.02359	0.02818	0.02765	0.02434	0.989 (0.961, 1.018)

* Analyses of variance and covariance were performed using procedure NESTED in SAS (SAS 1988). Intrinsic regression slopes at the various nesting levels were computed using their respective variance and covariance components and standard formulae for major axis regression in Sokal and Rohlf (1981: 594–599).

† Individual fruits within species.

TABLE 3. Random effects nested ANOVA for the effect of dispersal model ("bird" vs. "bird plus mammal") and phylogeny on the residuals of the fitted major axis regression of log fruit width on log fruit length shown in Fig. 1.

Variance source*	ANOVA table df	Mean square	F	P	Variance accounted for (% of total)
Dispersal mode	1	0.002836	0.36	.55	0.00
Family	38	0.007890	1.13	.38	6.75
Genus	26	0.006977	2.26	.0063	40.39
Error	51	0.003082			52.86

Significance of the model: $F = 2.56$, df = 65,51, $P = .00034$

* Dispersal mode was used as the main effect, and family and genus were hierarchically nested within each level of dispersal mode. The error term corresponds to variation among species within genera. The model was fitted using procedure GLM (Type III sum of squares) and proportions of variance were obtained using procedure VARCOMP (SAS 1988).

nificant. Phylogeny, in contrast, did have a significant influence, and accounted for 47.1% of variance in residuals. Variation of residuals among families within dispersal modes was not significant, while variation among genera within families was significant. Phylogenetic effects on residuals were thus almost entirely due to variation among genera within families (40.4% of residuals variance). It may be concluded that the degree of departure of individual species from the predicted log W–log L regression line is attributable to phylogenetic effects alone, being unrelated to dispersal mode. Departures from allometry are associated with genus-specific, intrafamilial variation in fruit shape independent of dispersal mode.

To further document the conclusion that interspecific variation in fruit shape is unrelated to dispersal mode, I examined in detail the patterns of variation in fruit dimensions occurring within the Rosaceae and the Caprifoliaceae, the two families contributing the largest number of species to the sample. In the Caprifoliaceae, fruit consumption by mammals has not been recorded to date for any of the 13 species in my sample, and apparently all species are exclusively bird dispersed. In the Rosaceae, in contrast, mammalian dispersal occurs in at least 24 of the 27 species in the sample. Regressions for the log W–log L plots of species means (not shown) were computed separately for each family (Table 4). Despite their contrasting dispersal modes, the two families were similar in having interspecific regression slopes not departing significantly from 1.

DISCUSSION

Bivariate regression analyses are routinely used in ecological research to elucidate relationships between variables. Most often, the objective of such analyses is just to determine the nature and statistical significance of the relationship between variables, the particular values of regression parameters (slope and intercept) having little or no relevance to results. In other cases, however, specific hypotheses concerning the values of regression parameters are the focus of analyses. In these instances, accuracy of parameter estimates is essential, and the reliability of results will depend on whether the assumptions required by the particular estimation method used actually hold in the data. Detailed descriptions of the assumptions involved in the various regression estimation methods have been presented, among others, by Seim and Sæther (1983), Rayner (1985), McArdle (1988), and Pagel and Harvey (1988*b*). These studies should make clear to everyone that the routinely used, simple least squares regression (LSR) is an inappropriate estimation method for most ecological applications requiring accurate estimates of regression parameters. The present study illustrates well the risks of using an inappropriate regression method, as its main conclusions would have been reversed had I used ordinary LSR estimation. Using LSR, the resulting slope for the regression of mean log W on mean log L across species (Fig. 1) is 0.888 (95% confidence interval = 0.808–0.968). In addition, intrinsic regression slopes at the various taxonomic levels in the nested ANCOVA (Table 2) likewise become significantly smaller than unity when LSR estimation is used. By underestimating regression slopes, uncritical application of LSR would have erroneously led to rejection of the null hypothesis and acceptance of one of the adaptive hypotheses (predicting that fruits become more elongated with increasing mass).

Predictions based on dispersal-related adaptive hypotheses are not supported by the present study. Instead, interspecific variation in fruit shape (as described by length and width) of Iberian vertebrate-dispersed plants does not depart significantly from that predicted

TABLE 4. Summary of interspecific regressions (major axis estimation method) of log fruit width on log fruit length for the two main families in the sample. N = number of species.

Regression parameters	Rosaceae ($N = 27$)	Caprifoliaceae ($N = 13$)
Slope	0.999	1.099
(95% confidence limits)	(0.851, 1.173)	(0.548, 2.318)
Intercept	−0.034	−0.149
(95% confidence limits)	(−0.221, +0.124)	(−1.235, +0.340)

TABLE 5. Differences in fruit size (mean ± 1 SD) between the two groups of species recognized in the sample on the basis of seed dispersal mode. N = number of species.

Fruit trait	Bird dispersed (N = 73)	Bird plus mammal dispersed (N = 44)	Difference*	
			F	P
Length (mm)	8.1 ± 2.9	12.4 ± 6.3	32.86	≪.0001
Width (mm)	7.4 ± 2.3	11.7 ± 6.1	38.66	≪.0001
Fresh mass (mg)	319 ± 439	1589 ± 2994	39.96	≪.0001

* Statistical tests conducted on log-transformed data.

by a simple null hypothesis based on allometry. Deviations of individual species from the predicted allometric relationship (regression residuals) are also unrelated to dispersal mode, and are best explained by the existence of genus- and species-specific variation in fruit shape. Nested analysis of covariance further shows that, after accounting for the influence of common descent on observed interspecific patterns (as inferred from taxonomical affiliation), the null hypothesis still holds within taxonomic categories above the species level.

No evidence was found that species groups, or families (comparison Rosaceae vs. Caprifoliaceae), of Iberian plants differing in seed dispersal modes had contrasting patterns of interspecific variation in fruit shape. The two dispersal modes recognized in the species sample ("birds" vs. "birds plus mammals," B and BPM species groups hereafter), involve partly overlapping arrays of dispersers. It might thus be argued that they are not distinct enough to provide an adequate basis for testing the adaptive predictions formulated here, and that here lies the reason for the failure to find supporting evidence. Nevertheless, species in the B and BPM groups differ significantly in average fruit length, width, and fresh mass (Table 5), BPM species having larger fruits than B species. Previous investigations have also documented additional differences between BPM and B Iberian species in other fruiting traits, including color and nutritional composition of the pulp (Herrera 1989; see also Debussche and Isenmann 1989). The two groups of species considered here are thus different enough in other fruit features as to deny the possibility that they could also exhibit differences in fruit shape. Furthermore, significant differences between the two groups in mean fruit size are consistent with the assumptions that led to the adaptive hypotheses tested here (see *Introduction: Hypotheses and predictions* and *Adaptive hypotheses*).

It is striking that the allometric prediction holds uniformly in the species set examined, given the broad variety of morphological fruit types represented. Out of 117 species, 46 (39.3%) produce berries and 48 (41.0%) produce drupes, while fruits from the remaining 23 species (19.7%) include a variety of morphological types (e.g., syconia of *Ficus*, strobili of *Juniperus*, arillate seeds of *Euonymus*, and a number of structural types found in the Rosaceae). An analysis of variance of the log W–log L regression residuals of individual species, using fruit type as a three level categorizing variable (berries, drupes, and "others"), does not reveal significant heterogeneity among the three species groups (F = 1.77, df = 2, P = .18). Homogeneity in the pattern of relative variation of mean fruit length and width in face of contrasting anatomical origins (and thus, presumably, developmental pathways) may be interpreted in terms of shared constraints. Examination of the factors influencing fruit shape within species may help to identify these constraints.

With regard to shape, large fruits are simply scaled-up versions of small ones, both within and among species. This suggests that the morphogenetic and physical constraints responsible for intraspecific patterns of shape variation may also apply to interspecific ones. Within species, fruit volume at ripeness largely depends on the volume of fleshy tissue, which, in turn, depends on cell number and cell volume (Coombe 1976, Esau 1977). The number and volume of cells in fruit flesh at ripeness depend on the number at anthesis and the rate and duration of cell division and cell expansion thereafter. Active cell division in the flesh is generally limited to a short period after anthesis, and ensuing cell enlargement is the process most directly determining final fruit volume (Bollard 1970, Coombe 1976, Staudt et al. 1986). Before cellular expansion takes place, fruit shape depends closely on the shape of the ovary (and/or ancillary structures involved) and the orientation of cell division planes. The final shape, however, will be largely determined by internal hydrostatic pressure and mechanical stresses on the fruit surface (generated by intense solute and water accumulation during cellular enlargement) (Considine and Brown 1981). Physical models demonstrate that surface stresses are strongly shape dependent, and that they are minimized in fruits with a length/width ratio of unity (Considine and Brown 1981, Considine 1982). Independently of fruit mass and anatomical structure, the combined action of internal hydrostatic pressures and surface stresses operating on a relatively adjustable mass of expanding cells will therefore lead to the observed convergence on length/width ratios close to unity. In interspecific comparisons, deviations from this prevailing pattern will reflect species-specific variation in ovary (and/or associated structures) shape, organization of cellular division planes, and duration of the cell division phase,

during the earlier stages of fruit development. All these factors are expected to be closely influenced by phylogeny, which is in agreement with the results found here (Table 3).

Nested analyses of variance of log fruit length and width have revealed a considerable phylogenetic component in the variation of these traits. Nearly half of their total variance is attributable to variation among genera within families, while variation among species within genera, and among families, is less important (Table 2). These figures suggest that, in the sample examined, diversification of fruit size has mainly occurred at the generic level. Further studies are needed on other species assemblages and other fruit features before the generality and implications of these results can be properly assessed, but the influence of phylogeny on interspecific variation in fruit traits is probably greater than ordinarily acknowledged (Herrera 1986, 1987, Gorchov 1990; P. Jordano, *personal communication*). Recognition of this fact will have important consequences for evolutionary interpretations of interspecific patterns of occurrence of fruit and fruiting features in local or regional multispecies assemblages. If interspecific variation in fruit and fruiting characteristics of animal-dispersed species is eventually proven to depend more on allometric effects and taxonomic affiliation above the species level than on the ecological conditions of the habitats concerned (including dispersal agents), adaptationist interpretations of interspecific patterns in fruit and fruiting features will have to be revised.

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