

INTER- AND INTRASPECIFIC VARIATION IN FRUIT TRAITS IN CO-OCCURRING VERTEBRATE-DISPERSED PLANTS

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A quantitative analysis of the patterns of intra- and interspecific variance of fleshy fruit traits (length, width, pulp mass, seed mass, percent pulp mass) in eight species of southeastern Spanish vertebrate-dispersed plants, *Berberis hispanica*, *Crataegus monogyna*, *Daphne laureola*, *Hedera helix*, *Juniperus communis*, *Juniperus phoenicea*, *Juniperus sabina*, and *Rosa canina*, shows a statistically significant individual variability in the five fruit traits considered. Individual variability tended to be largest for pulp mass and seed mass (coefficient of variation of individual means between 20% and 30%) and smallest for fruit width and length and for proportion of pulp (CV of 5%–12%). Most variance in fruit traits (67%–88%) was accounted for by taxonomic affiliation, while the remainder of the variance was partitioned in roughly similar proportions among and within plants of individual species. There were some differences between fruit traits in the relative proportion of variance contributed by within and among individual variation, but all fruit traits in all species consistently exhibited a remarkably high proportion of within-individual variance, roughly comparable to the variance among individuals. The potential ecological and evolutionary implications of observed patterns of fruit variability are discussed in relation to the foraging behavior of seed-dispersing frugivores.

Introduction

Individual variation is the indispensable raw material for natural selection, and quantitative investigations on patterns of intraspecific variation in plant reproductive traits have often been conducted in recent years. These studies have most commonly examined variability in seed size (Thompson 1984; Zimmerman 1987; Michaels et al. 1988; Winn 1988; Hendrix and Sun 1989), nectar production and availability (Herrera and Soriguer 1983; Pleasants and Chaplin 1983; Real and Rathcke 1988, 1991), and floral morphology (Nilsson 1988; Herrera 1990a, 1990b, 1993; Fenster 1991; Campbell 1992; Svensson 1992). Despite this growing interest in the natural patterns of variability of plant reproductive characters, comparatively few investigations have focused on assessing levels of intraspecific variability in fruit traits of fleshy-fruited, vertebrate-dispersed plants (Jordano 1984, 1991; Willson et al. 1990; Herrera 1992). This dearth of information on patterns of natural fruit variability contrasts sharply with the abundance of publications on seed dispersal by animals in the last 2 decades (Howe 1986; Jordano 1992; Willson 1992).

Evolutionary interpretations of plant-vertebrate seed dispersal systems will benefit from an improved knowledge of the patterns of natural variation in fruit features. Analyses of the apportionment among species, among individuals, and within individuals of variance in fruit characters will provide insights into the potential opportunities open to frugivorous animals for ex-

erting selection on these plant traits. Remarkably little is known about how much of natural variation in fleshy-fruit traits occurring in a given habitat results from variation among species and among individuals within species. The objective of this article is to provide a quantitative evaluation of patterns of variability in fruit traits in a southeastern Spanish local fruit assemblage. This is one of the few studies that partitions the variance components of all fruit traits. The following questions are addressed: (1) How is total variance in fruit traits apportioned among species and individuals within species? (2) Are different fruit traits similar with regard to patterns of intra- and interspecific variation? (3) Does the relative importance of variation within and among individual for particular fruit traits remain consistent across species?

Study area and methods

Variability in fruit characteristics was studied in eight co-occurring plant species growing in the Roblehondo area, Reserva de Navahondona-Guahornillos, Sierra de Cazorla (Jaén province, southeastern Spain; a description of the vegetation of the area can be found in Herrera [1984b]). The species studied were *Berberis hispanica* (Berberidaceae), *Daphne laureola* (Thymelaeaceae), *Crataegus monogyna*, *Rosa canina* (Rosaceae), *Hedera helix* (Araliaceae), *Juniperus sabina*, *Juniperus communis*, and *Juniperus phoenicea* (Cupressaceae). All of these are shrubs or small trees, except *H. helix*, a woody climber, found in the understory of a mixed forest dominated by *Pinus nigra* and *Quercus rotundifolia*, at elevations between 1,300 and 1,500 m a.s.l. Seeds of *Berberis*, *Daphne*, and *J. sabina* are dispersed exclusively by small- to medium-sized

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frugivorous birds (Obeso 1986; Jordano 1993). The remaining species are dispersed by both birds and carnivorous mammals (Obeso 1986; Herrera 1989). Excepting the summer-fruiting *D. laureola*, species considered here mature fruits in autumn-winter, and their ripe fruits are simultaneously available to frugivores in the study area.

Ripe fruits ($N = 20-30$ fruits/plant) were collected from five to 17 individual plants from each species, depending on local abundance and availability of fruit crops. In each sampled individual, ripe fruits were picked from as many infructescences as possible to reduce possible biases derived from differences between branches in fruit characteristics. Length (FLEN) and width (transversal diameter; FWID) were measured on individual fresh fruits to the nearest 0.1 mm. Fruits were then dried to constant weight, and pulp (PMASS) and seed (SMASS) mass obtained to the nearest 0.1 mg. A fifth variable included in the analyses was the proportion of the dry fruit made up by the pulp (%PULP). Percentage of pulp was arcsin-transformed for the analyses. Data from a total of 1,860 fruits were included in the analyses.

To partition the total population variance in each fruit trait, nested univariate ANOVAs were used according to two different models. In the first model, species were treated as the highest level for nesting, and individual plants were then nested within species. In the second model, a single nesting level (individual plants) was used and was analyzed separately for individual species. The NESTED procedure in the SAS package was used to obtain components of variance (SAS Institute 1988).

Results

All species exhibited significant individual variability in the five fruit traits considered, as revealed by univariate ANOVA ($P < .001$ in all cases, results not shown). Average values for fruit traits were computed separately for each plant and univariate statistics were obtained for each species using individual plant means. All species exhibited substantial individual variability in all fruit traits, as revealed by the broad ranges of individual plant means, the large CVs (often greater than 20%) and the variance of the log-transformed data (table 1). Traits differed broadly in their levels of relative individual variation. In all species, pulp mass and seed mass showed the largest CVs (typically between 20% and 30%), while fruit width and length and proportion of pulp exhibited the smallest ones (generally 5%–12%).

INTRA- VS. INTERSPECIFIC VARIATION

For all the fruit traits examined, most variance (66.7%–88.4%) was accounted for by taxonomic affiliation (the higher hierarchical level in the

Table 1

SUMMARY OF INDIVIDUAL VARIATION IN SELECTED FRUIT CHARACTERISTICS IN EIGHT SPECIES OF SOUTHERN SPANISH VERTEBRATE-DISPERSED PLANTS

Species	n	FLEN (mm)			FWID (mm)			PMASS (mg)			SMASS (mg)			%PULP		
		Range	CV	S ²	Range	CV	S ²	Range	CV	S ²	Range	CV	S ²	Range	CV	S ²
<i>Berberis hispanica</i>	14	6.8–9.4	7.6	1.23	4.2–5.3	7.4	1.08	14–28	19.9	4.99	15–25	17.7	6.08	44.2–65.3	10.2	1.95
<i>Crataegus monogyna</i>	7	7.0–10.0	11.1	2.91	6.6–8.9	8.7	1.76	56–110	22.6	14.19	58–115	30.6	19.82	45.1–59.3	8.2	1.42
<i>Daphne laureola</i>	8	8.8–9.9	4.7	.48	5.8–7.4	6.8	1.08	15–30	20.1	4.61	20–30	13.4	3.94	40.2–55.6	10.1	2.13
<i>Hedera helix</i>	5	5.5–7.5	11.5	3.26	5.5–8.7	15.1	5.71	15–39	36.1	27.67	17–50	33.0	28.36	40.6–46.9	5.6	.75
<i>Juniperus communis</i>	10	5.3–7.4	9.6	1.82	4.9–6.6	9.0	1.82	22–72	36.4	18.72	12–27	20.7	8.70	58.5–81.2	10.5	2.30
<i>J. phoenicea</i>	12	6.9–8.7	6.5	.85	7.0–9.0	7.0	1.10	118–208	17.9	7.93	27–85	30.0	19.91	69.8–83.0	5.3	.57
<i>J. sabina</i>	6	6.6–8.3	9.1	2.00	61–102	17.9	7.26	37–67	17.9	8.22	56.1–64.8	5.5	.71
<i>Rosa canina</i>	17	10.4–17.8	11.6	3.29	7.9–10.9	8.8	1.44	156–462	23.3	16.35	80–373	40.5	32.41	52.7–79.6	9.6	1.80

Note. Entries represent the range, the CV, and the variance (S², multiplied by 1,000 to improve presentation) of log₁₀ transformed individual plant means for each fruit character. FLEN = fruit length; FWID = fruit width; PMASS = dry pulp mass; SMASS = dry seed mass; %PULP = percent of dry fruit mass made up by pulp (arcsine-transformed). n = number of individual plants sampled per species. Fruit length data were not available for *J. sabina*.

Table 2
COMPONENTS OF VARIANCE (%) OF FRUIT TRAITS IN A SET OF EIGHT
CO-OCCURRING FLESHY-FRUITED PLANTS

Source of variation	FLEN	FWID	PMASS	SMASS	%PULP
All species:					
Species	88.42	77.35	85.74	67.86	66.69
Individuals	8.08	11.29	7.69	19.53	14.77
Within individuals...	3.50	11.36	6.57	12.61	18.54
<i>Juniperus</i> species only:					
Species	61.13	63.03	73.61	53.09	45.10
Individuals	17.76	19.51	11.83	21.51	26.76
Within individuals...	21.11	17.46	14.56	25.40	28.14

Note. FLEN = fruit length; FWID = fruit width; PMASS = dry pulp mass; SMASS = dry seed mass; %PULP = percent of dry fruit mass made up by pulp (arcsine-transformed). The analysis of FLEN for *Juniperus* species was based only on two species (*J. phoenicea* and *J. communis*). In each analysis, fruits were nested within individuals, and individuals nested within species.

ANOVA design), while the remainder of the variance (within species) was partitioned in roughly similar proportions among and within plants of individual species (table 2). These results might be influenced by the distribution of the species examined in six different genera and five families, thus representing considerable phylogenetic diversity. To examine this further, a similar analysis was conducted using only the three species in the genus *Juniperus*, hence reducing considerably the taxonomic diversity of the species sample. As expected, there was some reduction in the proportion of variance at the species level when the sample was restricted to the three *Juniperus* species, but most variance in all characters was still accounted for by taxonomic affiliation (45.1%–73.6%) (table 2). A most drastic reduction in the taxonomic diversity of the species sample thus brought about only a relatively minor reduction in the proportion of total variance in fruit traits accounted for by taxonomic affiliation alone.

WITHIN- VS. AMONG-INDIVIDUAL VARIATION

In the analyses above, components of intraspecific variance were pooled across species, and it was not possible to examine them on a species-by-species basis. To this end, separate ANOVAs and variance partitions were performed for each species, using individual plants as the single categorical factor (table 3). The first major conclusion emerging from these analyses is that, with only minor exceptions, all fruit traits examined exhibited a remarkably high proportion of within-individual variance in all species, roughly comparable to the variance among individuals.

There were some differences between fruit traits in the relative proportion of variance contributed by within- and among-individual variation, but the relative importance of within- and among-individual variation for individual fruit traits re-

mained consistent across species ($W = 0.450$, $P = .027$; Kendall coefficient of concordance [Siegel 1956]). Fruit length was the trait exhibiting, on average, the smallest proportion of within-individual variation (36.9%), and percent dry pulp mass the largest (74.5%) (table 3). Extreme values of the within-individual component of variation were exhibited by the proportion of pulp in *Hedera helix* (91.8%) and *Juniperus sabina* (74.5%), indicating that, in these species, almost all the variation in this trait occurring in the study population was represented within individual fruit crops. On the opposite extreme of the gradient, within-individual variation contributed only 17.6% of total variance in fruit length in *Crataegus monogyna*, and 20.0% of variance in fruit width in *H. helix*. In these results, most variance resulted from differences between individuals.

Species differed with regard to the relative importance of within-individual variation in fruit traits. *C. monogyna* was the species exhibiting, on average, the smallest proportion of within-individual variation (29.6%), and *Berberis hispanica* the largest (60.2%) (table 3).

Discussion

In all species studied, individual plants differed significantly in mean values of all fruit traits. Levels of individual variability, as assessed by the CV, were relatively high for pulp and seed mass (18%–40%), and appreciably lower for linear dimensions (fruit length and width) and the proportion of dry fruit mass made up by the pulp (5%–12%). Despite the significance of individual differences in mean fruit traits, however, it is remarkable that about 50% of intraspecific variance in fruit traits occurred within individual fruit crops. Although no previous studies on the comparative magnitude of within- and among-individual variation in fruit traits are available for reference (except the analysis of Jordano [1991]

Table 3
COMPONENTS OF INTRASPECIFIC VARIANCE IN FRUIT TRAITS

	FLEN	FWID	PMASS	SMASS	%PULP	Averages
<i>Berberis hispanica</i>	65.7/34.3	36.5/ 63.5	52.8/47.2	25.3/ 74.7	35.6/ 64.4	39.8/ 60.2
<i>Crataegus monogyna</i>	82.4/17.6	67.9/32.1	68.9/31.1	71.5/28.5	56.7/43.3	70.4/29.6
<i>Daphne laureola</i>	41.1/ 58.9	53.8/46.2	44.1/ 55.9	53.0/47.0	47.5/ 52.5	49.1/ 50.9
<i>Hedera helix</i>	77.5/22.5	80.0/20.0	76.8/23.2	46.1/ 53.9	8.3/ 91.8	55.2/44.8
<i>Juniperus communis</i>	67.8/32.2	49.2/ 50.8	66.2/33.8	32.7/ 67.3	61.0/39.0	53.8/46.2
<i>J. phoenicea</i>	34.7/ 65.3	44.3/ 55.7	37.6/ 62.4	46.1/ 53.9	42.7/ 57.3	41.8/ 58.2
<i>J. sabina</i>	65.6/34.4	50.8/49.2	38.9/ 61.1	25.5/ 74.5	45.4/ 54.6
<i>Rosa canina</i>	72.6/27.4	39.4/ 60.6	53.7/46.3	59.8/40.2	49.3/ 50.7	55.8/44.2
Averages	63.1/36.9	54.6/45.4	54.1/45.9	46.7/ 53.3	25.5/ 74.5	

Note. Figures in each entry represent the percentages of total variance accounted for by differences among (first figure) and within (second figure) individuals. FLEN = fruit length; FWID = fruit width; PMASS = dry pulp mass; SMASS = dry seed mass; %PULP = percent of dry fruit mass made up by pulp (arcsine-transformed). In each entry, the largest variance component is shown in bold type.

for *Juniperus phoenicea*, a species included also in this study), it is illustrative to compare the patterns of variation revealed by the present investigation with those reported for other plant reproductive structures.

For seed mass, a trait whose variability has been studied in detail for many species, reported CVs of individual plant means most commonly fall in the range 25%–40%, and about 35%–80% of total intraspecific variance occurs within plants (Stanton 1984; Thompson 1984; Zimmerman 1987; Michaels et al. 1988; Winn 1988; Hendrix and Sun 1989). For a variety of linear measurements of floral structures, reported CVs most often fall between 5% and 15%, and within-individual variation accounts for 35%–55% of total intraspecific variance (Stanton and Preston 1988; Tucic et al. 1990; Campbell 1992; Svensson 1992; Herrera 1993, and unpublished data). Compared with these figures, levels of variability in mass-related fruit characters (pulp and seed mass) documented by the present study are analogous to those reported for seed mass, whereas variability of the linear dimensions (fruit length and width) is more similar to that exhibited by linear measurements of floral structures. Dimensionality considerations predict that, all else being equal, the CVs of mass-related traits will be larger than those of linear or surface measurements (Lande 1977). Mass-related fruit traits (pulp and seed mass) are related to linear dimensions (fruit length and width) by a cubic function, and computer simulations show that this relationship alone may satisfactorily account for the larger CVs exhibited by the former group of traits (C. M. Herrera, unpublished). Plant reproductive structures studied to date (flowers, fruits, and seeds) thus do not seem to differ essentially with regard to patterns of individual variability, and the larger CVs exhibited by seed and pulp mass relative to linear dimensions are simply attributable to differences in dimensionality. The variance, or standard de-

viation, of the logarithms of measurements provides a measure of intrinsic variability that is invariant under a multiplicative change (Lewontin 1966), and it should thus be more appropriate than the CV in comparisons involving reproductive structures differing in dimensionality. Unfortunately, however, published analyses have rarely used this measure of variability (Fenster 1991). Variances of log-transformed data presented here showed the same order of magnitude as CVs, which supports the larger variability of mass-related traits relative to linear dimensions.

In the assemblage of fruit species studied here, interspecific differences accounted for the greatest proportion of the variance in fruit traits. A total of 16 fleshy-fruited plant species are found in the Roblehondo study area (Herrera 1982; Obeso 1986). Although all the most common species were included in the subsample chosen for this study, the proportional contribution of between-species variation to total local variance in fruit traits has been probably underestimated. In the sample of 114 Spanish species examined by Herrera (1992), variation among species is responsible for 92.8% of total variance in fruit width and 93.5% of variance in fruit length (C. M. Herrera, unpublished).

The potential ecological and evolutionary implications of the patterns of intra- and interspecific variability documented by this study will largely depend on the foraging responses of frugivores to this variability. Frugivorous birds, the main dispersal agents of the species studied here, are able to discriminate among co-occurring fruit species, individual fruiting plants within species, and fruits within individual fruit crops (Moermond and Denslow 1983; Herrera 1984a, 1988; Manzur and Courtney 1984; Jordano 1987; White and Stiles 1991). Plant and fruit features known to influence intra- and interspecific fruit selection by avian frugivores include some of the traits examined in this study, such as fruit size (Herrera

1984a, 1988; Jordano 1987; McPherson 1988) and relative pulp mass (Howe and Vande Kerckhove 1980). It thus seems reasonable to assume that variability in fruit traits reported in this study may actually influence fruit choice by frugivores in our study area. This has been confirmed by Obeso (1988, 1989) for *Berberis hispanica*, one of the species studied here. In this species, individual variation in fruit size and pulp/seed ratio was found to be related to differences in proportional fruit removal by birds.

The rules governing the foraging behavior of frugivores are imperfectly understood, and it has been recently suggested that they behave according to a hierarchical decision strategy (Sallabanks 1993). This would involve stepwise selection among species, among individuals within species, and among fruits within individuals. Under this hierarchical selection model, opportunities for fruit selection potentially open to frugivores at each of these three decision levels will be proportional to the magnitude of the variance in fruit traits occurring at each of them. Of the three fruit selection processes, only the second one (discrimination among conspecifics) is apt to have some evolutionary consequences for the plant species involved, for it may result in differential reproductive success (mediated by seed dispersal differences) between conspecific plants. If most of the local variance in those fruit traits that influence fruit selection by frugivores results from differences among species, and if a great part of the intraspecific variation occurs within crops, as shown by this study, then the likelihood that selection by frugivores based on these traits will translate into measurable fitness differentials among individual plants will be inherently low. Furthermore, this study has shown that the hierarchical apportionment of variance in fruit traits may differ among plant species and fruit traits.

This leads to the corollary that the opportunities for selection by frugivores on a given fruit trait may differ substantially among species. However, results presented here must be taken with caution due to the relative small number of individuals per species. More data are necessary on this subject to support above statements.

The consequences for the plants of the hierarchical structure of variance in fruit traits may only be tentatively guessed in absence of detailed data on the fruit selection patterns exhibited by the seed dispersal agents. A proper assessment of the ecological and evolutionary relevance of the patterns of variability documented by this study thus requires a more precise knowledge of the decision mechanisms involved in the foraging behavior of the frugivorous animals that eat the fruits and disperse the enclosed seeds, and particularly of those mechanisms involved in stepwise hierarchical discrimination processes among species, plants, and fruits. For want of investigations addressing this issue, however, analyses of variability of fruit traits in natural populations such as the present one may at least serve to draw the attention of researchers on plant-frugivore interactions on this neglected subject.

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