

Seed weight variation and differential avian dispersal in blackberries *Rubus ulmifolius*

Pedro Jordano

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Patterns of within- and between-crop variation in seed weight are described for a population of *Rubus ulmifolius* Schott in southern Spain. Broad variation in seed weight (1.1–4.9 mg) exists among clones; within-crop variation usually encompassed at least $\frac{1}{3}$ of this range and accounted on average for 23% of the total population variance. The four main avian seed dispersers in the study area differ in the frequency distributions of seed sizes found in faecal samples analyzed, indicating that they actually disperse different portions of the seed size distribution.

P. Jordano, Unidad de Ecología y Etología, Estación Biológica de Doñana, C/Paraguay, 1–2, Sevilla-12, Spain.

Описан характер весовых различий семян *Rubus ulmifolius* Schott. одного урожая и разных урожаев в южной Испании. Большие вариации веса семян (1,1–4,9 мг) установлены в разных клонах. Различия семян одного урожая составляют по меньшей мере треть этого перепада и дают в среднем 23 % общих популяционных вариаций. У четырех видов птиц, основных распространителей семян в исследованном участке, найдены различия частоты распределения семян разных размеров в пробах фекалий, что показывает, что они фактически распространяют разные размерные группы семян.

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1. Introduction

Evidence is accumulating which shows that frugivorous animals that are seed dispersers do not eat fruits at random with respect to fruit and seed detailed traits (Janzen 1981, Herrera 1981, Howe and Smallwood 1982, Moermond and Denslow 1983) and therefore the potential exists for the different fruit and seed types and sizes produced by a given plant individual or population being dispersed by rather different species of disperser (Janzen 1982). Other things being equal, the potential selective effect of animals on plant traits such as number of seeds, seed size and fruit features would depend upon the way in which the whole fruit crop variance is allocated among the potential array of seed dispersers and predators, provided this allocation is heritable and has a genetic component.

In this paper I first describe the fruit and seed variability shown by a population of blackberries (*Rubus ulmifolius* Schott, Rosaceae) within and between crops and then I document which dispersers actually disperse which segments of this range of seed variation. A detailed account of the seed dispersal ecology of this species is given in Jordano (1982). Approximately 80% of the seeds were removed by only four passerine species: blackcap *Sylvia atricapilla* (L.), garden warbler *Sylvia borin* (Bodd.), European robin *Erithacus rubecula* (L.) and blackbird *Turdus merula* (L.). These four species are considered here in detail, but the fruits are consumed by at least 16 other bird species.

2. Methods

Birds were netted weekly between 19 August and 14 October 1978 to obtain faecal samples for food analysis (see Herrera and Jordano 1981). *Rubus* seeds were sorted out of the faeces and measured (maximum length) to the nearest 0.25 mm under 10× magnification. Maximum seed length is easily measured and gives an adequate measure of *Rubus* seed weight, as it is significantly correlated with seed dry weight (see below).

During peak fruit ripening, fruit samples were taken from nine previously marked clones. Fruits were analysed for characteristics such as fresh and dry weights, number of seeds, pulp/seed ratios and percent water. Seeds were separated from pulp, air-dried, measured (maximum length) and weighed to the nearest 0.1 mg. Because of the small seed size, mean dry weights and s.d. were obtained for each clone by weighing n groups of 3 seeds each and then averaging over the $n_1/3$; $n_2/3$; $n_3/3$; . . . $n_i/3$ values. Regressions of maximum seed length on seed dry weight were obtained from this sample.



Fig. 1. Extreme types of fruit variation in *Rubus ulmifolius* in the study area, ranging from fruits with many, very small seeds (A) to fruits with few, large seeds (B). Note also differences in infructescence size (only $\frac{1}{3}$ shown in A). In addition to these visible features fruits also differ in pulp/seed ratio and water content. Black line is ≈ 1 cm.

3. Results

3.1. Patterns of seed variation

Striking differences exist in fruit characteristics of clones growing in different habitats but are also apparent between individual clones irrespective of habitat type (e.g. Fig. 1). Both within- and between-crop variation in fruit features is best exemplified by variability in seed weight (Fig. 2). Dry weights of filled seeds for the population range from 1.1 to 4.9 mg but within-crop variation usually encompasses at least $\frac{1}{3}$ of this range, revealing a large variation also at the clonal level. Within-crop variance in seed weight averages 23% of the total population variance.

Other fruit features which are important from the disperser's point of view covary with seed weight and number of seeds. Average seed dry weight is a decreasing function of average seed number (\bar{x} dry weight (mg) = $4.72 - 0.07 \bar{x}$ number of seeds/fruit, $r^2 = 0.89$, $p < 0.01$), reflecting a tendency to produce few large or many small seeds. Average number of seeds is nega-

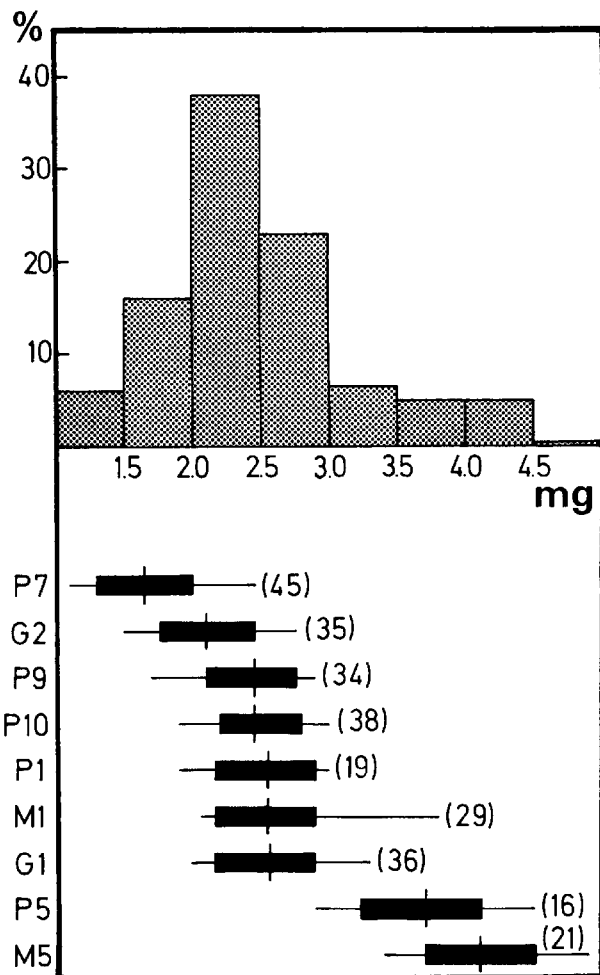


Fig. 2. Seed size frequency distribution (above; expressed as dry weight, in mg) in the *Rubus ulmifolius* population and average seed sizes and ranges for 9 individual clones (below). Segments in the bottom graph show mean \pm one s.d. and ranges (vertical lines, dark rectangles and horizontal lines, respectively) for individual clones of large (G), medium (M) and small (P) size.

tively correlated both with \bar{x} pulp/seed ratio ($r_s = -0.68$, $p = 0.03$, $n = 9$) and \bar{x} percent pulp ($r_s = -0.65$, $p = 0.04$). Thus, clones producing fruits with small seeds on the average tend to produce more seedy fruits with a relatively lower amount of pulp. Therefore, seed size frequency distributions in disperser faecal samples reflect the consumption of fruits of variable characteristics. It is reasonable to assume that the external fruit morphology of *Rubus polydrupes* (Fig. 1), directly reflecting both number of seeds and seed size, could be used by the birds as a visual cue to select fruits of variable profitabilities.

3.2. Seed dispersal

Variation in the sizes of seeds actually taken by dispersers was documented on the basis of seed length meas-

urements (see Methods). Since maximum seed length and seed dry weight are significantly and linearly correlated both at a population level (\bar{x} seed dry weight = $1.65 \bar{x}$ seed length - 1.37, $r^2 = 0.70$, $p = 0.004$, $n = 9$ clones) and within each individual clone ($0.40 \leq r^2 \leq 0.77$, all $p < 0.01$, $n = 20$ seeds for 9 clones), it is concluded that 1) seed length frequency distributions for different dispersers reflect seed dry weight frequency distributions and 2) between-species differences and variabilities in the former reflect those of the latter.

The frequency distributions of seed sizes, as described by seed lengths, in faecal samples of the four main dispersers and the whole disperser assemblage are compared in Fig. 3. Among the four main dispersers the only non-significant difference is *S. atricapilla* vs *T. merula*. The remaining possible comparisons are all significantly different (all $t \geq 3.35$, $p < 0.001$). Thus, dis-

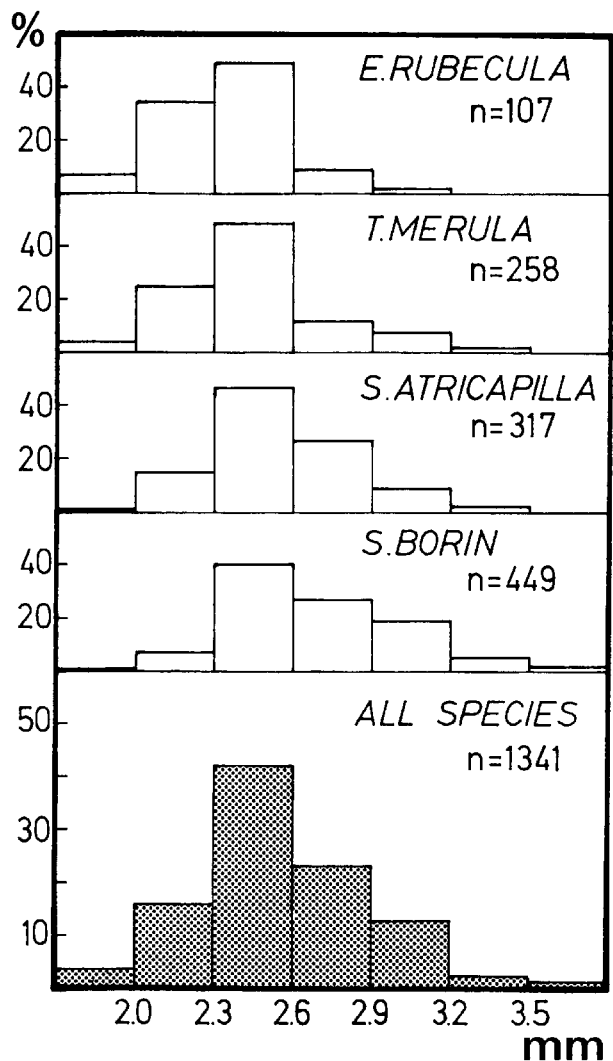


Fig. 3. Seed size frequency distributions (expressed as maximum seed length, in mm) found in the pooled faecal sample of the whole disperser assemblage (bottom) and samples of the four main disperser species.

persers differ in the sizes of seeds they actually disperse and therefore by inference in the kinds of fruits they have consumed, between-species differences being centered about the relative importance of extreme seed sizes in the faecal samples (Fig. 3).

An important aspect of the dispersal at the population level is the heterogeneity (i.e., variance) in seed size of the seed loads actually delivered by dispersers. As all four species have roughly similar short gut passage times (35–80 min, Herrera 1983), seed loads obtained in each faecal sample would reflect the average seed size and variance actually ingested by a foraging disperser during a relatively short feeding bout, probably 1–3 visits to a clone (Jordano 1982, pers. observ.). This implies that no mixing actually occurs in the gut system, but to my knowledge information on this subject for small passerines is lacking.

Mean seed length was computed for every individual faecal sample with ≥ 4 seeds for the four main dispersers (Fig. 3). Mean individual seed sizes thus obtained were averaged to get a grand mean seed size for each disperser species. Two components of heterogeneity in seed sizes dispersed would thus be obtained. Firstly, a within-individual average deviation of every seed in the individual faecal sample from the individual's mean over all the individuals sampled. Secondly, a between-individual average deviation results from averaging the deviation of every individual mean seed size from the specific grand mean (Tab. 1).

Between-species differences in both components were tested with the Levene's test (Van Valen 1978), which compares average deviations by means of a t-test. No differences were found in the within-individual component of heterogeneity in seed size (all $0.60 \leq t \leq 1.99$, $p > 0.10$), while only *S. borin* – *E. rubecula* ($t = 2.63$, $p < 0.01$) and *T. merula* – *E. rubecula* ($t = 2.28$, $p < 0.01$), among all the 6 possible comparisons, statistically differed in between-individual heterogeneity.

Tab. 1. Statistics of deviation from \bar{x} seed size of the *Rubus ulmifolius* seeds found in individual faecal samples of the four main avian seed dispersers. Figures are average \pm 1 s.d. of both the between- and within-individual components (see text for further details).

	Average between-individual deviation from \bar{x} seed size	Average within-individual deviation from \bar{x} seed size
<i>S. atricapilla</i> (n=24)	0.109 \pm 0.092	0.140 \pm 0.064
<i>S. borin</i> (n=34)	0.155 \pm 0.107	0.169 \pm 0.108
<i>E. rubecula</i> (n=9)	0.076 \pm 0.072	0.150 \pm 0.036
<i>T. merula</i> (n=9)	0.219 \pm 0.175	0.186 \pm 0.058

Thus, differences exist among the main disperser species both in the average seed size and average between-individual heterogeneity in seed size.

4. Discussion

4.1. Seed variability

The *Rubus* population studied has a wide range of phenotypic plasticity in seed size, with great variances in this trait at the population level and within individual crops. Wide intra-individual variation suggests wide phenotypic plasticity, making it difficult to separate the genetic and non-genetic components (Hickman 1979, Waller 1982) and therefore making it difficult to estimate the potential selection pressure of any kind of selective disperser.

Broad variation in seed size has been repeatedly reported both within and between populations suggesting several mechanisms favouring variable seed sizes: i.e., matching local environmental conditions (Thompson 1978, Ernst 1981, Waller 1982, among others), density effects (Rabinowitz 1974, Snell 1976), insect seed predation and herbivory (Mitchell 1977, Hare 1980, Bentley et al. 1980) and size, photosynthetic capacity and internal structure of the fruit (Janzen 1977, 1978, 1982, Bazzaz et al. 1979, Hole and Scott 1981, Melin and Paillard 1982). The relative influence of genetic differences and environmental components on seed size determination may thus vary between species as variance in seed size itself varies.

4.2. Implications in relation to dispersal

The results reported above indicate that different parts of a variable seed size distribution are differentially dispersed by birds. An immediate consequence of this process is that it would result in different seed banks of variable seed sizes as well. From the perspective of a colonizing species such as *Rubus ulmifolius* this is probably adaptive in generating a more homogeneous seed shadow than would be obtained with a narrower range of seed sizes (Janzen 1977, 1978).

The fact that different portions of the seed crop produced by the *Rubus* population studied are actually dispersed by different disperser species implies that the different seed shadows originated contain significantly different proportions of a given seed size class, while encompassing the complete range of seed sizes. Differences between the main dispersers of *Rubus* in flight patterns and first-stop sites after leaving a clone have been described elsewhere for this population (Jordano 1982). After a feeding bout *E. rubecula* usually perches close (< 20 m) to the feeding clone, along the forest edge surrounding the stream course where *Rubus* patches occur. In contrast, *T. merula* leaves the feeding clone with long flights along the stream course while the *Sylvia* warblers favour short flights in both directions.

These differences probably determine species-specific sites of faecal deposition and hence seed delivery. Great inter- and intra-individual heterogeneity in mean seed size therefore implies greater evenness of dispersal of a highly variable seed crop over a patchy environment. Coupling production of a variable range of seedling reserves with thorough seed dispersal would increase the chances of seedling survival over a greater proportion of the available soil surface (Janzen 1977), given the wide array of soil conditions potentially faced by a *Rubus* seed once dispersed.

The fact that no differences in within-individual heterogeneity in seed size were found among the four main dispersers was expected on the basis of the possible small scale variation in seed size encountered by a given bird during a short feeding bout. High constancy in seed size within a ramet or group of infructescences would cause individual faecal samples to contain seeds of homogeneous sizes, provided the four species peck on average two or three fruits per visit to the plant, and these are often located within the same infructescence. On the other hand, differences in between-individual heterogeneity are not so readily explained. The pattern of bird species replacement is such that each species probably finds a different variety of seed sizes available (all except *T. merula* are autumn passage migrants (Jordanano 1982) peaking in abundance at different dates in the study area). This could result from either 1) different dispersers differentially exhausting the range of seed sizes available in such a way that the later incoming species find a truncated seed size distribution (e.g. Howe in press) and 2) clones differing in average seed size ripen fruits at different dates. In fact the temporal sequence of peak abundances of the four main dispersers in the study area matches their respective positions over the seed size distributions (Fig. 3), with *S. borin* dispersing the largest seeds and *E. rubecula* the smallest ones. Most likely the observed pattern of seed dispersal results from the interaction of these two factors.

From the plant's point of view, the greater the variability in mean seed size carried by the disperser species (both in the within- and between-individual components as well as among species), the closer the current crop's collective seed shadow would reflect the pre-dispersal genetic variance resulting from pollination and seed set.

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