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FRUGIVORE-MEDIATED SELECTION ON FRUIT AND SEED SIZE: BIRDS AND ST. LUCIE'S CHERRY, *PRUNUS MAHALEB*[1]

PEDRO JORDANO
Estación Biológica de Doñana, CSIC, Apartado 1056, E-41080 Sevilla, Spain

Abstract. Frugivorous birds consumed >75% of the ripe fruits of a *Prunus mahaleb* population in southeastern Spain, but only half of the seed crop was successfully removed from parent plants by legitimate seed dispersers. For two consecutive years, I studied the sign and magnitude of phenotypic selection exerted by frugivorous birds on fruit size and seed mass, two key traits in this mutualistic plant–seed disperser interaction. Individual plants showed extensive phenotypic variation in these traits, but among-individual variation accounted for <30% of total trait variance. Selection patterns were assessed at two levels by separating the effects of selection acting on the parent tree (among-crop selection; comparing fruit removal and seed dispersal efficiency among individual plants) and selection acting at the individual seed level (comparing seed mass variation before and after dispersal by frugivorous birds). Dispersal efficiency (percentage of the seed crop dispersed) correlated negatively with crop size, fruit size, and seed mass. However, only crop size was significantly, positively, correlated with the absolute number of seeds dispersed relative to the population mean, used as the estimator for relative fitness. Greater visitation by dispersers to smaller plants compensated for their lower fecundity but, for plants with larger crops, a greater number of seeds was dispersed despite lower dispersal efficiency. Directional and stabilizing/disruptive selection gradients on fruit traits were not significant or, at best, only marginally significant, indicative of weak and inconsistent selection effects on maternal phenotypes. In contrast, selection on individual seed phenotypes was significant. Seeds on the ground, after successful dispersal by frugivorous birds, were significantly smaller than seeds 'available' at the start of the fruiting season. Observed selection differentials on individual seed mass were −0.12 (1992) and −0.13 (1993), suggesting that frugivores might exert strong selection on individual seed phenotypes irrespective of the maternal phenotype. This selection regime, with far-reaching demographic consequences but low potential for inducing evolutionary change in fruit traits, is expected on the basis of known hierarchical selection cues used by foraging frugivores. Fruit phenotypic variation might be irrelevant as a cue used by birds for discrimination among fruit crops, but, given extensive within-crop variation, frugivores might strongly select among seed phenotypes in a process not related consistently to among-crop selection on maternal phenotypes.

Key words: fruit size; frugivorous birds; mutualism; phenotypic selection; Prunus; *seed dispersal; seed mass.*

INTRODUCTION

Animals that obtain food from the pulp of fleshy fruits may have long-lasting effects on plant demography. By differentially selecting among fruiting individuals, they can translate the overall population fruit production into a very different population of dispersed seed (see reviews in Howe 1986, Jordano 1992). In other words, frugivores directly determine realized fecundity (in terms of seeds dispersed) in plant populations, and are thus potential selective agents on fruit, seed, and plant traits associated with dispersal. Although these ideas impregnated the early literature on plant–frugivore interactions (Snow 1971), there has been, to my knowledge, not a single attempt to estimate the selective effects of frugivores on fruit and seed traits and, thus, measure natural selection for these traits in the field. Only recently, Wheelwright (1993) has approached the question by examining relationships between fruit size and fruit removal, and by documenting patterns of phenotypic variation and heritability of fruit size in a tropical lauraceous tree. This situation contrasts with pollination studies, in which several workers have quantitatively assessed selection intensities and differentials exerted by pollinators on flower morphology (Campbell 1989, 1991, Galen and Stanton 1989, Schemske and Horvitz 1989, Campbell et al. 1991, Johnston 1991, Herrera 1993). The recent expansion of early adaptive explanations to include the effects of constraints in plant–frugivore coevolution (Wheelwright and Orians 1982, Howe 1984, 1986, 1993, Herrera 1986, Jordano 1987*b*, 1995, Wheelwright 1988) has unfortunately lacked this necessary background of field selection studies (but see Whelan and Willson 1994). Thus, we have ample evidence for the action of constraints on this interaction, but very scarce field data on the magnitude of selection on fruit traits exerted by frugivores.

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Documenting the sign and magnitude of phenotypic selection on characters is a first step in understanding their evolution (Endler 1986). When these characters are central to a mutualistic interaction, such as seed dispersal by frugivorous animals, this kind of analysis is indispensable for understanding the process of coevolution. If combined with adequate experimental evidence and causal analysis, the sign of both directional and nonlinear (quadratic) selection coefficients on phenotypic traits studied in wild populations (Lande and Arnold 1983, Arnold and Wade 1984*a,* Mitchell-Olds and Shaw 1987) can be used to assess the form and causes of selection (Wade and Kalisz 1990).

There is ample field and laboratory evidence that frugivorous vertebrates exhibit preferences for certain fruit traits, both among and within species (Turcek 1961, Herrera 1981, Sorensen 1984, Levey 1987, McPherson 1987, Foster 1990, Willson et al. 1990, Willson and Comet 1993, Whelan and Willson 1994), and that these preferences may sometimes translate into differential fruit and seed removal and dispersal efficiency, measured as the percentage of seeds leaving the parent tree (Howe and Vande Kerckhove 1981, Sallabanks 1992, Willson and Whelan 1993). Fruit and seed size, together with fruit seediness, have often been found to correlate negatively with fruit removal efficiency (see Wheelwright 1985, 1993). Nevertheless, recent field work on the interaction of frugivores and particular plant species (Jordano 1987*a,* Herrera 1988, Jordano 1989, Herrera et al. 1994) has shown that evolutionary responses to selection by frugivores can be seriously constrained by opposing selective effects derived from the predispersal phase (e.g., dispersal success limited by seed abortion), and from interaction with insect frugivores (e.g., opposed selection patterns by insect and vertebrate dispersers). Furthermore, the selective effects of frugivores might not translate into net phenotypic selection if outweighed by factors that operate later in the life cycle, as demonstrated by Howe and co-workers with *Virola* spp. (Howe and Vande Kerckhove 1980, 1981, Howe 1981, 1993, Howe et al. 1985; see also Herrera et al. 1994). Unfortunately, we lack the quantitative estimates of the magnitude of frugivore selection pressure needed to adequately gauge the net effects of these opposing selection forces.

Evidence for additional influences comes from the fact that the dispersal process of parental plants incorporates an effective decoupling of maternal and seed phenotypes. Frugivores not only select among maternal phenotypes while they forage for fruits, but also choose among individual seed phenotypes within a fruit crop. From this perspective, individual seed fitness is influenced not only by maternal inheritance, but also by the maternal characters that shape the interaction of the whole seed crop with frugivores (maternal selection: Kirkpatrick and Lande 1989). For example, consider how maternal inheritance and maternal selection operate simultaneously during dispersal. Seed mass is a trait of the offspring, yet its phenotypic value is largely determined by maternal inheritance (see Roach and Wulff 1987, Kirkpatrick and Lande 1989). Seed size also would be influenced by maternal selection during dispersal if the likelihood of dispersal success for individual seeds is shaped somewhat by the mother's phenotype. As far as I know, this decoupling of frugivore effects on maternal vs. seed phenotypes has not been explicitly considered in previous analyses of the plant–frugivore mutualism, yet its implications can be far-reaching, both from demographic and evolutionary perspectives.

I argue that we need an explicitly evolutionary approach to the study of fruit phenotypic traits in relation to frugivore activity and foraging preferences. Here, I analyze selection through realized seed dispersal by frugivorous birds acting on fruit size and seed size, two fruit traits that are central to the plant–bird mutualistic interaction. I address the following objectives, using data on fruit removal and seed dispersal efficiency from a population of wild cherry, *Prunus mahaleb* (Rosaceae), in southeastern Spain: (1) document patterns of phenotypic variation in fruit and seed size among individual plants; (2) quantify the sign and magnitude of phenotypic selection by frugivores on these traits; (3) evaluate to what extent the selection response can be outweighed by other effects, such as differences in absolute fecundity or selection on correlated characters; and (4) describe and quantify selection patterns on maternal (selection among fruit crops) and individual seed phenotypes (selection among individual fruits within a crop).

METHODS

Study area

This study was conducted during 1992 and 1993 in the Reserva de Navahondona-Guadahornillos (Parque Natural de las Sierras de Cazorla, Segura y las Villas, Jaén province, southeastern Spain). The study area is located in Nava de las Correhuelas, a site in the park highlands, at 1615-m elevation. The main study site extends over ≈100 ha and includes both deep soils and rocky, exposed slopes. Deciduous vegetation, including *Crataegus monogyna, Prunus mahaleb, Lonicera arborea, Berberis hispanica, Daphne laureola, Rosa canina,* and *Acer monspessulanus,* occupies the deep soils. Adjacent rocky slopes are dominated by open pine forest (*Pinus nigra,* subsp. *salzmannii*) with *Juniperus communis, J. phoenicea, J. sabina,* and scattered *Taxus baccatta* (Valle et al. 1989). *Prunus mahaleb* is relatively abundant at the site, with an estimated population of 350 reproductive individuals. The climate is of the Mediterranean montane type. Rainfall averages 1527 mm, concentrated in autumn and winter. Only 9% of the total annual precipitation falls during June and September, the main fruiting season for *P. mahaleb.* Average temperatures for the coldest and hottest months are 2.9° and 22.5°C, respectively. Snowfall is frequent from November to March.

Plant natural history and frugivore foraging

Prunus mahaleb, the Saint Lucie's or Mahoma's cherry, is a small tree (2–10 m in height) that grows scattered at mid-elevations (1250–1900 m) in southeastern Spanish mountains. The species extends from Morocco through central and eastern Europe, to Ukraine, Syria, and west-central Asia (Webb 1968). Fruits are one-seeded drupes, black when ripe, 8.0 ± 4.4 mm long (mean ± 1 SD) and 8.3 ± 0.5 mm wide ($N = 20$), with a sugary, water-rich pulp (Herrera and Jordano 1981). Chemical analyses of the fruit pulp reported by these authors yielded 3.2% crude fat, 2.8% crude protein, 6.3% ash, and 5.7% fiber, with 82.0% soluble carbohydrates. Fruit crops of individual trees usually range between 700 and 30 000 fruits.

Herrera and Jordano (1981), Herrera (1989), Guitián et al. (1992), and Jordano (1994) present information on interactions of *P. mahaleb* with animals that consume fruits and disperse seeds. At least 28 bird species, four mammals, and one lizard have been recorded feeding on the fruits at the study site (P. Jordano and E. W. Schupp, *personal observation*). The four main types of birds visiting *P. mahaleb* trees for fruits differ in foraging mode and immediate consequences for seed removal: (1) Legitimate seed dispersers (e.g., warblers, *Sylvia* spp.; thrushes, *Turdus* spp.; and redstarts, *Phoenicurus* spp.) swallow the fruits whole and defecate and/or regurgitate the seeds, usually after leaving the tree. (2) Pulp consumers (tits, *Parus* spp.; and Chaffinch, *Fringilla coelebs*) peck the fruit without detaching it from the peduncle or, after plucking, tear off the pulp while holding the fruit in the bill or against the perch. In both cases, the seed is dropped to the ground beneath the parent. (3) Pulp consumer–seed dispersers are pulp consumer species (*Parus ater, Garrulus glandarius,* and *Sitta europaea*) occasionally observed to pluck some fruits and exit from the tree to another perch to eat the pulp, thus actually dispersing some seeds. (4) Seed predators feed on the seed contents and drop the pulp and seed coat. Only the Hawfinch *Coccothraustes coccothraustes* has been recorded in this group.

Plant characteristics and fruit removal

Plant height, area of canopy projection, number of trunks, and trunk basal diameter were measured for each of $N = 60$ marked plants. I measured characteristics of the habitat immediately surrounding each cherry tree by determining the number of shrub species, substrate type, vegetation height, and vegetation and rock cover to the nearest 10%. I measured vegetation height in each of eight sectors, four beneath the canopy and four outside the canopy edge. The area beneath the canopy was divided into sectors by four lines at 90° starting from the trunk base. These lines were extended 10 m away from the canopy edge to define the four external sectors in the vicinity of the tree. Vegetation and rock cover were estimated for each entire sector, while vegetation height was measured at five random points in each sector.

Fruit removal was assessed for the 60 individually marked trees during the 1992 and 1993 fruiting seasons. The number of mature-sized fruits ("crop size") was estimated by a complete count on all marked plants during the last two weeks of July, when fruits start to ripen, just prior to massive fruit consumption. I tallied the number of fruits on individual branches within a defined portion of the canopy and then continued moving to new portions until the total crown volume had been scanned. To check for accuracy, I made periodic recounts for a large branch or group of branches. The count was repeated if the difference between successive counts exceeded 5% (crops $< 10^4$ fruits) or 10% (crop sizes $> 10^4$ fruits). I assumed counts were exact for crop sizes <2000 fruits.

The percentage of fruits taken by frugivores relative to the total fruit crop will be referred to as "fruit removal efficiency." Only a fraction of this fruit consumption is attributable to legitimate seed dispersers; thus, "seed dispersal efficiency" will be used to denote the percentage of seeds estimated to leave the tree through the activity of these species (Willson and Whelan 1993). Fruit removal and seed dispersal levels were assessed by sampling with seed traps beneath the trees. Traps consisted of 0.17-m^2 plastic trays covered with 1.23-cm mesh wire to prevent fruit and seed consumption by rodents. Between two and five traps were placed per tree, depending on canopy size, so that the average sampling area per tree was 7.4 ± 0.7% (mean ± 1 SE, $N = 60$) of the canopy area. Seed traps beneath *P. mahaleb* trees sampled six types of fruits or seeds: (1) ripe, desiccated fruits, not handled by frugivores; (2) unripe, dried fruits (largely abortions of undeveloped fruits); (3) ripe-damaged fruits (i.e., with signs of damage by invertebrates); (4) seeds dropped by pulp consumers, with pulp remains attached; (5) seeds of the same tree regurgitated or defecated by legitimate seed dispersers; and (6) seeds of other trees also delivered by legitimate seed dispersers. Categories 5 and 6 are obviously indistinguishable. The numbers of fruits consumed and seeds dispersed were estimated as follows. I calculated the number of fruits not consumed, or not handled, by frugivores by dividing the sum of fruits and seeds in categories 1, 2, and 3 by the fraction of canopy area sampled by the trays. The number of ripe fruits consumed by frugivores was estimated by subtracting this number from the fruit crop size. Similarly, I determined the number of nondispersed seeds for each tree by dividing the sum of the sampled numbers of ripe desiccated, unripe, and ripe damaged fruits, and dropped seeds (with pulp remains) by the fraction of canopy area sampled (see Howe 1981 for a similar method). To estimate the number of seeds dispersed, I subtracted this total from total crop size. Extensive data from direct watches of bird foraging (P. Jordano and E. W. Schupp, *unpublished data*) indicate that most ripe fruits taken by pulp consumers are handled and consumed in the same tree and dropped, so most category 4 fruits are offspring of the sampled tree. Foraging data for legitimate dispersers indicate that they deliver very few seeds beneath the parent tree while feeding, largely due to extremely short visit duration (P. Jordano and E. W. Schupp, *unpublished data*). Thus, for the purpose of this paper, seed dispersal efficiency will estimate the percentage of seeds that is dispersed away from the parent canopy.

Fruit and seed characteristics

Samples of fresh ripe fruits (N = 30–65 fruits per tree) were collected from all study trees in 1992 and 1993, mostly between 15 and 23 July, just before fruit consumption by frugivores started. I estimate that $\leq$1% of the fruit crop had been consumed by the time ripe fruits were sampled. I collected fruits from branches at each of six different canopy locations spaced regularly on the canopy perimeter. For each sampled branch, I picked up to three individual fruits from each of 5 to 25 infructescences. Descriptive statistics for fruit diameter and seed dry mass for each tree were obtained from these samples. Fruit diameter was measured with a digital caliper as the maximum cross width of the fruit to the nearest 0.1 mm. I manually removed the pulp from fresh fruits and air-dried the seeds at ambient temperature before storage. Seeds were then dried at 30–40°C for a minimum of 4 d and weighed to the nearest 0.01 mg. Repeatability estimates for fruit diameter and seed mass measurements are high: 0.9710 (95% confidence limits: 0.8895–0.9979) and 0.9986 (0.9945–0.9997), respectively.

Seed samples were used to estimate the distribution of seed masses available in the tree population before consumption by frugivores each year. Estimates of seed masses for fruits consumed by frugivores were obtained from the sample of fruits and seeds falling in trays used in the study of fruit removal. In addition, when most trees had their crops almost completely removed, different habitat patches were haphazardly selected and searched for the presence of bird feces and/or regurgitated seeds. Evidence from experimental monitoring of postdispersal seed survivorship (E. W. Schupp and P. Jordano, *unpublished data*) indicates that these ground samples were obtained before postdispersal seed predators could alter the distribution of seed sizes among seeds on the ground. Seeds from both the trays and ground samples were pooled and were cleaned manually before drying and weighing, following exactly the same protocol as for seeds sampled from the branches. These final samples thus included three categories of fruits and seeds handled by frugivores: (1) defecated seeds obtained from feces; (2) regurgitated seeds; and (3) seeds (with pulp remains attached) from fruits that had been handled by pulp consumers (also pulp consumer–seed disperser species) that usually drop the seed beneath the parent plant. Seeds in categories 1–3 will be referred to as 'removed' seeds, i.e., handled by frugivores visiting the trees. Note that only the seeds in categories 1 and 2 (defecated or regurgitated) can be considered as coming from fruits handled by legitimate seed dispersers that pluck and ingest fruits and deliver the seeds unharmed. These will be referred to as 'dispersed' seeds, as they most often land away from the canopy of the parent plant.

Data analyses

This study focused on selection on fruit and seed phenotypic variation exerted by birds that consume fruits and disperse seeds in a natural population. A selection episode includes the phase of fruit removal and seed delivery to the ground mediated by the activity of frugivorous birds. As only a fraction of the available fruit is consumed, two aspects are relevant: analysis of the ecological correlates of fitness variation among trees (estimated by the fecundity component, i.e., the number of seeds successfully removed); and comparison of fruit and seed characteristics before and after the fruit removal episode. Using fruit diameter and seed dry mass as the key phenotypic traits in this interaction, I examined two components of fitness: (1) seed dispersal efficiency (the percentage of seed production that is removed by legitimate seed dispersers); and (2) relative fitness, expressed as the number of seeds dispersed relative to the population mean. Thus, realized fecundity was calculated for each tree as W_i the absolute number of seeds estimated to leave the tree. Relative fitness, w_i, is expressed as $W_i/[\Sigma W_i/n]$, where n is the number of trees in the study population.

I used techniques developed by Lande and Arnold (1983) and Arnold and Wade (1984*a*, *b*; see also Mitchell-Olds and Shaw 1987) to estimate and quantify the sign and magnitude of natural selection on phenotypic traits. Selection differentials, S, describe the change in mean value of a character after a selection episode. If this change is described in units of standard deviations of the character, a standardized selection differential is obtained that estimates the selection intensity, i, on the character. The directional selection gradient, β, quantifies the magnitude of selection on the character and is computed as the slope of the regression of the fitness component on the character. Finally, the stabilizing selection gradient, γ, quantifies the direction and strength of stabilizing/disruptive selection. It is estimated by the regression coefficients of the fitness component on the quadratic terms of the polynomial regression on character values (Lande and Arnold 1983). Both β and γ are multiplied by the standard deviation of characters, σ_i, to obtain the standardized selection gradients β' and γ'. This transformation allows comparisons of the relative magnitudes of selection on traits in different populations or selection episodes. I used the nonparametric

TABLE 1. Yearly variation in mean individual plant fecundity and mean fruit characters of a *Prunus mahaleb* population in the 1992 and 1993 study seasons, southeastern Spain.

Variable	Mean ± 1 SD 1992	Mean ± 1 SD 1993	Paired t†
Fruit diameter (mm)‡	7.83 ± 0.37	7.84 ± 0.37	0.027^{NS}
Seed dry mass (mg)‡	77.35 ± 10.68	71.44 ± 8.28	5.18***
Crop size (no. of fruits)	2917 ± 2524	3692 ± 3214	−2.62**
Fruit removal efficiency§	76.20 ± 15.99	81.37 ± 15.81	−2.65**
Seed dispersal efficiency‖	53.37 ± 23.94	55.01 ± 25.17	-0.63^{NS}
No. of seeds dispersed	1412 ± 1773	1721 ± 1946	-0.57^{NS}

** $P < 0.01$; *** $P < 0.001$; ^{NS} not significant.

† Results of paired t test (df = 59) for between-year differences.

‡ Means for individual plant means in each year.

§ Percent of fruits removed (by both legitimate seed dispersers and pulp consumers) relative to fruit crop size.

‖ Percent of seeds removed (by legitimate seed dispersers only) relative to fruit crop size.

techniques described by Schluter (1988) to estimate the form of fitness functions.

A detailed analysis of among-year variation in selection patterns is beyond the scope of this paper and will be presented subsequently, with data for more study years and populations. Thus, I performed most analyses on the combined values for years 1992 and 1993 by summing fruit crop sizes and number of seeds dispersed to obtain cumulative 2-yr fecundities for individual plants. Data for fruit diameter and seed mass were averaged for each individual plant. Data on plant size and habitat characteristics were obtained in 1992. For individual seeds, I estimated selection differentials directly from the comparison of seed mass statistics before ("seeds available") and after ("seeds dispersed;" i.e., categories 1 and 2 defined in *Fruit and seed characteristics*) the selection episode, defined as the interaction with avian frugivores resulting in fruit removal and seed delivery.

I used the original, untransformed variables to estimate the selection parameters. As some of the traits examined, especially fruit crop size and plant size, exhibited strongly non-normal distributions, I used randomization tests (Manly 1991) to assess the significance of the selection gradients. Randomization tests were carried out with 5000 iterations and α set to 0.05, using routines provided in Manly (1991) and Press et al. (1992). The procedures CORR and REG (SAS 1988) were used to obtain correlations and regression coefficients among characters and fitness components. I used the SAS procedures GLM, VARCOMP, and NESTED to determine whether or not there was significant variation in plant traits among plants and years (both treated as random effects), and to estimate the associated variance components.

I used a structural equation approach to test causal models on relative fitness values (Crespi and Bookstein 1989). Linear structural equation (LSE) analysis permits the assessment and evaluation of more complex causal models than path analysis, and is basically an extension of this method (see Pedhazur 1982, Maddox and Antonovics 1983, and Mitchell 1992 for an introduction). Its advantages include the ability to incorporate measurement errors for observed variables, unmeasured general factors, such as 'fitness,' which are frequently determined by several correlated variables, and test of goodness-of-fit. Covariances are explained through the use of unmeasured factors (e.g., 'fecundity,' 'size,' 'shape,' etc.) that require estimation from the data. Observed variables are used as indicators for these unmeasured factors or constructs. Parameters for the LSE model and its significance were estimated with CALIS procedure, using maximum-likelihood estimation on the covariance matrix (SAS 1988).

RESULTS

Variation in plant traits

There was significant annual variation in individual plant means for seed mass, fruit crop size, and fruit removal efficiency, but not for fruit size (Table 1). Between-year differences in seed mass in the absence of significant variation in fruit size may be explained by parallel variation in average pulp allocation per fruit. Unfortunately, no data on pulp mass per fruit are available for the study years, but data for 1990 and 1991 suggest that significant variation in pulp mass per fruit remains after accounting for differences in fruit diameter ($F_{1,798} = 5.78$, $P = 0.016$ for the ANCOVA of pulp mass per fruit with year as the main effect and fruit diameter as the covariate). The individual plant effect accounts for 29.10% and 27.95% of the variation in fruit diameter and seed mass, respectively; the year effect accounts for 21.49% and 31.99%, respectively (nested ANOVA, SAS 1988). Approximately 40% of the variation in these two traits thus is due to within-plant variation.

Fruit removal efficiency increased generally in 1993, with 42 out of 60 individual plants showing a greater fruit removal efficiency in this year (Table 1; $P = 0.0137$, sign test). However, this increase did not translate into greater seed dispersal efficiency (Table 1); trees successfully dispersed about one half of the initial fruit crop each year. Most variance in fruit removal and

TABLE 2. Pearson product-moment correlation coefficients (upper half of matrix) and partial correlation coefficients (lower half) between plant characters and fecundity components, using data for years 1992 and 1993 pooled. $N = 60$ *Prunus mahaleb* trees sampled each year. Boldface figures, $P < 0.05$; boldface italic figures, $P < 0.01$.

Character	AREA	DIAM	SEEDM	CS	DISP	FRE
Canopy area (AREA)		***0.2496***	**0.1675**	***0.6830***	***0.5560***	**−0.2308**
Fruit diameter (DIAM)	0.0977		***0.6779***	***0.2244***	0.0539	0.0375
Seed dry mass (SEEDM)	−0.0621	***0.6495***		0.1436	0.0527	−0.0816
Crop size (CS)	***0.4373***	0.1443	−0.0491		***0.7243***	−0.1099
No. seeds dispersed (DISP)	**0.1862**	−0.1116	−0.0215	***0.3222***		−0.0851
Fruit removal efficiency (FRE)†	**0.1846**	0.1417	−0.0191	−0.0729	−0.0901	
Seed dispersal efficiency (SDE)‡	***−0.4024***	−0.0797	−0.0927	0.1053	0.1411	***0.7843***
Relative fitness (RF)	−0.0029	−0.0123	0.1346	***0.2180***	***0.5468***	−0.0333
Habitat PCI*	0.0597	−0.1246	0.0646	−0.0668	−0.0312	***−0.3304***
Habitat PCII*	−0.0545	−0.0680	−0.0691	0.0301	0.0132	−0.0007

* Tree scores on the first and second principal components of characteristics of the habitat surrounding the trees. PCI is positively correlated with shrub cover, vegetation height, and number of conspecifics within a 15-m radius. PCII is positively correlated with rock cover and negatively correlated with distance to the edge of the pine forest.

† Percent of fruits removed (by both legitimate seed dispersers and pulp consumers) relative to fruit crop size.

‡ Percent of seeds removed (by legitimate seed dispersers only) relative to fruit crop size.

seed dispersal efficiency was accounted for by the effect of year within plant (85.23% and 96.67%, respectively), with individual plant effect accounting for only 14.78% and 3.33%, respectively (nested ANOVA, SAS 1988).

Individual relative fitness (w_i, standardized number of seeds dispersed) was calculated as the number of seeds dispersed divided by the population mean. Variances of relative fitness were relatively high, (Var $w_{1992} = 1.132$ and Var $w_{1993} = 1.278$), but did not differ significantly between years ($F_{1,118} = 0.0068$, $P = 0.93$, Brown-Forsythe test). Use of nested ANOVA to account for between-year variation within plants revealed significant differences among plants in relative fitness ($F_{20,63} = 2.28$, $P = 0.006$), with 24.29% of the variation in plant fitness attributed to the plant effect and the remaining 75.77% to the year (within-plant) effect. The within-year ranks for individual plants in fitness values were significantly correlated between years ($t = 0.234$, $z = 2.63$, $P = 0.008$; Kendall correlation coefficient), suggesting that individual plant differences outweigh individual variation among years in fruit removal and seed dispersal efficiency.

Correlations and causal effects in the selection episode

Plant size (AREA) and fruit crop size were strongly and positively correlated with both the absolute number of seeds dispersed (DISP) and relative fitness (RF) (Table 2). In terms of realized dispersal, RF was more strongly correlated with the absolute number of seeds dispersed (DISP) ($r_{\text{part}} = 0.5468$) than with fruit removal (FRE) or seed dispersal (SDE) efficiencies ($r_{\text{part}} = -0.0333$ and 0.0494, respectively; Table 2). Fruit diameter and seed mass were negatively correlated with SDE (Table 2); plants with larger fruits showed a lower percentage of seeds dispersed (data from the two years combined). When differences in plant fecundity were taken into account by using the absolute number of seeds removed relative to the population average (RF), the correlation with fruit phenotypic variables was of opposite sign and only marginally significant (Table 2). Moreover, fruit size (indicated either by fruit diameter or by seed mass) did not correlate with any estimator of efficiency (FRE or SDE) when the influence of other variables was accounted for (Table 2, partial correlation coefficients). FRE was negatively correlated with the two principal components describing habitat characteristics; trees growing away from rocky substrates, surrounded by greater vegetation cover, and in the neighborhood of more conspecifics experienced higher percentages of fruits consumed.

Relative fitness residuals from a regression of RF on SDE were obtained to assess fitness variation independent of differences in the percentage of seeds dispersed, an indicator of visitation intensity by legitimate dispersers. A plot of residual fitness against fruit crop size (Fig. 1) reveals a non-increasing trend up to 4000 fruits and then a sharp increase. Thus, for less fecund plants, greater visitation by seed dispersers might compensate for differences in the number of fruits produced (i.e., a plant with a smaller crop visited largely by legitimate dispersers would disperse more seeds than a more fecund plant with greater visitation by pulp consumers). For larger plants, larger crop sizes imply a greater number of seeds dispersed despite lower dispersal efficiency.

A model of causal relationships between correlated causes acting upon relative fitness in each selection episode (Fig. 2) shows the disproportionate effect of plant size and fecundity. Both the direct and indirect effects of observed variables are included in this type of model, and both phenotypic and ecological variables are simultaneously analyzed. This LSE model resulted in an adequate fit, with the fit per degree of freedom being lower ($\chi^2/\text{df} = 2.46$) than the suggested ratio of 5 indicated by Wheaton et al. (1977) as minimally reasonable (see also Pedhazur 1982, Maddox and Antonovics 1983, and Mitchell 1992). The main influences of plant fecundity are determined by the strong effect

Table 2. Continued.

SDE	RF	HPCI	HPCII
−0.3788	***0.4885***	−0.0720	0.0217
−0.1496	0.1352	−**0.2019**	−0.1304
−**0.2000**	0.1609	−0.0788	−0.1102
−0.1175	***0.6716***	−0.0667	−0.0064
−0.0144	***0.7725***	0.0112	−0.009
0.7690	−0.0805	**−0.1873**	**−0.2076**
	−0.0228	0.0564	−***0.2265***
0.0494		0.0159	−0.0312
0.2777	0.0420		0.0371
−0.1572	−0.0138	0.0234	

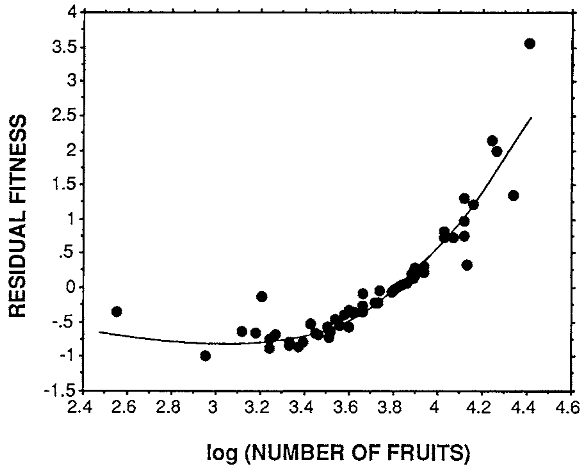

Fig. 1. Plot of residual relative fitness in *Prunus mahaleb,* after controlling for the effects of individual variation in seed dispersal efficiency (percentage of seeds dispersed relative to fruit crop size), against fruit crop size (log-transformed). The trend of covariation is shown by a spline fit to the data with a smoothing parameter, ln $\lambda = -2.3$ (Schluter 1988). Relative fitness was estimated as the no. of seeds dispersed relative to the population average no. of seeds dispersed per tree.

of crop size on "realized fecundity," a latent variable (F_FEC) indicated by the absolute number of seeds actually dispersed. Its effect, determined indirectly by plant size (Fig. 2), clearly outweighs the negligible negative effect of latent variable "fruit size" (F_FRUIT) on F_FEC. Moreover, the effects of habitat variables on "fitness" (F_FIT) are also obscured by the disproportionate influence of F_FEC on this variable (Fig. 2). The LSE model, as specified in Fig. 2, was highly consistent when applied separately to 1992 and 1993 data (goodness-of-fit indices, GFI > 0.88 for the two years).

Selection estimates

Selection gradients and differentials.—I observed no significant directional or stabilizing/disruptive selection gradients on fruit traits when using the proportion of seeds dispersed (Table 3A). However, the negative gradients for fruit crop size ($0.05 < P < 0.10$) and fruit diameter ($0.05 < P < 0.12$) were marginally significant, with more fecund plants and those with larger fruits tending to disperse a lower percentage of seeds. β' values were also negative, but nonsignificant, for both fruit diameter and seed mass when 1992 and 1993 data were analyzed separately. Values for the stabilizing/disruptive gradients also showed similar, nonsignificant variation between the two years. The only significant gradients were found when considering relative fitness (Table 3B). Plants with a greater number of fruits dispersed significantly more seeds relative to the population average. Both the directional and stabilizing/disruptive selection gradients were positive and significant.

Realized selection on seed mass.—Negative selection differentials, *i,* of fruit crop size and fruit and seed size on seed dispersal efficiency (Table 3A) are indicative of larger plants with larger fruits dispersing a smaller fraction of their seeds, a pattern evidenced with the phenotypic correlations (Table 2). I would expect negative realized selection on fruit and seed size (i.e., smaller seeds in the seed bank relative to the sizes available at the start of the fruiting season) if less fecund plants with smaller fruits tend to contribute disproportionately to the population seed rain. However, this might not be the case if total fecundity compensates for the negative effect of fruit size on seed dispersal effectiveness. To clarify this point, I compared seed masses available in the population before removal by frugivores with those of dispersed seeds sampled (just after dispersal, by the end of the fruiting season). This provided an estimate of the intensity of realized selection on seed mass by frugivores, independent of estimates based on fitness variation among maternal plants.

Mean mass of dispersed seeds, sampled just after the ripe fruit crops have been exhausted by frugivores, was significantly smaller than that of seeds available at the start of the fruiting season (Table 4), suggesting a realized negative selection pattern on seed size by frugivorous birds after the selection episode defined by the fruit removal phase. This pattern was highly consistent in the two study years: dispersed seeds weighed, on average, 1.2–1.4 mg less than full-size seeds on the trees before dispersal, and observed selection differentials were similar (−0.12, 1992; and −0.13, 1993; Table 4). The fitness functions relating probability of seed removal to seed mass also showed a very consistent pattern between years (Fig. 3), indicating that successful removal for individual seeds steadily decreases as seed size increases.

Discussion

Variation in fruit traits

Two main sources might contribute to the large within-individual component of variation in fruit size and seed mass. First, fruit traits show phenotypic variation due to the presence of functional hermaphrodites and

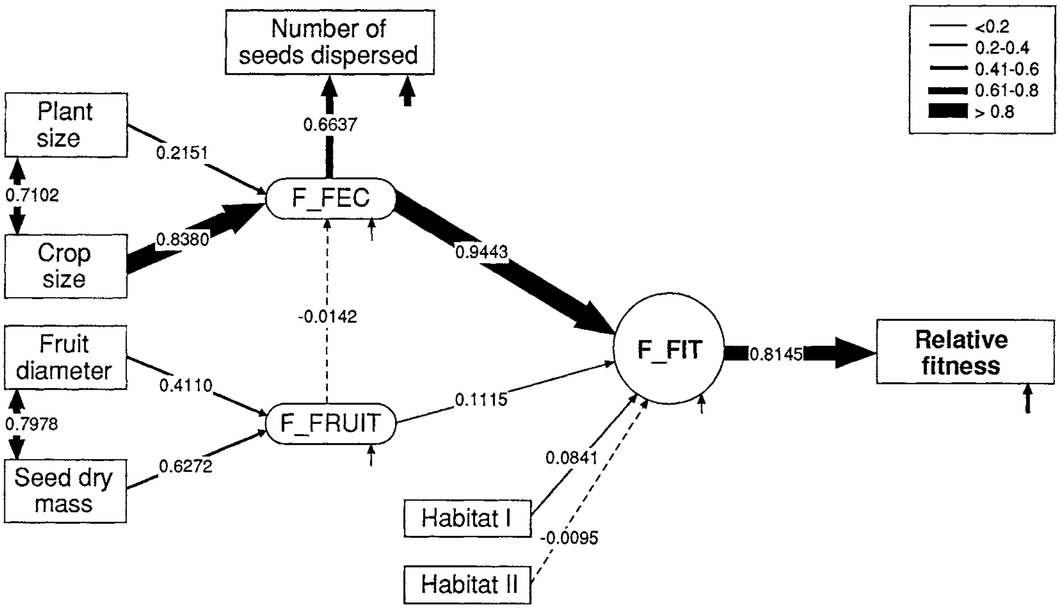

FIG. 2. Path diagram illustrating a causal model for the influences of plant fecundity and fruit phenotypic traits on fitness. The causal model states that plant fitness (F_FIT) is influenced by two latent variables representing a "fecundity factor" (F_FEC) and a "fruit size" factor (F_FRUIT), as well as influences of external characteristics of the habitat surrounding the trees, estimated by Habitat I and II. The no. of seeds dispersed and the relative fitness (no. of seeds dispersed relative to population average no. of seeds dispersed per tree) are the exogenous variables used to estimate F_FEC and F_FIT, respectively. F_FEC is influenced by plant size and fruit production; F_FRUIT is determined by fruit phenotypic variation related to size (fruit diameter and seed mass). Data for years 1992–1993 are pooled by calculating the cumulative fecundities for this period. Positive effects are indicated by solid lines and negative effects by dashed lines. Numbers on the arrows are the path coefficients. Error and disturbance terms in the structural equation are represented by small arrows.

female (androsterile) individuals in this population (see Jordano 1993 for details). Long-term (6-yr) data on seed mass variation for individual plants (P. Jordano, *unpublished observation*) reveal greater average seed dry mass among female, obligately outcrossed trees (75.54 ± 0.20 mg, $N = 3872$; mean ± 1 SD) than among hermaphrodites, which show a variable level of selfing in different years (74.04 ± 0.18 mg, $N = 5147$). Second, a pollination environment adverse to pollen movement between trees (e.g., adverse weather for pollinator foraging) might result in higher levels of selfing, and thus smaller seed mass (higher levels of outcrossing usually promote larger seed mass and fruit size; Mitchell-Olds and Waller 1985, Richards 1986, Jordano

TABLE 3. Multivariate standardized selection gradients (β', γ') and differentials (i, j) on fruit characters in *Prunus mahaleb*. Regression coefficients are given for directional and stabilizing/disruptive selection on untransformed variables. Two fitness estimators are used: seed dispersal efficiency (percentage of seeds dispersed relative to total fruit crop size) and relative fitness (number of seeds dispersed relative to the population mean). Coefficients express the rate of change in fitness with the characters (β') and with squared deviations from the character mean (γ'), accounting for the effects of correlated characters. Selection differentials indicate the expected change in mean (i) and variance (j) of the character after the selection episode, and were calculated on untransformed data. Note that j values include effects of directional selection. All coefficients are in units of character standard deviations. The significance of each selection gradient was tested using a randomization procedure.

Fitness component and character	Directional		Stabilizing/disruptive	
	β'	i	γ'	j
A. Seed dispersal efficiency				
Fruit crop size	-0.0819^{NS}	−0.001	0.0362^{NS}	−0.001
Fruit diameter	-0.0800^{NS}	−0.020	0.0355^{NS}	−0.019
Seed dry mass	0.0167^{NS}	−0.015	0.0255^{NS}	−0.013
B. Relative fitness				
Fruit crop size	0.8915***	0.796	0.3844***	0.765
Fruit diameter	-0.1161^{NS}	0.207	0.0391^{NS}	0.215
Seed dry mass	0.1298^{NS}	0.215	0.0982^{NS}	0.223

$^{\text{NS}}$, nonsignificant; *** $P < 0.001$.

TABLE 4. Dry mass (mg) of *Prunus mahaleb* seeds (mean ± 1 SD) sampled from trees at the start of the dispersal period (Control), and dispersed by frugivorous birds (Dispersed: sampled from feces and regurgitations beneath perches).

Year	Control	Dispersed	*F*†	*i*‡	*j*
1992	73.70 ± 10.65 (*N* = 721)	72.43 ± 10.36 (*N* = 2567)	8.45**	−0.1198	−0.0549
1993	71.83 ± 10.93 (*N* = 2409)	70.43 ± 11.05 (*N* = 677)	8.67**	−0.1284	−0.0224

† df = 1, 3286 (1992); df = 1, 3084 (1993); ** $P < 0.01$.

‡ *i*, standardized directional selection differential ($i = [\bar{X}_A - \bar{X}_B]/\sigma_B$); and *j*, standardized stabilizing selection differential ($j = [\sigma_A^2 - \sigma_B^2]/\sigma_B^2$). Both *i* and *j* are calculated on untransformed seed mass data. Subscripts *A* and *B* stand for "after" and "before" the selection episode.

1993; P. Jordano, *unpublished data*). The consequences of this effect might vary in different reproductive seasons. Not unexpectedly, considerable variance in seed mass was accounted for by between-year effects alone. Therefore, a sizeable fraction of variation in seed size in this population can be attributed to breeding system variation and the lasting consequences of the pollination phase.

Only one previous study (Wheelwright 1993) has documented long-term patterns of variation in fruit and seed size in fleshy-fruited species, showing extensive between-year variation in fruit size, but also marked individual differences with measurable heritability for this trait. Given sizeable selection intensity and additive genetic variance for the traits, evolutionary change in characters might still occur. Nevertheless, my preliminary results with diallel crossings for *P. mahaleb* reveal a large effect of the maternal environment on seed mass relative to the additive genetic component (P. Jordano, *unpublished data*). Therefore, large environmental and yearly variation, due to changes in the pollination environment during flowering, leave a small potential for selection by frugivores to work on individual differences.

Correlates of seed removal success

Despite relatively high fruit removal by frugivores in the two study years (>75% of the initial fruit crop), the activity of legitimate seed dispersers limited successful seed dispersal, as only half of the ripe fruit crop was consumed by this type of frugivore. I have documented elsewhere (Jordano 1994) that yearly average dispersal efficiency in this population is inversely related to the relative abundance of pulp consumer and seed predator species in the local frugivore avifauna. Variance in seed dispersal efficiency is high, but subject to ample between-year variation due to changes in composition of the frugivore assemblage (Jordano 1994), leading to a minor contribution of individual plant effects (<15%) to explain either fruit removal or seed dispersal efficiency (see also Willson and Whelan 1993). Despite the fact that individual differences ac-

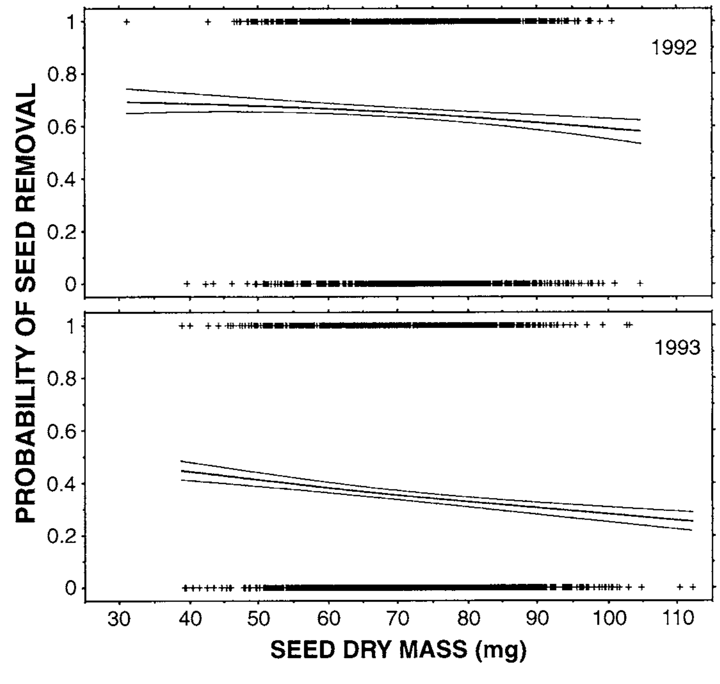

FIG. 3. Nonparametric estimates of fitness functions for seed dry mass of *Prunus mahaleb* in 1992 and 1993. Individual seeds were sampled from bird droppings or regurgitations ('dispersed,' scored as 1.0 on Removal axis) by the end of the fruiting season, or were obtained directly from the trees (control, scored as 0) at the start of the ripening season (see *Methods*). The "+" symbols indicate raw data values for individual seeds. The cubic splines (continuous lines) and confidence intervals (±1 SE of predicted values from 5000 bootstrap regression resamplings) were calculated using a nonparametric, generalized cross-validation method (Schluter 1988).

counted for only 24.3% of variance in relative fitness, the within-year ranks of individual plants were significantly correlated between years, indicating that absolute differences in number of seeds removed outweigh differences in proportion removed. (See Howe and Vande Kerckhove 1979, Davidar and Morton 1986, Jordano 1987*a,* 1989, Herrera 1988, Obeso 1989, and Willson and Whelan 1993 for previous reports of similar effects.)

Relative fitness, corrected for differences in legitimate disperser activity (Fig. 1), did not increase up to crop sizes of ≈4000 fruits, e.g., approximately the mean 2-yr fecundity of *P. mahaleb* trees. Above this fecundity, residual fitness increased sharply, suggesting that the fitness advantage of the more fecund individuals compensated for the decrease in disperser activity (lower dispersal efficiency) at more fecund trees. Thus, I expect factors affecting the absolute number of seeds dispersed to be more determinant of relative fitness than factors influencing the efficiencies of fruit removal or seed dispersal (see also Willson and Whelan 1993). Plant fecundity alone thus explains most variation in realized seed dispersal for individual plants, especially the larger ones.

Previous studies have reported negative correlations between both fruit crop size and fruit phenotypic traits and seed dispersal efficiency, arguing that large crops might eventually 'saturate' the disperser assemblage or increase fruit retention times, hence causing lower 'per fruit' probability of successful fruit removal (Howe and Vande Kerckhove 1979, Jordano 1987*a,* Herrera et al. 1994). On the other hand, large average fruit size might decrease seed dispersal efficiency by increasing foraging and handling costs for gape-limited frugivores (Wheelwright 1985, 1993). The causal model fit to pooled 1992 and 1993 data confirmed the disproportionate effect of plant fecundity on relative fitness. Both direct and indirect effects of this variable outweighed the negligible negative effect of overall fruit size on relative fitness. Larger mean fruit size had a measurable negative effect on fruit removal and dispersal efficiency, as predicted by models incorporating fruit foraging costs (Wheelwright 1985, Levey 1987), but had a negligible influence on relative fitness.

The fact that 'rate processes,' which are directly influenced by animal mutualists (e.g., the proportion of flowers pollinated, the fraction of the fruit crop removed by frugivores), rarely compensate for differences in absolute fecundities should not be surprising. Few studies, however, have addressed the important issue of whether or not the net effects of mutualists outweigh these effects of fecundity. The few that have either found negligible net effects of mutualists (Jordano 1987*a,* 1989, Herrera 1988, 1991, Willson and Whelan 1993, and this present study) or report minor but significant effects (Campbell 1991, Willson and Whelan 1993, Herrera et al. 1994, Mitchell 1994). Even with significant selection exerted by mutualists, net selection can be unpredictable from measures of 'success' of the interaction alone (Campbell 1991, Herrera 1991, Jordano and Herrera 1995).

Patterns of phenotypic selection on fruit traits

Can phenotypic variation in plant structures relevant to the interaction with animals (flowers, fleshy fruits) be interpreted as adaptations to enhance the interaction? The first steps to provide an answer to such a question are: (1) analysis of the ecological correlates and influences that mediate the plant–animal interaction; (2) study of phenotypic selection patterns; and (3) documentation of the genetic vs. environmental variation patterns in fruit traits. Results discussed here for *P. mahaleb* are relevant to the first issue, as are results from most previous research on the ecological scenario of the plant–seed disperser interaction (Howe 1986, Jordano 1992). As far as I know, no previous study has addressed the third issue (but see Wheelwright 1993). Here I concentrate on the second point, which, to my knowledge, has not been studied previously for plant–frugivore interactions.

The opportunity for selection through female function (seed production and realized seed dispersal) in the *P. mahaleb* population was high, as estimated by the variance of relative fitness (Arnold and Wade 1984*a*), and was similar in the two study years. Yet the analysis of both multivariate and univariate selection coefficients failed to detect significant selection on fruit and seed size. There was evidence for marginally significant ($0.05 < P < 0.12$) negative selection on fruit size when the first component of fitness (dispersal efficiency) was considered. Given the large effect of plant fecundity on realized seed dispersal, it is not unexpected that any correlated trait will show parallel directional selection in univariate analyses (see, e.g., Johnston 1991).

Frequently, frugivores might exert at best weak, statistically insignificant, selection on maternal fruit size and seed mass in wild populations, where plant fecundity differences usually obscure the influences of mutualists in 'rate processes' that marginally contribute to fitness differences (see, e.g., Herrera 1988, 1991, 1993, Jordano 1989, Campbell 1991, Johnston 1991, Mitchell 1994). It would be necessary, however, to assess the temporal constancy of this selective regime in the *P. mahaleb*–bird interaction, because weak selection gradients can result in phenotypic change if sustained over a long time (Lande 1976). Data from the two study years revealed consistent patterns similar to preliminary results from correlational analyses for 1988, 1989, and 1994 (P. Jordano and E. W. Schupp, *unpublished manuscript*): weak effects of fruit traits vs. plant fecundity in explaining among-tree variance in fruit removal and seed dispersal success.

Discordant selection on maternal and seed phenotypes

The probability for individual *P. mahaleb* seeds to be successfully dispersed was a decreasing function of seed mass, an evidence of net negative directional selection on individual seed mass in this population, despite absence of significant selection on maternal phenotypes. Immediately after the dispersal event, larger seeds tend to be underrepresented in the seed rain relative to their 'availability' at the start of the fruiting season. This effect was documented prior to the action of secondary seed dispersal and postdispersal seed predation as factors altering the phenotypic distribution of dispersed seeds.

Is there a mechanistic basis for such discordant consequences of frugivore activity for maternal and seed phenotypes? Frugivores not only determine fitness differences among fruit crops (maternal phenotypes) as a result of differential offspring dispersal, but also determine the success of the individual offspring themselves (the seed phenotypes). The relative dispersal success of an individual seed need not necessarily be associated with the relative success of its maternal average phenotype. For example, frugivores might selectively remove 70% of a fruit crop averaging 79.5 mg seed mass, with most seeds selected below the 60th percentile seed mass of the crop. This within-crop selection effect, if consistent across individual plants in the population, would yield a truncated distribution of seed masses that is independent of the original distribution of maternal seed mass averages. As the pulp/seed ratio of individual fruits is negatively correlated with seed mass in *P. mahaleb* drupes ($r = -0.2781$, $P < 0.01$, $N = 726$; P. Jordano, *unpublished data*), frugivores might process smaller seeds by selecting smaller fruits, yet obtain a greater relative amount of pulp per unit fruit mass processed. Negative directional selection on individual seed mass is thus largely attributable to strong within-crop selectivity by frugivorous birds against large fruit and seed size, and is expected from foraging models that incorporate feeding and fruit handling costs for gape-limited frugivores and fruit profitability (Wheelwright 1985, Levey 1987).

Consider the hierarchical nature of avian fruit-foraging cues (Sallabanks 1993). Preliminary evidence suggests that avian frugivores may use foraging cues based primarily on 'extrinsic' plant characteristics (type of surrounding habitat, number of neighbors, proximity of forest edges, etc.) when discriminating (selecting) among fruit crops (Sallabanks 1992, 1994, Traveset 1994; P. Jordano, *unpublished data* for *P. mahaleb*). Yet individual seeds might face strong selection if frugivores use within-crop foraging cues based on proximate 'intrinsic' fruit traits (color, seediness, overall size, etc.) (Herrera 1981, Jordano 1984, 1987*a*, Wheelwright 1985, 1993, Levey 1987, Willson et al. 1990). Thus, both the patterns and the consequences of frugivore selection regimes among maternal phenotypes and seed phenotypes need not be coupled or congruent, as illustrated in the present study. If 'extrinsic' plant traits determine among-crop selection patterns, we might expect weak selection regimes on maternal fruit phenotypes, as found in this study. Given extensive within-crop variation in fruit and seed size (nearly 40% of the total phenotypic variance in *P. mahaleb*) and overlap of individual values, the possibility exists for frugivores to "filter out" a distinct subset of the seed phenotypes without influencing differential dispersal success of the maternal phenotypes. Such a decoupled selection regime obviously has important demographic consequences, as seed mass is a key trait in plant recruitment (Harper 1977). However, it is probably irrelevant for inducing evolutionary changes in fruit traits, because maternal selection (direct influence of the mother plant on dispersal success of individual seeds; Kirkpatrick and Lande 1989) is scarcely influential on individual seed fitness in this episode of interaction with frugivores. Additional research is clearly needed for a deeper mechanistic understanding of frugivore foraging and how it translates into natural selection in the mutualistic plant–disperser interaction. A fundamental characteristic of this interaction is that it simultaneously influences maternal (mother plant) and offspring (individual seed) fitness but, as revealed by this study, in ways not necessarily analogous or consistent.

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