Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*

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**Introduction**

Seed dispersers play a role in the ecology and evolution of plants if their patterns of activity (fruit selection and dissemination of seeds) influence subsequent stages of the plant life cycle (Schupp, 1995; Jordano, 2000; Willson & Traveset, 2000; Wang & Smith, 2002). Although early studies on seed dispersal mention this requirement (Howe & Smallwood, 1982), explicit connections between dispersal and post-dispersal events have been made only recently (Herrera *et al.*, 1994; Rey & Alcántara, 2000; Wenny, 2000). These recent studies show that the spatial pattern of seed distribution generated by dispersers does not always match the pattern that would provide the highest probabilities of success during post-dispersal events (seed predation, germination, seedling survival and establishment). Thus later-acting interactions or abiotic factors can potentially counteract selective pressures exerted by dispersers.

Most fruit traits of vertebrate-dispersed plants show significant levels of phylogenetic inertia (Jordano, 1995a) or might be the result of selection other than by dispersers (Fuentes, 1992; Cipollini & Levey, 1997). As an important exception, fruit size is positively correlated with seed disperser size across the Angiosperms (Jordano, 1995a), among con-familial genera (Mack, 1993; Pizo, 2002), and possibly among con-generic species (Herrera, 1995). Thus dispersers appear to be selective agents in fruit size evolution. The ecological mechanism invoked to explain it is ‘gape limitation’, as gape and body size of dispersers limit the size of fruits they can manipulate and swallow (Moermond & Denslow, 1985; Wheelwright, 1985; Rey *et al.*, 1997). Therefore large fruits can evolve only in the presence of large frugivores (Herrera, 2002). Besides limiting maximum fruit size, gape limitation should select for smaller fruit size, both because smaller fruits can be dispersed by more and more diverse dispersers and because frugivores prefer smaller fruits (Jordano, 2000; and references therein). However, studies of selection on fruit size within populations show weak and variable selection pressures on this trait (Jordano, 1987; Sallabanks & Courtney, 1993; Herrera *et al.*, 1994; Alcántara *et al.*, 1997). Therefore, selection exerted by dispersers alone does not explain the observed positive correlation between the size of fruits and dispersers.

Several authors (Howe & Richter, 1982; Mack, 1993; Schupp, 1995; Jordano, 2000) have proposed that fruit size evolution is a correlated effect of selection for large seeds exerted by factors other than dispersers. Thus, this hypothesis states that the evolution of fruit size is the

**Abstract**

Recent evidence indicates that fruit size has evolved according to dispersers’ size. This is hypothesized to result from a balance between factors favouring large seeds and dispersers setting the maximum fruit size. This hypothesis assumes that (1) the size of fruits that can be consumed by dispersers is limited, (2) fruit and seed size are positively correlated, and (3) the result of multiple selection pressures on seed size is positive. Our studies on the seed dispersal mutualism of *Olea europaea* have supported the first and second assumptions, but valid tests of the third assumption are still lacking. Here we confirm the third assumption. Using multiplicative fitness components, we show that conflicting selection pressures on seed size during and after dispersal reverse the negative pattern of selection exerted by dispersers.
combined result of factors favouring large seed size and dispersers limiting the maximum fruit size. This hypothesis only considers patterns of selection and assumes that fruit and seed size are heritable traits not involved in other genetic correlations, for example a negative one with plant fecundity. To test the validity of this hypothesis it is necessary to demonstrate, in a within-species context, (1) that gape limitation limits maximum fruit size, (2) that fruit size is positively correlated with seed size, and (3) that the final result of the multiple selection pressures on seed size is positive. Gape limitation has been demonstrated by several authors (see references above). The correlation between seed and fruit size holds especially for single or few seeded fruits (Oheso, 1988; Sallabanks, 1993; Herrera et al., 1994; Jordano, 1995b). However, a cohesive summary of the multiple selection pressures on seed size exerted by dispersers and post-dispersal factors is still lacking. There is evidence for conflicting selection pressures on seed size during and after dispersal: small seeds had higher dispersal probabilities or distances, but also had lower germination probabilities or produced smaller, less competitive seedlings (Howe & Vande Kerckhove, 1981; Howe & Richter, 1982; Howe et al., 1985). Additional examples of seed-seedling conflicts over optimal seed size involving seed dispersal mutualism exist (Herrera et al., 1994; Parciak, 2002a). However, whether this combined selection favours larger or smaller seeds depends on the relative strength, shape, and direction of the multiple post-dispersal selection pressures on seed size. Therefore, demonstrating the existence of opposing selection pressures does not demonstrate that the dispersers’ pattern of selection has been reversed. Such reversal can only be demonstrated by obtaining comparable estimates of the strength of successive episodes of selection.

In previous studies with Olea europaea var. sylvestris (wild olive), we have shown that gape limitation actually sets a limit to the maximum size of fruits that its main dispersers can swallow (Rey et al., 1997). We have also shown that seed weight is positively correlated with fruit weight (Alcántara, 1995). The present study was designed to obtain comparable estimates of the strength of successive episodes of selection for a cohort of wild olive seeds, from dispersal to the survival of 2-year-old seedlings. By estimating multiplicative fitness components, in this study we assess the following main questions: (1) do different episodes of selection on seed size, from dispersal to seedling establishment, act in opposite directions? (2) If so, how is the pattern of selection on seed size exerted by dispersers modified by later episodes of selection?

The present study shows that selection on seed size during post-dispersal stages of recruitment can be strong enough to reverse the pattern of selection exerted by dispersers. Furthermore, our results confirm the roles of gape limitation and post-dispersal survival as ecological forces shaping the evolution of fruit size in O. europaea.

**Methods**

**Study area and species**

The study was conducted at La Parrilla site, Sierra Sur de Jaén (37°40’N, 3°45’W; Jaén province, southern Spain). The area is a mosaic of dense scrubland patches (several hectares each) dominated by Olea, Pistacia terebinthus, Phillyrea latifolia, and Quercus cocciifera, mixed with pine forests (Pinus halepensis) and old olive groves. The climate is Mediterranean type with mean annual temperature of 16 °C and mean annual rainfall of 539 mm.

Olea europaea (L.) forms a complex with four subspecies occurring from east and south Asia through the Mediterranean Basin to Macaronesia and east and southern Africa (Besnard et al., 2002). Olea europaea ssp. europaea var. sylvestris (Olea hereafter) is a small tree that occurs throughout the Mediterranean basin. The species is wind-pollinated and its drupes, which ripen through autumn and winter, contain a single seed (embryo plus endosperm) wrapped in a hard endocarp. Hereafter, the whole propagule (seed plus endocarp) will be referred to as ’seed’.

In southern Spain, small- to medium-sized frugivorous birds, mainly species of the genus Turdus and Sylvia, disperse the seeds. The range of seed sizes produced by wild olive trees can be classified according to the identity of their potential dispersal agents (Rey et al., 1997). Fruits containing small seeds (<100 mg) can be consumed by all the avian seed dispersers of the study area, Turdus philomelos (Song Thrush), Sylvia atricapilla (Blackcap), S. melanocphala (Sardinian Warbler), and Erithacus rubecula (European Robin); those containing medium-sized seeds (100–200 mg) can be swallowed only by S. atricapilla and T. philomelos; and those with the largest seeds (>200 mg) can be consumed only by T. philomelos.

Apodemus sylvaticus (Wood mouse) is the only rodent present in our study site (Rey, unpubl. data). Secondary dispersal by this species must be negligible, as it carries the seeds to deep larder-hoards (Montgomery & Gurnell, 1985) from which successful establishment of seedlings is unlikely. Olea seeds do not seem to be actively sought by A. sylvaticus in our study site, yet a significant preference for small and medium-sized Olea seeds has been shown (Alcántara et al., 2000a).

**Fitness components**

We defined multiplicative fitness components (Arnold & Wade 1984) as the probabilities of (1) being removed by a seed disperser, (2) reaching a suitable place for recruitment, (3) escaping from post-dispersal seed predators, (4) germination, and (5 and 6) surviving the first and second years after germination. All these fitness components are survival probabilities across stages; therefore, all are calculated as the ratio of the number of individuals completing a stage to the number of
individuals that entered the stage. The product of all these components is the probability that a seed produced in the study cohort became an established sapling 4 years later. Though this estimate is far from representing the lifetime fitness of the plant, it includes all the relevant stages at which individual seed size can be directly selected. We will assume that subsequent components of fitness (survival until reaching the reproductive state, age at first reproduction, life span and fecundity) are random with respect to individual size at the seed stage. This assumption seems reasonable as the effects of seed size on subsequent plant performance disappear soon after germination in many species (Westoby et al., 1997).

Unless otherwise stated, all the observations and experiments described below were conducted for the cohort of seeds produced in winter 1993/1994; the ‘study cohort’ hereafter.

Dispersal stages

Dispersal probability (P_D): probability of being consumed by a seed disperser. The absolute frequency (i.e. total number) of seeds of each size class in the pool of dispersed seeds (F_{D_i}; hereafter the suffix ‘s’ indicates the seed size classes 1–3 for small to large seeds) is the result of the probability of dispersal of each size (P_{D_i}) acting on the absolute frequency of this size produced by the trees (F_i):

\[ F_i \times P_{D_i} = F_{D_i}; \]

Thus, P_{D_i} can be estimated, for each size class, as the ratio F_{D_i}/F_i.

During winter 1993–1994 we estimated ripe fruit crop size and the distribution of seed size (i.e. fresh seed weight) for all the Olea trees fruiting in the study site (N = 39 trees, N = 30 seeds per tree). This information provided an estimate of F_i in the study cohort.

We can estimate F_{D_i} as the product of the relative frequency (i.e. proportion) of each size in the seed rain (f_{D_i}) multiplied by the total number of seeds dispersed (N_D):

\[ F_{D_i} = N_D \times f_{D_i}; \]

To obtain N_D we estimated the number of seeds consumed by frugivores on each tree. To estimate f_{D_i}, we collected and weighed dispersed seeds from the study site. The exact procedures used to obtain N_D and f_{D_i} can be found in Alcántara et al. (1997, 2000b). Here we will use the information shown in these publications but for different purposes, and collapse the distribution of seed sizes into the three classes described above.

Arrival probability (P_A): probability that a seed consumed by a disperser is deposited in a suitable place for recruitment. In the study site, and during the same study years included in the present study, the natural recruitment of Olea was negligible in places not covered by woody plants, and was inhibited under the crown of conspecifics (Rey & Alcántara, 2000). Therefore, the cover of woody plants other than conspecifics can be considered as ‘suitable sites for recruitment’. It is important to assess whether seeds of different size had different probabilities of reaching such sites. This probability can be defined, for each size class, as the ratio of seeds falling in suitable sites to the total number of seeds dispersed, P_A can be obtained from the information about the spatial distribution of seeds by seed size shown in Alcántara et al. (2000b).

Post-dispersal stages

In the subsequent experiments, we consider the effects of seed size, number of individuals entering the stage (i.e. initial density of individuals) and microhabitat (suitable sites for recruitment vs. open interspaces) on post-dispersal fitness components. Our interest in these experiments was to determine whether seed size effects depend on the environment (density and microhabitat), in which case selection on seed size would strongly vary depending on the patterns of distribution of seeds across the landscape. As no interaction effect was significant (see results), the survival probabilities for each post-dispersal stage are estimated only from experimental units located in suitable sites for recruitment.

Post-dispersal seed survival probability (P_PD): probability of escaping from post-dispersal seed predators. In spring 1994 we started an experiment to determine the effects of microhabitat (under the cover of three shrub species, Olea and open interspaces), density of seeds and seed size on the survival probability from dispersal to the time of germination. Unfortunately, goats destroyed this experiment. The same experiment, though not for seeds of the study cohort, was run again from February to October 1997. Detailed description of the experiment and results can be found in Alcántara et al. (2000a). From this experiment, we will use the estimates of predation as a function of seed size obtained in sites suitable for recruitment. For the present study this estimate has two shortcomings. First, as not calculated for the study cohort, these values may under- or over-estimate corresponding predation levels, because inter-annual variation in seed predation intensity by rodents seems to be common (Schupp, 1988, 1990; Ostfeld et al., 1997). However, our main interest is in obtaining a comparative estimate of survival for seeds of different sizes. Therefore, our results will be valid if seed size preferences of predators do not vary across years. Available evidence supports this assumption both within and across species (e.g. Kollmann et al., 1998; Parciak, 2002a; Rey et al., 2002). Secondly, the period that seeds were exposed to predation (11 months) was shorter than necessary for germination (around 20 months) so this measure may be an over-estimation of survival.
probability till germination. However, at the end of the experiment litter had naturally covered seeds, which strongly reduces their detectability by rodents (Hulme, 1994). Hence we feel that longer exposure would not have further reduced survival probabilities.

Probabilities of germination ($P_G$) and surviving the first and second year after germination ($P_1$ and $P_2$). In December 1994, 2400 seeds that had been dispersed by birds in the study site, were distributed across 72 plots. Each plot was protected with a 30 × 30 × 10-cm wire-mesh cage to prevent rodent predation. Before sowing, we removed all seeds present in these plots. In subsequent fruiting seasons we prevented seed input by covering each cage with a translucent piece of cloth. The experimental design considered the effects of microhabitat (suitable sites for recruitment vs. open sites), seed size (three size classes), and sowing density (16, 25, or 64 seeds per plot). Goats destroyed six plots in October 1995, but enough replicates remained for all the treatment combinations. Plots were monitored biweekly for germination throughout the period of natural seedling emergence (December–May). We considered that germination had occurred whenever the endocarp split and the radicle emerged. Although litter naturally buried seeds, they could be easily located and checked for germination by gently removing the litter. The survival of seedlings that emerged in this experiment was monitored monthly during the subsequent 2 years. Protecting the seedlings from vertebrate herbivores might result in overestimating survival probability. However, in a study of natural recruitment conducted simultaneously in the same study site and seasons (Alcáñiz, 1998) we detected that only 2.7% of deaths were caused by herbivores.

Statistical analyses

Results of the experiment of germination and seedling survival in the first and second year were analysed with Generalized Linear Model procedures of Statistica software (StatSoft, 2000) employing Binomial error distribution with logit link-function, entering microhabitat and seed size as categorical variables. In the analysis of germination probability, the number of seeds sown per plot (i.e. seed density) was included as a categorical factor. In the analysis of seedling survival probability during the first year, the number of seedlings emerged was included as a covariate. Similarly, in the analysis of the probability of seedling survival during the second year, the number of seedlings surviving the first year was entered as a covariate. In the analyses of seedling survival probability the first and second years, only plots with seedlings in the beginning of the respective period were included. The covariates used in some analyses (number of seeds germinated and number of seedlings surviving the first year) are correlated with some of the factors. Accordingly, the significance of the effects were assessed through step-wise deletion of terms from the maximal model (model containing all the factors, interaction terms and covariates), as suggested by Crawley (1993) to generate the minimal explanatory model.

Results

A summary of the estimates of fitness components as a function of seed size class is shown in Fig. 1. Figure 2 shows the cumulative fitness along the recruitment process.

Ripe crop size ranged from 4 to 10 166 fruits/tree, averaging 2519.02 ± 396.67 fruits ($n$ = 38 trees; one of the trees did not produce any ripe fruits) (otherwise stated, means are given ±1 SE). The distribution of seed size in the cohort was quite even: 35.74% of the seeds were small, 30.92% medium, and 33.3% large.

The mean percentage of seeds dispersed from sampled branches of individual trees was 31.23 ± 4.70%, ranging between 0 and 87.5%. From these percentages and tree crop sizes, we estimated the number of seeds dispersed from each tree, which averaged 1616.75 ± 390.42 seeds, ranging between 0 and 9494. These values render an estimate of $N_D$ = 61 437 seeds dispersed in the population.

The analysis of dispersed seeds collected from the seed rain (2657 seeds) indicates that 51.15% were small ($f_{D1}$).
29.36% medium (F₂₃) and 19.50% large (F₃₃). Using eqn 2 we can estimate the absolute frequency of seeds of each size class in the seed rain:

\[ F_D^1 = 31,424, \quad F_D^2 = 18,036, \quad \text{and} \quad F_D^3 = 11,977 \text{ seeds.} \]

Using eqn 1, the dispersal probabilities by size were:

\[ P_D^1 = 0.9183, \quad P_D^2 = 0.6094, \quad \text{and} \quad P_D^3 = 0.3753. \]

Among the seeds dispersed, very few were deposited in open interspaces, and only a small proportion managed to escape from the shade of conspecific trees (Alcántara et al., 2000b). Small, medium-sized and large seeds respectively had the probabilities (P₁₁) = 0.1329, (P₁₂) = 0.1589 and (P₁₃) = 0.1623 of reaching a suitable site.

Alcántara et al. (2000a) showed that PPD significantly differed among seed size classes, and the effect of size did not depend on the microhabitat. Survival probabilities by the end of the experiment were similar for small and medium seeds, and higher for the largest seeds: \( P_{PD}^1 = 0.4047, \quad P_{PD}^2 = 0.3946, \quad \text{and} \quad P_{PD}^3 = 0.5117. \)

Seeds remained dormant for around 2 years, as they were dispersed during winter 1993/1994 but did not start to germinate until winter 1995/1996. During this winter 22.13% of the seeds germinated, and during winter 1996/1997 an additional 4.48% germinated. The mean probability of germination in 1995/1996 was significantly higher in suitable sites for recruitment (40.16 ± 22.33%) than in open interspaces (16.58 ± 13.67%), and increased with increasing seed size. In contrast, germination was independent of seed density and none of the interactions between size and microhabitat or density were significant (Table 1a). Pooling data from the two germination seasons gives the same results (analysis not shown). The estimates for germination probabilities under scrub cover were \( P_{G}^1 = 0.2286, \quad P_{G}^2 = 0.3452, \quad \text{and} \quad P_{G}^3 = 0.6119. \)

The first germination season produced 472 seedlings, 101 survived 1 year and 91 survived 2 years. Average survival probability over the first year was higher under woody cover (0.27 ± 0.04) than in open interspaces (0.07 ± 0.04), and decreased with seedling density. None of the interactions between microhabitat, seed size and initial seedling density were significant (Table 1b). Survival also increased significantly with seed size; under scrub cover these probabilities were: \( P_{11} = 0.1867, \quad P_{12} = 0.2562, \quad P_{13} = 0.3382 \). Survival probabilities over the second year were much higher, and did not depend on any experimental factor (Table 1c). Under scrub cover, these probabilities were: \( P_{21} = 0.7857, \quad P_{22} = 0.9677, \quad P_{23} = 0.9130. \)

Finally, the total probability of recruitment (i.e. the product of all the fitness components) increased with seed size: \( P_{R}^1 = 0.0017, \quad P_{R}^2 = 0.0033, \quad \text{and} \quad P_{R}^3 = 0.0059. \)

![Fig. 2](cumulative_fitness.png) Cumulative fitness for seeds of different sizes across successive selection events. Point size and line widths are represented according to large, medium and small seed size.

**Table 1** Analysis of post-dispersal stages of recruitment in *Olea europaea*. Results of Generalized Linear Models testing the effect of seed size, microhabitat, and number of individuals entering each stage on: (a) probability of germination, (b) probability of survival from germination to 1 year, and (c) probability of survival between the first and second year. See methods for explanation of the testing procedure. Abbreviations are: microhabitat (M), seed size (SS), density of seeds sown (D), number of seeds germinated (NG), number of seedlings surviving the first year (N1Y).

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Discussion

In spite of the abundant literature documenting natural selection, few studies have actually coupled estimates of selection over more than one life-history trait or fitness component (Schluter et al., 1991; Preziosi & Fairbairn, 2000). Such consideration can be of major importance in explaining adaptive trends. The evolution of fruit size in vertebrate-dispersed plants provides one example, as it has been hypothesized that the evolution of fruit size is the combined result of dispersers setting the maximum fruit size and other factors favouring large seed size.

Selection pattern imposed by dispersers

Avian seed dispersers are expected to act as selective agents on individual seed size (1) because gape size limits the size of fruits that a bird can manipulate (Moermond & Denslow, 1985; Wheelwright, 1985; Rey et al., 1997), and seed and fruit size are usually positively correlated (Obeso, 1988; Sallabanks, 1993; Herrera et al., 1994; Jordano, 1995b); (2) because the abundance of dispersers of different size may be different (Parciak, 2002a); and (3) because dispersers of different size may move seeds of different size to places differing in suitability for recruitment (Schupp, 1995). This last reason does not hold in our study case because, once dispersed, the probability of reaching suitable recruitment sites was independent of seed size. However, gape-limitation and the abundance of dispersers may explain the observed decrease in dispersal probability with increasing seed size. Gape limitation imposes truncation selection on large seed size in Olea. Indeed caged birds are less able to manipulate and swallow larger Olea fruits, with fruits wider than 11.83 mm, corresponding to seeds larger than 310 mg, hardly swallowed even by the largest disperser (Rey et al., 1997). Consequently seeds larger than 310 mg should and do hardly appear in the seed rain (Alcántara et al., 2000b). The largest seed produced by the trees weighed 680 mg. However, the largest seed found in the seed rain weighed 450 mg, and seeds above 300 mg were severely underrepresented in the seed rain relative to their availability on trees.

Besides this truncation selection, disperser activity may select for smaller seeds from the remaining range of phenotypes. Direct measurements of the selection differential on seed size caused by dispersers come from the comparing seed sizes available on maternal plants and in the seed rain. Estimates of such a differential are scarce but consistent in showing a negative value (Jordano, 1995b; Alcántara et al., 2000b; Parciak, 2002b). Using data from Alcántara et al. (2000b), in the present study we have shown that the probability of dispersal was almost three times higher for small than large seeds. As noted, one possible explanation for this pattern of selection may be the relative abundance of dispersers of different size. During winter 1993–1994 there were 16.56 birds per hectare able to disperse small seeds in the study site (S. melanocphala, S. atricapilla, E. rubecula, and T. philomelos); for medium-sized seeds there were 10.42 birds per hectare (S. atricapilla and T. philomelos), and only 3.4 birds per hectare (only T. philomelos) were able to disperse large seeds (data on bird abundance from Alcántara et al., 1997). The mean number of fruits consumed per bird (i.e. the mean number of seeds dispersed per bird) might differ among bird species. However their significance as Olea fruit consumers seems to be related to their abundance in the area, and not to their dependence on the fruit for food (Jordano, 1987). Therefore, a positive correlation between the cumulative abundance of dispersers of different sizes and the dispersal probability of seeds of different sizes is expected.

Summarizing, the pattern of selection on seed size exerted by dispersers can be viewed as a decreasing function relating dispersal probability to seed size. This function crosses the x-axis within the range of phenotypes available in the population, effectively exerting truncation selection by excluding the phenotypes located to the right of the crossing point.

Selection pattern imposed by later-acting factors. After dispersal, recruitment was significantly affected by the microhabitat and seed size. The demographic implications of the microhabitat effect have been discussed elsewhere (Rey & Alcántara, 2000). In the absence of significant interaction terms involving seed size, we can discuss the size effect independent of microhabitat or density. Seed size had a significant positive effect on final recruitment, indicating that selection acts strongly during post-dispersal stages. A general benefit of seed size on multiple aspects of seed and seedling performance has been demonstrated in many species (Westoby et al., 1997). However selection on seed size during sequential post-dispersal stages may differ in direction across species. The probability of escape from post-dispersal predators may decrease (Van der Wall, 1994), or increase (Tripathy & Khan, 1990; Herrera et al., 1994) with seed size. Most frequently, germination increases with seed size (Herrera et al., 1994). Seed size translates into seedling size after germination (Morse & Schmitt, 1985; Moegenburg, 1996). In turn, seedling size is positively correlated with survival probability in some cases (Tripathy & Khan, 1990) but not in others (Howe et al., 1985). In the case of Olea, seed size was positively selected or selectively neutral during post-dispersal stages. Larger seeds had a higher probability of escaping from post-dispersal predators and of germination, and they produced seedlings with a higher probability of survival during their first year, but 2 years after germination, the survival probability had become independent of seed size.
Outcome of conflicting selection pressures

When a trait is selected through consecutive selection episodes, later acting selection pressures might oppose early-acting ones. Yet, the consequences of early truncation selection cannot be modified because some phenotypes are removed from the original pool. The present study is the first to demonstrate that the ‘conflict between seed dispersability and survivability’ (Howe, 1990; Schupp, 1995) can be strong enough to completely reverse the pattern of selection exerted by dispersers on individual seed size, at least within the range of phenotypes not affected by truncation selection. Large seed size decreased dispersal probability but increased survival probability during post-dispersal stages. Figure 2 illustrates the effect of this conflict for our study cohort: the survival rankings were completely reversed from dispersal to germination and early seedling survival. Germination and early survival influenced overall probability of recruitment more than dispersal, with the final selection pattern resembling the pressures exerted during post-dispersal stages rather than that produced by dispersers. Therefore, our results confirm the validity of the hypothesis about the selection pressures shaping the evolution of fruit size in vertebrate-dispersed plants: the role of dispersers as selective agents on individual seed size sets a maximum limit to the potential adaptive response of seed size (and fruit size as a correlated trait), although later-acting factors resulted in positive directional selection on seed size, and thereby fruit size, within the remaining range of phenotypes.

The final pattern of selection shown in Fig. 2, acting on the initial frequency of seed sizes produced by the trees, will produce a pattern of relative abundance of plants established from seeds of different size. If a trade-off exists between seed size and number as is assumed in many theoretical analyses of seed size evolution (Smith & Fretwell, 1974; Ganeshalaih & Uma Shaanker, 1991; Geritz, 1995), the pattern of selection might not necessarily generate a population dominated by individuals derived from large seeds. For example, the recruitment probability for large seeds was about three times that for small seeds. If the small seeds were initially three (or more) times more abundant than large seeds, the outcome would be a population with equal (or reversed) frequency of sizes. However, empirical studies often find positive or nonsignificant phenotypic and genetic correlations between maternal seed size and number within populations (Marshall et al., 1986; Wolf et al., 1986; Mazer, 1987; Michaels et al., 1988; Winn, 1988; Àgren, 1989; Andersson, 1990; Mojonnier, 1998). The absence of negative correlations is not necessarily evidence against the trade-off (Mojonnier, 1998). However, it suggests that: (1) if there is no correlation between seed size and number (as is the case for our study cohort; see results), the final distribution of seed sizes will resemble the pattern of selection; and (2) if there is a positive correlation between seed size and number, the pattern of selection will lead to an even more pronounced abundance of plants derived from large seeds.

Despite obvious limitations of our study of a single reproductive event in a single population, our approach has produced very suggestive results regarding the ways in which dispersers might affect the evolution of an important plant trait. It is clear that long term and broad spatial scale studies are required to improve our knowledge of the evolutionary dynamics of this type of interaction (Levey & Benkman, 1999). However, this study underscores the fact that more detailed analyses covering successive processes in the plant life are still needed for reaching insights on the many details determining final selection patterns.

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