EVOLUTIONARILY STABLE SEED POLYMORPHISM AND SMALL-SCALE SPATIAL VARIATION IN SEEDLING DENSITY

S. A. H. GERITZ*

Institute of Evolutionary and Ecological Sciences, University of Leiden, Kaiserstraat 63, 2311 GP Leiden, The Netherlands

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Abstract.—Using the evolutionarily stable strategy (ESS) approach in a model for the evolution of seed size, I show that small-scale spatial variation in seedling density favors the evolution of variation in seed size within individual plants if competition among seedlings is sufficiently asymmetric in favor of larger seeds. A single seed size is found to be never evolutionarily stable. I always find at least some continuous adaptive variation in seed size. The model generates the following predictions. At least some continuous variation in seed size is adaptive. Plants with many resources have more variable seeds than plants with few resources. Plants with low juvenile mortality have more variable seeds than plants with high juvenile mortality. Plants with aggregated seed dispersal have seed size distributions that are more biased toward small seeds compared to plants with more even seed dispersal. An explicit formula for the evolutionarily stable seed size distribution was obtained for Poisson-distributed seed numbers and for negative binomial distributed seed numbers per safe site. The application of the model to seed size distributions of entire populations or plant communities is discussed.

Among plant species, there is an enormous variation in seed size (Harper et al. 1970). Also among and within individual plants variation in seed size is widespread and common (Michaels et al. 1988). Some species produce seeds of only two particular sizes (e.g., Danthonia spicata [Clay 1983], Heterosperma pinna- tum [Venable et al. 1987], Spergularia marina [Telenius and Torstensson 1989], Taraxacum hamatiforme [Mogie et al. 1990]). Other species exhibit continuous variation in seed size (e.g., Rubus ulmifolius [Jordano 1984], Raphanus raphanis-trum [Stanton 1984], Ipomopsis aggregata [Wolf et al. 1986], Desmodium paniculatum [Wulff 1986a, 1986b, 1986c], Rubus chamaemorus [Ågren 1989], Crinum ernbescens [Manasse and Stanton 1991]). Various authors suggest that within-individual variation in seed size may have evolved as a bet-hedging strategy in a spatially or temporally unpredictable environment in which a single intermediate seed size has low fitness (Harper et al. 1970; Cavers and Steel 1984; Kaplan and Cooper 1984; Silvertown 1984; Rathcke and Lacey 1985; Symonides 1988). Mathematical models support this view but focus mainly on the effects of large-scale environmental variation and the evolution of seed dimorphism (Kaplan and Cooper 1984; Venable 1985; McGinley et al. 1987; García-Dorado 1990; Lalonde

* Present address: Department of Genetics, Eötvös University, Műzeum krt. 4/A, 1088 Budapest, Hungary; E-mail: GERITZ@LUDENS.ELTE.HU.
1991). In this article, I consider the possible evolutionary consequences of small-scale variation in seedling density and show that continuous variation in seed size within individual plants is favored if competition among seedlings is sufficiently asymmetric in favor of larger seeds.

Seed size affects a plant's fitness basically in two ways. First, seed size has marked effects on the expected reproductive yield per offspring. This relation may include seed size effects on seed dispersal (Levey 1987; Telenius and Tors-tenssen 1989), seed predation (Bailey and Polis 1987; Benkman 1991; Crist and MacMahon 1992; Reader 1993), seed burial (Grime 1979), germination (Mogie et al. 1990), seedling emergence (Winn 1988; Reader 1993), seedling growth and survival (Wulff 1986b; Winn 1988; Mogie et al. 1990; Bell et al. 1991; Houssard and Escarré 1991; Jurado and Westoby 1992), seedling competition (Black 1958; Wulff 1986c), and fecundity (Wulff 1986b; Bell et al. 1991; Cipollini and Styles 1991). The effects of seed size on the offspring may also depend on the environment. For example, Price and Podolsky (1989) showed that the selectivity of seed predation by desert-dwelling heteromyid rodents depends on soil texture. Moreover, a number of studies show that seed size may have a significant effect on seedling emergence and growth in shaded conditions under perennial vegetation or litter but not in open conditions (Gross 1984; Stanton 1984; Winn 1985). Correlations between seed size and the expected reproductive yield of the offspring in general tend to be positive.

Second, seed size constrains the total seed number of a plant. Given a certain amount of resources, fewer big seeds can be provisioned than small seeds. Empirical evidence for a trade-off between seed size and seed number is scarce (Wolf et al. 1986; Ågren 1989; Andersson 1990; Cipollini and Stiles 1991). Correlations between seed size and seed number often have been found to be neutral or even positive (Marshall et al. 1986; Mazer 1987; Michaels et al. 1988; Winn 1988). The absence of a negative correlation between seed size and number in natural populations is no evidence against a trade-off, however. Positive correlations between seed size and number may occur among individuals if variation in a third variable (such as plant size) is strong enough to mask any negative correlation between seed size and number within individuals (Maddox and Antonovics 1983; Haig 1989; Venable 1992). The trade-off between seed size and seed number, on the one hand, and the effects of seed size on the offspring, on the other, together set the stage for the seed size optimization problem.

Smith and Fretwell (1974) formulated a model that captures the essentials of the optimization problem. In their model the fitness of a plant, \( W(m) \), is equal to the per capita number of seeds multiplied by the expected reproductive yield per seed. Modeling the trade-off between seed size and seed number, the seed number is given by the total amount of resources available per plant, \( R \), divided by the amount invested per seed, \( m \). The expected reproductive yield per seed (confusingly called the "offspring fitness" by Smith and Fretwell) depends on seed size and is denoted by \( f(m) \). Thus, the fitness of a plant with seeds of size \( m \) is

\[
W(m) = f(m) \frac{R}{m}.
\]
The fitness is maximal for the value of $m$ that maximizes the ratio of $f(m)$ and $m$; that is, the seed size that maximizes the plant's fitness coincides with the point of contact where the graph of $f(m)$ is touched by a straight line through the origin (fig. 1). Generally, there is only a single (globally) optimal seed size that does not depend on $R$ but that may vary for different shapes of $f(m)$ corresponding to different types of environments. Any variation in seed size within or between individuals in a given environment in this model necessarily is nonadaptive.

The predictions of the Smith-Fretwell model critically depend on the implicit assumption that the expected reproductive yield per offspring is independent of population density or environmental variability. This assumption may wrongly lead to the conclusion that competitors could be treated simply as part of the environment so that the optimization approach should give a qualitatively correct answer when competition between individuals is taken into account. However, if seed size affects the competitive ability of seedlings, then the fitness of a plant is likely to depend not only on its own seed size but on that of its competitors as well. Seedling competition, therefore, may lead to frequency-dependent selection for seed size so that a simple optimization approach is no longer possible, and an ESS approach (Maynard Smith 1982) should be used instead.

In this article, I formulate an extension of the Smith-Fretwell model that explicitly takes into account competition among seedlings. Using the ESS approach, I investigate the possible effects of small-scale spatial variation in seedling density on the evolution of seed size. To model seedling competition, I use a "safe site" model, a type of model in which plants interact only with their nearest neighbors in local sites called "safe sites." (Safe-site models were first proposed by Skellam [1951]; for related examples of safe-site models, see, e.g., Chesson and Warner...
1981; Ågren and Fagerström 1984; Geritz et al. 1988; Klinkhamer and De Jong 1989). Safe sites are by definition just big enough to support only one adult plant each. After the random dispersal of seeds, some sites may remain empty, whereas others may receive one or more seeds. If several seeds happen to fall in the same site, then seedlings will compete for space, which eventually will leave only one (local) winner that will occupy the safe site. In the present model, I assume extremely asymmetric competition; that is, the winner within a safe site invariably is recruited from the largest seed present. All other seeds within the same site die. Seedlings from smaller seeds only have a chance if they happen to land in sites without any larger seeds present.

Previously (Geritz et al. 1988) I have shown that with these assumptions no single seed size is evolutionarily stable. Plants that produce seeds of only one particular size can always be outcompeted by plants with slightly larger seeds, which suggests an evolutionary trend toward the largest seed size possible. Also, however, plants with sufficiently smaller seeds can always invade. Their competitive disadvantage is compensated for by their larger seed number (due to the size-number trade-off) that enables them to exploit safe sites that by chance are left without the larger seeds of their competitors. Now having established that for the present model there is no evolutionarily stable seed monomorphism, I proceed in the next section to investigate the possibility of an evolutionarily stable seed polymorphism. I first develop the model for annual plants each with the same amount of resources. In the appendixes the model is extended for perennials as well as for plants each with a different amount of resources.

THE MODEL

Seed-Setting Strategies

Individual plants will be characterized by their seed-setting strategy that specifies what fraction of the available resources is allocated to the production of seeds of a particular size. Let $m$ denote seed size; then the mathematical representation of a plant’s strategy is some nonnegative function $p(m)$ such that the integral

$$\int_{m_1}^{m_2} p(m) \, dm$$

is the expected fraction of resources allocated to the production of seeds with sizes between $m_1$ and $m_2$. With $R$ denoting the total amount of resources in a safe site available for seed production, integration from zero to $R$ by definition should yield a value of one. Notice that $R$ is also equal to the maximum possible seed size in the sense that all available resources must be used to produce a single seed of size $R$. Seeds larger than $R$ would require more resources than are available and therefore are not possible. Only seeds for which $p(m)$ is positive are actually produced. Seeds for which $p(m)$ is zero are absent. Modeling the trade-off be-
tween seed size and seed number in a way similar to Smith and Fretwell’s (1974), we find the seed size distribution is given by \( p(m)R/m \) so that

\[
\int_{m_1}^{m_2} \frac{R}{m} p(m) \, dm
\]

(3)

is the expected per capita number of seeds with sizes between \( m_1 \) and \( m_2 \). Integration from zero to \( R \) yields the total number of seeds per plant.

The shape of \( p \) as a function of seed size is the evolutionary variable. A seed-setting strategy \( p \) is evolutionarily stable if no mutant seed-setting strategy can invade a resident population in which \( p \) is common. If mutations occur only infrequently relative to the rate of the resident’s population dynamics, then the resident population can be assumed to be stable by the time a mutant comes along; that is, the number of the adult individuals in the resident population is not changing anymore. The resident population at its equilibrium defines the biotic environment in which the new mutants occur. To see which mutants can invade, let \( W_p(q) \) denote the per capita number of offspring for a mutant with seed-setting strategy \( q \) within a population of residents, all of which have seed-setting strategy \( p \). If \( W_p(q) \) is larger than one, then the mutant can invade. For \( p \) to be evolutionarily stable, \( W_p(q) \) should not exceed one for any \( q \).

**Mutant’s Fitness**

Consider an initially rare mutant with seed-setting strategy \( q \) within a population of residents with seedsetting strategy \( p \). The total per capita number of seeds of a mutant plant is

\[
\int_{0}^{R} \frac{R}{m} q(m) \, dm
\]

(4)

(see eq. [3]). During dispersal, germination, and early seedling growth, seeds and seedlings may get lost because of (density-independent) predation, desiccation, burial, trampling, and so forth, or simply because of seed landings outside of safe sites. To account for all density-independent mortality in the early phase still before competition comes into effect, let \( f(m) \) denote the precompetitive seed and seedling survival probability for a seed of size \( m \). Hence, the effective per capita seed number (i.e., the per capita number of seeds that actually land in safe sites, germinate, and enter the competitive phase) is given by

\[
\int_{0}^{R} f(m) \frac{R}{m} q(m) \, dm.
\]

(5)

Due to the mutant’s initial rareness (and consequently low mutant seed densities), the probability for a safe site to receive more than one mutant seed each is negligibly small. Mutant seedlings therefore do not compete among themselves but only with the seedlings of residents. Let \( U_p(m) \) denote the probability that a mutant seed of size \( m \) wins the local competition and occupies the safe site it has landed in. Assuming that seed size and the number of competitors in a safe site
have no further effect on the offspring beyond the competitive phase (and do not affect the survival or fecundity of the offspring once established), the mutant’s per capita number of offspring is

\[ W_p(q) = \int_0^R U_p(m) f(m) \frac{R}{m} q(m) \, dm. \]  

(6)

The product of \( U_p(m) \) and \( f(m) \) is the expected reproductive yield per seed of size \( m \). If \( p(m) \) and \( q(m) \) are equal for all \( m \), then mutants and residents are effectively indistinguishable, and hence the per capita offspring number should be the same for both. In a stable resident population, the per capita offspring number for a resident plant necessarily is equal to one. It follows that \( W_p(p) = 1 \) a priori for any \( p \).

**Relation between \( U_p \) and \( p \)**

The probability of establishment, \( U_p(m) \), depends on the position of the mutant’s seed within the competitive hierarchy among the resident seeds. Since invariably the largest seed present in a safe site wins the local competition and eventually occupies the safe site, \( U_p(m) \) is equal to the probability that a safe site does not contain any resident seeds larger than \( m \). Without having to specify the precise probability distribution for the number of seeds per safe site, it can be seen that \( U_p \) must have the following general properties:

**Proposition 1**

(a) \( \frac{d}{dm} U_p(m) \geq 0 \) for all \( m \),

(b) \( \frac{d}{dm} U_p(m) = 0 \) if and only if \( p(m) = 0 \), and

(c) \( U_p(R) = 1 \).

To see this, notice that in equation (a) increasing the mutant’s seed size either has no effect or improves the seed’s position within the competitive hierarchy, in equation (b) increasing seed size by a small amount improves the seed’s position within the competitive hierarchy if and only if there are resident seeds of similar size the mutant could swap ranks with, and in equation (c) the largest seed theoretically possible is at the top of the competitive hierarchy and will certainly occupy the safe site it has landed in. (Competition with resident seeds of size \( R \) can be ruled out. As all available resources must be used for the production of even a single seed of size \( R \), the effective per capita seed number of a resident plant with seeds of size \( R \) could not be larger than one. Additional mortality due to competition would yield a per capita offspring number strictly less than one whenever the population has a positive density. No resident population with seeds of size \( R \), therefore, could maintain a population at positive densities.) Proposition 1 is true a priori for any \( p \) and does not require that \( p \) be evolutionarily stable.

For an explicit expression relating \( U_p \) to \( p \), additional assumptions are required
for the exact probability distribution for the number of seed landings in a given safe site. I derive \( U_p \) for the Poisson distribution and for the negative binomial distribution. The Poisson distribution presumes independent dispersal of individual seeds, unhindered by distance and irrespective of seed size. The negative binomial distribution has a higher variance and represents a more aggregated (or clumped) distribution of seed numbers per safe site. The biological relevance of each will be discussed later. Let \( \alpha_p(m) \) denote the per capita number of resident seeds larger than \( m \), such that

\[
\alpha_p(m) = \int_m^R f(\mu) \frac{R}{\mu} p(\mu) \, d\mu \tag{7}
\]

(see eq. [5]). Moreover, let \( N_p \) denote the resident equilibrium population density expressed as the fraction of safe sites occupied by adult plants. The average number per safe site of resident seeds larger than \( m \) is \( \alpha_p(m)N_p \). Hence, with Poisson-distributed seed numbers per safe site, the probability that a safe site does not receive any resident seed larger than \( m \) is

\[
U_p(m) = \exp(-\alpha_p(m)N_p). \tag{8}
\]

As \( N_p \) is equal to the fraction of safe sites that receive at least one resident seed of any size, \( N_p \) can be solved from \( N_p = 1 - U_p(0) \). Differentiation of equation (8) with respect to \( m \) and use of equation (7) yield

\[
p(m) = C_1 \frac{m}{f(m)} (U_p(m))^{-1} \frac{dU_p(m)}{dm}, \tag{9}
\]

where \( C_1 \) is a normalization constant such that the integral of \( p(m) \) from zero to \( R \) is one. With negative binomial-distributed seed numbers per safe site, the probability that a safe site does not receive any resident seed larger than \( m \) is

\[
U_p(m) = \left( \frac{\alpha_p(m)N_p}{k} + 1 \right)^{-k}. \tag{10}
\]

The degree of aggregation is inversely related to the parameter \( k \). For \( k \to 0 \) aggregation becomes arbitrarily high so that most safe sites remain empty and \( U_p(m) \) approaches one. In the limit for \( k \to \infty \) the negative binomial distribution and the Poisson distribution coincide. Differentiation of equation (8) with respect to \( m \) and use of equation (7) yield

\[
p(m) = C_2 \frac{m}{f(m)} (U_p(m))^{-1 - 1/k} \frac{dU_p(m)}{dm}. \tag{11}
\]

Here \( C_2 \) again is a normalization constant such that the integral of \( p(m) \) is one. For both the Poisson distribution and the negative binomial distribution, it can be seen that there is a one-to-one relationship between the functions \( U_p \) and \( p \).
ESS Conditions

A seed-setting strategy $p^*$ is evolutionarily stable (ESS) if no mutant can invade, that is, if $W_{p^*}(q) \leq 1$ for all possible mutants $q$. On inspection of equation (6) it can be seen that the following must hold:

Proposition 2
If $p^*$ is evolutionarily stable, then necessarily
(a) $U_{p^*}(m)f(m)R/m \leq 1$ for all $m$, and
(b) if $U_{p^*}(m)f(m)R/m < 1$, then $p^*(m) = 0$.

To see this, first notice that $U_{p^*}(m)f(m)R/m$ is the per capita number of offspring for a monomorphic mutant with seeds of size $m$ only. For $p^*$ to be stable against invasion by all monomorphic mutants, $U_{p^*}(m)f(m)R/m$ should not exceed one for any $m$. As $W_{p^*}(q)$ is the weighted average of $U_{p^*}(m)f(m)R/m$ over all values of $m$ with weighing factor $q(m)$, it immediately follows that $W_{p^*}(q) \leq 1$ for all polymorphic strategies $q$ as well. Second, a strategy such that there is some investment of resources in seeds for which $U_{p^*}(m)f(m)R/m$ is strictly less than one cannot be evolutionarily stable, because any mutant allocating resources to other, more profitable seeds instead (i.e., for which $U_{p^*}(m)f(m)R/m$ is equal to one) would have a higher offspring number and hence could invade. (Proposition 2 is an application of the Bishop-Cannings [1978] theorem for continuous strategies).

A mutant strategy $q$ such that $q(m)$ is positive for only those values of $m$ for which $p^*(m)$ is positive as well is selectively neutral; that is, $W_{p^*}(q) = 1$. Whether it can invade or not depends on whether it will gain a fitness advantage or disadvantage relative to the resident if present at higher densities when it actually starts to change the seed size frequencies within the population as a whole. In the terminology of Uyenoyama and Bengtsson (1982), $p^*$ is a “weak form” ESS (as opposed to a “strong form” in which rare mutants have a per capita offspring number that is strictly less than one). Notice from proposition 2 that the expected reproductive yield per unit of seed cost, $U_{p^*}(m)f(m)/m$, is the same for all $m$ for which $p^*(m)$ is positive.

Construction of the ESS

Suppose $p^*$ is evolutionarily stable. Its shape as a function of seed size is implicitly given by proposition 2. As an intermediate step, I first derive the shape of $U_{p^*}$ and translate the results for $p^*$ later. From proposition 2 we know that either $U_{p^*}(m) = m/f(m)R$ or $U_{p^*}(m) < m/f(m)R$, where in the latter case necessarily $p^*(m) = 0$. From proposition 1 we know that $p^*(m) = 0$ if and only if $d/dm U_{p^*}(m) = 0$, and otherwise $d/dm U_{p^*}(m) > 0$. It follows that $U_{p^*}(m)$ is a nondecreasing function of seed size that is either equal to $m/f(m)R$ or smaller and constant. Starting from the largest possible seed size $R$ (which is the only seed size for which $U_{p^*}[m]$ is known in advance irrespective of the shape of $p^*$) and proceeding down toward smaller seeds, we can construct the graph of $U_{p^*}(m)$
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Fig. 2.—Construction of the ESS. Here $U_p(m)$ (solid line) is a nondecreasing function of $m$ and either coincides with $m/f(m)R$ (dashed line) or is smaller and constant. At the rightmost end of the graph (i.e., at $m = R$), $U_p(m)$ is equal to one, which typically is below the graph of $m/f(m)R$. For smaller seeds, therefore, $U_p(m)$ remains constant until it meets the graph of $m/f(m)R$ at $m = m_3$. Between $m_3$ and $m_4$, $U_p(m)$ and $m/f(m)R$ necessarily coincide, because if continued as a constant function, then $U_p(m)$ would end up above the graph of $m/f(m)R$, which is excluded by the ESS conditions. Since $U_p(m)$ is a nondecreasing function of seed size, it can no longer follow the graph of $m/f(m)R$ once $m_4$ has been reached, and therefore it must be continued as a constant function until the graph of $m/f(m)R$ is joined again at $m = m_4$. Between $m_4$ down $m_1$ (and hence $p^*(m)$ is positive. The graph of $m/f(m)R$ is based on $f(m)$ as used in fig. 3.

from the graph of $m/f(m)R$ (fig. 2). It can be seen in figure 2 that $U_p(m)$ is strictly increasing (and therefore $p^*[m]$ is positive) only for those values of $m$ where $m/f(m)R < 1$, and, moreover, $m/f(m)R < m'/f(m')R$ for any $m'$ larger than $m$. This is reformulated in the following proposition:

**Proposition 3**

If $p^*$ is evolutionarily stable, then $p^*(m)$ is positive if and only if

(a) $f(m)/m > 1/R$, and

(b) $f(m)/m > f(m')/m'$ for all $m' > m$.

As $f(m)/m$ is the slope of a straight line connecting the graph of $f(m)$ with the origin, proposition 3 provides a shortcut method to derive directly from the graph of $f(m)$ for which seed sizes $p^*(m)$ is positive and for which it is not (fig. 3). Notice that $1/R$ is the slope of the diagonal in figure 3 connecting the origin with the point $(R,1)$.

The results from figure 3 can be generalized as follows: If $p^*$ is evolutionarily stable, then there are one or more disjunct ranges of continuous variation in seed size depending on the precise shape of $f(m)$. Among the seeds produced, $f(m)/m$ is always a decreasing function of seed size. The seed size that (globally) maxi-
The very left boundary of the total seed size range and coincides with the (global) fitness optimum in the model of Smith and Fretwell (1974). The very right boundary of the total range is characterized by \( f(m)/m = 1/R \) and corresponds to the largest possible seed size beyond which the effective per capita seed number would always be less than one, and hence no positive population density could be maintained. A single range of seed sizes occurs if \( f(m)/m \) has only a single global maximum. For two or more disjunct ranges, \( f(m)/m \) should exhibit as many local maxima with decreasing magnitudes toward larger seeds. For each separate range, the minimal seed size coincides with a local maximum of \( f(m)/m \) and hence with a local fitness optimum in the Smith-Fretwell model (cf. fig. 1).

Construction of the range of seed sizes does not depend on any property of \( U_p^* \) other than the few general properties given in proposition 1. The derivation of an explicit expression for the precise shape of \( p^* \) requires specific assumptions about the exact probability distribution for the number of seeds that land in a given safe site. From proposition 2 it follows that if \( p^*(m) \) is positive, then \( U_{p^*}(m) = m/f(m)R \), which on substitution into equation (9) and equation (11), respectively, gives

\[
p^*(m) = C_1 \frac{d}{dm} \left( \frac{m}{f(m)} \right)
\]

for Poisson-distributed seed numbers per safe site and

\[
p^*(m) = C_2 \left( \frac{m}{f(m)} \right)^{-1/k} \frac{d}{dm} \left( \frac{m}{f(m)} \right)
\]
for negative binomial-distributed seed numbers per safe site. Given a certain probability distribution for the number of seeds per safe site, the shape of $p^{*}(m)$ depends on the shape of $f(m)$ only, except for the truncation at the upper limit of the seed size range, which also depends on $R$. The seed size distribution of a plant is given by $p^{*}(m)R/m$ (fig. 4).

**DISCUSSION**

The main conclusion of this article is that in the present model a single seed size is never evolutionarily stable and that there is always selection for at least some continuous variation in seed size within individual plants. Which seeds are included in the evolutionarily stable seed setting strategy can be graphically determined from the precompetitive seed and seedling survival, $f(m)$, and the amount of resources per safe site, $R$. The model generates several predictions—for example, prediction 1: At least some continuous within-individual variation in seed size is adaptive and does not arise from constraints on a plant’s ability to produce seeds of uniform size.

Comparing seed-setting strategies for different amounts of resources (fig. 5), it can be seen that the range of seed sizes increases as $R$ increases. The left boundary of the range remains unchanged, however, and increasing $R$ amounts to merely truncating the seed size distribution at a larger seed size. The fraction of resources invested in small seeds then necessarily decreases. There is a threshold value for $R$ below which the effective per capita seed number is too low for a population to thrive. Approaching the threshold from above, the seed size range shrinks to a single seed size that corresponds to the optimal seed size in the model of Smith and Fretwell (1974). Thus we have prediction 2: Plants with many
resources have more variable seeds than plants with few resources. The minimum seed size is independent of the amount of resources.

Comparing seed-setting strategies for different levels of precompetitive seed and seedling survival (fig. 6), we can see that decreasing \( f(m) \) decreases the seed size range. If \( f(m) \) is reduced by a single factor independent of seed size, then the minimum seed size remains constant, and reducing \( f(m) \) amounts to truncating the seed size distribution at a smaller seed size (see prediction 2). If \( f(m) \) is reduced by a factor that is different for different seed sizes, then both minimum and maximum seed size may change. For survival rates below a certain threshold, the effective per capita seed number is too low for population survival. Approaching the threshold from above reduces the seed size range to a single seed size that coincides with the optimum in the Smith-Fretwell model. Now we have prediction 3: Plants in environments in which (precompetitive) juvenile mortality is high have less variable seeds than plants in environments in which juvenile mortality is low. If mortality varies by a factor independent of seed size, then the minimum seed size remains constant, but otherwise both minimum and maximum seed size may change.

Comparing seed-setting strategies for different seed dispersal modes for plants with the same seed size range (fig. 4), we can see that with aggregated seed dispersal (negative binomial-distributed seed numbers per safe site), the seed size distribution is more biased toward small seeds than in the case of more even seed dispersal (Poisson-distributed seed numbers per safe site). Thus we have prediction 4: Plants with aggregated seed dispersal have seed size distributions that are more biased toward small seeds than plants with a similar seed size range but with more even seed dispersal.

The predictions presume that the evolutionarily stable seed-setting strategy has
Fig. 6.—Seed size variation for different levels of juvenile survival. A, When precompetitive seed and seedling survival is high (curve 1), seed size varies between $m_1$ and $m_5$ (long horizontal bar). When survival is low (curve 2), seed size varies between $m_2$ and $m_4$ (short horizontal bar). For very low survival (curve 3), the seed size range reduces to a single size $m_3$. B, If the precompetitive seed and seedling survival varies by a factor independent of seed size, then the minimum seed size remains constant. When survival is high (curve 1), seed size varies between $m_1$ and $m_5$ (long horizontal bar). When the survival is low (curve 2), seed size varies between $m_1$ and $m_5$ (short horizontal bar). For very low survival (curve 3), the seed size range reduces to a single seed size $m_1$.

been established in the population. Specific data to test the predictions are largely missing from the literature but should otherwise be easily obtainable. To test whether the present model could account for seed size variation found in real plants, we can experimentally estimate $f(m)$ by the proportion of establishment among seeds of size $m$ when sown in situ at low density such that competition with conspecific seedlings can be ruled out. The total amount of resources per safe site available for seed production, $R$, can be estimated by a plant’s total seed weight. Plant biomass often correlates well with total seed weight and therefore could be used as an indirect estimate of $R$. An explicit formula for the evolutionarily stable seed-setting strategy requires the exact probability distribution for the number of seeds that land in a given safe site and was obtained for the Poisson distribution and the negative binomial distribution.

The model’s conclusions depend mainly on the interaction of two assumptions, that is, random seed dispersal and extremely asymmetric seedling competition. Seeds are assumed to be randomly dispersed such that different safe sites receive varying numbers of seeds of different sizes. Small seeds contribute to a plant’s fitness by exploiting safe sites that by chance are left without any larger seeds. If there were no variation among safe sites at all, then small seeds would never have the opportunity to occupy a safe site, and only the largest possible seeds would yield established plants. Investment of resources in small seeds would be lost and hence be selected against. However, if seed dispersal is random so that small seeds do have a chance to reach safe sites that remain unoccupied by bigger seeds, then the production of small seeds is beneficial if the competitive
disadvantage is outweighed by a larger seed number and hence a higher efficiency for colonizing unoccupied safe sites. If seed dispersal is random but relatively even so that the differences in seed numbers among safe sites are small (e.g., Poisson-distributed seed numbers per safe site), then the chances for small seeds to land in a safe site with no larger seeds present are less than with more aggregated seed dispersal (e.g., negative binomial-distributed seed numbers). The potential advantage of producing small seeds, therefore, is most pronounced in cases of aggregated seed dispersal (see prediction 4). Poisson-distributed seed numbers per safe site presume independent dispersal of individual seeds over distances that are large compared to the distances between safe sites and may be best approximated in wind- or water-dispersed species. The negative binomial distribution describes a more aggregated seed dispersal as may be expected when seeds are dispersed by animals, especially if carried internally and deposited in the droppings (Fenner 1985).

Seedling competition is assumed to be extremely asymmetric in the sense that seedlings from seeds of a given size always win from seedlings from smaller seeds whenever present in the same safe site. It can be shown that with less asymmetric competition (such that seedlings from smaller seeds have a small but nevertheless positive chance to become established), there still is selection for a variation in seed size. The continuous range, however, breaks up into many discrete seed sizes, the number of which depends on the precise level of competitive asymmetry (S. A. H. Geritz, unpublished manuscript). If competition were fully symmetric (i.e., if seed size had no effect on the competitive ability of seedlings at all), then the higher costs of bigger seeds (in terms of resources invested) no longer would be balanced by a higher competitive ability, and therefore big seeds would be selected against. The single seed size that maximizes the effective per capita seed number (and that maximizes fitness in the Smith-Fretwell model) would be the evolutionary optimum. However, if competition is asymmetric, then the production of big seeds is beneficial if the lower total seed number is compensated for by a higher competitive ability of the seedlings. A continuum of seed sizes occurs if competition is extremely asymmetric, because then an arbitrarily small increase in seed size gives already a sufficiently large competitive advantage to outweigh the lower seed number. Competitive asymmetry as extreme as in the present model may be unlikely to occur in nature, however. Initially positive correlations between seed size and plant vigor often turn out to be insignificant by the end of the season (Stanton 1984). Nevertheless, evidence for strong competitive asymmetry comes from a study by Black (1958), who showed that in *Trifolium subterraneum* seedlings from small seeds were totally overgrown by seedlings from large seeds when sown together. Cipollini and Stiles (1991) concluded that in *Phaseolus vulgaris* and *Phaseolus coccineus* plants from larger seeds were faster growing and probably able to outcompete plants from smaller seeds. Houssard and Escarré (1991) found that in *Rumex acetosella* seedlings from heavy seeds appeared to be strong competitors, whereas seedlings from light seeds showed less growth in the presence of neighbors and may thus be considered subordinate competitors.

Random seed dispersal and extreme competitive asymmetry yield opposite
selective forces on seed size. Without random seed dispersal the competitive ability of seedlings is maximized, whereas without competitive asymmetry the efficiency for colonizing empty safe sites is maximized. At the ESS the two forces are in equilibrium. The evolutionarily stable seed-setting strategy, however, is not an evolutionary compromise in the sense of single intermediate seed size: Mutants with larger (and hence more competitive) seeds or mutants with sufficiently smaller (and hence more numerous) seeds could always invade a monomorphic resident population. Instead, the ESS consists of a continuous range of seed sizes, each with the same expected reproductive yield per unit of seed cost. The upper size limit is the largest possible seed size beyond which the effective per capita seed number would always be less than one, and hence no positive population density could be maintained. Clearly, the upper size limit increases as the amount of resources increases or as the precompetitive seed and seedling mortality decreases (see predictions 2 and 3). Smaller seeds persist because of two effects that counteract each other: Each seed size is superior to all smaller sizes with regard to its ability to compete in safe sites, and each seed size produced by the ESS is superior to all larger sizes with regard to its efficiency for finding safe sites that remain unoccupied by seeds larger than itself (see proposition 3). The lower size limit of the range corresponds to the fitness optimum in the Smith-Fretwell model and is the most efficient of all possible sizes for colonizing empty safe sites. As the optimal size in the Smith-Fretwell model is independent of the amount of resources and also remains unaffected by a proportional change in the precompetitive seed and seedling survival, the lower size limit of the ESS does not change, either (see predictions 2 and 3). Seeds smaller than the optimal size in the Smith-Fretwell model are not present at the ESS, because compared with slightly larger seeds, they are inferior with regard to both their competitive ability and their efficiency for finding unoccupied safe sites.

The differences between the present model and the Smith-Fretwell model are due only to the imposition of safe-site competition, because the formulations are otherwise equivalent. In the Smith-Fretwell model the expected reproductive yield per seed is given by a single factor, $f(m)$, that accounts for frequency-independent seed and seedling mortality only. In the present model, the expected reproductive yield per seed is given by the product of two factors: one, $f(m)$, to account for frequency-independent seed and seedling mortality and the other, $U_p(m)$, to account for mortality due to competition in safe sites. The two models are effectively equivalent if $U_p(m)$ is constant (i.e., seed size has no effect on the competitive ability of seedlings) or when competition in safe sites is rare as a consequence of low seed numbers per plant (due to few resources or high precompetitive mortality) so that most safe sites remain unoccupied (see predictions 2 and 3) or extremely aggregated seed dispersal so that competition is confined to only few safe sites, whereas most safe sites remain empty and the seed size distribution is extremely skewed in favor of the smallest seeds and only a very small proportion of resources is invested in big seeds (see prediction 4).

The model was developed for annual plants each with the same amount of resources. The conclusions also hold for perennials if $R$ is replaced by the expected lifetime amount of resources of a plant (app. A) and for plants each with
a different amount of resources if \( R \) is replaced by its population average (app. B). Below I highlight some of the other model assumptions.

Seed size is assumed to have no lasting effects beyond the seedling stage; that is, seed size does not affect a plant's survival or fecundity once it has become established. Also, the number of competitors in a safe site is assumed to be ineffective after seedling establishment. In some plants, however, competition may affect plant fecundity rather than seedling survival (see, e.g., Wulf 1986c). The two cases of a single, unaffected winner per safe site and of several survivors, each with reduced fecundity, are mathematically equivalent if the probability of winning in the first case is interpreted as the fraction of resources secured by an individual plant in the second case. Extremely asymmetric competition in the latter case implies that among the survivors within a safe site, the plant from the largest seed present captures all resources and hence will be the only plant with offspring of its own.

The calculation of the mutant’s per capita offspring number presumes that, because of the mutant’s initial rareness, mutant seedlings do not compete among themselves but with resident seedlings only. In plants in which the fruit or the flower head is the unit of dispersal, however, competition among siblings may occur even at very low plant densities if the seeds fail to separate from one another.

The calculation of the mutant’s per capita offspring number further presumes that the resident population is stable; that is, the resident population density is constant over time. In a nonequilibrium resident population, the production of small seeds will be more beneficial in years when population density is low (and only few seeds in total are produced so that many safe sites remain unoccupied), whereas in crowded years the production of larger seeds is more advantageous. Temporal variation in population density, therefore, may reinforce rather than counteract the evolution of seed size variation. The assumption of a stable resistant population implies that the total number of safe sites in the population must be large in order to exclude population fluctuations due to demographic stochasticity.

Most annuals have a substantial seed bank that was not accounted for in the model. Dormancy and seed bank accumulation are favored under circumstances when most of the seedlings fail to become established in certain years (see, e.g., Cohen 1966; Ellner 1984) but is disadvantageous in the present model in which the probability of establishment is constant over time. To investigate the possible consequences, the model should be considered under circumstances that favor the evolution of a seed bank. As small size tends to increase the chances of a seed’s being incorporated in the pool of buried seeds (Grime 1979) and also increases seed longevity (Harper 1977), some selective interaction between dormancy and seed size variation is likely to occur, presumably in favor of smaller seeds.

Precompetitive seed and seedling survival in the model depends on seed size but not on seed or seedling density. The only cause of density-dependent mortality in the model is competition in safe sites. In the real world, however, the risk
of death by seed predators, seedling herbivores, or fungal pathogens may increase as seed or seedling density increases (Hutchings 1986). The (on first sight appealing) hypothesis that a higher risk of density-dependent mortality favors the production of larger (and hence less numerous) seeds in order to decrease overall seed and seedling density certainly is false. A mutant with smaller but more numerous seeds will be able to invade, because the risk of precompetitive density-dependent mortality is the same for mutant and resident seeds, whereas the larger number of safe sites left unoccupied by the resident gives the mutant a definite advantage. Below I formulate an alternative hypothesis. For simplicity, assume that the probability of a safe site’s being affected by precompetitive density-dependent mortality increases as the number of seeds in the safe site increases but is independent of seed size. Moreover, assume that if a safe site is affected, then all seeds and seedlings will be destroyed. When a seed has landed in a given safe site, two conditions must be satisfied for seedling establishment: no larger seeds must be present, and the total number of seeds present must be low. Even though seed size by assumption does not directly affect the risk of precompetitive density-dependent mortality, the two requirements are statistically dependent. Safe sites with many seeds probably give a fairly representative sample of all seed sizes present in the population and hence contain both small and big seeds. Safe sites with only a few seeds will often lack big seeds simply because of sampling error. In other words, safe sites lacking big seeds tend to be the least crowded. The reproductive yield of small seeds, therefore, depends mainly on establishment in less crowded safe sites. The reproductive yield of big seeds, on the other hand, also depends on establishment in crowded safe sites, that is, if there were no precompetitive density-dependent mortality. Since the risk is highest for crowded safe sites, the imposition of precompetitive density-dependent mortality will affect big seeds more severely than small seeds and therefore will modify the shape of the ESS seed size distribution in favor of smaller seeds. Different assumptions about precompetitive density-dependent mortality (e.g., different risks for different seed sizes or incomplete depletion of affected safe sites) may yield different results. For a definite answer, explicit modeling is necessary.

In the model, a seed-setting strategy by definition describes seed size variation within individual plants, and hence the ESS conditions specify the ESS as a polymorphic strategy of an individual plant. However, Tomas (1984) argues that if (like in the present model) the fitness of an initially rare mutant is given as a (weighted) arithmetic average over a number of alternative monomorphic strategies, then the ESS can be interpreted not only as a single, polymorphic phenotype but more generally as a population frequency distribution. Such a distribution could be the result of all individuals producing a distribution that matches the population distribution or each monomorphic strategy being produced by a different type of individual, with the frequency of these types matching the population distribution or any mixture of these two. The model’s predictions can be interpreted accordingly, and thus they allow for a comparison between seed size distributions of whole populations or plant communities as well. The more general
interpretation of the ESS as a population distribution of seed sizes, however, presuming that the resident population is stable, because in a temporally varying environment the fitness of a mutant no longer is the arithmetic average over the various monomorphic strategies (which is a prerequisite for Tomas’s argument) but instead is given by the geometric average of the fitness in different year types (see, e.g., Cohen 1966; Metz et al. 1992). For a more intuitive insight, consider that in a population with a single, polymorphic phenotype, the population frequency distribution of seed sizes is fixed independently of population fluctuations. However, in a population consisting of several monomorphic phenotypes each with a different, single seed size, the relative frequencies of the seed sizes will vary if different types are favored in different years (É. Kisdi, personal communication). In a fluctuating population, therefore, the alternative interpretations of the ESS either as a single, polymorphic phenotype or as a population distribution of seed sizes produced by a number of monomorphic phenotypes each with a different seed size are no longer equivalent.

Kaplan and Cooper (1984), Venable (1985), and McGinley et al. (1987) showed in models that the evolution of variable offspring is promoted by high temporal environmental variation if the reproductive yield of the various offspring types is negatively correlated among different years. McGinley et al. (1987) found that in a spatially heterogeneous environment the production of variable offspring sizes is favored only if the reproductive yield of the offspring is strongly reduced by high population density and parents can control the dispersal of the offspring to the appropriate habitats. García-Dorado (1990), however, found that spatial heterogeneity may favor variation in offspring sizes also if population density is regulated locally in different patches and the offspring optimally adapted in one patch cannot survive in the other. Lalonde (1991) showed that variation in offspring size may occur if the amount of resources that become available during the provisioning period is unpredictable and if resources that have already been allocated are at least partially unrecoverable. In all these models, the variation in offspring size is an adaptation for reducing risk in a temporally or spatially unpredictable environment that varies in a “coarse-grained” manner. The present model differs from those above in two ways. First, the physical environment itself is constant both in time and in space. The spatial heterogeneity, which accounts for the variable offspring, results from the nonuniform distribution of the seedlings themselves. Second, the environment varies in a “fine-grained” manner; that is, the scale of spatial variation is small compared to the dispersal distances of seeds.

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APPENDIX A

Perennial Plants

For perennials seed-setting strategies may be conditional on plant age. A seed-setting strategy therefore will be represented as a vector-valued function \( p(m) = (p_1[m], \ldots, p_k[m]) \), where \( p_i(m) \) describes the allocation of resources for a plant of age \( i \in \{1, \ldots, k\} \), where \( k \) is the maximum age. Let \( \sigma_i \) denote the probability that a plant will survive up to age \( i \), and let \( R_i \) denote the amount of resources in a safe site available at age \( i \). The amount of resources may vary with plant age because of the nutrient dynamics within the soil of the safe site (which may deteriorate or improve with time) or because of changes in the allocation of resources among growth, survival, and reproduction within the plant itself.

The number of offspring produced at age \( i \) by a mutant plant with seed-setting strategy \( q \) in a population of residents with seed-setting strategy \( p \) is

\[
\int_0^{R_i} U_p(m) f(m) \frac{R_i \sigma_i}{m} q_i(m) \, dm.
\]

The expected lifetime offspring number therefore is

\[
W_p(q) = \sum_{i=1}^k \sigma_i \left[ \int_0^{R_i} U_p(m) f(m) \frac{R_i \sigma_i}{m} q_i(m) \, dm \right].
\]

If \( p^* \) is evolutionarily stable, then \( W_{p^*}(q) \leq 1 \) for all \( q \). Since \( W_{p^*}(q) = 1 \) for \( q = p^* \), the ESS maximizes \( W_{p^*}(q) \) as a function of \( q \). Using the Lagrange multiplier method for maximizing \( W_{p^*}(q) \) as a function of \( q \) subject to

\[
\int_0^{R_i} q_i(m) \, dm = 1,
\]

we get

\[
U_{p^*}(m) f(m) \frac{R_i \sigma_i}{m} \leq \lambda_i
\]

for \( m \in (0, R_i) \) and for certain constants \( \lambda_i \) with \( i \in \{1, \ldots, k\} \). A strict inequality in equation (A4) for a given \( m \) implies that \( p_i^{*\infty}(m) = 0 \). If \( p_i^{*\infty}(m) > 0 \), then both sides of equation (A4) are equal, and hence \( \lambda_i / R_i \sigma_i = U_{p^*}(m) f(m)/m \), which is independent of \( i \). Substitution of equation (A4) into equation (A2) with \( q = p^* \) reveals that \( \lambda_i = 1 \). It thus follows that

\[
\lambda_i = \frac{R_i \sigma_i}{\sum_{i=1}^k R_i \sigma_i}
\]

Substitution of equation (A5) into equation (A4) yields

\[
\frac{U_{p^*}(m) f(m)}{m} \sum_{i=1}^k R_i \sigma_i \leq 1
\]

for \( m \in (0, R_i) \), where both sides are equal if \( p_i^{*\infty}(m) > 0 \) and where a strict inequality implies that \( p_i^{*\infty}(m) = 0 \). With equation (A6) we recover the ESS conditions of proposition 2, but with \( \sum_{i=1}^k R_i \sigma_i \) (i.e., the expected lifetime amount of resources) instead of \( R \).

As equation (A6) does not depend on any particular \( i \), it follows that if \( p_i^{*\infty}(m) > 0 \) at a
given age $i$, then it is positive for all ages for which $m < R_i$. The other way around also holds; that is, if $p^*_i(m) = 0$ for some given age $i$ and $m < R_i$, then it is zero for any age. In other words, if $p^*$ is evolutionarily stable, then the range of the sizes of the seeds produced is independent of plant age, except for the possibility of truncation at $R_i$. Although the seed size ranges for different ages necessarily coincide, the shape of $p^*_i$ as a function of seed size may still be different. These differences, however, will be selectively neutral. For perennials there is not a one-to-one relationship between $U_{p^*}$ and $p^*$. Instead, $U_{p^*}$ specifies the seed size distribution within the population as a whole rather than for individual plants. There are infinitely many possible individual seed-setting strategies $p^*_i$ that satisfy the ESS conditions and that give together the same population seed size distribution. The graph $U_{p^*}(m)$ can be constructed from the graph of $m/f(m) \sum_{i=1}^n R_i \sigma_i$ in a way identical to the one followed in the model for annuals.

**APPENDIX B**

**Variation in Resources**

If individual plants have different amounts of resources (e.g., because of differences in safe-site quality or in predation on leaves or roots, etc.), then seed-setting strategies may be conditional on $R$. Let $p(m, R)$ denote the seed-setting strategy for a plant in a safe site with an amount of resources $R \in (0, R_{max})$, where $R_{max}$ is the maximum amount of resources in a safe site in the population. Let $r(R)$ denote the probability distribution for $R$ such that the integral

$$
\int_{R_1}^{R_2} r(R) \, dR
$$

is the probability that a given plant has an amount of resources between $R_1$ and $R_2$. Notice that this probability is assumed to be independent of seed size. Integration from zero to $R_{max}$ by definition should yield a value of one.

The expected per capita offspring number for an initially rare mutant with seed-setting strategy $q$ within a population of residents with seed-setting strategy $p$ is

$$
W_{p^*}(q) = \int_0^{R_{max}} r(R) \left[ \int_0^R U_{p^*}(m) f(m) \frac{R}{m} q(m, R) \, dm \right] dR. \tag{B2}
$$

If $p^*$ is evolutionarily stable, then maximization of $W_{p^*}(q)$ as a function of $q$ subject to

$$
\int_0^R q(m, R) \, dR = 1 \tag{B3}
$$

gives

$$
U_{p^*}(m) f(m) \frac{R}{m} r(R) \leq \lambda(R) \tag{B4}
$$

for $m \in (0, R)$ and for some function $\lambda(R)$. A strict inequality in equation (B4) for given $m$ implies that $p^*(m, R) = 0$. If $p^*(m, R) > 0$, then both sides of equation (B4) are equal, and hence $\lambda(R)/R r(R) = U_{p^*}(m) f(m)/m$, which is independent of $R$. Substituting equation (B4) into equation (B2) with $q = p^*$ shows that $\int_0^{R_{max}} \lambda(R) \, dR = 1$, and thus

$$
\lambda(R) = \frac{R r(R)}{\int_0^{R_{max}} R r(R) \, dR}. \tag{B5}
$$

Substituting equation (B5) into equation (B4) gives

$$
\frac{U_{p^*}(m) f(m)}{m} \int_0^{R_{max}} R r(R) \, dR \leq 1 \tag{B6}
$$
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for \( m \in (0, R) \), where both sides are equal if \( p^*(m, R) > 0 \) and where a strict inequality implies that \( p^*(m, R) = 0 \). With equation (B6) we again recover the ESS conditions of proposition 2 but with \( \int_{0}^{R} mR(R) \, dR \) (i.e., the population average of \( R \)) instead of \( R \).

As equation (B6) does not depend on any particular \( R \), it follows that if \( p^* \) is evolutionarily stable, then the range of the sizes of the seeds produced is independent of the amount of resources, except for the possibility of truncation. The shape of \( p^* \) as a function of seed size may still be different for different values of \( R \). These differences, however, will be selectively neutral. As in the model for perennials, \( U^*_p \) specifies the seed size distribution within the population as a whole rather than of individual plants. The graph of \( U^*_p(m) \) can be constructed from the graph of \( m f(m) \int_{0}^{R} mR(R) \, dR \) in a way identical to the one followed in the model for annuals with a fixed amount of resources.

LITERATURE CITED


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