

# Life history evolution of seed-bank annuals in response to seed predation

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## Summary

We present a model of life history evolution for seed-bank annuals in temporally varying environments in which both the seed bank and the distribution of fecundity across year types evolve in response to seed predation. The fecundity distribution refers to the expected reproductive success of germinating seeds across a range of different year types. We assume that it is a function of traits pertaining to growth and survival under different environmental circumstances. Such traits are assumed to result in a trade-off between reproduction in favourable and less favourable years. The model is used to explore how seed predation selects for changes in the seed bank and fecundity distribution and how changes in each of these further select for changes in the other. The direction of selection is contingent upon: whether or not a seed bank exists; whether predation has a greater effect on fresh or buried seed; whether the predation rate differs in different year types, and if so, if it is positively or negatively density-dependent; whether or not predation rate is sensitive to individual variation in seed yield, and if so, whether and how such dependency varies in different kinds of year. Under a variety of predation regimes, seed predators select for a temporal clumping of reproduction; i.e. a specialisation on a favourable subset of year types. This effect usually requires negatively density-dependent seed predation of the sort created by predator satiation. In fact, the classic scenario favouring masting in perennials creates the strongest such effect in our model. Yet unlike the masting of perennial plants, this effect is favoured in a seed-bank annual. It can even occur in a strict annual without a seed bank, and it can occur in a seed-bank annual even if seed predation is density-independent.

*Keywords:* Seed predation; annual plants; life history evolution; dormancy; fitness sets; environmental variability; reproductive ecology; masting; density-dependence.

## Introduction

Seed predators typically consume over half of a plant's seed crop (Price and Jenkins, 1986; Hendrix, 1987). Such damage creates strong selective pressures that favour the evolution of anti-herbivore traits such as the production of toxic chemicals in seeds (Janzen, 1969; Breedlove and Ehrlich, 1968; Center and Johnson, 1974; Green and Palmblad, 1975; Hare and Futuyama, 1978), protective tissue such as thick seed coats or fruit walls (Davey, 1965; Janzen, 1969; Elliot, 1974), defensive seed coat shapes and textures (Pulliam and Brand, 1975; Hare, 1980), small seed size (Smith, 1970; Abramsky, 1983; Davidson *et al.*, 1985), dispersal structures that may result in removal from areas of high predation risk (Bullock, 1974; O'Dowd and Hay, 1980; Heithaus,

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1981; Clark and Clark, 1984), cryptic seed coloration (Cook *et al.*, 1971), and mast fruiting (Ebell, 1967; Janzen, 1976; Harper, 1977; Silvertown, 1980).

Here, we explore the selective impact of seed predation on the life histories of annual plants in variable environments. Specifically, we explore its impact on seed dormancy and other traits determining the distribution of reproductive success in different year types. Such traits are not normally thought of as anti-herbivore adaptations and in fact the likely selective effects of seed predation on annual plant life history evolution remains uninvestigated. Examples of traits that affect the distribution of reproductive success in different year types include seed size (in the context of its effects on shade tolerance or drought resistance in variable environments rather than its direct role in predator defense; Baker, 1972; Gross, 1984), root/shoot ratios (which can affect success in wet versus dry years) and mesic/xeric leaf morphology and anatomy (which can also affect success in wet versus dry years; Brown and Venable, 1986). The selection dynamics explored here can result in temporal clumping of seed production (bloom years) by annual plants in response to seed predation. Temporal clumping of seed production is a life history response to herbivory previously considered significant only for long-lived masting perennials (Bulmer, 1977).

Our model considers an annual plant species in a temporally varying environment that relies on between-year dormancy to avoid conditions unfavourable for vegetative growth (Cohen, 1966; Ellner, 1985a; b; Holsinger, 1985; Leon, 1985). Cohen (1966) and Ellner (1986) considered the evolution of dormancy assuming that the rest of the life history does not change. Templeton and Levin (1979), by investigating how the presence of a seed bank affects the evolution of post-germination traits, considered the converse and showed that dormancy encourages an annual plant to specialise on a favourable subset of the conditions normally encountered. Elsewhere, we considered the evolutionary effects of selection operating simultaneously on dormancy, post-germination traits (Brown and Venable, 1986), and dispersal (Venable and Brown, 1988). Here, we apply this framework to study the selective effects of seed predation on an annual plant subjected to a variety of realistic seed predation regimes. Specifically, we consider the evolutionary effects of positively and negatively density-dependent (DD) predation when the predation intensity may vary among high and low seed production years, and among high and low seed producing individuals within a given year. Our goal is to capture some essential features of the life cycle of annual plants and to explore how different patterns of seed predation may favour changes in dormancy and year-type specialisation. Such phenomena are not only of interest as adaptations to variable environments, but also because of their increasing relevance to variance mediated mechanisms of species coexistence (Venable, 1989).

### The model

We envision an annual plant in a temporally variable environment (Fig. 1). At the beginning of a growing season a fraction,  $G$ , of seeds in the seed bank germinate. Of the remainder, a proportion,  $R$ , will survive until the next growing season. Among germinating seeds, a fraction,  $c$ , will survive to adulthood at which time each adult produces  $B$  seeds ( $cB = S$ , the mean seed yield per germinating seed). A fraction of these new seeds,  $(1 - m)$ , die either on the parent plant or in the soil prior to the start of the next growing season.

Annual fitness,  $\lambda$ , is the expected number of seed progeny at the start of the next growing season per seed alive at the start of the present growing season:

$$\lambda = GSm + (1 - G)R$$

Temporal variation is incorporated by permitting the yield of germinating seeds and the

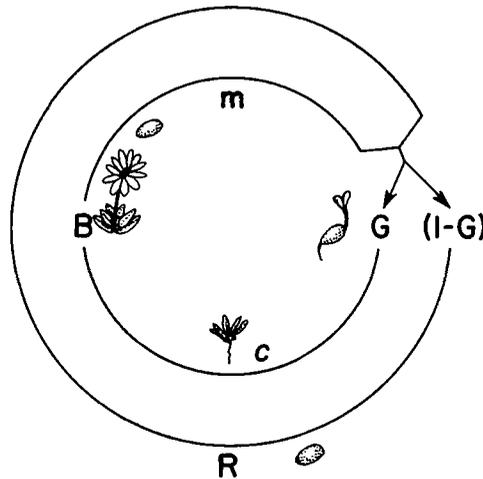


Figure 1. Diagrammatic life cycle of a seed bank annual showing the model's parameters.  $G$  = proportion of seeds germinating at the start of the growing season;  $c$  = probability of surviving from germination to adulthood;  $B$  = expected seed set per adult;  $S = cB$  = expected seed yield per germinating seed;  $m$  = probability that a seed survives from seedset to the start of the next growing season;  $R$  = probability that a dormant seed survives to the next growing season.

probability of survival from seed set to the beginning of the next growing season to vary. Let  $\mathbf{S} = (S_1, \dots, S_n)$  be the expected seed yield of a germinating seed in each of  $n$  year types which occur randomly in time. Let the vector  $\mathbf{p} = (p_1, \dots, p_n)$  denote probabilities of occurrence of each year type. If the time from germination to seed set is less than a year, fresh seeds must survive in or on the soil surface until the following germination season. Let the vector  $\mathbf{m} = (m_1, \dots, m_n)$  denote probabilities that a seed survives from seed set to the start of the next growing season in each year type.

Fitness (the expected per capita growth rate),  $W$ , is given by the geometric mean of annual fitness (Cohen, 1966; Leon, 1985):

$$W = \prod_{i=1}^n [GS_i m_i + (1 - G)R]^{p_i}$$

We assume that  $\mathbf{p}$  and  $R$  are strictly environmental variables that do not evolve. However,  $G$ ,  $S$ , and  $\mathbf{m}$  are biological variables that depend partially on the value of traits under the evolutionary control of the plant.

In the above model, fitness,  $W$ , is independent of plant density. If seed yield is influenced by plant density then changes in dormancy and the distribution of fecundity over year types can provide mechanisms for avoiding overcrowding (Levin *et al.*, 1984) and sib competition (Hamilton and May, 1977; Comins, *et al.*, 1980). Here, by assuming that seed yield per germinating seed is independent of seedling and plant density, we are investigating the plants' use of dormancy and reproductive schedule as tools for bet-hedging against environmental unpredictability (Cohen, 1966; Venable and Brown, 1988); the selection forces are independent of plant density.

#### Germination fraction

The model lets seed dormancy evolve by permitting the germination fraction,  $G$ , to take on any

value from 0 to 1 (predictive dormancy could be introduced using the approach of Cohen (1967) and Leon (1985), see Venable (1989)). Actual mechanisms that permit the evolution of dormancy include changes in seed coat thickness, changes in the action of germination inhibitors (Mayer and Poljakoff-Meyber, 1982), and changes in the maturity of embryos at seed maturation (cf Amen, 1968). The germination fraction which yields highest fitness is less than one step greater than zero if the harmonic mean of  $m_i S_i$  is less than  $R$  and if the arithmetic mean of  $m_i S_i$  is greater than  $R$  (Cohen, 1966; Brown and Venable, 1986).

*Fecundity distribution*

Throughout, we refer to  $S$  as the fecundity distribution. We consider it to be an implicit function of specific evolutionarily adjustable traits that determine seed yield in different year types. The term can be read either as: (1) the vector of mean seed yields per germinating seed; or (2) a shorthand for all the traits,  $x$ , which determine mean seed yield in different year types,  $S(x)$ . As an example, consider the effect of leaf anatomy on the fecundity distribution of a population that experiences low and variable rainfall. As compared to mesophytic leaf anatomy, xerophytic traits such as low leaf surface–volume ratio, sunken stomata, and thick cuticle improve a plant’s ability to survive and reproduce in dry years. Yet in years when water is not limiting, these same traits result in lower fecundity than mesophytic traits due to lower photosynthetic efficiency and higher nutrient and energy costs.

We assume that the fecundity distribution,  $S$ , can evolve subject to the constraint that there are trade-offs among seed yields in different year types. This constraint can be thought of as a multidimensional fitness set,  $F(S) = 0$  (Fig. 2; Levins, 1968; Brown and Venable, 1986). We assume that there are diminishing returns to mean seed yield in a given year type from exaggerating a trait which promotes seed yield in that year type. Also, there are increasing losses

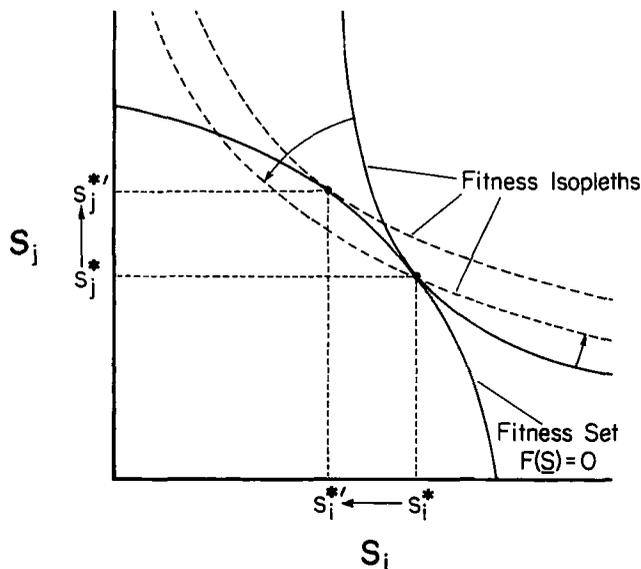


Figure 2. Graphical presentation of the evolutionary constraint on reproductive successes given germination in two different kinds of years,  $i$  and  $j$ . The arrows show the effect of increasing predation when the derivative of the slope of the fitness isopleth with respect to predation is positive, i.e.  $\partial g(\cdot)/\partial d > 0$ . The result is greater specialisation on unfavourable conditions ( $S_j^*$  increases) and less specialisation on favourable conditions ( $S_i^*$  decreases). This occurs, for example, when seed predation is strongly positively density dependent.

to mean seed yield in other year types as a result of exaggerating the trait. For example, each increment of mesophytic adaptations may generate less additional seed yield during wet years and result in greater losses of seed yield during dry years. (These convexity assumptions ensure a unique optimal fecundity distribution.)

### *Seed predation*

Seed predation may occur when seeds are still on the parent plant, when seeds have freshly fallen and remain exposed, or after seeds have worked their way into the substrate. Many natural history details of plant and seed consumer influence when predation is most severe. In the model, predation on freshly produced seeds, either prior to dispersal or on the soil, lowers  $m$ . Seeds that have survived to the beginning of the next growing season are more likely to have worked themselves into the soil seed bank; so, predation on buried seeds will have a greater effect on  $R$  than on  $m$ . It turns out that the  $R$  versus  $m$  distinction strongly affects the kinds of life history shifts favoured by seed predation. The selective consequences of changes in  $R$  were explored in Brown and Venable (1986). A reduction in  $R$  selects for an increased germination fraction and decreased specialisation on conditions pertaining to good years. Here we focus on the effects of seed predation on  $m$ .

A variety of insect, avian, and mammalian seed predators are known to harvest seeds directly from plants resulting in up to 100% of seed crop loss (Elliot, 1974; Janzen, 1975; Moore, 1978). Fresh seeds that have recently dispersed from the parent are often exposed and clumped; both exposure and clumping may increase seed predation risk (Brown *et al.*, 1975; Mittelbach and Gross, 1984; Clark and Clark, 1984). The diet of heteromyid rodents may reflect plants currently in seed rather than the composition of the soil seed bank (M'Closkey, 1983). Furthermore, position in the substrate can influence the seed's risk of predation. Beetles and ants only remove seeds which are lying on the surface while some mammals and birds will dig in the substrate for seeds (Brown *et al.*, 1975). However, increasing burial depth, and the hardness and coarseness of the substrate decreases the risk of predation by these mammals and birds (Price and Heinz, 1984). The preceding observations suggest that seed predation may frequently be more severe on fresh seeds (lowering  $m$ ) than on those of the between-year seed bank.

For  $i = 1, \dots, n$ , let:

$$m_i = (1 - dq_i)$$

where  $d$  is the intensity of predation and might reflect predator density or seed susceptibility to predation, and  $q_i$  is a weighting factor which allows us to set the predation rate higher or lower in any particular year type,  $i$ , depending on the peculiarities of the particular seed-predator interaction. Thus,  $dq_i$  is the per capita mortality rate of fresh seeds due to predation.

The predation rate may be constant regardless of year type (if all  $q_i$ 's are equal) or it may depend on year type, possibly in a density-dependent fashion. Also, predation rates may depend upon the seed yield of an individual plant within a given year type. For example, even if predation rates were higher in low seed production years, predation rates might be higher on high seed yielding individuals during such years (see Price and Jenkins, 1986). That is, we can let the per capita rate of predation in a given year type  $i$  be a function of the individual's mean seed yield in that year type (which can evolve), i.e.  $q_i(S_i)$ . Furthermore, the form of  $q_i(S_i)$  may vary among year types.

### **The evolution of dormancy**

The initial question is: for a given set of environmental parameters, including a particular

predation regime, and a given set of evolutionary constraints, what dormancy and fecundity distribution yield highest fitness? Formally, the problem is to maximise long term per capita growth rate

$$W = \prod_{i=1}^n \{[1 - dq_i(S_i)]GS_i + R(1 - G)\}^{p_i} \quad (1)$$

with respect to  $G$  and  $S$  subject to the constraints:  $F(S) = 0$ ,  $S_i \geq 0$ , and  $0 \leq G \leq 1$ .

To examine the selective effects of seed predation on dormancy, we assume that the optimal germination fraction,  $G^*$ , is on the open interval  $(0, 1)$ . If  $G^*$  is between 0 and 1 then it is found by taking the derivative of the fitness function (Equation 1) with respect of  $G$  and setting the derivative equal to zero (Brown and Venable, 1986). From this operation it follows that  $G^*$  satisfies:

$$h(\cdot) = \sum_{i=1}^n \frac{p_i[(1 - dq_i)S_i - R]}{[(1 - dq_i)GS_i + R(1 - G)]} = 0 \quad (2)$$

where  $(\cdot)$  is shorthand for  $(S, p, G, d, q)$ , and  $q = (q_1, \dots, q_n)$ .

The qualitative selection effects of changing the intensity of pre-dispersal or early post-dispersal seed predation on dormancy can be determined by taking the derivative of Equation 2 with respect to  $d$ :

$$\frac{\partial h(\cdot)}{\partial d} = \sum_{i=1}^n \frac{-R}{[(1 - dq_i)GS_i + R(1 - G)]^2} < 0 \quad (3)$$

At the old optimum, the slope of the fitness function with respect to  $G$  was 0. Since Equation 3 is always negative, increasing  $d$  results in a decrease of the slope of the fitness function, i.e.  $\partial W(\cdot)/\partial G < 0$ . Thus, starting at the old equilibrium, increasing  $d$  creates a new situation in which fitness increases if the germination fraction declines.

Seeds of an annual plant have two avenues for persisting to the next year. They may either remain dormant or germinate and gamble on seed production (see Fig. 1). Increasing the intensity of predation on fresh seeds,  $d$ , hurts the second avenue, and reduces the value of germinating relative to remaining dormant.

### Evolution of the fecundity distribution

We use the technique of Lagrange multipliers to maximise fitness,  $W(\cdot)$ , subject to the constraints on the fecundity distribution defined by  $F(S)$ . For this model, Brown and Venable (1986) showed that the fitness maximising fecundity distribution,  $S^*$ , is given by the point in the state space of seed yields in different year types where the fitness isopleth is tangent to the convex constraint function,  $F(S)$  (Fig. 2). A fitness isopleth is a line or surface representing the different values of  $S$  that have equal fitness, i.e.  $W(\cdot) = k$  where  $k$  is a constant. For all pairs of year types  $i, j = 1, \dots, n$ , the fitness maximising fecundity distribution  $S^*$ , satisfies:

$$\frac{-[\partial W(\cdot)/\partial S_i]}{[\partial W(\cdot)/\partial S_j]} = \frac{-[\partial F(S)/\partial S_i]}{[\partial F(S)/\partial S_j]} \quad (4)$$

where the left-hand side of Equation 4 is the slope of the fitness isopleth and the right-hand side is the slope of the constraint function in the state space of  $S_i$  versus  $S_j$  (Fig. 2).

The condition shown in Equation 4 provides a means for exploring the way selection will modify the fecundity distribution,  $\mathbf{S}$ , in response to changing parameter values. At the fitness maximum, the slope of the fitness isopleth is a function of all parameters but the slope of the constraint function depends only on  $\mathbf{S}$ . Thus, changing the value of a parameter other than  $\mathbf{S}$  effects the slope of the fitness isopleths only. Selection will favour changes in the fecundity distribution that re-establish equality (Equation 4).

Let  $g(\cdot)$  denote the slope of the fitness isopleths (the left-hand side of Equation 4). Taking the derivatives of the fitness function (Equation 1) with respect to  $S_i$  and  $S_j$  and substituting these into  $g(\cdot)$  yields, for all pairs  $i, j$ :

$$g(\cdot) = \frac{-p_i\{[1 - dq_i(S_i)] - dS_i[\partial q_i(S_i)/\partial S_i]\}\{[1 - dq_j(S_j)]GS_j + R(1 - G)\}}{p_j\{[1 - dq_j(S_j)] - dS_j[\partial q_j(S_j)/\partial S_j]\}\{[1 - dq_i(S_i)]GS_i + R(1 - G)\}} \quad (5)$$

In this general form of the equation, we have written  $q_i$  as an explicit function of  $S_i$  in recognition of the possibility that predation rates may depend on the mean seed yield of individual plants. If the derivative of  $g(\cdot)$  with respect to a parameter of interest is positive then the slopes of the fitness isopleths become less negative when the parameter is increased; i.e. all fitness isopleths rotate in a counter-clockwise direction (Fig. 2). This selects for a decrease of  $S_i^*$  relative to  $S_j^*$  (to re-establish equality (4)). If the derivative is negative, an increase of  $S_i^*$  relative to  $S_j^*$  is favoured.

In the Appendix, we determine the derivative of the slope of the fitness isopleth with respect to the intensity of predation on fresh seeds,  $\partial g(\cdot)/\partial d$ . In what follows, we use this result to determine the effects of specific predation regimes on the optimal distribution of fecundities among year types. We discuss the outcomes in terms of two year types,  $i$  and  $j$ , that are 'favourable' and 'unfavourable' in the sense that  $S_i^* > S_j^*$ . In a desert animal, for example, favourable might signify wet years and unfavourable, dry years.

### When seed yield of an individual does not influence predation rate

Consider the case where a change in the mean value of an individual's seed production,  $S_i$ , does not immediately change its seed predation rate,  $q_i$ , at least not until the new mutant becomes predominant in the population; i.e.  $\partial q_i/\partial S_i = 0$  for all  $i = 1, \dots, n$ . This means that the probability that a fresh seed is consumed is independent of a change in the number of seeds produced by the parent plant. This could occur in plant populations where the predators respond to the overall background population seed density (which can vary between years) as opposed to the local density of a particular plant's progeny. The biology underlying this situation might involve a predator with coarse grained responses to spatial variation in seed density or a plant with sufficient dispersal capabilities so that several seed progenies become mixed. If seeds of several plants become mixed, then even with DD seed predation, a change in the reproductive output of an individual may have negligible impact on total seed density and, thus, on the predation rate. Of course, the assumption of independence of predation intensity to a change in individual plant behaviour is met if the numerical or functional responses of a predator are not cued to seed density at all (density-independent predation).

For the case considered in this section, if there is no seed bank, changing predation intensity does not alter the fitness maximising fecundity distribution,  $\mathbf{S}^*$ . If, in Equation A.6 of the Appendix,  $G = 1$  and  $\partial q_i/\partial S_i = 0$  for all  $i = 1, \dots, n$ , then  $\partial g(\cdot)/\partial d = 0$ . Under the assumption of

no predator response to individual plant reproductive level, it is the existence of between-year dormancy ( $G < 1$ ) that encourages the plant to respond to seed predation by altering its reproductive schedule.

*Density-independent seed predation*

In the model, density-independent (DI) seed predation implies that  $q_1 = \dots = q_n = q$ . Substituting  $q = q_i = q_j$  into Equation A.6 gives:

$$\frac{\partial g(\cdot)}{\partial d} = \frac{p_i q R G (1 - G) (S_j - S_i)}{p_j [(1 - dq) G S_i + R(1 - G)]^2} < 0 \quad (6)$$

Because  $i$  is the favourable year type ( $S_i^* > S_j^*$ ), Equation 6 is always negative. Increasing the intensity of predation on fresh seeds results in an increase of  $S_i^*$  relative to  $S_j^*$ .

The existence of a between-year seed bank causes the population to specialise on favourable years in response to an increase in DI predation on fresh seeds. To understand why, remember that a seed bank annual has two paths for reaching the next year (dormancy and germination, Fig. 1), and that we are assuming that predation affects fresh seeds only (part of the germination path). Dormant seeds are a more important component of fitness during unfavourable years than during favourable years. Because we have assumed that predation only affects fresh seeds, increasing per capita seed predation harms fitness more in favourable years so that both fitness mean and variance are reduced. This results in compensating selection for an increased fitness mean and variance to restore a fitness-maximising balance between them (cf. Brown and Venable, 1986). This is achieved by increasing seed yield in favourable years at the expense of unfavourable years. Seed predation on fresh seeds of seed bank annuals selects for greater specialisation on favourable years with the results that reproduction is more clumped in time. As we shall see, however, DD seed predation can exaggerate or override this tendency.

*Density dependent seed predation*

As a result of the predators' functional and numerical responses, seed predation should, in general, be density-dependent (DD). There are examples of both positive (Wilson and Janzen, 1972; Platt, 1976; O'Dowd and Hay, 1980) and negative DD seed predation (Smith, 1970; Gardner, 1977; Ashton, 1979). In the model, positive DD implies  $q_i > q_j$  and negative DD implies  $q_i < q_j$ .

In Equation A.6 of the Appendix, when  $\partial q_i / \partial S_i = 0$  for all  $i = 1, \dots, n$ , (i.e. individual plant behaviour does not influence its seed predation rate) the derivative of the fitness isopleth with respect to the intensity of predation reduces to the sum of two terms. The sign of the first term is determined by  $(q_j S_j - q_i S_i)$  (this is Equation 6 in the DI case), and the sign of the second by  $(q_i - q_j)$  (which cancelled out in the DI case because  $q_i = q_j$ ). Because, in general, the total number of seeds consumed by predators will be greater in favourable years, we expect  $q_i S_i \geq q_j S_j$ . Hence, the first term should be negative. This term represents the pressure to specialise on favourable years in response to seed predation on fresh seeds (as in the DI case). The sign of the second term is determined by whether predation is positively or negatively DD. Seed predation selects for increased seed yield in year types that suffer a lower per seed predation rate. Thus, negative DD (higher predation in unfavourable years) reinforces the tendency of the plant to specialise on favourable years while positive DD dampens it.

Positive DD seed predation on fresh seeds can override the inherent tendency of seed bank annuals to specialise on favourable years in response to seed predation. Consider an extreme case of positive DD in which the seed consumers have a threshold seed density (Hubbell, 1980;

Brown, 1988) below which it is not profitable to forage. Assume that the foragers attempt to consume fresh seeds to this 'giving-up density' which is somewhat independent of year type. In other words, the number of seeds that survive seed predation in unfavourable years is approximately equal to the number that survive predation in favourable years, i.e.  $(1 - dq_i)S_i = (1 - dq_f)S_f$ . When this assumption is substituted into Equation A.6, the total derivative of the fitness isopleth with respect to predation intensity is positive. With a constant consumer giving up density, increased predation favours specialisation on unfavourable years. Conversely, predator satiation at high yields favours specialisation on favourable year types.

#### *Total evolutionary effect of changing the intensity of predation*

In Brown and Venable (1986), we showed that increasing dormancy selects for greater specialisation on favourable years and that increased specialisation on favourable years selects for greater dormancy. Here, we have shown that increasing the intensity of DI or negatively DD predation on fresh seeds will directly select for increased specialisation on favourable years and an increase in dormancy. Indirectly, the increased specialisation on favourable years further encourages increased dormancy, and, indirectly, the increased dormancy further encourages specialisation on favourable years. Thus, when the seed bank and the fecundity distribution both evolve they should show greater responses to changes in seed-predation intensity than if one or the other were fixed (Fig. 3).

If there is extreme positively DD predation on fresh seeds, the direct selective effects favour plant specialisation on unfavourable years and increased dormancy. In this case the direct and indirect effects of changing the intensity of predation are of opposite sign and the net effects are damped.

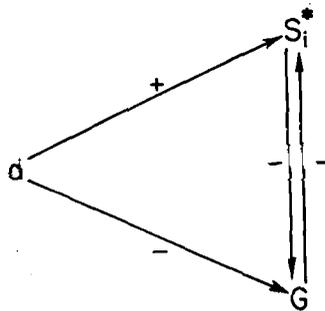


Figure 3. Summary of the direct and indirect selective effects of increasing the intensity of seed predation,  $d$ , on the germination fraction,  $G$ , and seed yield in favourable years,  $S_i$ , when seed predation is density-independent or negatively density-dependent. Under these circumstances the direct and indirect selective effects are reinforcing. Increasing predation intensity selects for increased specialisation on favourable years which in turn selects for decreased germination fraction. This reinforces the direct effect of seed predation on the germination fraction which is negative. If seed predation is strongly positively density dependent then the direct effect of seed predation is to reduce the specialisation on favourable years. The other effects remain the same and so the direct and indirect effects are damping.

#### **When seed yield of an individual influences predation rate**

The seed yield of an individual plant may influence its per seed rate of predation, particularly when predation occurs prior to dispersal. For example, Elliot (1974) found that the number of

seeds per cone influenced the probability that a given pine tree was foraged by squirrels. Bradford and Smith (1977) found that the number of seeds per fruit influenced, in opposite ways, the probability that a seed would be destroyed by insect or rodent predators. Clark and Clark (1984), in summarising evidence from tropical trees, found that seed predation under maternal plants is often density-dependent. Janzen (1969) concluded that smaller seed size should decrease the rate of predation suffered by a parent plant. In our model, when a change in an individual's expected seed yield changes the expected rate of seed predation on those seeds,  $q_i$  becomes a function of  $S_i$ ,  $q_i(S_i)$ .

If  $q_i$  is a function of  $S_i$ , between-year dormancy ( $G < 1$ ) is no longer required for predation on fresh seeds to have a selective effect on the reproductive schedule. To explore this evolutionary force for a variety of seed predation regimes we set  $G = 1$ . If  $G < 1$ , the evolutionary effects discussed in the previous section will dampen or reinforce the new selective effects explored here.

After substituting  $G = 1$  into Equation A.6, the sign of the derivative of the fitness isopleth with respect to the intensity of predation depends upon the sign of the sum of the following three terms:

$$S_i[1 - dq_j(S_j)]^2[\partial q_i(S_i)/\partial S_i] \quad (7a)$$

$$- S_j[1 - dq_i(S_i)]^2[\partial q_j(S_j)/\partial S_j] \quad (7b)$$

$$+ d^2 S_i S_j [q_j(S_j) - q_i(S_i)][\partial q_i(S_i)/\partial S_i][\partial q_j(S_j)/\partial S_j] \quad (7c)$$

We must now consider whether DD predation responds to high and low seed production years, high and low seed producing individuals within a year, or to different combinations of both. The change in per seed rate of predation in response to the level of seed production in different year types (the only density dependence considered in the previous section) will be called *among* year type DD. A change in per seed rate of predation in response to individual seed yield will be called *within* year type DD. Within year type DD is positive when  $\partial q_i(S_i)/\partial S_i > 0$  and is negative when  $\partial q_i(S_i)/\partial S_i < 0$ . Among year type DD is positive when  $q_i(S_i) > q_j(S_j)$  and is negative when  $q_i(S_i) < q_j(S_j)$ .

Expression 7a is a selective effect favouring specialisation on favourable years if increasing seed production of individuals in favourable years results in a lower per seed rate of predation (if within year type DD is negative in favourable years). Expression 7b is a selective effect favouring specialisation on unfavourable years if increasing seed production in unfavourable years results in a lower rate of predation (if within year type DD is negative in unfavourable years). Equation 7c is more complex. If within year type DD is positive or negative in both favourable and unfavourable year types (i.e. if  $\partial q_i(S_i)/\partial S_i$  and  $\partial q_j(S_j)/\partial S_j$  have the same sign), Equation 7c encourages specialisation on the year type with the greater per seed rate of predation (favourable years if among year type DD is positive, unfavourable years if negative). If  $\partial q_i(S_i)/\partial S_i$  and  $\partial q_j(S_j)/\partial S_j$  have opposite signs, Expression 7c encourages specialisation on the year type with the lower per seed rate of predation. Equation 7 combines all of these different effects to determine the net selective effect of seed predation on the fecundity distribution.

These selective effects are independent of the selective effects which require a seed bank, and only occur when the predation rate on fresh seeds is sensitive to changes in seed yield of individuals within specific year types. Thus, as the within year type DD approaches zero in all year types, Equations 7a-c all approach zero and the effect disappears. Any combination of within and among year type DD is feasible and the selective effects of increased seed predation depend upon the details (Table 1). In general, increased predation on fresh seeds favours specialisation away from year types in which the predation rate rises with seed yield and toward year types in which it is less sensitive or actually drops with increasing seed yield. If the predation

Table 1. Summary of how within and between year type DD influences the selective effects of increased seed predation on fresh seeds in the absence of a seed bank. The rows and columns give all combinations of DI, +DD, and -DD seed predation for within year type DD ('O' = DD, '+' = +DD, '-' = -DD). The entries indicate whether increased seed predation favours no change (O), an increase ( $\uparrow$ ), a decrease ( $\downarrow$ ), or ambiguous changes (A) in specialisation on favourable years,  $S_i$ . In the presence of a seed bank these selective effects of seed predation are in addition to those shown in Fig. 3.

	Within year type DD in unfavourable years								
	DI			+DD			-DD		
Between year type DD	O	+	-	O	+	-	O	+	-
DI	O	O	O	$\uparrow$	$\uparrow$	$\uparrow$	$\downarrow$	$\downarrow$	$\downarrow$
Within year type +DD	$\downarrow$	$\downarrow$	$\downarrow$	A	A	A	$\downarrow$	$\downarrow$	A
DD in favourable years									
-DD	$\uparrow$	$\uparrow$	$\uparrow$	$\uparrow$	A	$\uparrow$	A	A	A

rate in one year type is insensitive to yield, then Equation 7c and either Equations 7a or b disappear. The one remaining term favours specialisation away from the sensitive year type if the predation rate increases with individual seed yield or toward the sensitive year type if it decreases. If the predation rate rises with seed yield in one year type and drops in the other, Equations 7a and b will favour specialisation away from the year type with positive within year type DD and toward the year type with negative DD. Equation 7c will favour specialisation on favourable years if the among year type DD is negative, or favour specialisation on unfavourable years if it is positive.

Less intuitive effects of seed predation occur when the magnitude and sign of within year type DD is the same in both favourable and unfavourable years. In such cases, diverting seed yield from one year type to another no longer provides an obvious escape from predation. When within year type DD is negative, plants will specialise on favourable years if the among year type DD is positive (and vice versa if it is negative). When within year type DD is positive, the selective effects are ambiguous and depend on particular parameter settings because the net contribution from Equations 7a and 7b will be of opposite sign to the contribution from Equation 7c.

In summary, allowing seed predation rates to be sensitive to changes in seed set within years opens a rich array of evolutionary possibilities that are independent of the previously discussed effects that operate through the presence of a seed bank. We have explored these in the unambiguous case of no seed bank. Plants will specialise away from year types in which predation rate increases strongly with seed set and toward year types with less sensitivity or negative sensitivity, because such specialisation lowers the experienced predation rate. However, even if the within year type sensitivity to seed yield is the same in all year types, the fecundity distribution responds to increased predation. If a seed bank exists, we must consider the additional reinforcing or damping selective effects that operate through this avenue. To make this exploration more concrete we now consider several specific forms of predation on fresh seeds that have been discussed in the literature.

#### *Predator satiation: fixed quantity seed predation*

The most extreme form of predator satiation occurs when a predator can only consume a fixed number of seeds over the course of a growing season. To explore this extreme form of negatively within year type DD seed predation, we assume that predators harvest a fixed number of seeds per individual plant independently of year type.

A fixed number of seeds harvested per individual plant and per unit of predation intensity,  $d$ , implies that

$$q_i(S_i)S_i = c \quad (8)$$

for  $i = 1, \dots, n$ , where  $c$  is the constant amount of seeds harvested. Manipulating Equation 8 yields the following relationships

$$q_i(S_i) = c/S_i$$

$$[1 - dq_i(S_i)] = (S_i - dc)/S_i$$

$$\partial q_i(S_i)/\partial S_i = -c/S_i^2.$$

Substituting these relationships into Equations 7a–c shows that Equation 7b and 7c are positive, and that 7b dominates 7a. The derivative of the fitness isopleth with respect to the intensity of predation on fresh seeds has the same sign as  $(S_i - S_j)$ , thus  $\partial g(\cdot)/\partial d > 0$ . In an annual plant without a seed bank, increasing fixed quantity seed predation on fresh seeds will select for greater specialisation on unfavourable years. In contrast, the effect of negative among year type DD operating through a seed bank does favour specialisation on favourable years. Thus, if a seed bank exists, strict predator satiation creates effects operating through within year type predator sensitivity and the between year seed bank that are in opposition and we might expect little evolutionary change in such situations (Table 1).

### Masting

Masting is the temporal clumping of seed production by a population of plants in response to fruit or seed predation (Janzen, 1971). The concept of masting has generally been applied to perennials because presumably only they can afford to forgo seed yield for years at a time. According to the standard theory, masting provides two potential benefits. First, during high seed yield years (favourable years in our terminology) there may be predator satiation and thus negative DD seed predation (negative within year type DD in our terminology). Second, the numerical response of predators may be severely hampered by bottlenecks imposed by low seed yield years creating negative DD between years (our negative among year type DD). In the bottleneck of low seed yield years, predators are likely to consume efficiently everything they can, which may be a higher proportion of the seed yield of high yielding plants (positive within year type DD in unfavourable years). When these assumptions are substituted into Equation A.6, Equations 7a–c are all negative and all favour greater specialisation on favourable years (Table 1).

Thus, the classical scenario proposed to favour the evolution of masting in perennials also generates strong selection for specialisation on favourable years regardless of whether a seed bank is present or not. If a seed bank exists, the masting effect is further accentuated because among year type DD is negative.

What conditions produce the strongest selection for specialisation on unfavourable years, i.e. positive values for Equations 7a–c? During favourable years, within year type DD predation must be positive,  $\partial q_i(S_i)/\partial S_i > 0$ , and during unfavourable years it must be negative,  $\partial q_i(S_j)/\partial S_j < 0$ . Among year type density dependence must also be positive,  $q_i > q_j$ . With such a predation regime, increased seed predation will select for greater temporal uniformity of seed production (Table 1).

### Discussion

Increasing seed predation generates a set of selection dynamics that operate in a variety of ways

on dormancy and the fecundity distribution for annual plants. The predictions of the model, which depend on the selection regime, can be summarised in a dichotomous key (Table 2). For a specific consumer/seed relationship, this key indicates the direction of plant life-history evolution in response to increased seed predation and it also indicates the kinds of data that are required in order to make such predictions.

Although many possible outcomes exist, the net direction of selection on life histories is determined by four aspects of the natural history of the plant–animal interaction: (1) presence or absence of a seed bank; (2) whether fresh or buried seeds are most affected by predators; (3) presence and type of DD seed predation; and (4) the grain of predator response to changes in seed yield (individual versus population).

The presence or absence of a seed bank has been shown here and elsewhere (Templeton and Levin, 1979; Brown and Venable, 1986) to be more than just an isolated trait aiding in population persistence. It provides a basis for altered selection dynamics on other aspects of life history such as the year type specialisation generated by the present model. The relative extent of damage to fresh seeds (either pre-dispersal or on the soil surface) versus buried seeds depends on predator behaviour, plant phenology, and habitat characteristics. While the studies cited herein suggest that most predators preferentially remove fresh seeds, good case studies are rare and it is currently difficult to make generalisations for different kinds of seeds and predators. The same can be said for density dependence. With some notable exceptions, the presence and nature of DD are not reported in studies of seed predation and it is currently difficult to make generalisations for different kinds of predators and plants. Furthermore, different selective effects result if predators respond to local variations in seed density than if behavioural or numerical responses are cued to the whole population's seed density. A rich set of poorly understood predator and plant behaviours determines this predator sensitivity to variation in seed yield. These include dispersal distance of seeds, predator's home range and search behaviour, spatial scale of predator's numerical response, and degree of predator specialisation on a particular plant species. Because the model's predictions depend on the details of plant and predator natural history, empirical and theoretical advances will be interdependent in this area of research. We urge researchers to carefully consider the aforementioned details of plant and predator behaviour in studies of seed predation.

In the model, several predation regimes created selective pressures favouring temporal clumping of seed production. This effect is similar to the classic concept of masting. Masting is normally considered to be an evolutionary response to predator satiation, i.e. negative DD (among years) in the per capita seed predation rate due to the inability of a predator's numerical or functional response to track sudden increases in seed density (Janzen, 1971). Masting is assumed to evolve only in perennials which can live long enough to cause predator population bottlenecks by storing energy and nutrients and releasing them in occasional large bursts of synchronised reproduction (Bulmer, 1977). In the model, the presence of the seed bank ('perenniality'), negatively DD predation among years, negatively DD predation between individuals within favourable years, or positively DD predation between individuals within unfavourable years select for bursts of reproduction due to specialisation on a subset of favourable conditions. Interestingly, the 'perenniality' of seed bank annuals promotes a masting effect even in the absence of predator satiation (or in the absence of DD predation of any kind). Furthermore, if predator satiation is occurring, the masting effect can evolve in an annual plant without a seed bank. This model extends the range of mechanisms by which reproductive clumping may evolve in response to seed predation.

In the model, the dormancy fraction, and the fecundity distribution evolve to mitigate the negative effects of seed predators. These are not the sorts of anti-predator adaptations usually

Table 2. Dichotomous key of selective effects of seed predation on the fecundity distribution.

- 
- 1a Predation rate is not sensitive to the seed yield of individual plants.
- 2a The plant does not produce a seed bank: regardless of the presence or absence of DD, seed predation will not select for changes in the fecundity distribution.
- 2b The plant does produce a seed bank.
- 3a Predation high on buried seeds (on the inter-year seed bank): increased seed predation favours a decreased seed bank and more specialisation on unfavourable years.
- 3b Predation high on fresh seeds: increased seed predation favours an increased seed bank.
- 4a Seed predation is either DI or negatively DD: increased seed predation favours specialisation on favourable years.
- 4b Seed predation is positively DD: increased seed predation favours specialisation on unfavourable years if the DD is sufficiently strong.
- 1b Predation rate is sensitive to the seed yield of individual plants.
- 5a The sensitivity to seed yield of individuals is different in favourable and unfavourable year types.
- 6a Only one year type is sensitive.
- 7a DD in the sensitive year type is positive.
- 8a No seed bank: specialise on the insensitive year type.
- 9a Among year type DD is negative or zero: the presence of a seed bank creates a selective effect favouring specialisation on favourable years (4a).
- 9b Among year type DD is sufficiently positive: the seed bank effect favours specialisation on unfavourable years (4b). This reinforces the effect described in 8a if the insensitive year type is favourable years but dampens the effect if it is unfavourable years.
- 7b DD in the sensitive year type is negative.
- 10a Species with no seed bank: specialise on the sensitive year type.
- 10b Seed bank exists
- 11a Among year type DD is negative or zero: the presence of a seed bank creates a selective effect favouring specialisation on favourable years (4a). This reinforces the effect described in 10a if the sensitive year type is favourable years but dampens the effect if it is unfavourable years.
- 11b Among year type DD is sufficiently positive: the seed bank effect favours specialisation on unfavourable years (4b).
- 6b Seed predation rate is sensitive to individual seed yield in both favourable and unfavourable years, but the DD is of opposite sign in the different year types.
- 12a Within year type DD is negative in favourable years and positive in unfavourable years.
- 13a Among year type DD is negative: specialise on favourable years. If there is a seed bank that plants should specialise even more (4a).
- 13b Among year type DD is positive: the selective effect is ambiguous. Adding a seed bank shifts the equilibrium toward unfavourable years if the between year DD is sufficiently strong (4b).
- 12b Within year type DD is positive in favourable years and negative in unfavourable years.
- 14a Among year type DD is positive: specialise on unfavourable years. If there is a seed bank and the among year DD is sufficiently positive the specialisation on unfavourable years will be accentuated (4b).
- 14b Among year type DD is negative: the selective effect of seed predation is ambiguous. If there is a seed bank the equilibrium will be shifted towards favourable years (4a).
- 5b The sensitivity to seed yield of individuals is similar in both favourable and unfavourable year types.

- 15a Among year type DD is positive.
    - 16a Within year type DD is negative: seed predation favours specialisation on favourable years. If there is a seed bank this effect will be damped (4b).
    - 16b Within year type DD is positive: the selective effect of seed predation is ambiguous. If there is a seed bank the equilibrium will be shifted towards unfavourable years (4b).
  - 15b The among year type DD is negative.
    - 17a If the within year type DD is negative: seed predation favours specialisation on unfavourable years. If there is a seed bank this effect will be damped (4a).
    - 17b If the within year type DD is positive: seed predation has ambiguous selective effects.
- 

discussed in the literature (e.g. spines, defensive chemistry, or thick seed coats). While these more typical adaptations could be considered in the model's framework, they influence fitness in a fundamentally different fashion than the traits we have considered. Adjusting the dormancy fraction or the fecundity distribution involves a trade-off between fitness in different year types. Direct anti-predator adaptations such as toxic chemicals and protective tissue probably benefit the plant by reducing the rate of seed predation in all year types and cost the plant by reducing growth and thus seed yield in all year types. Independently of temporal variation, these direct adaptations to seed predators involve a trade-off between the per seed rate of predation and seed yield. The rather straightforward prediction would be that increasing predation selects for lower seed yield and greater anti-predator adaptations.

The model can be used to explore other issues besides seed predation. Other sources of seed mortality such as competition, drought stress, temperature stress, and their dependencies on density can be explored. Yet, the great advantage of the dormant seed as a life history stage is its resistance to most forms of biotic and abiotic hazards. By considering seed predation, we have perhaps isolated a critical selective factor. In a broader context, the seed mortality parameter,  $m = (1 - dq)$ , could be redefined to be any other mortality component in the germination pathway around the yearly cycle (Fig. 1). If this is done, the results we obtained by varying  $d$  and  $q$  could be reinterpreted in terms of, say, seedling establishment and its possible forms of DD. Likewise, the model's results may be applicable to the evolution of other organisms that have discrete generations and a persistent dormant stage. Regardless of the specific biological context to which the model is applied, complex and predictable life-history phenomena can be generated from a simple annual life cycle when several aspects of the life history are allowed to co-adapt in a variable environment.

### Acknowledgements

This paper grew from a presentation given by the second author at a symposium on Seed Producers and Seed Consumers in Arid Environments held at UCLA in May 1985. We are grateful to the insightful comments of P. R. Grant, D. Lloyd, S. Pacala, J. Powlesland and an anonymous reviewer. We thank the late Don Thompson for drafting the figures and Angie Valenzuela for typing several drafts of the manuscript. This work was supported by NSF grant BSR-8516971 and by the Mitrani Center for Desert Ecology of the Blaustein Institute, Ben-Gurion University, Sede Boqer Campus, Israel. This is publication #100 of the Mitrani Center.

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**Appendix**

The slope of the fitness isopleth is given by Equation 5. To take its derivative with respect to the intensity of predation,  $d$ , it is helpful to define the following:

$$A(\cdot) = [(1 - dq_i(S_i))GS_i + R(1 - G)] \quad (\text{A.1})$$

$$B(\cdot) = [(1 - dq_j(S_j))GS_j + R(1 - G)] \quad (\text{A.2})$$

$$C(\cdot) = [(1 - dq_i(S_i)) - dS_i(\partial q_i(S_i)/\partial S_i)] \quad (\text{A.3})$$

$$D(\cdot) = [(1 - dq_j(S_j)) - dS_j(\partial q_j(S_j)/\partial S_j)] \quad (\text{A.4})$$

Substituting Equation A.1–A.4 into 5 yields:

$$g(\cdot) = \frac{-p_i C(\cdot) B(\cdot)}{p_j D(\cdot) A(\cdot)} \quad (\text{A.5})$$

To calculate  $\partial g(\cdot)/\partial d$  we first take the derivative of A.5 with respect to  $d$ . Then, the derivatives of A.1–A.4 with respect to  $d$  are substituted. The resulting expression reduces to:

$$\frac{\partial g(\cdot)}{\partial d} = \frac{p_i p_j}{[p_j D(\cdot) A(\cdot)]^2} \cdot \left\{ A(\cdot) B(\cdot) \left[ (q_i(S_i) - q_j(S_j)) + \left( S_i \frac{\partial q_i(S_i)}{\partial S_i} - S_j \frac{\partial q_j(S_j)}{\partial S_j} \right) \right] + C(\cdot) D(\cdot) [G^2 S_i S_j (q_j(S_j) - q_i(S_i)) + RG(1-G) (S_j q_j(S_j) - S_i q_i(S_i))] \right\} \quad (\text{A.6})$$