

## SIZE-NUMBER TRADE-OFFS AND THE VARIATION OF SEED SIZE WITH PLANT RESOURCE STATUS

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*Abstract.*—I develop a general treatment of the effects of parental resource status on optimal offspring size. The model shows that even when there is a resource trade-off between size and number of offspring within individuals, positive correlations between size and number may occur among individuals due to individual variation in resources. Such positive correlations imply that parental resource status affects the fitness-maximizing offspring size, in contrast to the predictions of the standard Smith-Fretwell model. I show that parental resource status affects the fitness-maximizing offspring size whenever the size-number fitness function is nonhomogeneous in offspring number. This condition implies some sort of density-dependent interactions among offspring, although it is possible to have either positive or negative sib interactions in fitness functions that are homogeneous in offspring number. In the latter case offspring size should be insensitive to parental resource status. I explore several cases including linear (Smith-Fretwell), nonlinear but homogeneous, and nonhomogeneous seed-number functions with independent size and number effects, as well as models with interacting offspring size-number effects. I briefly review the plant literature on offspring density dependence and seed-size variation with parental resource status. Some suggestions for testing the ideas with plants and some alternative explanations of positive seed-size/plant-size and seed-size/seed-number correlations are discussed.

Seed size varies tremendously among plant species and was investigated early by plant ecologists as a life-history trait of obvious importance (Salisbury 1942). Open or mesic habitats tend to have species with smaller seeds than low-light or arid habitats (Salisbury 1942, 1974; Baker 1972; Foster and Janson 1985; Mazer 1989). Studies of individual species often indicate that, under competitive conditions, large seed size confers an advantage of higher seedling survival (Weller 1985; Marshall et al. 1986) or growth (Howe and Richter 1982; Weis 1982; Stanton 1984), greater success in emerging from deep burial (Weller 1985), and increases in various components of reproductive success (Stanton 1984; Wulff 1986; Mazer 1987). Seed-size variation within species has traditionally been regarded as low (Harper et al. 1970), although in recent years increased attention has been given to quantifying and mechanistically explaining intraspecific variation (see reviews in Haig and Westoby [1988] and Silvertown [1989]). The standard theoretical treatment of offspring size and number is that of Smith and Fretwell (1974), which has been extended in a number of directions in the plant literature (Temme 1986; Lloyd 1987; McGinley et al. 1987; Haig and Westoby 1988; Venable and Brown 1988). These models address the apportionment of resources between two fitness components: seed size and seed number.

Here I address the importance of individual plant size or the size of the resource pool available for seed production as a determinant of the fitness consequences of offspring size and number. The model extends and generalizes two others (Parker and Begon 1986; McGinley 1989) that also considered the sensitivity of offspring size to resource status. Plant populations usually consist of individuals of widely varying sizes, and models of their ecology and evolution can often gain in realism and insight by explicitly taking this into account (cf. Ebenman and Persson 1988).

NEUTRAL AND POSITIVE CORRELATIONS OF SEED SIZE  
AND SEED NUMBER WITHIN SPECIES

Since the standard models assume a trade-off between offspring size and number, plant ecologists have often looked for empirical evidence of such trade-offs. While negative correlations are sometimes found among populations or species, intraspecific correlations of seed size and number have often been found to be neutral or positive (Schaal 1980; Marshall et al. 1986; Mazer 1987; Michaels et al. 1988; Winn 1988). Data of this sort are frequently interpreted as a violation of the trade-off assumption in models of size-number evolution (Michaels et al. 1988). Such negative evidence sometimes forms part of more general arguments questioning the role of continuing selection acting on seed size (Silvertown 1989). But before rejecting the trade-off idea and, by implication, evolutionary-ecological models of size-number evolution, we must ask whether these empirical observations were made under conditions in which a trade-off would be expected to be revealed. In part because of their iterative, modular growth, individual plants are notoriously variable in size and in the amount of resources available for seed production. It is not unusual to find individuals that vary by three to five orders of magnitude in size, even in the same population (Harper 1977). Offspring size-number models address the issue of how to partition a given amount of resources. Variation in a third variable, such as plant size or the size of the reproductive resource pool, could be strong enough to mask any negative correlation between seed size and number for a given amount of resources (fig. 1a; and see van Noordwijk and de Jong [1986] for a lucid discussion of the related issue of trade-offs between growth and reproduction). A clear case of this masking phenomenon was documented by Maddox and Antonovics (1983), who carefully measured many aspects of plant size through time and applied a path analysis to explain variation in seed size and number. For *Plantago aristata* the simple correlation between seed size and number per plant was positive, yet the relationship was negative when the effects of plant size were partialled out via the path analysis.

While the distinction between genetic and environmental correlations is clearly relevant to this issue, even genetic correlations of seed size and number can be confounded by genetic variation in plant size or resource-garnering ability unless these are carefully accounted for. After all, the expectation of a negative genetic correlation is still based on an allocational constraint for a given amount of resources.

We might conclude from this discussion that the absence of negative correla-

$$s \cdot n = r \Rightarrow \ln n = -\ln s + \ln r$$

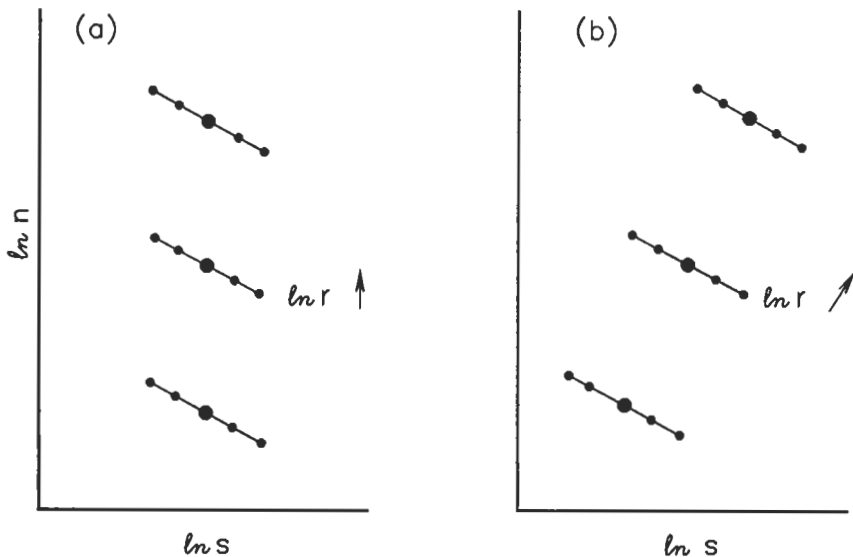


FIG. 1.—*a*, Correlation between offspring size and offspring number when resource status varies more than offspring size. Variation in resource status,  $r$ , can obscure a trade-off between offspring size,  $s$ , and number,  $n$ , for a given amount of resources, especially if resource status varies more than offspring size. *b*, Correlation between offspring size and offspring number when offspring size increases with resource status. Variation in resource status may result in a positive correlation between offspring size and number, even in the presence of a trade-off for a given amount of resources, if mean offspring size increases with resource status.

tions in the empirical literature does not necessarily invalidate the trade-off assumption of size-number models (cf. Haig 1989). Yet, one troublesome detail remains: a positive correlation between seed size and number requires seed size to also be positively dependent on resource status (fig. 1*b*). The basic Smith-Fretwell model suggests that this should not be so (Smith and Fretwell 1974; Lloyd 1987; Haig and Westoby 1988). However, a number of species (though by no means all) show clear patterns of larger seeds being produced on plants with more resources (e.g., corn [Stickler and Pauli 1961], sorghum [Hanway 1969], *Rumex crispus* [Maun and Cavers 1971], *Senecio sylvaticus* [van Andel and Vera 1977], *Catalpa speciosa* [Stephenson 1980], *Asclepias syriaca* [Willson and Price 1980], *Plantago aristata* [Maddox and Antonovics 1983], *Aster acuminatus* [Pitelka et al. 1983], *Sesbania vesicaria* [Marshall et al. 1986], *Raphanus raphanistrum* [Mazer 1987], and *Prunella vulgaris* [Winn and Werner 1987]).

#### SIB INTERACTIONS

It turns out, as will be explained below, that the prediction of seed-size constancy in the Smith-Fretwell model derives from the assumption that parental

fitness is a linear or, more generally, a homogeneous function of offspring number. How reasonable is this assumption for plants? A high concentration of seeds beneath the maternal plant and diminishing numbers of seeds with distance is the commonly observed dispersal pattern in plants (Levin and Kerster 1974; Harper 1977). Such limited dispersal capacities suggest that sib interactions are frequent; these may lead to situations favoring a shift in seed size with plant size, as will be explained below. Density-dependent reduction of survival or growth of seeds or seedlings clumped under maternal plants have been frequently documented and may be due to competition, predation, or pathogens (Platt 1976; Augspurger 1983; examples for tropical woody plants are reviewed in Clark and Clark 1984).

The opposite effect, an accelerating fitness return for increased seed number, is theoretically possible, based on either local predator satiation or a disproportionate increase in successful seed dispersal for larger seed crops. Predator satiation has usually been investigated on a population rather than individual level (Silvertown 1980), although some evidence suggests that individuals with larger seed crops or more seeds per fruit may occasionally have a greater proportion of seeds escape from predators (Willson 1983, pp. 205–208). Most studies looking for disproportionate dispersal success (per seed) of larger fruit crops have not found it (Howe and De Steven 1979; Howe and vande Kerckhove 1979; Howe 1980, 1981; Moore and Willson 1982; Denslow 1987). Thus, the available empirical evidence seems to suggest that sib interactions are typically negative, although positive interactions may sometimes occur.

#### THE MODEL

In what follows, the Smith-Fretwell model is modified to account explicitly for the effects of variation in resource availability and to relax the assumption of linear fitness returns from offspring number. In the Smith-Fretwell model the fitness of a parent is given by  $w = n \cdot f(s)$ , where  $n$  is the offspring number and  $f(s)$  is the per capita offspring fitness, which is considered to be a function of offspring size,  $s$ . Positive or negative sib interactions can be incorporated into the Smith-Fretwell model by letting fitness be some more general function of seed number,  $g(n)$ . If the number component of fitness also varies with seed size, fitness could be described as a general function of seed size and number,  $h(s, n)$ .

Assume that reproduction is limited by resources and that there are no fixed costs that are not proportional to seed size or number. Then a constraint equation,  $s \cdot n = r$ , describes the trade-off between offspring size and offspring number;  $r$  is the amount of resources available for seed production (which I will call "resource availability" in this article). Resource availability may vary considerably among individuals within populations either genetically or environmentally, which would potentially mask the implied size-number trade-off.

The problem is to find the size-number strategy that maximizes  $w = g(n) \cdot f(s)$ , or, more generally,  $w = h(s, n)$ , subject to  $s \cdot n = r$ , and to see how it varies with resource availability. It turns out that many of the interesting properties of offspring size-number models are determined by the consequences of proportional changes in seed size, number, resources, and fitness. Since any strategy that maximizes  $w$  will also maximize  $\ln(w)$ , the problem can be converted to

logarithms as follows: maximize  $\ln(w) = \ln(h(\ln(s), \ln(n)))$ , subject to  $\ln(s) + \ln(n) = \ln(r)$ . For shorthand I will use uppercase letters to refer to the logarithm of variables or functions that are normally represented by lowercase letters. According to this notational convention, the problem is restated as follows: maximize  $W = H(S, N)$ , subject to  $S + N = R$ .

The technique of Lagrange multipliers is useful for maximization subject to an equality constraint such as  $S + N = R$ . It proves especially useful for examining the consequences of variation in resource levels because it treats the resource constraint explicitly. The technique involves writing down a Lagrange function, which brings the constraint into the equation to be maximized (Chiang 1984). In the present case the Lagrange function is

$$L = H(S, N) - \lambda(S + N - R). \quad (1)$$

If we can somehow make sure that the resource constraint is satisfied (i.e., that  $S + N = R$ ), then the last term of equation (1) vanishes and  $L$  equals the original expression for fitness,  $H(S, N)$ . Also, since the constraint will be satisfied, any fitness maxima will be constrained maxima. The way to make the last term of the Lagrange function vanish is to treat  $\lambda$  (which is called the "Lagrange multiplier") as an additional variable and simultaneously solve the zero derivatives of  $L$  with respect to  $S$ ,  $N$ , and  $\lambda$ :

$$\frac{\partial L}{\partial S} = \frac{\partial H(S, N)}{\partial S} - \lambda = 0, \quad (2)$$

$$\frac{\partial L}{\partial N} = \frac{\partial H(S, N)}{\partial N} - \lambda = 0, \quad (3)$$

and

$$\frac{\partial L}{\partial \lambda} = S + N - R = 0. \quad (4)$$

Note that the last zero derivative guarantees that the constraint is satisfied. The simultaneous solution to these equations gives constrained maxima (assuming appropriate sufficiency conditions are satisfied to exclude the possibility of a minimum or saddle point). The sufficiency condition ensuring a maximum is

$$\frac{\partial^2 H(S^*, N^*)}{\partial S^2} - \frac{\partial^2 H(S^*, N^*)}{\partial S \partial N} + \frac{\partial^2 H(S^*, N^*)}{\partial N^2} - \frac{\partial^2 H(S^*, N^*)}{\partial N \partial S} < 0, \quad (5)$$

where  $S^*$  and  $N^*$  are the fitness-maximizing values of  $S$  and  $N$  (see Chiang 1984, pp. 381–386, on sufficiency conditions for extremes in more than one variable). Thus, by bringing the constraint into  $L$  and treating  $\lambda$  as an extra variable, we can find the size-number strategy that maximizes fitness subject to the resource constraint.

Solving the first two simultaneous equations for  $\lambda$  and setting the two resulting expressions equal to one another shows that at the fitness maximum

$$\frac{\partial H(S^*, N^*)}{\partial N} = \frac{\partial H(S^*, N^*)}{\partial S}. \quad (6)$$

This generalized Smith-Fretwell model, equation (6), is an equal-marginal-advantage model (*sensu* Lloyd 1988; Lloyd and Venable 1992). It states that, at the fitness maximum, the marginal fitness advantage of seed number equals the marginal fitness advantage of seed size when everything is measured as proportional changes (i.e., logarithms). In the rest of the article I will call the left and right sides of equation (6) the proportional marginal advantages of seed number and seed size, respectively. The logarithmic transformation of the resource-constraint equation states that proportional changes in size and number balance each other (e.g., for a given amount of resources, a 1% increase in seed size requires a 1% decrease in seed number). The equal marginal advantage equation, (6), can be restated roughly as follows: Fitness is maximized when the percentage increase in fitness resulting from a 1% increase in seed size equals the percentage increase in fitness resulting from a 1% increase in seed number. If these are not equal, fitness could be increased by shifting resources to whichever reproductive component (size or number) gave the higher percentage increase in fitness.

To see if and when seed size should vary with resource availability we can calculate  $\partial S^*/\partial R$ . This is done by recognizing that the fitness-maximizing seed size and number in equation (6) are implicit functions of resource availability and by taking the derivatives of both sides of equation (6) with respect to resource availability:

$$\frac{\partial^2 H(S^*(R), N^*(R))}{\partial N^2} \cdot \frac{\partial N^*(R)}{\partial R} + \frac{\partial^2 H(S^*(R), N^*(R))}{\partial N \partial S} \cdot \frac{\partial S^*(R)}{\partial R} = \frac{\partial^2 H(S^*(R), N^*(R))}{\partial S \partial N} \cdot \frac{\partial N^*(R)}{\partial R} + \frac{\partial^2 H(S^*(R), N^*(R))}{\partial S^2} \cdot \frac{\partial S^*(R)}{\partial R}. \quad (7)$$

From the constraint equation,  $N^*(R) = R - S^*(R)$ , so  $\partial N^*(R)/\partial R = 1 - \partial S^*(R)/\partial R$ . Substituting this into equation (7), letting the notation  $H(\cdot)$  stand for  $H(S^*(R), N^*(R))$ , and solving for  $\partial S^*(R)/\partial R$  give

$$\frac{\partial S^*(R)}{\partial R} = \frac{1}{1 + A}; \quad A = \frac{\frac{\partial^2 H(\cdot)}{\partial S^2} - \frac{\partial^2 H(\cdot)}{\partial S \partial N}}{\frac{\partial^2 H(\cdot)}{\partial N^2} - \frac{\partial^2 H(\cdot)}{\partial N \partial S}}. \quad (8)$$

This is the general analytical formula that tells how the fitness-maximizing seed size changes with plant resource availability for any offspring size-number fitness equation,  $w = h(s, n)$ . The magnitude of  $\partial S^*(R)/\partial R$  is determined by  $A$ , and the fitness-maximizing seed size will not change with resource availability if the denominator of  $A$  is zero. Notice that the numerator of  $A$  equals the first two terms of equation (5), the sufficiency conditions that guarantee a fitness maximum, while the denominator equals the other two terms. Thus, there are some restrictions on the values  $A$  can take if  $S^*$  is to be a fitness maximum. Either the numerator or the denominator must be negative, and if they are of opposite sign, the negative term must predominate (i.e., numerator + denominator < 0).

The numerator of  $A$  is the sensitivity of the proportional marginal advantage of seed size to changes in seed size and number. The denominator is the sensitiv-

ity of the proportional marginal advantage of seed number to changes in seed size and number. In other words, the effect that increasing resource availability has on the fitness-maximizing seed size depends on how rapidly the left and right sides of the equal marginal advantage equation, (6), change with a change in allocation to seed size or seed number.

### *Likely Outcomes*

The analysis has been done without stipulating specific forms of the function relating fitness to seed size and number; thus, the answers are general and phrased in terms of the shapes (signs of derivatives) of the fitness curves. Likely outcomes can best be seen by considering some specific situations. Unfortunately, it is difficult to empirically establish the shapes of fitness gain curves. McGinley et al. (1987) cite a number of studies relating early life-history traits to seed size that suggest that fitness typically increases with seed size but with diminishing gains. It is reasonable to expect that a minimum seed size is required for any fitness and that, beyond the minimum, fitness increases with seed size, but not indefinitely. Such seed-size fitness curves have proportional marginal advantages that decline with increasing seed size ( $\partial^2 F(S^*)/\partial S^2 < 0$ ). If sib interactions are typically negative, as the empirical evidence seems to suggest, then we expect either constant or declining proportional marginal advantages of seed number as well. As can be seen from equation (8), under these conditions the model predicts either constant or increasing seed size with improved resource availability (i.e., the two patterns commonly observed in nature). This point is elaborated below.

### *The Smith-Fretwell Model: Linear Seed-Number Functions with Independent Size and Number Effects*

In the standard Smith-Fretwell model the effects of size and number on fitness are independent, and number has a linear effect on fitness ( $w = n \cdot f(s)$ ). In logarithms, the fitness equation is  $H(S, N) = N + F(S)$ , and the equal marginal advantage equation, (6), is  $\partial H(S^*, N^*)/\partial S = 1$ . The proportional marginal advantage of seed number always equals one, so that a 1% increase in seed number (with seed size held constant) always results in a 1% increase in fitness. Thus, following equation (6), the standard Smith-Fretwell model predicts that the fitness-maximizing seed size should be the one for which the proportional marginal advantage of seed size equals one. Rewriting this in the more familiar arithmetic form of the marginal advantages gives

$$\frac{s^* \left( \frac{\partial f(s^*)}{\partial s} \right)}{f(s^*)} = 1$$

$$\Rightarrow \frac{f(s^*)}{s^*} = \frac{\partial f(s^*)}{\partial s}. \quad (9)$$

This gives the standard graphic interpretation of the basic Smith-Fretwell model when plotted on a graph of per capita seed fitness versus seed size (fig. 2a): at the fitness-maximizing seed size,  $s^*$ , the slope of the seed-size fitness curve equals

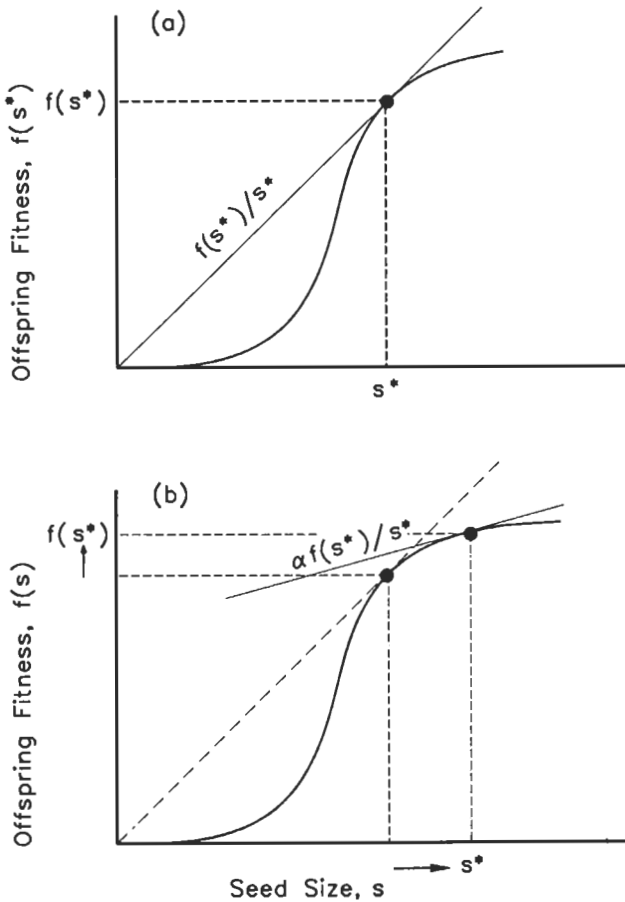


FIG. 2.—*a*, Fitness-maximizing offspring size for the Smith-Fretwell model. In the standard Smith-Fretwell model the fitness-maximizing offspring size is found where the average offspring fitness per unit investment equals the marginal fitness advantage of seed size. *b*, Fitness-maximizing offspring size for a nonlinear homogeneous model of offspring size and number. If average offspring fitness declines with the number of siblings, the fitness-maximizing offspring size is found at a point where the marginal advantage of offspring size is less than the average offspring fitness per unit investment. Since the marginal advantage of seed size declines with seed size, this point corresponds to a larger seed size than that for the standard Smith-Fretwell model.

the slope of a straight line through the origin. For this value of  $s$  to give a fitness maximum, the second derivative of  $f(s)$  must be negative (i.e., there must be a decelerating fitness gain from increasing seed size).

For present purposes the important result is that, as long as fitness is a linear function of seed number (as is assumed in the Smith-Fretwell model), the fitness-maximizing seed size does not depend on the amount of resources available for seed production. In terms of equation (8), the cross-partial derivatives are zero because seed-size and seed-number effects are independent. Since  $\partial H(\cdot)/$

$\partial N$  is constant,  $\partial^2 H(\cdot)/\partial N^2 = 0$  as well. Thus, the denominator of  $A$  equals zero. As the denominator of  $A$  approaches zero,  $\partial S^*(R)/\partial R$  approaches zero, so the fitness-maximizing seed size is insensitive to variation in resource availability.

*Homogeneous Nonlinear Seed-Number Functions  
with Independent Size and Number Effects*

Actually, although linearity of fitness with respect to seed number will always result in a prediction of constant seed size in response to variation in resource availability, certain nonlinear forms for the seed-number fitness function also give this result. Technically, whenever  $h(s, n)$  is a homogeneous function in  $n$ ,  $\partial H(\cdot)/\partial N$  will be a constant, and fitness-maximizing seed size will not vary with resource availability. A function is said to be homogeneous of degree  $c$  if multiplication of each of its independent variables by an arbitrary constant  $j$  will alter the value of the function by the proportion  $j^c$ , that is, if  $g(jx_1, \dots, jx_p) = j^c \cdot g(x_1, \dots, x_p)$  (Chiang 1984). A function is said to be homogeneous of degree  $c$  in a particular variable if multiplication of that variable by an arbitrary constant alters the value of the function by the proportion  $j^c$ , for example, if  $h(s, j \cdot n) = j^c \cdot h(s, n)$ . This last condition can be written logarithmically as  $H(S, J + N) = cJ + H(S, N)$ . Thus, if a fitness equation is homogeneous in  $n$ , it directly follows that  $\partial H(S, J + N)/\partial N = \partial H(S, N)/\partial N$  and  $\partial H(S, J + N)/\partial S = \partial H(S, N)/\partial S$ . Since  $J$  is an arbitrary constant, the proportional marginal advantage of number is a constant, and  $\partial^2 H(\cdot)/\partial N^2$  and  $\partial^2 H(\cdot)/\partial S \partial N$  both equal zero. Thus, homogeneity in  $n$  implies that the denominator of  $A$  equals zero and  $\partial S^*/\partial R = 0$ .

For example, consider what happens if sibling density influences fitness according to a power equation so that  $h(s, n) = bn^\alpha f(s)$ , where  $\alpha$  is a constant describing the nonlinearity of the seed-number effect on fitness, and  $b$  is a constant scaling  $n^\alpha$  to units of fitness. Notice that the fitness equation is homogeneous in  $n$  since  $h(s, j \cdot n) = b(j \cdot n)^\alpha f(s) = j^\alpha bn^\alpha f(s) = j^\alpha \cdot h(s, n)$ . In logarithms the fitness equation becomes  $H(S, N) = B + \alpha N + F(S)$ . The number derivatives are  $\partial H(\cdot)/\partial N = \alpha$ ,  $\partial^2 H(\cdot)/\partial N^2 = 0$ , and  $\partial^2 H(\cdot)/\partial N \partial S = 0$ . Thus, from equation (8) the fitness-maximizing seed size will not change with resource availability. The equal marginal advantage equation, (6), becomes

$$\alpha = \frac{\partial H(\cdot)}{\partial S} = \frac{s^* \left( \frac{\partial f(s^*)}{\partial s} \right)}{f(s^*)}$$

$$\Rightarrow \frac{f(s^*)}{s^*} = \alpha \frac{\partial f(s^*)}{\partial s} \quad (10)$$

If, for example,  $\alpha = 1/2$  so that the average seed fitness declines with an increasing number of sibling seeds, the proportional marginal advantage of seed number will always equal one-half. Thus, from equation (6), the fitness-maximizing seed size will be the one at which the proportional marginal advantage of seed size equals one-half. Graphed on arithmetic axes (fig. 2b),  $s^*$  will be determined by the point of tangency of the seed-size fitness curve with a line having half the slope of a straight line from the origin. Given the shape of the seed-size fitness curve at the

Smith-Fretwell fitness maximum (negative second derivative), the new point of tangency will be to the right, where the slope is lower (fig. 2*b*). Thus, if the per seed fitness declines with seed number (because of sibling density dependence), the fitness-maximizing seed size will be larger than for the case of no sib interactions. If average seed fitness increases with seed number ( $\alpha > 1$ ), the fitness-maximizing seed size will be smaller than for the Smith-Fretwell case of no sib interactions. However,  $s^*$  should not vary with resource availability.

These conclusions make intuitive sense in terms of the equal marginal advantage equation, (6). If, under a particular regime of sib interactions (i.e., for a particular value of  $\alpha$ ), the proportional marginal advantage of seed number (the left side of eq. [6]) does not change with seed number, seed size, or resource availability, then neither will the seed size that satisfies the equal marginal advantage equation. Yet, changing the nature of sibling density dependence by lowering  $\alpha$  reduces the marginal advantage of seed number as a fitness component. This favors a reallocation of resources away from seed number toward another source of fitness, seed size (but only up to the point on the seed-size curve where the marginal advantage of seed size has dropped down to equal the new lower marginal advantage of seed number).

#### *Nonhomogeneous Seed-Number Functions with Independent Size and Number Effects*

We have seen that  $s^*$  does not change with resource availability if the proportional marginal advantage of seed number ( $\partial H(\cdot)/\partial N$ ) is constant. However, if the proportional marginal advantage of seed number changes with either seed size or seed number (i.e., either  $\partial^2 H(\cdot)/\partial N^2$  or  $\partial^2 H(\cdot)/\partial N \partial S$  does not equal zero), then variation in resource availability will change the fitness-maximizing seed size. This occurs whenever  $h(s, n)$  is not homogeneous in  $n$  (i.e., whenever  $h(s, j \cdot n) \neq j \cdot h(s, n)$ ). The change in seed size is necessary to maintain the equal marginal advantages of size and number (eq. [6]) in the face of a changing marginal advantage of seed number.

Two cases of specific functional forms in which  $h(s, n)$  is not homogeneous in seed number but that have independent size and number effects have been previously explored (Parker and Begon 1986; McGinley 1989). Each of these models represents the offspring-size component of fitness with a different specific function having the common standard shape: fitness increases from a minimum seed size with diminishing gains. These functions both have declining proportional marginal advantages for seed size ( $\partial^2 H(\cdot)/\partial S^2 < 0$ ). Parker and Begon's (1986) model of insect egg size explores an offspring-number component of fitness incorporating negative sib interactions ( $g(n) = n[1 - kn]$  where  $k$  is a positive constant and  $kn < 1$ ). Here  $g(n)$  increases from zero at  $n = 0$  to a maximum at  $n = 1/(2k)$ , from which it declines to zero at  $n = 1/k$ . McGinley (1989) considers an offspring-number component that incorporates positive sib interactions by assuming that predators consume all offspring below, and none above, a threshold offspring number  $t$  so that  $g(n) = n - t$ . Since in both of these models the size and number components of fitness are considered to be independent,  $\partial^2 H(\cdot)/\partial N \partial S = \partial^2 H(\cdot)/\partial S \partial N = 0$ .

Using equation (8) with Parker and Begon's (1986) and McGinley's (1989) functional forms, one can see that  $s^*$  and  $n^*$  will both increase with improved resource availability for any feasible parameter values of either of their models because both size and number have declining proportional marginal advantages ( $\partial^2 H(\cdot)/\partial S^2$ ,  $\partial^2 H(\cdot)/\partial N^2 < 0$ ). For example, according to Parker and Begon's (1986) number function,  $H(S, N) = N + \ln(1 - kn) + F(S)$ , so  $\partial H(\cdot)/\partial N = 1 - kn/(1 - kn)$  and  $\partial^2 H(\cdot)/\partial N^2 = -kn/(1 - kn)^2$ . Since  $k$  and  $n$  are positive, the latter expression is always negative, which indicates that the proportional marginal advantage of seed number declines with seed number.

McGinley's (1989) model is especially interesting because it illustrates that, even with a predator-satiation-type seed-number effect incorporating positive sib interactions, the proportional marginal advantage of a change in seed number may decrease as seed number increases ( $\partial^2 H(\cdot)/\partial N^2 < 0$ ). Thus, the fitness-maximizing seed size may increase with improved resource availability even with positive sib interactions. In his model  $H(\cdot) = \ln(n - t) + F(S)$  so that  $\partial H(\cdot)/\partial N = n/(n - t)$  and  $\partial^2 H(\cdot)/\partial N^2 = -nt/(n - t)^2$ . Since  $t$  and  $n$  are both positive, the latter expression is negative, which indicates that the proportional marginal advantage declines with seed number. Thus, in both of these models the numerator and denominator of  $A$  are negative, and the fitness-maximizing seed size will increase with resource availability (see eq. [8]). Both studies reach this same conclusion by simulation of numerical examples for particular parameter values.

In general, if the numerator and denominator of  $A$  are of the same sign, they must be negative, as in the Parker-Begon (1986) and McGinley (1989) models, in order to satisfy the secondary conditions for a fitness maximum (inequality [5]). As long as the numerator and denominator are both negative,  $A$  will be positive and the fitness-maximizing seed size and number will both increase with resource availability; that is,  $\partial S^*(R)/\partial R$ ,  $\partial N^*(R)/\partial R \in (0, 1)$  (if  $\partial S^*(R)/\partial R \in (0, 1)$ , then  $\partial N^*(R)/\partial R \in (0, 1)$  since  $\partial S^*(R)/\partial R + \partial N^*(R)/\partial R = 1$ ). For example, if the numerator and denominator of  $A$  are equal, the proportional marginal advantage of seed size declines at the same rate as the proportional marginal advantage of seed number. Also,  $A$  will equal one, and  $\partial S^*(R)/\partial R$  will equal one-half; that is, half of any increase in resources available should go to making larger seeds and half to making more seeds. This makes sense when we remember that the proportional marginal advantages of seed size and number are equal at the fitness maximum and that when more resources are added they will be allocated preferentially to whichever fitness component has a higher proportional marginal fitness advantage. Thus, if the proportional marginal fitness advantage diminishes at the same rate for both size and number, then half of the additional resources should be allocated to each.

It is theoretically possible to have an internal fitness maximum with the numerator and denominator of  $A$  being of opposite signs, as long as the negative term predominates (i.e., numerator + denominator  $< 0$ ; see inequality [5]). If the proportional marginal advantage of seed number actually increases with allocation to seed number while the proportional marginal advantage of seed size declines with allocation to seed size ( $A < -1$ ), then improved resource availability would favor the production of more but smaller seeds. If the proportional mar-

ginal advantage of seed size actually increases with allocation to seed size ( $-1 < A < 0$ ), then improved resource availability would favor the production of fewer but larger seeds. These situations seem biologically unlikely.

### *Interacting Effects of Offspring Size and Number*

In contrast to the previous examples, it is not difficult to imagine that the fitness effects of offspring size and number interact, which implies nonzero cross-partial derivatives in equation (8). For example, a common result of experimental studies of interactions of seed size and density is that seed size has relatively little impact on per capita seed fitness at low sowing density. Yet, at higher densities seed size may become increasingly important in determining success (Gross 1984; Stanton 1984). In this scenario the proportional marginal advantage of seed size is likely to be an increasing function of seed number (i.e.,  $\partial^2 H(\cdot)/\partial S \partial N > 0$ ). Since  $\partial^2 H(\cdot)/\partial S \partial N = \partial^2 H(\cdot)/\partial N \partial S$ , the effect of a positive cross-partial is to subtract the same positive number from the second derivatives in the numerator and denominator of  $A$ . In the likely case that the second derivatives are negative (as discussed in the previous section), the numerator and denominator will still be negative after subtracting the cross-partial derivative. If the second derivative in the numerator were negative and that in the denominator zero (as in the traditional Smith-Fretwell case), subtracting positive cross-partials will leave both numerator and denominator negative. Thus, when compared to species with independent size and number effects, species for which seed-size effects on fitness are more pronounced at higher sowing density should be even more likely to respond to improved resource availability with an increase in seed size. Since the same number is subtracted from the (negative) numerator and (negative or zero) denominator, this will tend to equalize them. Having a more equal numerator and denominator in  $A$  favors a more equal response of offspring size and number to resource availability. Since the empirical studies cited at the beginning of this article suggest that most plants adjust seed number more than seed size when resource availability varies, a more equal response implies a stronger response of seed size and a weaker response of seed number. Thus, the most likely consequences of nonzero cross-partial derivatives in the general model is to increase the responsiveness of seed size to resource availability. The effects of size-number fitness interactions for other, less likely scenarios (negative cross-partials, second derivatives of opposite sign, etc.) can be deduced from an examination of equation (8) in a similar fashion.

### TESTING THE IDEAS

The model presented here suggests that certain forms of sib interactions (non-homogeneous ones) may favor a shift in seed size with resource availability. This could be tested in a variety of ways. It is clear from the plant literature cited above that some species have a pronounced tendency to vary seed size with resource availability, whereas many others do not. If the dynamics of the model help to explain this interspecific pattern, it should be possible to predict which

species should have greater or lesser shifts in seed size based on the nature of their sibling interactions.

Many aspects of plant growth form and seed dispersibility should affect the likelihood of sib competition. For example, a plant that allocates most of an increase in resources to horizontal vegetative spread should be less likely to experience greater sib competition with greater resource availability. It is possible that small herbaceous plants differ systematically from large woody plants in the degree to which sib competition is correlated with plant size.

Seed number in plants is actually a hierarchical packaging strategy (e.g., number of seeds per fruit, number of fruits per inflorescence), and the consequences of increased seed number for sib competition depends on the details in potentially predictable ways. For example, if fruits are indehiscent (either dry or fleshy) and seeds tend to be dispersed in a clump, there should be strongly diminishing returns on seed number per fruit. In a grass for which variation in resource availability is reflected in number of culms with a fairly constant number of seeds per culm, the consequences of improved resource availability for sib competition would depend critically on whether the species is caespitose or rhizomatous (bunch vs. sod formers, phalanx vs. guerrilla).

Also, plants with effective dispersal vectors that are more attracted to or otherwise work more effectively on larger plants would be predicted to have little variation in sib competition (and thus seed size) with variation in resource availability. Plant species with effective dispersal adaptations that result in most seeds' being dispersed (e.g., small wind-dispersed seeds or "profitable" vertebrate-dispersed seeds) may not experience greater sib competition as a result of increases in parental resources allocated to seed production. Increased sib interaction with increased parental resources might be more likely in adhesively dispersed seeds that are unattractive to dispersal agents and many of which are not dispersed (e.g., *Heterosperma pinnatum*; D. L. Venable, personal observation).

What would happen if a plant or clone were subdivided into quasi-independent resource modules (Watson and Casper 1984)? In principle this should not affect the fitness maximization process since the same density-dependent seed number processes will operate regardless of the metabolic subdivision of the parent. However, it may be that the quasi-independent resource modules cannot effectively sense the resource status of the whole genet and can only vary seed size with the resource status of the module. Such physiological limitation on the fitness maximization process could lead to variable seed size within genets. A similar situation arises at the individual seed-crop/population-density level. Individual plants could adaptively vary seed size according to the neighbor-dependent seed density their offspring are likely to experience. Yet, it may not be possible for individual plants to sense and respond to variation in the density of seeds produced by neighbors.

It would be interesting to explore some of these issues by comparing related species with and without a seed-size correlation to resource availability (e.g., *Sesbania macrocarpa* and *Sesbania vesicaria*). How do the intensity and homoge-

neity of sib interactions vary with plant size in such species pairs? What aspects of the species biology determine differences in the intensity and nature of sib interactions?

#### SOME ALTERNATIVE EXPLANATIONS

A positive or neutral correlation between seed size and number is perfectly consistent with, and even predicted by, size-number models in a system in which resource availability is likely to vary among individual plants. Thus, such positive and zero correlations do not invalidate the assumption of trade-offs or offspring size-number models. The question now becomes, What other explanations exist for such correlations besides this particular adaptive hypothesis?

Thompson and Rabinowitz (1989), in a discussion of interspecific seed-size/plant-size relationships, concluded that simple allometric relationships between adult and juvenile sizes are less likely in plants than animals because of modular growth. Differences in plant size often depend more on differences in the number of modules than on module size, but allometric constraints on seed size are more likely to be related to the latter than to the former.

Thompson and Rabinowitz (1989) also suggest that, since plant height influences dispersibility, small plants may be constrained to produce smaller seeds for dispersal purposes. Yet, this mechanism is not likely to be general across dispersal mechanisms. For example, adhesive fruits may be less likely to encounter dispersal vectors on tall plants than short (see Venable and Levin 1984). The present model actually makes the opposite prediction at the intraspecific level: if larger plants have substantially better seed dispersal than smaller ones, siblings may not experience stronger interactions when many seeds are produced on larger plants. Thus, seed size should show less variation with plant size under this set of conditions.

If early allocation "decisions" regarding the number of seeds per fruit and fruits per inflorescence are fixed before the exact amount of resources available for reproduction is determined, secondary adjustments in traits such as seed size might result (Lloyd 1980). Yet, by this mechanism large plants might be expected to overcommit as well as undercommit when making early number decisions. They would thus sometimes be forced to make smaller rather than larger seeds, so this mechanism does not necessarily produce positive size-number correlations.

There are a variety of ways, not treated in this model, by which the seed-size fitness function might vary within species (Haig and Westoby 1988; Haig 1989). The resulting seed-size variation could be "conditional," or contingent on the specific environment in which the individual plant finds itself. It is possible that in some species more resources or a larger maternal plant size is predictive of an offspring environment requiring larger seeds (for mechanisms other than those discussed above). Perhaps a greater resource supply or larger plant size is a reliable cue that offspring will experience more competition either with the maternal parent or with other plants. However, such relationships between resource availability and competition are less direct than the relationship between the number of siblings and sib competition or other types of sib interactions. Also, a

positive association of resource availability with seed size would not necessarily be favored if different individuals experience different seed-size fitness functions. For example, it appears that for *Hakea sericea* smaller seeds may represent an adaptive conditional response to improved resource status (Haig and Westoby 1988). Smaller seeds are produced when the plant is grown on nutrient-enriched soils, which suggests that seed reserves may be less important for establishment in nutrient-enriched sites (i.e., that the plants experience a different seed-size fitness function on nutrient-enriched soils).

#### CONCLUSIONS

Neutral or positive size-number correlations within species are sometimes cited as apparent violations of the trade-off assumption of seed size-number models. Yet, most plant species vary more in plant size or the size of the resource pool available for seed production than in seed size. Any trade-off between seed size and number is likely to be masked by this variation in resource availability. A potentially more serious problem for size-number models is that, contrary to the standard theoretical expectation, seed size increases with plant size in a number of species.

Offspring size-number models are standard equal marginal advantage models when variation in fitness, offspring size, and number are measured as proportions (logarithms). In the standard Smith-Fretwell model, offspring size is independent of resource availability because the proportional marginal fitness advantage of seed number does not vary with seed number, seed size, or resource availability. When the proportional marginal fitness advantage of seed number does vary, the fitness-maximizing seed size will change (usually increase) with the size of the pool of resources available for seed production. The formal condition for seed-size change is that the size-number fitness function be nonhomogeneous in offspring number. Both positive and negative sib interactions can give rise to an increase in the fitness-maximizing seed size with an increase in resource availability. It is also possible to have either positive or negative sib interactions with fitness functions that are homogeneous in offspring number, and in such cases the fitness-maximizing seed size remains constant in the face of varying resource availability. If seed-size and seed-number effects on fitness interact in such a way that seed size is more important at higher seed densities, a greater responsiveness of seed size to resource availability is favored. Some other models (Smith and Fretwell 1974; Parker and Begon 1986; McGinley 1989) are shown to be special cases of the independent size-number-effects version of the model presented here.

Variation in resource availability and sib interactions are not necessarily the only factors that can explain neutral or positive size-number correlations within species or the increase in seed size sometimes associated with improved resource availability. However, the selective mechanisms presented here do predict these patterns under conditions broadly applicable to seed plants, and it is important to sort out these conceptual issues for further progress to be made in understanding seed size.

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## LITERATURE CITED

- Augsburger, C. K. 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* 71:759–771.
- Baker, H. G. 1972. Seed mass in relation to environmental conditions in California. *Ecology* 53:997–1010.
- Chiang, A. C. 1984. *Fundamental methods of mathematical economics*. McGraw-Hill, New York.
- Clark, D. A., and D. B. Clark. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Naturalist* 124:769–788.
- Denslow, J. S. 1987. Fruit removal rate from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. *Canadian Journal of Botany* 65:1229–1235.
- Ebenman, B., and L. Persson. 1988. *Size-structured populations: ecology and evolution*. Springer, New York.
- Foster, S. A., and C. H. Janson. 1985. The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* 66:773–780.
- Gross, K. L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology* 72:369–387.
- Haig, D. 1989. Seed size and adaptation. *Trends in Ecology & Evolution* 4:145.
- Haig, D., and M. Westoby. 1988. Inclusive fitness, seed resources, and maternal care. Pages 60–79 in J. Lovett Doust and L. Lovett Doust, eds. *Plant reproductive ecology: patterns and strategies*. Oxford University Press, New York.
- Hanway, J. J. 1969. Defoliation effects on different corn (*Zea mays* L.) hybrids as influenced by plant population and stage of development. *Agronomy Journal* 61:534–538.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, New York.
- Harper, J. L., P. H. Lovell, and K. G. Moore. 1970. The shapes and sizes of seeds. *Annual Review of Ecology and Systematics* 1:327–356.
- Howe, H. F. 1980. Monkey dispersal and waste of a Neotropical fruit. *Ecology* 61:944–959.
- . 1981. Dispersal of a Neotropical nutmeg (*Virola sebifera*) by birds. *Auk* 98:88–98.
- Howe, H. F., and D. De Steven. 1979. Fruit production, migrant bird visitation, and seed dispersal of *Gaurea glabra* in Panama. *Oecologia (Berlin)* 39:185–196.
- Howe, H. F., and W. M. Richter. 1982. Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia (Berlin)* 53:347–351.
- Howe, H. F., and G. A. vande Kerckhove. 1979. Fecundity and seed dispersal of a tropical tree. *Ecology* 60:180–189.
- Levin, D. A., and H. W. Kerster. 1974. Gene flow in seed plants. *Evolutionary Biology* 7:139–220.
- Lloyd, D. G. 1980. Sexual strategies in plants. I. An hypothesis of serial adjustment of maternal investment during one reproductive session. *New Phytologist* 86:69–79.
- . 1987. Selection of offspring size at independence and other size-versus-number strategies. *American Naturalist* 129:800–817.
- . 1988. A general principle for the allocation of limited resources. *Evolutionary Ecology* 2:175–187.
- Lloyd, D. G., and D. L. Venable. 1992. Some properties of selection with single and multiple constraints. *Theoretical Population Biology* 41:110–122.

- Maddox, G. D., and J. Antonovics. 1983. Experimental ecological genetics in *Plantago*: a structural equation approach to fitness components in *P. aristata* and *P. patagonica*. *Ecology* 64: 1092–1099.
- Marshall, D. L., D. A. Levin, and N. L. Fowler. 1986. Plasticity of yield components in response to stress in *Sesbania macrocarpa* and *Sesbania vesicaria* (Leguminosae). *American Naturalist* 127:508–521.
- Maun, M. A., and P. B. Cavers. 1971. Seed production and dormancy in *Rumex crispus*. I. The effects of removal of cauline leaves at anthesis. *Canadian Journal of Botany* 49:1123–1130.
- Mazer, S. J. 1987. The quantitative genetics of life history and fitness components in *Raphanus raphanistrum* L. (Brassicaceae): ecological and evolutionary consequences of seed mass variation. *American Naturalist* 130:891–914.
- . 1989. Ecological, taxonomic, and life history correlates of seed mass among Indiana dune angiosperms. *Ecological Monographs* 59:153–175.
- McGinley, M. A. 1989. The influence of a positive correlation between clutch size and offspring fitness on the optimal offspring size. *Evolutionary Ecology* 3:150–156.
- McGinley, M. A., D. H. Temme, and M. A. Geber. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *American Naturalist* 130:370–398.
- Michaels, H. J., B. Benner, A. P. Hartgerink, T. D. Lee, S. Rice, M. F. Wilson, and R. I. Bertin. 1988. Seed size variation: magnitude, distribution, and ecological correlates. *Evolutionary Ecology* 2:157–166.
- Moore, L. A., and M. F. Wilson. 1982. The effect of microhabitat, spatial distribution and display size on dispersal of *Lindera benzoin* by avian frugivores. *Canadian Journal of Botany* 60:557–560.
- Parker, G. A., and M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *American Naturalist* 128:573–592.
- Pitelka, L. F., M. E. Thayer, and S. B. Hansen. 1983. Variation in achene weight in *Aster acuminatus*. *Canadian Journal of Botany* 61:1415–1420.
- Platt, W. J. 1976. The natural history of a fugitive prairie plant (*Mirabilis hirsuta* [Pursh] MacM.). *Oecologia* (Berlin) 22:399–409.
- Salisbury, E. J. 1942. *The reproductive capacity of plants*. Bell, London.
- . 1974. Seed size and mass in relation to environment. *Proceedings of the Royal Society of London Series B, Biological Sciences* 186:83–88.
- Schaal, B. A. 1980. Reproductive capacity and seed size in *Lupinus texensis*. *American Journal of Botany* 67:703–709.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* 14:235–250.
- . 1989. The paradox of seed size and adaptation. *Trends in Ecology & Evolution* 4:24–26.
- Smith, C. C., and S. Fretwell. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108:499–506.
- Stanton, M. L. 1984. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* 65:1105–1112.
- Stephenson, A. G. 1980. Fruit set herbivory, fruit reduction, and the fruiting strategy of *Catalpa speciosa*. *Ecology* 61:57–64.
- Stickler, F. C., and A. W. Pauli. 1961. Leaf removal in grain sorghum. I. Effects of certain defoliation treatments on yield and components of yield. *Agronomy Journal* 53:784–794.
- Temme, D. H. 1986. Seed size variability: a consequence of variable genetic quality among offspring? *Evolution* 40:414–417.
- Thompson, K., and D. Rabinowitz. 1989. Do big plants have big seeds? *American Naturalist* 133: 722–728.
- van Andel, J., and F. Vera. 1977. Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. *Journal of Ecology* 65:747–758.
- van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist* 128:137–142.
- Venable, D. L., and J. S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* 131: 360–384.

- Venable, D. L., and D. A. Levin. 1984. Morphological dispersal structures in relation to growth habit in the *Compositae*. *Plant Systematics and Evolution* 143:1-16.
- Watson, M. A., and B. B. Casper. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. *Annual Review of Ecology and Systematics* 15:233-258.
- Weis, I. M. 1982. The effects of propagule size on germination and seedling growth in *Mirabilis hirsuta*. *Canadian Journal of Botany* 60:1868-1874.
- Weller, S. G. 1985. Establishment of *Lithospermum caroliniensis* on sand dunes: the role of nutlet mass. *Ecology* 66:1893-1901.
- Willson, M. F. 1983. *Plant reproductive ecology*. Wiley, New York.
- Willson, M. F., and P. W. Price. 1980. Resource limitation of fruit and seed production in some *Asclepias* species. *Canadian Journal of Botany* 58:2229-2233.
- Winn, A. A. 1988. Ecological and evolutionary consequences of seed size in *Prunella vulgaris*. *Ecology* 69:1537-1544.
- Winn, A. A., and P. A. Werner. 1987. Regulation of seed yield within and among populations of *Prunella vulgaris*. *Ecology* 68:1224-1233.
- Wulff, R. D. 1986. Seed size variation in *Desmodium paniculatum*. III. Effects on reproductive yield and competitive ability. *Journal of Ecology* 74:115-121.

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