



More on Optimal Rates of Dispersal: Taking into Account the Cost of the Dispersal Mechanism

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NOTES AND COMMENTS

MORE ON OPTIMAL RATES OF DISPERSAL: TAKING INTO ACCOUNT
THE COST OF THE DISPERSAL MECHANISM

Most plants furnish their seeds with special dispersal devices, such as wings, tufts, thorns, or fleshy fruit. The dispersal mechanism, which can have many different forms, guarantees that only part of the progeny remain near the parent, while the rest are scattered to compete for other living sites. In many species, the division between progeny that remain near the parent and those that are dispersed is made in advance, for example, by producing two kinds of fruit or seeds (heterocarpy), with one kind possessing a dispersal apparatus and the other lacking such a device. In most species, however, all the seeds are equipped with the dispersal apparatus, and the seemingly less-than-perfect dispersal mechanism is responsible for achieving the desired rate of dispersal. It is interesting to note that even in several heterocarpous species (of the Compositae family), all the seeds are initially equipped with the dispersal device, and only later do some lose their ability to disperse (Shmida 1985).

Since the resources used by the parent plant for its reproduction are not unlimited, a larger investment in the dispersal mechanism, which results in the scattering of a larger fraction of the progeny, can also affect the total number of seeds produced. More specifically, the fecundity of each individual is expected to be a decreasing function of the amount it invests in the dispersal of its seeds.

An interesting question is how much of its total expenditure for reproduction a plant should devote to the dispersal mechanism of its seeds. To answer this question, we analyze the evolutionarily stable dispersal rate. Since the dispersal rate is an increasing function of the amount invested in dispersal, the evolutionarily stable investment strategy can then be obtained.

Evolutionarily stable rates of dispersal have been investigated previously (Hamilton and May 1977; Motro 1982*a,b*, 1983; Frank 1986; Taylor 1988). The major contribution of these works to the understanding of the evolution of dispersal is the conclusion that it is advantageous to disperse a substantial fraction of the progeny, even under constant environmental conditions. However, these works considered the fecundity of each individual constant, independent of its dispersal strategy. The present work attempts to redress this somewhat atypical assumption and consider the case in which the cost of the dispersal mechanism is taken into account.

THE MODEL

We consider an infinite population of haploid organisms and denote by μ the expected number of seeds produced by an individual in that population. A fraction $1 - \alpha$ ($0 \leq \alpha \leq 1$) of the seeds remains near the parent plant, whereas a fraction α is scattered uniformly across the entire population range. The dispersal rate, α , is an increasing function of the amount invested in the seed's dispersal mechanism, and this amount is assumed to be a genetically determined trait. Hence, dispersal rate is also genetically determined.

The cost of producing each seed complex—that is, the seed together with its dispersal apparatus—is the sum of the costs of the seed itself plus the cost of the dispersal apparatus for that seed. By appropriately choosing the price units, we can equate the cost of the seed itself to one. Thus, the cost of the dispersal apparatus is x units per seed, and the total price of each seed complex is $1 + x$. Clearly, the more the plant invests in its dispersal mechanism, the larger is the proportion of its progeny that leaves the parental site. Thus, the dispersal rate, α , is an increasing function of x . The total number of seeds produced by an individual is inversely proportional to the cost of producing each seed complex. Hence, the fecundity, μ , is a decreasing function of α .

Generations are discrete and nonoverlapping. At the end of each season, the preceding generation is eliminated, and each site is reoccupied by a single individual. The successor at a site is chosen at random from among all the seeds at that place, which consist of the nondispersed seeds of the preceding occupant or the immigrant seeds of other individuals of the preceding generation.

Because of the risks concomitant with dispersal, such as the possibility of being lost while dispersing, the probability of acquiring a site is assumed to be less for a dispersed seed than for a nondispersed one. Thus, the probability of a dispersed seed's surviving to compete at a site is only a fraction β ($0 < \beta \leq 1$) of that probability for a sessile seed. A reduced β signifies that more-stringent environmental conditions are endured by the dispersed seeds.

Under these assumptions, we examine the evolutionarily stable dispersal strategy. Except for the assumed dependence of fecundity on dispersal rate, our model is the same as earlier haploid models (Hamilton and May 1977; Motro 1982*a*).

In order to find the evolutionarily stable dispersal strategy α^* , we assume that α^* is the prevailing strategy in the population and consider the fate of a mutant strategy α , where $\alpha \neq \alpha^*$. If $\epsilon > 0$ is the frequency of the mutants, then their frequency in the next generation is

$$\epsilon' = \epsilon \frac{\mu(1 - \alpha) + \mu\alpha\beta\epsilon}{\mu(1 - \alpha) + \lambda} + (1 - \epsilon) \frac{\mu\alpha\beta\epsilon}{\mu^*(1 - \alpha^*) + \lambda}, \quad (1)$$

where $\lambda = \mu\alpha\beta\epsilon + \mu^*\alpha^*\beta(1 - \epsilon)$ is the expected number of immigrating seeds per site, μ and μ^* are the corresponding fecundities (recall that fecundity is a decreasing function of the dispersal rate, α), and $1 - \beta$ is the proportion lost during dispersal (see Motro 1982*a*).

After some algebraic manipulations, we obtain

$$\Delta\epsilon = \epsilon' - \epsilon = \beta\epsilon(1 - \epsilon) \left[\frac{\mu\alpha}{\mu^*(1 - \alpha^*) + \lambda} - \frac{\mu^*\alpha^*}{\mu(1 - \alpha) + \lambda} \right]. \quad (2)$$

Define

$$\phi(\alpha; \alpha^*) = \mu\alpha[\mu(1 - \alpha) + \lambda] - \mu^*\alpha^*[\mu^*(1 - \alpha^*) + \lambda].$$

The sign of $\phi(\alpha; \alpha^*)$ is identical to the sign of $\Delta\epsilon$. For a rare mutant (i.e., for small ϵ) and for α^* between 0 and 1, we have

$$\phi(0; \alpha^*) < -(\mu^*)^2\alpha^*(1 - \alpha^*) < 0$$

and

$$\phi(1; \alpha^*) < -(\mu^*)^2\alpha^*(1 - \alpha^*)(1 - \beta) < 0.$$

Hence, a necessary condition for α^* to be an evolutionarily stable strategy (ESS) is that it satisfies

$$d\phi(\alpha; \alpha^*)/d\alpha|_{\alpha=\alpha^*} = 0. \quad (3)$$

For a rare mutant, this equation is equivalent to

$$(d\mu/d\alpha)\alpha[2 - \alpha(2 - \beta)] + \mu[1 - \alpha(2 - \beta)] = 0 \quad (4)$$

(where the asterisks have been omitted for simplicity). Solutions for which the function on the left-hand side of equation (4) intersects the horizontal axis from above represent maxima (and are thus ESS's), whereas intersections from below represent minima.

Note that if μ does not depend on α , the first term on the left-hand side of equation (4) vanishes, and we get the ESS $\alpha^* = 1/(2 - \beta)$, which is the result obtained previously (Hamilton and May 1977; Motro 1982a). This evolutionarily stable dispersal rate is an increasing function of β , the survival probability of the dispersed seeds, and is larger than $1/2$.

The value of the left-hand side of equation (4) is positive for $\alpha = 0$, whereas it is negative for all α where $1/(2 - \beta) \leq \alpha \leq 1$. Hence, there always exists an ESS α^* , which lies between 0 and $1/(2 - \beta)$. This implies that if the cost of the dispersal mechanism puts a pressure on the total number of seeds produced by the plant, the evolutionarily stable dispersal strategy is that of reduced dispersal. From the solution of α^* in equation (4), the ESS of investment $x^* = x(\alpha^*)$ can be obtained.

AN EXAMPLE

The increasing function that describes the dependence of α on x can have different forms. One such form, which is both plausible and easy to analyze, is the case in which α is proportional to x , that is, α equals kx (k is a constant greater than 0). The parameter k measures the efficiency by which investment in the dispersal mechanism is converted into actual dispersal rates. The fecundity, μ , which is proportional to $1/(1 + x)$, is proportional in this case to $1/(1 + \alpha/k)$.

Substituting in equation (4), we obtain the ESS's

$$\alpha^* = 1/(2 - \beta + 1/k) \quad \text{and} \quad x^* = 1/[k(2 - \beta + 1/k)].$$

(Note that since $0 < \beta \leq 1$, both α^* and x^* are less than 1.)

Thus, if α is proportional to x , the evolutionarily stable dispersal rate (α^*) is an increasing function of k , the efficiency with which investment in dispersal is converted into dispersal rates. As this efficiency increases, the ESS α^* converges to the results obtained previously (Hamilton and May 1977; Motro 1982a) for the constant-fecundity case. The evolutionarily stable investment in the dispersal apparatus of each seed (x^*) is, by contrast, a decreasing function of the efficiency parameter. However, regardless of the value of the parameter k , x^* should always be smaller than one. Thus, even with low efficiency, evolutionary stability implies that if the outcomes of the investment in dispersal, in the form of dispersal rates, are additive, the amount invested in the dispersal mechanism of the seeds should always be smaller than the amount invested in the production of the seeds themselves. (This conclusion, however, is not necessarily valid for other than a linear dependence of α on x .)

CONCLUSIONS

This paper examines evolutionarily stable dispersal strategies under the natural assumption that larger investment in the dispersal mechanism, which facilitates seed dispersal, inevitably results in reducing the total number of seeds produced. The strategies that have been considered are the amount invested in the dispersal apparatus and the realized rate of dispersal (i.e., the proportion of the progeny that leaves the parental site), and it is assumed that dispersal rate is an increasing function of the amount invested in dispersal. Thus, whenever the cost of the dispersal mechanism restricts the total number of seeds produced by the plant, the evolutionarily stable dispersal strategy implies that a *smaller*, yet always positive, fraction of the progeny should be dispersed.

The results of this note were obtained under the basic assumption that all parents have the same total amount of resources for producing progeny and that variability in fecundity is a result of the variable fraction of the amount allocated to the dispersal mechanism of the seeds. The *total* amount of resources that should be devoted to reproduction may depend on ecological factors, such as population density (Gadgil and Solbrig 1972; Christiansen and Fenchel 1977) or the availability of pollinators (Bierzychudek 1981).

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