

Dispersal Polymorphisms in Subdivided Populations

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Price's method for analyzing natural selection in subdivided populations is applied to the problem of dispersal polymorphism strategies in a stable habitat. The results agree with the more traditional Mendelian models for this same problem that have recently been published. Further, by using Price's method, the results obtained are simpler and more general, and the causal evolutionary mechanisms underlying the predicted patterns are more easily recognized. The most interesting new result is that the equilibrium proportion of dispersed individuals is a simple function of the risk of dispersing and the regression coefficient of relatedness among individuals who, in the absence of dispersal, would compete for a limited, local resource. This regression coefficient refers to the genotypes that control the dispersal phenotype. For example, when mothers control the phenotype of their progeny, then the regression is from the mother onto an offspring chosen randomly from the local group before dispersal; while when offspring control their own phenotype, the regression is taken directly from offspring onto a randomly chosen cohort member before dispersal. This use of controlling genotypes to calculate regressions explains the form of the parent-offspring conflict over dispersal noted by previous authors. The simplicity and generality of these results suggest that Price's method is a useful approach for studying the class of phenomena known as "games among relatives".

1. Introduction

Many organisms have two distinct dispersal morphs. Colonization of new patches and extinction of extant patches are two commonly discussed explanations for the maintenance of these polymorphisms (e.g. Van Valen, 1971; Gadgil, 1971). A complementary factor that also favours dispersal polymorphisms is competition among relatives for a limited local resource. Hamilton & May (1977) isolated the effects of the kin selection factor by studying a series of simple ESS models in which the size and number of patches in the population remain constant. Motro (1982*a,b*, 1983) repeated and extended Hamilton & May's (1977) work by using a fully dynamic Mendelian approach. Here I subsume a number of separate results of Hamilton & May and Motro within a single simple formulation by applying Price's (1970, 1972) method for the hierarchical analysis of natural selection.

2. Methods

The Price equation has been reviewed and discussed several times (e.g. Price, 1972; Wade, 1985). The expanded form of the equation used here is described by

Hamilton (1975) and Frank (1986*a*). This selection equation is

$$\bar{w}\Delta q = \text{COV}(w_s, q_s) + \sum_s \alpha_s [\text{COV}_s(w_{si}, q_{si}) + E_s(w_{si}\Delta q_{si})]. \quad (1)$$

One advantage of the Price equation is flexibility in the definition of terms. I restrict definitions here to those that will be most useful for the applications in the next section: \bar{w} is population fitness; Δq is the change in frequency of a particular allele after one generation; s is the index for types of subpopulations, where $q_s = s/N$ is the frequency of a particular genotype within an s -type subpopulation, and si is the index for the i th individual in an s -type subpopulation, where q_{si} is the allele frequency within the s th individual—i.e., q_{si} is proportional to the individual's additive genotypic value, here assumed to be at a single locus; w_s is the relative contribution of an s -type group to the next generation (i.e., group fitness), and w_{si} is the absolute fitness of the i th individual within an s -type group (i.e., individual fitness in the context of a group); E_s is the expectation over all individuals, i , within an s -type group; and α_s is the frequency of s -type groups.

The term Δq_{si} is the change in the allele frequency among the set of successful gametes of the s th individual, due to meiotic drive, gametic selection, or sampling effects (drift). For the models in this paper, I will make the usual assumption that these within-individual effects are negligible, and Δq_{si} will be set to zero. Replacing the second covariance term in (1) with the product of the regression and the variance yields

$$\bar{w}\Delta q = \text{COV}(w_s, q_s) + \sum_s \alpha_s R_s(w_{si}, q_{si}) V_s(q_{si}) \quad (2)$$

where the R_s term is the slope of the within-group fitness (number of progeny) on additive genotypic value for individuals in an s -type group, and the V_s term is the within-group variance in additive genotypic values.

3. The General Model

Hamilton & May (1977) and Motro (1982*a,b*, 1983) studied a series of simple models in which they searched for the equilibrium proportion of dispersing individuals in each generation. I show here that a single model obtained by Price's method subsumes many of these results. Assumptions of the model are (Motro, 1982*b*): (i) The habitat consists of an infinite number of discrete patches, each containing N reproducing adult females. (ii) Each female produces the same number of progeny, k . (iii) A proportion $1 - d$ ($0 \leq d \leq 1$) of the progeny remains in its natal patch, while a proportion d is scattered randomly over all patches in the population. (iv) Generations are discrete and non-overlapping. Each patch is recolonized at the beginning of each season both by females born in that patch and by immigrants. N females are chosen at random from among both nondispersed individuals and colonizing immigrants from other patches, and these N females produce the next generation. (v) Dispersed progeny incur the risks of travel. Assume non-dispersed progeny have an expected fitness of one, and dispersed progeny a fitness of β ($0 < \beta \leq 1$), so that the cost of dispersal is $c = 1 - \beta$.

I will search for a solution only at the boundaries of the gene frequency space (the ESS technique; see Maynard Smith, 1982). Assume that heterozygotes have an intermediate phenotype between the two homozygotes. Let there be two dispersal phenotypes: an a -type that disperses at rate d_a , corresponding to the resident homozygote AA; and a b -type that disperses at the rate d_b , corresponding to the rare mutant heterozygote. The formal translation from (essentially haploid) types to diploid genotypes will require an additional step, discussed below. The dispersal rate refers to the controlling genotype in the following way. If the mother controls the dispersal of her progeny, then an a -type mother disperses d_a of her progeny, and if the offspring controls the probability of its own dispersal, then a -type offspring disperse with probability d_a .

Let the frequency of b -types in the population be q , and that of a -types, $1 - q$. Let the number of b -types in a subpopulation be s , $0 \leq s \leq N$, and $q_s = s/N$. The proportion of dispersing propagules from an s -type subpopulation is $d_s = (1 - q_s)d_a + q_s d_b = d_a - q_s \Omega$, where $\Omega = d_a - d_b$. Finally, let the frequency of s -type subpopulations be α_s ($\sum \alpha_s = 1$), and the average dispersal rate be $d = \sum \alpha_s d_s$. The average number of arrivals in a patch is therefore $Nk\beta d$.

With this notation, we can construct the expected fitness of a b -type individual relative to an average member of an s -type subpopulation, where, under maternal control, an offspring's type during the dispersal phase is determined by its mother's genotype. $k(1 - d_b)$ is the expected number of progeny of a b -type that do not disperse, and $Nk(1 - d_s + \beta d)$ is the expected number of young individuals competing for a spot in an s -type patch. Since there are N places to fill in a patch, $k(1 - d_b)/[Nk(1 - d_s + \beta d)]$ multiplied by N is the average success of the non-dispersed progeny of a b -type individual. Likewise, kd_b is the expected number of dispersed progeny of a b -type, and $Nk(1 - d + \beta d)$ is the expected number of young individuals competing for a spot in an average patch within the population, so $\beta kd_b/[Nk(1 - d + \beta d)]$ multiplied by N is the average success of dispersed progeny of a b -type individual. Thus the expected number of progeny w_{si} of a b -type in an s -type patch is

$$w_{si}(b) = (1 - d_b)/(1 - d_s + \beta d) + \beta d_b/(1 - d + \beta d) \quad (3)$$

where group membership in an s -type patch is defined by location of the mother if control of the phenotype is maternal, or by birthplace if control of the phenotype is by the offspring—i.e., group membership is determined by the site of phenotypic action.

$w_{si}(a)$ takes the same form as (3), when b is replaced with a . The remainder of the expressions for use in (2) can now be written as

$$w_s = (1 - q_s)w_{si}(a) + q_s w_{si}(b) = (1 - d_s)/(1 - d_s + \beta d) + \beta d_s/(1 - d + \beta d) \quad (4)$$

$$\text{COV}(w_s, q_s) = \sum \alpha_s w_s (q_s - q) \quad (5)$$

$$R_s(w_{si}, q_{si}) = w_{si}(b) - w_{si}(a) = \Omega/(1 - d_s + \beta d) + \beta \Omega/(1 - d + \beta d) \quad (6)$$

$$V_s(q_{si}) = q_s(1 - q_s). \quad (7)$$

A candidate for the ESS can be obtained from eqn (2) by equating to zero the derivative of $\bar{w}\Delta q$ with respect to d_b , and then setting $d_a = d_b = d^*$ (see Maynard Smith, 1982). Following through, one obtains d^* , the ESS dispersal fraction

$$d^* = \frac{\rho - c}{\rho - c^2} \quad 0 \leq c < \rho \leq 1 \quad (8)$$

$$\rho = \frac{V(q_s)}{V(q_s) + \sum \alpha_s V_s(q_{si})}$$

where $c = 1 - \beta$ and $d^* = 0$ when $\rho < c$. $V(q_s)$ is the variance in the frequency of b -types among subpopulations, $\sum \alpha_s V_s(q_{si})$ is the expected within-subpopulation variance in types, so ρ is the expected among-subpopulation variance divided by the total population variance, and is thus a measure of the similarity of group members. So far, the model is essentially haploid, since the two types can be construed as alternative haploid genotypes. Any reasonable definition of ρ will yield the same results (e.g., correlation of additive genotypic values, regression coefficient of relatedness). However, if we wish to consider other genetic systems, the choice of ρ will affect the results. In order for eqn (8) to hold for any genetic system, let ρ be Hamilton's (1972) regression coefficient of relatedness of the controlling genotype onto a member of the cohort of offspring chosen randomly before dispersal. The rationalization for this choice is that regression was specifically designed so that fitness valuations for any genetic system could be translated into a common currency. A discussion of the use of regression in ESS sex ratio models based on the Price equation is in Frank (1986*a,b*); see also the *Note* at the end of this paper. The purpose of the present paper is to illustrate the value of this approach for simplifying and extending a set of known models that are complex and conceptually opaque.

Values of d^* as a function of ρ and β are given in Fig. 1. As the regression of controlling genotype on offspring, ρ , increases, the proportion of dispersing offspring increases. As β decreases and the cost of dispersal, c , increases, the proportion of

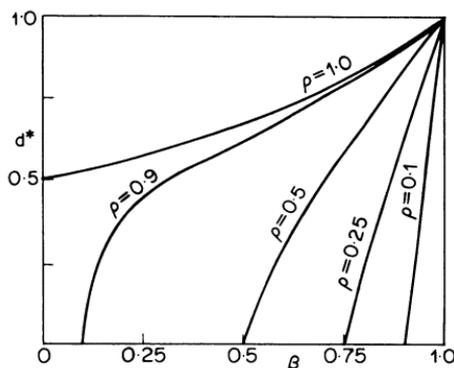


FIG. 1. The ESS dispersal fraction, d^* , as a function of the relative value of a dispersing individual, $\beta = 1 - c$, and the regression coefficient of relatedness of controlling genotypes onto competing individuals, ρ . The curves are obtained from eqn (8).

dispersed offspring decreases. Comins *et al.* (1980) and Comins (1982) obtained similar results under more complex model assumptions. However, their methods are much more complicated than those presented here, and the simple role of regression coefficients of controlling genotypes onto offspring is more difficult to interpret from their models.

One interesting result that follows from the general formulation presented here is that when the probability of successful dispersal, β , is very low, ρ may be high (close to one) even for moderately large N . This would favor a high dispersal rate even though patch size is moderately large and the probability of successful dispersal is vanishingly small.

4. Special Cases

Presenting the dispersal fraction as a function of ρ generalizes a series of models by Hamilton & May (1977) and Motro (1982*a,b*, 1983). In this section I examine some special cases of eqn (8), which include many of the results of these authors.

Assume the number of reproducing adult females in a patch is N , and that mothers control the dispersal fraction. If the N mated composites (adult females plus stored sperm) are genetically uncorrelated, then the regression of a mother onto a randomly chosen offspring is $\rho = 1/N$, since the regression of a mother on an offspring that is not her own would be zero, and

$$d^* = \frac{(1/N) - c}{(1/N) - c^2}. \quad (9)$$

The mated composites are likely to be correlated, however, since $1 - d^*$ of the mothers are sampled from among N families in each generation. Therefore $\rho = [1 + (N - 1)\rho']/N$, where ρ' is the average pairwise regression of mothers on mated composites, and eqn (9) is a lower bound for d^* for the usual case in which $\rho' \geq 0$.

When $N = 1$, $\rho = 1$ and $d^* = 1/(1 + c) = 1/(2 - \beta)$, as in Hamilton & May (1977) and Motro (1982*a*) for haploid models. Motro (1982*b*) also obtained this result for a diploid model with maternal control and $N = 1$, in which mating is a mixture of selfing and random mating. Since ρ measures the regression of the controlling maternal genotypes onto a randomly chosen offspring, it is easy to see that eqn (8) holds in general for any sort of selfing and random mating when the mated composites are uncorrelated ($\rho' = 0$), and this explains Motro's result.

Both Hamilton & May (1977) and Motro (1983) studied a diploid model with $N = 1$, in which the dispersal probability is controlled by the genotype of the offspring. Hamilton & May (1977) limited the mothers to a single mating, so the regression of controlling genotypes on offspring is $\rho = 1/2$; the regression among outbred full-sibs. Their solution is obtained by using $\rho = 1/2$ in eqn (8). In Motro's (1983) model, he allowed mothers to mate many times, so $\rho = 1/4$, the correlation among outbred half-sibs. His result is obtained by using $\rho = 1/4$ in eqn (8). This use of ρ as the regression of controlling genotypes onto offspring clarifies the nature of the parent-offspring conflict over the optimal dispersal fraction that was noted by these authors. Also, by appropriate calculation of ρ , the ESS can be calculated

directly from eqn (8) under the relaxed assumptions of multiple adults per patch ($N > 1$) and inbreeding.

Consider another model by Motro (1982*b*) as the final example of the generality of Price's method. In this case the mother controls the dispersal fraction; $1 - d$ of the reproductive investment is in vegetatively produced descendants; and d of the investment is in sexually produced, dispersing progeny. To incorporate this within the approach of the present paper, weight the relative fitness of the stay-at-home fraction, $1 - d$, by a factor of two on the right-hand-side of eqn (3). This factor of two represents the fact that vegetatively produced offspring carry twice as many alleles identical by descent from the mother, when compared to outcrossed sexuals; and by construction of the model, the vegetative investment is kept at home, while the sexually produced offspring are forced to disperse. For $N = 1$, and hence $\rho = 1$, the solution by this method is $d^* = 1/(3 - \beta)$, as in Motro (1982*b*).

5. Discussion

The most interesting result obtained by using Price's method is that the equilibrium dispersal fraction is a simple function of the cost of dispersal and the regression of the controlling genotype onto a member of the local cohort chosen randomly before dispersal. This agrees with a result for sex ratios obtained by Price's method: the reproductive value to a mother of a son that competes with male relatives for a limited resource (e.g., mates) is discounted by the regression of the mother on a male chosen randomly from among the local group (Frank, 1986*a,b*).

The results presented here for dispersal and elsewhere for sex ratios are more easily obtained and more general than those that have been derived by other methods. Price's method is therefore useful for studying the class of phenomena known as "games among relatives" (Grafen, 1979; Hines & Maynard Smith, 1979).

Notes (i) The use of Hamilton's regression coefficient of relatedness for this model is really a conjecture at present. In a paper soon to be published Taylor (1987) proves an important theorem that links the Price equation with inclusive fitness arguments and regression (or pedigree) coefficients of relatedness. This theorem greatly strengthens my conjecture, although I still cannot claim a formal proof for the particular dispersal model presented here. The sex ratio models in Frank (1986*a,b*) also provide strong support for this conjecture.

(ii) Crow (1955) is apparently the first to provide a hierarchical selection equation of the form used here. Previous reviews of hierarchical selection theory have not, to my knowledge, cited this work by Crow.

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