Population Stability and the Evolution of Dispersal in a Heterogeneous Environment

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Summary. A model is presented which demonstrates that a stable polymorphism for dispersal tendency can be generated under a wide range of conditions. These conditions include both different genetic models and different "dispersal probability" functions. It is shown that individual selection for or against dispersers may result in a stable polymorphism which depresses population numbers and prevents population fitness from being maximized. Changes in the genotypic probabilities of dispersal may lead to very large changes in other parameters both with regard to their means and their spatial distribution. The effect of increasing environmental stability does not effect the proportion of dispersers maintained in the population in identical ways; the effect depends upon the parameter altered and the genetic model used.

1. Introduction

Dispersal is a phenomenon which is of great interest to both geneticists and ecologists. The geneticists are largely concerned with the question of how dispersal between populations affects the genetic structure of the population whilst ecologists are interested in how dispersal contributes towards population stability. Naturally these two questions are complementary; excessive dispersal between populations occupying different habitats may prevent these populations from becoming adapted to the particular conditions in which they exist but too little dispersal may prevent areas in which a population has, for one reason or another, died out from being recolonized by neighbouring populations.

In two previous papers (Roff, 1974a, b) I presented a simulation model designed to test the hypothesis that dispersal can significantly decrease the probability of extinction, within a given time interval, of a population living in a heterogeneous environment. The model demonstrated that dispersal may increase the time to extinction of a population by at least three orders of magnitude and often more. In the model a number of different dispersal strategies were used but in no case was the probability of dispersal considered as a function of genotype. However, there exists evidence which indicates that genotype is important in this regard (Sakai et al., 1958; Howard, 1960; Collier, 1968; Dingle, 1968; Narise, 1962, 1969; Krebs et al., 1973).

The present paper describes the behaviour of a population model in which dispersal is genetically determined. The model is used to answer two questions:

(i) Is a stable "dispersal" polymorphism possible?

(ii) What effect do changes in the stability of the environment have upon the frequency of dispersers in the population?
2. The Population Model

The model simulates a population which is distributed amongst 36 discrete “island” habitats, the environmental parameters of which are allowed to vary independently. These environmental parameters are \( K \), the carrying capacity of the environment, and the effect of density-independent environmental factors on the rate of increase, \( \lambda \). For simplicity the effect of environmental factors on \( \lambda \) was simulated by simply making \( \lambda \) a random variable with mean \( \mu(\lambda) \) and variance \( \sigma^2(\lambda) \). In reality the correlation between these environmental parameters and between habitats will depend upon the number of factors which determine either parameter and upon the distance between habitats; increasing either of these will, in general, decrease the correlation. In the present model I have assumed no correlation over time or space both for computational simplicity and because there exists no data to indicate what a reasonable correlation might be. Moreover, any instability that might result from a correlation between habitats or parameters could be overcome simply by increasing the dispersal distance of the “animals” and by increasing the number of island habitats.

The stability of the habitat is a function of the four statistics \( \mu(\lambda) \), \( \sigma^2(\lambda) \), \( \mu(K) \) and \( \sigma^2(K) \). The environment is made more stable if either \( \mu(\lambda) \), \( \mu(K) \) are increased or \( \sigma^2(\lambda) \), \( \sigma^2(K) \) are decreased.

The model assumes non-overlapping generations and random mating within any subpopulation. Population changes are generated by the following sequential operations:

- **Reproduction**
  \[ N_i(t+1) = N_i^*(t) \lambda_i(t) \]

- **Dispersal**
  \[ N_i^{**}(t+1) = N_i(t+1) - \text{Emigrants} + \text{Immigrants} \]

- **Density-dependent Regulation**
  \[ N_i^*(t+1) = N_i^{**}(t+1) \text{ if } N_i^{**}(t+1) < K_i(t+1) \]
  \[ N_i^*(t+1) = K_i(t+1) \text{ if } N_i^{**}(t+1) > K_i(t+1) \]

\( N_i(t) \) is the size of the \( i \)th subpopulation at time \( t \) (or equivalently generation \( t \)), \( \lambda_i(t) \) is the “potential” finite rate of increase and \( K_i(t) \) is the carrying capacity of the \( i \)th habitat at time \( t \). A subpopulation is considered extinct if it comprises less than two “animals” (i.e., \( N_i^*(t) < 2 \)). Dispersal occurs from one habitat only into its immediate neighbours and the boundary of the whole environment is reflecting so there is no dispersal completely out of the area except as explained below. Of those “animals” dispersing only a proportion \( S \) find new habitats. This “mortality” of dispersers may be due to death of the disperser or due to its dispersing completely out of the environment in which case it is effectively “dead” to the population. Genotype frequencies were calculated after density-dependent regulation had occurred.

Three “dispersal models”, each involving three different strategies, were used. The three models are:

- a) Dispersal not under genetic control.
- b) The probability of dispersal determined by a single gene with two alleles, \( d_1, d_2 \).
- c) The probability of dispersal a quantitative genetic trait. In this model it is assumed that there is a linear relationship between the mean dispersal “tendency” (not probability as explained below) of the parents and their offspring.