The evolution of life histories in spatially heterogeneous environments: optimal reaction norms revisited

TADEUSZ J. KAWECKI* and STEPHEN C. STEARNS
Institute of Zoology, University of Basel, Rheinsprung 9, CH-4051 Basel, Switzerland

Summary

Natural populations live in heterogeneous environments, where habitat variation drives the evolution of phenotypic plasticity. The key feature of population structure addressed in this paper is the net flow of individuals from source (good) to sink (poor) habitats. These movements make it necessary to calculate fitness across the full range of habitats encountered by the population, rather than independently for each habitat. As a consequence, the optimal phenotype in a given habitat not only depends on conditions there but is linked to the performance of individuals in other habitats. We generalize the Euler-Lotka equation to define fitness in a spatially heterogeneous environment in which individuals disperse among habitats as newborn and then stay in a given habitat for life. In this case, maximizing fitness (the rate of increase over all habitats) is equivalent to maximizing the reproductive value of newborn in each habitat but not to maximizing the rate of increase that would result if individuals in each habitat were an isolated population. The new equation can be used to find optimal reaction norms for life history traits, and examples are calculated for age at maturity and clutch size. In contrast to previous results, the optimal reaction norm differs from the line connecting local adaptations of isolated populations each living in only one habitat. Selection pressure is higher in good and frequent habitats than in poor and rare ones. A formula for the relative importance of these two factors allows predictions of the habitat in which the genetic variance about the optimal reaction norm should be smallest.

Keywords: reaction norms; phenotypic plasticity; life history evolution; age at maturity; spatial heterogeneity; fitness measures; fitness sensitivity

Introduction

When a population inhabits an environment that varies in space and time, each individual in the population should express a phenotype that is appropriate for the conditions that it encounters. Evolution can in principle solve that problem by moulding the population reaction norm to produce the optimal phenotype in every habitat (Via and Lande, 1985; Stearns and Koella, 1986; de Jong, 1990).

In a previous paper, Stearns and Koella (1986) introduced the concept of an optimal reaction norm. The optimal reaction norm determines the optimal value of a trait – they considered age and size at maturity – as a function of environmental conditions, which they summarized as individual growth rate. They also proposed a framework for finding optimal reaction norms. The critical feature of their method is that each point on the optimal reaction norm is calculated independently of every other point. It is as though the reaction norm were made up of a large
Figure 1. When individuals in each habitat constitute an isolated population (left), each of the populations grows with its own rate and tends to evolve local adaptations. However, when individuals of one population encounter different habitats (right), the flow of individuals among habitats results in one overall rate of increase and creates an opportunity for the evolution of reaction norms that produce the optimal phenotype in each habitat.

Figure 1. When individuals in each habitat constitute an isolated population (left), each of the populations grows with its own rate and tends to evolve local adaptations. However, when individuals of one population encounter different habitats (right), the flow of individuals among habitats results in one overall rate of increase and creates an opportunity for the evolution of reaction norms that produce the optimal phenotype in each habitat.

number of populations each of which had achieved its optimal point in its own separate habitat (Fig. 1, left hand side). For this reason the phenotype optimal in a given habitat did not depend on the quality and frequency of other habitats. They used the Euler-Lotka equation:

\[ 1 = \int_0^\infty e^{-rx} L(x)B(x)dx \]  

where \( x \) stands for age, \( L(x) \) for the probability of surviving to age \( x \), \( B(x) \) for the number of offspring expected by females aged \( x \), and \( r \) for the rate of increase (the Malthusian parameter). The survivals, fecundities, and the tradeoffs among them specific for a given habitat (i.e. resulting from a given individual growth rate) were entered into Equation 1, and the age at maturity maximizing the rate of increase \( r \) was considered optimal in this habitat. The optimal reaction norm for age at maturity was generated by repeating this for a series of growth rates. In general the optimal reaction norm for any life history trait could be found by using a similar procedure for a range of habitats characterized by survival and fecundity schedules and a trade-off structure.

The Euler-Lotka equation defines \( r \), and hence fitness, as an implicit function of the survival and fecundity schedules in a constant, uniform environment in which offspring experience the same conditions as parents. In a population inhabiting a spatially heterogeneous environment, however, some offspring experience conditions different from their parents because they migrate to other habitats. This results in source-sink population structure with a net flow of individuals from better to poorer habitats (Pulliam, 1988; Pulliam and Danielson, 1991). The resulting rate of increase will be a summed effect of births and deaths taken across all habitats (Fig. 1, right hand side). In this case the Euler-Lotka equation applied separately to each habitat (each set of conditions) fails to predict the overall rate of increase. It could only be used to predict the optimal reaction norm that should evolve in a spatially heterogeneous environment if the contributions of individuals from each habitat to overall population growth were proportional to the value of \( r \) calculated for each habitat separately. As shown below, this is not generally the case.

In this paper, we generalize the Euler-Lotka equation to get the rate of increase for a