

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

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## 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

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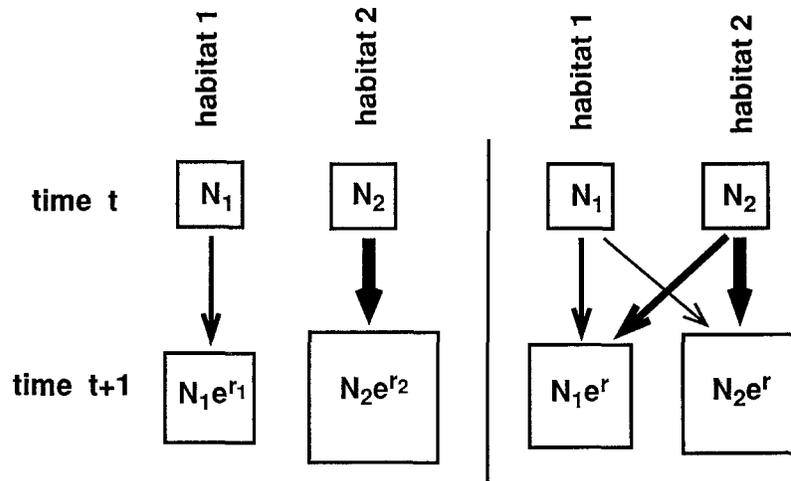


Figure 1. When individuals in each habitat constitute an isolated population (left), each of the populations grows with its own rate and tends to evolve local adaptations. However, when individuals of one population encounter different habitats (right), the flow of individuals among habitats results 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:

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

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

population living in a spatially heterogeneous environment and show how the equation can be used to predict optimal reaction norms for life history traits. We compare a few examples of optimal reaction norms for age at maturity and for clutch size predicted with the new equation with those predicted by the approach taken in Stearns and Koella (1986). Finally, the new equation is used to calculate the sensitivity of fitness to departures of life history phenotypes from the optimal reaction norm when habitat quality and frequency vary. The model we present is a phenotypic model that implicitly assumes clonal inheritance (cf. Stearns and Crandall, 1981). While aware of the limitations of this approach, we believe that its results are also relevant to sexually reproducing organisms. We discuss this problem further below.

Recently, Houston and McNamara (1992) independently reached some of our conclusions using matrix population models.

### The model

We consider overlapping generations and a life cycle in which an individual disperses as a newborn (e.g. egg, seed, or spore), settles in a given habitat, and stays there for life. The proportion of offspring born in a habitat A that settle in another habitat B is time-independent. However, this proportion may differ from the proportion of offspring born in some habitat C that settle in habitat B, except for the section on fitness sensitivity, where completely random dispersal is assumed. Only females are considered. Habitat differences are expressed in survival and fecundity schedules and the structure of tradeoffs among them and are summarized by the parameter  $h$ .  $h$  may be a single number (e.g. a growth rate), or a vector (e.g. temperature, food abundance, and the intensity of predation), and may vary continuously or in a discrete manner. We assume that the frequency distribution of habitats remains constant.

#### *The characteristic equation for a spatially heterogeneous environment*

In this section we generalize the Euler-Lotka equation to populations living in spatially heterogeneous environments. We derive it for continuous variation in  $h$  and continuous time, but an analogous equation can be derived for discrete habitats or time units.

Let  $N(x, h, t)$  be the number of individuals living in habitat  $h$  aged  $x$  at time  $t$  (a probability density function). The number of offspring produced by individuals in habitats within a narrow range  $(h, h+dh)$  during a short time interval  $dt$  is

$$dt \, dh \int_0^{\infty} N(x, h, t) B(x, h) \, dx \quad (2)$$

where  $B(x, h)$  is the fecundity of an individual aged  $x$  in habitat  $h$ . Individuals aged  $x$  at time  $t$  were born and settled in habitat  $h$ ,  $x$  time units ago and survived to age  $x$ , or

$$N(x, h, t) = N(0, h, t-x) L(x, h) \quad (3)$$

where  $L(x, h)$  is the survival to age  $x$  in habitat  $h$ . The number of individuals born in a given habitat during time  $dt$  differs from the number of individuals settling in this habitat at this time because some offspring emigrate and some settlers come from other habitats. However, the total number of individuals born at a given time in the population must be the same whether they are classified by the habitat of origin (i.e. their parents' habitat) or by the habitat in which they are destined to live. Hence

$$dt \int_{\mathbf{H}} N(0, h, t) \, dh = dt \int_{\mathbf{H}} \left[ \int_0^{\infty} N(0, h, t-x) L(x, h) B(x, h) \, dx \right] \, dh \quad (4)$$

If no habitats are isolated and if there are no dead-end habitats (i.e. given enough time all individuals have ancestors that lived in all habitats), so that the corresponding projection matrix

is primitive, the population will converge to a stable distribution in which the proportions of individuals living in each of the habitats will remain constant through time and the number of individuals will grow exponentially with rate  $r$  (Caswell, 1989a; McNamara, 1991). Thus the number of newborn settling in habitat  $h$   $x$  time units ago has the following relation to the number of newborn settling in habitat  $h$  now:

$$N(0, h, t-x) = N(0, h, t)e^{-rx} \quad (5)$$

By substituting this relation into Equation 4 and dividing both sides by the total number of individuals born during period  $dt$ , one obtains the characteristic equation:

$$1 = \int_{\mathbf{H}} \left[ q(h) \int_0^{\infty} e^{-rx} L(x, h) B(x, h) dx \right] dh \quad (6)$$

where  $q(h)$  is a probability density function describing the proportion of total offspring produced in the population in stable distribution that settle in habitat  $h$ . If the dispersal of newborn is completely random,  $q(h)$  equals the frequency of particular habitats. In general it depends on the frequency of habitats, dispersal strategy and performance of individuals in particular habitats.

Equation 6 defines the population growth rate  $r$  as an implicit function of both (1) the survival and fecundity schedules of individuals in all habitats and (2) the distribution of newborn among habitats. If reproduction is asexual,  $r$  measures the fitness of a clone when age specific survivals and fecundities of individuals belonging to this clone are substituted in Equation 6. Under restricted conditions (random mating, density and frequency independence),  $r$  should also measure the fitness of a phenotype in sexually reproducing organisms (cf. Charlesworth, 1980). Because the right hand side of Equation 6 is a strictly decreasing function of  $r$ , it has only one real solution. It generalizes the Euler-Lotka equation (Equation 1) and reduces to it if survival and fecundity functions are independent of  $h$ . One or both integrals can be replaced by appropriate sums if habitats or time are better handled as discrete entities.

Equation 6 is analogous to an equation describing the growth rate of a population genetically heterogeneous with respect to vital rates and hence undergoing selection (Charlesworth, 1980; p.156). Because allele frequencies occurring in that equation change in the course of selection, the variation in survival and fecundity schedules was viewed as transient (unless there was heterozygote advantage), and the equation was regarded as a tool to investigate selection dynamics but not to find optimal life histories.

The characteristic equation derived above can be used to predict optimal reaction norms for life history traits and to calculate the sensitivity of fitness, and thus the strength of selection pressure, in different habitats as it depends on their frequency and quality.

#### *Optimal reaction norms*

The reaction norms of life history traits can be seen as adaptations that depend conditionally on habitat conditions. If there is no frequency-dependence, the optimal reaction norm is the variant with maximum fitness measured by the rate of increase. If no genetic or developmental constraints prevent it, and if the developing organism can perceive the necessary information about its habitat, then the optimal reaction norm should evolve. Equation 6 specifies the rate of increase  $r$  as a function of survival and fecundity schedules in all habitats in a spatially varying environment. Therefore, if one knows how survival and fecundity depend on the habitat and on a trait, this equation can be used to predict what reaction norm for this trait should evolve in response to spatial variation in habitats.

Denote the reaction norm of the optimized trait  $u$  as  $u(h)$ , where  $h$  characterizes the habitat. The survivals and fecundities are now not only age- and habitat-dependent, but are also functions of the trait  $u$ . From the rules for finding the maxima of implicit functions and the fact that the

right hand side of Equation 6 is a decreasing function of  $r$ , we can find the  $u(h)$  that maximizes  $r$  in two steps:

*Step 1.* Substitute an arbitrary discounting factor  $r_c$  for  $r$  in Equation 6. Find a reaction norm  $\hat{u}(h, r_c)$  maximizing the right hand side of Equation 6. Do it for a range of values of  $r_c$ .

As long as the optimized trait  $u$  does not influence the dispersal of offspring and thus  $q(h)$ , maximizing the right hand side of Equation 6 is equivalent to maximizing

$$J(h, r_c) = \int_0^{\infty} e^{-r_c x} L(x, h) B(x, h) dx \quad (7)$$

for each habitat  $h$ . The resulting value of the trait  $u$  for a given habitat  $h_i$ ,  $\hat{u}(h_i, r_c)$  depends on the conditions encountered in habitat  $h_i$  and on the value of the parameter  $r_c$ . It is however still independent of conditions encountered in other habitats. Therefore in this step the knowledge of what the other habitats are, how frequent they are, and how they differ from the habitat  $h_i$  does not affect calculations made for habitat  $h_i$ .

*Step 2.* Among many possible  $r_c$ s find the  $r^*$  which together with corresponding  $\hat{u}(h, r^*)$  found in Step 1 satisfies Equation 6.  $\hat{u}(h, r^*) = u^*(h)$  is the optimal reaction norm, and  $r^*$  is its rate of increase.

In this second step the optimization of the trait for an individual living in a particular habitat is put in the context of total habitat variation encountered by the population. This is done because  $r^*$ , the overall rate of increase, is a summed effect of births and deaths occurring in all habitats. For example, if better habitats are rarer,  $r^*$  will be lower. In turn  $r^*$  determines which of the  $\hat{u}(h, r_c)$ s maximizing the right hand side of Equation 6 is the optimal reaction norm  $u^*(h)$ . This step requires the knowledge of the conditions in other habitats and of the way the newborn distribute themselves among habitats  $q(h)$ . Therefore, in contrast to the predictions of Stearns and Koella (1986), the optimal value of a trait in a given habitat is not independent of the conditions encountered by other members of the same population.

Using the Euler-Lotka Equation 1 as suggested by Stearns and Koella (1986) is equivalent to finding the life histories  $u_{EL}(h, r_c)$  maximizing  $J(h, r_c)$  for which the maximum  $J(h, r_c) = 1$  for each habitat  $h$  (see also Goodman, 1982). The optimal phenotype for a given habitat predicted with the Euler-Lotka Equation will thus generally differ from  $u^*(h)$ . Therefore the rate of increase that would result if individuals in a given habitat constituted an isolated population cannot be used to predict the optimal phenotype in this habitat if the population is in fact living in a spatially heterogeneous environment.

If the actual rate of increase of the optimal strategy  $r^*$  is substituted for the arbitrary constant (discounting factor)  $r_c$  in Equation 7, the resulting quantity

$$R(h) = \int_0^{\infty} e^{-r^* x} L(x, h) B(x, h) dx \quad (8)$$

is the discounted lifetime reproductive success of an individual living in habitat  $h$ . Thus when parents do not affect the dispersal of their offspring among habitats, maximizing the rate of increase  $r$  in the spatially heterogeneous environment is equivalent to maximizing the discounted lifetime reproductive success of individuals in each habitat. Note that when  $r^* = 0$  the quantity defined in Equation 8 becomes the net reproductive rate (lifetime reproductive success)  $R_0$ .

As shown by Houston and McNamara (1992), in the more general case where individuals differ with respect to habitat or physiological condition (state in their terminology), maximizing the rate of increase  $r$  is equivalent to maximizing the reproductive value of newborn in each habitat  $V_0(h)$ . The newborn reproductive value differs from the discounted lifetime reproductive success (as defined in Equation 8) in that fecundity  $B(x, h)$  itself is expressed in the units of reproductive value rather than in the number of offspring.  $V_0(h)$  and  $R(h)$  become equivalent if offspring habitat is independent from parent habitat (i.e. if dispersal is completely random).

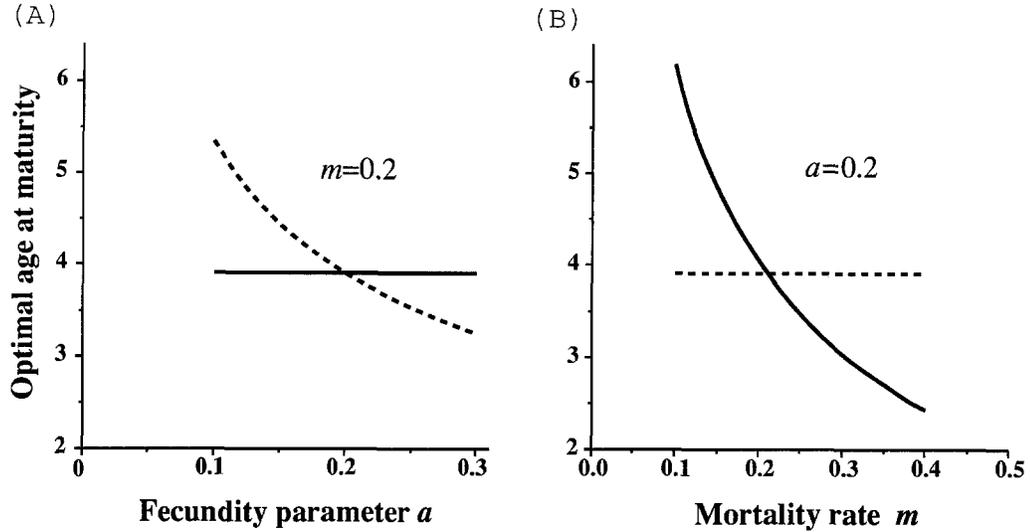


Figure 2. Optimal reaction norms for age at maturity in a hypothetical organism in which fecundity =  $a^*$  (age at maturity)<sup>1,2</sup> and mortality rate  $m$  is age independent, predicted using the method developed in this paper (solid lines) and the approach proposed by Stearns and Koella (1986) (broken lines). (A) Habitat differences expressed in the fecundity parameter  $a$ . (B) Habitat differences expressed in the mortality parameter  $m$ . In both cases a uniform frequency distribution of habitats was assumed.

#### Examples of optimal reaction norms for age at maturity and for clutch size

To illustrate how the above general model can be applied to particular traits, we give below two examples of calculating optimal reaction norms for age at maturity and for clutch size. We also compare the predictions of our model with those obtained by using the classical Euler-Lotka equation.

*Example 1: age at maturity in a hypothetical organism.* Consider the optimal reaction norm for age at maturity ( $\alpha$ ) in an organism for which survival  $L(x) = e^{-mx}$  and fecundity  $B(x) = a\alpha^b$  for  $x \geq \alpha$  (and  $B(x)=0$  for  $x < \alpha$ ).  $m$ ,  $a$  and  $b$  may differ among habitats; the optimal reaction norm  $\alpha^*(m,a,b)$  predicts at what age individuals experiencing particular values of these three parameters should mature.

*Step 1:* First we find  $\alpha(h,r_c)$  maximizing the right hand side of Equation 6 with  $r_c$  treated as a parameter and  $h$  being a set of three parameters:  $m$ ,  $a$  and  $b$ . After substitution of the functions for fecundity and survival, and integration,  $J(h,r_c)$  (Equation 7) becomes:

$$J(h,r_c) = a\alpha^b \left( \frac{e^{-(r_c+m)\alpha}}{r_c+m} \right) \quad (9)$$

where  $\alpha = \alpha(h)$  is the age at maturity in the habitat  $h$ . To find the  $\alpha(h,r_c)$  maximizing  $J(h,r_c)$ ,  $dJ/d\alpha$  must be set to 0:

$$\frac{dJ}{d\alpha} = ac^{-(r_c+m)\alpha} \alpha^{b-1} \left( \frac{b}{r_c+m} - \alpha \right) = 0 \quad (10)$$

and solved for  $\alpha$ :

$$\hat{\alpha}(h, r_c) = \frac{b}{r_c + m} \quad (11)$$

The second derivative  $d^2J/d\alpha^2$  evaluated at  $\alpha$  is negative, and thus  $J(h, r_c)$  has a maximum at  $\alpha$ .

Note that it has not yet been necessary to specify whether the differences among habitats are actually expressed in  $a$ ,  $b$ ,  $m$ , or all three parameters. Although we do not yet know the  $r^*$  to be substituted for  $r_c$ , Equation 11 tells a lot about the optimal reaction norm. Because  $a$  – the coefficient of the function relating fecundity to age at maturity – does not appear in Equation 11, it is optimal for individuals that live in habitats differing only with respect to  $a$  to mature at the same age – the optimal reaction norm  $\alpha^*(a)$  is flat (Fig. 2A, solid line). If the differences among habitats are reflected in mortality rates  $m$ , then, other things being equal, the higher the mortality in a given habitat, the earlier the individuals inhabiting it should mature (Fig. 2B, solid line). And if the habitat variation is reflected in  $b$ , the exponent to which age at maturity is raised in determining fecundity, then individuals should mature later when  $b$  in their habitat is larger. Therefore, the approximate shape of the optimal reaction norm is established to a certain degree without knowing the distribution of habitat variation. That distribution will influence the position and shape of the reaction norm through its effect on  $r^*$ .

*Step 2:* Now we have to find the actual rate of increase  $r^*$  that should be substituted for the discounting parameter  $r_c$ . To do this, we must specify the nature and range of habitat variation. Two cases will be considered: (A) when the habitats differ with respect to  $a$ , and (B) when the differences among habitats are reflected in  $m$ .

*Case A:* Variation in the fecundity coefficient  $a$  ( $h=a$ ). Substituting  $\alpha(h, r_c)$  from Equation 11 into Equation 6 gives

$$1 = \int_{a_1}^{a_2} q(a) a e^{-b} \frac{b^b}{(r_c + m)^{b+1}} da \quad (12)$$

where  $a_1$ ,  $a_2$  specify the range of variation in  $a$ , and  $q(a)$  is the distribution of newborn among habitats characterized by  $a$ . Solving this equation for  $r_c$  gives the maximum possible rate of increase, i.e. the fitness of the optimal reaction norm,  $r^*$ ,

$$r^* = [E(a) b^b e^{-b}]^{\frac{1}{b+1}} - m \quad (13)$$

where  $E(a)$  is the arithmetic mean value of  $a$ . The optimal reaction norm itself can be found by substituting  $r^*$  for  $r_c$  in Equation 11 (and rearranging):

$$\alpha^*(a) = \left[ \frac{b e^b}{E(a)} \right]^{\frac{1}{b+1}} \quad (14)$$

Thus spatial environmental variation affecting the fecundity of individuals of all ages proportionally (e.g. variation in egg or infant survival), and uncorrelated with variation in any other environmental parameter, produces no differences in the optimal age at maturity:  $\alpha^*$  depends only on the mean conditions encountered by the population.

*Case B:* Variation in mortality rate  $m$  ( $h=m$ ). In this case the characteristic equation becomes (cf. Equation 12):

$$1 = \int_{m_1}^{m_2} q(m) a e^{-b} \frac{b^b}{(r_c + m)^{b+1}} dm \quad (15)$$

and cannot be solved explicitly for  $r_c$ . Consider a case in which the distribution of newborn among habitats with different mortality rates is uniform, i.e.  $q(m) = 1/(m_2 - m_1)$ . Then Equation 15 becomes

$$1 = \frac{a}{m_2 - m_1} b^{b-1} e^{-b} \left[ \frac{1}{(r_c + m_1)^b} - \frac{1}{(r_c + m_2)^b} \right] \quad (16)$$

The  $r_c$  satisfying Equation 16 ( $r^*$ ) can be found numerically. Substituting  $r^*$  into Equation 11 yields the optimal reaction norm  $\alpha^*(m)$  (Fig. 2B, solid line).  $r^*$  could be found numerically for any distribution  $q(m)$ .

If habitat differences were expressed in both  $a$  and  $m$ , the optimal reaction norm would be a curved surface in three dimensional space ( $a, r, \alpha$ ) still described by Equation 11. Its position would be found by determining  $r^*$  from Equation 6 in which

$$\int_{\mathbf{H}} dh$$

would be replaced by

$$\int_{a_1}^{a_2} \int_{m_1}^{m_2} dm da$$

The optimal reaction norms in cases where environmental variables are correlated can also be predicted within this framework. For example, if some habitats were abundant with both food and predators, high  $a$  would be associated with high  $m$ . This correlation would influence  $r^*$ , but once  $r^*$  is known, the optimal age at maturity for a given set of  $m$ ,  $a$  and  $b$  can be found from Equation 11.

Using the Euler-Lotka Equation 1 as suggested by Stearns and Koella (1986) results in qualitatively different predictions. In the example above, substituting

$$r_c + m = \frac{b}{\alpha} \quad (17)$$

from Equation 11 into Equation 9 and setting it equal to 1 yields:

$$1 = \frac{a}{b} e^{-b} \alpha^{b+1} \quad (18)$$

From Equation 18 the age at maturity in habitat  $h$ , resulting from the Euler-Lotka equation,  $\alpha_{EL}(h)$ , can be found

$$\alpha_{EL}(h) = \left( \frac{b}{a} e^b \right)^{\frac{1}{b+1}} \quad (19)$$

This reaction norm,  $\alpha_{EL}(h)$ , differs qualitatively from  $\alpha^*(h)$ : the optimal age at maturity is not sensitive to spatial variation in mortality rate  $m$ , but it is sensitive to variation in the fecundity parameter  $a$  (Fig 2A and B, broken lines).

Figure 3 depicts the optimal reaction norms for age and size at maturity for *Drosophila*

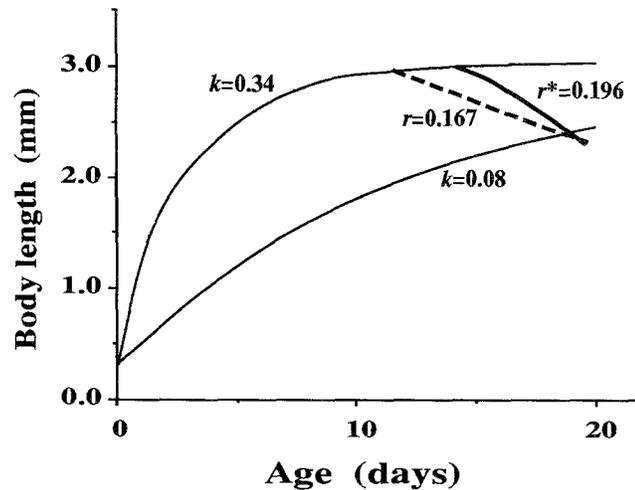


Figure 3. The optimal reaction norm for age and size at maturity in *Drosophila* predicted by Stearns and Koella (1986) (broken heavy line) and that predicted with the approach developed in this paper (solid heavy line) when conditions encountered by an individual influence its growth rate,  $k$ , and  $k$  is assumed to be evenly distributed. Light lines depict growth curves for two growth rates. Note that the axes differ from Fig. 2. Data from Stearns and Koella (1986).

encountering different growth conditions for two models: as predicted by Stearns and Koella (1986) (broken line) and calculated using Equation 6 (solid line) for the same assumptions concerning growth curves and relations between juvenile survival, growth rate and mother's age at maturity (details in Stearns and Koella, 1986). The qualitative difference is not great, but predicted ages at maturity still differ by about 2 days for fast growing flies, a difference large enough to measure.

*Example 2: Optimal clutch size in an iteroparous organism.* Consider an organism maturing at a fixed age  $\alpha$  and then having one clutch of size  $F$  each year. The probability of survival to maturity  $S_j$  and the extrinsic component of adult survival  $S_{ex}$  are assumed to depend on environmental conditions, whereas intrinsic adult survival  $S_{in}$  is a decreasing function of clutch size  $F$  laid by an individual. (More generally,  $F$  can be seen as a measure of parental effort, and  $S_j$  as the number of offspring surviving to maturity produced per unit of parental effort.) For iteroparity to be an optimal strategy, this trade-off function must be, at least for some clutch sizes, concave (viewed from below), i.e.  $d^2S_{in}/dF^2 < 0$  (cf. Schaffer, 1974). How should the optimal clutch size respond to spatial variation in juvenile or adult extrinsic survival, i.e. what is the optimal reaction norm for clutch size? As shown in the Appendix, in habitats characterized by higher  $S_{ex}$  the optimal clutch size is always lower (leading to higher  $S_{in}$ , and thus enhancing habitat differences in total adult mortality) whereas differences in juvenile survival (or in the number of surviving offspring produced per unit of parental effort) do not influence predicted clutch size (reproductive effort) (see Fig. 4 A and B, solid lines).

In contrast, applying the Euler-Lotka equation to isolated populations that each experience different environmental conditions predicts smaller clutches in populations experiencing lower survival to maturity (Fig. 4A, broken line; cf. Schaffer, 1974; Sibly and Calow, 1986). The relationship between the optimal clutch size and adult extrinsic survival is also negative but is

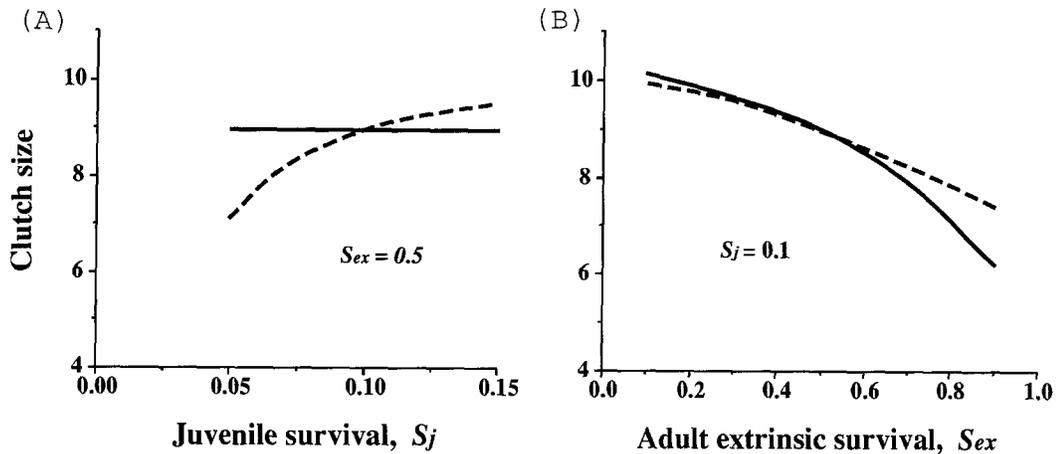


Figure 4. Optimal reaction norms for clutch size in the iteroparous organism described in Example 2, predicted with the method developed in this paper (solid lines) and with that proposed by Stearns and Koella (1986) (broken lines). The trade-off function assumed:  $(\text{adult extrinsic survival})^2 + (0.1 \cdot \text{clutch size})^2 = 1$ . (A) Spatial variation in juvenile survival; (B) Spatial variation in extrinsic adult survival.

always less steep than the optimal reaction norm predicted with the method developed in this paper (Fig. 4B, broken line, see Appendix for the proof).

To summarize, spatial variation in the environment and the resulting source-sink population structure have profound consequences for optimal values of life history traits. The optimal reaction norms predicted with this approach are sometimes qualitatively different from predictions obtained with the Euler-Lotka equation.

#### *Habitat quality and frequency and the sensitivity of fitness*

If the rate of increase  $r$  measures fitness, then the selection pressure on a given trait is proportional to the sensitivity of  $r$  to a marginal change in the trait (Charlesworth, 1980; Caswell, 1989b). Fitness sensitivity analysis has proven useful in analysing the evolution of senescence (Hamilton, 1966; Emlen, 1970). Here we show how the new characteristic equation (Equation 6) can be used to investigate relations between fitness sensitivity and habitat quality and frequency in a spatially heterogeneous environment.

In addition to the general assumptions of our model, in this section we assume that the dispersal of offspring is completely random, i.e. that the offspring habitat is independent of that of the parents. This assumption ensures that the frequency distribution of newborn among habitats  $q(h)$  is not affected by a change in the life history in some habitats, and the discounted lifetime reproductive success ( $R(h)$  as defined in Equation 8) becomes equivalent to the reproductive value of a newborn  $V_0(h)$ . These assumptions are restrictive, but relaxing the last one should not influence the predictions about fitness sensitivity much unless the population is very 'viscous', i.e. unless offspring are very likely to stay near the place of birth.

The discrete habitat version of Equation 6,

$$1 = \sum_{\mathbf{H}} \left[ q(h) \int_0^{\infty} e^{-rx} L(x,h) B(x,h) dx \right] \quad (20)$$

will be used because the meaning of sensitivity can then be more easily grasped. The change in

fitness resulting from a change in a trait  $u$  in a habitat  $z$ ,  $\Delta u(z)$ , can be approximated by the Taylor series:

$$\Delta r = \frac{\partial r}{\partial u(z)} \Delta u(z) + \frac{1}{2} \frac{\partial^2 r}{\partial u^2(z)} [\Delta u(z)]^2 + \dots \quad (21)$$

Under the assumptions of this section the first derivative of the rate of increase with respect to  $u(z)$  is

$$\begin{aligned} \frac{\partial r}{\partial u(z)} &= \frac{q(z) \int_0^\infty e^{-rx} \frac{\partial}{\partial u(z)} [L(x,z)B(x,z)dx]}{\sum_{\mathbf{H}} \left[ q(h) \int_0^\infty x e^{-rx} L(x,h)B(x,h)dx \right]} \\ &= \frac{q(z)}{T} \frac{\partial V_0(z)}{\partial u(z)} \end{aligned} \quad (22)$$

where  $T$  is generation time (cf. Charlesworth, 1980). Thus, ignoring the second and higher order terms, the effect on fitness of a marginal change in a trait in a given habitat is proportional to its influence on the reproductive value of newborn and to the proportion of newborn settling in that habitat. In turn, the absolute effect of a change in a trait on reproductive value is likely to be greater for individuals with higher  $V_0$ , i.e. living in better habitats. (It is certain to be greater if the change occurs in a juvenile trait.) For example, the sensitivity of fitness to the same change in mortality rate for all ages in a habitat  $z$  equals:

$$\frac{\partial r}{\partial m(z)} = - \frac{q(z)}{T} \int_0^\infty x e^{-rx} L(x,z)B(x,z)dx \quad (23)$$

and the sensitivity of fitness to proportional change of fecundity for all ages in a given habitat is

$$\frac{\partial r}{\partial B(z)} = \frac{q(z)}{T} \int_0^\infty e^{-rx} L(x,z)B(x,z)dx \quad (24)$$

and hence is proportional to  $V_0$  in that habitat and to the habitat frequency (the second order terms have been omitted).

Sensitivity analysis also allows us to quantify the fitness consequences of a departure of a life-history trait (e.g. age at maturity) from the optimal reaction norm and thus to compare the strength of stabilizing selection pushing the population towards the optimal reaction norm in different habitats. Right on the optimal reaction norm, the first derivative of fitness with respect to the optimized trait is 0, and the second derivative tells us how the first derivative changes as we move away from the optimum. The second derivative of fitness evaluated on the optimal reaction norm is

$$\left. \frac{\partial r}{\partial u(z)} \right|_{u^*(z)} = \frac{q(z)}{T} \frac{\partial^2 V_0(z)}{\partial u^2(z)} \quad (25)$$

which is also likely to be positively correlated with  $V_0(z)$ .

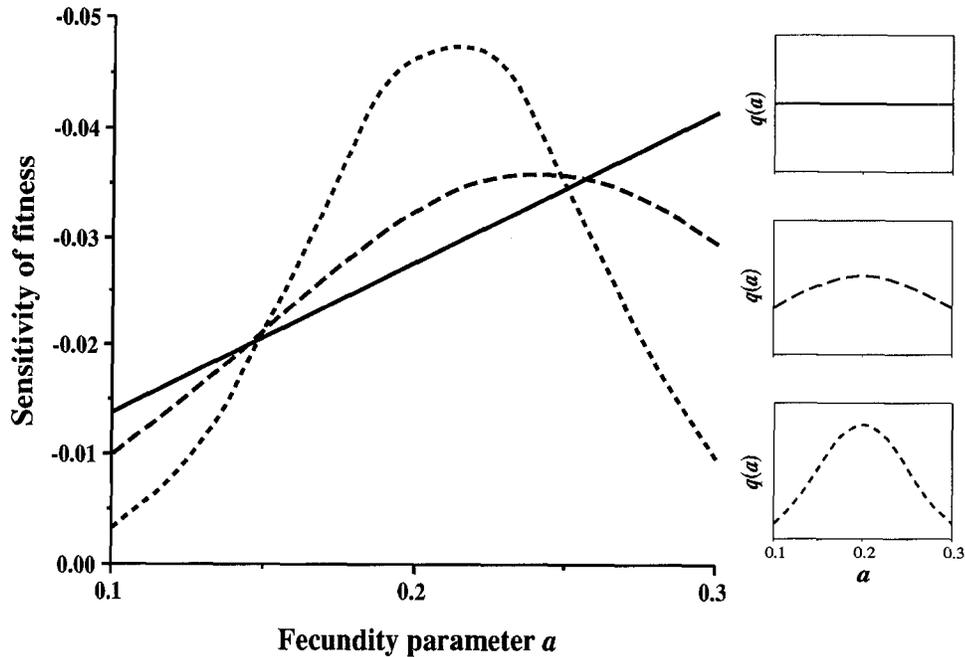


Figure 5. The sensitivity of fitness to departures of age at maturity in particular habitats from the optimal reaction norm depicted in Fig. 2A, for three different habitat frequency distributions (shown on the small graphs).

Figure 5 illustrates for Example 1, Case A, how habitat quality and frequency influence the sensitivity of fitness to departures from the optimal reaction norm (the solid line in Fig. 2A). When all habitats are equally frequent, the selection pressure on age at maturity is much higher in better habitats, and thus age at maturity in the latter should be better tuned to the optimal reaction norm. As, however, some habitats become common and others rare, the habitat frequency starts to dominate over the quality of the individual habitats, and selection in good but rare conditions becomes weak.

One can also use fitness isoclines to illustrate the sensitivity of fitness to deviations from the optimal reaction norm. Figure 6 depicts the fitness of organisms from Example 1 in an environment consisting of two equally frequent habitats as a function of age at maturity in each of the habitats. Although the optimal age at maturity is the same in both habitats (recall Fig. 2A), fitness decreases much faster when age at maturity deviates from the optimum in the good habitat than when it does so in the poor one.

To summarize, the selection pressure on a trait in a particular habitat is positively correlated with its frequency and quality as measured by the reproductive value of newborn that live there. The fitness sensitivity formula (Equation 22) derived from the new characteristic equation allows us to evaluate the relative role of these two factors.

## Discussion

When the optimization of a reaction norm is carried out across the range of habitats inhabited by a population, the predicted reaction norm differs from that expected when one predicts the

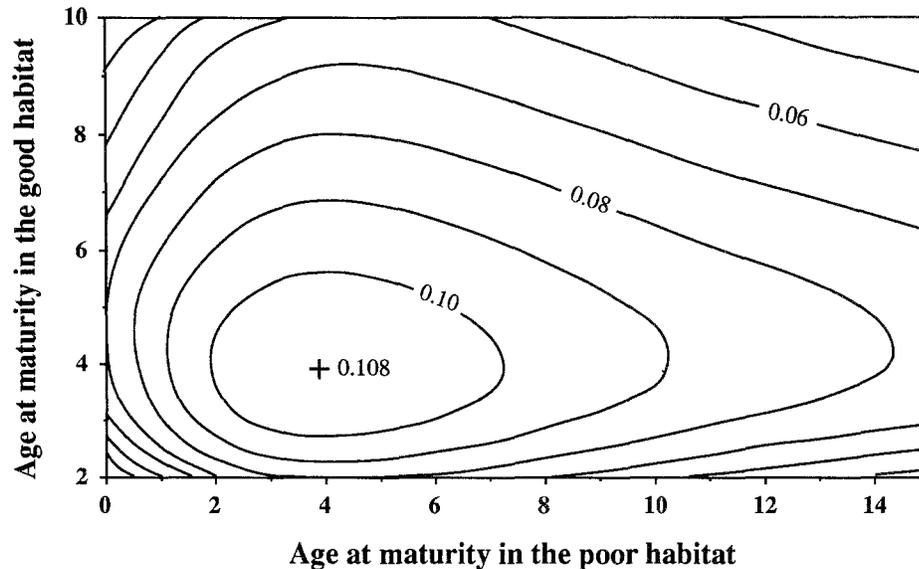


Figure 6. Fitness ( $r$ ) isoclines of a population of organisms described in the legend to Fig. 2, encountering two equally frequent habitats differing in the fecundity coefficient  $a$ . Poor habitat:  $a = 0.1$ ; good habitat:  $a = 0.3$ .

optimal life history for each habitat conceived of as an isolated population cut off from the rest of the environmental heterogeneity. The intuitive reason is that in this model offspring from all habitats can grow and reproduce in all other habitats. The movement of offspring results in a sink-source population structure and connects performance in one habitat with performance in others. The rate of increase becomes a summed effect of births and deaths taking place in all habitats, whereas the rates of increase of isolated populations each encountering only one habitat are coupled only with conditions in the local habitat. Because the rate of increase is the discounting factor that determines the relative value of offspring born at different ages, predictions of optimal life history traits for the same local habitat conditions will differ for different global rates of increase, and thus for different frequency distributions of habitats encountered by the population. The characteristic equation derived in this paper (Equation 6) gives the rate of increase in the heterogeneous environment as a function of frequency distribution of habitats and the mortality and fecundity schedules in each habitat.

Therefore, in a spatially heterogeneous environment, fitness cannot be defined separately for each habitat in which the organism finds itself. An individual encountering a given habitat  $h$  should maximize her discounted reproductive success  $R(h)$ , or more generally, her reproductive value at birth  $V_0$ . However, measuring discounted reproductive success  $R(h)$  requires knowledge of the discounting factor  $r^*$ , and this in turn depends on the quality and frequency of all habitats; measuring reproductive value requires knowledge both of  $r^*$  and of the habitats in which a given individual's offspring will live.

Most of the successful offspring in the population will originate from the best habitats and from the habitats that are at high frequency, and thus natural selection in these habitats can be expected to be strongest. The effects of a trait expressed in a local habitat on the global rate of increase (fitness) is proportional to its influence on the newborn reproductive value and to the proportion of total offspring produced by the population which settle in this habitat. The reproductive value of a newborn expressing the optimal phenotype can thus be used as a measure

of habitat quality, for example to compare two habitats in one of which both fecundity and mortality are higher than in the other.

When the rate of increase of the optimal reaction norm is equal to 0, the newborn reproductive value becomes equivalent to the net reproductive rate  $R_0$ . This result is by no means new (Haldane, 1927), but in contrast to previous results (e.g. Hastings, 1978; Charnov, 1990) it does not require that the net reproductive rate resulting from the survival and fecundity functions determined by a particular habitat equals 1; only the population mean over all habitats must equal 1.

Our model also creates a link between models using the rate of increase  $r$  and those using the net reproductive rate  $R_0$  that have produced contradictory predictions in the past. The qualitative predictions of optimal reaction norms we arrived at in Examples 1 and 2 using  $r$  as a measure of fitness are the same as those obtained by other authors using  $R_0$  as a measure of fitness: spatial variation in egg or infant survival should not influence the optimal age at maturity (Kozłowski and Wiegert, 1986; Charnov, 1990), and optimal reproductive effort should not be affected by spatial differences in juvenile survival (Kozłowski and Uchmanski, 1987) or the number of offspring produced per unit of reproductive effort (Charnov, 1986), but should increase with decreasing adult survival (Kozłowski and Uchmanski, 1987).

The calculation of an optimal reaction norm requires that the dispersal of offspring among habitats and the conditions in each habitat are known. However, by maximizing a quantity analogous to  $R(h)$  but with an arbitrary discounting factor, i.e. performing only Step 1 of the calculations, one can predict some qualitative features of the optimal reaction norm. This can be done even when mortality and fecundity functions are known only for a part of the range of habitat variation and when only some of the environmental parameters influencing individual performance are measured. For example, in Example 1, after performing Step 1 it could be concluded that spatial variation in the parameter  $a$  (resulting from variation in fecundity or egg survival) should have no influence on the optimal age at maturity, whereas individuals in habitats with higher age-independent mortality should mature earlier.

Our model assumes that an individual migrates as a newborn and then stays in a given habitat for life. It can, however, be easily modified for cases where dispersal occurs at a different life stage. It can also be adapted to organisms that change their habitat during life. For example, many insect larvae live in a completely different habitat than adults; here the habitat parameter  $h$  would have to describe conditions for both larval and adult stages. It could be a vector composed of parameters determining larval mortality, larval growth conditions, adult mortality, food abundance in adult environment, and relation between adult size and fecundity. In other words the assumption of 'staying in the same habitat' requires that 'habitat' describes conditions for the whole individual lifespan rather than that parameters like mortality or fecundity remain constant through life. However, as the number of habitat alterations increases, the number of parameters required to describe the conditions for the whole life becomes large and applying our model becomes impractical. This approach can also be extended to individual differences other than those resulting from variation in habitat, e.g. maternal effects or developmental noise, that cause differences in survival and fecundity and in the tradeoffs between them.

Our phenotypic model assumes *de facto* clonal inheritance, and for clones the rate of increase that we calculate (Equation 6) is a proper measure of fitness. Phenotypic optimization models seem to be consistent with classical quantitative genetic assumptions (Charnov, 1989; Charlesworth, 1990). It is not clear to what extent they are consistent with single locus population genetics, in particular where there are deviations from random mating and weak selection (Charlesworth, 1980, p. 197). If, in our model, individuals in all habitats release gametes to a common mating pool (e.g. many sessile marine invertebrates), the assumption of random mating may be

reasonable. However, if mating takes place within habitats, even if it is locally random, it will generally not be random on the population level because the allele frequencies in mating individuals will differ among habitats. One of us is currently working on a population genetic version of this model in which the problem of non-random mating will be addressed. Despite their limitations, phenotypic models of life history evolution have been useful because their predictions are more easily tested than those of quantitative genetic models, and in particular than those of population genetic models.

#### *Comparison with other models*

The use of the Euler-Lotka equation to predict the optimal reaction norm, as proposed by Stearns and Koella (1986), seems to be incorrect. It predicts local adaptations of isolated populations with inter- but not intrapopulation habitat differences. In such a case no adaptive reaction norm can evolve, for each population will be adapted only to the habitat it encounters. It does predict the evolutionary response to a change of some environmental factor over time (provided that selection is weak), and thus can be used to predict the life history responses of exploited populations.

Many of our conclusions independently confirm those reached by another route by Houston and McNamara (1992). They also found:

- (1) That the reaction norm that maximizes the overall rate of increase  $r$  in a spatially heterogeneous environment differs from the line connecting the local adaptations of isolated populations.
- (2) That the optimal strategy for an individual in a given state (or habitat) depends on the performance of the other individuals (living in other habitats), i.e. on their relative influence on the overall  $r$ .
- (3) That one cannot define fitness separately in each habitat.

The matrix model used by Houston and McNamara (1992) allows them to treat the habitat (or more generally state) of an individual as a variable that changes during life, and to consider cases where the quality of offspring (or the habitat in which they will live) is under parental control. Our approach can deal with continuous variation in the environment while in theirs the number of discrete states (habitats) that can be handled is limited.

The results of the fitness sensitivity analysis correspond to those obtained by Via and Lande (1985) in a quantitative genetic model. They found that a trait evolved toward its optimal reaction norm most rapidly in the habitat that contributed most offspring to the population, and this could even occur at the cost of departing from the optimum in poor or rare habitats if the cross-habitat genetic correlation structure was unfavourable.

We assume that individuals possess perfect information about their habitats so that they can finely adjust their life history in response to encountered conditions. This will be unlikely in most cases, and adaptations to habitat uncertainty analogous to those proposed for unpredictable temporal variation (reviewed by Seger and Brockmann, 1987) can be expected to evolve. We also assume that the proportion of individuals born in a habitat 1 migrating to a habitat 2 is constant, thus ignoring the possibility of habitat choice (reviewed in Rosenzweig, 1991). Pulliam and Danielson (1991) identified conditions favouring migration to poor habitats and explored the consequences of habitat choice for population structure and dynamics.

#### *Corroborating evidence*

Wide variation in the quality of habitats was a centrepiece of Andrewartha and Birch's (1954) view of the environment (their figures 1.01 and 1.02), based on many years of experience in insect

ecology. Pulliam (1988) developed this view into a picture of the environment as consisting of source habitats (good ones) that produce most of the surviving offspring and sink habitats (bad ones) that contribute little. A good, early example of this sort of population structure was described by Connell (1961), who demonstrated that only a small portion of the population of barnacles living in the rocky intertidal in Scotland, living in the most favourable habitat, was responsible for the great majority of offspring produced. Since then a few other cases of source-sink population structure have been documented, including great and blue tits (Dhont *et al.*, 1990), reindeer (Bergerud, 1988) and northern elephant seals (Reiter and Le Boeuf, 1991).

Sink-source population structure results in dependence of the optimal phenotype in one habitat on the quality and frequency of the other habitats. There is some evidence that organisms adjust their life histories quite flexibly to react to *relative* differences in the quality of different habitats. Charnov *et al.* (1981) found that the sex ratio of eggs laid by parasitoid wasps on the larvae of beetles living inside seeds of grain changed with the size of the larvae, laying males into small larvae and females into large ones, and they found further that the definition of what is large and what is small varied with the frequency of the size classes of seeds encountered in the recent past. Results obtained by Wright *et al.* (1988) suggest that female mice adjust the sex ratio of their offspring in response not to their absolute food intake and physiological conditions, but to their condition relative to that of other females in the group and to the position in social hierarchy.

In a spatially heterogeneous environment, adaptations should be more precise in the better and in the more frequent habitats and less precise in infrequent habitats and in habitats where reproductive performance is poor. In good, frequent habitats there should be less genetic variation around the presumed optimum. Stearns and Sage (1980) found that mosquitofish living in a small, peripheral freshwater habitat connected to a large, brackish habitat were poorly adapted to the freshwater habitat and well adapted to the brackish one. In a population of blue tits living in a mosaic environment, the reproductive phenology of individuals breeding in good habitat was well synchronized with food availability, whereas individuals breeding in the poor habitat were apparently maladapted. Another population of tits confined to poor habitat with no good habitat available was well adapted to the conditions of the poor habitat (Blondel *et al.*, 1992).

#### *Potential applications and tests*

A pessimistic conclusion that our model holds for field studies is that the fitness effect of an adaptation in a particular set of environmental conditions cannot be measured precisely without knowledge of the conditions encountered by all population members and their performance in all situations. In a given habitat (say, oak forest), whether it is better to lay a clutch of five or seven may depend, through the discounting factor (the rate of increase of the best genotype calculated across all habitats), on the dispersal of offspring among habitats (e.g. how many live in oak forest, and how many in pine forest). Such data would be particularly hard to get for a species with a large continuous range in which only arbitrary boundaries can be drawn between populations and the movement of individuals forces us to consider the whole species as one population.

An optimal value for a trait in a particular habitat might also be found by using reproductive value with a discounting factor inferred from the population growth rate, as done successfully by Daan *et al.* (1990) to predict the correlation between food abundance, laying date, and clutch size in kestrels. This, however, could mislead because the actual population growth rate can differ from the genotypic rate of increase of the optimal reaction norm, and thus the robustness of predictions to changes in the discounting factor should be examined. Our model also suggests

that lifetime reproductive success can be used to predict qualitatively how a trait should change along a spatial environmental gradient.

It is not easy to find data that could be used to distinguish between the model presented here and that put forth by Stearns and Koella (1986), primarily because data on the quality and frequency of habitats are rare and exact data on the shape of tradeoffs are difficult to obtain even in the laboratory. However, some qualitative predictions that differ between the two models can be made and tested. For example, our model predicts that, independently of other life history parameters, the optimal age at maturity should not vary across habitats that differ only with respect to egg or hatchling mortality (i.e. mortality occurring far before maturation is possible). The Stearns and Koella model would predict early maturity when egg mortality is lower.

Another test takes advantage of a prediction concerning the reproductive value of newborn in each habitat. One can manipulate the (presumably optimized) life history trait in a series of different habitats and see whether the trait actually expressed leads to the highest reproductive value for newborn in that habitat. Daan *et al.* (1990) have shown how the consequences of such a manipulation could be measured for clutch size in kestrels, and Sinervo (1990) has carried out analogous manipulations for size at hatching in lizards.

### Conclusion

The growing number of papers on environmental heterogeneity and phenotypic plasticity reflects the increasing recognition of their importance in evolution. We show that in a spatially heterogeneous environment, the fitness of a phenotype expressed in a given habitat cannot be defined except in the context of the environmental variation encountered by the whole population. This result emphasizes the need for thorough studies of natural source-sink populations and their reaction norms.

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**Appendix: optimal reaction norms for clutch size in an iteroparous organism**

$J(h, r_c)$  as defined in Equation 7 for the organism described in Example 2 becomes

$$J(h, r_c) = \sum_{x=\alpha}^{\infty} S_j (S_{in} S_{ex})^{x-\alpha} e^{-rx} F = \frac{S_j e^{-r\alpha} F}{1 - S_{in} S_{ex} e^{-r}} \quad (\text{A1})$$

Setting  $dJ/dF = 0$  yields the equation

$$1 = S_{ex} e^{-r_c} \left( S_{in} - \frac{dS_{in}}{dF} F \right) \quad (\text{A2})$$

defining the optimal clutch size  $F^*$  if  $r_c$  is replaced by the genotypic rate of increase of the optimal reaction norm  $r^*$  (to be found using Equation 6). The equation does not contain  $S_j$ , and thus variation in juvenile survival does not affect optimal clutch size: the corresponding optimal reaction norm is flat. To find out how the optimal clutch size changes with  $S_{ex}$  its derivative with respect to  $S_{ex}$  must be calculated by differentiating Equation A2:

$$\frac{\partial F^*}{\partial S_{ex}} = \frac{S_{in} - (dS_{in}/dF)F^*}{(d^2 S_{in}/dF^2)S_{ex}F^*} < 0 \quad (\text{A3})$$

(recall that both first and second derivative of  $S_{in}$  with respect to  $F$  are negative). Hence, the optimal reaction norm for clutch size is a decreasing function of extrinsic adult survival.

Applying the Euler-Lotka equation to each set of conditions separately (setting  $J(h, r_c)=1$ ) leads to different predictions. Rearranging Equation A2 yields

$$e^{r_c} = S_{ex} \left( S_{in} - \frac{dS_{in}}{dF} F \right) \quad (\text{A4})$$

Substituting Equation A4 into Equation A1 and setting  $J(h)=1$  gives

$$1 = \frac{-S_j}{S_{ex}^{\alpha} (S_{in} - (dS_{in}/dF)F_{EL})^{\alpha-1} dS_{in}/dF} \quad (\text{A5})$$

where  $F_{EL}$  is the predicted clutch size. The derivative of  $F_{EL}$  with respect to  $S_j$  is

$$\frac{\partial F_{EL}}{\partial S_j} = \frac{(dS_{in}/dF)(S_{in} - (dS_{in}/dF)F)}{S_j(d^2 S_{in}/dF^2)(S_{in} - \alpha(dS_{in}/dF)F)} > 0 \quad (\text{A6})$$

which means increasing clutch size with increasing juvenile survival. The derivative of  $F_{EL}$  with respect to  $S_{ex}$  is

$$\frac{\partial F_{EL}}{\partial S_{ex}} = \frac{-\alpha(dS_{in}/dF)(S_{in} - (dS_{in}/dF)F)}{S_{ex}(d^2 S_{in}/dF^2)(S_{in} - \alpha(dS_{in}/dF)F)} < 0 \quad (\text{A7})$$

Thus, similarly to Equation A3 a decrease of the optimal clutch size with increasing adult mortality is predicted. Dividing  $\partial F^*/\partial S_{ex}$  by  $\partial F_{EL}/\partial S_{ex}$  yields

$$\frac{\partial F^*/\partial S_{ex}}{\partial F_{EL}/\partial S_{ex}} = 1 - \frac{S_{in}}{\alpha(dS_{in}/dF)F} > 1 \quad (\text{A8})$$

and since both derivatives are negative this means

$$\frac{\partial F^*}{\partial S_{ex}} < \frac{\partial F_{EL}}{\partial S_{ex}} \quad (\text{A9})$$

i.e. faster decrease of clutch size with increasing adult extrinsic survival predicted by the method developed in this paper than predicted using the Euler-Lotka equation.