

Adaptation and constraint in the evolution of environmental sex determination

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Abstract

When environments differentially influence male and female performance, environmental sex determination (ESD) might evolve. The conclusion from several previous theoretical models was that reaction norms for sex determination should have a single, sharp threshold, with only females being produced in some environments and only males in others. These reaction norms can be disadvantageous in fluctuating environments, however, because they lead to sex-ratio fluctuations. We analysed the evolution of ESD, looking for equilibrium strategies in unconstrained as well as constrained strategy spaces. We identified situations where a single-threshold reaction norm is not evolutionarily stable. In these cases, we found stable strategies in the form of complex reaction norms, showing an oscillatory pattern of sex determination with respect to variation in an environmental variable. Considering that constraints could prevent such phenotypes from being realized, we found that certain randomized reaction norms, with probabilistic sex determination for a range of environments, would achieve nearly the same fitness. We also investigated reaction norms constrained to have a single threshold and found that genetic polymorphism in the environmental threshold value could evolve, producing a similar effect as a randomized reaction norm. We argue that the appearance of genetic variation can be regarded as an alternative outcome when constraints prevent the evolution of a more complex or a randomized strategy.

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1. Introduction

Environmental sex determination (ESD) is a form of phenotypic plasticity, where an individual's sex is determined by environmental cues. Organisms may experience variation in conditions like temperature or nutrient availability during development, which can influence their performance as adults. Although certain environments will be more favorable, one sex may gain relatively more by developing in these conditions, whereas the other sex may lose less by developing in unfavorable circumstances. When the differential fitness effects are sufficiently strong, environmental conditions could become used as cues for sex determination. This possibility is an important ingredient in the traditional

explanation for the occurrence of ESD, originally put forward by [Charnov and Bull \(1977\)](#).

In some theoretical models of the evolution of ESD, sex was found to be a threshold trait, determined by a quantitative environmental variable ([Bull, 1981b, 1983](#); [Bulmer and Bull, 1982](#); [Charnov and Bull, 1989](#)). For these models, the outcome is that one sex is produced in environments where the variable is above a threshold and the other sex below the threshold, according to which gains relatively more from high or low values. Similar results were obtained for other models with discrete classes of environments or patch types, with only one sex being produced in patch types favoring that sex, except that both sexes may be produced in a single, intermediate condition ([Bull, 1981a](#); [Charnov and Bull, 1985, 1989](#)). When there are many patch types, such sex-determination strategies will approach those for continuously varying environments. The results are analogous to what has been found for the parental control of

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sex ratio envisaged by Trivers and Willard (1973), where females determine the sex of offspring based on an environmental variable or phenotypic condition (Charnov et al., 1981; Charnov, 1982). A basic assumption behind such results is that the sex-determining environmental conditions experienced by different individuals in the same mating group are statistically independent.

When these conditions are correlated, however, strategies with a single, sharp threshold that relates sex to environmental condition may suffer from fluctuations in the adult sex ratio of mating groups. These can be detrimental to the reproductive success of individuals of the sex in excess in a particular group. The reason for correlated conditions could be large-scale environmental fluctuations over time, affecting all members of a cohort, but local fluctuations can also have this effect, provided there is limited dispersal of individuals from juvenile development to mating.

For situations where ESD with a sharp threshold would lead to pronounced sex-ratio fluctuations, there may be other outcomes. One possibility is that ESD is abandoned, through a transition to genetic sex determination (GSD). This idea was developed by Bulmer and Bull (1982), who argued that genes with major effects on sex determination could invade if environmental fluctuations were strong compared to differential developmental advantages of the sexes. Subsequent theoretical investigation has confirmed that GSD could evolve in this manner (Van Dooren and Leimar, 2003). Another possibility is that strategy evolution leads to increasing randomness in sex determination, so that both sexes are produced over a wider range of environmental conditions.

It is well known that fluctuating environments can favor the evolution of mixed strategies (Haccou and Iwasa, 1995; McNamara, 1995; Sasaki and Ellner, 1995), sometimes referred to as bet-hedging. For sex determination, this could mean a strategy with even chances of becoming either sex or, more generally, a randomized reaction norm where the probability varies with environmental conditions. This latter type has been analysed for the special case of two patch types, for which Bull (1981a) found that more pronounced fluctuations over time in the frequencies of patch types resulted in a larger parameter region where both sexes were produced in one of the patches. More recently, Van Dooren and Leimar (2003) studied the evolution of sigmoid-shaped reaction norms for ESD in a metapopulation setting. They found that gradually sloping reaction norms could evolve in situations where a sharp threshold would lead to pronounced local sex-ratio fluctuations. Nevertheless, the general question of whether one should expect environmental fluctuations to select for a component of randomness in the expression of phenotypic plasticity has been rather little studied (Walker, 1986; Haccou and Iwasa, 1995; Van Dooren, 2001).

Genetic polymorphism and mixed strategies are both capable of producing a mixture of phenotypes and tend to be favored by similar circumstances (Maynard Smith, 1982; Sasaki and Ellner, 1995), so they could be regarded as alternative evolutionary outcomes. Mixtures of phenotypes might also result from a randomized reaction norm, as well as from a multi-threshold reaction norm that oscillates between alternative phenotypes as one increases the value of an environmental variable. In this work, we compare these different ways in which population mixtures might appear, in the context of the evolution of sex determination. We also investigate if genetic polymorphism is more likely to appear when constraints prevent the evolution of an appropriate randomized or oscillating reaction norm, which might correspond to a phenotype that is difficult to realize. Our general aim is to shed light on the nature of evolutionarily stable sex determination strategies in fluctuating environments, and to discuss to what extent these strategies might be attained or, at least, approximated by real organisms.

2. The model

Our model is similar to the one studied by Van Dooren and Leimar (2003). During a sensitive period of development, environmental conditions are used as cues for sex determination. A strategy x consists of probabilities x_i of becoming female in condition e_i . For mathematical convenience, we assume a finite number of conditions, for instance $e_i = i\delta$, $i = -i_0, \dots, i_0$, $\delta > 0$. With many finely spaced values this can approximate continuous variation. Development in e_i affects the adult phenotype and thus the competitive ability. We use f_i and m_i to denote the competitive abilities of females and males reared in e_i (Fig. 1a) and interpret them as probabilities of successfully delivering a gamete when a reproductive opportunity arises.

Local environmental fluctuations are modeled using a metapopulation distributed over N patches. A patch is characterized by an environmental condition E_j , and the particular e_i of an individual developing in the patch is drawn from a conditional distribution $\hat{h}_{i|j}$. In our examples, the patch environments are given by $E_j = j\delta$, $j = -j_0, \dots, j_0$, and the individual deviations $e_i - E_j$ can take values $k\delta$, $k = -k_0, \dots, k_0$, so that $i_0 = j_0 + k_0$. Generations are non-overlapping and, for each generation, the E_j are drawn from a distribution g_j . Per patch, a fixed number K of new individuals are formed. The probability that a random metapopulation member develops in e_i is then

$$h_i = \sum_j \hat{h}_{i|j} g_j \quad (1)$$

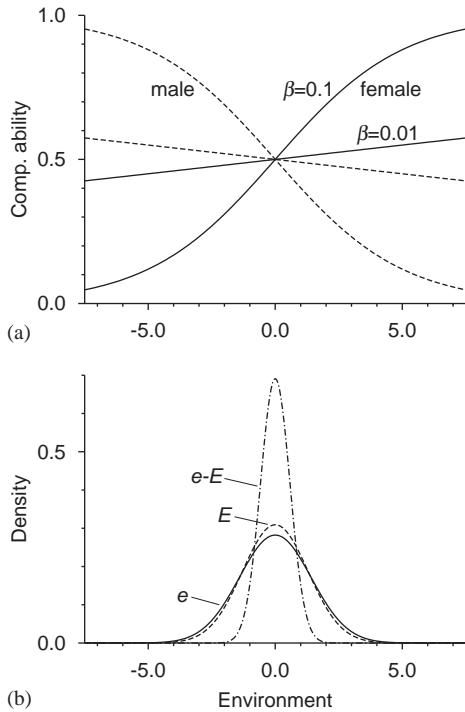


Fig. 1. (a) Two examples of individual competitive abilities, as functions of e . The female curves, $f(e) = 1/(1 + \exp(-4\beta e))$, are labeled with the slope at $e = 0$ and the corresponding (dashed) male curves, $m(e) = 1/(1 + \exp(4\beta e))$, have negative slopes at $e = 0$; (b) the distributions of the environmental variables, portrayed as densities for a case with many finely spaced environmental conditions ($\delta = 0.0125$, $i_0 = 720$, $j_0 = 480$, $k_0 = 240$). The distribution of the within-patch deviation $e - E$ has variance $\sigma_{e-E}^2 = \frac{1}{3}$, the distribution g of the patch variable E has variance $\sigma_E^2 = \frac{5}{3}$ (dashed curve), and the resulting distribution h (solid curve) of the individual variable e has variance $\sigma_e^2 = 2$. The distributions have Gaussian shapes.

(see Fig. 1b). Development occurs in the patch of conception, without juvenile mortality, after which an individual has probability p of dispersing to a random patch. In each patch, adults contribute to reproduction in proportion to their competitive abilities. At a point in time after migration but before reproduction, the probability that an individual competing for reproduction in an E_j patch has developed in condition e_i is

$$\tilde{h}_{ij} = (1 - p)\hat{h}_{ij} + ph_i. \tag{2}$$

We assume that N and K are both very large, so that Eqs. (1) and (2) approximate the distributions of e_i for the individuals actually present in a given generation. For a population with strategy x , we can then define per capita female and male competitive abilities in an E_j patch as

$$\phi_j(x) = \sum_i f_i x_i \tilde{h}_{ij}, \tag{3}$$

$$\psi_j(x) = \sum_i m_i (1 - x_i) \tilde{h}_{ij}. \tag{4}$$

The reason for the terminology is that a female with competitive ability f_i would have reproductive success f_i/ϕ_j relative to the expected female reproductive success of a random individual in the patch. The corresponding quantity for a male is m_i/ψ_j .

2.1. Invasion fitness

From our simplifying assumptions, the rearing conditions of parents and offspring are statistically independent. This means that reproductive success measured as the expected number of offspring, weighted by genetic contribution, is a relevant fitness measure. Suppose a small proportion of individuals use a mutant strategy x' and the remainder the resident strategy x . Provided that the mutant proportion is small in each patch, the expected reproductive success of a random mutant individual attempting to reproduce in an E_j patch is

$$\begin{aligned} R_j(x', x) &= \frac{1}{2} \sum_i \left[\frac{x'_i f_i}{\phi_j(x)} + \frac{(1 - x'_i) m_i}{\psi_j(x)} \right] \tilde{h}_{ij} \\ &= \frac{1}{2} \left[\frac{\phi_j(x')}{\phi_j(x)} + \frac{\psi_j(x')}{\psi_j(x)} \right]. \end{aligned} \tag{5}$$

The factor one-half is present because each parent contributes half of an offspring's genes. By averaging over the distribution of E_j , we get the overall expected mutant reproductive success as

$$R(x', x) = \sum_j R_j(x', x) g_j. \tag{6}$$

The relative rate of increase of the mutant gene, when small, is given by the logarithm of $R(x', x)$. If gene flow from inter-patch migration keeps the frequency of the mutant gene spatially homogeneous, we can regard $\log R(x', x)$ as the invasion fitness of the mutant (Metz et al., 1992). For very low rates of migration, gene frequencies may differ between local populations, and it is not clear that Eq. (6) can be used as a basis for invasion fitness. However, since Eq. (6) will describe the change of mutant frequency in the migrant pool, it can be used for any given $p > 0$, provided that N and K are large enough that the influx of migrants to a patch can be viewed as a deterministic process. For the special case of no migration ($p = 0$), each subpopulation of the metapopulation evolves independently in a temporally fluctuating environment. In such a situation we should use geometric mean reproductive success to determine the possibility of mutant invasion (Lewontin and Cohen, 1969). Thus,

$$G(x', x) = \sum_j \log[R_j(x', x)] g_j \tag{7}$$

is an appropriate invasion fitness when $p = 0$.

We can view each x_i as a quantitative character that can vary over the range $0 \leq x_i \leq 1$. For the analysis of

evolutionary stability we will make use of the selection gradient, which consists of the partial derivatives of invasion fitness with respect to mutant traits, evaluated at $x' = x$. From Eq. (5) we see that $R_f(x, x) = 1$, implying that the selection gradient is given by

$$s_i(x) = \left. \frac{\partial R(x', x)}{\partial x'_i} \right|_{x'=x} = \frac{1}{2} \sum_j \left[\frac{f_i}{\phi_j(x)} - \frac{m_i}{\psi_j(x)} \right] \tilde{h}_{ij} g_j, \quad (8)$$

both for invasion fitness $\log R(x', x)$ and for invasion fitness $G(x', x)$. The selection gradient turns out to be equal to the gradient of a real-valued function defined on the space of strategies, namely the function

$$P(x) = L(\phi(x)) + L(\psi(x)) \quad (9)$$

with

$$L(y) = \frac{1}{2} \sum_j \log(y_j) g_j, \quad (10)$$

since we have

$$s_i(x) = \frac{\partial P(x)}{\partial x_i}. \quad (11)$$

The reason it is possible to write s as the gradient of a function on the trait space is that the reproductive success (5) has the special Shaw–Mohler form (Shaw and Mohler, 1953), where the contribution of a mutant strategy to the next generation is expressed as a sum of mutant/resident ratios of functions of male and female traits.

3. Evolutionary stability

When evaluating the evolutionary stability of a strategy x^* , we will consider both uninvadability (i.e., whether $F(x', x^*) \leq F(x^*, x^*)$ for all mutant x' , where F is invasion fitness) and convergence stability. For our model, invasion fitness depends on the strategies through ϕ and ψ and the same is true for the function $P(x)$ in Eq. (9). We will make use of this dependence to develop our main theoretical result, namely that there is a unique pair (ϕ^*, ψ^*) of evolutionarily stable per capita competitive abilities, in the sense that a strategy x^* is an ESS if and only if $\phi(x^*) = \phi^*$ and $\psi(x^*) = \psi^*$. There will be at least one such strategy x^* , but in degenerate cases a set of relatively neutral strategies can satisfy the condition.

To see this result, we first study maxima of the function P (a more rigorous treatment appears in the appendix). Note that P is a concave function, defined on a convex set of strategies x , so we can deduce that P has a maximum on the trait space. Since P is a weighted sum of logarithms of the per capita competitive abilities, and the logarithm is strictly concave, it also follows that there is a unique pair (ϕ^*, ψ^*) such that $\phi(x^*) = \phi^*$ and $\psi(x^*) = \psi^*$ for a maximizing x^* . Any such x^* must

satisfy the condition

$$\begin{aligned} s_i(x^*) &\leq 0 && \text{when } x_i^* = 0, \\ s_i(x^*) &= 0 && \text{when } 0 < x_i^* < 1, \\ s_i(x^*) &\geq 0 && \text{when } x_i^* = 1. \end{aligned} \quad (12)$$

The concavity of P also implies that condition (12) is sufficient for a maximum, so that x^* maximizes P if and only if condition (12) holds.

Next, a necessary condition for x^* to be uninvadable is that the selection gradient satisfies condition (12). This applies to both $\log R(x', x^*)$ and to $G(x', x^*)$. The reproductive success $R(x', x^*)$ depends linearly on x' , so that

$$R(x', x^*) = R(x^*, x^*) + \sum_i s_i(x^*) (x'_i - x_i^*). \quad (13)$$

Using this we can conclude that $R(x', x^*) \leq R(x^*, x^*)$ for all x' when condition (12) holds, so the condition is also sufficient for uninvadability. From Jensen's inequality it follows that $G(x', x^*) \leq \log R(x', x^*)$, so $G(x', x^*) \leq G(x^*, x^*)$ for all x' when condition (12) holds. This verifies our result with respect to uninvadability.

Concerning convergence stability (Eshel and Motro, 1981; Eshel, 1983; Christiansen, 1991), we need to take into account that the trait space, which consists of the x with $0 \leq x_i \leq 1$, is multidimensional. Because the selection gradient has the form given in Eq. (11), an x^* that maximizes $P(x)$, i.e. one that satisfies condition (12), will be absolutely convergence stable (Leimar, 2001) (alternatively, if a set of strategies satisfy condition (12), that set will be absolutely convergence stable). Briefly, since the selection gradient satisfies Eq. (11), gradual evolutionary change must increase $P(x)$, eventually approaching a maximizing x^* . The verification of our result is then complete.

To gain an intuitive understanding of evolutionary change in the trait space, it is helpful to think in terms of x being mapped to $(\phi(x), \psi(x))$, which in turn are mapped to a value of P . As x ranges over all possible strategies, the corresponding (ϕ, ψ) range over some set and (ϕ^*, ψ^*) is the point in this set for which P has the maximal value. If x maps to (ϕ, ψ) that are very close to (ϕ^*, ψ^*) , the selection gradient will be very small at x , leading to weak selection for further change in x . As we will illustrate in the examples, there may be strategies x that are seemingly quite different from an ESS x^* but map to (ϕ, ψ) that are very close to (ϕ^*, ψ^*) .

For a constrained trait space, consisting of some subset of all possible x , one can ask how closely (ϕ^*, ψ^*) can be approximated with a strategy from the subset. Gradual evolution tends to increase $P(x)$ toward a maximal value on the subset. Without further conditions on the subset, it is not certain that a strategy \hat{x} corresponding to a constrained maximum is uninvadable for mutants x' belonging to the subset. If the subset

is convex, it is rather easy to see that \hat{x} must be uninvadable within the subset, but for a non-convex subset there may be disruptive selection at \hat{x} , in which case genetic polymorphism could evolve. Nevertheless, if a constrained maximum is close to that given by (ϕ^*, ψ^*) , uninvadability will hold as an approximation, and there will be little reason to expect further evolutionary change.

4. Examples of ESSs

Although our model can be applied to situations with just a few environmental conditions, our aim here is to consider many finely spaced values of e . For the dependence of competitive ability on e , we use the functions illustrated in Fig. 1a. These f and m have opposite slopes, which introduces a symmetry with respect to female/male advantage and positive/negative e , but our qualitative results do not depend on this assumption. For the distributions of environmental variables, we use discrete versions of Gaussian distributions (Fig. 1b), but also distributions with non-Gaussian shapes. To compute equilibria, we implemented gradual evolutionary change numerically, using the selection gradient, in this way searching for maxima of the function $P(x)$. Our approach corresponds to an adaptive dynamics approximation of gradual evolutionary change (Dieckmann and Law, 1996; Geritz et al., 1998), where an evolutionary sequence is built up of mutations of small effect that invade and replace resident strategies.

A notable fact about our model is that constrained strategies can be rather different from an unconstrained ESS, while at the same time being close in terms of fitness (Fig. 2). The explanation for this lies in the convolution-like nature of the transformation (3), (4) from strategy to per capita competitive abilities. When this transformation acts to smooth out irregularities or oscillations in a reaction norm, an oscillating x can give rise to very similar ϕ and ψ as an x that varies in a simpler fashion. Since the strength of selection to replace one strategy with another only depends on differences in ϕ and ψ , those strategies with very similar ϕ and ψ will be effectively neutral relative to each other. In such a case, the strategy that actually evolves ought to be a matter of what most readily can be implemented by a particular organism.

From our theoretical results, we know that the equilibrium per capita competitive abilities in Fig. 2 are unique, and our investigations also suggest that the unconstrained ESS is unique (see the appendix). Furthermore, we found that different starting x for the evolutionary sequence in our computation lead to the same maximizing x^* (to get a starting x , each x_i was drawn from the uniform distribution on the unit

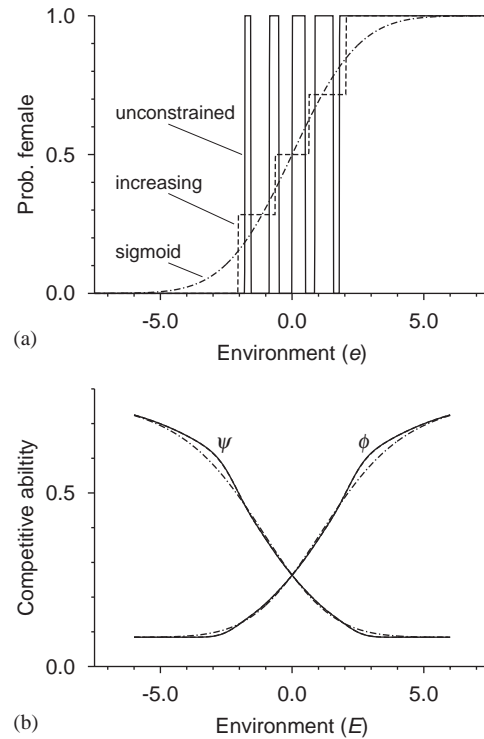


Fig. 2. (a) Equilibrium reaction norms in three strategy spaces, with either unconstrained, increasing, or sigmoid reaction norms with shapes like cumulative normal distributions. In the unconstrained space there is a unique ESS (defined as being uninvadable and convergence stable) that has a number of abrupt switches between only males and only females. In the space of increasing functions, there is a unique ESS with a number of discrete upward steps. Among the sigmoid reaction norms we found a similar-looking, smoother function that is convergence stable but may fail to satisfy uninvadability. Competitive abilities are as in Fig. 1a with $\beta = 0.1$, environmental distributions as in Fig. 1b, and $p = 0.3$; (b) corresponding patch-level per capita female (ϕ_j) and male (ψ_j) competitive abilities (for the unconstrained and increasing strategy spaces, they are almost identical). The values of the function $P(x)$ for the three strategies are -1.362169 (unconstrained), -1.362176 (increasing) and -1.362769 (sigmoid).

interval). For the unconstrained ESS in Fig. 2, x_i^* is either zero or one for the great majority of e_i , but for conditions where there is a switch between zero and one, the x_i^* are intermediate. We also computed ESSs for successively finer spacings between the e_i , and these seem to approach a limiting form with a finite number of abrupt switches, as the one illustrated in Fig. 2. Thus, for continuously varying e one would expect a reaction norm lacking randomization. We found the same qualitative form of the ESS also with other shapes than Gaussian for the environmental distributions, suggesting that this kind of ESS may be rather typical.

Of the two constrained equilibria in Fig. 2, the increasing strategy is very close to x^* in term of fitness, although it prescribes intermediate x_i for a substantial range of e_i . Because the subset of reaction norms consisting of increasing functions of e is convex, we

know that this strategy is uninvadable within the subset. The sigmoid strategy is constrained to the shape of a cumulative normal distribution, which corresponds to a two-dimensional, non-convex subset. Based on the theory in the previous section we cannot conclude uninvadability within the subset, but since the value of $P(x)$ for this strategy is rather close to the unconstrained maximum, selection for further modification will not be strong.

4.1. Weak environmental effects

When the environment has a weak effect on competitive ability, one can ask to what extent equilibrium sex-determination strategies will be close to Fisherian. One way to investigate the issue is to assume that f and m have small slopes and look for equilibria in the subset of ‘linear’ reaction norms of the form

$$x_i = 0.5 + a + be_i, \tag{14}$$

where $|a|$ and $|b|$ are small enough that $0 \leq x_i \leq 1$ for all e_i (this defines a convex subset). Assuming that $f(e_i) \approx 0.5 + \beta_f e_i$ and $m(e_i) \approx 0.5 + \beta_m e_i$, where $|\beta_f|$ and $|\beta_m|$ are small, a straightforward calculation gives the equilibrium constrained strategy as $a \approx 0$ and

$$b \approx \frac{\sigma_{e|E}^2 + p(2-p)\sigma_E^2}{2(1-p)^2\sigma_E^2} (\beta_f - \beta_m), \tag{15}$$

where p is the migration rate and $\sigma_{e|E}^2$ and σ_E^2 are variances of environmental distributions. Fig. 3 shows two examples of numerically computed ESSs where the competitive abilities have small slopes. The reaction

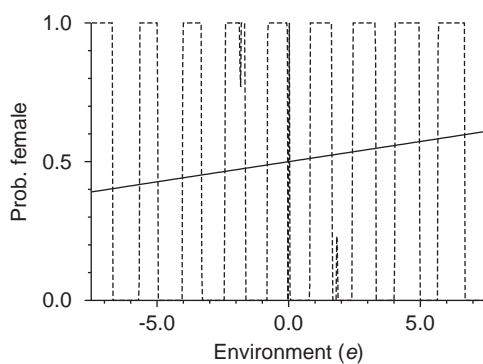


Fig. 3. ESS reaction norms for weak environmental effects (f and m as in Fig. 1a with $\beta = 0.01$) and two shapes of the environmental distributions. For the solid line, the distributions (depicted in Fig. 1b) have Gaussian shapes. For the dashed line, with many switches between only males and only females (and some additional oscillation), the distributions are platykurtic (having the same variances as in Fig. 1b and obtained by superimposing two Gaussians, centered at, respectively, plus/minus the width parameter of each). Although the two strategies seem very different, the corresponding (ϕ, ψ) are quite similar (not shown), as are the maximal values of the functions $P(x)$ for the two cases (-1.386114 vs. -1.386107).

norm for Gaussian distributions is close to the result of the above calculation for linear reaction norms. For the other example, the shape of the distributions was changed to platykurtic (but with the same variances as before), and the ESS shows a pattern of abrupt shifts between only males and only females, as well as some additional oscillations. Although this strategy appears different from a linear reaction norm, it is in fact very close in terms of fitness to the corresponding constrained strategy. At any rate, the reaction norms in Fig. 3 are not of the kind where one sex is produced above a threshold and the other below it.

4.2. Single-threshold reaction norms

To see when a single-threshold reaction norm is an ESS, we have checked over a range of parameter values whether such a strategy fulfills condition (12). As can be seen in Fig. 4, a single-threshold reaction norm is an ESS when p is high and/or when f and m differ strongly in their dependence on environmental conditions. Concerning the environmental distributions, a single-threshold reaction norm is an ESS for large variance $\sigma_{e|E}^2$ of the within-patch individual deviation in relation to the between patch variance σ_E^2 .

A threshold pattern of morph determination has frequently been postulated, both for the two sexes and for other morphs (Roff, 1996; Lynch and Walsh, 1998), so it may be of interest to inquire about the evolutionary outcome in our model when strategies are constrained to be of a single-threshold kind (for discrete conditions we could use $x_i = 0$ for $i < i_s$, $x_i = 1$ for $i > i_s$ and $0 \leq x_i \leq 1$,

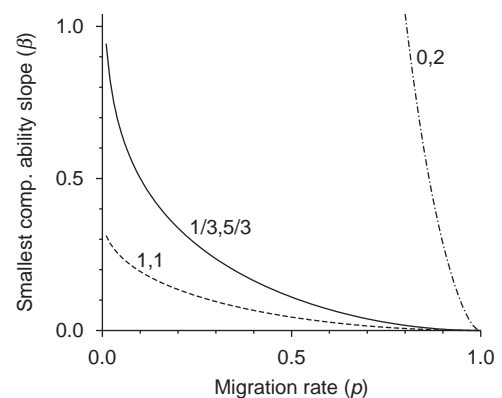


Fig. 4. Examples of parameter regions where a single-threshold strategy ($x_i = 0$ for $i < 0$, $x_0 = 0.5$, and $x_i = 1$ for $i > 0$) is an ESS. For given, positive p , the strategy is an ESS when the slope β of f is above the curve (assuming the slope of m is $-\beta$; Fig. 1a). The curves are labeled with the variances $\sigma_{e|E}^2, \sigma_E^2$ of the environmental distributions (Fig. 1b). The curves have been computed for $p = 0.01, 0.02, \dots, 1.00$, but not for $p = 0$. Without migration, a single-threshold strategy will never be an ESS for the environmental distributions used here, so the curves tend towards infinity as p goes to zero.

with ‘threshold’ at $e = e_{i_s} + (1 - 2x_{i_s})\delta$. This subset of strategies is one dimensional and can be parametrized with the location e of the threshold. For competitive abilities as in Fig. 1a, one can show that the reaction norm with threshold at $e = 0$ will maximize $P(x)$ and thus be convergence stable in the constrained subset. However, the subset is not convex, so we cannot conclude that this strategy is uninvadable within the subset. For parameter values where a single-threshold strategy is an ESS (Fig. 4), uninvadability will of course hold, but otherwise the convergence stable x will typically be exposed to disruptive selection, which is illustrated in Fig. 5a.

When there is disruptive selection, genetic variation will accumulate. One possibility is evolutionary branching (Geritz et al., 1998) of alleles coding for threshold location, possibly leading to GSD (Bulmer and Bull, 1982; Van Dooren and Leimar, 2003), but the outcome could also be intermediate between environmental and genetic sex determination, with a distribution of

reaction-norm genotypes. Less genetic variation in the location of the threshold is expected when a single-threshold reaction norm is an ESS, although a certain amount will be present in mutation-selection balance. To illustrate these points, we performed individual-based simulations corresponding to the two cases in Fig. 5a. The resulting equilibrium cumulative distributions in Fig. 5b can be interpreted as population average reaction norms, giving the probability that an individual with random genotype would develop into a female if reared in condition e . Comparing with the reaction norms in Fig. 2, there is rough agreement between the cumulative distribution for the case corresponding to disruptive selection in Fig. 5 and the constrained equilibrium for increasing reaction norms in Fig. 2 (the model parameters are the same for these). Thus, depending on the nature of constraints, genetic polymorphism can play a similar role as strategic randomization.

5. Discussion

An important characteristic of sex-determination strategies in fluctuating environments is that they can have the effect of dampening fluctuations in the sex ratio of mating groups. Such strategies may evolve when sex-ratio fluctuations would otherwise be greater than is warranted by differences in competitive ability. We found ESSs where the dampening effect was achieved by seemingly complex reaction norms, with several abrupt switches between only males and only females, but in these cases we also found gradually varying, randomized reaction norms with nearly the same fitness. The interpretation would be that the precise oscillating shape of such an ESS represents adaptive fine tuning, perhaps with little practical relevance. Nevertheless, these strategies illustrate that direct randomization is not the only way of producing a more stable distribution of sexual morphs: a reaction norm that varies in an oscillating manner with environmental conditions can also have this property.

There are several ways in which organisms might achieve effects like those of a randomized reaction norm. One possibility is that morph determination is influenced by developmental noise (Van Dooren and Leimar, 2003), and another could be that several environmental variables influence morph determination, with some of these variables being approximately uncorrelated between individuals in the same mating group. A somewhat different possibility is that the organism’s response to environmental conditions is of a threshold type, but that the within-patch variability in environmental conditions is modified by an evolutionary change in another trait. For instance, although a developing individual may have little possibility to

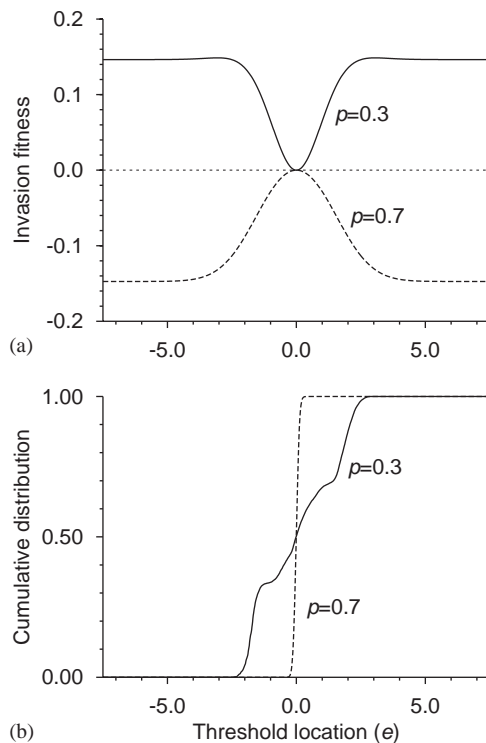


Fig. 5. (a) Invasion fitness of single-threshold x' (with threshold at e) for resident single-threshold x (with threshold at 0). Two cases, labeled with the migration rate, illustrate disruptive and stabilizing selection at a convergence stable equilibrium (other parameters as in Fig. 2). The cases correspond to points below ($p = 0.3$) and above ($p = 0.7$) the solid line in Fig. 4; (b) equilibrium genetic variation in threshold location from individual-based simulations with constrained, single-threshold strategies, corresponding to the two cases. The curves are empirical cumulative distributions of individual threshold locations, determined by a diploid locus ($N = 100$, $K = 500$, mutation rate = 0.001, and SD of mutational increments in location value = 0.1; dominance between alleles could also evolve).

influence its rearing conditions, it is possible that mothers could be responsible for such variability, perhaps through variability in their preferences for egg-laying sites. We found that a single-threshold reaction norm is favored by greater within-patch to between-patch environmental variability, and one way of viewing this result is that the within-patch variability has the effect of producing a sufficiently stable distribution of sexual morphs.

If constraints prevent organisms from evolving adaptations with the effect of producing a sufficiently stable distribution of sexual morphs, genetic variation may play the role of an alternative. Complete genetic sex determination will prevent any influence of the rearing environment, but genetic variation in constrained reaction norms represents a wider spectrum of possibilities. For reaction norms with a single, sharp threshold, we found that an accumulation of genetic variation in the location of the threshold could approximate the action of a well-adapted randomized reaction norm. This is an illustration of the general point that constraints can be important for the buildup of genetic variation. When constraints prevent strategies from evolving near to an ESS, there is scope for stronger disruptive selection, which in turn may lead to genetic polymorphism.

Several of the features of ESD that we have discussed correspond to empirical observation, such as variability in the slope of reaction norms (Girondot, 1999; Shine et al., 2002), influence of several variables on reaction norms (Bowden et al., 2000), variability in egg-laying preferences (Janzen and Morjan, 2001), and genetic variation in reaction norms (Rhen and Lang, 1998; Shine et al., 2002). Although it is not known if any of these features evolved in response to sex-ratio fluctuations of local mating groups, our analysis suggests that this could be the case. Concerning GSD, which is very wide spread, it is not known whether its emergence sometimes was related to sex-ratio fluctuations.

Apart from sex determination, our results may have bearing on the general issue of randomization in decision making. If an individual has two or more strategic options, but also some 'private' information about the relative value of the options, one might expect a strategy where the individual chooses the option with highest value to evolve, rather than a mixed strategy. In classical game theory, this idea has been expressed in the form of the celebrated Harsanyi purification theorem (Harsanyi, 1973; Binmore, 1992). A basic assumption for the theorem is that the private variables of different players of the game are statistically independent. Our analysis suggests that the applicability of the idea is limited to this case. When the private variables of interacting individuals are correlated, randomized or complex, oscillating strategies might instead be the typical outcome.

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Appendix A

To study maxima of the function $P(x)$, we use the idea of viewing P as the composition of an affine (linear-plus-constant) mapping, given by the per capita competitive abilities $(\phi(x), \psi(x))$, and a real-valued function, using that a strictly concave, continuous function must have a unique maximum on a compact, convex set. We assume that the competitive abilities satisfy $0 < f_i, m_i < 1$ for all i , which implies that $0 \leq \phi_j, \psi_j \leq 1$ for all j . We also assume that all E_j and e_i have positive probability of occurring, i.e. that all $g_j > 0$ and all $h_i > 0$.

An x with $0 \leq x_i \leq 1$ for all i can be regarded as a point in a unit cube $X \subset \mathbb{R}^I$ (with $I = 2i_0 + 1$ in our examples). Based on Eqs. (3), (4) and (9), (10) in the text, let us write P as

$$P(x) = Q(S(x)) = L(\phi(x)) + L(\psi(x)),$$

where $S(x) = (\phi(x), \psi(x))$ is an affine mapping from \mathbb{R}^I to $\mathbb{R}^{2J} = \mathbb{R}^J \times \mathbb{R}^J$ (with $J = 2j_0 + 1$ in our examples), and L is the mapping (10) defined from the positive orthant of \mathbb{R}^J to \mathbb{R} . Since L is a sum of concave functions it is concave, so that Q is concave. Furthermore, since the logarithm of a coordinate is a strictly concave function of that coordinate, and all coordinates appear with positive g_j in the sum in Eq. (10), it follows that L is a strictly concave function from the positive orthant of \mathbb{R}^J to \mathbb{R} and, similarly, that Q is a strictly concave function.

Since X is a convex set and S is affine, the set $Z = S(X) \subset \phi(X) \times \psi(X)$ is also convex. There will however be $x \in X$ for which one or more $\phi_j(x)$ or $\psi_j(x)$ are zero, and therefore $P(x)$ is undefined (or $-\infty$). Note that for positive migration rate p , this can only happen if all $x_i = 0$ or all $x_i = 1$, in which case the metapopulation goes extinct, and for $p = 0$ the consequence will also be extinction if some $\phi_j(x)$ or $\psi_j(x)$ is zero, so that such an x cannot be an ESS.

To deal with this technical problem, introduce Z_+ as the subset of Z where each coordinate is positive and Z_ε as the subset where each coordinate is at least ε . Let Q^* be the supremum of Q on Z_+ . By choosing ε small enough, we can ensure that $Q(z) < Q^* - 1$ for all $z \in Z_+ \setminus Z_\varepsilon$ (for instance, choose $\varepsilon < \exp[2(P(\bar{x}) - 1) / \min(g_j)]$ where \bar{x} is the strategy with all $x_i = 0.5$). Since Z_ε is a compact, convex set and Q is a strictly concave function, we know that Q achieves a unique maximum

at some point $z^* \in Z_\varepsilon$. It then follows that $Q(z^*) = Q^*$, so that Q has a unique maximum on Z_+ at $z^* = (\phi^*, \psi^*)$. Let us use the notation X_+ for the set of strategies corresponding to Z_+ , i.e. $X_+ = S^{-1}(Z_+)$. These are the strategies for which all $\phi_j(x)$ and $\psi_j(x)$ are positive.

A.1. Main result

We have then proved the following result: P has a maximum on X_+ and there is a unique pair (ϕ^*, ψ^*) such that x^* maximizes P if and only if $\phi(x^*) = \phi^*$ and $\psi(x^*) = \psi^*$.

Since P is a smooth function of x on X_+ , it is clear that condition (12) must hold for a maximizing x^* . Since P is concave on the convex set X_+ , it is also clear that an x^* satisfying condition (12) must yield a maximum of P on X_+ . Thus, x^* maximizes P if and only if condition (12) holds.

A.2. The set of maximizing strategies

Several strategies x could in principle satisfy $\phi(x) = \phi^*$ and $\psi(x) = \psi^*$. To gain an understanding of when this might happen, we can look at the linear component of the mapping $S(x)$, which we can write as $Ax = (\phi(x), \hat{\psi}(x))$ with

$$\phi_j(x) = \sum_i f_i x_i \tilde{h}_{ij},$$

$$\hat{\psi}_j(x) = - \sum_i m_i x_i \tilde{h}_{ij},$$

since

$$\psi_j(x) = \sum_i m_i \tilde{h}_{ij} + \hat{\psi}_j(x).$$

One would expect that the linear mapping A , from \mathbb{R}^I to $\mathbb{R}^{2J} = \mathbb{R}^J \times \mathbb{R}^J$, should be injective in our examples, since the dimension $2J$ is greater than I . If this is the case, only a single x^* maps to (ϕ^*, ψ^*) and there is thus a unique ESS. However, since we have no proof of this, we have tried to investigate the issue numerically, by using different starting points for an evolutionary sequence that leads to a maximum of P . These investigations indicated uniqueness of x^* in our examples.

Nevertheless, in degenerate cases the mapping A can have a non-trivial kernel. For instance, this will happen if male and female competitive abilities depend on the environment in the same way, i.e. $m_i = f_i$ for all i , since we then have $\hat{\psi} = -\phi$ and the mapping ϕ is not injective (because $I > J$ in our examples). In the latter case $x_i^* = 0.5$ for all i will maximize P , but there will be additional maximizing strategies.

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