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Sexual dimorphism or evolutionary branching?

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ABSTRACT

Disruptive selection due to ecological causes can lead to different types of phenotypic polymorphism. For a broad range of ecological scenarios, we investigate the odds that disruptive selection leads to sexual dimorphism relative to polymorphisms that appear after evolutionary branching. These involve genetic polymorphism, such as sympatric species or Mendelian genes with strong dominance-recessivity. When models that allow for sexual dimorphism are compared with constrained models with equal phenotypes in males and females, a sexual dimorphism is expected to evolve instead of the evolutionary branching in the constrained model. This is an important general result on the odds of different types of ecological polymorphism. It implies that the possibility for sympatric speciation caused by ecological selection pressures can be removed by the evolution of ecological differences between the sexes. Evolutionary branching becomes more likely when: (1) there is a strong constraint on sex differentiation; (2) secondary branching events occur after sexual dimorphism has already evolved; (3) assortative mate choice occurs before trait divergence starts. The possibility of sexual selection driving sympatric speciation is not affected by our conclusions.

Keywords: dominance evolution, ecological polymorphism, evolutionary branching, sexual dimorphism, sympatric speciation.

INTRODUCTION

Sexual dimorphism is widespread in the animal kingdom. Sexual selection is generally seen as the major driving force behind these differences (Shine, 1989), but ecological selection can also play a role (Temeles *et al.*, 2000; Temeles and Kress, 2003). In theoretical studies, there is a similar focus on sexual selection. Many studies (e.g. Lande, 1980; Iwasa *et al.*, 1991; Pomiankowski *et al.*, 1991) have examined how sexual and natural selection both contribute to the evolution of sexual dimorphism, whereas Slatkin (1984) focused on its ecological causes. One of the selection scenarios he considered was a character displacement scenario in which competition over a limiting resource causes disruptive selection and phenotypic differences between the sexes. Thus, Slatkin (1984) had already drawn parallels between sympatric speciation models and models for sexual dimorphism.

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The ecological conditions that lead to dimorphic sexes or diverging species were identical in his models, but he never compared the odds for either outcome directly.

Recently, the evolution of sympatric speciation due to ecological causes is again receiving a lot of attention (Dieckmann and Doebeli, 1999; Matessi *et al.*, 2001; van Doorn and Weissing, 2001; Doebeli and Dieckmann, 2003), with the same resource competition scenario playing a prominent role in several studies. There is a growing consensus among theoreticians (Dieckmann and Doebeli, 1999; van Doorn and Weissing, 2001; Gavrilets and Waxman, 2002) that sympatric speciation often requires evolutionary branching (Metz *et al.*, 1996; Geritz *et al.*, 1998). On that evolutionary scenario, an ecological generalist with intermediate trait values usually evolves first, but, once it has become common in the population, competition intensifies. It then pays to specialize again and the generalist becomes replaced by a genetic and phenotypic polymorphism of more specialized strategies. In ecological selection models, selection occurs on the use of available resources. With sexual selection, it is the distribution of potential mates that is the resource that individuals can specialize on. Evolutionary branching occurs at the phenotypic value of the generalist strategy that is replaced by co-existing specialists. It is defined as convergence of the evolutionary process to a point in trait space where directional selection disappears and disruptive selection dominates (Metz *et al.*, 1996; Geritz *et al.*, 1998). At that point in trait space, disruptive selection drives the emergence of a polymorphism of very different major genes (Kisdi and Geritz, 1999a; Van Dooren, 1999) or an increase in the genetic variance when there are only polygenes with small effects (Bulmer, 1980). That increase in the amount of standing genetic variation can trigger the evolution of assortative mate choice (Dieckmann and Doebeli, 1999), with the origin of two new species as a consequence. There is a snag, however, when major genes appear. Many traits and properties of the genetic system start to evolve differently in the presence of major genes (Dickinson and Antonovics, 1973), and not all of them lead to sympatric species. For instance, Balkau and Feldman (1973), Meszéna *et al.* (1997) and Kisdi and Geritz (1999b) have suggested that evolutionary branching can trigger the evolution of reduced migration, inducing parapatric or allopatric speciation. Van Dooren (1999) has shown that major genes that appear after evolutionary branching can evolve pronounced dominance interactions, which eliminates the selective advantage of assortative mate choice and speciation. If completely assortative mate choice is already present before evolutionary branching, two species must emerge instantly (van Doorn and Weissing, 2001), but there is a possibility that dominance evolution might still occur in a population with incomplete assortative mating.

Considering the existence of alternative evolutionary outcomes in the same ecological context, it becomes important to investigate the odds among different evolutionary outcomes. The odds of evolutionary branching relative to phenotypic polymorphisms where a genetic or environmental switch provokes alternative phenotypes from a single set of genes are also important. In this paper, we investigate the odds for the evolution of sexual dimorphism, modelled as a reaction norm with two alternative states, versus polymorphisms that require evolutionary branching. We generalize the resource competition model of Slatkin (1984) to a broad range of ecological scenarios. Then we focus on a specific question: Starting from a constrained model in which phenotypic differentiation between the sexes is not allowed, will evolutionary branching still occur at the same trait values as before, once dimorphic sexes are allowed to evolve? Bolnick and Doebeli (2003) consider a specific model within our modelling framework and conclude that sexual dimorphism is more likely to evolve than sympatric species. The distinction

addressed here between phenotypic polymorphism requiring evolutionary branching and sexual dimorphism is more fundamental. Moreover, the results presented are analytical and do not depend on model details, such as the independent diallele loci sometimes assumed in sympatric speciation models (Dieckmann and Doebeli, 1999; Bolnick and Doebeli, 2003), or specific ecological functions used (Slatkin, 1984; Bolnick and Doebeli, 2003).

INVASION FITNESS

We assume that sex-specific phenotypic traits of females and males are determined by a single set of autosomal genes with potentially pleiotropic effects or sex-specific expression. One can therefore consider these genes to specify a reaction norm with two alternative states (i.e. for the phenotypes expressed in each sex). An unspecified environmental or genetic switch controls sex determination, independent of the genes for sex-specific phenotypes. We assume that there is an even sex ratio at birth, which is the evolutionarily stable strategy (ESS) sex ratio of the models we consider.

The calculations presented use the invasion fitness of rare mutants (Fisher, 1930; Metz *et al.*, 1992; Rand *et al.*, 1994; Diekmann *et al.*, 2003), since that fitness measure is used to characterize evolutionary branching (Metz *et al.*, 1996; Geritz *et al.*, 1998). Invasion fitness corresponds to the fitness of a strategy in an ecological environment which is given. The effects of such an environment on demographic parameters are summarized in a vector $\boldsymbol{E}$, which has to be determined from a population dynamical model for all common strategies in the population. Usually, populations with a single common strategy are considered to determine the existence and location of evolutionary branching points.

We will look at environments $\boldsymbol{E}(\boldsymbol{z})$, set by a single common resident strategy with trait vector $\boldsymbol{z}$, assume that $\boldsymbol{E}(\boldsymbol{z})$ is constant over time (the population dynamics of common phenotypes is at equilibrium) and that the population is not spatially structured in a manner that creates local mating pools. The population can still be age-, stage- or otherwise structured. We consider two-sex models where the resident trait vector is $\boldsymbol{z} = (z_\mathrm{f}, z_\mathrm{m})$, with a continuous phenotypic trait in females and in males. The trait vector of the invading mutant is written as $\boldsymbol{z}'$. Invasion fitness, the per capita number of mutant individuals contributed to the next generation by the mutant strategy $\boldsymbol{z}'$ in the environment set by the resident strategy $\boldsymbol{z}$, then has the form (Shaw and Mohler, 1953; Charnov, 1982; Diekmann *et al.*, 2003)

$$\lambda(\boldsymbol{z}',\boldsymbol{z}) = \frac{1}{2}\left(\frac{R^{\mathrm{female}}(z'_\mathrm{f},\boldsymbol{E}(\boldsymbol{z}))}{R^{\mathrm{female}}(z_\mathrm{f},\boldsymbol{E}(\boldsymbol{z}))} + \frac{R^{\mathrm{male}}(z'_\mathrm{m},\boldsymbol{E}(\boldsymbol{z}))}{R^{\mathrm{male}}(z_\mathrm{m},\boldsymbol{E}(\boldsymbol{z}))}\right) \tag{1}$$

where functions $R^i(z,\boldsymbol{E})$ denote the number of offspring contributed to the next generation, by a phenotypic strategy z taking the reproductive role of females (i = female) or males (i = male) in environment $\boldsymbol{E}$. When phenotypic differentiation between males and females is ignored, the trait vector is reduced to a scalar trait and invasion fitness becomes

$$\lambda(z',z) = \frac{R(z',\boldsymbol{E}(\boldsymbol{z}))}{R(z,\boldsymbol{E}(\boldsymbol{z}))} \tag{2}$$

There are two obvious cases where invasion fitness (equation 1) simplifies and becomes more similar to invasion fitness (equation 2). First, when there are no intrinsic differences in reproductive roles between the sexes, numbers of offspring only depend on phenotypic values. Functions R^i are then identical in both sexes, such that invasion fitness simplifies to

$$\lambda(\boldsymbol{z}',\boldsymbol{z}) = \frac{1}{2}\left(\frac{R(z'_{\mathrm{f}},\boldsymbol{E}(\boldsymbol{z}))}{R(z_{\mathrm{f}},\boldsymbol{E}(\boldsymbol{z}))} + \frac{R(z'_{\mathrm{m}},\boldsymbol{E}(\boldsymbol{z}))}{R(z_{\mathrm{m}},\boldsymbol{E}(\boldsymbol{z}))}\right) \tag{3}$$

When the phenotypes of females and males are constrained to be equal, we obtain equation (2). The complete reproductive symmetry of equation (3) is unrealistic for many organisms. However, if the traits that evolve are not involved in fecundity or sexual selection, we can ignore selection in the mating process and focus on the number of times or the probability that offspring enter the mating pool. In that case, we also obtain an invasion fitness with the symmetry of equation (3).

EVOLUTIONARY DYNAMICS

Assuming large population sizes and small mutation rates, ecological and evolutionary time-scales become separated (Roughgarden, 1979). The common strategies in the population then determine the environments $\boldsymbol{E}$ in which each new mutant will invade or not, and after each successful invasion the resident environment will have reached equilibrium before a new successful mutant rises in frequency. With a single common strategy and a unique equilibrium of the population dynamics, we can write environments as functions of that strategy $\boldsymbol{E}(\boldsymbol{z})$. We can then use the invasion fitness functions (equations 1–3) to study the evolutionary dynamics of sex-specific phenotypes.

Additionally, assuming small mutational effects, a multivariate equation similar to the breeder's equation can be derived, which describes gradual phenotypic change over evolutionary time if fitness depends on the state of the population (Dieckmann and Law, 1996).

Equation (4) describes the rate of change of the resident phenotype in a population:

$$\frac{d}{dt}\boldsymbol{z} = \boldsymbol{G}\boldsymbol{\beta}(\boldsymbol{z}) \tag{4}$$

$\boldsymbol{G}$ is the mutational-variance covariance matrix times a scaling factor for the rate of appearance of mutants (which depend on $\boldsymbol{z}$ as well, but keeping that implicit does not affect our conclusions) and $\boldsymbol{\beta}$ is the selection gradient, given by equation (5) below. In comparison to the approach of Iwasa *et al.* (1991) and Abrams *et al.* (1993), the matrix $\boldsymbol{G}$ does not incorporate any standing genetic variation among the residents, because the separation of evolutionary and ecological time-scales eliminates it.

The invasion fitness gradient $\boldsymbol{\beta}$ (equation 5) is the vector of partial derivatives of invasion fitness with respect to the mutant traits, evaluated at equal mutant and resident traits. We can write that gradient vector as

$$\boldsymbol{\beta}(\boldsymbol{z}) = \nabla'\lambda(\boldsymbol{z},\boldsymbol{z}) = \begin{pmatrix} \dfrac{\partial}{\partial z'_{\mathrm{f}}}\,\lambda(\boldsymbol{z}',\boldsymbol{z})\big|_{\boldsymbol{z}'=\boldsymbol{z}} \\ \dfrac{\partial}{\partial z'_{\mathrm{m}}}\,\lambda(\boldsymbol{z}',\boldsymbol{z})\big|_{\boldsymbol{z}'=\boldsymbol{z}} \end{pmatrix} \tag{5}$$

The ∇' notation stresses that we only take partial derivatives with respect to the mutant traits. When gradient (5) equals zero and directional selection is absent, then we are at a potential endpoint of evolution, a candidate ESS (Metz *et al.*, 1996). For the two-sex model with invasion fitness (3), such singular or critical points $\boldsymbol{z}^*$ can have equal phenotypes in females and males; we denote these points $\boldsymbol{z}^*_= = (z^*,z^*)$, or they can be sexual dimorphisms $\boldsymbol{z}^*_{\neq} = (z^*_{\mathrm{f}},z^*_{\mathrm{m}})$, with $z^*_{\mathrm{f}} \neq z^*_{\mathrm{m}}$. Whether evolution will really halt at such a point depends on the pattern of invasion fitness over trait space, and on the mutational variances and covariances that can make paths of evolution deviate from the direction in which the fitness gradient points.

SEXUAL DIMORPHISM OR EVOLUTIONARY BRANCHING?

Symmetric two-sex models (equation 3) reduce to models without differentiated sexes when phenotypes of females and males are equal. This property makes it easy to turn many models that do not allow for sexual dimorphism into obvious extensions that do. In a model without separate sexes, individuals can be equally partitioned over classes that can be interpreted as males and females without introducing any differences in total equilibrium densities and so forth. That also creates specifications of the environment $\boldsymbol{E}$, which can be used in a simple two-sex model.

In this section, we use reproductive success functions R as if they have three ordered arguments: the mutant trait value z', the trait value of resident females, z_{f}, and that of resident males, z_{m}. Specifying partial derivatives of R can be done by writing indicators of the three arguments. For example, the second-order partial derivative for the mutant trait, evaluated at the point where all three phenotypes are equal to $\boldsymbol{z}^*$, can be written as $R_{11}(z^*,z^*,z^*)$, since it requires taking a partial derivative for the first argument twice.

Singular points $\boldsymbol{z}^*$ of models with differentiated sexes (equation 3) are found at points where the invasion fitness gradient (equation 5) equals zero. In terms of partial derivatives of function R, that translates into $R_1(z^*_{\mathrm{f}},z^*_{\mathrm{f}},z^*_{\mathrm{m}}) = 0$ and $R_1(z^*_{\mathrm{m}},z^*_{\mathrm{f}},z^*_{\mathrm{m}}) = 0$. For the constrained model with undifferentiated females and males, a singular point $\boldsymbol{z}^*$ satisfies $R_1(z^*,z^*,z^*) = 0$. That immediately shows that singular points of the constrained model must appear as singular points $\boldsymbol{z}^*_= = (z^*,z^*)$ in the unconstrained model, on the diagonal in trait space where phenotypes z_{f} and z_{m} are equal (Fig. 1).

With a supply of the appropriate mutational variation, evolutionary branching occurs at a point $\boldsymbol{z}^*$ that attracts evolutionary orbits from nearby, which at the same time is a local fitness minimum in at least one direction (Geritz *et al.*, 1998; Leimar, 2001, in press). The main question we want to address is whether rewriting a constrained model that does not allow for sexual dimorphism such that it allows phenotypic differences between the sexes maintains the evolutionary branching of the original model or not. That implies that singular points $\boldsymbol{z}^*_=$ with equal phenotypes in females and males are of special interest.

In the constrained model, those $\boldsymbol{z}^*$ that are evolutionary branching points are invadable by similar strategies (Geritz *et al.*, 1998). Invadability requires that the curvature h of invasion fitness is positive at $\boldsymbol{z}^*$, with h given by

$$h = \frac{R_{11}(z^*,z^*,z^*)}{R(z^*,z^*,z^*)} \tag{6}$$

such that invadability corresponds to the condition $R_{11}(z^*,z^*,z^*) > 0$.

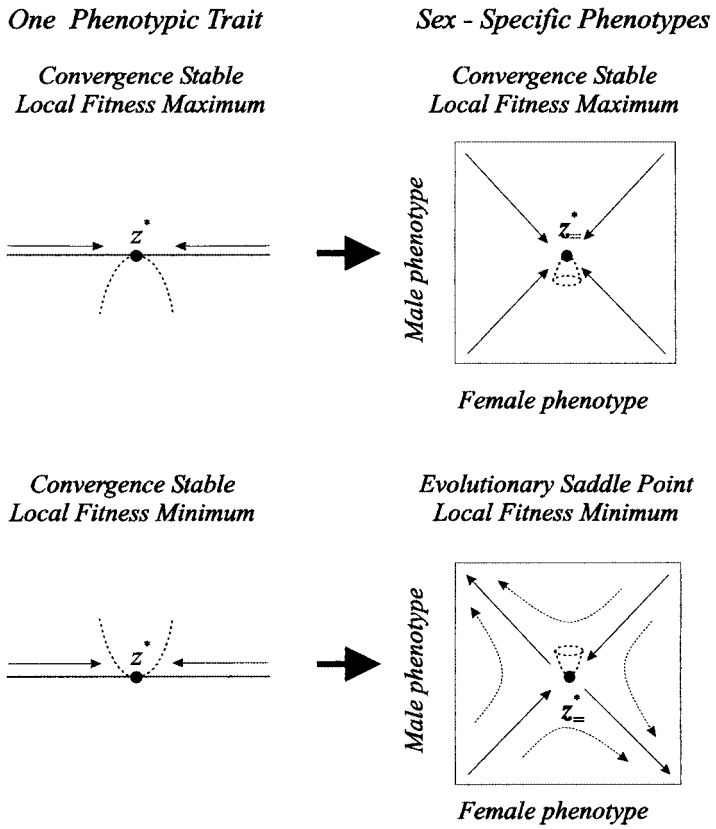

Fig. 1. Separate phenotypes for each sex. Diagram showing changes in convergence stability and invadability that are expected when sex-specific phenotypes are introduced in an evolutionary model with a singular point z^*. A strategy $z^*_= = (z^*, z^*)$ with equal phenotypes in the two sexes appears as a singular point. Non-invadability at z^* or $z^*_=$ corresponds to a local fitness maximum at the singular point (drawn as an attached parabola or a dome), invadability to a local fitness minimum. If z^* was convergence stable and non-invadable in the original model, then $z^*_=$ has these properties too. For z^* that were evolutionary branching points, $z^*_=$ becomes a strategy that is still invadable but not convergence stable, such that evolutionary branching will not occur. The dashed lines in the two-sex panels indicate the typical pattern of evolutionary trajectories.

For the unconstrained model, a two-by-two matrix, called the fitness Hessian $\boldsymbol{H}(z^*)$ (Leimar, 2001, in press), specifies the curvature of invasion fitness at z^* and determines whether a singular point can be invaded by mutants. It consists of second-order partial derivatives

$$\boldsymbol{H}_{i,j}(z^*) = \frac{\partial}{\partial z_i' \partial z_j'} \lambda(\boldsymbol{z}', \boldsymbol{z})|_{z' = z = z^*} \tag{7}$$

where the indices i and j take on the values female or male. When the Hessian has two eigenvalues with negative real parts, then the singular point is a local fitness maximum and uninvadable for any mutational variance covariance matrix (Leimar, 2001, in press). Otherwise, there is at least one direction where selection is neutral or disruptive. When

disruptive selection is present, the strategy $\boldsymbol{z}^*$ is invadable. If the Hessian has only positive eigenvalues, invasion fitness has a local minimum at $\boldsymbol{z}^*$, invadable by any phenotypically similar mutant strategy. At $\boldsymbol{z}^*_=$, $\boldsymbol{H}(\boldsymbol{z}^*_=)$ is a diagonal matrix with two eigenvalues equal to $h/2$ (equation 6). Invasion fitness therefore has a local minimum at $\boldsymbol{z}^*_=$ if the singular point of the constrained model was an evolutionary branching point.

The matrix $\boldsymbol{J}(\boldsymbol{z}^*)$ (equation 8; Leimar, 2001, in press), together with the mutational variance–covariance matrix, determines whether a singular point is evolutionarily attracting. This fitness Jacobian is used to decide whether mutants can invade that bring the population closer to $\boldsymbol{z}^*$ when nearby. $\boldsymbol{J}(\boldsymbol{z}^*)$ is the derivative of the selection gradient for the resident traits, evaluated at the point $\boldsymbol{z}^*$. One finds that the Jacobian $\boldsymbol{J}(\boldsymbol{z}^*)$ is the sum of two matrices:

$$\boldsymbol{J}(\boldsymbol{z}^*) = \boldsymbol{H}(\boldsymbol{z}^*) + \boldsymbol{Q}(\boldsymbol{z}^*) \tag{8}$$

Namely, the Hessian of equation (7) and a square matrix $\boldsymbol{Q}(\boldsymbol{z}^*)$, which consists of elements

$$\boldsymbol{Q}_{i,j}(\boldsymbol{z}^*) = \frac{\partial}{\partial z_i' \partial z_j} \lambda(\boldsymbol{z}', \boldsymbol{z})|_{\boldsymbol{z}' = \boldsymbol{z} = \boldsymbol{z}^*} \tag{9}$$

When all eigenvalues of the Jacobian have negative real parts, then the singular point is attracting from all directions and for any mutational covariance matrix. This property is called strong convergence stability (Leimar, 2001, in press) and extends the convergence stability (Eshel and Motro, 1981; Eshel, 1983; Christiansen, 1991) used in single-trait models to multiple traits. We will call both convergence stability. When all eigenvalues of $\boldsymbol{J}$ have positive real parts, then $\boldsymbol{z}^*$ repels for any mutational covariance matrix. In the case of indefinite $\boldsymbol{J}$, different choices of mutational covariance can affect convergence to $\boldsymbol{z}^*$.

In the constrained model, a local stability analysis shows that convergence stability holds at $\boldsymbol{z}^*$ when the scalar $j = h + q_2 + q_3$ is negative, with h defined by equation (6) and q_2 and q_3 by equation (10):

$$\begin{aligned} q_2 &= \frac{R_{12}(z^*, z^*, z^*)}{R(z^*, z^*, z^*)} \\ q_3 &= \frac{R_{13}(z^*, z^*, z^*)}{R(z^*, z^*, z^*)} \end{aligned} \tag{10}$$

Parameters q_2 and q_3 will be equal when a small change in the phenotype of resident females or males affects the environment $\boldsymbol{E}$ equally. Combinations of a negative Jacobian j and a negative Hessian h are called a continuously stable strategy (CSS; Eshel and Motro, 1981; Eshel, 1983). Figure 1 also depicts the pattern of invasion fitness in the neighbourhood of that type of convergence stable strategy.

The Jacobian of the unconstrained model at a point $\boldsymbol{z}^*_=$ has the form

$$J(\boldsymbol{z}^*_=) = \frac{1}{2}\begin{pmatrix} h & 0 \\ 0 & h \end{pmatrix} + \frac{1}{2}\begin{pmatrix} q_2 & q_3 \\ q_2 & q_3 \end{pmatrix} \tag{11}$$

This matrix has eigenvalues $h/2$ and $j/2$. Convergence to $\boldsymbol{z}^*_=$ depends on the convergence stability parameter j of the constrained model in the direction where male and female ecological phenotypes are kept equal (Fig. 1). Convergence in another direction depends on invadability parameter h, such that a branching point implies a repelling direction in the

two-sex model (Fig. 1). Summarizing, convergence stability of $\boldsymbol{z}^*$ is preserved in the unconstrained model when non-invadability holds, but changes when the constrained model has an evolutionary branching point. Figure 1 illustrates that the fitness gradient then points towards the two-sex candidate ESS $\underline{\underline{\boldsymbol{z}}}^*$ in one direction and away from it in another. Evolutionary branching becomes unlikely when phenotypic differentiation between the sexes is allowed. Evolutionary trait substitution sequences veer away from $\underline{\underline{\boldsymbol{z}}}^*$ into an area where phenotypes of females and males are different, with females having either larger or smaller phenotypic values than males. Using the ordinary differential equation (equation 4) to describe the evolutionary dynamics around $\underline{\underline{\boldsymbol{z}}}^*$, this strategy turns out to be a saddle point. This point is not approached even though fitness is a local minimum exactly at $\underline{\underline{\boldsymbol{z}}}^*$. One can calculate from the eigenvalues of the product $\boldsymbol{GJ}(\underline{\underline{\boldsymbol{z}}}^*)$ that $\underline{\underline{\boldsymbol{z}}}^*$ only attracts when the genetic correlation between the female and male trait values equals -1 or $+1$. We then, in fact, return to a constrained model that does not allow for any change in the amount of sexual dimorphism, but does allow for different mutational variances in females and males.

Our results show the generality of the pattern observed by Bolnick and Doebeli (2003), where the evolution of sexual dimorphism greatly hampers evolutionary branching, potentially leading to sympatric speciation. For cases of sex-linked inheritance with dosage compensation, Lande (1980) has shown that the selection gradient is not affected by the genetic mechanism of sex differentiation. Only the variance–covariance matrix becomes re-scaled relative to genetics with autosomal inheritance. Our results therefore hold for sex-linked inheritance with dosage compensation too. The Appendix generalizes the results of this section to multivariate phenotypes for each sex.

EXAMPLES

We will show by means of two examples that evolutionary branching remains a possibility after the evolution of sexual dimorphism. The first example is a version of a time-honoured model of resource competition (Roughgarden, 1979; Slatkin, 1984; Metz *et al.*, 1996). A peculiarity of the model of Bolnick and Doebeli (2003) is that it never has an evolutionarily stable sexual dimorphism. We modified their resource competition model to demonstrate that it does allow for ESS sexual dimorphisms after a minor change. We also provide an example of asymmetric competition, showing the intuitive pattern that the number of co-existing phenotypes each time increases or decreases by one when an ecological parameter is varied in small steps.

Symmetric competition

Figure 2 contains results from a resource competition model without competitive asymmetries. Phenotypic values are limited to the interval $(-1,1)$. The number of offspring is controlled by females. Each female has r offspring of which half are males. Offspring viability is a function of their phenotype z and of the vector of population densities of offspring of different types, $\boldsymbol{N}$, and of the vector of all corresponding phenotypes, $\boldsymbol{y}$, in the population:

$$R(z,(\boldsymbol{N},\boldsymbol{y})) = \left(1 + \frac{(r-1)}{k(z)} \sum_i \alpha(z, y_i) N_i\right)^{-1} \tag{12}$$

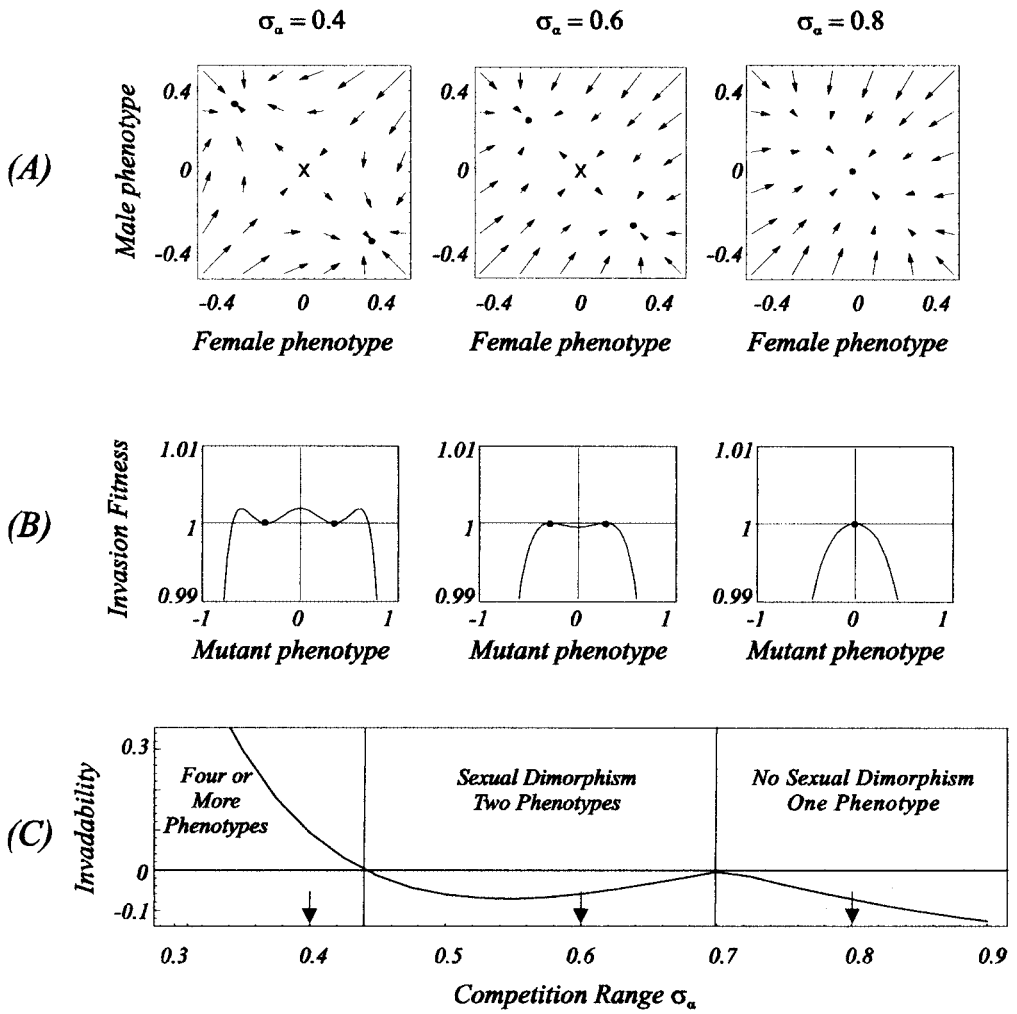

Fig. 2. Model example. Results from a resource competition model with symmetric competition. (A) Pattern of the invasion fitness gradient for three values of a parameter σ that controls the range over which phenotypes compete. These values are also indicated with arrows in panel (C). The convergence stable singular points are either a monomorphic convergence stable strategy, or two dimorphic singular points. Convergence stable singular points are indicated by a dot, evolutionary saddles by a cross. (B) Invasion fitness functions at singular points of (A). Because of the symmetry in the functions used to model competition, these are equal for mutants with either a change in the female or the male trait. Resident trait values at convergence stable singular points are indicated by dots. (C) Values of the Hessian parameter determining invadability, calculated at convergence stable singular points ($z_f \leq z_m$), such as the ones in panels (A) and (B). When this curvature measure is positive, the singular points are local fitness minima. When increasing the range of similar phenotypes over which competition occurs, a polymorphism of four morphs (or higher-order polymorphisms for the smallest values), a dimorphism and a single phenotype are the evolutionary outcomes.

with competition intensity function $\alpha(z, y) = \exp[-(z-y)^2/2\sigma_\alpha^2]$ and with $k(z) = 1 - z^2$ (as in Metz *et al.*, 1996), which can be interpreted as the distribution of a limiting resource. Equilibrium densities and invasion fitnesses are calculated from these equations and from equation (3). Bolnick and Doebeli (2003) use a Gaussian for function k. In the example of Fig. 2, we fixed parameter r at a value of 3. Figure 2A shows the pattern of the invasion fitness gradient (equation 5) for three values of the parameter σ_α that controls the range over which phenotypes compete. The convergence stable singular points are either a single monomorphic one, or two sexually dimorphic singular points. However, such a convergence stable trait vector can still be invadable (Fig. 2B). It can be seen that the singular point is a local fitness minimum for value $\sigma_\alpha = 0.4$ of the ecological parameter, and secondary evolutionary branching is expected in both sexes simultaneously. This joint secondary branching of the sexes is a consequence of the symmetry in competition. Figure 2C shows the value of the eigenvalue of the Hessian at convergence stable candidate singular points, which determines invadability.

Asymmetric competition

We present a simple example of a model with asymmetric competition, similar to Kisdi (1999). We calculate viabilities from equation (12) but now use

$$\alpha(z, y) = 1 - \frac{1}{1 + e^{-v(z-y)}} \text{ and } k(z) = \frac{1}{\sqrt{2\pi\sigma_k^2}} e^{-\frac{z^2}{2\sigma_k^2}} \tag{13}$$

The trait space ranges over positive real numbers in this example. The competition intensity function α assumes that individuals have a competitive advantage when they are larger. Parameter v controls the competition intensity between different phenotypes. Parameter σ_k controls the width of the resource distribution function k. One can calculate that the constrained version of this model has a convergence stable singular point at $\boldsymbol{z}^* = v\sigma_k^2/2$. The sign of the Hessian h is positive when $\sigma_k > 1$; then $\boldsymbol{z}^*$ is invadable, otherwise it is not. Figure 3 shows results from this model, with $r = 3$ and $v = 2$. When σ_k is smaller than one, the singular point $\boldsymbol{z}^*_=$ for the two-sex model attracts and it is not invadable. When σ_k is larger than one, this singular point with equal phenotypes in males and females becomes an evolutionary saddle and two other singular points appear that have different phenotypes for males and females. These singular points are non-invadable for a small range of σ_k. In Fig. 3B, we see that at a dimorphic singular point for larger values of σ_k, fitness can be a local minimum for the phenotype of one sex and a maximum for the other. In this case, a secondary polymorphism in only one sex originates through evolutionary branching. Such evolutionary branching can potentially lead to speciation, with species-specific phenotypes in a single sex.

DISCUSSION

Our results show that constraints play an important role in ecological diversification via evolutionary branching. When two classes of individuals can become phenotypically different and reduce competition in that manner, then it becomes much less likely that an evolutionary dynamics passes through an evolutionary branching point. We derived this conclusion from a study on the evolution of sexual dimorphism, but the same phenomenon

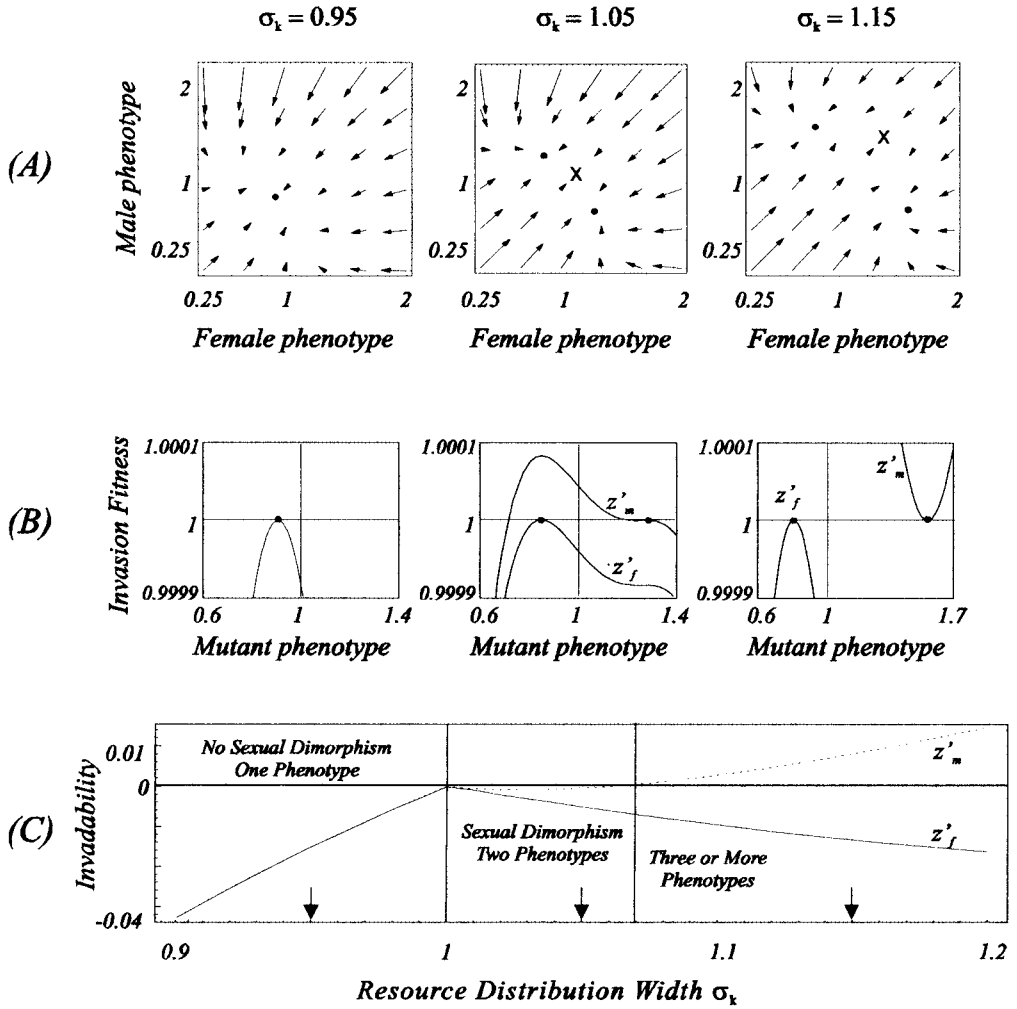

Fig. 3. Model example. Results from a resource competition model with asymmetric competition. (A) Pattern of the invasion fitness gradient for three values of a parameter σ_k that controls the width of resource distribution function k. (B) Invasion fitness functions at singular points of (A). We calculated them at resident trait values where the phenotype of females is smaller than or equal to that of males. Resident trait values at convergence stable singular points are indicated by dots. Mutants with changes in the female (indicated by z'_{f}) or in the male trait (indicated by z'_{m}) have different invasion fitness functions. (C) Values of the double partial derivatives of the Hessian that determine invadability, calculated at convergence stable singular points. For dimorphic singular points, we chose the one with the largest male phenotype. When increasing σ_k, a single phenotype, a dimorphism, then three morphs or a higher-order polymorphism are expected.

might also be relevant when there are other types of classes of individuals with facultatively different phenotypes. Evolutionary branching appears to thrive on constraints that keep these classes phenotypically equal, so that the only route towards phenotypic polymorphism and reduced competition is via a genetic polymorphism.

With autosomal genes for alternative sex phenotypes, some sort of gene regulation must occur to provoke the right phenotype in each situation. Severe genetic constraints on this plasticity can make the evolution of sexual dimorphism impossible, but the evolution of regulatory modifier sequences does not seem to be very restricted (Badyaev, 2002). Merilä *et al.* (1998) do show that genetic correlations between undifferentiated sex phenotypes can sometimes be equal to +1. However, not all evidence for strong genetic correlations between sex phenotypes excludes the possibility of sex differentiation. Some studies have reported strong positive genetic correlations between already dimorphic sex phenotypes (Rogers and Mukherjee, 1992). In that case, one can only conclude that the scope of further sex differentiation is limited, once sexual dimorphism is present. We also must keep in mind that, strictly speaking, our model requires a strong constraint on the *mutational* variance to prevent the evolution of sexual dimorphism. Little is known about such constraints (Mackay, 2001), and the main study in this respect did not find it (Mackay *et al.*, 1992). Bolnick and Doebeli (2003) simulate the effects of a genetic constraint by modifying the ratio of loci with sex-specific expression to loci without, and derive the same conclusion concerning constraints and sympatric speciation as we do with respect to evolutionary branching: sexual dimorphism evolves unless a genetic constraint prevents it. Additionally, they show that stochastic effects from finite population size affect the probability of sexual dimorphism versus branching, indicating that the adaptive dynamics approximation (Dieckmann and Law, 1996) that we used to investigate the evolutionary dynamics has its limitations. Bolnick and Doebeli (2003) also note in their simulations that a partial constraint limiting sex differentiation, as in Rogers and Mukherjee (1992), can lead to the loss of sexual dimorphism followed by sympatric speciation. This could depend on the amount of standing genetic variation in the simulated populations and on the sexual selection it creates, which allows for the evolution of assortative mate choice even when evolutionary branching for ecological reasons has not occurred (Lande, 1981).

Our examples show that evolutionary branching remains possible after the evolution of dimorphic sexes. Intuitively, this must occur less often than evolving sexual dimorphism. Competition parameters must be more extreme to obtain it, if the character displacement between the sexes already manages to annihilate disruptive selection caused by competition. Surprisingly, Bolnick and Doebeli (2003) find that the evolution of sexual dimorphism in their model comes together with disruptive selection and potential secondary branching at the dimorphic candidate ESS. However, genetic constraints from the diallele model they use generally prevent what they call 'adaptive splitting'. For some parameter combinations though, the evolution of (dis-)assortative mating does seem to make secondary branching possible. When the Gaussian carrying capacity function in Bolnick and Doebeli's model is replaced by a different function, such as a parabola, the coupling between sexual dimorphism and secondary branching disappears. Selection can then be stabilizing at a convergence stable sexual dimorphism. When competition is asymmetric, selection can be stabilizing for one sex and disruptive for the other. In that case, secondary branching will occur in a single sex, leading to three co-existing phenotypes. In any case, the route to speciation via secondary branching is not implausible.

Another possibility that will lead to evolutionary branching, and sympatric species by necessity, is the presence of (completely) assortative mate choice before phenotypic sex differentiation evolves. Females only mating with phenotypically equal males inhibit the emergence of sexual dimorphism, and the only ecological differentiation that can occur is through sympatric speciation. This can imply that branching will be restored, but

van Doorn and Weissing (2001) have shown that the presence of assortative mate choice also reduces the likelihood of evolutionary branching, because it stabilizes selection.

Sexual selection has been put forward as another driving force behind evolutionary branching leading to sympatric speciation (e.g. van Doorn and Weissing, 2001). We did not consider it here, but we do note that our conclusions do not directly affect the plausibility of sympatric speciation via sexual selection. In sexual selection models, evolutionary branching occurs in traits that are already specific to a single sex. That rules out the possibility for the appearance of a new phenotypic difference between the sexes capable of preventing branching caused by sexual selection. Thus, using our results indirectly, the odds for sexual selection versus ecological selection as the force driving sympatric speciation seem to veer towards sexual selection because the evolution of sexual dimorphism reduces the likelihood of the ecological route to speciation.

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APPENDIX

With multivariate ecological phenotypes per sex, say n traits, the complete trait vector becomes $\boldsymbol{z} = (\boldsymbol{z}_f, \boldsymbol{z}_m)$, which is a vector of length $2n$.

Selection gradient

Singular points are determined using equation (5), but with partial derivatives for each element in the trait vector $\boldsymbol{z}$. When the fitness gradient $\nabla' \lambda(\boldsymbol{z},\boldsymbol{z})$ equals zero, evolution is potentially halted.

Invadability

At a singular point with equal male and female multivariate phenotypes, the Hessian $\boldsymbol{H}(\underline{\underline{z}}^*)$ (equation 7) becomes a block diagonal matrix with two blocks $\boldsymbol{h}/2$, and off-diagonal zero matrices. The eigenvalues of each $\boldsymbol{h}$ are determined by a constrained model without sex differentiation. If we append n zeroes to an eigenvector $\boldsymbol{u}_h$ of such an eigenvalue λ_h, then that vector $\boldsymbol{u} = (\boldsymbol{u}_h, \boldsymbol{0})$ solves the eigenvalue equation $\boldsymbol{H}(\underline{\underline{z}}^*)\boldsymbol{u} = \lambda \boldsymbol{u}$ of the two-sex model with $\lambda = \lambda_h/2$. The vector $(\boldsymbol{0}, \boldsymbol{u}_h)$ similarly solves this equation such that each eigenvalue of the constrained model corresponds to an eigenvalue of the Hessian of the two-sex model with double multiplicity.

Convergence stability

The Jacobian $\boldsymbol{J}(\underline{\underline{z}}^*)$ of the two-sex model is a real matrix with blocks of second-order (mixed) partial derivatives corresponding to the entries in matrices $\boldsymbol{H}(\underline{\underline{z}}^*)$ and $\boldsymbol{Q}(\underline{\underline{z}}^*)$ (equations 7–9). Concerning convergence stability, we first show that the eigenvalues of the Hessian $\boldsymbol{h}$ are always equal to two times an eigenvalue of the Jacobian $\boldsymbol{J}(\underline{\underline{z}}^*)$. The eigenvalues of a square matrix $\boldsymbol{J}(\underline{\underline{z}}^*)$ are equal to the eigenvalues of the transpose $\boldsymbol{J}(\underline{\underline{z}}^*)^T$. These eigenvalues solve the equality $\boldsymbol{J}(\underline{\underline{z}}^*)^T\boldsymbol{u} = \lambda \boldsymbol{u}$, which is equal to

$$\frac{1}{2}\begin{pmatrix} \boldsymbol{q}_2^T + \boldsymbol{h}^T & \boldsymbol{q}_2^T \\ \boldsymbol{q}_3^T & \boldsymbol{q}_3^T + \boldsymbol{h}^T \end{pmatrix}\boldsymbol{u} = \lambda \boldsymbol{u}$$

If we take an eigenvector $\boldsymbol{u}_h$ of $\boldsymbol{h}^T$, with eigenvalue λ_h, concatenate it with $-\boldsymbol{u}_h$, then we see that $\boldsymbol{u} = (\boldsymbol{u}_h, -\boldsymbol{u}_h)$ solves this equality. Eigenvalue λ equals $\lambda_h/2$, and λ_h is an eigenvalue of the Hessian $\boldsymbol{h}$.

Second, to show that halves of the eigenvalues of the Jacobian $\boldsymbol{j} = \boldsymbol{q}_2 + \boldsymbol{q}_3 + \boldsymbol{h}$ of the model without sex differentiation also occur in the two-sex model, we rewrite the eigenvalue equation of the two-sex Jacobian $\boldsymbol{J}(\underline{\underline{z}}^*)$ as

$$\frac{1}{2}\begin{pmatrix} -\boldsymbol{q}_3 & \boldsymbol{q}_3 \\ \boldsymbol{q}_2 & -\boldsymbol{q}_2 \end{pmatrix}\boldsymbol{u} + \frac{1}{2}\begin{pmatrix} \boldsymbol{q}_2 + \boldsymbol{q}_3 + \boldsymbol{h} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{q}_2 + \boldsymbol{q}_3 + \boldsymbol{h} \end{pmatrix}\boldsymbol{u} = \lambda \boldsymbol{u}$$

If we use as eigenvector an eigenvector $\boldsymbol{u}_j$ of the Jacobian $\boldsymbol{j}$ repeated twice, $\boldsymbol{u} = (\boldsymbol{u}_j, \boldsymbol{u}_j)$, and plug it into the eigenvalue equation of the two-sex Jacobian, the elements in the first matrix cancel. This last eigenvector $\boldsymbol{u}$ solves the two-sex eigenvalue equation with one-half of the eigenvalue of the original model, corresponding to $\boldsymbol{u}_j$.