

Reproductive character displacement by the evolution of female mate choice

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ABSTRACT

Background: Interspecific mating often results in the loss of female reproductive success and can lead to the extinction of a species. In such situations, females evolve a stronger mate preference to avoid heterospecific mating, which promotes pre-mating barriers between species.

Questions: What is the magnitude of reproductive character displacement and how large is the damage done by reproductive interference? What is the effect of female mate preference on reproductive character displacement? Can the character displacement prevent extinction of the species?

Key assumptions: There are two closely related species whose individuals can mate but whose hybrids are inviable. One, the resident, lives in an isolated area where it is common. Individuals of the other, the invader, regularly migrate to the isolated area. Resident females accept mates based on a male ornament or other secondary sexual trait. Both female preference and the male trait are determined by sex-limited autosomal loci.

Methods: Build mathematical models for male and female fitnesses. Analyse the evolution of male and female traits. Deduce the amount of character displacement caused by resident females evolving to prefer males that do not resemble invaders. Deduce the evolutionary change of resident male traits. Determine the effect on character displacement of varying the fitness cost of interspecific mating to the females. Calculate numerically the course of the evolutionary transition as well as the time required to complete it. Study the chance that the invasion will cause the extinction of the resident species.

Conclusions: Both the resident male trait and the resident female preference evolve away from the male trait of the invader. The evolutionary shift in the male trait is largest at an intermediate intensity of female mate choice. Equilibrium in male and female traits is maintained by the balance between natural and sexual selection, and the male trait value most preferred by females is more exaggerated than the actual male trait. Sexual dimorphism may evolve if female morphology (as opposed to female preference) remains at the viability optimum. The risk of extinction of the resident species strongly depends on the speed of extinction relative to the time it takes for the adaptation to evolve.

Keywords: extinction, heterospecific mating, pre-zygotic isolation, quantitative trait, reproductive character displacement, sexual selection.

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INTRODUCTION

Interspecific mating, which often results in the loss of female reproductive success, can lead to species extinction. In such situations, females may evolve a mate preference to avoid heterospecific mating and promote pre-mating barriers between species. This process is called ‘reproductive character displacement’ (Butlin, 1987). The male traits of the species that are used by conspecific females in their mate choice should diverge, promoting pre-zygotic isolation where the species co-occur. Reproductive character displacement is one of the common evolutionary consequences of reproductive interference, especially when heterospecific mating occurs because of the lack or insufficiency of pre-mating barriers (for a review, see Gröning and Hochkirch, 2008). Heterospecific mating results either from unavoidable forced copulations by heterospecific males or from a misdirected female preference for heterospecific males. Its costs are higher if the number of opportunities for the female to mate is limited, and post-mating barriers are in place (Ribeiro and Spielman, 1986; Liou and Price, 1994). If two species do not produce viable hybrid offspring, the females must pay the cost of heterospecific mating in the form of time, energy, and nutrient expenditure caused by a heterospecific male’s mating attempts (harassment), sperm competition, sterility, and developmental anomaly (Barton and Hewitt, 1985; Bull and Burzacott, 1994; Howard, 1999; Hill and L’Hernault, 2001; Price *et al.*, 2001; Servedio and Noor, 2003). Reproductive interference is normally distinguished from standard competition for shared limited resources, although it may sometimes be regarded as ‘a type of competition’ (Birch, 1957). In this situation, a ‘mistake’ by females results in a loss of fitness.

Theoretical and experimental studies have shown that reproductive interference can result in the extinction of one species if the reduction in reproductive success is larger in one of the species, or if one of the species is much more abundant (Kuno, 1992; Fujimoto *et al.*, 1996; Takafuji *et al.*, 1997; Reitz and Trumble, 2002; Westman *et al.*, 2002). Nevertheless, reproductive interference may produce reproductive character displacement as demonstrated in recent field studies (Sætre *et al.*, 1997; Höbel and Gerhardt, 2003; Smadja and Ganem, 2005; Uit De Weerd *et al.*, 2006; Johanet *et al.*, 2009). When a pair of species with incomplete pre-zygotic isolation becomes sympatric, a chain of evolutionary events may occur that results in a more efficient avoidance of heterospecific mating.

While reproductive character displacement occurs between different species, a similar process can occur between two different populations of the same species. This is called ‘reinforcement’ (Dobzhansky, 1937; Butlin, 1989; Pfennig and Pfennig, 2009). When the viability of a hybrid between different populations is lower than that of individuals mating within each population, pre-zygotic isolation becomes stronger and contributes to the process of speciation (Coyne and Orr, 2004). Many models of reinforcement focus on the situation where hybrids have zero fitness (e.g. Spencer *et al.*, 1986). They address the evolution of assortative mating (Kelly and Noor, 1996) [see also Servedio (2000) for a comparison with choice based on preference, and Yukilevich and True (2006) for the relative importance of assortative mating and migration modification], the factors overcoming gene mixing due to the partial viability of hybrids (Servedio and Kirkpatrick, 1997), loci resulting in hybrid incompatibilities (Kirkpatrick and Servedio, 1999), or the problem between pre-zygotic and post-zygotic isolation fitness (Servedio, 2001).

Sawyer and Hartl (1981) calculated changes in allele frequency for a mutation that reduces the probability of mating with a second species given that the viability of hybrids is zero, and they demonstrated that the mutation can always invade, implying the evolution

of pre-zygotic isolation. In contrast, Sved (1981) explicitly considered the mechanism for reproductive character displacement, namely the evolution of female mate preference and the male sexual trait. He showed that in a quantitative genetic model, character displacement occurs much more effectively if a difference exists in the male trait between the initial populations.

Reproductive interference may also cause the displacement of traits controlling resource use. Ecological traits between species tend to differ more between species in sympatry than those in allopatry (Brown and Wilson, 1956; Huey, 1974; Slatkin, 1980; Schluter *et al.*, 1985; Taper and Case, 1985; Schluter and McPhail, 1992; Doebeli, 1996; Schluter, 2000), which was traditionally interpreted as a consequence of the evolutionary avoidance of interspecific resource competition termed ‘ecological character displacement’. If a trait is used both for resource utilization and for mate choice, Konuma and Chiba (2007) showed that body size separation becomes more pronounced in the presence of reproductive interference. Using different numbers of quantitative traits affecting competition and hybridization between species, Goldberg and Lande (2006) surveyed the importance of spatial environmental gradients for ecological displacement, reproductive character displacement, and combinations of the two. Thibert-Plante and Hendry (2009) studied an individual-based model of two separate traits (one for determining adaptation and the second for mate choice) and concluded that ecological character displacement can be enhanced by selection against hybrids.

In the present paper, we consider the evolution of pre-mating isolation by reproductive character displacement between two species whose hybrid is not viable. We explicitly model the evolution of a male’s secondary sexual trait and the female’s preference for it when an alien species invades. The male’s trait can be any trait used by the females for discriminating conspecific males from males of different species – visual, olfactory, auditory, behavioural, etc. The situation is similar to the one studied by Sved (1981), but Sved focused on the initial speed of character displacement. He did not discuss the evolutionary outcomes or the eventual degree of character displacement. The latter may also depend on the cost of the trait – a high cost should modulate or reduce further exaggeration of the trait. In this paper, we focus on modelling the evolutionary outcomes.

Our model will show that the evolutionary shift in the male trait is largest when the intensity of female mate choice is at an intermediate magnitude. Equilibrium in the strength of the male shift is maintained by the balance between natural and sexual selection, and the male trait value most preferred by females is more exaggerated than the modal male trait. Sexual dimorphism may evolve if the female morphological trait remains at the viability optimum. Finally, evolutionary adaptation of both sexes may reduce the risk of extinction.

THE MODEL

Consider an island or an island-like habitat occupied predominately by one species (the resident species). A second species, closely related to the resident species, recurrently invades the habitat. Some females of the resident species may accept males of the invader if the two species are similar in male morphological traits. These females will suffer a loss of fitness if the hybrid is not viable. In the absence of complete pre-zygotic isolation, the risk of mating with heterospecific males might select for females with a more careful mate choice.

Suppose the resident species has two sex-limited quantitative traits: a male mating ornament, x , and a female mating preference, y . Let all loci be autosomal. We denote the

population mean values of x and y by $\bar{x}$ and $\bar{y}$, respectively. We denote the mating trait of the male of the invader species by z , and its mean value by $\bar{z}$.

The fitness function for a male with phenotype x is

$$W_m(x | \bar{y}) = \exp \left\{ \lambda_m - \frac{x^2}{2w^2} - a(x - \bar{y})^2 \right\}, \quad (1a)$$

where λ_m is a constant indicating the maximum fitness level for males in the population. We set $x = 0$ as the male trait that achieves the maximum viability. We assume that the survivorship of the male is Gaussian, as indicated by the second term in the exponent ($-x^2/2w^2$). w is the standard deviation, indicating the range of male phenotypes around the optimum with high viability. Hereafter this is referred to as male tolerance. A small w implies that male fitness declines sharply as the trait deviates from 0. The third term in the exponent of equation (1a) indicates mate choice: males with x close to $\bar{y}$ have the highest reproductive success. $\bar{y}$ is the trait most preferred by females in the population. a indicates the effectiveness of the female mate choice.

The fitness function for a female is

$$W_f(y | \bar{x}, \bar{z}) = \exp \{ \lambda_f - b(y - \bar{x})^2 \} \frac{N \exp \{ -a(y - \bar{x})^2 \}}{N \exp \{ -a(y - \bar{x})^2 \} + mN' \exp \{ -a(y - \bar{z})^2 \}}. \quad (1b)$$

The first factor in the right-hand side of equation (1b) shows that the female fitness has a Gaussian distribution, achieving a maximum when it is close to the average male trait $\bar{x}$ and declining as it deviates from $\bar{x}$. b indicates the cost of mate choice paid by females. (Females must pay an additional cost in the form of time and energy if they prefer males that are not abundant in the current population.) The second factor on the right-hand side of equation (1b) is the fraction of conspecific mating. Heterospecific mating results in failure. Here, we assume that conspecific mating occurs in proportion to the number of conspecific and heterospecific males multiplied by factors indicating female mate preferences. When the mean trait of invasive males $\bar{z}$ is similar to that of resident males $\bar{x}$, females suffer a substantial cost due to frequent misidentification. The ratio of the population sizes of the conspecific males to the heterospecific males is N to N' . However, only a fraction m of heterospecific individuals have invaded (m is the migration rate per generation). We neglect the effect of the heterospecific females because they fail to reproduce effectively in a population in which most males belong to the resident species. Because of this failure, the invader population cannot maintain itself in the habitat it invades and the model system needs to receive migrants every generation. We can safely assume that the effectiveness of mate choice a is greater than the cost of female mate choice b .

The resident female fitness given by equation (1b) considers the risk of heterospecific mating and the female cost of mate preference. It reflects a per capita population growth rate. In the presence of the heterospecific males, female fitness is reduced. In contrast, when the resident males evolve an exaggerated trait, they experience a reduction in survivorship.

Since each offspring inherits from a father and a mother equally, the mean male and female fitness should be the same. Those males fortunate enough to survive may have a greater than average chance to compensate for the reduction in male survivorship. However, equation (1a) does not represent this aspect explicitly because it does not affect the evolution of the male trait that we consider in this study.

The evolution of the mean values of two sex-limited quantitative traits in a resident population with discrete, non-overlapping generations is modelled as the product of the additive genetic variance–covariance matrix and the selection gradient vector,

$$\begin{pmatrix} \Delta \bar{x} \\ \Delta \bar{y} \end{pmatrix} = \frac{1}{2} \begin{pmatrix} G_x & B \\ B & G_y \end{pmatrix} \begin{pmatrix} \frac{\partial}{\partial x} \ln W_m \\ \frac{\partial}{\partial y} \ln W_f \end{pmatrix}. \quad (2)$$

This particular formalism was first derived by Iwasa *et al.* (1991). Here, the selection gradient is given as a derivative of individual fitness with respect to an individual trait evaluated at the population mean. A slightly different formalism was previously proposed by Lande (1976, 1981), in which the selection gradient was a derivative of the mean fitness as a function of mean traits. Lande's formalism requires that the breeding values for the trait and the preference be strictly bivariate-normally distributed, which is difficult to satisfy (Barton and Turelli, 1987, 1991). In contrast, the formalism in equation (2) is valid when fitness functions change little over the range of phenotypic variations in the population (weak selection), but it does not require normality of the breeding value distribution. Equation (2) has been applied to the evolution of both mate choice (Pomiankowski *et al.*, 1991; Pomiankowski and Iwasa, 1993; Iwasa and Pomiankowski, 1994, 1995) and genomic imprinting (Mochizuki *et al.*, 1996). The factor of $1/2$ represents the sex-limited trait expression of the fitness functions. We assume that the variance–covariance matrix is not degenerate (i.e. that the inverse of the matrix also exists).

Co-evolutionary dynamics

Under weak selection, additive genetic covariance B is much smaller than the additive genetic variances (G_x and G_y) (see Pomiankowski and Iwasa, 1994). In the following, we focus only on leading order terms with respect to selection intensity. Then from equations (1a), (1b), and (2), we obtain the dynamics for the mean trait values as follows:

$$\Delta \bar{x} = \frac{1}{2} G_x \left\{ -\frac{\bar{x}}{w^2} - 2a(\bar{x} - \bar{y}) \right\}, \quad (3a)$$

$$\Delta \bar{y} = \frac{1}{2} G_y \left[-2b(\bar{y} - \bar{x}) + \frac{2a(\bar{x} - \bar{z})}{1 + \frac{1}{\gamma} \exp \{a(\bar{x} - \bar{z})(2\bar{y} - \bar{x} - \bar{z})\}} \right], \quad (3b)$$

where γ is the magnitude of invasion, defined as $\gamma = mN'/N$. Here we regard G_x and G_y as constants. Figure 1 illustrates the fitness function before and after the invasion. The symbols represent the traits at the new equilibrium and those at the initial state $x = x_0$, $y = y_0$, the latter being the viability optimum ($x_0 = y_0 = 0$).

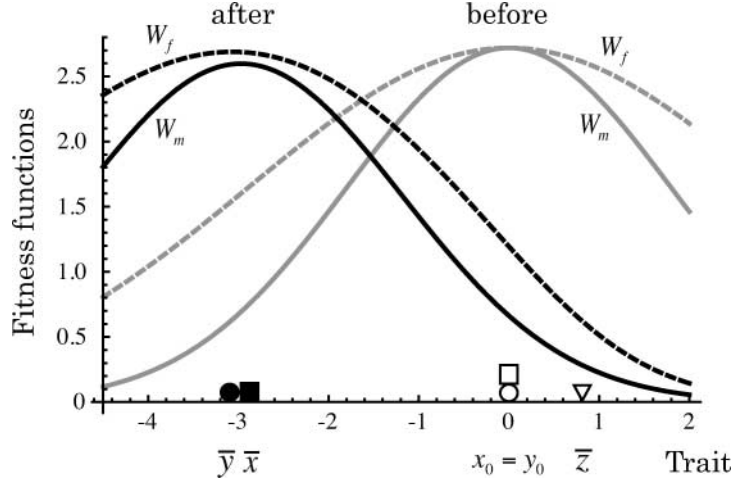


Fig. 1. Fitness functions before and after the reproductive character displacement. The x -axis is a trait expressed in a certain generation. Solid lines show male fitness functions and dashed lines denote female fitness functions. The grey colour indicates the initial state (before invasion), and the black colour shows the equilibrium. Open squares, circles, and inverted triangles are for the mean trait values of male, female, and invading species, respectively. Solid squares and circles are the values at equilibrium after the reproductive character displacement. Parameter values are $\lambda_m = 1$, $\lambda_f = 1$, $w = 10$, $a = 0.15$, $b = 0.06$, $\bar{z} = 0.8$, and $\gamma = 0.1$.

REPRODUCTIVE CHARACTER DISPLACEMENT

If the resident species does not go extinct, its traits should evolve to a new stable equilibrium. For a broad range of parameters, the dynamics given by equation (3) have two stable equilibria with an unstable intermediate equilibrium. The population evolves to converge at one of the two stable equilibria because both the male trait and female preference of the resident species evolve away from the male trait of the invader. If the optimum viability is selected as zero, the equilibrium of the resident traits before invasion is located at the origin. At the equilibrium after character displacement, female preference $\bar{y}^*$ and male trait $\bar{x}^*$ have the same sign (both are positive or both are negative), and it is the opposite of the sign of the trait of the invader males.

In addition, at equilibrium, the trait preferred by females deviates more from the male trait of the invader. This is illustrated by the following relationship:

$$\bar{y}^* = \bar{x}^* \left(1 + \frac{1}{2aw^2} \right), \quad (4)$$

where $\bar{x}^*$ and $\bar{y}^*$ are equilibrium values. Note that the magnitude of $\bar{y}^*$ is greater than that of $\bar{x}^*$. The females try to avoid harmful heterospecific mating. The male trait of the resident species is affected also by the survivorship that constrains the male trait closer to the optimum viability, resulting in a smaller evolutionary change of the male trait than of the female preference, as shown by equation (4). Accordingly, the evolutionary equilibrium is determined by the balance between sexual selection and natural selection. These selection processes keep acting at the equilibrium.

Parameter dependence of the final magnitude of evolutionary shift

Figure 2 illustrates the mean male trait at the equilibrium after the evolutionary response to the invasion. A larger shift in the trait implies a clearer reproductive character displacement.

(i) Male tolerance w :

Figure 2(a) illustrates that the magnitude of the shift in the male trait caused by contact with the invaders increases with an increase in the male tolerance of the resident w . If the resident male trait is strongly constrained (w is very small), it is difficult to change

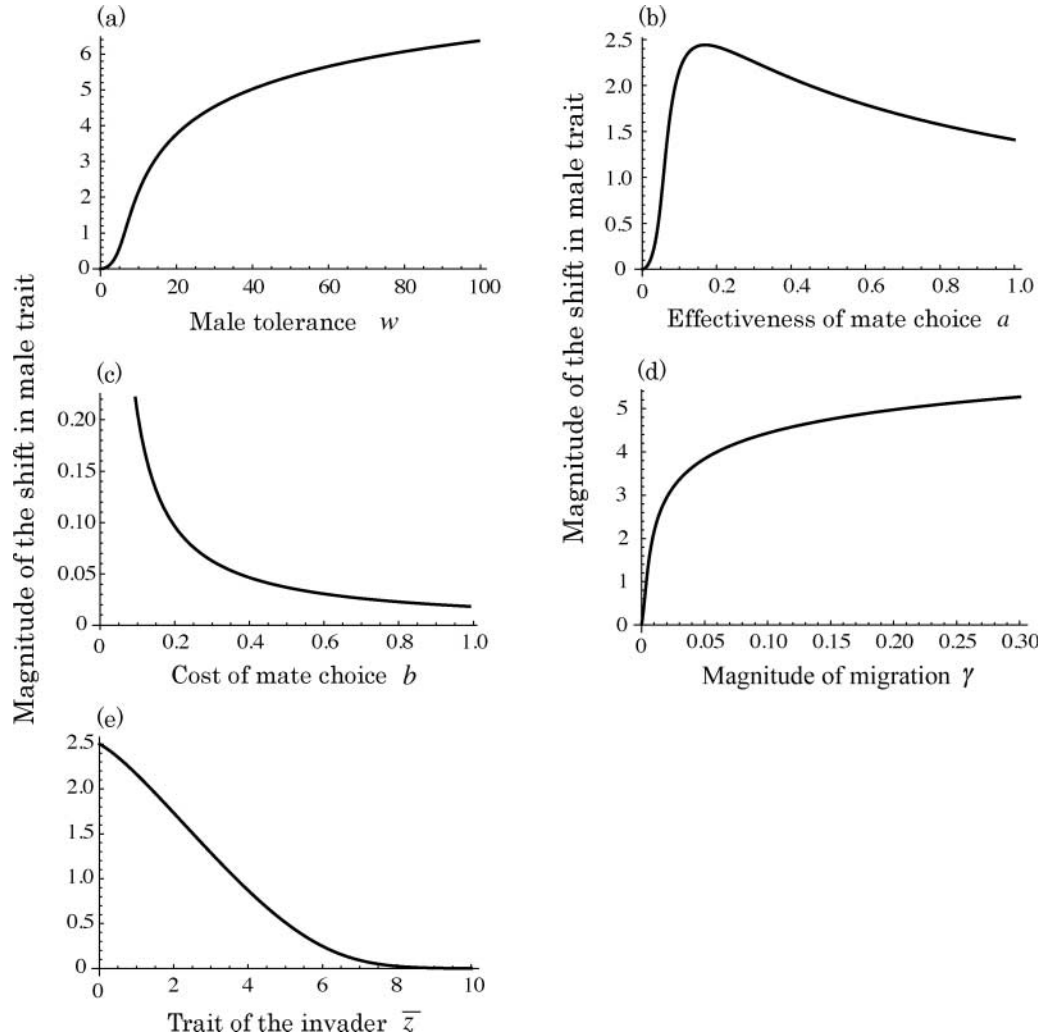


Fig. 2. Magnitude of the shift in the male trait after adaptive evolution, $|\bar{x}(\infty) - \bar{x}(0)|$. Different graphs indicate the dependence on different parameters in the model. The x-axes are: (a) male tolerance, w ; (b) the effectiveness of female mate choice, a ; (c) the cost of mate choice, b ; (d) the magnitude of migration, γ ; and (e) the mean trait of the invasive species, $\bar{z}$. Parameter values are $w = 10$, $a = 0.1$, $b = 0.01$, $\gamma = 0.01$, and $\bar{z} = 1$, unless stated otherwise.

the male trait much by female mate preference. As w increases, the male trait value becomes less restricted, and the male trait can show a stronger response to the presence of an invader.

(ii) Effectiveness of mate preference a :

Figure 2(b) illustrates the magnitude of the shift in the male trait as a function of the effectiveness of mate preference. Note that the dependence is not monotonic – an intermediate value of a engenders the maximum shift in the male trait. If mate choice is weak, it is difficult for a trait shift to occur. But if mate choice is very strong, a small shift in the trait value is sufficient to establish species recognition.

(iii) Cost of female mate choice b :

Figure 2(c) illustrates that the magnitude of the shift in the male trait at equilibrium decreases monotonically with the cost of the female mate choice b . A larger value of b constrains the female mate preference and reduces the magnitude of reproductive character displacement.

Figure 3 is a contour map of the character displacement. The two axes are the effectiveness of mate choice a and the cost of mate choice b (where $b < a$). Figure 3 shows that the effect of the cost of mate choice b depends on the effectiveness of mate choice a . When

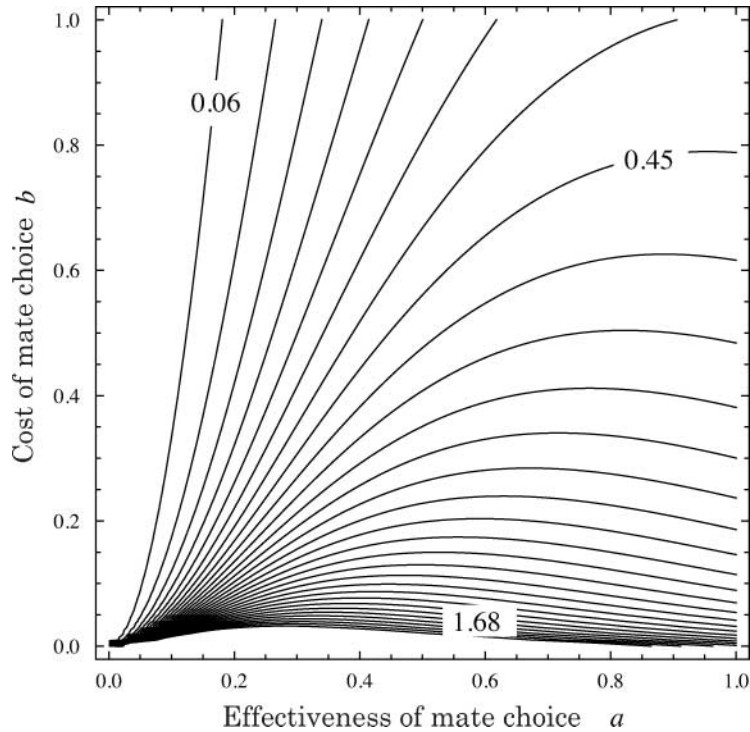


Fig. 3. Contour plot of the magnitude of the shift in the male trait after adaptive evolution, $|\bar{x}(\infty) - \bar{x}(0)|$. The x -axis represents the effectiveness of female mate choice, a ; the y -axis the cost of female mate choice, b . Numbers on the contours indicate the magnitude of trait shifts. Other parameter values are $w = 10$, $\bar{z} = 1$, and $\gamma = 0.01$.

a is small, the shift in the trait value decreases sharply with the cost of mate choice. In contrast, when a is large, a large displacement can occur even when mate choice is costly.

(iv) Magnitude of migration γ :

Figure 2(d) illustrates the magnitude of character displacement for different magnitudes of migration $\gamma = mN'/N$. (γ correlates with the encounter frequency between the two species.) The trait shift increases with the magnitude of migration.

(v) Trait of the invasive species $\bar{z}$:

Figure 2(e) illustrates how the magnitude of character displacement depends on the male trait of the invader $\bar{z}$. If the cost of mate choice b is small, the equilibrium value of character displacement decreases monotonically with $\bar{z}$. If b is large, the magnitude of character displacement is largest at intermediate values of $\bar{z}$. Thus the trait shift is small whether the invader is very similar to the resident or very different from the resident. The value of the parameters will determine whether this non-monotonic dependence is observable in natural systems.

Transient behaviour

Next we consider the speed of the evolutionary response of the resident population following contact with invaders. At t_0 , the population starts to make contact with the invader. In subsequent generations, the male trait $\bar{x}(t)$ converges to the new equilibrium $\bar{x}(\infty)$. The following quantity indicates the average time required for the response:

$$\tau = \frac{1}{\bar{x}(\infty) - \bar{x}(t_0)} \int_0^\infty t \frac{d\bar{x}}{dt}(t) dt. \quad (5)$$

We calculated this quantity numerically.

Figure 4 illustrates the mean response time for different magnitudes of invasion, $\gamma = mN'/N$. As γ increases, the total shift $|\bar{x}(\infty) - \bar{x}(t_0)|$ increases (see Fig. 2d), but the mean

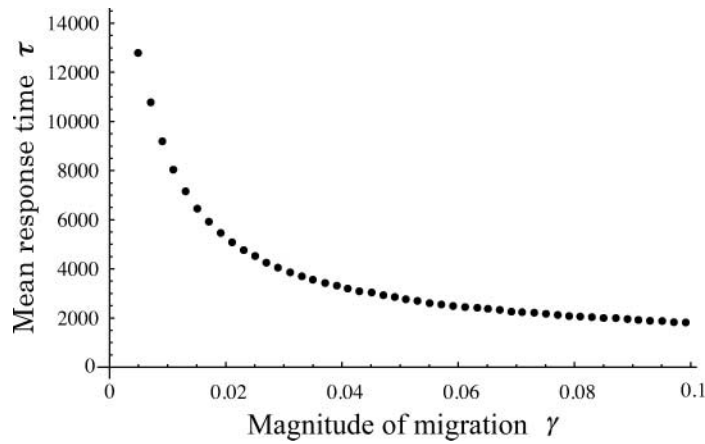


Fig. 4. Mean response time, τ . The x -axis represents the magnitude of migration, $\gamma = mN'/N$. The other parameter values are $w = 10$, $a = 0.1$, $b = 0.01$, and $\bar{z} = 1$.

response time becomes shorter. This result contrasts with all the other parameters; for them a larger shift in the trait tends to slow down the response (leading to a longer mean response time) (data not shown).

FITNESS EFFECTS OF REPRODUCTIVE CHARACTER DISPLACEMENT

Figure 5 illustrates the mean fitness of the population over time, which is $W_y(\bar{y} | \bar{x})$ given in equation (1b). Female fitness drops just after the contact with invaders, but the evolutionary change in female mate preference mitigates the shock as fitness recovers because females become more skilful at avoiding heterospecific mating, even considering the cost of mate choice. If traits change each generation, we can derive the following inequality from equation (2) with B neglected,

$$\Delta W_y(\bar{y}) = W_y \frac{1}{2} G_y \left(\frac{\partial}{\partial y} \ln W_y \right)^2 \geq 0, \quad (6)$$

where equality holds at equilibrium. Hence, the mean fitness increases monotonically over time by adaptive evolution. This is basically the same as Fisher's fundamental theorem (Fisher, 1930).

In the following, $W_f(t)$ is the female fitness value at time t , and $S_m(t) = \exp\{\lambda_m - x^2/2w^2\}$ is the male survivorship. Male survivorship declines over time because the male trait shifts and deviates from the trait value with optimum viability.

Decrease in female fitness following interspecific contact

Let $\hat{W}_f$ be the fitness before the contact with the invader and be equal to the optimal value. The ratio $W_f(t_0)/\hat{W}_f$ is the initial reduction in relative fitness following contact with

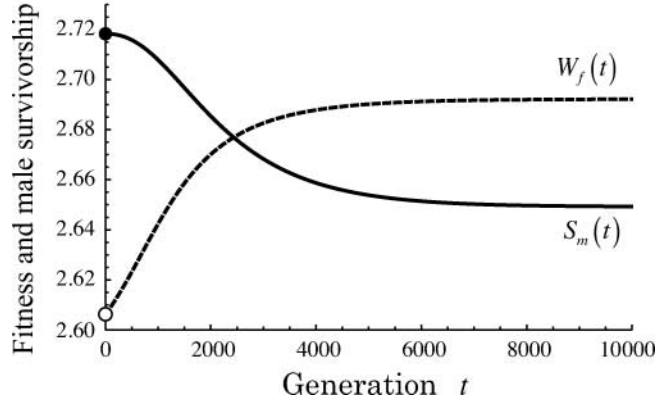


Fig. 5. Fitness and male survivorship of the resident population relative to the levels before invasion. The x -axis represents time expressed in terms of the number of generations. Solid and dashed lines indicate male survivorship $S_m(t)$ and female fitness $W_f(t)$, respectively. Solid and open circles are the initial female fitness before the invasion and just after the contact with the invader, respectively. Parameter values are $\lambda_m = 1$, $\lambda_f = 1$, $w = 10$, $G_x = 0.1$, $G_y = 0.1$, $a = 0.15$, $b = 0.06$, $\bar{z} = 1$, and $\gamma = 0.05$.

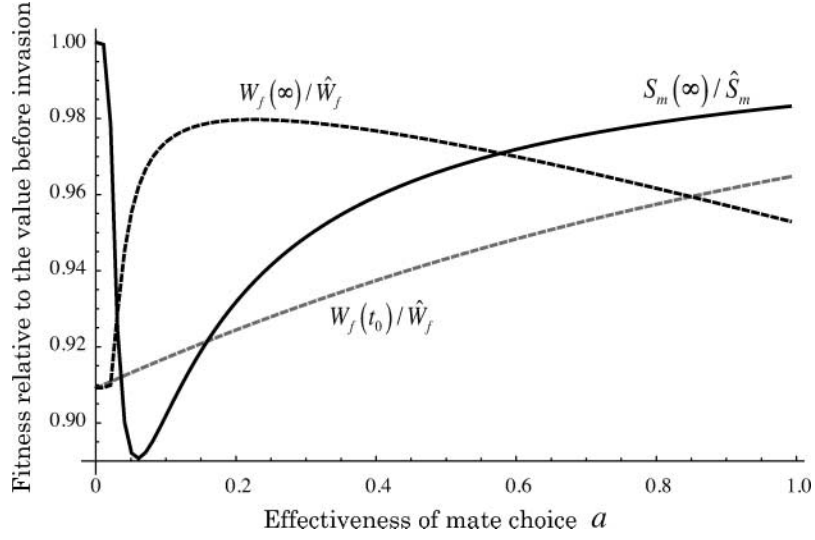


Fig. 6. Fitness after contact with the invader relative to the value before the invasion. The x -axis represents the effectiveness of female mate choice a . The dashed grey line represents the female fitness in the situation just after the first heterospecific contact, $W_f(t_0)/\hat{W}_f$, and at the equilibrium after fitness recovery is completed, $W_f(\infty)/\hat{W}_f$. The black solid line shows male survivorship at equilibrium. Parameter values are $w = 10$, $a = 0.1$, $b = 0.01$, $\bar{z} = 1$, and $\gamma = 0.01$.

the invader. A small value of $W_f(t_0)/\hat{W}_f$ implies substantial damage to resident females. Intuitively, small (similar) values of the male trait for the invasive species $\bar{z}$ and a higher value of γ generate more harm to the female fitness. Male tolerance w has no effect on the decrease in the fitness because no immediate shift of the male trait exists at t_0 . The cost of mate choice b also has little effect because the shift of female preference is small. In contrast, a more effective mate choice (large a) prevents the decline in fitness just after interspecific contact, as demonstrated in Fig. 6. Even before the adaptive evolution of female mate preference and an exaggerated conspecific male trait, females can avoid heterospecific mating more effectively if a is larger.

Recovery of female fitness after the trait shift

Although the evolution of female preference and the conspecific male trait allow the female fitness to recover, the recovery will not be complete. Instead, the level of fitness at the new equilibrium, denoted by $W_f(\infty)$, will lie between the fitness just after the heterospecific contact, $W_f(t_0)$, and the fitness before the invasion, $\hat{W}_f$. The relative female fitness after evolutionary adaptation is $W_f(\infty)/\hat{W}_f$.

The male trait evolves from the original optimal trait value to a new equilibrium that deviates from the male trait of the invader. This evolution helps females to discriminate against heterospecific males more effectively. So the risk of heterospecific mating for females declines and female fitness partly recovers. However, male survivorship decreases because the male trait shifts away from its viability optimum.

Figure 6 illustrates $W_f(\infty)/\hat{W}_f$ for differences in the effectiveness of mate choice a . An intermediate optimal value of a realizes the largest trait shift and the smallest decrease in female fitness. In contrast, relative male survivorship $S_m(\infty)/\hat{S}_m$ is lowest at the point of largest trait shift.

Extinction by reproductive interference

The invasion of an alien species may result in the extinction of the resident species. Traditionally, resource competition has been considered a major reason for such extinctions, but more recently reproductive interference has been considered a potential factor (Dame and Petren, 2006; Liu *et al.*, 2007; Takakura *et al.*, 2009; Matsumoto *et al.*, 2010). Here, we consider the case in which the resident species may go extinct when it encounters an invasive species and heterospecific mating results in a substantial loss of reproductive success among females. Specifically, we study three criteria, focusing on different phases in evaluating the likelihood of extinction of the resident species.

When a population is completely isolated, it can become extinct if its fitness becomes low for a small number of generations. Evolutionary adaptations that take many generations may not be helpful in preventing extinction in such a case. Here the initial drop in fitness may be the most important factor in evaluating extinction risk.

$$(i) \text{ Initial drop of fitness: } W_f(t_0)/\hat{W}_f < \theta_1, \quad (7a)$$

where θ_1 is a threshold.

However, most species live in spatially heterogeneous environments. They often live in a metapopulation composed of many local populations connected by occasional dispersal. When an invading species makes contact with a resident species, it may invade only a part of the resident's range. Other portions may remain in a state in which the resident population is abundant. In such situations, the extinction of the whole population can be avoided if the resident species can evolve so that females can avoid heterospecific mating effectively. In this case, the fitness after evolutionary adaptation is the most important factor determining the likelihood of extinction. We may use the following criterion:

$$(ii) \text{ Final value of fitness: } W_f(\infty)/\hat{W}_f < \theta_2, \quad (7b)$$

where θ_2 is a threshold.

Even though evolutionary adaptation can sometimes eventually bring the species back to a state of survival, if the evolutionary process is very slow, the extinction of the whole metapopulation might occur before the effective adaptation takes place. Hence, the mean number of generations required for the evolutionary adaptation to arise might be a useful criterion for determining the extinction risk:

$$(iii) \text{ Mean time required for the population's response: } \tau > \theta_3, \quad (7c)$$

where θ_3 is a threshold. This can be calculated from equation (5), where the male trait $\bar{x}(t)$ should be replaced by fitness $W_f(t)$.

Using these criteria, we can evaluate situations in which extinction is less likely to take place.

DISCUSSION

Two sympatric species with similar reproductive traits may evolve altered traits that avoid heterospecific mating if the hybrids have poor viability. We modelled and analysed the co-evolution of a male secondary sexual trait and of female preference for it, based on simple multivariate quantitative genetics. Examples of such quantitative traits can include colour pattern, morphology, songs, dance, and any signals used in species recognition during mating. Our results may explain the observation that closely related species often differ markedly in sexual morphology (e.g. Sætre *et al.*, 1997; Johanet *et al.*, 2009). Moreover, this biological situation results in sexual dimorphism because the morphological trait of females stays close to the viability optimum, whereas the corresponding male trait deviates from its viability optimum due to female mate preference. From this, we may infer that a species showing a sexual dimorphism only in some part of its geographical range may have experienced reproductive interference in the recent past.

Our analysis indicates that the magnitude of the shift in the traits is large when the resident species suffers substantial costs. For example, when the range overlap is large, the male trait is similar between species, the male tolerance of the male trait is broad, or the cost of female mate choice is small. However, an intermediate optimum for the effectiveness of mate choice exists that generates the largest reproductive character displacement. This non-monotonic dependence is explained by the adaptive response being weak if mate choice is not effective, whereas a small difference in the male trait results in an almost complete pre-zygotic isolation when mate choice is very effective.

In the present study, we considered the male's cost of producing an enhanced trait and the female's cost of mate choice. One of our conclusions is that at the equilibrium in the presence of heterospecific males, females evolve to prefer males that deviate more from the heterospecific males than the current conspecific male, as shown by equation (4). The equilibrium male trait is maintained by the balance between the female mate choice that ensures the male trait deviates more from the heterospecific males and the cost of having an enhanced male trait. Both sexual and natural selection continue to act at the equilibrium. Figure 5 illustrates that the reproductive character displacement allows the female fitness to recover by avoiding heterospecific mating, whereas male survivorship is reduced.

In contrast, some models of ecological character displacement do not consider the effect of female mate preference as the principal force for character displacement. For example, Konuma and Chiba (2007) developed a quantitative genetic model for ecological character displacement that included reproductive interference. In their model, females were assumed always to prefer the trait of their conspecific males, and the male morphological trait at the equilibrium was not affected by the female mate choice itself (for individual-based simulations, see Thibert-Plante and Hendry, 2009).

The importance of the evolution of mate choice in the process of reinforcement was also addressed by Coyne and Orr (2004), who observed that a model including the evolution of mate choice (Liou and Price, 1994) displayed a much wider range of parameters for reinforcement than the corresponding model without sexual selection (Spencer *et al.*, 1986). Sved (1981) studied evolutionary changes in female mating behaviour when the focal population was in contact with heterospecific males. However, the study focused on the initial evolutionary changes, and did not consider the evolutionary endpoint that is realized by the balance between the need for avoidance of interspecific mating and the costs to both sexes that constrain the evolution of traits. In our study, we considered the whole evolutionary process, not only

the initial rate of evolution but also the evolutionary equilibrium, as well as the speed of the adaptive response. These factors are important when considering the likelihood of extinction caused by the interspecific contact.

To evaluate the extinction risk of the contact with the invader, we examined three different criteria which focus the extinction risk at different stages of evolutionary adaptation. The results differ depending upon the criteria. For example, when the effectiveness of mate choice a was large, the potential for extinction was reduced immediately after the interspecific contact, as shown by equation (7a) (see Fig. 6). A stronger mate choice intensity results in females being more likely to choose conspecific males and avoid harmful heterospecific mating, thus reducing the risk of extinction. Alternatively, extinction risk may be controlled more strongly by the fitness resulting from adaptive evolution of the resident species than by the fitness just after the invasion. In such situations, the fitness at the new equilibrium is more important and an intermediate intensity of a would realize the smallest risk of extinction (see Fig. 6). This corresponds to the situation in which female mate preference deviates from the male trait of the invader by the largest magnitude. However, the greatest magnitude of trait shift achieved by an intermediate mate choice intensity takes the longest time to shift, which may lead to a high risk of extinction. Hence, the three criteria for extinction lead to different optimal values of mate choice intensity. The different criteria focus on different aspects of extinction risk, and it is important to specify how the extinction is likely to occur before discussing the relationship between extinction risk and biological parameters.

Although we drew many useful biological implications from the model, many limitations need to be resolved in future theoretical studies. First, the current model focused on the co-evolution of a male trait and female mate preference and did not consider the dynamics of the number of individuals. In addition, males of the two species may differ in aspects other than the focal trait, and females may encounter conspecific males more frequently than the heterospecific male encounters assumed in the current model. Second, as Moore (1957) pointed out, the traits resulting in reproductive character displacement have a selective advantage only within the zone of geographical overlap. The traits cannot spread outside the region of species overlap to the whole area in which the resident species lives if selection in the overlap zone is swamped by gene flow from outside. Third, we assumed that hybrid fitness is zero. In general, hybrid viability may be low but positive and reproductive character displacement may evolve to a smaller degree. The effect of introgression through surviving hybrids should then be considered. Finally, we considered one asymmetric situation in which one species is invaded by another. The evolutionary outcomes when two such species encounter each other should be a focus of future theoretical research.

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