

Sexual selection and the detection of ecological speciation

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ABSTRACT

Context: Ecological speciation is commonly inferred with evidence of the parallel evolution of pre-mating isolation: individuals from populations in similar environments show higher mating success in laboratory experiments than do individuals from different environments. Critically, this should hold even for mating crosses among populations that are from different locations that represent independent evolutionary lineages.

Problem: This prediction may not hold when conserved sexual selection (e.g. good genes benefits) constrains the evolution of mate preferences. In this case, ecological pre-mating isolation may be developing but is difficult to infer using the typical experimental approach.

Solution: We show how comparisons of mate preference functions among replicate populations in divergent environments can be used to reveal subtle signatures of ecological speciation. These functions can then be used to develop predictions of relative mating success in population crosses.

Significance: This general approach, based on mate preference functions, facilitates the simultaneous analysis of both pattern and process during ecological speciation.

Keywords: divergent natural selection, local adaptation, mate choice, parallel evolution, preference function, pre-mating isolation.

ECOLOGICAL SPECIATION

A connection between divergent natural selection and speciation has long been acknowledged (Mayr, 1963; Coyne and Orr, 2004), but only recently have definitive examples from nature begun to accumulate (Schluter, 2000). In general, ecological speciation is the evolution of reproductive isolation as a by-product of adaptation to different ecological environments (Schluter, 2000; Rundle and Nosil, 2005). This process can be inferred when assortative mating evolves repeatedly in response to similar differences between environments (Nosil *et al.*, 2002). In recognition of this expectation, a common approach to testing ecological speciation has involved mate choice experiments that examine whether parallel adaptive divergence between environments is accompanied by a parallel reduction of mating probabilities

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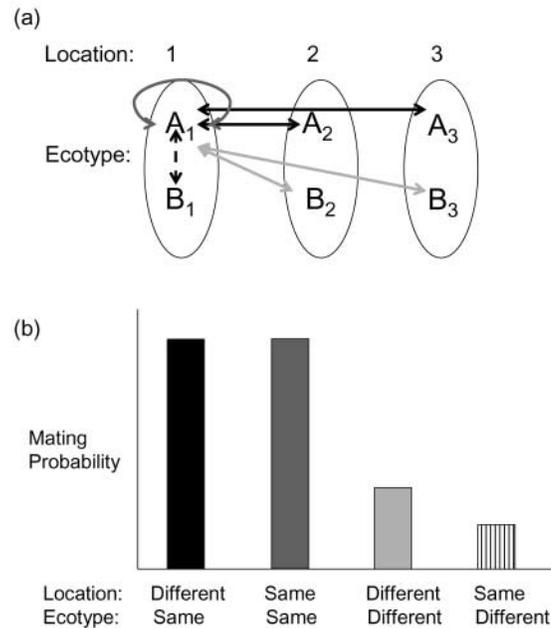


Fig. 1. An illustration of the typical approach and prediction for testing ecological speciation using mate choice trials. (a) Hypothetical parallel evolution of two ecotypes (A and B) in response to the same divergent selection in three different locations (e.g. different lakes). Arrows indicate pair-wise crosses performed in mating trials designed to test for ecological speciation. (Arrows are shown only for population A₁ but are assumed for the other five populations.) (b) The pattern of mating probabilities expected under the typical prediction of ecological speciation. Also shown is the expectation that reinforcement would lead to higher mate discrimination (lower mating probability) in sympatry (same location) than in allopatry (different locations).

(e.g. Rundle *et al.*, 2000). In a typical experiment (Fig. 1), multiple independent populations of at least two ecological types are subjected to mate choice experiments in the laboratory, and the probabilities of mating are then compared among the various types of population crosses (Seehausen, 1997; Funk, 1998; Nagel and Schluter, 1998; Rundle *et al.*, 2000; Nosil *et al.*, 2002; McKinnon *et al.*, 2004; Boughman *et al.*, 2005). Ecological speciation is inferred when the probability of mating is higher between individuals adapted to the same ecological conditions, even if they come from different locations, than between individuals adapted to different ecological conditions (Fig.1). We refer to this comparison as the ‘typical approach’ and the expected pattern as the ‘typical prediction’.

Our motivation for this article stems from a realization that although the typical approach and prediction do indeed suggest ecological speciation, a larger range of mate choice patterns are also consistent with this process. These other patterns are important to consider as they can arise when sexual selection is conserved between diverging populations for other reasons (see below) and when signalling traits diverge faster than do mate preferences. In these cases, the constraining effects of similar sexual selection between environments may limit the ability to detect ecological speciation by the typical approach. This limitation is particularly unfortunate because populations early in the process of divergence are also the best candidates for studying the influence of natural selection on the

evolution of reproductive isolation. It therefore becomes important to examine how both mating traits and preferences evolve throughout the process of speciation.

THE COMPLICATION OF SEXUAL SELECTION

For the sake of convenience only, we henceforth assume ‘conventional’ sex roles, where males signal and females choose. Following previous work on ecological speciation (Rundle *et al.*, 2000; Nosil *et al.*, 2002; Boughman *et al.*, 2005), we consider ecological pre-mating isolation to be signalled by non-random mating that leads to a bias against individuals from different environments. Such isolation is thought to evolve when traits used in mate choice or mate recognition diverge in response to natural selection (Schluter, 2001). Although ecological pre-mating isolation could evolve by a variety of mechanisms (Coyne and Orr, 2004), we focus here on behavioural isolation (via mate choice) as it has been the subject of many empirical tests, and because it appears important in some of the best-documented cases.

When considering behavioural isolation, it is necessary to discriminate between two major categories: (i) isolation that involves overall preferences for a general ‘type’, and (ii) isolation that requires the evolution of preferences for specific traits. Consider, for example, mate choice that is based on body size (Nagel and Schluter, 1998; Sisodia and Singh, 2004). In the first category of isolation, females might have a general mate choice rule, such as ‘mate with own type’, which leads females to prefer males that are similar to their own size (McKinnon *et al.*, 2004; Boughman *et al.*, 2005). In the second category, females in one population might show a directional preference for larger males, whereas females in another population might show a directional preference for smaller males. Now assume that natural selection causes divergence in body size between populations in the two environments. Under either category of isolation, females from the environment where large (small) size is favoured will prefer to mate with large (small) males. That is, females will mate readily with males from similar selective environments, but will discriminate against males from different environments.

These two types of isolation have different consequences for the evolution and detection of ecological pre-mating isolation. Felsenstein (1981) demonstrated that speciation evolves most readily between sympatric populations when the same allele is substituted in both populations. Speciation is much more difficult if assortative mating is the result of different alleles being substituted in different populations. Similarly, divergence in male traits in our first category can lead to pre-mating isolation even if mate choice itself does not evolve, whereas isolation in the second category requires the additional *evolution* of mate choice. In the second category, forces stabilizing female preferences can therefore constrain the evolution of ecological pre-mating isolation, or at least make it difficult to observe in natural populations.

We focus further on this second category of isolation because it is here that the typical approach for inferring ecological pre-mating isolation encounters difficulties. In this case, females will favour males from their own environment only to the extent that male signals and female preferences have co-evolved (Fisher, 1930; Lande, 1982; Liou and Price, 1994; Servedio, 2000; Kirkpatrick and Ravigné, 2002). And yet the extent of this co-evolution can be variable, as traits subject to divergent natural selection could be subject to some conserved components of sexual selection (Ryan and Keddy-Hector, 1992) (see Table 1). When male traits and female preferences do not closely co-evolve, an asymmetry can be evident in mate choice trials: females from one population type might favour their own males, whereas females from the

Table 1. Recent studies of sexually selected traits under divergent natural selection: do female preferences evolve in parallel with male traits?

Species	Sexually selected trait	Ecological variation in trait	Source of selection	Ecological variation in preference	Direction of preference and trait divergence ^e	Evidence of pre-mating isolation	Reference
Acoustic signals							
Field cricket <i>Teleogryllus oceanicus</i>	Calling songs	YES	Parasites	Unknown	Mismatch	NO	Simmons <i>et al.</i> (2001), Zuk <i>et al.</i> (2001)
Katydid <i>Ephiggea ephiggea</i>	Song	YES	Unknown	Unknown	Correlated	YES	Ritchie (1996)
Crickets <i>Acris crepitans</i>	Call and body size	YES	Habitat sound transmission	YES	Correlated with some mismatch	YES	Kime <i>et al.</i> (1998, 2004)
Tungara frog <i>Physalaemus pustulosus</i>	Call and body size	YES	Predation	NO	Unidirectional	NO	Ryan and Rand (1990), Ryan <i>et al.</i> (1990)
Chemical signals							
Grasshopper <i>Chortippus parallelus</i>	Song and CHCs	YES	Altitude (inconsistent)	Inconsistent	Correlated	YES	Dagley <i>et al.</i> (1994), Tregenza <i>et al.</i> (2000)
Jewel wasp <i>Nasonia viripennis</i> and <i>N. longicornis</i>	Pheromones and courtship displays	Unknown	Host preference	Unknown	Unknown	Weak	Bordenstein <i>et al.</i> (2000)
Leaf beetle <i>Neochlamisus bebbianae</i>	Life-history traits associated with host use	YES	Host plant preference	Unknown	Correlated	Incomplete	Funk (1998)
Drosophila <i>D. mojavensis</i>	Epicuticular hydrocarbons	YES	Host plant preference	YES	Correlated	YES	Etges and Ahrens (2001)

Visual signals	Coloration	YES	Predation	YES	Unidirectional mismatch*	Weak	Endler (1980), Houde and Endler (1990)
Guppy <i>Poecilia reticulata</i>	Coloration	YES	Predation	YES	Unidirectional mismatch*	Weak	Endler (1980), Houde and Endler (1990)
Sticklebacks <i>Gasterosteus aculeatus</i>	Coloration	YES	Water transmission	YES	Correlated	YES	Boughman (2001), Boughman <i>et al.</i> (2005)
Seaweed flies <i>Coelopa frigida</i>	Body size; karyotype	NO	Tide/food availability	YES	Unidirectional*	YES	Gilburn and Day (1994)
Amphipods <i>Hyalella azteca</i>	Body size	YES	Predation	YES	Unknown	YES	McPeck and Wellborn (1998)
Colias butterfly <i>C. philodice eriphyle</i>	Female wing colour	YES	Elevation; thermal environment	NO	Unidirectional	NO	Ellers and Beggs (2002, 2003)
Iguanid lizard <i>Sauromalus obesus (ater)</i>	Coloration	YES	Population size; resource limitation	YES	Correlated with asymmetry among populations	Weak	Kwiatkowski and Sullivan (2002)
Wolf spider <i>Schizocosa</i> spp.	Courtship behaviour	YES	Physiographical environment	Unknown	Unknown	Unknown	Miller <i>et al.</i> (1998)
Drosophila <i>D. melanogaster</i> , <i>D. simulans</i> , <i>Zaprionus tuberculatus</i>	Weight, symmetry, oviposition site	YES	Microclimate: temperature and drought stress tolerance	YES	Unknown	YES	Korol <i>et al.</i> (2000)
African cichlids <i>Haplochromis nyererei</i>	Coloration	YES	Light environment	YES	Correlated	YES	Seehausen (1997), Seehausen and Schluter (2004)

^a 'Mismatches' refer to situations where females prefer a higher value of the trait than the population average. 'Unidirectional' indicates that all females prefer high values of the trait. * The special cases in which the population with the widest mismatch shows a weaker preference for the trait. Under the typical predictions of ecological speciation, pre-mating isolation is expected when both the male trait and the female preference respond to divergent selection in the same direction. Therefore, only those marked 'correlated' would be expected to produce mate choice patterns in line with the typical predictions.

other population type might not, or may do so to a lesser extent. These asymmetries might arise in a variety of ways, including a difference in the strength of overall female discrimination, the specifics of experimental conditions, or a lack of divergence in preferences for particular traits (Kaneshiro, 1980; Fraser and Boake, 1997). In the last case, components of sexual selection may act to constrain preference evolution. For example, a sexually selected trait may be a reliable indicator of mating benefits, whether direct (e.g. resources or paternal care) or indirect (e.g. 'good genes' or 'sexy sons') (Kokko, 2003). If so, females may derive a high enough benefit from choosing males with larger trait values in both environments so that the expected signature of ecological speciation would not be evident in population crosses. Conserved preferences resulting from a pre-existing bias in the female sensory system (Ryan and Rand, 1993; Fuller *et al.*, 2005) could have a similar effect. Even if preferences are not constrained by sexual selection, they may nonetheless evolve at a slower rate than the mating traits on which they are based (Schluter and Price, 1993). For example, colonization of a new environment may lead to rapid changes in phenotypic traits (Kinnison and Hendry, 2001), some of which may be related to mate choice, but to slower changes in preference functions. Although this scenario is plausible, we are not aware of any studies that have determined the rate at which preference functions evolve in natural populations. If female preferences evolve more slowly than male traits, pre-mating isolation may not be detectable based on the typical prediction at the early stages of divergence (Fig. 1b), even if it would be after a longer period of time.

To further illustrate this critical point, assume that environments A and B in Fig. 1a impose divergent selection that has led to adaptive divergence in male size, with the population in environment A evolving larger size. If all females prefer large males because large size indicates greater health or simply makes males more conspicuous, 'B' females would appear to discriminate against males of their own type because the largest males presented to them will be from environment A. Complete understanding of how divergent natural selection leads to ecological pre-mating isolation thus requires an explicit consideration of within-population sexual selection. We will show how the analysis of preference functions allows the incorporation of such considerations.

The validity of our concerns with the typical approach hinges on evidence that mating traits and preferences do not always co-evolve tightly. We therefore reviewed empirical studies that might indicate the incidence of such co-evolution between populations that have diverged in an ecologically important trait (Table 1). Although many studies have examined inter-population variation in secondary sexual traits, relatively few have examined variation in both traits and preferences. Even fewer have been able to determine the specific selective factors driving the observed patterns. This relative scarcity of information reflects a general lack of integration between studies of mating isolation and studies of natural selection acting on the traits involved in mating isolation. Based on our review, we can conclude that mating signals often diverge between populations in different ecological environments, but that mating preferences often do not co-evolve to tightly match this trait divergence. In some cases, preferences do not diverge at all between environments and a lack of ecological pre-mating isolation would be correctly inferred using the typical approach. In other cases, however, preferences have diverged to some extent but may be partly masked by conserved components of sexual selection. The approach we now outline allows inferences of ecological pre-mating isolation in this latter case.

PREFERENCE FUNCTIONS AS A POTENTIAL RESOLUTION

Preference functions represent the relationship between male trait values and the probability of mating with females of a given type. The shapes of these preference functions can be used to estimate the strength and form of sexual selection acting on the trait (Lande, 1981; Ritchie, 1996; Widemo and Saether, 1999; Brooks and Endler, 2001). As such, the parallel divergence of preference functions between ecological environments may indicate that divergent natural selection is causing divergent sexual selection, which may then contribute to ecological pre-mating isolation. Preference functions can also be used to infer ecological pre-mating isolation in the case of conserved sexual selection or when preferences evolve at a different rate than signalling traits. In the following, we consider possible ways in which preference functions can evolve in response to divergent selection. We then show how patterns of divergence in preference functions can be translated into expectations of mating frequencies among populations, and how to interpret the degree of ecological pre-mating isolation.

When female choice is based on a single male trait that is expressed to varying degrees in two (or more) population types, both natural and sexual selection should be considered simultaneously. Although the specific selective agents will change from system to system, we can here distinguish two population types based on the strength of natural selection acting *against* a trait (*strong* vs. *weak*) that is favoured by sexual selection – a situation that may be common in nature (Etges, 2002). In principle, we would expect the mean value for the trait to evolve to the optimum, as determined by the balance between these two forces in any particular population. Figure 2 illustrates a hypothetical example where sexual selection favours large values of the trait in both populations, perhaps because of good genes effects or sensory bias. In contrast, natural selection acts against the trait in both populations, although more strongly so in one population type (*strong*) than in the other (*weak*) (Fig. 2a).

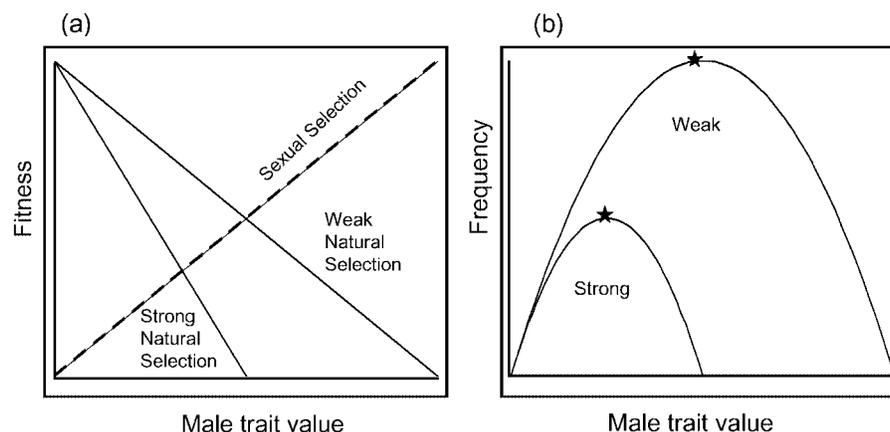


Fig. 2. The joint effects of natural and sexual selection on the evolution of male phenotypes in two selective environments. (a) Hypothetical patterns and relative strengths of natural selection (solid lines) acting on a male trait in the two environments. Sexual selection (dashed line) is assumed to be identical in the two environments. (b) Resulting fitness functions determined by the product of natural and sexual selection in (a). The optimal trait value (star) is lower in the environment where natural selection against it is stronger.

Accordingly, the *strong* population type will evolve a smaller mean trait value than the *weak* population type (Fig. 2b).

Sexual selection is, for the present, assumed to favour the trait to the same extent in both environments. The opposing forces of natural and sexual selection thus lead to different optima for the traits, which generates divergent selection between environments. This type of divergent selection contributes to ecological speciation because it is caused solely by differences in natural selection between the two environments, even though the direction of natural selection is the same in both environments.

We now consider the possible divergence of sexual selection through changes in preference functions. These functions then allow for the flexible prediction of among-population mating probabilities, and the estimation of ecological pre-mating isolation. In particular, the height of the female preference function for a given population at the average phenotypic value of males from a given population yields the expected mating probability for that cross. In the typical approach to testing ecological speciation, these mating probabilities would be used to quantify female acceptance of males from her own population type, relative to males of other population types. Because the direction of sexual selection may be similar among all females, we suggest that a more general approach is to quantify the mating success of *males* with females from their own population type, relative to females from other population types.

Theoretical models and empirical studies suggest that ecological speciation may depend on (i) the correlation between traits and preferences (Lande, 1981, 1982), (ii) the reliability of the trait as a signal (Schluter and Price, 1993), and (iii) the signalling environment (Endler, 1992). Our approach most directly considers the first condition, which can be visualized by varying the slope of linear preference functions. Such functions can be derived by regressing a measure of relative male mating success (e.g. spawning rate, female acceptance rate) onto male trait values. We illustrate this approach using our hypothetical populations experiencing different strengths of natural selection (i.e. *weak* vs. *strong*) that act in opposition to sexual selection. We then vary sexual selection to establish how different patterns of preference function divergence may influence pre-mating isolation. We further assume that divergent selection has led to (at least partial) adaptive divergence of the population types. For the purposes of illustration, we then assume that males at the low and high ends of trait variation are representative of mean phenotypes in the *strong* and *weak* population types. The height of the preference function for females at these average male values can then be used to predict mating frequencies for the different cross types. (Note that a more precise prediction may be obtained by multiplying the distribution of male trait values by the distribution of female preference values and calculating the average.) In this case, the strength of pre-mating isolation can be quantified as male mating success with females from the same selective environment (homotypic) relative to male success with females from the opposing selective environment (heterotypic). We can then quantify the total ecological pre-mating isolation (EPMI) as:

$$\text{EPMI} = [\text{MS}_{\text{ww}} - \text{MS}_{\text{sw}}] + [\text{MS}_{\text{ss}} - \text{MS}_{\text{ws}}]$$

where MS refers to mating success, and the subscripts refer to crosses between individuals from *weak* (W) and *strong* (S) population types, with the first letter indicating the female.

We now specify four plausible scenarios for preference function divergence (Fig. 3). In each scenario, we assume that *weak* females show an open-ended linear preference function (solid line). We then vary preference functions for females in the *strong* population type (dashed lines). For each scenario, we allow overall mating propensity in the *strong* population to vary (i.e. different elevations in preference functions; lines A–C in each figure). This allows us to consider whether overall mating propensity influences our conclusions (Arnold *et al.*, 1996; Rolan-Alvarez and Caballero, 2000). Using preference functions as a guide, we also show predictions for homotypic and heterotypic mating probabilities in the four scenarios.

We begin with a null model in which the shape of the preference function remains constant even though its height (i.e. overall mating propensity) may vary (Fig. 3a). This scenario generates no pre-mating isolation between population types, whether assessed by the typical approach or by our approach. With respect to the typical approach, females from both population types prefer to mate with males of a single type (here, the *weak* males) because these males have larger trait values. With respect to our approach, males of one type are favoured to a certain extent by females of that type, but males of the other type are disfavoured to a similar extent by females of their own type. In this scenario, natural selection is divergent but because sexual selection is not, ecological pre-mating isolation has not evolved. Our suggested index of ecological pre-mating isolation (EPMI = 0 for our hypothetical preference functions) reflects this fact regardless of mating propensity.

We next consider a situation in which preference function divergence parallels male trait divergence (Fig. 3b). That is, males in *strong* (*weak*) populations have smaller (larger) trait values, and females in *strong* (*weak*) populations prefer males with smaller (larger) trait values. With respect to the typical approach, this generates a situation where females of each population type prefer males of their own type over males of the alternative type, which is the pattern typically used to infer ecological pre-mating isolation (Fig. 1b). Our approach yields a similar conclusion because males always have greater success with females of their own type than with females of the alternative type. Our suggested index of ecological pre-mating isolation (EPMI = 1.2) reflects this fact regardless of mating propensity.

We now turn to scenarios where the typical approach and prediction may fail to detect ecological pre-mating isolation, whereas our approach succeeds. One such scenario is the evolution of a flat preference function in the *strong* population, indicating no discrimination with respect to the male trait (Fig. 3c). This might occur if, for example, female preference has direct costs associated with searching time or predation risk in the *strong* environment (Houde and Endler, 1990; Grafe, 1997). A flat preference function may also indicate that females have shifted their basis for mate choice to a different trait. With respect to the typical approach, females from one population type prefer males of their own type, but females of the other population type make no such discrimination – a pattern that might be interpreted as inconsistent with ecological speciation. With respect to our approach, males of both types have greater success with their own females than with females of the alternative type. If overall mating propensities also diverge substantially, this may no longer be true, and males of both types can have their highest success with females of a single type (as would be the case in any scenario). Fortunately, however, our index reveals the same amount of ecological pre-mating isolation (EPMI = 0.6) regardless of overall mating propensity.

Our final scenario is of particular interest given our supposition that some male traits under divergent natural selection may be consistently favoured by some components of

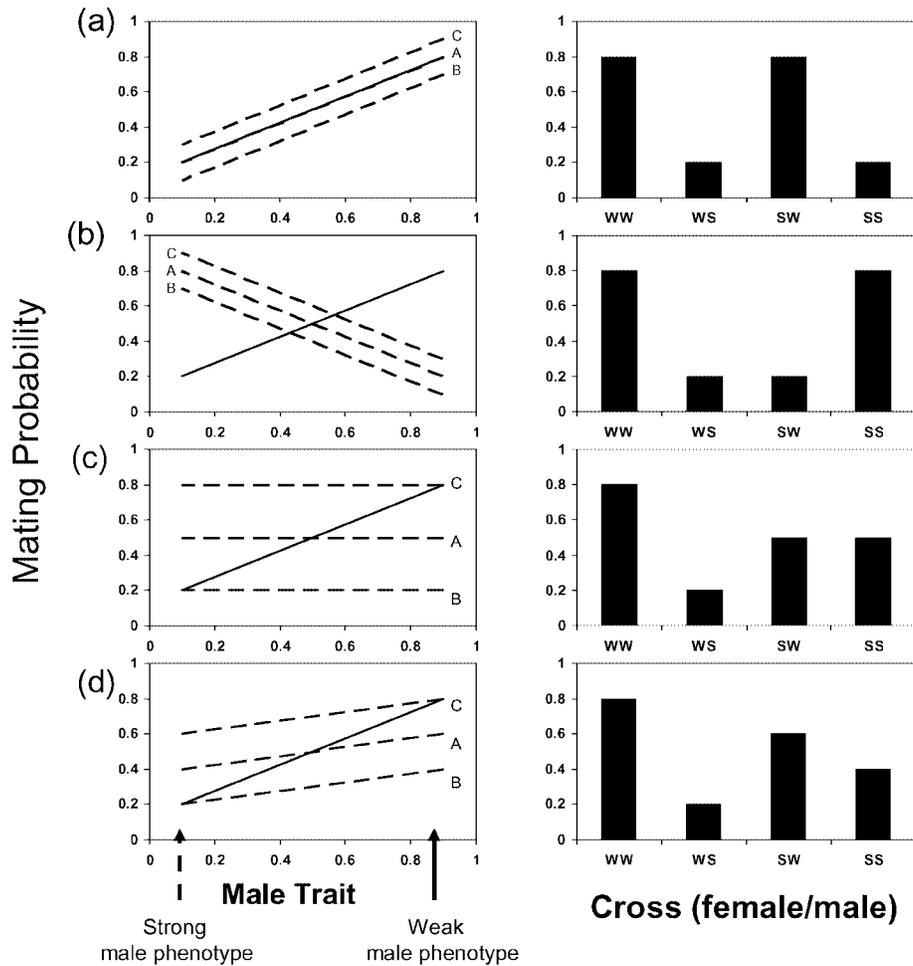


Fig. 3. Preference function evolution and ecological premating isolation. Hypothetical scenarios of preference function evolution in response to divergent natural selection (left panels) and the corresponding expected patterns of homotypic and heterotypic mating probabilities (right panels). Solid lines show directional female preference for the trait in *weak* populations. Dashed lines show hypothetical female preference functions in *strong* populations. Bars in the mating probability panels are determined as the height of the *weak* and *strong* (Function 'A') preference functions at hypothetical male trait values in *strong* and *weak* population types (indicated by arrows at the bottom of the preference function panels). Symbols below the bars show particular mating combinations between *weak* (W) and *strong* (S) populations, with the first letter representing the female. (a) *A null model*. Females from *strong* and *weak* population types show identical directional preferences for a male trait under divergent natural selection. Ecological pre-mating isolation is asymmetric and absent overall (EPMI = 0) regardless of overall mating propensity. (b) *The 'typical prediction' of ecological speciation: co-evolution of traits and preferences*. *Weak* and *strong* female preference functions have equal slopes, but in opposite directions. Females from *strong* (*weak*) population types thus prefer lesser (greater) trait values, which are typical of *strong* (*weak*) male phenotypes. Ecological pre-mating isolation is symmetric and strong (EPMI = 1.2) regardless of overall mating propensity. (c) *No discrimination in one population*. Females in *strong* population types have a flat preference

sexual selection. Here female discrimination based on the male trait (i.e. the slope of the preference function) may be in the same direction in both populations, but might be weaker in the *strong* population type than in the *weak* population type (Fig. 3d). This might occur if female discrimination carries a higher cost in the *strong* selective environment, but still has an average overall benefit (e.g. good genes). With respect to the typical approach, females of only one population type (*weak*) prefer males of their own type, and ecological pre-mating isolation might not be inferred. With respect to our approach, males of one type are discriminated against by both female types, but they are discriminated against less by their own female type than by the alternative female type. Overall ecological pre-mating isolation is therefore detectable because the heterotypic preference of the one female type is weaker than the homotypic preference of the other female type. We also offer the following interpretation: although males of one type are preferred by females of the other type (contrary to the typical prediction), this preference is less than expected had the preference function not evolved. As in all the scenarios, our index of ecological pre-mating isolation reliably detects the signature of at least partial ecological pre-mating isolation (EPMI = 0.4) regardless of overall mating propensity.

SUMMARY AND FUTURE DIRECTIONS

Empirical and theoretical evidence suggests that divergent natural selection may affect mate signalling traits more strongly than mating preferences (Schluter and Price, 1993). In such cases, large differences in male traits between ecological environments may not be closely tied to parallel differences in female preferences (Table 1). If so, females may not always prefer males from their own population type. This does not necessarily mean that ecological pre-mating isolation is absent. For example, an increase in natural selection acting against a male trait may increase mating costs to females who choose that trait. A decrease in the strength of female preference for the trait would thus amount to ecological pre-mating isolation. We have shown how the shapes of preference functions can be coupled with comparisons of mating probabilities among and within population types to reliably infer the strength of ecological pre-mating isolation.

The present exposition represents only a starting point for more detailed considerations of how to infer ecological speciation using mate choice trials. For example, we have presented our approach using population-level preference functions. Although these preference functions can reveal the strength and nature of selection currently acting on preferences, it may mask within- or between-female variation in preferences. If this individual variation is high, predictions of relative mating success from population averages may be misleading. Ideally, one would measure individual preference functions repeatedly for a large number of females (Wagner, 1998) and then use this to predict population average

function. Where *strong* and *weak* females mate at the same rate (line A), the direction of ecological pre-mating isolation is symmetric. Where *strong* females mate at lower (line B) and higher (line C) rates, the patterns are asymmetric, but in opposite directions (not shown). Our index of ecological pre-mating isolation gives the same result (EPMI = 0.6) regardless of overall mating propensity. (d) *Similar directions but different strengths of preferences.* Preference functions are in the same direction but weaker in the *strong* populations than the *weak* populations. Ecological pre-mating isolation is asymmetric but of similar strength for all mating propensities (EPMI = 0.4).

mating frequencies. However, given the difficulty of measuring a large number of individual preference functions, population-level functions offer a useful first approximation, so long as females are exposed to a wide range of male trait values.

We have assumed that all preference functions are linear, whereas they can actually take a variety of non-linear shapes (Brodie *et al.*, 1995; Widemo and Saether, 1999). Regardless of these shapes, our general approach may still be applied in the following way. First, preference functions can be estimated for individual populations, preferably using the full range of potential mating signals. Second, the distribution of male traits in each population can be superimposed on the preference functions in each population to predict the relative mating frequency for among-population mate choice trials. This might be done by calculating the height of the preference function for particular male trait values, weighted by the frequency of males expressing those trait values in the population. Mate choice trials can then be performed among population pairs and compared to these predictions. Finally, the relative performance of males of each type with females of each type (our index of ecological pre-mating isolation) can be used to infer the extent of pre-mating isolation caused by divergent natural selection.

All of this, however, still presupposes that the relevant traits for pre-mating isolation have been identified and used to construct preference functions. And yet, mating traits may be used differently within and between populations (e.g. Boughman *et al.*, 2005). Although this difference in itself can reveal a signature of divergent sexual selection, a failure to measure preference functions for the entire range of variation in mating traits could lead to a disconnect between predicted and observed mating propensities. Furthermore, subtle differences in local environments will affect how signals are generated, transmitted and received between mating partners (Endler, 1992). Experimental designs should therefore consider the environment of signal detection to ensure that mate choice is an accurate representation of mating preferences for particular traits.

Many additional complications have yet to be considered, including particular mechanisms of preference evolution, multiple cues for mate choice (multivariate preference functions) (Blows *et al.*, 2003; Van Doorn and Weissing, 2004), and demographic factors such as frequency-dependent selection or asymmetric population sizes. Gene flow can have especially important effects. Some migration between populations is necessary to initiate reinforcement of mate discrimination, and yet too much gene flow can limit the opportunity for local adaptation (Servedio, 2000; Hendry, 2004; Nosil, 2004). Furthermore, when traits favoured by sexual selection are subject to stronger natural selection in one environment type than in the other, the costs of moving between environments will be asymmetric. In our example, *strong* males moving to *weak* environments, where natural selection is relaxed, may suffer reduced mating success but no viability selection. On the other hand, *weak* males moving to *strong* environments may experience high mating success but suffer both direct (increased mortality) and indirect (maladapted offspring) fitness costs. This difference in the success of migrants between different environments could affect the shapes of preference functions and lead to asymmetrical patterns of mate choice. Sex-biased dispersal may also dictate whether male-based or female-based assessments of ecological pre-mating isolation are more relevant for inferences about isolation in natural conditions.

The study of ecological pre-mating isolation is best accomplished through empirical studies that integrate signal variation, covariance of traits and preferences, and signalling environments. Our general approach allows inferences about ecological pre-mating isolation even when female preferences and male traits do not tightly co-evolve. Incorporating studies

of preference function evolution within the growing field of ecological speciation can allow for more realistic predictions of sexual isolation and provide clues to the mechanisms by which natural selection exerts its effects during the course of reproductive isolation.

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