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Sympatric Speciation by Sexual Selection: A Critical Re-Evaluation

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Contents

Abstract

Several empirical studies put forward sexual selection as an important driving force of sympatric speciation. This idea agrees with recent models suggesting that speciation may proceed by means of divergent Fisherian runaway processes within a single population. Notwithstanding this, the models so far have not been able to demonstrate that sympatric speciation can unfold as a fully adaptive process, driven by sexual selection alone. Implicitly or explicitly, most models rely on non-selective factors to initiate speciation. In fact, they do not provide a selective explanation for the considerable variation in female preferences required to trigger divergent runaway processes. We argue that such variation can arise by disruptive selection, but only when selection on female preferences is frequency-dependent. Adaptive speciation is therefore unattainable in traditional female choice models, which assume selection on female preferences to be frequency-independent. However, when frequency-dependent sexual selection processes act alongside mate choice, truly adaptive sympatric speciation becomes feasible. Speciation is then initiated independently of non-adaptive processes, and does not suffer from the theoretical weaknesses associated with the current Fisherian runaway model of speciation. However, adaptive speciation requires the simultaneous action of multiple mechanisms, and therefore it occurs under conditions far more restrictive than earlier models of sympatric speciation by sexual selection appear to suggest.

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Introduction

Classical research into the potential mechanisms of sympatric speciation has sought to explain sympatric speciation primarily from ecological causes (reviewed, e.g., in Johnson & Gullberg, 1998; Schluter, 2001), often presupposing the presence of an assortative mating structure allowing for a high degree of reproductive isolation. Recent research, on the other hand, has put emphasis on the evolution of the mating structure itself and focuses on sexual selection as a driving force of sympatric speciation (reviewed in Panhuis *et al.*, 2001).

The view that sexual selection plays a significant role in sympatric speciation is supported by comparative studies, which indicate that closely related species often differ most pronouncedly in their secondary sexual characters, rather than in other, ecologically relevant, morphological traits (Eberhard, 1985; Wilson *et al.*, 2000). Moreover, DNA sequence analysis has revealed an extraordinary divergence of sex-related genes, particularly between closely related species (e.g., Vacquier, 1998; Wyckoff *et al.*, 2000), lending support to the hypothesis that strong (sexual) selection has acted on these genes during speciation (Van Doorn *et al.*, 2001).

Also from a theoretical point of view, the involvement of sexual selection in sympatric speciation seems plausible. It is now well established that sexual selection by female mate choice may lead to rapid evolution of exaggerated male traits and corresponding female preferences by means of a Fisherian runaway process (Fisher, 1930; Lande, 1981; Kirkpatrick, 1982). In contrast to good-genes processes, female preferences in a runaway process may be based on arbitrary male traits, conferring no inherent fitness advantage. In principle, it is therefore conceivable that multiple runaway processes simultaneously occur within the same population. A theoretical study by Higashi *et al.* (1999) has shown that this is a feasible scenario and that sexual selection alone can split a population into two reproductively isolated parts.

As indicated by Higashi *et al.* (1999), sufficient initial genetic variation of female preferences has to be present in order to trigger two simultaneous runaway processes. This prerequisite is not surprising, since classical female-choice models demonstrated that already a single runaway process will only occur if the initial level of choosiness exceeds a certain threshold value (Kirkpatrick, 1982; Andersson, 1994). It is therefore to be expected that, in order to trigger two simultaneous runaway processes, the level of choosiness for two distinct male traits has to be sufficiently high. Consequently, multiple preference alleles, coding for choosiness with respect to different male traits will have to be present in sufficiently high frequencies, which implies that there should be considerable variation of female preferences in the initial population. Although female preference variation has been documented (Kirkpatrick, 1987; Bakker, 1990), the origin and maintenance of such a large amount of variation in natural systems is not self-evident.

Two paths along which sufficient genetic variation in female preferences could arise have been discussed in the literature. First, there is the possibility that a sudden change in environmental conditions changes the parameters of mate choice in such a way that previously hidden genetic variation of female preferences is suddenly exposed (Higashi *et al.*, 1999). For example, it has been argued that the deterioration of the underwater light conditions in Lake Victoria has led to a decline in haplochromine cichlid diversity, since the increased turbidity of the water has severely compromised female mate choice based on male coloration (Seehausen *et al.*, 1997). If the water would suddenly become clear again, a large variation of female preferences that was hidden under the turbid water conditions would be expressed, possibly leading to new speciation events. It is hard to determine whether such sudden environmental changes are very likely to occur. Moreover, if such events were required to induce sympatric speciation, then sympatric speciation, like allopatric speciation requiring imposed geographic isolation, would largely be dependent on unpredictable external events. This conclusion not only conflicts with the historical interpretation of sympatric speciation as an internally driven and adaptive process, but also has implications for several of the arguments commonly raised in favor of sympatric speciation and against allopatric speciation. For example, the argument that allopatric speciation, unlike sympatric speciation, is too slow to be able to account for the presently observed biodiversity, loses much of its strength when also sympatric speciation is driven by external processes. In fact, the supposed higher rate of sympatric speciation is commonly substantiated by arguing that sympatric speciation is internally driven by selection.

The second possibility that has been considered is that the mutation-selection balance on female preference allows for the maintenance of significant preference variation. If selection on female preference were very weak or absent and if the mutation rate were sufficiently high, mutations in female preference genes would accumulate over time, resulting in a sufficiently broad distribution of female preferences in the population (as illustrated in Wu, 1985; Van Doorn & Weissing, 2001; Takimoto, 2002). The condition of weak selection (and/or high mutation rate) is not likely to hold in general, although in some species (e.g., marine invertebrates) selection on female preference has been shown to be very weak (Swanson & Vacquier, 1998).

Surprisingly, an obvious third possibility has largely been overlooked in the literature on sympatric speciation (but see mutual mate choice models by Lande *et al.*, 2001; Almeida & Vistulo de Abreu, 2003): genetic variation of female preferences could be maintained by disruptive selection. In contrast to the other possibilities, this option allows sympatric speciation to be described as a directed and adaptive process governed by selective forces – thus eliminating a critical dependence on external events, weak preference selection, or high mutation rates.

The aim of this paper is to critically investigate whether sexual selection by female mate choice can drive adaptive speciation. Specifically, we ask whether female mate choice, through its effect on the joint evolution of male and female mating characters, is capable of generating the conditions under which a polymorphism of female preferences can arise and be maintained. As we will show, by means of individual-based simulations and numerical analysis of a model for the evolution of male and female mating types, the answer to this question is negative. In the traditional models of female choice, mate choice cannot induce *frequency-dependent* disruptive selection on female preferences, which, as we argue, precludes the occurrence of adaptive speciation (Dieckmann *et al.*, 2003). We subsequently propose specific inter- and intrasexual interactions that do generate frequency-dependent disruptive selection. With these additional sources of sexual selection, acting alongside mate choice, sympatric speciation by sexual selection becomes feasible, without any dependence on non-adaptive processes. However, since it is far from trivial to generate frequency-dependent disruptive selection in both sexes simultaneously, we expect that the occurrence of sympatric speciation by sexual selection will be limited to rather specific biological conditions.

A model of female choice

We consider the evolution of two continuous phenotypic traits: female preference (denoted p) and the male trait on which female preference acts (denoted q). In every generation, a constant number of N offspring is produced (other forms of population density regulation give identical results, as long as female preference and male trait are ecologically neutral traits, Van Doorn & Dieckmann, ms. in prep.). For every offspring, a female (denoted i) is randomly selected from the population. She is then allowed to choose a mate (denoted j) from the available males. The probability that a particular male j succeeds to fertilize the female is proportional to the male's "attractiveness" to female *i*, denoted a_{ij}, which depends on both the female preference value p_i and the male trait value q_j. We keep the model as general as possible and make no assumptions regarding the mechanism of female choice: attractiveness and mate choice may be based on any active or passive process (behavioral, morphological, or other) affecting the probability that a female is successfully fertilized by a particular male. For convenience however, our terminology will not always reflect this general interpretation of the model. "Mating", for example, will often be used as shorthand for "successful fertilization".

We assume that attractiveness is highest when the male trait q_j matches the value preferred by the female. Naively, one could be tempted to specify the male trait q that optimally matches a given female preference p as $q = p$, thereby equalizing traits with preferences. However, this convenient choice is only justified if male trait and female preference phenotypes can be measured on the same scale. This assumption is implicitly made in many models of sexual selection – yet it is problematic, since the choice of scale is not arbitrary, but prescribed by the assumptions made on the mutation process at the genetic level. Since trait and preference represent different entities that are governed by different biological processes (e.g., a color trait may be governed by pigment formation, while a color preference may be governed by processes at the level of color receptors), it is unlikely that a convenient choice of scale at the genotypic level, will also allow us to measure trait and preference on the same scale at the phenotypic level.

There are two more or less equivalent ways to deal with this issue. One could simply define trait and preference such that they are measured on the same scale on the phenotypic level. However, this would require a relatively complicated description of processes at the genetic level, involving, e.g., mutation biases. It has been shown previously that the latter may strongly affect the outcome of sexual selection models (Bulmer, 1989). Alternatively, one could choose to measure trait and preference on a scale determined by their respective mutation processes, rendering the description at the genetic level simple. In that case, one has to assume, as we do in our model, that female preferences are "translated" into (preferred values of) male traits by means of a "choice function" c, where $q = c(p)$ is the male trait preferred by a female with preference p. By identifying traits with preferences, most classical models implicitly assume that this choice function is linear, but it is easily conceivable that developmental processes and the mechanisms of perception create all kinds of nonlinearities. Such nonlinearities can have important consequences, since the shape of the function c determines the strength and direction of sexual selection. This can be illustrated as follows. Consider the male trait value that is, on average, preferred by the females in the population. It follows from standard error analysis theory that this quantity, which we denote $\overline{c(p)}$, is approximated by

$$\overline{c(p)} \approx c(\overline{p}) + \frac{1}{2} c''(\overline{p}) \operatorname{var}(p). \qquad (1)$$

If the choice function is linear, its second and higher derivatives will be zero, which, according to equation (1), implies that $\overline{c(p)} = c(\overline{p})$. Hence, the male type that is on average preferred by the females is the same as the male type that is preferred by the female with the average preference. By contrast, nonlinearities in the female choice function translate into a discrepancy between $\overline{c(p)}$ and $c(\overline{p})$. Such a discrepancy generates directed sexual selection, since it directly results in a discrepancy between the optimal and the mean trait and preference values. The direction and intensity of sexual selection depend, respectively, on the sign and magnitude of $c''(\overline{p})$, that is, on the local curvature of the female choice function. For illustration we will choose a particular function c allowing for divergent evolution (see Figure 2 later on).

We assume that females tolerate some deviation of male traits from their preferred value, such that attractiveness is described by

$$a_{ij} = g_m\big(c(p_i) - q_j\big) , \qquad (2)$$

where here and henceforth g_a denotes a gaussian function with mean zero and standard deviation σ_a. In particular, the standard deviation of the gaussian distribution used here, σ_m, determines the specificity of mate choice: higher values of σ_m correspond to less discriminate mate choice. This model of mate choice assumes fixed absolute preferences and is more conservative than models based on fixed relative, or open-ended preferences (Lande, 1981).

Preferences are potentially costly, especially if a female does not mate when she cannot find a sufficiently attractive male. This occurs, for instance, when searching for mates is time-consuming, or when sperm is limiting. Let us assume that a female encounters any given male at rate $1/\eta$, such that the female can locate and evaluate at most N/η potential mates in a time unit (a time unit is conveniently defined as the time needed to produce a single offspring). Every time the female encounters a male, she may reject him or accept him as a mate. The latter occurs with probability a_{ij}, defined in (2). A female will produce a single offspring per time unit, as long as she has mated at least once in the previous time interval. Under these assumptions, we can easily compute α_i, the offspring production rate of female i. We find

$$\alpha_i = \frac{\sum_{\text{males } k} a_{ik}}{\eta + \sum_{\text{males } k} a_{ik}}. \tag{3}$$

If a female encounters many attractive males, she mates multiple times per time unit. In that case, all males that were accepted by the female have an equal probability to father the offspring, such that the probability that a particular male j succeeds to fertilize female *i*, denoted α_{ij}, is given by

$$\alpha_{ij} = \frac{a_{ij}}{\eta + \sum_{\text{males } k} a_{ik}}. \tag{4}$$

The parameter η can be interpreted as the time needed to locate and evaluate a particular potential male. When $\eta = 0$, females are not time-constrained and they will always find an attractive mate, regardless of their mating preference. Consequently, there is no direct selection on female mating type *p*. By contrast, when $\eta > 0$, there is a time-cost associated with mate rejection. Females with deviating preferences will reject most of the potential mates they encounter. Such females will produce offspring at a lower rate, since they waste time searching for more attractive mates. Consequently, when $\eta > 0$, selection will act to match female preference with the predominant male trait.

In this model for female choice, females with different mating types differ only in their preferred male trait value, not in the effort invested in mate choice or the degree of choosiness. All females encounter potential mating partners at the same rate, and the average probability that the female will accept a male as mating partner, which is defined as the integral of a_{ij} over q_j, is independent of female preference (the integral of a gaussian function is independent of its mean). Consequently, no female preference type is inherently favored. Rather, the selective advantage or disadvantage of a particular preference type is dependent on its match with the male types that are currently present in the population.

Underlying equations (3) and (4) is the assumption that females are limited in the total number of offspring they may produce and that males, on the other hand, may potentially father an unlimited number of offspring, since their reproductive success is limited only by the number of females they succeed to fertilize. This assumption is habitually made in many models of sexual selection, and we will therefore refer to it as the ‘typical sex-role assumption’. Note that, under this typical sex-role assumption, the sex roles themselves are hardly ‘typical’ but rather extremely asymmetric. Later on, we will therefore relax this restrictive assumption.

For simplicity, we assume discrete and non-overlapping generations. After a new generation of offspring has been produced, viability selection occurs. We assume that male survival probabilities vary according to a gaussian function $g_s(q)$, such that the male trait value $q = 0$ is optimal for survival and extreme male traits suffer a viability disadvantage. Viability selection is stabilizing, and the width of the viability selection function, σ_s, is inversely related to the intensity of direct selection on the male trait.

The model was implemented as an individual-based simulation program. We assumed multi-locus genetics underlying male trait and female preference. Specifically, phenotypic preference and trait values both consist of a genetic and an environmental component. The genetic components are determined by L diploid loci for male trait and another L diploid loci for female preference. We assume a continuum of alleles, that is, the phenotypic effect of each allele is a continuous quantity. All genes are unlinked and alleles interact additively within and between loci, that is, genotypic trait and preference values are the average of the phenotypic effects of the trait and preference alleles. Trait and preference genes are transmitted according to normal Mendelian genetics. Mutations occur with a frequency of μ per allele per generation and are modeled by altering the phenotypic effect of an allele by a number drawn from a normal distribution with a narrow width $\sigma_v \sqrt{2L}$. Under this scaling of the size of mutations, the phenotypic variation caused by mutation is independent of the number of loci L. The environmental component of trait and preference is drawn from a normal distribution with width σ_p for female preference and σ_q for male trait. Hence, the non-heritable environmental variance of female preference and male trait is σ_p^2 and σ_q^2, respectively.

In addition, we approximated the individual-based simulation model by assuming mutation-limited evolution and single-locus haploid genetics underlying female preference and male trait (Appendix A). This approximation yields equations for the expected growth rate of rare female preference or male trait mutants interacting with a monomorphic resident population. We then use adaptive dynamics theory (Metz *et al.*, 1996; Dieckmann & Law, 1996; Geritz *et al.*, 1998) to numerically calculate the expected evolutionary trajectories of female preference and male trait (Appendix B). Throughout the manuscript, results based on this adaptive dynamics approximation will be used to complement results obtained from the individual-based simulations.

Disruptive sexual selection, but no sympatric speciation

The individual-based simulations show that populations starting out from arbitrary initial conditions quickly converge to combinations of male trait and female preference values such that $q \approx c(p)$ (Figure 1). This is not surprising, since, at those combinations of trait values, the trait expressed by the males optimally matches the mating preference exerted by the females, and sexual selection on the male trait selects

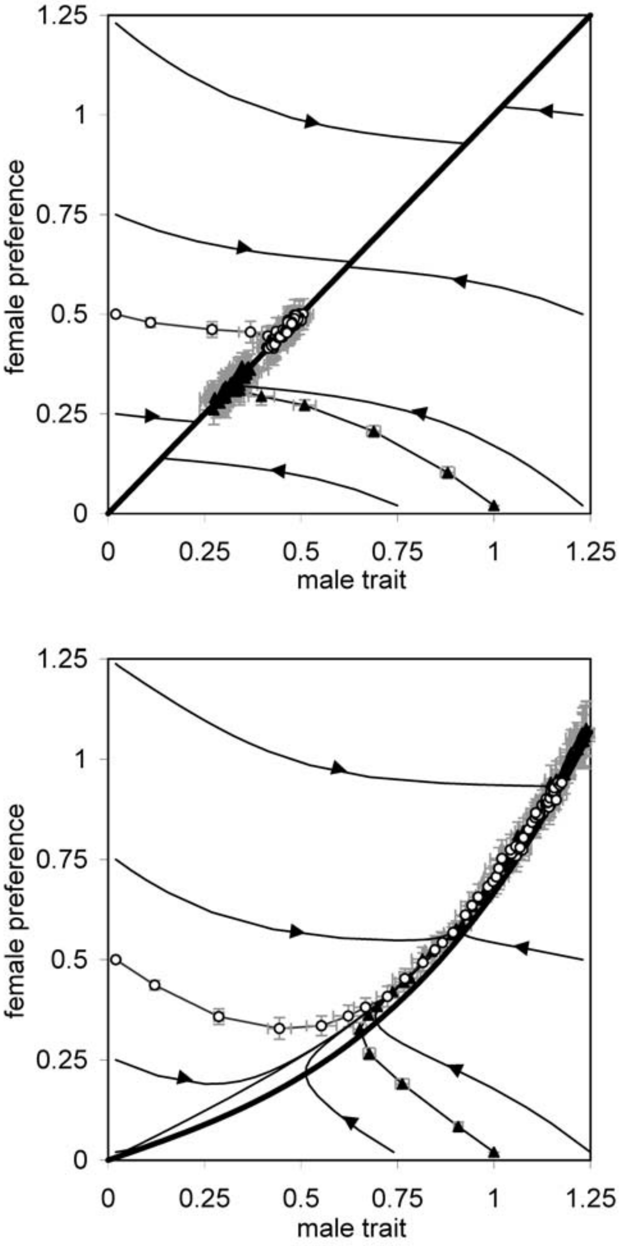

Figure 1: Evolution along the female-choice function. For a given female-choice function (thick black curves), the two panels show the evolutionary trajectories of male trait and female preference from different initial conditions as obtained by individual-based simulations (open circles and filled triangles show simulations from two different starting conditions) and numerical integration of the deterministic equations derived in Appendices A and B; equation (16) (thin black curves with arrows). Parameters: $N = 500$, $\sigma_m = 0.15$, $\sigma_p = \sigma_q = 0.2$, $\eta = 25.0$, $L = 2$, $\mu = 0.025$, $\sigma_v = 0.05$, and $\sigma_s \to \infty$ (no viability selection on male trait). Individual-based simulations lasted for 3000 generations, with data plotted every 50 generations. The resulting individual-based trajectories represent averages over five independent simulations; error bars indicate the standard errors of the mean across the replicate simulations. For details about the nonlinear female-choice function see Appendix B.

for such optimal matching. The same is true for direct selection on female preference, since females with deviating preferences suffer more from the cost of mate choice.

After this initial phase of rapid evolution, a slower phase of adaptive change along the female-choice function sets in. In the absence of viability selection on the male trait, the direction of evolution along the female-choice function is completely determined by the local curvature of that function (Figure 1). If the function is linear, the female choice function defines a line of equilibria, along which the population drifts neutrally (Figure 1, upper panel). This line of equilibria disappears as soon as the female choice function becomes nonlinear (Figure 1, lower panel). In that case, the local curvature of the female choice function generates directed sexual selection, thus forcing the population to move slowly along the female choice function. This can be understood from the fact that the local curvature of the female choice function translates into a discrepancy between the average preferred male trait value and the male trait value that is preferred by a female expressing the average preference value (equation (1); Van Doorn *et al.*, 1998). Because of this discrepancy, the optimal male trait value will be different from the population mean male trait value, which will therefore shift towards the optimal value. However, this will immediately induce a corresponding change in the population mean female preference value, since the female preference value at which the costs of choice are minimized is the one that matches the population mean male trait value.

In general, the female-choice function could have any shape and it need not necessarily be smooth, as in Figure 1. For different biological systems, the shape of the respective female choice functions will vary with specific nonlinearities induced by processes such as development and perception. Here we will not attempt to model this biological complexity in any detail. Instead, without harm to our argument, we will simply choose an example female-choice function in such a way that disruptive sexual selection is generated. In Figure 2, the female-choice function (thick black line) is shaped such that sexual selection can drive the population in two different directions, towards two possible endpoints of evolution. The latter are located at the intersection points of the null-isoclines for the rate of change of trait and preference (thick gray lines). Females prefer costly and exaggerated male traits in both of these endpoints. However, despite a potential for the occurrence of evolution in multiple directions, diversification of female mate preferences was never observed in our simulations. The two replicate runs (circles and triangles) represented in Figure 2 were both started from the initial conditions $p_0 = q_0 = 0$, i.e., exactly at the point where sexual selection is disruptive. Nevertheless, the two simulations show no speciation, but evolution towards either one of the two possible stable endpoints of evolution. For some parameter conditions, a polymorphic transient (as in Figure 2) or a permanent genetic polymorphism of male trait arose, but the distribution of female preference always remained unimodal. In fact, there is always a clear boundary line (dashed curve in Figure 2) that separates the initial conditions from which the respective endpoints of evolution are reached.

Why does the distribution of female preference remain unimodal in all of our simulations, whereas genetic polymorphism in the male trait does arise under suitable conditions? The answer to this question lies in the fact that the selective forces acting on

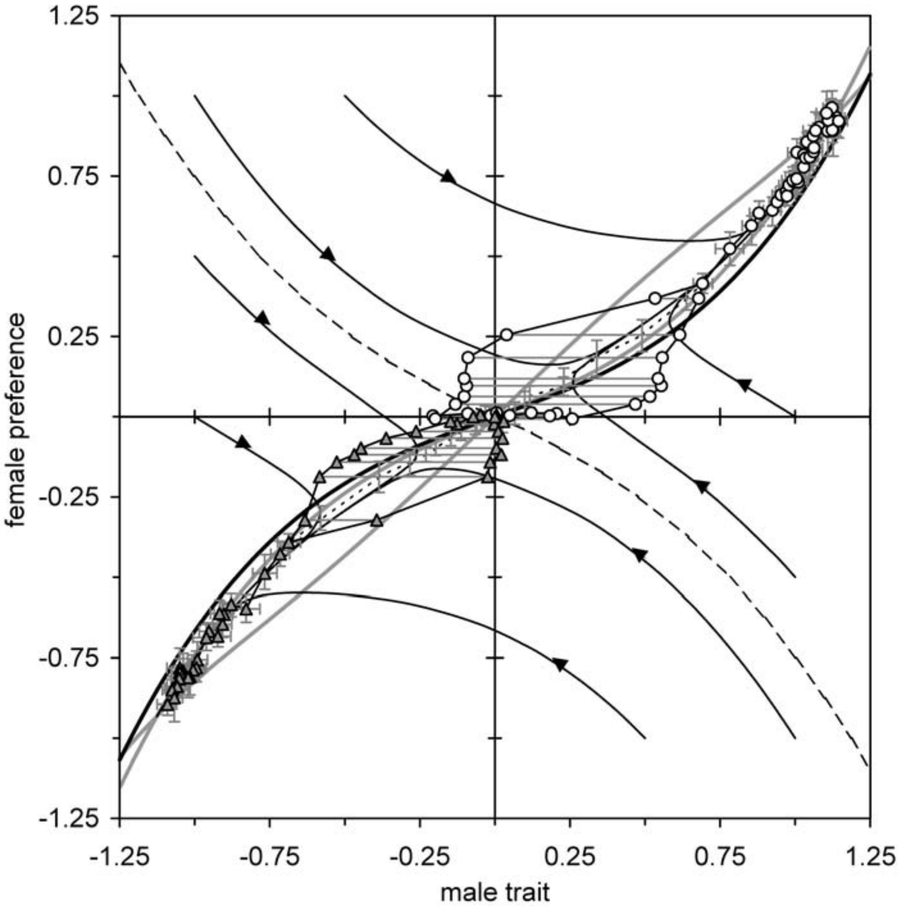

Figure 2: Disruptive sexual selection, but no speciation. Two replicate individual based simulations (circles and triangles) were started from the initial conditions $p_0 = q_0 = 0$, i.e., exactly at the point where sexual selection is disruptive. The simulations do not show speciation, but evolution towards one of two possible endpoints of evolution. At the start of both simulations, male traits are polymorphic. There are two clearly distinct male trait alleles, indicated separately in the graph, as circles or triangles joined by horizontal gray lines. Later, the populations again become monomorphic for male trait. Grey error bars indicate within-population variation of preference and trait (not, as in Figure 1, variation between replicate runs). Other lines in this graph represent the female choice function (thick black line), null-isoclines for the rate of change of trait and preference, corresponding to the solutions of the separate equations (16) in Appendix B (thick gray lines), evolutionary trajectories predicted by the adaptive dynamics approximation (thin black lines with arrows), and the boundary line that separates the basins of attraction of the two stable equilibria (dashed curve). Parameters: $N = 1000$, $\sigma_m = 0.15$, $\sigma_p = \sigma_q = 0.3$, $\eta = 25.0$, $L = 1$, $\mu = 0.0125$, $\sigma_v = 0.01$, and $\sigma_s = 1.0$. Individual-based simulations lasted for 10000 generations, with data plotted every 200 generations. For details about the nonlinear female-choice function see Appendix B.

female preference are fundamentally different from those acting on the male trait. This difference derives from a basic assumption of our model: females are limited in the number of offspring they may produce by time or energy constraints. These factors are not influenced by the preferences of the other females in the population. As a consequence, female fitness is not affected at all by the strategies of other females, and, therefore, selection on female preference is independent of the frequencies of other preference strategies in the population. Male fitness, on the other hand, varies with the strategies of other males, since it is determined mainly by success in competition between the males for access to the females.

This difference has important consequences. Frequency-independent selection, such as the selection on female preference in the model above, is unable to support genetic polymorphism (Appendix C), at least when the underlying genetics is not governed by strong constraints (as, for example, in the case of over-dominance). This is illustrated in the upper panel of Figure 3. For this figure, we first calculated an evolutionary trajectory of female preference (thick black curve). At every point in time we subsequently computed the fitness of rare female preference mutants in an equilibrium population with the current resident female preference. As reflected by the bimodal shape of the resulting female-preference fitness landscape, selection on female preference is disruptive at the start of the simulation. Due to the fact that selection on female preference is frequency-independent, the fitness landscape does not change in response to changes in the resident female strategy. As a result, the population can easily escape from a point where selection is disruptive and will do so without polymorphism being generated.

Frequency-dependent selection, by contrast, allows for the origin and maintenance of stable genetic polymorphisms under far more general conditions. The effects of frequency-dependent disruptive selection are highlighted in the lower panel of Figure 3. First, an evolutionary trajectory of the male trait (white curves) was calculated. In the simulation, the male trait first converges to $q = 0$, where matching with the average female preference is maximal. Then a stable polymorphism of two male-trait genotypes emerges. This course of events is typical of the process of evolutionary branching (Metz *et al.*, 1996; Geritz *et al.*, 1998; Dieckmann *et al.*, 2003), as formulated by the theory of adaptive dynamics. The underlying male-trait fitness landscape, calculated in analogy to the female-preference fitness landscape described above, drastically changes over time, responding to changes in the resident male trait because of frequency-dependent selection on that trait. The dynamically changing fitness landscape makes it possible that evolution, even though always moving uphill, first converges to the bottom of a fitness valley, that is, to a point where selection turns disruptive. A monomorphic population cannot escape from such a valley, since any step away from the bottom of the valley would change the landscape in such a way that the population is driven back. The only way for the population to escape from the fitness minimum is to become dimorphic in the male trait.

If selection on female preferences is frequency-independent, three inter-related problems arise, all potentially preventing speciation:

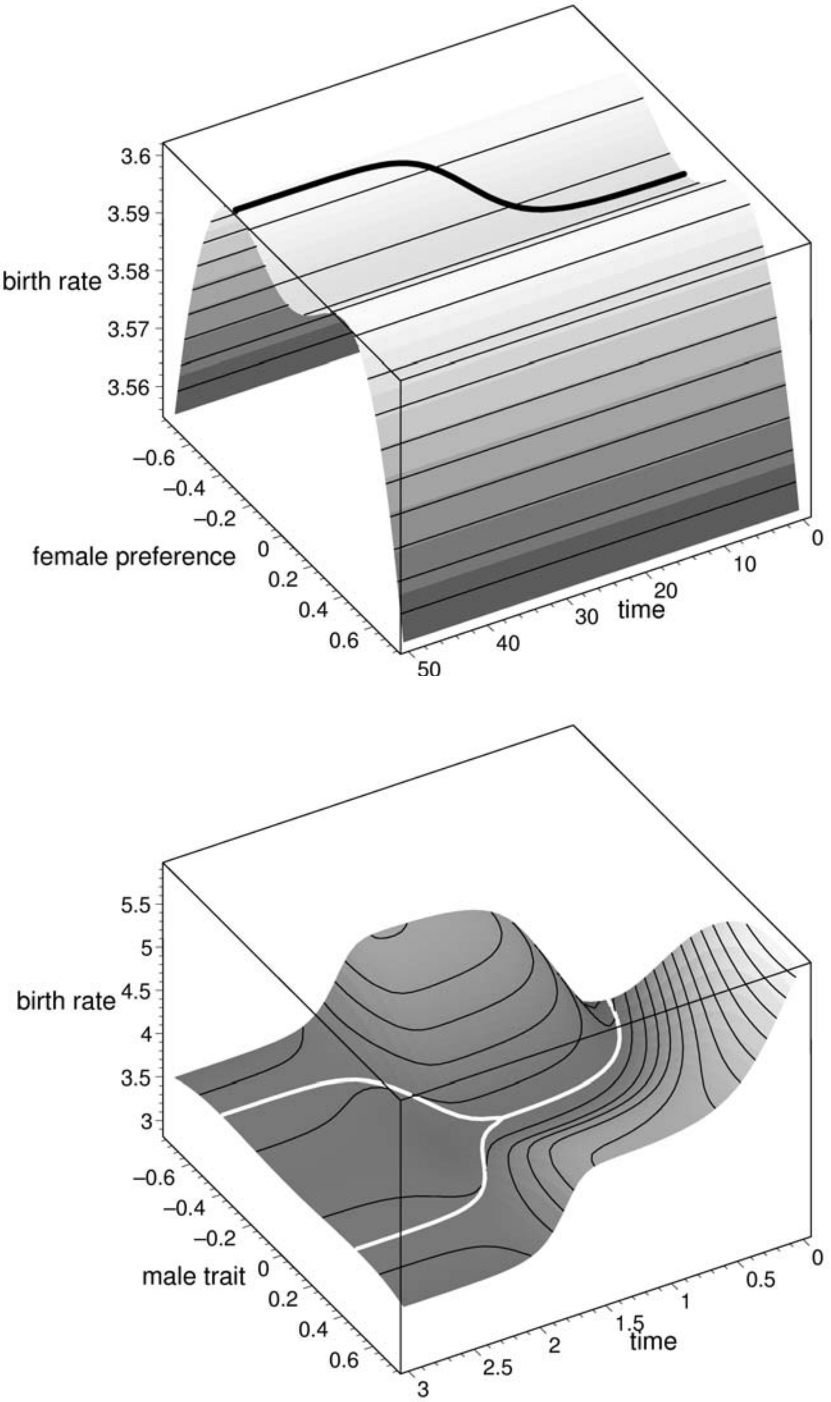

Figure 3: Differences between frequency-independent and frequency-dependent selection. The adaptive dynamics approximation was used to calculate an evolutionary trajectory of female preference (upper panel, thick black curve). For this illustration, a fixed dimorphism of male trait was considered, with two equally frequent male types at $q_1 = -q_2 = 0.75$. At every point in time, we determined the birth rate of rare female preference mutants in an equilibrium population with the current resident female preference; Selection on female preferences is frequency-independent. Consequently, the fitness landscape does not change in response to changes of the resident female preference. The lower panel shows evolutionary branching of the male trait (evolutionary trajectories are represented by white curves), and the associated dynamic change of the fitness landscape caused by frequency-dependent selection. For this simulation, female preference was kept at a constant value, $p = 0$. Parameters are as in Figure 2.

- Sexual selection on female preference is disruptive only when the population mean trait values are close to the boundary line between the two stable equilibria (of the order of a standard deviation away), but directional everywhere else.
- A population tends to evolve away from the area in which selection is disruptive.
- Even if a population spends a long time in the area of disruptive sexual selection and a polymorphism arises, this polymorphism quickly disappears because there are no selective forces to stabilize it.

Although the first and second problem can be overcome if the initial conditions are suitably chosen (the initial population should exhibit considerable variation and it should be perched on the boundary line between the two stable equilibria), the third problem cannot. At best, female preferences may transiently diversify, but due to the lack of stabilizing forces, the two resulting daughter species can only coexist ephemerally. Note that this transient phase might seem deceptively long in deterministic models (as in Takimoto *et al.*, 2000), an artifactual feature that disappears as soon as only a minimal amount of stochasticity is introduced. This aggravates the problem mentioned in the introduction: even if a large amount of genetic variation of female preferences is initially present – by a sudden change of the environment, or by mutation pressure – speciation is still impossible, since there is no selection that will stabilize the coexistence of the daughter species.

Female competition for males renders selection on female preference frequency-dependent

The solution to the problems highlighted above might seem to be straightforward: in order to allow for sympatric speciation, selection on female preference must be made dependent on the strategies of other females in the population. It is not at all unlikely that such dependence exists. For example, if we replace the assumption that males can potentially father an unlimited number of offspring by the more realistic assumption that also male matings are limited (to a small extent) by time or energy constraints, then selection on female preference immediately becomes dependent on the strategies of other females in a population.

Male limitation of this type can arise in many different ways. For example, males may be limited in the amount of time they can invest in parental care, such that a male that has fathered many offspring cannot provide paternal care for all of them. Alternatively, males may have to spend time on courting a female, which makes them temporarily unavailable for other females. Another possibility that may be of relevance for specific natural systems is that males are limited in the amount of sperm they can produce. In all these cases, male limitation introduces (indirect) mate-competition between the females, such that females preferring males not already chosen by other females will enjoy elevated fitness.

Although the above examples show that male limitation is biologically plausible, work is needed to delineate the biological conditions under which male limitation is also strong enough to result in appreciable intensities of competition between females. We leave this issue unresolved, and, for the sake of our argument, examine an example in which competitive interactions between females are quite strong. For this purpose, we slightly extend our model by allowing for the fact that the quality of a male partner may deteriorate with the number of times the male has already mated during a season (for example, because the male can only offer a fixed amount of parental care, which has to be shared among all his offspring); we also assume that a female cannot ascertain how many times a male has mated before. The female therefore still selects a male on the basis of her preference. We assume that if she selects a male that has mated n times before, she produces viable offspring with probability φ^n ($0 < \varphi < 1$). The parameter φ determines how fast male quality deteriorates with the number of matings. For $\varphi = 1$, we recover the model analyzed above.

With this modification of the model, there are parameter conditions under which a genetic polymorphism of female preference evolves. In Figure 4, we systematically varied the environmental variances of male trait and female preference (σ_q^2 and σ_p^2, respectively), thereby manipulating the population variances of trait and preference (when mutations are rare, genetic variation can be neglected). As we will explain shortly, the latter variances determine, relative to the other parameters, whether selection on the male trait and the female preference will be stabilizing or disruptive.

A polymorphism of female preference can evolve when the variation of female preference in the population is small with respect to the population variation of male trait (Figure 4). Under these conditions, males in the tails of the distribution of trait values are rarely chosen, and, therefore, females that choose such males are favored. Because of the fitness advantage of females that prefer extreme male types, female preference is expected to diversify, and this is accomplished by evolutionary branching. Notice that in this situation the evolution of female preference is governed by the same mechanism underlying the evolution of resource-utilization traits: the population-level phenotypic distribution of male trait acts like a resource availability spectrum, the individual-level phenotypic distribution of female preference acts like a resource utilization spectrum, and evolutionary branching occurs if the former is wider than the latter (see, e.g., Dieckmann & Doebeli 1999). This highlights a structural similarity between selection pressures acting on ecological characters and those acting on sexual traits (Van Doorn & Weissing, 2001).

The conceptual relevance of this similarity, however, is much undermined by the following observation: parameter conditions under which female-preference branching occurs do not overlap with those under which the male trait undergoes evolutionary branching (Figure 4). Indeed, male branching occurs when the variation of female preference in the population is large with respect to the population variation of the male trait. In that case, disruptive selection favors male-trait specialization on females in the tails of the relatively broad distribution of preferences, since those females are hardly competed for in a monomorphic male population (Van Doorn & Weissing, 2001). Irrespective of the strength of competition between females (determined by the parameter φ), we never found overlapping conditions for female preference and male trait branching. Since there is no reproductive isolation without a polymorphism evolving in both female preference and male trait, speciation does not occur.

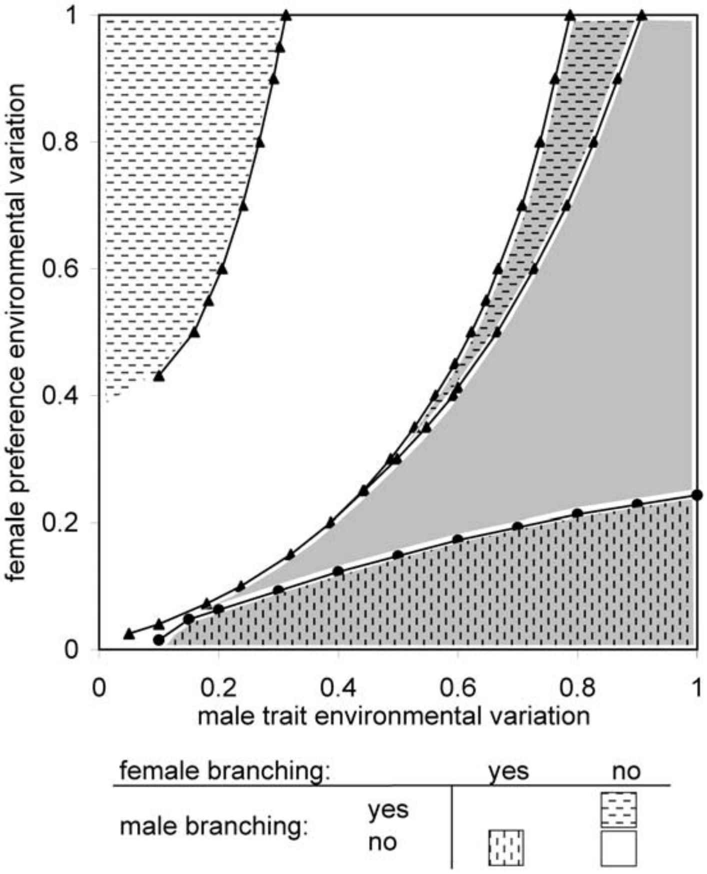

Figure 4: Impossibility of simultaneous evolutionary branching. As explained in the text, male branching occurs when the (environmental) variation in female preference (σ_p) is large relative to the (environmental) variation in male trait (σ_q). By contrast, female primary branching occurs in the opposite corner of parameter space. The picture is complicated slightly by the fact that, in the initial phase of evolution, females do not always evolve preferences for costly male traits (this depends on the stability of the equilibrium $p = q = 0$, which can be assessed from equation (16) in Appendix B). In the white region, monomorphic evolution leads to an equilibrium at which female preference for costly male traits has been established. In the gray region, this does not occur, and the endpoint of monomorphic evolution is the equilibrium that optimizes male survival. When male-trait environmental variation is large, extreme male traits suffer (on average) more from viability selection, and therefore female preferences for costly male traits evolve less easily. For a similar reason, male-trait branching requires more extreme parameter combinations when females exhibit preference for costly male traits, since branching will then on average lead to larger viability disadvantages. All boundary lines in this plot (triangles: male primary branching, circles: female primary branching) were calculated using the adaptive dynamics approximation. Parameters are as in Figure 2, with $\varphi = 0.75$. Numerical instabilities prevented accurate calculation of selection gradients for very small σ_q; no points are therefore shown for the leftmost region of parameter space.

The reason for the mutual exclusiveness of the conditions for male-trait and female-preference branching lies in the fact that male fitness increases when a male mates with more females, whereas female fitness decreases in the same situation. This fundamental conflict between the sexes translates into opposing selective forces: when it pays the males to diversify and undergo branching, the females will experience stabilizing selection, and vice versa. A simple calculation shows that this intuitive explanation applies under general conditions (Appendix D).

Male-male competition provides additional disruptive selection

The results of the previous section show that the areas in parameter space in which female preference and male trait undergo evolutionary branching do not overlap and must thus be enlarged in order to create a potential for sympatric speciation. This can only be accomplished by assuming an additional source of disruptive selection acting on either females or males, separate from the disruptive selection already generated by mate choice and female-female competition. Such additional disruptive selection could be caused by a variety of mechanisms, and any process that leads to an intrinsic advantage of rarity (Weissing, 1996) would be adequate.

For the sake of concreteness, we consider a particular example, in which the trait subject to female preference is also involved in male-male competition. This is, for example, well known for sticklebacks, where the red coloration of the male is used as a signal by females (in the context of mate choice) as well as by males (in the context of aggressive interactions). Intuitively, one would also expect males to make their competitive strategies dependent on the traits on which female preference acts, at least, as long as males compete for no other resource than the female's attention. In that case, it makes no sense to waste valuable energy in fighting a male with whom no potential partners are shared (Verkiel, 2002). More specifically, one would expect that males behave less aggressively towards one another if their mating traits are less similar. This idea is currently under empirical investigation for haplochromine cichlids, where it has been suggested that males behave less aggressively towards rare male color morphs and that these rare morphs are therefore favored in male-male competition (Dijkstra & Groothuis & Dijkstra, *ms. in prep.*).

Inspired by this biological example, we therefore assume that all males compete to establish mating territories. When a male tries to establish a territory, he has to compete with the other males already owning a territory. In accordance with the preceding discussion, the intensity of competition, f_{ij}, between two males i and j is taken to be dependent on the difference between their trait values,

$$f_{ij} = g_c\left(q_i - q_j\right) \ . \tag{5}$$

The width of the gaussian g_c, σ_c, determines how strongly male aggression is influenced by male trait differences. Male aggression is independent of male trait differences when σ_c approaches infinity, whereas males fight only with identical males when σ_c is very small.

A male experiencing very intense competition is assumed not to be able to establish or maintain a territory. The total strength of competition experienced by a male, $\bar{f}_i$, is given by

$$\bar{f}_i = \sum_{\substack{\text{territory owners } j \\ j \neq i}} f_{ij} \ . \tag{6}$$

When this total strength exceeds a threshold value θ, the male loses his territory. If, on the other hand, $\bar{f}_i$ falls below the threshold, a male is allowed to establish a territory, if he does not already possess one. Throughout the rest of this paper the threshold value θ is chosen such that one quarter of a population consisting of identical males is able to maintain a mating territory (the precise numerical value of θ depends on the model parameters σ_c, σ_s and the population size N). In the individual-based simulations, all males were given several opportunities to establish a territory, allowing for a stable composition of territory owners to be reached. After that, females were allowed to choose a mate from the males that had succeeded to obtain a territory.

As shown in Figure 5, the additional disruptive selection generated by male-male competition may indeed result in sympatric speciation. The figure shows a complicated sequence of events, eventually resulting in speciation: over the first 10,000 generations, females evolve preferences for costly male traits, after which a polymorphism of male trait arises (t =20,000 to 35,000 generations). Each of the four loci coding for the male trait undergoes evolutionary branching, transiently giving rise to nine genotypic clusters (inset A). Triggered by a sudden change of female preference around that time, the polymorphism in male trait is lost at three of the four loci, whereas the polymorphism at the remaining locus continues to grow. This divergence induces female-preference branching around $t = 40,000$ generations. Females specialize on one of the extreme male traits, leading to a highly skewed distribution of male-trait alleles in the population. At $t = 65,000$ generations, the female-preference polymorphism has grown sufficiently in order to allow for the build-up of linkage disequilibrium of trait and preference alleles; the distribution of genotypes at this moment in time is shown in inset B. Full linkage disequilibrium then evolves quickly, and as, a consequence, the heterozygotes (middle branches) carrying two different male-trait or female-preference alleles at the polymorphic locus disappear. In the end, two stably coexisting and reproductively isolated daughter species remain.

For the parameters used in the multi-locus simulation represented in Figure 5, there is good agreement between simulation and the corresponding adaptive dynamics approximation (Appendix E; also shown in Figure 5), even though our adaptive dynamics approximation is based on haploid single-locus genetics and on the assumption of mutation limited evolution. We tested other parameter conditions and found that the adaptive dynamics approximation always correctly predicted the evolutionary equilibrium eventually attained in the individual based simulations. For the transient behavior, we found better quantitative agreement between adaptive dynamics approximation and the simulations for smaller mutation step size σ_v. Larger mutation step sizes result in increasingly rapid evolutionary branching in the simulations, such that the population already undergoes evolutionary branching before the predicted evolutionary equilibrium for the monomorphic population is reached. These observat-

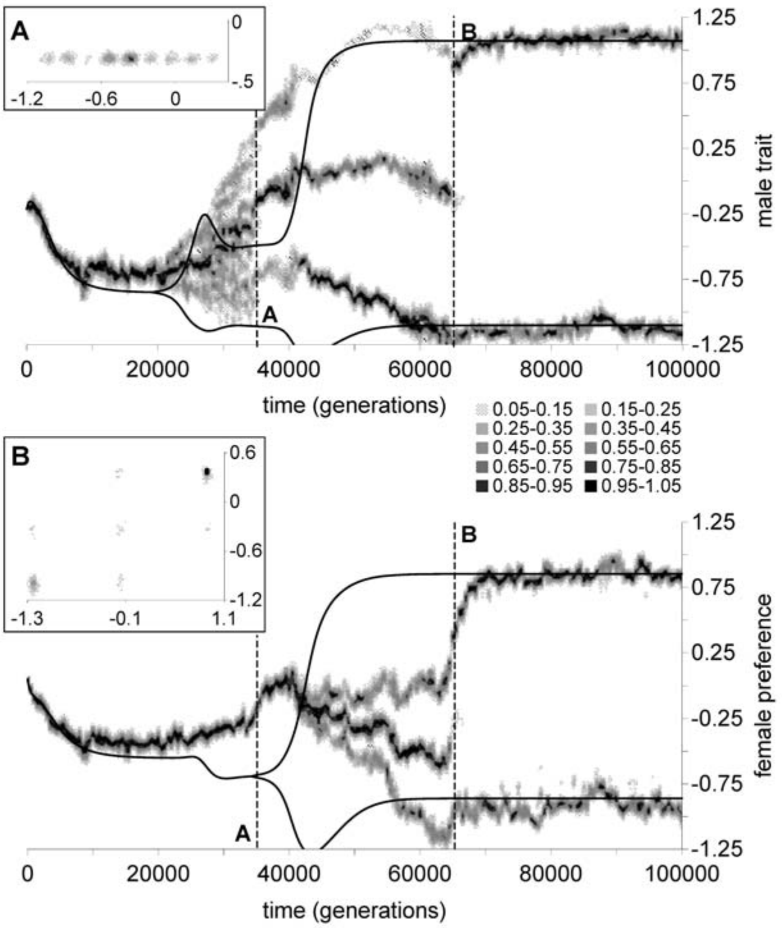

Figure 5: Sympatric speciation. Two plots show the relative frequency distributions of male-trait and female-preference genotypes (indicated on a gray-scale) in a population with $N = 1000$ in which both trait and preference are based on four diploid loci, $L = 4$. The thin black curves represent trajectories of the corresponding adaptive dynamics approximation. Small insets depict the frequency distribution of male trait (horizontal axis) and female preference (vertical axis) at two moments during the simulation (inset A: $t = 35,000$ generations, just before polymorphism is lost at all but one male trait locus, inset B: $t = 65,000$ generations, just before full linkage disequilibrium develops). Parameters are as in Figure 4, with $\sigma_c = 1$.

ions are in line with theoretical results predicting that the rate of evolutionary change in a monomorphic population is proportional to $\mu\sigma_v^2$, whereas the rate of evolutionary branching is proportional to $\mu\sigma_v^3$ (Metz *et al.*, 1996). For this reason, we use small mutation step sizes ($\sigma_v = 0.01$) in our simulations, and a high mutation rate ($\mu = 1.25 \cdot 10^{-2}$, due to limitations on computer time). Simulations with a more realistic mutation rate ($\mu = 1 \cdot 10^{-5}$), and a larger mutation step size ($\sigma_v = 0.15$), however, reach the same evolutionary end state and show speciation on the same timescale as the simulation represented in Figure 5.

We have used the more tractable adaptive dynamics approximation to further explore the parameter space of our model. Figure 6 shows that the parameter space is subdivided in two regions. In the first region (white background), sexual selection drives the monomorphic evolution (i.e., the adaptive change before branching has occurred) to an equilibrium characterized by female preference for exaggerated (costly) male traits (as in the first 2000 generations in Figure 5). In the second region (gray background), this process does not occur and monomorphic evolution converges to the equilibrium $p = q = 0$, where the male trait value is optimal for survival. In both regions (white and gray), there are large areas in which female preference and male trait undergo branching. Crucially, there now is a substantial overlap between these areas, in which speciation is possible. Depending on parameter values, the speciation process may unfold in different ways.

First, the order in which female preference and male trait undergo evolutionary branching may vary. In some regions, both male trait and female preference may undergo branching from a monomorphic population (both traits are capable of ‘primary branching’), in other regions, branching of one of the traits is possible only after the other trait has undergone branching and has diversified sufficiently (see Doebeli & Dieckmann (2000) for another model in which such ‘secondary branching’ occurs).

Second, speciation may occur with or without the initial establishment of mating preferences for costly male traits. In the former case the population first evolves towards a stable equilibrium at which females show preference for costly male traits, in the latter case monomorphic evolution converges to the viability optimum for the male trait. Surprisingly, the outcome of this initial monomorphic phase of evolution does not seem to influence the further speciation process qualitatively. Quantitatively, there is an effect, though. Ironically, the establishment of female preferences for costly male traits inhibits male-trait branching. When males express costly mating traits, male-trait branching occurs only when there is a large difference between the environmental variances of male trait and female preference (Figures 4 and 6), indicating that male-trait branching now requires much stronger disruptive selection. The reason for this effect is that branching after the establishment of female preferences for costly male traits results in two male types that, on average, suffer more from viability selection. This stabilizing force counteracts male-trait branching. Not surprisingly, female preference branching is facilitated under these conditions (Figure 6). When females have evolved preferences for costly male traits, females, on average, prefer extreme males from one of the tails of the male distribution, rather than the most common males.

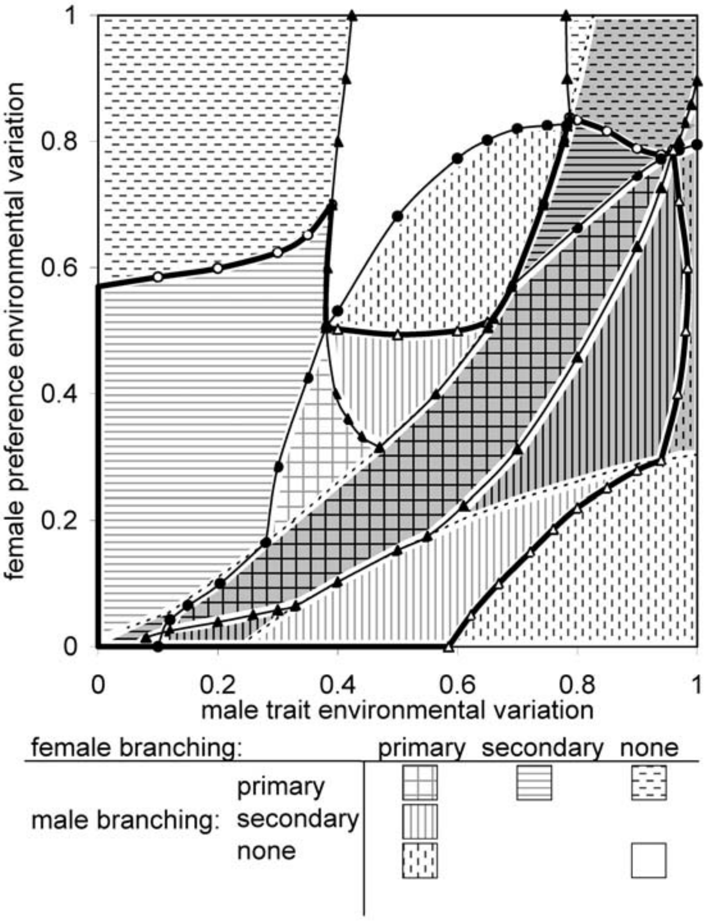

Figure 6: Possible outcomes of female-female and male-male competition. In comparison with Figure 4, additional disruptive selection on the male trait has enlarged the regions in parameter space in which male and female branching occur, now allowing for sympatric speciation in the region delimited by the thick black curve. There are now regions in which female and male branching are possible simultaneously or in arbitrary sequence (male *and* female primary branching), and, in addition, regions in which branching in one of the traits induces branching in the other one (secondary branching). Sympatric speciation is possible in all these regions, but not in regions where only a single trait or none of the traits undergoes branching. Like in Figure 4, the gray background extends over parameter combinations where females do not evolve preferences for costly male traits. As in Figure 4, lines with triangles delimit male branching areas, and circles delimit female branching areas. Filled and open symbols are used to distinguish between primary and secondary branching, respectively. Parameters are as in Figure 4, and male-male competition was incorporated as explained in the text.

This increases the intensity of competition between the females, and hence the intensity of disruptive selection on female preference.

Discussion

The essential ingredients of sympatric speciation by sexual selection are selective forces that not only account for the evolution of male-trait polymorphism, but also generate and maintain a polymorphism of female preference. It is already well established that female mate choice can cause frequency-dependent disruptive selection on male traits, allowing for evolutionary branching of male secondary sexual characters. However, under the typical sex-role assumption, female mate choice does not result in any dependence of female mating success on the strategies of other females present in the population. Consequentially, female choice cannot generate frequency-dependent selection on female preference, and, therefore, the emergence and maintenance of a polymorphism in female mating preferences is precluded. Even when one is willing to accept that non-selective agents, such as sudden changes of environmental conditions or strong mutation pressure, are responsible for generating female preference polymorphism, the problem of maintaining such polymorphisms remains unresolved. This is a neglected but fundamental problem (Appendix C) for the theory of sympatric speciation by sexual selection, which underlies and explains several undesirable features of current models, such as the unstable coexistence of daughter species after divergent runaway processes.

Even though frequency-dependent interactions between females are neglected in traditional models, there are many ways in which female fitness could be dependent on the strategies of other females. One obvious mechanism, investigated in the present paper, is competition between females, which occurs as soon as males are limited in the number of offspring they can father. This immediately results in (indirect) competition between the females, generating frequency-dependent disruptive selection on female preference. Under suitable conditions, this disruptive selection is sufficiently strong to maintain a stable polymorphism in female preference. As Figure 4 showed, however, competition for males among females can only generate disruptive selection on female preference under conditions for which indirect competition for females between males (by means of female choice) results in stabilizing selection on male trait (and vice versa). Speciation, requiring both female-preference and male-trait polymorphism, therefore remains impossible under this relaxation of the typical sex-role assumption. The mutual exclusion between the conditions under which selection on males is disruptive and of those under which females experience disruptive selection derives from a fundamental conflict between the sexes regarding the mating rate of males (Appendix D): males benefit from mating as often as possible, whereas females benefit when they mate with males that have not mated very often before.

Because of the non-overlapping conditions for male-trait and female-preference branching, additional and independent disruptive selection is required to make sympatric speciation possible. Direct competition between males was presented here as a possible selective agent favoring rare male-trait varieties. This source of additional disruptive selection, acting together with sexual selection by female choice and with competition between females for mates, can then drive adaptive sympatric speciation (Dieckmann *et al.*, 2003), without requiring a dependence on high mutation rates or external events. We have shown that this conclusion applies for a range of model parameters and even when trait and preference are based on several diploid loci with free recombination. Because of the frequency-dependent nature of the combined selection pressures, the daughter species stably coexist after speciation, even without ecological divergence.

These results permit us to conclude that the sympatric speciation observed in our simulations is a robust phenomenon, as far as genetic details and parameter conditions are concerned. However, this does not imply that sympatric speciation by sexual selection will occur under general biological conditions. For that, one needs to consider the robustness of speciation on the level of the processes involved in speciation. We have shown that sympatric speciation occurs only when several independent biological processes are acting simultaneously on the same mating traits. In our example model, the required interactions are represented by mate choice, significant female-female competition for males and male-male competition based on the trait also used in mate choice. Although the individual components of this cocktail appear to act in a wide variety of species, their simultaneous presence seems to be restricted to a few specific cases.

Therefore, we conclude that sympatric speciation by sexual selection is possible, but unlikely in general, since it requires rather specific conditions: first of all, selection must be frequency-dependent in *both* sexes, and second, selection must be disruptive in both sexes *simultaneously*. The latter will often require an additional and independent source of disruptive selection acting on the same traits. That these conditions are independent of the specific model structure and the biological scenarios used to illustrate our points follows from verbal and formal arguments (Appendices C and D). In particular, our arguments are equally valid for models with different assumptions regarding the mate choice process (open-ended preferences, relative preferences). Moreover, the core of our argumentation applies to three recent models of sympatric speciation that include interactions between the sexes other than (just) female mate choice. We will now discuss these models in some detail, in order to illustrate that the processes underlying frequency-dependent selection on females could be diverse in nature and that competition between females for males, although a likely factor, is certainly not the only candidate mechanism.

The first model describes sympatric speciation by sexual conflict (Gavrilets & Waxman, 2002). The basic assumptions are that mating rates, as in our present model, depend on the match between male and female mating characters. However, the sexes have conflicting interests, since mating is assumed to be costly for females but advantageous for males. As a consequence, the male mating character evolves to optimally match the female mating character, but the female mating character evolves away from the male mating character, resulting in a coevolutionary chase between the sexes. Under suitable parameter conditions, however, this coevolutionary chase can be stopped. This occurs when a female mutant arises by a large mutational step, such that the males are now trapped between the old female mating character and the new mutant type. The females then diversify into two separate clusters, which may subsequently also trigger diversification in the male mating character, resulting in sympatric speciation. Gavrilets and Waxman observed speciation while assuming unlimited availability of males and without introducing any additional processes to generate frequency dependence, an observation that, at first sight, would appear to contradict our conclusions. However, Gavrilets and Waxman assumed a large population, in which several mutants with rather different phenotypes were already present in low densities. As a result, frequency-dependent selection on female preference could arise from the *antagonistic interactions between females and a genetically polymorphic male population*. In a polymorphic male population, the fitness of a female mating strategy depends on the shape of the frequency distribution of male mating characters in the population. At the same time, the frequency distribution of male mating characters will always accommodate itself to the mating strategies of females in the population in such a way that male fitness is maximized. Due to this feedback on the population dynamical timescale between female mating strategies and the “environment” (i.e., the frequency distribution of male mating characters), selection on female mating characters is clearly frequency-dependent. We emphasize that interactions with genetically polymorphic populations result in frequency-dependent selection, but not necessarily frequency-dependent disruptive selection. In the Gavrilets and Waxman model, however, selection is disruptive due to the nature of the interactions between males and females: the frequency distribution of male mating characters will tend to be skewed in such a way that it matches with the most abundant female mating character, and therefore, due to the sexual conflict, rare female mating characters are favored. Whereas our model focused on mechanisms influencing the availability of potential partners, the model of Gavriltes and Waxman illustrates that also mechanisms influencing the density of potential partners can generate the required frequency-dependent disruptive selection on female mating characters.

The second model (Almeida & Vistulo de Abreu, 2003) is again a model of sympatric speciation by mate choice, but it deviates from traditional sexual selection models in that it analyses the consequences of *mutual mate choice*. In this model, both females and males engage in mate choice, and both sexes may abandon their current partner when encountering one that better matches their mate choice criteria. Only pairs that persist for some minimal period of time produce offspring. Mutual mate choice generates competition between males for females as well as competition between females for males. The simultaneous action of these two types of competition can drive sympatric speciation, since it leads to an intrinsic advantage of rarity for both male and female mating characters. Individuals exhibiting rare mate choice criteria are favored because those individuals will be less likely to abandon their partner or to be abandoned by their partner before the minimal period required to produce offspring has elapsed. Although Almeida and Vistulo de Abreu modeled quite different biological processes than we did, the two models are almost identical at the level of the mechanisms involved in speciation. In both models the source of frequency-dependent disruptive selection on both sexes is competition for mates. In our model this competition is caused by direct male-male competition for mating territories and indirect competition between females due to limited male availability. In the model of Almeida and Vistulo de Abreu, there is indirect competition within both sexes due to the fact that the lifetime of a pair bond is determined by the mate choice criteria of other individuals in the population.

The third model (Van Doorn & Weissing, 2001) integrates sexual selection with the ecological approach to sympatric speciation, and, as such, builds on classical (Felsenstein, 1981) and recent models (Dieckmann & Doebeli, 1999) of ecological speciation. The model does not deviate from the typical sex role assumption and, as in the present paper, it is assumed that mating rates are determined by the match between male and female mating characters. In addition to female preferences and male mating traits, the model also involves ecological characters, which determine an individual's success in competing for ecological resources and, through processes like habitat choice, also pleiotropically affect mating rates. On this basis Van Doorn & Weissing (2001) show that sympatric speciation can be initiated by the simultaneous and mutually dependent diversification of mating characters and ecological characters. This option only exists when the pleiotropic interaction between ecological characters and mating rates is sufficiently strong. In the light of the conclusions of the present study, these results, which are in line with those based on earlier models (e.g., Felsenstein, 1981), can now be explained as follows. If sufficiently strong, the pleiotropic interaction between ecological characters and mating types allows for the development of a linkage disequilibrium between ecological characters and mating characters. The linkage disequilibrium, in turn, is responsible for generating the necessary frequency-dependent selection on female preference. Rare preference alleles are favored, not because of processes related to mate choice, but because rare preference alleles are, due to the linkage disequilibrium, often associated with rare ecological characters, which are favored in ecological resource competition. This illustrates that, through *linkage disequilibria*, frequency dependent disruptive selection on characters unrelated to mate choice can indirectly generate frequency-dependent selection on female preferences. It is clear that models of this type (Felsenstein, 1981; Dieckmann & Doebeli, 1999; Van Doorn & Weissing, 2001) exhibit sympatric speciation not so much 'through' sexual selection as merely 'involving' sexual selection, since the speciation process is driven primarily by the disruptive selection acting on the (ecological) characters and not in the first place by disruptive sexual selection.

Also mate choice itself tends to generate non-random genetic associations (i.e., linkage disequilibria), particularly between female preference and male trait alleles. In fact, this is what actually drives the Fisherian runaway process of sexual selection (Fisher, 1930; Lande, 1981; Andersson, 1994). Given that linkage disequilibria with other traits under disruptive selection can generate frequency-dependent selection on female preferences, the above would seem to imply that Fisherian runaway sexual selection could generate the frequency-dependent and disruptive selection needed for adaptive sympatric speciation. Although this possibility exists in theory (see Takimoto, 2002), it does in practice not conflict with our conclusion that, as a general rule, mate choice alone is insufficient to support sympatric speciation. We provide three arguments to support this claim. First, sympatric speciation models based on divergent Fisherian runaway processes (Higashi *et al.* 1999; Takimoto, 2000) and also the simulations presented in this paper (Figure 2), illustrate that the indirect frequency-dependent selection on female preference generated through its genetic covariance with the male mating trait is typically only weak and unable to support stable coexistence of the daughter species. Second, although our adaptive dynamics approximation does not take into account the genetic covariances between traits, our analysis provides a valid limit for the case in which genetic covariances are small. Third, an extended analysis, which does take into account genetic covariances, reveals that the establishment of linkage disequilibrium between female preference and male trait will not qualitatively affect the outcome when both male trait and female preference are capable of undergoing evolutionary branching, or, alternatively, when evolutionary branching is precluded for both traits. Consequently, qualitatively different outcomes can only be expected when female choice generates frequency-dependent disruptive selection on males. This, however, requires selection on female preferences to be very weak, such that considerable genetic variation of female preferences can build up through mutation pressure (Van Doorn & Weissing, 2001). In other words, unless genetic covariances are large and selection on female preferences is very weak, the effects of indirect selection on female preferences through genetic linkage with male mating traits can be neglected.

Although we have shown that sympatric speciation by sexual selection is feasible, this by no means suggests that it is ubiquitous. On the contrary, our main point here is that sympatric speciation by sexual selection requires far more specific biological conditions than is generally recognized. We argue that essential ingredients of the sympatric speciation process have been overlooked. For several empirical systems it has been investigated in quite some detail how female mate choice may exert frequency-dependent disruptive sexual selection on males (Andersson, 1994), but the analysis of processes capable of generating such selection on female preference has been neglected so far. Moreover, since it is far from trivial, as we have seen, that the frequency-dependent interactions in both sexes are capable of inducing disruptive selection simultaneously, empirical and theoretical attention needs to be devoted to additional sources of disruptive selection that may well be required to explain sympatric speciation. Only after these issues have been clarified will we be able to decide in which biological systems and under what conditions sympatric speciation by sexual selection, rather than another mode of speciation, is indeed the more plausible alternative.

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Appendices

Appendix A: Derivation of mutant invasion fitness

We approximate the dynamics of our stochastic individual-based model by deterministic equations using methods derived from adaptive dynamics theory (Metz *et al.*, 1996; Dieckmann & Law, 1996; Geritz *et al.*, 1998). To enable this complementary treatment we make a number of simplifying assumptions. First of all, we assume that population sizes are sufficiently large such that we may neglect stochasticity in the dynamics of the resident population. Second, we consider mutation-limited evolution, so that mutants arise in genetically monomorphic resident populations. Third, we assume single-locus haploid genetics to underlie male trait and female preference (our approach can be extended to more complicated diploid genetics, but we refrain from doing so to keep our analysis tractable). Our aim is to derive the invasion fitness $\lambda(p,q,\hat{p},\hat{q})$ of a rare male trait or female preference mutant with genotypic values (p,q) that has arisen at low frequency in a resident population characterized by the genotypic values $(\hat{p},\hat{q})$. The invasion fitness measures the initial exponential growth rate of the mutant: only when it is larger than zero, i.e., larger than the resident growth rate at equilibrium, the mutant generically can replace the resident (Metz *et al.*, 1996; Geritz *et al.*, 2002). Moreover, the evolutionary rates of change in male trait and female preference can be derived from the invasion fitness (Dieckmann & Law 1996).

As introduced above, we denote *genotypic* trait and preference values p and q, and use hats to distinguish resident from mutant traits. The *phenotypic* trait and preference values, which consist of a genotypic component and added environmental noise, are denoted x and y for preference and trait, respectively. In the following, the variables $\tilde{x}$ and $\tilde{y}$ are always used as auxiliary integration variables. Finally, as in the main text, we use the notation g_i to denote gaussian functions $g_i(x) = \exp\left(-\frac{1}{2}x^2/\sigma_i^2\right)$ and $\bar{g}_i$ to denote normalized gaussian functions $\bar{g}_i(x) = g_i(x)/\left(\sigma_i\sqrt{2\pi}\right)$.

Analogous to equation (4), the probability $\alpha(x,y,\hat{q})$ that a female with phenotypic preference x chooses a particular male with phenotypic trait y, when she also encounters males from a resident population with genotypic trait value $\hat{q}$, is given by

$$\alpha(x,y,\hat{q}) = \frac{a(x,y)}{\eta + A(x,\hat{q})} \quad , \tag{7}$$

where, as in equation (2), $a(x,y) = g_m\left(c(x) - y\right)$ is the “attractiveness” of the focal male to the female, and $A(x,\hat{q})$ sums the attractivities of all competing resident males to the female, that is,

$$A(x,\hat{q}) = \sum_{\text{males } \tilde{y}} \mathrm{N}_{\text{male}}(\tilde{y},\hat{q})\, a(x,\tilde{y}) \,. \tag{8}$$

In a resident population in which all males posses the genotypic trait value $\hat{q}$, the number of males with a phenotypic trait value between $\tilde{y}$ and $\tilde{y}+d\tilde{y}$ is $\mathrm{N}_{\text{male}}(\tilde{y},\hat{q}) = N\, \bar{g}_q(\hat{q}-\tilde{y})\, g_s(\tilde{y})\, d\tilde{y}$. Recall that we assumed the environmental component of the male trait to be distributed according to a normal distribution with width σ_q. This distribution is described by the normalized gaussian function $\bar{g}_q$. The gaussian function g_s gives the probability density that a male survives viability selection. Finally, the constant N denotes the population size of the resident, expressed as the number of males or females before viability selection. These considerations allow us to write

$$A(x,\hat{q}) = N \int_{-\infty}^{\infty} \bar{g}_q(\hat{q}-\tilde{y})\, g_s(\tilde{y})\, a(x,\tilde{y})\, d\tilde{y}\,. \tag{9}$$

To find the per capita mating rate of a mutant male interacting with the female resident population, denoted $M_m(q,\hat{p},\hat{q})$, the expression in equation (7) has to be weighted according to the frequencies of the phenotypes x and y, and integrated over all possible phenotypic values y of the mutant male trait and over all possible phenotypic preference values x resulting from the resident female preference with genotypic value $\hat{p}$. The density of values x is described by the normalized gaussian $\bar{g}_p(\hat{p}-x)$. This yields

$$M_m(q,\hat{p},\hat{q}) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \bar{g}_p(\hat{p}-x) N\, \bar{g}_q(q-y)\, g_s(y)\, \frac{a(x,y)}{\eta + A(x,\hat{q})}\, dx\, dy\,, \tag{10}$$

which can be written more concisely as

$$M_m(q,\hat{p},\hat{q}) = \int_{-\infty}^{\infty} \bar{g}_p(\hat{p}-x) \frac{A(x,q)}{\eta + A(x,\hat{q})}\, dx\,. \tag{11}$$

Similarly, we may compute the per capita mating rate of a mutant female with preference p interacting with the resident male population as

$$M_f(p,\hat{q}) = \int_{-\infty}^{\infty} \bar{g}_p(p-x) \frac{A(x,\hat{q})}{\eta + A(x,\hat{q})}\, dx\,. \tag{12}$$

Note that $M_f(p,\hat{q})$ does not depend on the resident female preference $\hat{p}$, and that $M_m(\hat{q},\hat{p},\hat{q}) = M_f(\hat{p},\hat{q})$.

We may now establish a recurrence equation for the number of mutants $n_t(p,q,\hat{p},\hat{q})$ when rare. Under our assumption of constant population size N, the number of mutants n_t changes according to

$$n_{t+1}(p,q,\hat{p},\hat{q}) = n_t(p,q,\hat{p},\hat{q}) \frac{1}{2} \left(M_m(q,\hat{p},\hat{q}) + M_f(p,\hat{q})\right) S(\hat{p},\hat{q})\,. \tag{13}$$

The factor $1/2$ reflects that only half of the offspring of a mutant parent will inherit the mutant strategy. The function $S(\hat{p},\hat{q})$ captures the effects of density dependence. It absorbs the per capita survival probabilities, as well as the number of matings per female per generation.

When the mutant is identical to the resident ($p=\hat{p}, q=\hat{q}$) and the resident population is at equilibrium, the mutant's density must neither decline nor increase, which means that

$$\frac{1}{2}S(\hat{p},\hat{q}) = \frac{1}{M_m(\hat{q},\hat{p},\hat{q}) + M_f(\hat{p},\hat{q})} = \frac{1}{2\,M_f(\hat{p},\hat{q})}. \tag{14}$$

Equations (13) and (14) show that the geometric rate of increase of the number of mutants equals the ratio of mutant mating rates over resident mating rates. Since the invasion fitness is defined as the natural logarithm of the geometric rate of increase, we find that

$$\lambda(p,q,\hat{p},\hat{q}) = \ln\left(\frac{M_m(q,\hat{p},\hat{q}) + M_f(p,\hat{q})}{2\,M_f(\hat{p},\hat{q})}\right). \tag{15}$$

Appendix B: Numerical procedures

In generic cases, the fact that $\lambda(p,q,\hat{p},\hat{q}) > 0$ implies that $\lambda(\hat{p},\hat{q},p,q) < 0$ and that the mutant will go to fixation (Geritz *et al.*, 2002). This means that mutants with positive invasion fitness can grow in the resident population until the resident is completely replaced. A series of such trait substitution events results in directed evolution, the direction and expected rate of which is dependent on the sign and magnitude of the local fitness gradients (Dieckmann & Law, 1996). Specifically, it can be shown that

$$\begin{aligned} \frac{d\hat{p}}{dt} &= \kappa \left.\frac{\partial \lambda(p,q,\hat{p},\hat{q})}{\partial p}\right|_{\substack{p=\hat{p}\\ q=\hat{q}}} = \frac{\kappa}{2\,M_f(\hat{p},\hat{q})} \left.\frac{\partial M_f(p,\hat{q})}{\partial p}\right|_{p=\hat{p}}, \\ \frac{d\hat{q}}{dt} &= \kappa \left.\frac{\partial \lambda(p,q,\hat{p},\hat{q})}{\partial q}\right|_{\substack{p=\hat{p}\\ q=\hat{q}}} = \frac{\kappa}{2\,M_f(\hat{p},\hat{q})} \left.\frac{\partial M_m(q,\hat{p},\hat{q})}{\partial q}\right|_{q=\hat{q}}. \end{aligned} \tag{16}$$

Similar equations can be derived within a quantitative genetics framework (Lande, 1976). The constant $\kappa = \frac{1}{2} N \sigma_v^2 \mu$ captures the effects of population size, mutation ratio, μ, and mutational variance, σ_v^2, on the rate of evolution. An assumption underlying equations (16) is that mutations do not have pleiotropic effects and that mutation ratio and variance are equal for female preference and male trait. Generalizations can be readily considered; in particular, unequal mutation rates and/or mutational variances can be dealt with by rescaling the female-choice function.

Equations (16) were solved numerically using a standard algorithm for the numerical integration of ordinary differential equations (the Cash-Karp Runge-Kutta algorithm with adaptive stepsize control, Press *et al.*, 1992). The resident trajectories were calculated until a monomorphic evolutionary equilibrium was attained. We then determined whether further polymorphic evolution would occur by checking the local evolutionary stability of the monomorphic equilibrium. If so, numerical integration was then continued with an extended system of equations, with initial conditions slightly displaced around the monomorphic equilibrium. For a population that is dimorphic in both trait and preference, the evolutionary dynamics can be described by a system of four equations

$$
\begin{aligned}
\frac{d\,\hat{p}_1}{dt} &= \frac{\kappa\psi}{2\,M_{\mathrm{pol},f}\left(\hat{p}_1,\hat{q}_1,\hat{q}_2\right)} \left.\frac{\partial M_{\mathrm{pol},f}\left(p,\hat{q}_1,\hat{q}_2\right)}{\partial p}\right|_{p=\hat{p}_1}, \\
\frac{d\,\hat{p}_2}{dt} &= \frac{\kappa\left(1-\psi\right)}{2\,M_{\mathrm{pol},f}\left(\hat{p}_1,\hat{q}_1,\hat{q}_2\right)} \left.\frac{\partial M_{\mathrm{pol},f}\left(p,\hat{q}_1,\hat{q}_2\right)}{\partial p}\right|_{p=\hat{p}_2}, \\
\frac{d\,\hat{q}_1}{dt} &= \frac{\kappa\phi}{2\,M_{\mathrm{pol},f}\left(\hat{p}_1,\hat{q}_1,\hat{q}_2\right)} \left.\frac{\partial M_{\mathrm{pol},m}\left(q,\hat{p}_1,\hat{p}_2,\hat{q}_1,\hat{q}_2\right)}{\partial q}\right|_{q=\hat{q}_1}, \\
\frac{d\,\hat{q}_2}{dt} &= \frac{\kappa\left(1-\phi\right)}{2\,M_{\mathrm{pol},f}\left(\hat{p}_1,\hat{q}_1,\hat{q}_2\right)} \left.\frac{\partial M_{\mathrm{pol},m}\left(q,\hat{p}_1,\hat{p}_2,\hat{q}_1,\hat{q}_2\right)}{\partial q}\right|_{q=\hat{q}_2}.
\end{aligned}
\tag{17}
$$

The constants ψ and φ determine the relative abundance of, respectively, the two resident female preferences and male traits. The mating rates in a polymorphic population are straightforward generalizations of the mating rates in a monomorphic population. For example,

$$
\begin{aligned}
&M_{\mathrm{pol},m}\left(q,\hat{p}_1,\hat{p}_2,\hat{q}_1,\hat{q}_2\right)= \\
&\int_{-\infty}^{\infty}\left[\psi\,\bar{g}_p\left(\hat{p}_1-x\right)+\left(1-\psi\right)\bar{g}_p\left(\hat{p}_2-x\right)\right]\frac{A\left(x,q\right)}{\eta+\varphi A\left(x,\hat{q}_1\right)+\left(1-\varphi\right)A\left(x,\hat{q}_2\right)}dx\,.
\end{aligned}
\tag{18}
$$

The stable coexistence of two resident female-preference types requires that both types have equal fitness. The same applies for the coexistence of two resident male-trait types. In other words, in a polymorphic population,

$$
\begin{aligned}
M_{\mathrm{pol},f}\left(\hat{p}_1,\hat{q}_1,\hat{q}_2\right)&=M_{\mathrm{pol},f}\left(\hat{p}_2,\hat{q}_1,\hat{q}_2\right), \\
M_{\mathrm{pol},m}\left(\hat{q}_1,\hat{p}_1,\hat{p}_2,\hat{q}_1,\hat{q}_2\right)&=M_{\mathrm{pol},m}\left(\hat{q}_2,\hat{p}_1,\hat{p}_2,\hat{q}_1,\hat{q}_2\right).
\end{aligned}
\tag{19}
$$

These two equations define the values of the constants ψ and φ for any given set of resident preference and trait values.

We used an efficient way (based on fast Fourier transforms, details available upon request) to calculate the mating rate gradients. However, our algorithm required us to specify the inverse of the female choice function $c^{\mathrm{inv}}\left(q\right)$, rather than the female choice function $c\left(p\right)$ itself. In all simulations where the female choice function was nonlinear, we used

$$
c^{\mathrm{inv}}\left(q\right)=\frac{q+q^3}{3}
\tag{20}
$$

The graph of this function can clearly be recognized in Figure 2. This simple function is convex to the right of $q=0$, and concave to the left. Therefore it allows for divergent evolution: sexual selection will drive the population towards higher values of q when $q>0$, and to lower values when $q<0$. At $q=0$, sexual selection is disruptive.

Appendix C: Consequences of frequency-independent selection on female preference

Here we show in general that a polymorphism of female preference can never arise without frequency-dependent selection on female preference. As will become apparent, these general arguments are valid for a whole class of models sharing the property that the mating rate of females is independent of the resident female strategy. Our arguments can also be worked out on a more abstract and even more general level by considering the dimensionality of the environmental feedback (Meszéna & Metz, in press).

From equations (16), it can be seen that the endpoints of monomorphic evolution are strategy pairs $(\hat{p},\hat{q})=(p^*,q^*)$ at which the fitness gradients with respect to both trait and preference are zero. So, at those points

$$\left.\frac{\partial\lambda(p,q,\hat{p},\hat{q})}{\partial p}\right|_{\substack{p=\hat{p}=p^*\\ q=\hat{q}=q^*}}=0 \quad\text{and}\quad \left.\frac{\partial\lambda(p,q,\hat{p},\hat{q})}{\partial q}\right|_{\substack{p=\hat{p}=p^*\\ q=\hat{q}=q^*}}=0. \tag{21}$$

In view of equation (15), this is equivalent with

$$\left.\frac{\partial M_f(p,q^*)}{\partial p}\right|_{p=p^*}=0 \quad\text{and}\quad \left.\frac{\partial M_m(q,p^*,q^*)}{\partial q}\right|_{q=q^*}=0. \tag{22}$$

These conditions ensure that (p^*,q^*) is a pair of so-called evolutionarily singular strategies (Metz *et al.*, 1996), at which the rates of monomorphic evolution vanish. However, not all singular strategy pairs are relevant as endpoints of monomorphic evolution, since not all singular strategy pairs are attainable by gradual evolutionary change. Attainability of a singular strategy pair must be assessed by investigating its convergence stability. To ensure that evolution converges to the singular strategy pair irrespective of the mutational variance-covariance matrix, the singular strategy pair must satisfy the conditions for strong convergence stability (Leimar, 2001). Necessary (but not sufficient) conditions for strong convergence stability are

$$\frac{\partial}{\partial\hat{p}}\left(\left.\frac{\partial\lambda(p,q,\hat{p},\hat{q})}{\partial p}\right|_{\substack{p=\hat{p}\\ q=\hat{q}}}\right)\Bigg|_{\substack{\hat{p}=p^*\\ \hat{q}=q^*}}<0 \quad\text{and}\quad \frac{\partial}{\partial\hat{q}}\left(\left.\frac{\partial\lambda(p,q,\hat{p},\hat{q})}{\partial q}\right|_{\substack{p=\hat{p}\\ q=\hat{q}}}\right)\Bigg|_{\substack{\hat{p}=p^*\\ \hat{q}=q^*}}<0, \tag{23}$$

which, in our case, following from equation (15), translate into

$$\left.\frac{\partial^2 M_f(p,q^*)}{\partial p^2}\right|_{p=p^*}<0 \quad\text{and}\quad \left.\frac{\partial^2 M_m(q,p^*,q^*)}{\partial q^2}\right|_{q=q^*}+\left.\frac{\partial^2 M_m(q,p^*,q^*)}{\partial q\,\partial q^*}\right|_{q=q^*}<0. \tag{24}$$

The fact that monomorphic evolution comes to a halt at convergence stable singular strategy pairs does not imply that further evolution from such singular strategies is impossible. In fact, convergence stable singular strategy pairs need not be evolutionarily stable, that is, they need not be resistant against invasion by alternative strategies. In particular, the resident population at the singular strategy can be invaded by female preference or male trait mutants, when, respectively,

$$\left.\frac{\partial^2 \lambda\left(p,q,p^*,q^*\right)}{\partial p^2}\right|_{\substack{p=p^*\\ q=q^*}} > 0 \quad \text{or} \quad \left.\frac{\partial^2 \lambda\left(p,q,p^*,q^*\right)}{\partial q^2}\right|_{\substack{p=p^*\\ q=q^*}} > 0, \tag{25}$$

or, equivalently, when

$$\left.\frac{\partial^2 M_f\left(p,q^*\right)}{\partial p^2}\right|_{p=p^*} > 0 \quad \text{or} \quad \left.\frac{\partial^2 M_m\left(q,p^*,q^*\right)}{\partial q^2}\right|_{q=q^*} > 0\ . \tag{26}$$

When this situation occurs, the population will undergo evolutionary branching. It can only escape from the evolutionarily *un*stable singular strategy by becoming dimorphic, since, because of convergence stability, a monomorphic population is rapidly driven back to the singular strategy.

It is obvious that the left halves of conditions (24) and (26) are mutually exclusive, implying that there can be no female-preference branching in this model. By contrast, male-trait branching is possible, and occurs when

$$-\left.\frac{\partial^2 M_m\left(q,p^*,q^*\right)}{\partial q\,\partial q^*}\right|_{q=q^*} > \left.\frac{\partial^2 M_m\left(q,p^*,q^*\right)}{\partial q^2}\right|_{q=q^*} > 0. \tag{27}$$

Note that the contradiction between conditions (24) and (26) with regard to female-preference branching is unavoidable and simply results from the fact that M_f is independent of the resident female strategy.

Appendix D: Extension of the model with female-female competition

Competition between females can easily be incorporated in the equations by multiplying all mating rates with a function Φ, measuring the number of offspring produced per mating and decreasing with increasing mating rates of the male. Using the shorthand notation

$$\xi(y,p,q) = \int_{-\infty}^{\infty} \frac{N\,\bar{g}_p(p-x)\,a(x,y)}{\eta + A(x,q)}\,dx \tag{28}$$

for the mating rate of a male with trait y, the mutant male mating rate transforms into

$$\tilde{M}_m(q,\hat{p},\hat{q}) = \int_{-\infty}^{\infty} \bar{g}_q(q-y)\,g_s(y)\,\xi(y,\hat{p},\hat{q})\,\Phi\big(\xi(y,\hat{p},\hat{q})\big)\,dy \tag{29}$$

and the mutant female mating rate becomes

$$\tilde{M}_f(p,\hat{p},\hat{q}) = \int_{-\infty}^{\infty} \bar{g}_q(\hat{q}-y)\,g_s(y)\,\xi(y,p,\hat{q})\,\Phi\big(\xi(y,\hat{p},\hat{q})\big)\,dy\,. \tag{30}$$

This expression now also depends on the resident female preference, the importance of which was shown in Appendix C. Under our assumptions, the function Φ decreases with ξ, that is, a female will produce less and less offspring as her partner has mated more often. It seems biologically reasonable, however, to assume that males will still benefit from additional matings. Mathematically, this implies that

$$\text{for all } \xi: \quad \frac{d\Phi(\xi)}{d\xi} < 0 \quad \text{and} \quad \frac{d\left(\xi\Phi(\xi)\right)}{d\xi} > 0 \tag{31}$$

Using only these two properties of Φ, the semi-formal argumentation given below demonstrates that the conditions for male and female mating-type branching are mutually exclusive. A more rigorous proof, involving expansions of ξ and $\Phi(\xi)$ in terms of Hermite polynomial series, can be given, but this proof involves lengthy and complicated calculations and is therefore omitted here.

Let us suppose first that male mating-type branching is possible. This requires that, at the singular strategy $\left(p^*, q^*\right)$,

$$\left.\frac{\partial^2 \tilde{M}_m(q,\hat{p},\hat{q})}{\partial q^2}\right|_{\substack{\hat{p}=p^* \\ q=\hat{q}=q^*}} = \int_{-\infty}^{\infty} \bar{g}_q''\left(q^*-y\right) g_s(y)\, \xi\left(y,p^*,q^*\right) \Phi\left(\xi\left(y,p^*,q^*\right)\right) dy > 0\,. \tag{32}$$

By repeatedly applying the product rule for integration, one can easily see that the integral in equation (32) represents the smoothed second derivative with respect to y and evaluated at $y = q^*$ of the product $g_s(y)\, \xi\left(y,p^*,q^*\right) \Phi\left(\xi\left(y,p^*,q^*\right)\right)$. Consequently, the inequality (32) can only be fulfilled when $\xi\left(y,p^*,q^*\right) \Phi\left(\xi\left(y,p^*,q^*\right)\right)$ has a minimum with respect to y close to $y = q^*$. Because of conditions (31), this implies that $\Phi\left(\xi\left(y,p^*,q^*\right)\right)$ must have a maximum close to $y = q^*$. This in turn means that

$$\begin{aligned} \left.\frac{\partial^2 \tilde{M}_f(p,\hat{p},\hat{q})}{\partial p^2}\right|_{\substack{p=\hat{p}=p^* \\ \hat{q}=q^*}} &= \int_{-\infty}^{\infty} \bar{g}_q\left(q^*-y\right) g_s(y) \left.\frac{\partial^2 \xi\left(y,p,q^*\right)}{\partial p^2}\right|_{p=p^*} \Phi\left(\xi\left(y,p^*,q^*\right)\right) dy \\ &< \int_{-\infty}^{\infty} \bar{g}_q\left(q^*-y\right) g_s(y) \left.\frac{\partial^2 \xi\left(y,p,q^*\right)}{\partial p^2}\right|_{p=p^*} dy = \left.\frac{\partial^2 M_f(p,\hat{q})}{\partial p^2}\right|_{\substack{p=p^* \\ \hat{q}=q^*}} . \end{aligned} \tag{33}$$

In most models of female choice without female-female competition, the only selective force on female preference is the cost of choosiness. Usually this source of stabilizing selection will drive female preference to a *stable* evolutionary equilibrium value at which the costs of choice are minimized. Because of condition (24), convergence stability of equilibria in the preference direction implies that

$$\left.\frac{\partial^2 M_f(p,\hat{q})}{\partial p^2}\right|_{\substack{p=p^* \\ \hat{q}=q^*}} < 0 \tag{34}$$

and therefore

$$\left.\frac{\partial^2 \tilde{M}_m(q,\hat{p},\hat{q})}{\partial q^2}\right|_{\substack{\hat{p}=p^* \\ q=\hat{q}=q^*}} > 0 \;\Rightarrow\; \left.\frac{\partial^2 \tilde{M}_f(p,\hat{p},\hat{q})}{\partial p^2}\right|_{\substack{p=\hat{p}=p^* \\ \hat{q}=q^*}} < 0\,. \tag{35}$$

A similar reasoning shows that the reverse inference is also true. This demonstrates that there can be no simultaneous male and female mating-type branching, and, hence, no sympatric speciation in our model involving only female choice and female-female competition.

Appendix E: Extension of the model with male-male competition

Competition between males (e.g., for mating territories) can be dealt with by replacing in equations (28)-(30) the distribution of males after viability selection by the distribution $z(y,q,\hat{q})$, which denotes the distribution of males after both viability selection and male-male competition.

The distribution $z(y,q,\hat{q})$ was determined as follows. Following equation (6), the competition experienced by a male trying to establish a territory is

$$\overline{f}(y,\hat{q}) = \int_{-\infty}^{\infty} z(\tilde{y},\hat{q},\hat{q})\, g_c(y-\tilde{y})\, d\tilde{y}\,. \tag{36}$$

If $\overline{f}(y,\hat{q})$ falls below the threshold θ, the density of males of type y that occupy a territory grows, otherwise it decreases, such that an equilibrium is reached when

$$z(y,q,\hat{q}) = H\left(\theta - \overline{f}(y,\hat{q})\right)\overline{g}_q(q-y)\, g_s(y). \tag{37}$$

The function H is the Heaviside step function ($H(x)=0$ for $x<0$; $H(x)=1$ for $x>0$, and $H(x)$ is undefined at $x=0$), which we approximated for numerical reasons by the smoothed threshold function Θ, where

$$\Theta(y) = \frac{1}{2}\left(1+\tanh\left(\frac{y}{\sigma_w}\right)\right). \tag{38}$$

The smoothing parameter σ_w was chosen as $\sigma_w = 0.01$.

In our adaptive dynamics simulations, we solved equations (36) and (37) efficiently using Fast Fourier Transforms for the resident male distribution $z(y,\hat{q},\hat{q})$. The mutant male distribution $z(y,q,\hat{q})$ was then determined by using that

$$z(y,q,\hat{q}) = z(y,\hat{q},\hat{q})\frac{\overline{g}_q(q-y)}{\overline{g}_q(\hat{q}-y)}. \tag{39}$$

Equation (39) follows from the fact that $z(y,\hat{q},\hat{q})$ is a solution of (37) when $q=\hat{q}$.