Sympatric Speciation by Sexual Selection: A Critical Reevaluation

G. Sander van Doorn,[1,*] Ulf Dieckmann,[2,3] and Franz J. Weissing[1]

1. Centre for Ecological and Evolutionary Studies, University of Groningen, Kerklaan 30, 9751 NN Haren, The Netherlands;
2. Adaptive Dynamics Network, International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria;
3. Section Theoretical Biology, Institute of Biology, Leiden University, Kaiserstraat 63, 2311 GP Leiden, The Netherlands

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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 nonselective 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 nonadaptive 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.

Keywords: evolutionary branching, frequency-dependent disruptive selection, male-male competition, sexual conflict, Fisherian runaway, individual-based simulations.

* Corresponding author; e-mail: doorngs@biol.rug.nl.

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Classical research into the potential mechanisms of sympatric speciation has sought to explain sympatric speciation primarily from ecological causes (reviewed, e.g., in Johnson and Gullberg 1998; Schluter 2001), often presupposing the presence of an assortative mating structure that allows for a high degree of reproductive isolation. Recent research, in contrast, 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 that 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 because classical female

choice models already demonstrated that a single runaway process will occur only 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 because 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 were 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 be largely dependent on unpredictable external events. This conclusion not only conflicts with the historical interpretation of sympatric speciation as an internally driven and adaptive process (Dieckmann et al. 2004) 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 sympatric speciation is also 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 and 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 and Vacquier 1998).

Surprisingly, an obvious third possibility has been largely overlooked in the literature on sympatric speciation (but see mutual mate choice models by Lande et al. [2001]; Almeida and 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 article is to investigate critically 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. 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 nonadaptive processes. However, because 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 are produced (other forms of population density regulation give identical results as long as female preference and male trait are

ecologically neutral traits; G. S. van Doorn and U. Dieckmann, unpublished manuscript). 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_i 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 justified only 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 because the choice of scale is not arbitrary but prescribed by the assumptions made on the mutation process at the genetic level. Because 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, for example, 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 because 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

$$\overline{c(p)} \approx c(\bar{p}) + \frac{1}{2} c''(\bar{p}) \operatorname{Var}(p). \tag{1}$$

If the choice function is linear, its second and higher derivatives will be 0, which, according to equation (1), implies that $\overline{c(p)} = c(\bar{p})$. 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 $c(\bar{p})$. Such a discrepancy generates directed sexual selection because 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 $c''(\bar{p})$, 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 fig. 2).

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

$$a_{ij} = g_m[c(p_i) - q_j], \tag{2}$$

where here and henceforth g_a denotes a Gaussian function with mean 0 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 discriminative mate choice. This model of mate choice assumes fixed absolute preferences and is more conservative than models based on open-ended or fixed relative 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 equation (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

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

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

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

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 because they waste time searching for more attractive mates. Then, 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). Therefore, 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, in contrast, may potentially father an unlimited number of offspring because 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 nonoverlapping 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 multilocus genetics underlying male trait and female preference. Specifically, phenotypic preference and trait values consist of both 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 $\sigma_v(2L)^{1/2}$. 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 nonheritable 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 (see appendix in the online edition of the *American Naturalist*). 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 (Dieckmann and Law 1996; Metz et al. 1996; Geritz et al. 1998) to calculate numerically the expected evolutionary trajectories of female preference and male trait (appendix). Throughout the article, 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 $q \approx c(p)$ (fig. 1). This is not surprising because 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 for such optimal matching. The same is true for direct selection on female preference because 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 (fig. 1). If the function is linear, the female choice function defines a line of equilibria along which the population drifts neutrally (fig. 1, *upper panel*). This line of equilibria disappears as soon as the female choice function becomes nonlinear (fig. 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 (eq. [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 toward the optimal value. However, this will immediately induce a corresponding change in the population mean female preference value because 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 toward two possible endpoints of evolution. The latter are located

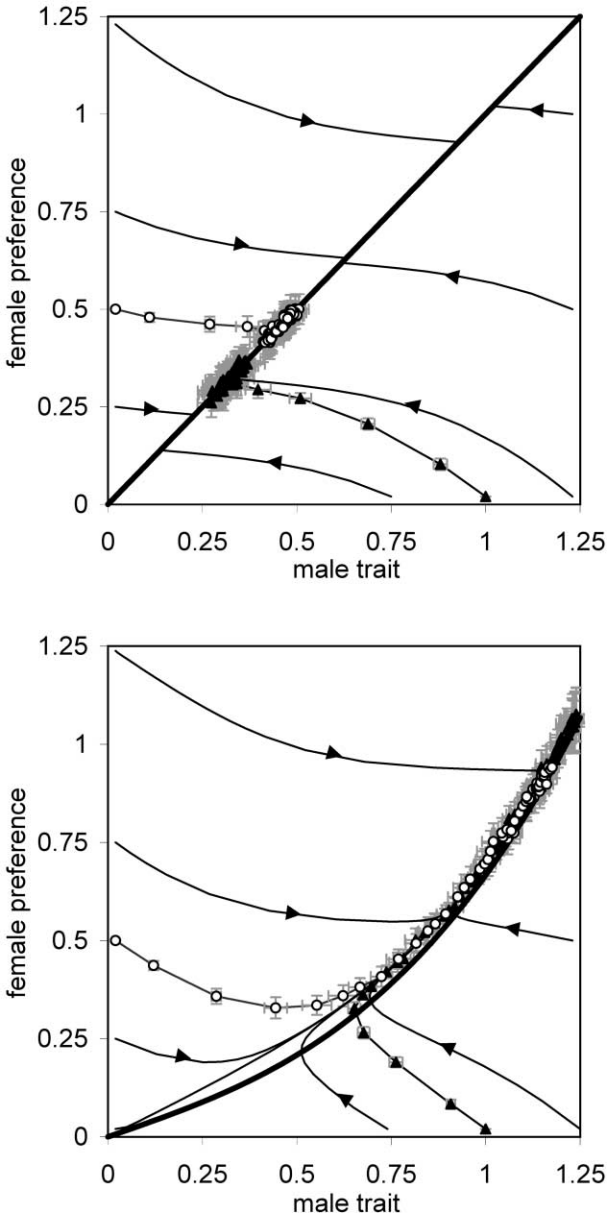

Figure 1: Evolution along the female choice function. For a given female choice function (*thick black curves*), the two panels show the evolutionary trajectories of male trait and female preference from different initial conditions as obtained by individual-based simulations (*open circles* and *filled triangles*) and numerical integration of the adaptive dynamics approximation (*thin black curves with arrows*; see appendix in the online edition of the *American Naturalist*). Parameters are as follows: $N = 500$, $\sigma_m = 0.15$, $\sigma_p = \sigma_q = 0.2$, $\eta = 25.0$, $L = 2$, $\mu = 0.025$, $\sigma_v = 0.05$, and $\sigma_s \to \infty$ (no viability selection on male trait). Individual-based simulations lasted for 3,000 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.

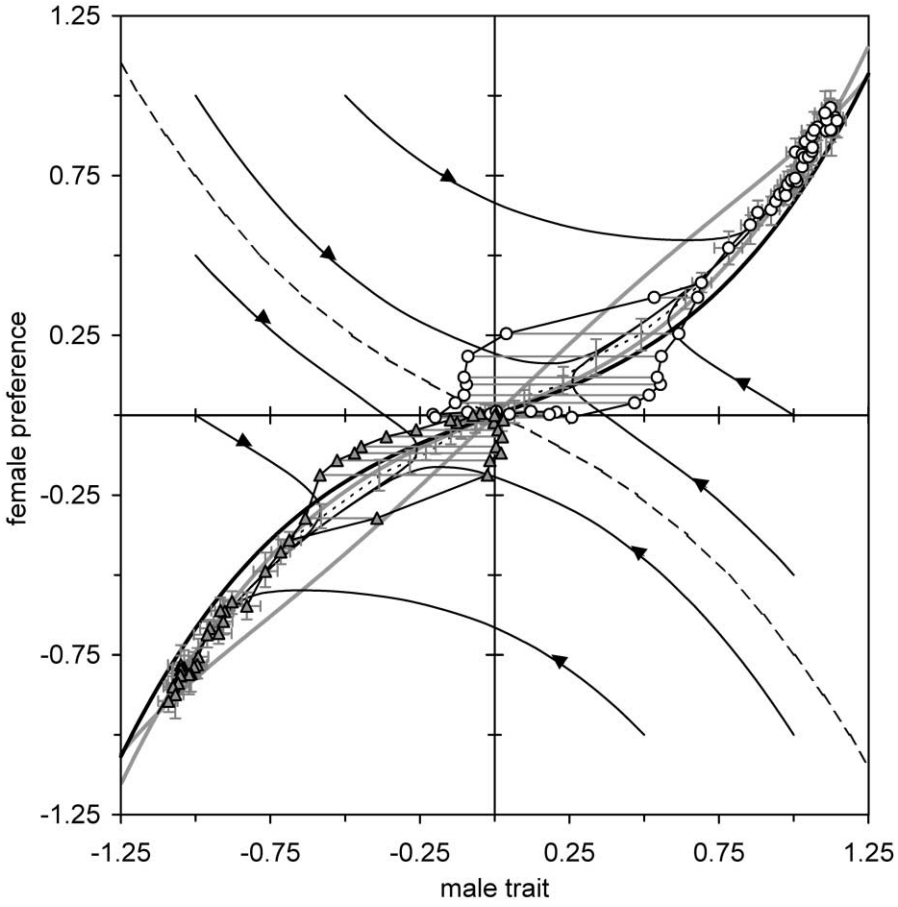

Figure 2: Disruptive sexual selection but no speciation. Two replicate individual-based simulations (*open circles* and *filled triangles*) were started from the initial conditions $p_0 = q_0 = 0$, that is, exactly at the point where sexual selection is disruptive. The simulations do not show speciation but evolution toward one of two possible endpoints. In the starting phase 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. Gray error bars indicate within-population variation of preference and trait (not, as in fig. 1, variation between replicate runs). Other lines in this graph represent the female choice function (*thick black line*), null isoclines (*thick gray lines*) for the rate of change of trait and preference according to the adaptive dynamics approximation (see appendix in the online edition of the *American Naturalist*), 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 are as follows: $N = 1{,}000$, $\sigma_m = 0.15$, $\sigma_p = \sigma_q = 0.3$, $\eta = 25.0$, $L = 1$, $\mu = 0.0125$, $\sigma_v = 0.01$, and $\sigma_s = 1.0$. Individual-based simulations lasted for 10,000 generations, with data plotted every 200 generations. For details about the nonlinear female choice function, see appendix.

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 $p_0 = q_0 = 0$, that is, exactly at the point where sexual selection is disruptive. Nevertheless, the two simulations show no speciation but evolution toward either one of the two possible stable endpoints of evolution. For some parameter conditions, a polymorphic transient (as in fig. 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 (fig. 2, *dashed curve*) 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 female preference are fun-

damentally 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, in contrast, varies with the strategies of other males because 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), at least when the underlying genetics are not governed by strong constraints (as, for example, in the case of overdominance). 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. Because of 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. 2004), as formulated by the theory of adaptive dynamics. The underlying male trait fitness landscape, calculated in analogy to the female preference fitness landscape, 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 because 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 preference is frequency independent, three interrelated problems arise, all potentially preventing speciation. First, 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 are directional everywhere else. Second, a population tends to evolve away from the area in which selection is disruptive. Finally, 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 problems 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 because of the lack of stabilizing forces, the two resulting daughter species can coexist only 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 because 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 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 with the more realistic assumption that 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

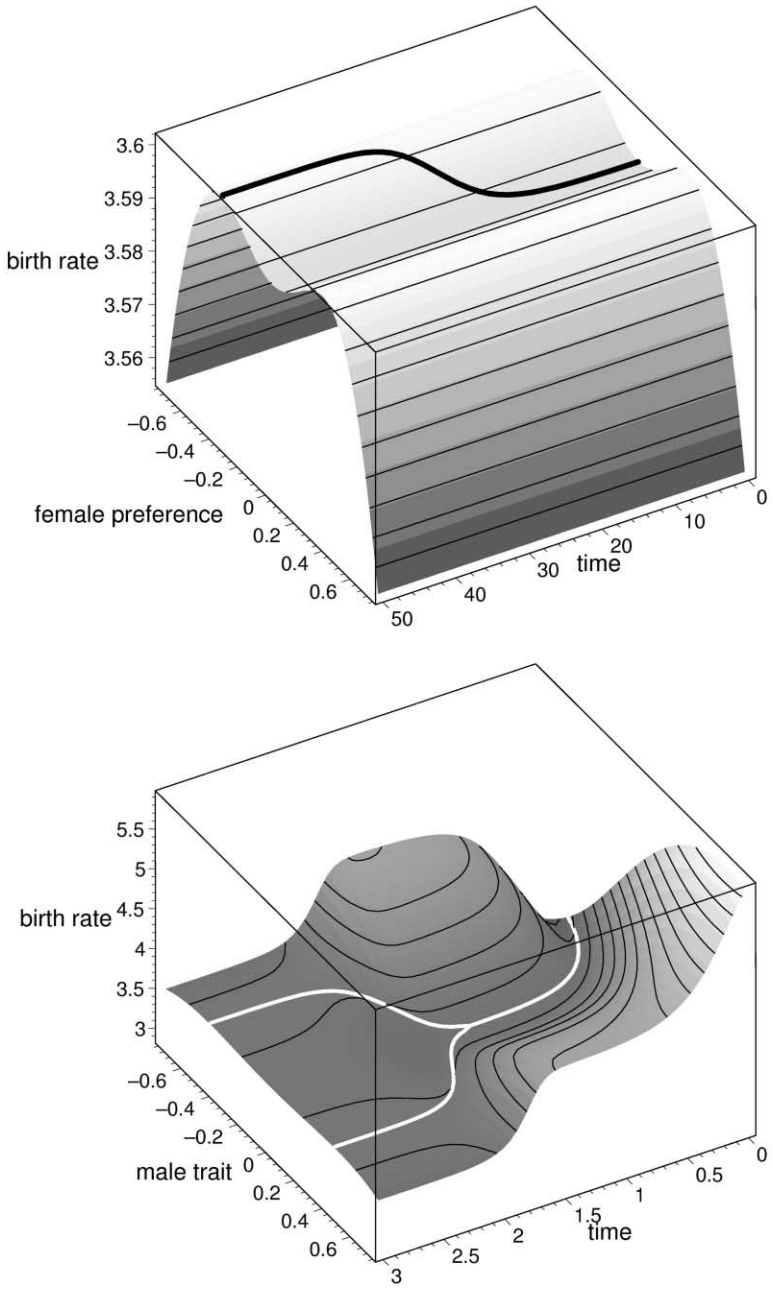

Figure 3: Differences between frequency-independent and frequency-dependent selection. The adaptive dynamics approximation was used to calculate an evolutionary trajectory of female preference (*upper panel*, *thick black curve*). For this illustration, a fixed dimorphism of male trait was considered, 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.

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 these 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 offer only 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). 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 (fig. 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 and Doebeli

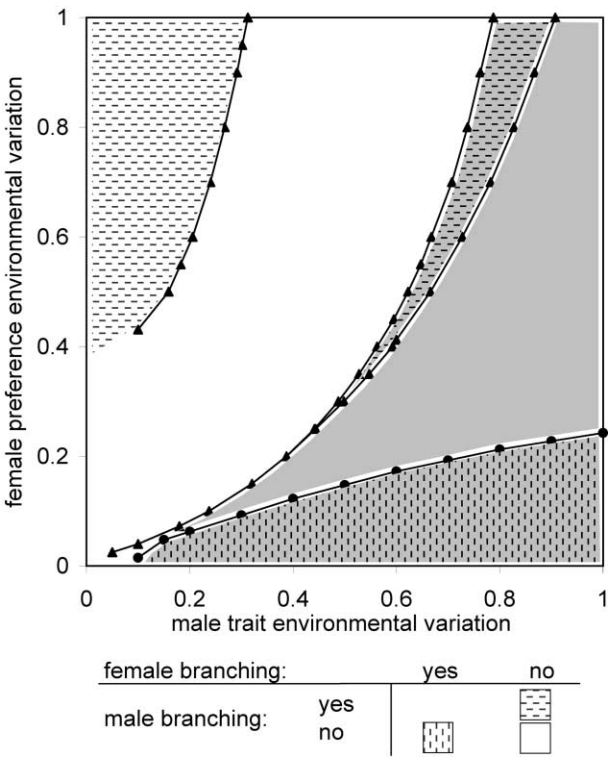

Figure 4: Impossibility of simultaneous evolutionary branching. Male branching occurs when the (environmental) variation in female preference (σ_p) is large relative to the (environmental) variation in male trait (σ_q). By contrast, female primary branching occurs in the opposite corner of parameter space. The picture is slightly complicated 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 eq. [A10] in the appendix in the online edition of the *American Naturalist*). In the white region, monomorphic evolution leads to an equilibrium at which female preference for costly male traits gets 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 because 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.

1999). This highlights a structural similarity between selection pressures acting on ecological characters and those acting on sexual traits (van Doorn and 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 (fig. 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 because those females are hardly competed for in a monomorphic male population (van Doorn and 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. Because there is no reproductive isolation without a polymorphism evolving in both female preference and male trait, speciation does not occur.

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 for 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).

Male-Male Competition Provides Additional Disruptive Selection

The results 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 be accomplished only 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 toward 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 toward rare male color morphs and that these rare morphs are therefore favored in male-male competition (P. D. Dijkstra and T. J. J. Groothuis, unpublished manuscript).

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. The intensity of competition, f_{ij}, between two males i and j is taken to be dependent on the difference between their trait values,

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

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 with identical males only 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

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

When this total strength exceeds a threshold value θ, the male loses his territory. However, if $\bar{f}_i$ falls below the threshold, a male is allowed to establish a territory if he does not already possess one. Throughout the rest of this article, 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

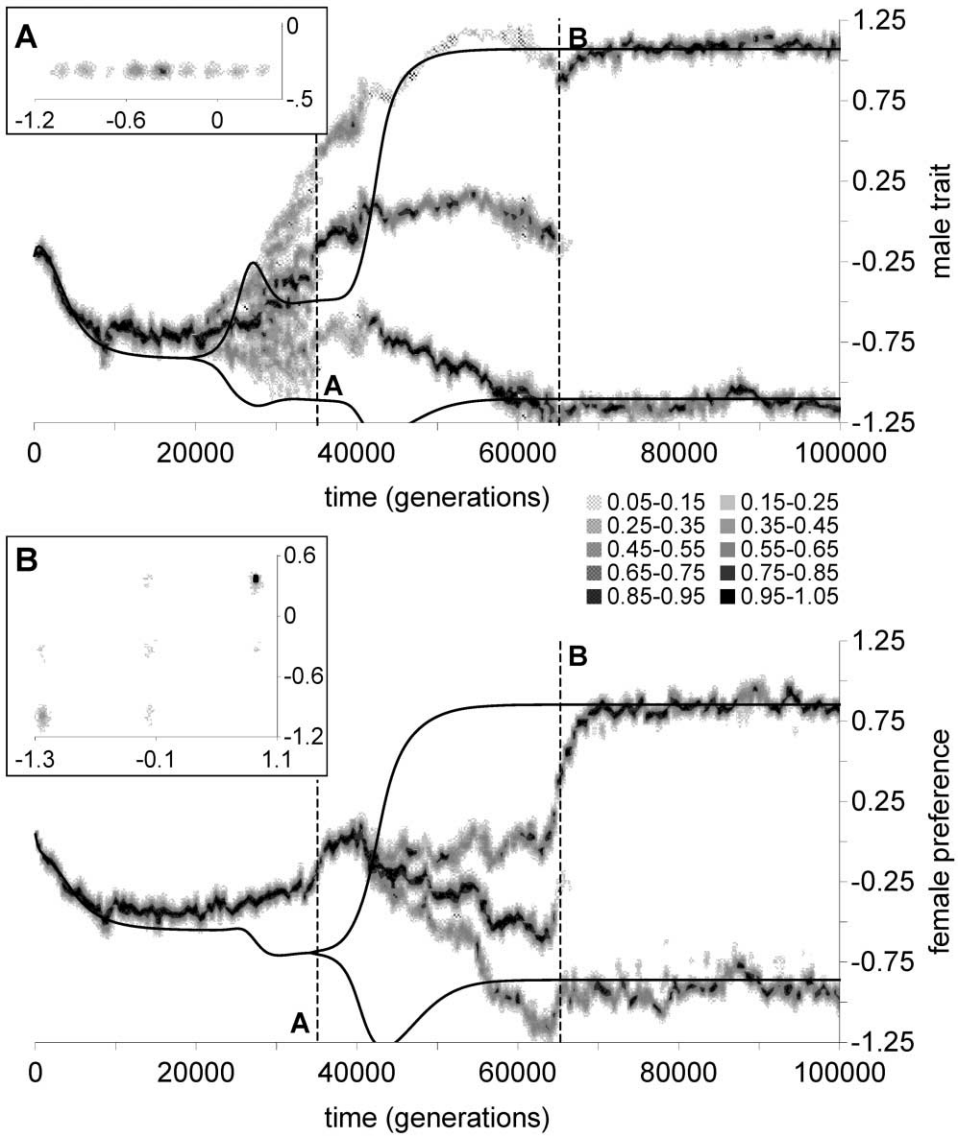

Figure 5: Sympatric speciation. Two plots show the relative frequency distributions of male trait and female preference genotypes (indicated on a gray scale) in a population with $N = 1{,}000$ in which both trait and preference are based on four diploid loci, $L = 4$. The thin black curves represent 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 $\sigma_c = 1$.

generated by male-male competition may indeed result in sympatric speciation. The figure shows a complicated sequence of events that eventually result in speciation: over the first 10,000 generations, females evolve preferences for costly male traits, after which a polymorphism of male trait arises ($t = 20{,}000$–$35{,}000$ generations). Each of the four loci coding for the male trait undergoes evolutionary branching, transiently giving rise to nine genotypic clusters (fig. 5, *inset A*). Triggered by a sudden change of female preference around that time, the polymorphism in the 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 figure 5 (*inset B*). Full-linkage disequilibrium then evolves quickly, and as a consequence, the heterozygotes (fig. 5, *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 multilocus simulation represented in figure 5, there is good agreement between simulation and the corresponding adaptive dynamics approximation (appendix; also shown in fig. 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 observations 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 ($\mu = 1.25 \times 10^{-2}$, as a result of limitations on computer time). Simulations with a more realistic mutation rate ($\mu = 1 \times 10^{-5}$) 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 explore further the parameter space of our model. Figure 6 shows that the parameter space is subdivided in two regions. In the first region (fig. 6, *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 2,000 generations in fig. 5). In the second region (fig. 6, *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.

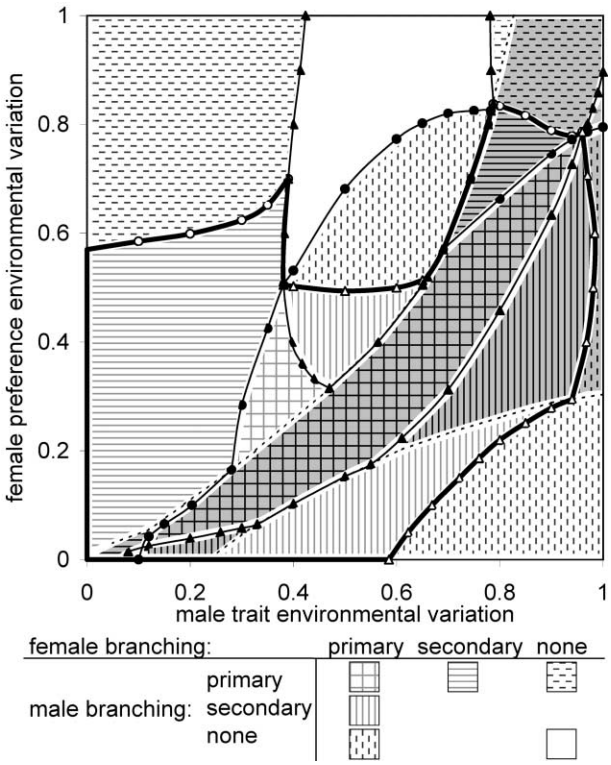

Figure 6: Possible outcomes of female-female and male-male competition. In comparison with figure 4, additional disruptive selection on the male trait has enlarged the regions in parameter space in which male and female branching occur, now allowing for sympatric speciation in the region delimited by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

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 and 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 toward a stable equilibrium at which females show preference for costly male traits, and 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 (figs. 4, 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 (fig. 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. 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. As a consequence, the emergence and maintenance of a polymorphism in female mating preferences by frequency-dependent disruptive selection on female choice is precluded. Even when one is willing to accept that nonselective 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) 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 this article, 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 generate disruptive selection on female preference only 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); 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 nonoverlapping conditions for male trait and female preference branching, truly adaptive (i.e., selection-driven) sympatric speciation requires some additional and independent form of disruptive selection. Direct competition among 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 without requiring a dependence on high mutation rates or external events. We have shown that this conclusion applies for a range of model parameters even if 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 pro-

cesses involved. 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 because 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 (appendix). 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 and 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 because mating is assumed to be costly for females but advantageous for males. As a consequence, the male mating character evolves optimally to 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 and result in sympatric speciation. Gavrilets and Waxman (2002) observed speciation while assuming unlimited availability of males and without introducing additional processes to generate frequency dependence, an observation that, at first sight, would appear to contradict our conclusions. However, Gavrilets and Waxman (2002) 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. Because of 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 becomes implicitly frequency dependent. We emphasize that interactions with genetically polymorphic populations result in frequency-dependent selection but not necessarily frequency-dependent disruptive selection. In Gavrilets and Waxman's (2002) model, however, selection is disruptive because of 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, as a result of sexual conflict, rare female mating characters are favored. Whereas our model focused on mechanisms influencing the availability of potential partners, the model of Gavrilets and Waxman (2002) also illustrates that mechanisms influencing the density of potential partners can generate the required frequency-dependent disruptive selection on female mating characters.

The second model (Almeida and 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 analyzes 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 because 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 (2003) 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 as a result of limited male availability. In the model of Almeida and Vistulo de Abreu (2003), there is indirect competition within both sexes because of 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 and Weissing 2001) integrates sexual selection with the ecological approach to sympatric speciation and, as such, builds on classical (Felsenstein 1981) and recent models (Dieckmann and Doebeli 1999) of ecological speciation. The model does not deviate from the typical sex role assumption, and, as in this article, 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 that determine an individual's success in competing for ecological resources and, through processes such as habitat choice, also pleiotropically affect mating rates. On this basis, van Doorn and Weissing (2001) show that sympatric speciation can be initiated by the simultaneous and mutually dependent diversification of mating characters and ecological characters. This option exists only when the pleiotropic interaction between ecological characters and mating rates is sufficiently strong. In light of the conclusions of this 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, as a result of 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 and Doebeli 1999; van Doorn and Weissing 2001) exhibit sympatric speciation not so much through sexual selection as merely involving sexual selection because 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 nonrandom 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), in practice it does not conflict with our conclusion that as a general rule, mate choice alone is insufficient to support sympatric speciation. In fact, sympatric speciation models based on divergent Fisherian runaway processes (Higashi et al. 1999; Takimoto et al. 2000) and also the simulations presented in this article (fig. 2) illustrate that the indirect frequency-dependent selection on female preference generated by its genetic covariance with the male mating trait is typically too weak to support stable coexistence of the daughter species. This conclusion is confirmed by an analysis of an extended version of the adaptive dynamics approximation, which takes into account genetic covariances. This analysis reveals that the establishment of linkage disequilibrium between female preference and male trait will not qualitatively affect the outcome either 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 be expected only 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 and 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.

In conclusion, we have shown that sympatric speciation driven by sexual selection is feasible. However, this does not imply that adaptive speciation by sexual selection 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, because 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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Literature Cited

Almeida, C. R., and F. Vistulo de Abreu. 2003. Dynamical instabilities lead to sympatric speciation. Evolutionary Ecology Research 5:739–757.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, N.J.

Bakker, T. C. M. 1990. Genetic variation in female mating preference. Netherlands Journal of Zoology 40:617–642.

Bulmer, M. 1989. Structural instability of models of sexual selection. Theoretical Population Biology 35:195–206.

Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. Nature 400:354–357.

Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. Journal of Mathematical Biology 34:579–612.

Dieckmann, U., M. Doebeli, J. A. J. Metz, and D. Tautz, eds. 2004. Adaptive speciation. Cambridge University Press, Cambridge.

Doebeli, M., and U. Dieckmann. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. American Naturalist 156(suppl.):S77–S101.

Eberhard, W. G. 1985. Sexual selection and animal genitalia. Harvard University Press, Cambridge, Mass.

Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? Evolution 35: 124–138.

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon, Oxford.

Gavrilets, S., and D. Waxman. 2002. Sympatric speciation by sexual conflict. Proceedings of the National Academy of Sciences of the USA 99:10533–10538.

Geritz, S. A. H., É. Kisdi, G. Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology 12:35–57.

Geritz, S. A. H., M. Gyllenberg, F. J. A. Jacobs, and K. Parvinen. 2002. Invasion dynamics and attractor inheritance. Journal of Mathematical Biology 44:548–560.

Higashi, M., G. Takimoto, and N. Yamamura. 1999. Sympatric speciation by sexual selection. Nature 402:523–526.

Johnson, P. A., and U. Gullberg. 1998. Theory and models of sympatric speciation. Pages 79–89 *in* D. J. Howard and S. H. Berlocher, eds. Endless forms. Oxford University Press, Oxford.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female preferences. Evolution 36:1–12.

———. 1987. Sexual selection by female choice in polygynous animals. Annual Review of Ecology and Systematics 18:43–70.

Lande, R. 1976. Natural selection and random drift in phenotypic evolution. Evolution 30:314–334.

———. 1981. Models of speciation by sexual selection on polygenic traits. Proceedings of the National Academy of Sciences of the USA 78:3721–3725.

Lande, R., O. Seehausen, and J. J. M. van Alphen. 2001. Mechanisms of rapid sympatric speciation by sex reversal and sexual selection in cichlid fish. Genetica 112–113:435–443.

Leimar, O. 2001. Evolutionary change and Darwinian demons. Selection 2:65–72.

Meszéna, G., and J. A. J. Metz. In press. The role of effective environmental dimensionality. *In* U. Dieckmann and J. A. J. Metz, eds. Elements of adaptive dynamics. Cambridge University Press.

Metz, J. A. J., S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs, and J. S. van Heerwaarden. 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. Pages 147–194 *in* S. J. van Strien and S. M. Verduyn Lunel, eds. Stochastic and spatial structures of dynamical systems. Elsevier/North-Holland, Amsterdam.

Panhuis, T. M., R. Butlin, M. Zuk, and T. Tregenza. 2001. Sexual selection and speciation. Trends in Ecology & Evolution 16:364–371.

Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1992. Numerical recipes in C. 2d ed. Cambridge University Press, Cambridge.

Schluter, D. 2001. Ecology and the origin of species. Trends in Ecology & Evolution 16:372–380.

Seehausen, O., J. J. M. van Alphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277:1808–1811.

Swanson, W. J., and V. D. Vacquier. 1998. Concerted evolution in an egg receptor for a rapidly evolving abalone sperm protein. Science 281:710–712.

Takimoto, G. 2002. Polygenic inheritance is not necessary for sympatric speciation by sexual selection. Population Ecology 44:87–91.

Takimoto, G., M. Higashi, and N. Yamamura. 2000. A deterministic genetic model for sympatric speciation by sexual selection. Evolution 54:1870–1881.

Vacquier, V. D. 1998. Evolution of gamete recognition proteins. Science 281:1995–1998.

van Doorn, G. S., and F. J. Weissing. 2001. Ecological versus sexual selection models of sympatric speciation: a synthesis. Selection 2:17–40.

van Doorn, G. S., A. J. Noest, and P. Hogeweg. 1998. Sympatric speciation and extinction driven by environment dependent sexual selection. Proceedings of the Royal Society of London B 265:1915–1919.

van Doorn, G. S., P. C. Luttikhuizen, and F. J. Weissing. 2001. Sexual selection at the protein level drives the extraordinary divergence of sex-related genes during sympatric speciation. Proceedings of the Royal Society of London B 268:2155–2161.

Verkiel, H. 2002. Male-male competition and sympatric speciation. M.S. thesis. University of Groningen.

Weissing, F. J. 1996. Genetic versus phenotypic models of selection: can genetics be neglected in a long-term perspective? Journal of Mathematical Biology 34:533–555.

Wilson, A. B., K. Noack-Kunnmann, and A. Meyer. 2000. Incipient speciation in sympatric Nicaraguan crater lake fishes: sexual selection versus ecological diversification. Proceedings of the Royal Society of London B 267:2133–2141.

Wu, C.-I. 1985. A stochastic simulation study on speciation by sexual selection. Evolution 39:66–82.

Wyckoff, G. J., W. Wang, and C.-I. Wu. 2000. Rapid evolution of male reproductive genes in the descent of man. Nature 403:304–309.

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