Coevolution of male and female mate choice can hamper speciation

Thomas G. Aubier[1,2,*], Hanna Kokko[3] & Mathieu Joron[1,*]

1. Centre d'Ecologie Fonctionnelle et Evolutive, CEFE - UMR 5175 - CNRS, Université de Montpellier, EPHE, Université Paul Valéry, 1919 route de Mende, F-34293, Montpellier 5, France

2. Institut de Systématique, Evolution, Biodiversité, ISYEB - UMR 7205 - CNRS, MNHN, UPMC, EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités, 57 rue Cuvier, CP50, F-75005, Paris, France

3. Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057, Zurich, Switzerland

∗ Corresponding authors; e-mail: thomas.aubier@cefe.cnrs.fr; mathieu.joron@cefe.cnrs.fr

Abstract

Sexual interactions are diverse and play a considerable role for speciation with gene flow. In particular, when mating cues are under disruptive selection, female preference for mates from their own kind should evolve, thereby forming premating isolation between diverging taxa. Male preference during courtship has been tacitly ignored in mathematical models of speciation despite increased empirical evidence for it. In a population genetics model of speciation in which female and male choosiness can evolve independently and feedback to each other, we show that selection favouring mutual mate choice should be common. Yet, we also find that coevolution of female and male choosiness often leads to episodes during which no sex is choosy and gene flow is unrestricted. Thus, premating isolation between taxa could be more reversible than previously thought. This prediction encourages further research on the lability of isolating barriers and sheds new light on the genomics of reproductive isolation.

INTRODUCTION

Positive assortative mating – the tendency of individuals of similar phenotype to mate together more often than expected at random – is widespread in animals[1]. It contributes to premating isolation between taxa and may therefore play a key role in speciation with gene flow[2]. Positive assortative mating can arise as an automatic by-product of adaptive divergence via temporal or spatial isolation[3], but can also be driven by various behavioural processes[4,5]. Of particular interest is the case of homotypic mate preferences, where individuals express a preference for mates of their own phenotype based on cues such as colour[6–9], acoustic signal[10,11] or pheromone[12,13]. When mating cues are diverging in a population because of environmental or ecological pressures, indirect selection favouring homotypic preferences can theoretically lead to premating isolation between emerging ecotypes[14–20]. Such mating cues subject to disruptive selection and contributing to non-random mating may have favoured speciation with gene flow in many species[3,21,22].

In most mathematical models of speciation accounting for homotypic preferences[14–19], premating isolation is only caused by female mate choice. The assumption that male mate preference is unlikely to evolve rests on the so-called Darwinian sex roles in courtship[23]; in many animal species, males are typically eager to copulate (even with heterospecific females), whereas females are choosy about mates[24–29]. In accordance with Bateman's principle[30], a greater variability in mating success is often observed in males than in females[31], probably because females' mating success is not limited by mate acquisition, but instead by gamete and offspring production. Mate choice ensuring offspring quality should therefore be under stronger selection in females than in males.

Sexual dimorphism with promiscuous males and choosy females is not inevitable. Males and females do not always follow Darwinian sex roles; sexual interactions show great diversity[32]. Interspecific sexual interactions in which males are the choosy sex are also observed[28,33–36]. In yet other interspecific sexual interactions, both males and females discriminate against heterospecifics, and are therefore engaged in mutual mate choice[28,29,37,38]. Evolution of choosiness in either sex should occur when the benefits of choosiness outweigh the costs, which in turn are impacted by differences in parental investments, mate encounter rates and mate quality variation[39,40]. In cichlid fishes[41–43] and *Heliconius* butterflies[7,44–50], which are text-book examples of taxa undergoing speciation with gene flow, both males and females can display homotypic preferences based on colour. Yet, the consequences of male mate preferences for speciation remain underexplored.

Variability in the degree of reproductive isolation between incipient species has been observed[50–52]. Divergence among taxa is a continuous process that may not always lead to complete speciation[53]. Increased divergence among taxa may require the addition of several isolating dimensions, such as decreased hybrid fertility, microspatial partitioning and divergence in other ecological traits[50,51]. Stable premating isolation may be required to allow sufficient time for those additional factors to evolve. Here, we are interested in whether allowing evolution of mutual mate preferences can lead to such stable premating isolation.

We investigate the evolution of mutual mate choice and its implication for speciation by analyzing a population genetics model. Driven by the prior evolution of female homotypic preference, male homotypic preferences frequently evolves in response to indirect selection. Intriguingly, despite selection favouring mutual mate choice, the coevolution of male and female mate choice strongly increases gene flow in stochastic simulations.

MODEL OVERVIEW

We construct a three-locus diploid population genetics model of speciation in sympatry. Disruptive selection acts on an ecological locus. With random mating behaviour, hybridization between divergent ecotypes maintains gene flow and would prevent speciation. We implement two distinct homotypic preference loci that are independently expressed in females or in males, such that the ecological trait can be used as a mating cue ('one-allele mechanism'[54]). Alleles coding for choosiness (i.e., for strong homotypic preference) are recessive; choosy males and females are homozygous for the 'choosy' allele on the corresponding preference locus. Therefore, assortative mating caused either by female, male or mutual homotypic preferences can reduce gene flow between ecotypes.

At each generation, disruptive selection first occurs with strength s, such that heterezygotes at the ecological locus suffer viability costs. Males then court females and are 'visible' to females (i.e. available as potential mates) proportionally to the courtship effort that they invest. Only choosy males prefer females that match their own ecological trait. In case

of a mismatch, choosy males reduce their courtship effort to a very small fraction ϵ_{m} of what nonchoosy males would invest. Saved courtship effort can be reallocated to court preferred females more vigorously. The extent of this reallocation of courtship effort is described by the parameter α. In particular, if choosy males reallocate all saved courtship effort towards preferred females ($\alpha = 1$), they enjoy a mating advantage over nonchoosy males with these particular females. Females also express different propensities to accept 'visible' males. Only choosy females prefer males that match their own ecological trait. We assume that, in case of a mismatch, choosy females reduce the probability of mating to a very small value ϵ_{f}. The mating success of choosy and nonchoosy females is equal, contrary to the mating success of males that depends on their choosiness (polygyny scenario). Based on the resulting fractions of mating among genotypes and assuming Mendelian inheritance of all loci with no linkage, we obtain the theoretical genotype frequencies at the next generation.

We first determine numerically the deterministic behaviour of the model. We then perform stochastic simulations to account for drift affecting traits under weak selection. At each generation, following the theoretical genotype frequencies, K offspring individuals are randomly picked and each locus can mutate. The genotype frequencies in this offspring population are therefore subject to sampling errors and mutations. To account for drift, the deterministic dynamic described above is not applied on the theoretical genotype frequencies, but instead on these offspring frequencies at each generation.

DETAILED METHODS

Genotypes

In a population genetics model, we consider three autosomal diploid loci. Alternative alleles at each locus are represented by small and capital letters, respectively. An ecological locus, A, is subject to disruptive selection and can be used as a mating cue. A female preference locus, F, alters the strength of female homotypic preference (female choosiness). A male preference locus, M, alters the strength of male homotypic preference (male choosiness) during courtship. We assume that preferences vary from indiscriminate to full assortative. Since there are three genotypes per locus (e.g., AA, Aa and aa for the A locus), we track the frequencies of $3^3 = 27$ genotypes in the population.

Deterministic simulations

Assuming discrete generations, we follow the evolution of genotype frequencies $\mathbf{p}(t)$ within an infinite population over time. $\mathbf{p} = \{p_i\}$ is a vector consisting of 27 elements $\{p_1, p_2, ..., p_{27}\}$ and refers to the frequencies of the 27 genotypes present in newborn offspring. The life cycle is as follow:

(1) Natural selection

We assume that heterozygotes Aa suffer a viability cost with parameter s representing the strength of disruptive selection on locus A. The two homozygotes AA and aa occupy niches that are assumed to occur equally abundantly in the environment, such that neither allele will outcompete the other based on ecological competition. Parameter s' quantifies the extent of such niche partitioning (if $s' = 0$, one allele can outcompete the other; 'gene swamping'[55]). Following these assumptions, the genotype frequencies after disruptive natural selection has occurred are:

$$p_i^{\mathrm{S}} = \begin{cases} p_i \left(1 + s' \left(0.5 - \frac{\sum\limits_{k \in \mathrm{aa}} p_k}{\sum\limits_{k \in \mathrm{aa} \cup \mathrm{AA}} p_k}\right)\right), & \text{if } i \in \mathrm{aa} \\ p_i \left(1 + s' \left(0.5 - \frac{\sum\limits_{k \in \mathrm{AA}} p_k}{\sum\limits_{k \in \mathrm{aa} \cup \mathrm{AA}} p_k}\right)\right), & \text{if } i \in \mathrm{AA} \\ p_i \left(1 - s\right), & \text{if } i \in \mathrm{Aa} \end{cases} \tag{1}$$

We normalize the elements of $\mathbf{p}^{\mathrm{S}} = \{p_i^{\mathrm{S}}\}$, such that the sum of the vector equals unity.

(2) Male choice and courtship

$P_{m,f}^{\text{♂}}$ denotes the courtship effort of a male with genotype m towards females with genotype f (m and $f \in \{1, 2, .., 27\}$). We assume that males with genotypes mm or Mm at the locus M are nonchoosy and court all females with the same intensity ($P_{m,f}^{\text{♂}} = 1$ towards all females). Only homozygous MM males are choosy (i.e., they express homotypic preferences). They exhibit courtship that depends on the match between the ecological trait (locus A) of the female and their own. In case of a mismatch (e.g., between a male with genotype AA and a female with genotype Aa or aa), choosy males reduce their courtship effort to a small fraction $P_{m,f}^{\text{♂}} = \epsilon_{\mathrm{m}} << 1$ of what nonchoosy males would invest. In other words, choosy males reduce resource use (e.g., time or energy) to court unpreferred females. Saved courtship effort can be reallocated (partially, totally, or not at all) to court preferred females matching their ecological trait more vigorously. The extent of this reallocation of courtship effort is described by the parameter α. Overall, of all possible courtship that could happen in the population, a fraction $C_{m,f}$ will occur between males of genotype m and females of genotype f:

$$C_{m,f} = p_m^{\mathrm{S}}\, p_f^{\mathrm{S}} \overbrace{\left(\overbrace{P_{m,f}^{\text{♂}}}^{\substack{\text{Baseline courtship effort of} \\ \text{a male of genotype } m \text{ towards} \\ \text{a female of genotype } f}} + \overbrace{\alpha \left(1 - \sum_{f'} p_{f'}^{\mathrm{S}} P_{m,f'}^{\text{♂}}\right)}^{\substack{\text{Courtship effort that} \\ \text{a male of genotype } m \\ \text{reallocates}}} \times \overbrace{\frac{P_{m,f}^{\text{♂}}}{\sum\limits_{f'} p_{f'}^{\mathrm{S}} P_{m,f'}^{\text{♂}}}}^{\substack{\text{Proportion of courtship effort that} \\ \text{a male of genotype } m \text{ reallocates} \\ \text{towards a female of genotype } f}} \right)}^{\text{Total courtship effort of a male of genotype } m \text{ towards a female of genotype } f} \tag{2}$$

where p_m^{S} and p_f^{S} are the frequencies of males of genotype m and females of genotype f after natural selection has occurred. If $\alpha \neq 1$, all possible courtship effort is not necessarily allocated ($\sum\limits_m \sum\limits_f C_{m,f} < 1$) and all males do not have equal overall courtship effort ($\sum\limits_f C_{m,f} \neq p_m^{\mathrm{S}}$).

If $\alpha = 0$, choosy males cannot reallocate saved courtship effort towards preferred (matching) females. If $\alpha = 1$, all saved courtship effort can be redirected towards preferred females, making males enjoy a mating advantage over their competitors with these particular females. This is modulated by the propensity of females to accept these matings (see below).

(3) Female choice and mating

We assume that males are 'visible' to females (i.e. available as potential mates) proportionally to the courtship effort that they invest. The baseline mating rate with males is therefore proportional to their courtship effort but can then be adjusted downwards or upwards by female choice. $P_{f,m}^{\text{♀}}$ denotes the willingness of a female with genotype f to mate with

courting males with genotype m. Females with genotype ff or Ff at the locus F mate indiscriminately ($P^{♀}_{f,m} = 1$ with all males), leading to mating rates that are directly proportional to courtship. Only homozygous FF females are choosy (i.e., they express homotypic preferences). Their decision to mate depends on the match between the ecological trait of the male and their own. In case of a mismatch, choosy females reduce the occurrence of mating to a small fraction $P^{♀}_{f,m} = \epsilon_{\mathrm{f}}$ of the baseline. Thus, the overall fractions of matings $F_{m,f}$ between males of genotype m and females of genotype f are:

$$F_{m,f} = \frac{C_{m,f} P^{♀}_{f,m}}{\widehat{F_f}} \tag{3}$$

with the normalization term $\widehat{F_f}$:

$$\widehat{F_f} = \sum_m C_{m,f} P^{♀}_{f,m} \ \ / \ \ p^{\mathrm{S}}_f \ \ , \quad \text{given } p^{\mathrm{S}}_f \neq 0 \tag{4}$$

$\widehat{F_f}$ ensures that all females, even the ones that are less preferred by males, are mating. Likewise, the mating success of females with and without a preference is equal ($\sum_m F_{m,f} = p^{\mathrm{S}}_f$). This assumption that all females have the same mating success is realistic for a polygynous mating system, but note that relaxing this assumption by implementing a cost of female choosiness ($\sum_m F_{m,f} < p^{\mathrm{S}}_f$ for $f \in$ FF) does not change our results (Appendix C).

(4) Recombination

From the overall fractions of mating $F_{m,f}$, we can calculate the theoretical genotype frequencies $\mathbf{p}(t+1)$ in the next generation, assuming Mendelian inheritance of all loci with no linkage. Zygote production follows recombination by summing the appropriate elements of the matrix $\mathbf{F}$, determining the frequencies of all possible progeny genotypes after recombination and segregation.

Stochastic simulations

Based on the above deterministic system, we also perform stochastic simulations to account for drift on traits that are under weak selection. At each generation, we pick randomly K offspring individuals from the theoretical genotype frequencies $\mathbf{p}(t)$, to form a new vector $\mathbf{p}(t)$ for which deterministic dynamics (Eq. 1 to 4) is then applied. We additionally assume that each allele of each offspring mutates to the alternative allele with probability μ.

Parameters

Unless stated otherwise, we perform simulations with strong choosiness associated to genotypes FF and MM ($\epsilon_{\mathrm{f}} = 0.01$, $\epsilon_{\mathrm{m}} = 0.01$). We also implement strong disruptive natural selection with $s = 0.2$ and $s' = 0.5$. In stochastic simulations, we model populations of appreciable size $K = 500$ with a probability of mutation $\mu = 10^{-3}$ per individual and per allele.

RESULTS

Selection gradients for female and male choosiness

We first quantify the change in frequencies of choosy females and choosy males over 3 generations, which is sufficient to account for the effects of indirect selection on frequencies but short enough so that we are not yet tracking long-term evolutionary changes. This timescale allows us to describe how female and male choosiness affect each others' selection gradients (vector fields in Fig 4).

In the model, all females have the same mating success (i.e., female choosiness incur no opportunity costs; but see Appendix C). Thus, selection on female choosiness is solely dependent on the type of offspring produced. Here female choosiness is favoured (Fig 4) because choosy females avoid producing hybrid offspring that suffer viability costs. Yet, selection favouring female choosiness becomes weak when all males are choosy. As females are exclusively courted by choosy males of their own ecotype, even nonchoosy females produce few hybrid offspring. Nonchoosy females may therefore easily persist by chance; female choosiness may drift.

Male choosiness is not always favoured. Contrary to females, the mating success of males depends on their choosiness. Here choosiness brings about an opportunity cost, since choosy males lose mating opportunities with those females that they choose not to court. If choosy males do not reallocate courship effort to court preferred females, male choosiness is deleterious ($\alpha = 0$, Fig. 4a). On the other hand, if choosy males reallocate all courtship effort to court preferred females, male choosiness is favoured ($\alpha = 1$, Fig. 4e). In that case, the increased chances to mate with females of the same ecotype overcome the cost of missed mating opportunities with females who would have offered inferior fitness prospects (with respect to the viability of offspring produced).

With partial reallocation of courtship effort ($\alpha \in]0, 1[$, Fig. 4b, c and d), male choosiness is favoured when the frequency of choosy females is high enough. When females are choosy, neither choosy nor nonchoosy males mate with females from the other ecotype (they are rejected upon courtship), but only the choosy ones enjoy the benefit of having saved some of their courtship effort for pursuing within-ecotype matings ($\alpha > 0$). This creates a net benefit that favours choosy males, changing the direction of selection on male choosiness. More details about the sensitivity of the selection gradient for male choosiness to other parameters are available in Appendix A.

Deterministic outcome: selection favouring mutual mate choice is common

In deterministic simulations, the equilibrium frequency of choosy females is 1. As explained above, when females are choosy, selection also favours male choosiness. As a result, the equilibrium frequency of choosy males is 1 even if choosy males reallocate only little of their courtship effort towards preferred females (for $\alpha \geq 0.01$, Fig. 1). Female and male choosiness synergistically reduce hybridization between ecotypes (Fig. 2) because we assume that choosy individuals do not completely avoid courting/mating across ecotype boundaries ($\epsilon_{\mathrm{m}} \neq 0$ and $\epsilon_{\mathrm{f}} \neq 0$). Therefore, even if choosy males reallocate little courtship effort towards preferred females, mutual mate choice is a stable equilibrium, reducing gene flow.

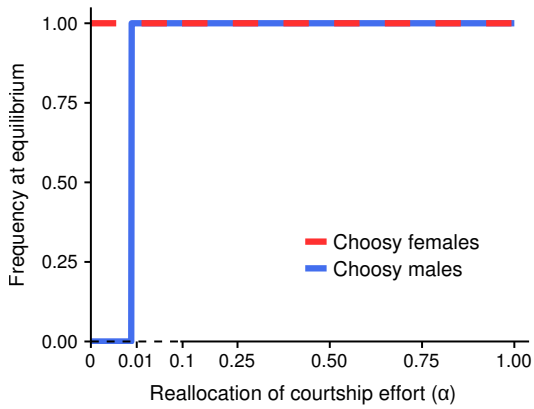

Figure 1: Frequencies of choosy females and males at deterministic equilibrium. Mutual mate choice evolves even if choosy males reallocate little courtship effort towards preferred females ($\alpha \geq 0.01$).

Stochastic simulations: coevolution of male and female mate choice increases gene flow

The regime of choosiness can evolve away from mutual mate choice. – We next implement drift in populations of appreciable size ($K = 500$). To describe the evolutionary dynamics of female and male choosiness, we define a frequency treshold ($= 0.85$) above which female or male populations are considered to be mainly choosy. We thereby characterize four regimes of choosiness: female choice only ($\mathcal{F}$), male choice only ($\mathcal{M}$), mutual choice ($\mathcal{MF}$) and partial choice (i.e., both female and male populations are only partly choosy, $\mathcal{P}$) (Fig. 2). For $\alpha > 0.01$, our deterministic analysis predicts mutual mate choice to be a stable equilibrium, yet when accounting for the effects of drift, preference traits can evolve away from this equilibrium (Fig. 3). Over evolutionary time, assortative mating is often driven by male choosiness only (regime $\mathcal{M}$). Assortative mating can also decay when both female and male populations are partly choosy (regime $\mathcal{P}$).

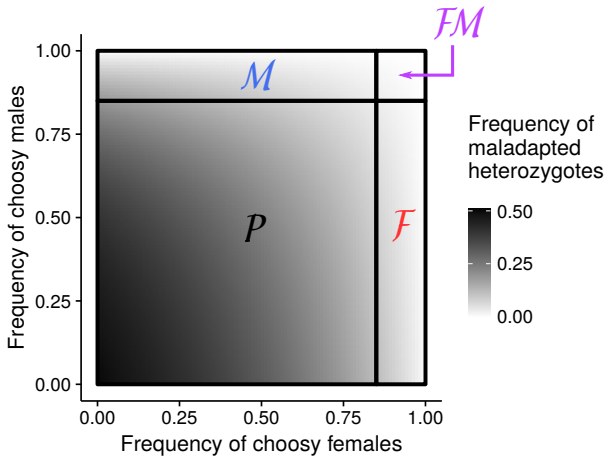

Figure 2: Deterministic frequencies of maladapted heterozygotes at the ecological locus (inversely proportional to gene flow) in populations with given frequencies of choosy females and males. We arbitrarily define four regimes of choosiness: mutual mate choice ($\mathcal{MF}$), male mate choice ($\mathcal{M}$), female mate choice ($\mathcal{F}$) and partial mate choice (i.e., female and male populations are only partly choosy, $\mathcal{P}$).

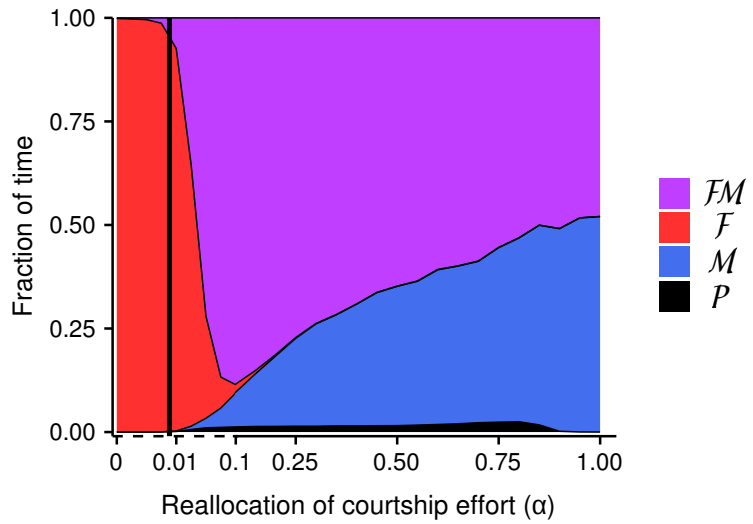

Figure 3: Fraction of time spent in each regime of choosiness in stochastic simulations ($K = 500$). The vertical line corresponds to the treshold above which mutual mate choice is the deterministic equilibrium (see Fig. 1). Assortative mating is often driven by male choosiness only (regime $\mathcal{M}$) despite selection favouring mutual mate choice ($\alpha > 0.01$). Moreover, for partial reallocation of courtship effort ($\alpha \in [0.01, 0.9]$), female and male populations are partly choosy (regime $\mathcal{P}$) for significant time periods.

Despite selection favouring mutual mate choice, assortative mating is often driven by male choosiness only (regime $\mathcal{M}$). When females are choosy, male choosiness is strongly favoured with little influence of drift. However, when males are choosy, selection favouring female choosiness is weak; the frequency of choosy females may decrease by drift (see simulations in Fig. 4). Despite selection favouring mutual mate choice, nonchoosy females can persist for significant time periods, during which assortative mating is mainly driven by male choosiness only (regime $\mathcal{M}$) (Fig. 3).

Female and male populations are rarely simultaneously partly choosy (regime $\mathcal{P}$) (Fig. 3). When $\alpha < 0.01$, selection favouring female choosiness is strong enough to keep female choosiness at high frequency, and the same applies for male choosiness when $\alpha > 0.9$. However, in simulations with intermediate α values, female and male populations are partly choosy (regime $\mathcal{P}$) for significant time periods. This is caused by the coevolutionary dynamics of female and male choosiness. As male choosiness is favoured only when the frequency of choosy females is high (selection gradients in Fig. 4b, c and d), drift on female choosiness changes the direction of selection on male choosiness, which can then lead to a regime of partial choosiness (regime $\mathcal{P}$). Although this predicts a return to mutual mate choice (i.e. regime $\mathcal{P}$ is only transient), the process takes time, and an observed outcome at a particular point in time features large fractions of both females and males being nonchoosy (regime $\mathcal{P}$) (simulations in Fig. 4b, c and d). Hereafter, 'preference cycling' refers to this coevolutionary dynamics of female and male choosiness.

Implementing continuous choosiness traits (Appendix B) and relaxing the hypothesis of polygyny (Appendix C) do not qualitatively change our results.

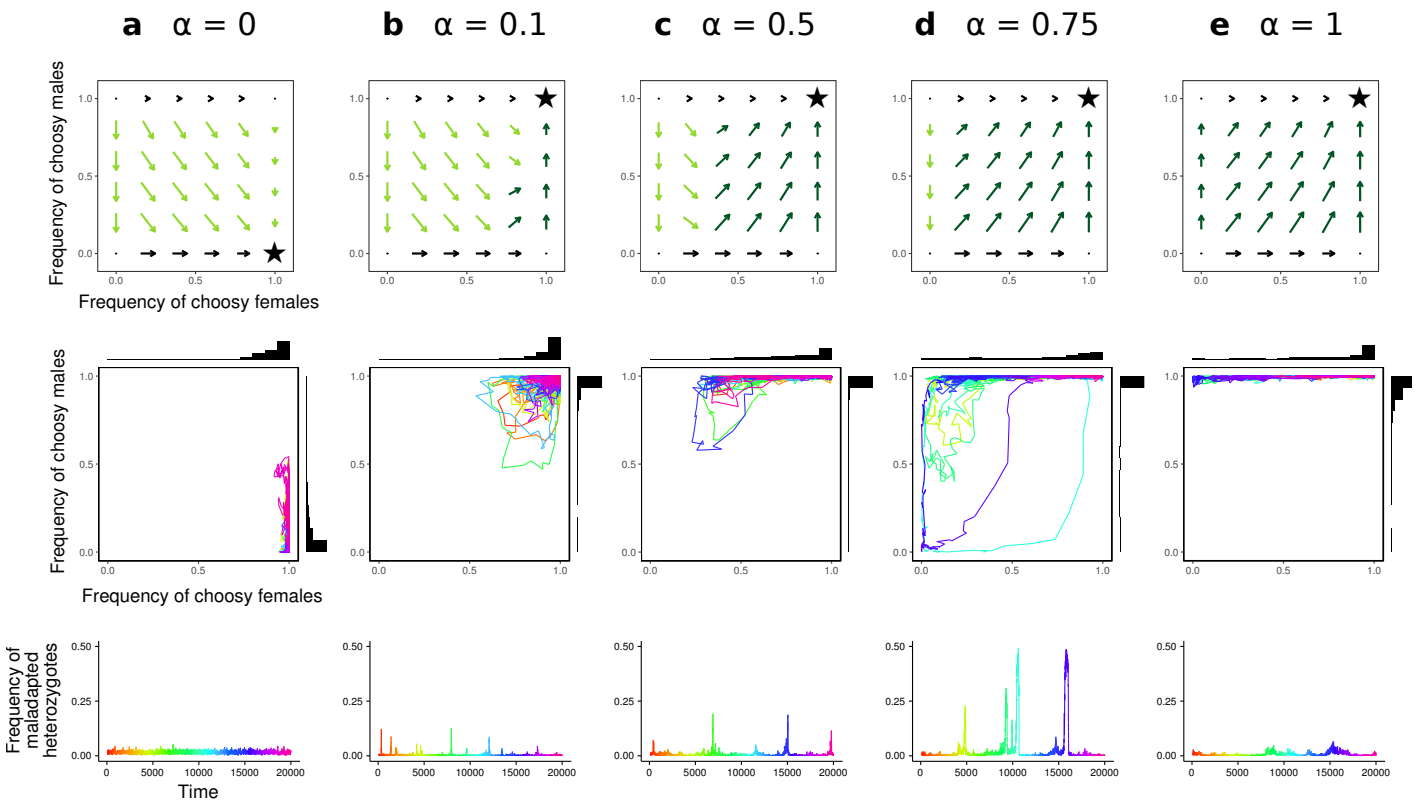

Figure 4: Selection gradients for female and male choosiness and stochastic simulations ($K = 500$) with different α values. From top to bottom, we represent the deterministic selection gradients for female and male choosiness, the evolutionary dynamics of choosiness and the resulting frequencies of maladapted heterozygotes at the ecological locus (from the same simulations). The selection gradients for choosiness correspond to the relative change in frequencies of choosy vs. nonchoosy females and males after 3 generations (dark green arrows represent selection favouring male choosiness). To highlight weak selection on choosiness, we use a logarithmic scale to draw arrow vectors. Stars corresponds to the regimes of choosiness at deterministic equilibrium. In the bottom graphs, stochastic simulations are runned, and rainbow colour gradients correspond to the passage of time. In stochastic simulations, the frequencies of choosy females and choosy males do not converge to the deterministic equilibrium.

Consequences for gene flow. – When assortative mating is driven by male choosiness only (regime $\mathcal{M}$) because of drift on female choosiness, gene flow is higher than with mutual mate choice (blue area in Fig. 5d). If choosy males reallocate all courtship effort to court preferred females ($\alpha = 1$), there is no preference cycling (Fig. 5a); populations may drift in regime $\mathcal{M}$ for a long time (Fig. 3), increasing gene flow (Fig. 5d).

If choosy males partially reallocate courtship effort (intermediate $\alpha \in [0.01, 0.9]$), preference cycling also increases gene flow (black area in Fig. 5d). The coevolutionary dynamics underlying preference cycling greatly depends on how much courtship effort can be reallocated by choosy males (e.g., Fig. 4b vs. 4d). Overall, preference cycling strongly increases gene flow among ecotypes in simulations with $\alpha \simeq 0.75$ (Fig. 5d). For $\alpha \simeq 0.75$, preference cycling is rare (Fig. 5a). However, it associates with a long duration into regime $\mathcal{P}$ (Fig. 5b) during which gene flow is especially high (i.e., both female and male choosiness reach low frequencies) (Fig. 5c).

Drift into regime $\mathcal{M}$ and preference cycling strongly increase gene flow in a context of weak disruptive selection (low s, Fig. S7) and in small populations (low K, Fig. S6) – i.e., if selection favouring female choosiness is too weak to oppose genetic drift. Because of the coevolutionary dynamics of female and male choosiness, highly accurately expressed choosiness are weakly favoured by selection and have the counterintuitive effect of increasing gene flow (low ϵ_{m} and ϵ_{f}, Fig. S8).

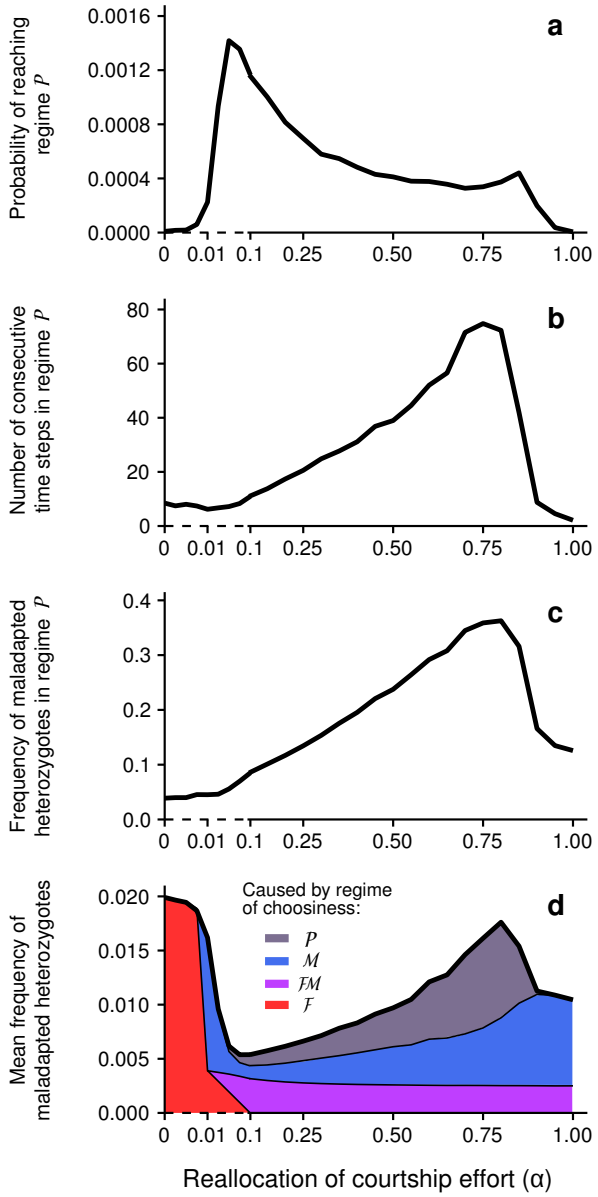

Figure 5: Coevolutionary dynamics of choosiness and resulting gene flow in stochastic simulations ($K = 500$). To describe the coevolutionary dynamics of female and male choosiness, we record the probability of reaching regime $\mathcal{P}$ (a), the number of consecutive time steps in regime $\mathcal{P}$ (b) and the frequency of maladapted heterozygotes in regime $\mathcal{P}$ (c). To assess the resulting gene flow, we record the mean frequency of maladapted heterozygotes over evolutionary time (d). In subfigure d, we also represent the contribution of each regime of choosiness to gene flow. In stochastic simulations, the coevolutionary dynamics of female and male choosiness increases gene flow despite selection favouring mutual mate choice ($\alpha > 0.01$).

DISCUSSION

Male mate choice is observed in cichlid fishes[41–43] and *Heliconius* butterflies[7,44–50], taxa that are undergoing speciation with gene flow. Despite these observations, the potential role of male mate choice in reproductive isolation has been tacitly ignored in the large majority of mathematical models of speciation. To our knowledge, only Servedio (2007) accounted for male mate choice in a model of speciation, showing that male choosiness can evolve if choosy males reallocate all their courtship efforts towards preferred (matching) females[56]. Our model builds on this to investigate the evolutionary dynamics of choosiness when courtship reallocation only functions partially. Our model also allows the joint evolution of female and male choosiness at the same time (choosiness in one sex is known to influence the evolution of choosiness in the other[57–60]), errors in decision-making, genetic drift and consider their outcome in term of gene flow and speciation. We show that male mate choice can evolve even if males reallocate only 1% of the courtship effort saved by not courting unpreferred females. This result comes from the importance of the female reaction to male courtship. Male choosiness is a poor courtship strategy if females are nonchoosy (it brings about opportunity costs), but saves energy and time to be used in more productive courtships if females are choosy. Selection favouring mutual mate choice should therefore be common in a context of speciation with gene flow.

Speciation is often viewed as a directional process characterized by a constant accumulation of barriers to gene flow. When comparing multiple pairs of incipient or closely related *Heliconius* species which vary in their divergence, increased divergence is associated with stronger and more numerous barriers to gene flow[46,50]. Yet, speciation can also be "undone"; barriers to gene flow can dissolve and genetic discontinuities may vanish, thereby merging two taxa into a single population by hybridization[61–63]. Premating isolation is often considered to initiate the process of divergence among taxa and its stability is therefore a key component for other barriers to evolve. For instance, only stable premating isolation leads to accumulation of genetic incompatibilities among taxa and to subsequent postzygotic isolation[64,65]. Yet, our model predicts that the coevolutionary dynamics of female and male mate preferences ('preference cycling') may lead to transient breakdown of emergent reproductive isolation, allowing temporary peaks of gene flow, despite selection favouring mutual mate choice. This occurs because selection pressures acting on female and male choice follow different rules. Female choice tends to favour male choice. On the contrary, male choice tends to relax selection on female choice; even nonchoosy females avoid getting unfit hybrids, as males focus their efforts on females of their own ecotype. The fact that choosiness in either sex can lead to reproductive isolation makes it difficult for mate choice to be maintained simultaneously in both sexes by selection; female choosiness can drift, triggering preference cycling and increasing gene flow. Overall, therefore, selection favouring mutual mate choice may even be considered to inhibit speciation because it makes premating isolation easily reversible. Besides, preference cycling among distant taxa could explain the formation of 'hybrid swarm' and subsequent genetic introgression[66] or hybrid speciation[67].

Empirical research often estimates isolating barriers between pairs of populations varying in their level of differentiation to track the 'speciation continuum'[46,50,52,68]. However, the strength of those barriers may actually fluctuate and even cycle, so empirical measures are only point measurements, which may not reflect the long-term level of gene flow among populations. In particular, given the coevolutionary dynamics of male and female mate preferences, observing premating isolation driven by mutual mate choice does not necessarily mean that gene flow is reduced over long time scale. In the same vein, if a species is partially fragmented across its range, preference cycling could cause different evolutionary

histories among populations. For instance, spatial variation in reproductive isolation in *Catostomus* fish species over a large geographic area has been documented[69,70]. Yet, variation in hybridization is rarely quantified across several natural populations and it could mislead conclusions about the overall dynamics of reproductive isolation among taxa. More studies characterizing the strength of isolating barriers at a broader spatial and temporal scale are therefore needed to assess the variability of reproductive isolation.

The coevolutionary dynamics of female and male mate preference (and resulting gene flow) depends crucially on how much courtship effort males reallocate towards preferred females, as a result of foregoing courting unpreferred females. By considering the reallocation of courtship effort (α), our model encompasses the ecological diversity in courtship and mating systems in animals. Choosy males can reallocate resources, which are required to court females (e.g., resources-demanding spermatophores[71] or nourishment gifts[72]). They can also reallocate time into searching preferred females or into improving the quality of the courtship display (e.g., complex courtship display[73,74]) (except if courting males can broadcast their messages to all nearby females simultaneously). Of course, the reallocation of resources and time into the courtship of preferred females also depends on the risk of mortality associated with mate searching. Therefore, to better understand the process of divergence between diverging taxa, it may be informative to consider estimating how much resources or time (i.e., courtship effort) choosy males reallocate to court preferred females. Based on the predictions of our model, selection should favour mutual mate choice as long as there is some reallocation of courtship effort; otherwise male choice should be deleterious. However, if reallocation is only partial, preference cycling is likely to occur, possibly hampering further differentiation between those taxa.

The magnitude of gene flow also depends on how accurately preferences are expressed. Perhaps counterintuitively, our model suggests that errouneously expressed preferences lead to less gene flow as a whole by strengthening selection favouring choosiness. In a context of local adaptation, error-prone female choice is more strongly favoured by selection than error-free choice because it maintains a higher diversity of male types in the population[75]. Likewise, similar effects can stabilize cooperation in mutualism[76]. In our context, this leads to the prediction that the genetic architecture of the preference traits expressed in females and males greatly affects the divergence process. For instance, female and male preference loci are not associated to the same colour pattern loci in *Heliconius melpomene* and *Heliconius cydno*[47]. Therefore, individuals may not completely avoid courting/mating accross ecotype boundaries (error-prone choice) because each sex relies on a given property of the trait under disruptive selection. Our model predicts this error-proneness could strengthen selection favouring mutual mate choice, which could in turn inhibit preference cycling and enhance speciation. This provides new light explaining the genetic architecture of speciation, i.e. the number and linkage of traits and genes underlying preferences in one or the other sex.

Overall, our theoretical model adds support to the idea that premating isolation may often be readily reversible[63,65,77]. Intriguingly, we show that premating isolation should be especially unstable when selection favours mutual mate choice. We highlighted some factors that could inhibit preference cycling (strong selection against hybrid, numerous erroneous mate choices). The geographical context of speciation and more detailed genetic architectures may also change the modalities of preference cycling and should therefore be investigated theoretically. On the empirical side, the occurence of preference cycling and its impact on gene flow remains to be tested. More generally, our study should stimulate further research on the stability of barriers to gene flow and on the genomics of reproductive isolation.

References

[1] Y. Jiang, D. I. Bolnick, and M. Kirkpatrick, "Assortative mating in animals," *The American Naturalist*, vol. 181, no. 6, pp. E125–E138, 2013.

[2] J. A. Coyne and H. A. Orr., *Speciation*. Sunderland: Sinauer Associates, 2004.

[3] M. R. Servedio, G. S. Van Doorn, M. Kopp, A. M. Frame, and P. Nosil, "Magic traits in speciation: 'magic' but not rare?," *Trends in Ecology & Evolution*, vol. 26, no. 8, pp. 389–397, 2011.

[4] M. Kirkpatrick and V. Ravigné, "Speciation by natural and sexual selection: models and experiments.," *The American Naturalist*, vol. 159, pp. S22–35, 2002.

[5] F. Cézilly, "Assortative mating," in *Bekoff, M., Encyclopedia of animal behavior*, pp. 876–881, Westport CT: Greenwood, 2004.

[6] K. Summers, R. Symula, M. Clough, and T. Cronin, "Visual mate choice in poison frogs," *Proceedings of the Royal Society B: Biological Sciences*, vol. 266, no. 1434, pp. 2141–2145, 1999.

[7] C. D. Jiggins, R. E. Naisbit, R. L. Coe, and J. Mallet, "Reproductive isolation caused by colour pattern mimicry.," *Nature*, vol. 411, no. 6835, pp. 302–305, 2001.

[8] R. G. Reynolds and B. M. Fitzpatrick, "Assortative mating in poison-dart frogs based on an ecologically important trait," *Evolution*, vol. 61, no. 9, pp. 2253–2259, 2007.

[9] G. R. Bortolotti, L. M. González, A. Margalida, R. Sánchez, and J. Oria, "Positive assortative pairing by plumage colour in Spanish imperial eagles," *Behavioural Processes*, vol. 78, no. 1, pp. 100–107, 2008.

[10] R. L. Rodríguez, K. Ramaswamy, and R. B. Cocroft, "Evidence that female preferences have shaped male signal evolution in a clade of specialized plant-feeding insects.," *Proceedings of the Royal Society B: Biological Sciences*, vol. 273, no. 1601, pp. 2585–2593, 2006.

[11] L. K. Snowberg and C. W. Benkman, "The role of marker traits in the assortative mating within red crossbills, Loxia curvirostra complex.," *Journal of evolutionary biology*, vol. 20, no. 5, pp. 1924–1932, 2007.

[12] C. Löfstedt, W. M. Herrebout, and S. B. J. Menken, "Sex pheromones and their potential role in the evolution of reproductive isolation in small ermine moths (Yponomeutidae)," *Chemoecology*, vol. 2, no. 1, pp. 20–28, 1991.

[13] J. W. Zhu, B. B. Chastain, B. G. Spohn, and K. F. Haynes, "Assortative mating in two pheromone strains of the cabbage looper moth, Trichoplusia ni," *Journal of Insect Behavior*, vol. 10, no. 6, pp. 805–817, 1997.

[14] U. Dieckmann and M. Doebeli, "On the origin of species by sympatric speciation.," *Nature*, vol. 400, no. 6742, pp. 354–357, 1999.

[15] M. Doebeli and U. Dieckmann, "Speciation along environmental gradients.," *Nature*, vol. 421, no. 6920, pp. 259–264, 2003.

[16] D. I. Bolnick, "Waiting for sympatric speciation.," *Evolution*, vol. 58, no. 4, pp. 895–899, 2004.

[17] M. Kopp and J. Hermisson, "Competitive speciation and costs of choosiness.," *Journal of evolutionary biology*, vol. 21, no. 4, pp. 1005–1023, 2008.

[18] X. Thibert-Plante and A. P. Hendry, "Factors influencing progress toward sympatric speciation.," *Journal of evolutionary biology*, vol. 24, no. 10, pp. 2186–2196, 2011.

[19] X. Thibert-Plante and S. Gavrilets, "Evolution of mate choice and the so-called magic traits in ecological speciation," *Ecology Letters*, vol. 16, no. 8, pp. 1004–1013, 2013.

[20] M. Kopp, M. R. Servedio, T. C. Mendelson, R. J. Safran, R. L. Rodríguez, M. E. Hauber, E. C. Scordato, L. B. Symes, C. N. Balakrishnan, D. M. Zonana, and G. S. van Doorn, "Mechanisms of assortative mating in speciation with gene flow: connecting theory and empirical research," *The American Naturalist*, vol. 191, no. 1, pp. 1–20, 2018.

[21] H. D. Rundle and P. Nosil, "Ecological speciation," *Ecology Letters*, vol. 8, no. 3, pp. 336–352, 2005.

[22] J. M. Sobel, G. F. Chen, L. R. Watt, and D. W. Schemske, "The biology of speciation.," *Evolution*, vol. 64, no. 2, pp. 295–315, 2010.

[23] C. Darwin, *The Descent of Man, and Selection in Relation to Sex*. Princeton University Press, 1871.

[24] B. Engeler and H. U. Reyer, "Choosy females and indiscriminate males: mate choice in mixed populations of sexual and hybridogenetic water frogs (Rana lessonae, Rana esculenta)," *Behavioral Ecology*, vol. 12, no. 5, pp. 600–606, 2001.

[25] M. Friberg, N. Vongvanich, A. K. Borg-Karlson, D. J. Kemp, S. Merilaita, and C. Wiklund, "Female mate choice determines reproductive isolation between sympatric butterflies," *Behavioral Ecology and Sociobiology*, vol. 62, no. 6, pp. 873–886, 2008.

[26] G. M. Kozak, M. Reisland, and J. W. Boughmann, "Sex differences in mate recognition and conspecific preference in species with mutual mate choice," *Evolution*, vol. 63, no. 2, pp. 353–365, 2009.

[27] S. Noh and C. S. Henry, "Sexually monomorphic mating preferences contribute to premating isolation based on song in European green lacewings," *Evolution*, vol. 64, no. 1, pp. 261–270, 2010.

[28] T. J. Ord, L. King, and A. R. Young, "Contrasting theory with the empirical data of species recognition," *Evolution*, vol. 65, no. 9, pp. 2572–2591, 2011.

[29] R. J. West and A. Kodric-Brown, "Mate Choice by Both Sexes Maintains Reproductive Isolation in a Species Flock of Pupfish (Cyprinodon spp) in the Bahamas," *Ethology*, vol. 121, no. 8, pp. 793–800, 2015.

[30] A. J. Bateman, "Intra-sexual selection in Drosophila," *Heredity*, vol. 2, no. 3, pp. 349–368, 1948.

[31] T. Janicke, I. K. Haderer, M. J. Lajeunesse, and N. Anthes, "Darwinian sex roles confirmed across the animal kingdom," *Science Advances*, vol. 2, no. 2, pp. e1500983–e1500983, 2016.

[32] J. Gröning and A. Hochkirch, "Reproductive interference between animal species.," *The Quarterly review of biology*, vol. 83, no. 3, pp. 257–282, 2008.

[33] P. A. Gowaty, R. Steinichen, and W. W. Anderson, "Indiscriminate females and choosy males: Within-and between-species variation in Drosophila," *Evolution*, vol. 57, no. 579, pp. 2037–2045, 2003.

[34] C. M. Espinedo, C. R. Gabor, and A. S. Aspbury, "Males, but not females, contribute to sexual isolation between two sympatric species of Gambusia," *Evolutionary Ecology*, vol. 24, no. 4, pp. 865–878, 2010.

[35] R. L. Moran, M. Zhou, J. M. Catchen, and R. C. Fuller, "Male and female contributions to behavioral isolation in darters as a function of genetic distance and color distance," *Evolution*, vol. 71, no. 10, pp. 2428–2444, 2017.

[36] T. C. Mendelson, J. M. Gumm, M. D. Martin, and P. J. Ciccotto, "Preference for conspecifics evolves earlier in males than females in a sexually dimorphic radiation of fishes," *Evolution*, pp. 1–11, 2018.

[37] C. T. Bergstrom and L. A. Real, "Towards a theory of mutual mate choice: Lessons from two-sided matching," *Evolutionary Ecology Research*, vol. 2, pp. 493–508, 2000.

[38] M. P. Shahandeh, A. Pischedda, and T. L. Turner, "Male mate choice via cuticular hydrocarbon pheromones drives reproductive isolation between Drosophila species," *Evolution*, vol. 72, no. 1, pp. 123–135, 2018.

[39] H. Kokko and P. Monaghan, "Predicting the direction of sexual selection," *Ecology Letters*, vol. 4, no. 2, pp. 159–165, 2001.

[40] H. Kokko and R. A. Johnstone, "Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 357, no. 1419, pp. 319–330, 2002.

[41] M. E. R. Pierotti, M. E. Knight, S. Immler, N. J. Barson, G. F. Turner, and O. Seehausen, "Individual variation in male mating preferences for female coloration in a polymorphic cichlid fish," *Behavioral Ecology*, vol. 19, no. 3, pp. 483–488, 2008.

[42] M. J. Pauers, T. J. Ehlinger, and J. S. McKinnon, "Female and male visually based mate preferences are consistent with reproductive isolation between populations of the Lake Malawi endemic Labeotropheus fuelleborni," *Current Zoology*, vol. 56, no. 1, pp. 65–72, 2010.

[43] P. Zoppoth, S. Koblmüller, and K. M. Sefc, "Male courtship preferences demonstrate discrimination against allopatric colour morphs in a cichlid fish," *Journal of Evolutionary Biology*, vol. 26, no. 3, pp. 577–586, 2013.

[44] J. Mavárez, C. A. Salazar, E. Bermingham, C. Salcedo, C. D. Jiggins, and M. Linares, "Speciation by hybridization in Heliconius butterflies.," *Nature*, vol. 441, no. 7095, pp. 868–871, 2006.

[45] N. L. Chamberlain, R. I. Hill, D. D. Kapan, L. E. Gilbert, and M. R. Kronforst, "Polymorphic butterfly reveals the missing link in ecological speciation.," *Science*, vol. 326, no. 5954, pp. 847–850, 2009.

[46] R. M. Merrill, Z. Gompert, L. M. Dembeck, M. R. Kronforst, W. O. McMillan, and C. D. Jiggins, "Mate preference across the speciation continuum in a clade of mimetic butterflies.," *Evolution*, vol. 65, no. 5, pp. 1489–1500, 2011.

[47] R. M. Merrill, B. Van Schooten, J. A. Scott, and C. D. Jiggins, "Pervasive genetic associations between traits causing reproductive isolation in Heliconius butterflies.," *Proceedings of the Royal Society B: Biological Sciences*, vol. 278, no. 1705, pp. 511–518, 2011.

[48] R. M. Merrill, A. Chia, and N. J. Nadeau, "Divergent warning patterns contribute to assortative mating between incipient Heliconius species," *Ecology and Evolution*, vol. 4, no. 7, pp. 911–917, 2014.

[49] C. Mérot, B. Frérot, E. Leppik, and M. Joron, "Beyond magic traits: Multimodal mating cues in Heliconius butterflies," *Evolution*, vol. 69, no. 11, pp. 2891–2904, 2015.

[50] C. Mérot, C. Salazar, R. M. Merrill, C. D. Jiggins, and M. Joron, "What shapes the continuum of reproductive isolation? Lessons from Heliconius butterflies," *Proceedings of the Royal Society B: Biological Sciences*, vol. 284, no. 1856, p. 20170335, 2017.

[51] P. Nosil, L. J. Harmon, and O. Seehausen, "Ecological explanations for (incomplete) speciation.," *Trends in Ecology & Evolution*, vol. 24, no. 3, pp. 145–156, 2009.

[52] P. Nosil, J. L. Feder, S. M. Flaxman, and Z. Gompert, "Tipping points in the dynamics of speciation," *Nature Ecology & Evolution*, vol. 1, no. 2, p. 1, 2017.

[53] R. K. Butlin, J. Galindo, and J. W. Grahame, "Sympatric, parapatric or allopatric: the most important way to classify speciation?," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 363, no. 1506, pp. 2997–3007, 2008.

[54] J. Felsenstein, "Skepticism towards Santa Rosalia, or why are there so few kinds of animals?," *Evolution*, vol. 35, no. 1, pp. 124–138, 1981.

[55] T. Lenormand, "Gene flow and the limits to natural selection," *Trends in Ecology and Evolution*, vol. 17, no. 4, pp. 183–189, 2002.

[56] M. R. Servedio, "Male versus female mate choice: sexual selection and the evolution of species recognition via reinforcement," *Evolution*, pp. 2772–2789, 2007.

[57] G. A. Parker, "Mate quality and mating decisions," in *Mate Choice* (P. Bateson, ed.), ch. Mate quali, pp. 141–164, Cambridge: Cambridge University Press, 1983.

[58] R. A. Johnstone, J. D. Reynolds, and J. C. Deutsch, "Mutual mate choice and sex differences in choosiness," *Evolution*, vol. 50, no. 1996, pp. 1382–1391, 1996.

[59] R. A. Johnstone, "The tactics of mutual mate choice and competitive search," *Behavioral Ecology and Sociobiology*, vol. 40, no. 1, pp. 51–59, 1997.

[60] A. Courtiol, L. Etienne, R. Feron, B. Godelle, and F. Rousset, "The evolution of mutual mate choice under direct benefits," *The American Naturalist*, vol. 188, no. 5, pp. 521–538, 2016.

[61] O. Seehausen, "Conservation: Losing biodiversity by reverse speciation," *Current Biology*, vol. 16, no. 9, pp. 334–337, 2006.

[62] E. B. Taylor, J. W. Boughman, M. Groenenboom, M. Sniatynski, D. Schluter, and J. L. Gow, "Speciation in reverse: Morphological and genetic evidence of the collapse of a three-spined stickleback (Gasterosteus aculeatus) species pair," *Molecular Ecology*, vol. 15, no. 2, pp. 343–355, 2006.

[63] S. Kleindorfer, J. A. O'Connor, R. Y. Dudaniec, S. A. Myers, J. Robertson, and F. J. Sulloway, "Species collapse via hybridization in Darwin's tree finches," *The American Naturalist*, vol. 183, no. 3, pp. 325–341, 2014.

[64] T. Dobzhansky, "Studies on Hybrid Sterility. I. Spermatogenesis in pure and hybrid Drosophila pseudoobscura," *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, vol. 21, no. 2, pp. 169–223, 1934.

[65] H. J. Muller, "Isolation mechanisms, evolution and temperature," *Biology Symposium*, vol. 6, pp. 71–125, 1942.

[66] P. W. Hedrick, "Adaptive introgression in animals: Examples and comparison to new mutation and standing variation as sources of adaptive variation," *Molecular Ecology*, vol. 22, no. 18, pp. 4606–4618, 2013.

[67] A. W. Nolte and D. Tautz, "Understanding the onset of hybrid speciation," *Trends in Genetics*, vol. 26, no. 2, pp. 54–58, 2010.

[68] A. P. Hendry, D. I. Bolnick, D. Berner, and C. L. Peichel, "Along the speciation continuum in sticklebacks," *Journal of Fish Biology*, vol. 75, no. 8, pp. 2000–2036, 2009.

[69] E. G. Mandeville, T. L. Parchman, D. B. McDonald, and C. A. Buerkle, "Highly variable reproductive isolation among pairs of Catostomus species," *Molecular Ecology*, vol. 24, no. 8, pp. 1856–1872, 2015.

[70] E. Mandeville, T. Parchman, S. Song, K. Thompson, R. Compton, K. Gelwicks, and C. Buerkle., "Inconsistent reproductive isolation revealed by interactions between Catostomus fish species," *Evolution Letters*, vol. 1, no. 5, pp. 255–268, 2017.

[71] G. A. Parker, "Sperm competition and its evolutionary consequences in the insects," *Biological Reviews*, vol. 45, no. 4, pp. 525–567, 1970.

[72] R. Thornhill, "Sexual selection and paternal investment in insects," *The American Naturalist*, vol. 110, no. 971, pp. 153–163, 1976.

[73] M. H. Robinson, "Courtship and mating behavior in spiders," *Annual Review of Entomology*, vol. 27, no. 2, pp. 1–20, 1982.

[74] M. B. Girard, D. O. Elias, and M. M. Kasumovic, "Female preference for multi-modal courtship: multiple signals are important for male mating success in peacock spiders," *Proceedings of the Royal Society B*, vol. 282, no. 1820, p. 20152222, 2015.

[75] L. Holman and H. Kokko, "Local adaptation and the evolution of female choice," in *Genotype-by-Environment Interactions and Sexual Selection* (J. Hunt and D. Osken, eds.), pp. 41–62, Wiley-Blackwell, 2014.

[76] K. R. Foster and H. Kokko, "Cheating can stabilize cooperation in mutualisms," *Proceedings of the Royal Society B: Biological Sciences*, vol. 273, no. 1598, pp. 2233–2239, 2006.

[77] M. R. Servedio and R. Burger, "The counterintuitive role of sexual selection in species maintenance and speciation," *Proceedings of the National Academy of Sciences*, vol. 111, no. 22, pp. 8113–8118, 2014.