Mating Instabilities Lead to Sympatric Speciation
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ABSTRACT

One of the most challenging issues of evolutionary biology concerns speciation, the emergence of new species from an initial one. The huge amount of species found in nature demands a simple and robust mechanism. Yet, no consensus has been reached concerning a reasonable disruptive selection mechanism that prevents mixing genes among the emerging species, especially when they live in sympatry. Usually it is assumed that females select males according to their displaying traits, but males perform no selection on female traits. However, recent experimental evidence accumulates towards the existence of male choice. Here we propose a robust mechanism for sympatric speciation, based on the assumption that sexual selection operates in two directions: selection of males by females and of females by males. Complex mating instabilities emerge, creating differential fitness depending on the individuals displaying traits and preferences. When a secondary sexual trait is introduced in a population, due to mutations, the activation of previously neutral genes or due to a different perception of already existent displaying traits, sympatric speciation may result (together with a species recognition system) from a competitive exclusion principle. We suggest that potential candidates to test our theory could be yeasts.

Key index words: sympatric speciation, sexual competition, mating systems
Traditionally, two main classes of models try to explain speciation. Allopatric speciation models are the most consensual and assume that the initial population is suddenly divided in two geographically isolated subpopulations, that then diverge until they become reproductively isolated, even after a secondary contact (Mayr 1963). There is however, mounting evidence (Albertson et al. 1999; Panhuis et al. 2001; Schliewn et al. 1994) that speciation might have emerged in sympatry (without geographical isolation). Examples like the cichlids in lake Victoria or many migratory birds, do not seem to fit the basic requirement of long periods of geographical isolation needed for allopatric speciation. Laboratory experiments have also shown that in principle, sympatric speciation is possible (Rice & Hostert 1993). Understanding how sympatric speciation can be driven, has thus attracted much theoretical effort. However, some early works showed that finding a biologically reasonable and robust model seems not to be an easy subject (Felsenstein 1981; Maynard Smith 1966).

Recently, several models have been proposed to explain sympatric speciation. Nevertheless, no consensus has been reached concerning the main driving mechanism, nor the conditions required in practice. One class of models concentrates on sexual competition for mates. So far, these models have been the least convincing models (Turelli et al. 2001) as they have been incapable of providing a robust mechanism, valid under reasonable initial conditions (Takimoto et al. 2000; Turelli et al. 2001). The other class of models assumes that competition for resources is essential to create disruptive selection (Doebeli & Dieckmann 2000; Kondrashov & Kondrashov 1999; see a discussion in van Doorn & Weissing). However it also requires a non-trivial association between traits relevant for ecological adaptation and traits used for sexual discrimination. Further, and in particular in the Doebeli and Dieckmann theory, phenotypes using scarce resources may substitute phenotypes using more abundant resources, as a result of a strong competition for resources in the later case. This is a somehow counter-intuitive result. Again it remains uncertain which species should be more speciation prone, in practice.

Here we propose an alternative approach that leads to a robust theory for sympatric speciation. We give a special emphasis to pair formation. Pair formation is an essential issue in any sexual population, as it is at the basis of the species reproductive success. As we will show, modelling pair formation is essential to create linkage disequilibrium due to
the emergence of complex mating instabilities.

In our model we assume that any individual possesses a preference list, where all individuals of the opposite sex are ranked, in descending priority order. The goal of any individual is to optimise his satisfaction by mating with convenient partners. How the preference list is established depends on a response to a sensory stimulus induced by varied secondary sexual traits displayed by the opposite sex individuals. In principle, it could also have an ecological component, to model, for instance, the preference for certain habitats (Bush 1969).

As the number of displaying traits can be quite large and perceived differently by different individuals, a simple assumption will be to consider that each individual has his own preference list and that this is approximately random. In this way we assume that sexual selection has already eliminated non-favoured traits, so that only neutral traits, concerning sexual selection, remain. Note that sexual selection does not necessarily mean the selection of traits relevant for adaptation. Sexual selection may only improve the fitness of a population, by optimising the consequences of the mating conflicts created.

Sexual conflicts lead to intricate dynamics, as both males and females pursue selfish goals, with conflicting wishes. Consider the following preference lists, for a population with three males and three females.

|   | M1 | M2 | M3 |
|---|----|----|----|
| 1 | F1 | F2 | F2 |
| 2 | F2 | F3 | F1 |
| 3 | F3 | F1 | F3 |

|   | F1 | F2 | F3 |
|---|----|----|----|
| 1 | M2 | M1 | M2 |
| 2 | M1 | M3 | M3 |
| 3 | M3 | M2 | M1 |

If all individuals search continuously for better partners, then we can imagine the following algorithm. First, males propose sequentially to females ranking higher in their preference lists, and females accept the new partners only if they improve their satisfaction. Then females and males switch roles. In this case, both males and females adopt active strategies towards mating (they both search for better mates). We could sketch that M1 mates F1, M2 mates F2, but then F2 divorces M2 and mates with M3 because he is higher in her preference list, and so on. It is easy to conclude that no stable arrangement is reached. That is, the system has no Nash equilibrium (Gale & Shapley 1962; Omero et al. 1997). While these instabilities are not the rule (for instance, a couple can be stable if they prefer each other), they produce differential costs for reproduction, as fitness depends on the stability of the
couples. There is an algorithm, due to Gale and Shapley (Gale & Shapley 1962; Omero et al. 1997), that leads to stable arrangements. This happens if males propose to females, and females dispose, accepting to mate new pretenders only if they improve their satisfaction. Nevertheless, even if a stable solution exists, the time needed to reach it, tGS, tends to be quite large, due to the large number of degrees of freedom and the complex dynamics. In practice, the results we will present do not depend on the strategy adopted by females towards mating.

Methods

We consider discrete generations of a population with an equal number, \( N_{\text{tot}} \), of males and females. The genetic information on each individual controls several characters. A sexual locus may control the strategy towards mating if one would want to study the selection of these strategies, but this, we checked, does not change the results concerning speciation. Henceforth males and females are assumed to take active and passive strategies towards mating, respectively.

One locus with two alleles (we assume dominance) accounts for a secondary sexual trait \((A \text{ or } B)\). Several independent loci with two alleles (+ or −) define a quantitative preference for one trait. Each individual ranks in a list of preferences individuals of the opposite sex. Preference lists are defined with a simple step-like structure. Calling \( n_+ \) the fraction of positive alleles, then a positively (negatively) biased arrangement corresponds to a preference for mates with trait \( A \) (\( B \)), such that there is a fraction \( f_\nu(n_+) = [4n_+(1-n_+)]^{\nu}/2 \) of non-preferred mates ranked within the first \( N_A \) (\( N_B \)) positions (\( N_A \) and \( N_B \) being the number of individuals respectively with phenotype \( A \) and \( B \)). The positive exponent \( \nu \) controls how efficiently individuals with a biased arrangement of alleles discriminate mates with preferred traits. For small values of \( \nu \), deviations from an unbiased arrangement produces poor discrimination, as can be seen in figure 1.

On each iteration, randomly picked individuals (with an active strategy towards mating) are given one opportunity to find a better partner. New matings happen only if they improve the satisfaction of both elements of the couple. The process repeats until \( 2N_{\text{tot}} \) offspring are born. One offspring of each sex is born if a couple stays together during a courtship time \( tc \),
plus a reproduction time $t_r$ (results concerning the emergence of speciation do not change if offsprings are only allowed to born after a stabilization time). During reproduction time, females cannot engage in new matings, but males may find a better partner (in relation to speciation, the relevant parameter is simply $t_c + t_r$). Offspring genotypes are found using Mendel genetic rules.

By introducing a probability $m$ of changing each allele controlling the trait of the offspring, we can model phenomenologically a many genes dependence on the trait or the effect of mutations. A similar procedure can be applied to the loci controlling the preference.

Finally, ornamentation costs can be introduced within our framework by assigning a birth probability, related to the parent’s trait. We checked that speciation is not prevented if the ornamentation costs are not too different, and thus this point will not be discussed further here.

**Results and Discussion**

Consider first a population with only one trait. In figure 2, the distribution function of mating lifetimes is shown. It exhibits clear power law decay. This scale invariant behaviour means that there is a large amount of stable matings, but also a large amount of very unstable short-lived matings, relatively to what one would expect if matings were random. Thus pair formation will certainly play a role in a sexual selection theory, as it distinguishes individual fitnesses over several scales. In what concerns speciation, another important consequence is that couples stability is context dependent: the same couple may have very different lifetimes depending on the preferences present in the whole population.

Note that scale invariant laws are often associated to self-organized criticality (Jensen 1998). Here, however, it results from the existence of preference lists. It is nevertheless conceivable that other alternative rules exist leading to the emergence of a similar scale invariant behaviour in a self-organized way.

For speciation to emerge as a result of sexual selection, a new sexual secondary trait must be introduced in a population (due to mutations, or to the activation of certain genes (Rutherford & Lindquist 1998), induced by new ecological conditions), or already existent displaying traits should be perceived differently under new ecological conditions (for instance, water quality or light intensity in a lake (Boughmann 2001)), differentiating the individuals.
Thus, a population subject to new ecological conditions may be driven into a sexual selection process, from which, we will show, sympatric speciation can be the outcome.

Consider the limit case in which an individual would rank all the mates with the preferred trait first. In general, if a new trait ($A$ or $B$) is introduced in a population, some individuals may prefer a mate with trait $A$, while others, one with trait $B$. We can classify males and females in four groups, $AA$, $AB$, $BA$ and $BB$, the first letter standing for the trait, the second for the preference. If only males adopt active strategies towards mating, then both, $AA$ and $BA$ males, compete for the same females, $AA$ or $AB$. A potential opportunity cost exists if, for instance, a $BA$ male mates with an $AA$ female, as there is a high probability that this mating will not last enough time to accomplish reproduction. We have checked that the mating instabilities reduce strongly the lifetime of couples where traits and preferences do not match. From the female’s point of view, $AA$ and $BA$ females prefer $AA$ or $AB$ males, which produces an indirect competition between $AA$ and $AB$ males. Neglecting the effects of recombination and assuming that the average number of males $ij$, $m_{ij}$, is equal to the average number of females with matched preferences, $f_{ji}$, then $m_{ij}$ grows roughly with the probability of forming stable couples, $dm_{ij} \simeq \alpha m_{ij}^2/m_j$, where $m_j$ is the total number of males with preference for $j$. Sexual selection will only keep those individuals reproducing at the highest rate, leading to a competitive exclusion principle with a symmetry breaking, where only $AA\times AA$ and $BB\times BB$ couples or $BA\times AB$ and $AB\times BA$, are selected. Introducing recombination with one dominant locus for each, trait and preference, this competitive scenario can be tackled analytically as shown in the appendix. Then, only $AA\times AA$ and $BB\times BB$ couples are selected, which corresponds to the emergence of homotypic preferences.

Our general model considers a quantitative genetic preference, determined by several additive independent loci. The number of these loci does not need to be only one, as considered in the simple case in the appendix. If we consider a large number of loci controlling the preferences, then random configurations produce only small preference tendencies. The more biased arrangements of preference alleles are, the larger will be the number of individuals with the preferred trait ranked in the first positions. As discussed above, the function $f_\nu(n_\nu)$, establishes the relation between bias in preference loci and the intensity of discrimination. In figure 3a we show how sympatric speciation emerges, starting from a population with random genotypes. Even for species with a considerable number of independent genes
controlling the preferences, speciation is remarkably achieved within just a few generations. Due to trait dominance, only $AA$ or $BB$ individuals last in the end, all heterozygous being eliminated. This corresponds to the emergence of two new species and a species recognition system. Prezygotic isolation is thus achieved giving way to species divergence. In this example, trait discrimination is the same for males and females (same $\nu$). However, for this example speciation could also be achieved if we had chosen higher trait discrimination for females (higher $\nu$, $\nu_{\text{females}} = 1.5$ and $\nu_{\text{males}} = 0.5$) as it is likely to happen in nature. In fact, trait discrimination needs to operate on both sexes, but its intensity may vary.

If $f_\nu(n_+)$ departs slowly from the unbiased arrangement of alleles corresponding to a difficult discrimination, disruptive sexual selection can be prevented (figure 3b). It is also possible to prevent speciation if traits are not straightforwardly inherited, due to complex dependencies on a large number of other genes (a trait may result from intricate interactions of a large number of proteins, leading to a complex inheritance) or as a result of mutations. These effects are taken into account through the $m$ parameter. Large values of $\mu$ (for the example of figure 3a, $\mu \approx 6 \times 10^{-3}$ mutations per generation and per allele) reduce the effects of the non-random pair formation created by the complex dynamics. Consequently above a certain threshold value speciation is prevented and a population with genotype frequencies in the Hardy-Weinberg proportions remains.

Our theory assumes that in a population, each individual presents many phenotypic traits, each contributing in a complicated way to establish the other individuals mate choice. Many of these traits may not have a strong impact in mate choice, in such a way that a phenotypic polymorphism remains in a population (they would be approximately neutral in what concerns sexual selection). In figure 4a we show a population in which discrimination relatively to a given trait is poor in the first 200 generations. The population consists of individuals with both traits and small preferences relatively to both traits. There is no relevant correlation between traits and preferences in the individuals. At generation 200, discrimination for the trait is increased and a quick speciation event emerges. An alternative picture is presented in figure 4b. Starting from a monomorphic population and sufficiently strong trait discrimination, mutations and a release of natural selection pressure (as a result of change of habitat, for instance) allows genetic drift. Preferences acquire variability, until individuals with preferences for both traits exist in the population. Then sympatric speciation emerges. In practice this later scenario needs more generations to reach
the speciation disruptive configuration.

The theory presented here explains, under minimal assumptions, how sympatric speciation emerges or not, together with a species recognition system. It is a robust mechanism, not requiring special assumptions on the initial species (Doebeli & Dieckmann 2000; Kondrashov & Kondrashov 1999; Lande 1982; Turner & Burrows 1995; van Doorn & Weissing), on male-female incompatibilities (Gavrilets 2000; Parker & Partridge 1998), on the ecological conditions (Turner & Burrows 1995), or on non obvious connections between sexual and ecological traits (Doebeli & Dieckmann 2000; Felsenstein 1981; Maynard Smith 1966; Turelli et al. 2001; van Doorn & Weissing). Our theory assumes that males and females have preferences over the same traits. While female preferences have been extensively studied (Andersson 1994; Futuyma 1998), male preferences are usually neglected. Nevertheless, there is now mounting experimental evidence for the existence of male choice (Andersson 1994; Burley et al. 1982; Rutowski 1982; Roulin et al. 2000; Katvala & Kaitala 2001; Amundsen & Forsgren 2001). This is actually a natural outcome of natural selection as males would otherwise incur in potential opportunity costs: those having the ability to elicit healthier females, or predators mimicry, should certainly be favoured. However, in practice, they should be more difficult to detect, as males usually adopt active strategies towards mating, and thus are seen performing courtship to many females. This is certainly an issue deserving more research.

A unified understanding of sexual selection, starting from simple organisms like yeasts to complex organisms like mammals, may be attempted with our model. Indeed, in yeasts it is now clear that both mates in a couple choose their partners (Jackson & Hartwell 1990). Further, many genes can be involved in the several complex steps of this process (White & Rose 2001). Hence, analogues to the preference lists used in our model may already be built in. For this reason we propose yeasts as potential candidates to test our theory in the laboratory. And if, as predicted, robust sympatric speciation is observed, then many implications can result not only on a conceptual level. Indeed we believe that sympatric speciation could be used as a general framework for studying the interactions between receptors and pheromones, and to construct a better understanding on how these correlate with the intracellular state. This issue will be addressed in a forthcoming publication.
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Appendix: Mathematical approach of the sexual competitive scenario for a population with two locus, for traits and preferences, with a dominant allele each.

Here we outline a mathematical approach to the emergence of an exclusion principle from our results. The dynamical correlations in the model reduce strongly the fitness of non-optimal couples. Assume then that fitness is proportional to the probability of forming couples where traits and preferences match. In a two-locus, two-allele model, we have 9 genotypes, denoted by $ij$, respectively associated with displaying traits and preferences, with $i, j = 1, 2, 3$. Genotype 2 is heterozygous, and 1 is a dominant homozygous. Denote the number of males (females) with genotype $ij$ by $m_{ij}$ ($f_{ij}$). The evolution of the number of genotypes $ij$ is proportional to:

$$dm_{ij} \simeq \sum_{klmn} \alpha_{ijklmn}^{klmn} m_{kl} f_{mn}/f_{M},$$

where $f_{M}$ is the number of females with trait corresponding to genotype mn ($M = A, B$) and $\alpha_{ijklmn}^{klmn}$ is a matrix giving the reproduction frequencies following Mendel rules. This equation is quite general but simplifies considerably in the present case, as most entries in the matrix are zero (see below). For instance, the equation associated with phenotype $BB$ (genotype $m_{33}$) is:

$$dm_{33} \simeq m_{33} f_{33}/f_B + m_{23} f_{32}/(4f_B) + m_{32} f_{23}/(4f_B) + m_{22} f_{22}/(16f_A).$$

An exclusion principle emerges as genotypes try to grow the fastest possible (following similar growth equations) while interacting and as we concentrate on populations with a fixed number of individuals. Only those growing at the highest rate will remain.

If we sum all genotypes contributing to the same phenotype, we arrive to similar equations to the evolution of the phenotypes. It is possible to check that all terms contributing to $dm_{AB} = dm_{13} + dm_{23}$ and $dm_{BA} = dm_{31} + dm_{32}$ appear in $dm_{AA} = dm_{11} + dm_{12} + dm_{21} + dm_{22}$ but with larger coefficients in the later. Thus $m_{AB}$ and $m_{BA}$ are eliminated (unless the starting population had only genotypes 13 and 31). Phenotypes $m_{AA}$ and $m_{BB}$ can coexist.
as both have a non-mixed contribution corresponding to the union of genotypes $m_{11} + f_{11}$ and $m_{33} + f_{33}$.

The non-zero matrix entries are: ($\alpha_{i,j}^{klmn} = \alpha_{i,j}^{mknl}$)

\[
\begin{align*}
1/2 &= \alpha_{111121} = \alpha_{111211} = \alpha_{121112} = \alpha_{121121} = \alpha_{211121} = \alpha_{212112} = \\
1/4 &= \alpha_{111112} = \alpha_{111121} = \alpha_{111211} = \alpha_{121121} = \alpha_{211212} = \alpha_{212121} = \alpha_{221122} = \\
&= \alpha_{131212} = \alpha_{211122} = \alpha_{211221} = \alpha_{212112} = \alpha_{221112} = \alpha_{221212} = \\
&= \alpha_{222122} = \alpha_{222222} = \alpha_{222332} = \alpha_{312121} = \alpha_{322332} = \alpha_{332332} \\
1/8 &= \alpha_{111122} = \alpha_{112122} = \alpha_{121222} = \alpha_{122122} = \alpha_{122212} = \alpha_{131222} = \alpha_{211222} = \alpha_{212222} = \alpha_{231222} = \\
&= \alpha_{232222} = \alpha_{312122} = \alpha_{321222} = \alpha_{322222} \\
1/16 &= \alpha_{111222} = \alpha_{132222} = \alpha_{312222} = \alpha_{332222} \\
1 &= \alpha_{111111} = \alpha_{221331} = \alpha_{333333}
\end{align*}
\]

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FIG. 1: Preference lists are constructed with a step-like structure. In the first positions there is a fraction $f(n_\pm)$ of individuals with non-preferred traits. The parameter $n$ controls how efficiently individuals with a biased arrangement of alleles ($n_\pm$ away from 1/2) discriminate mates with preferred traits. The function $f_\nu$ is shown for $\nu = 0.1, 0.3(\star), 1(\blacklozenge)$ and 4. Dots and diamonds show the discrete values of $f_\nu$ for the results of figure 3 (preferences with 30 alleles).
FIG. 2: Number of matings $N_m(t)$ lasting for $t$ iterations. 500 populations were sampled over 10000 iterations, for the model without reproduction events ($t_c = t_r = +\infty$). The distribution shows power law behaviour, $N_m(t) \sim t^{-\tau}$, with $\tau \simeq 2.5$. $\tau$ is independent of the number of individuals and the strategies of females. This distribution shows that, due to the correlated dynamics, individuals are expected to have fitness varying over several orders of magnitude. Thus correlated dynamics must play an essential role on the evolution of the population.
FIG. 3: Evolution of phenotype frequencies starting from a population with random initial genotypes. One dominant locus with two alleles controls the trait, and 15 independent loci with two alleles each, the preference intensity. For $n_+ \text{ close to } 1(0)$, mates with trait $A$ ($B$) tend to be preferred. Sympatric speciation $a$ quickly emerges if sufficient discrimination of mating traits exists ($\nu = 1.0$), or $b$ is prevented if discrimination is insufficient ($\nu = 0.3$) ($N_{\text{tot}} = 200, t_c = t_r = 40$).
FIG. 4: Evolution of phenotype frequencies (one dominant locus controls the trait; 15 independent loci, the preference intensity): a starting from a population with random initial genotypes, $\mu = 3 \times 10^{-4}$ per allele, and weak trait discrimination ($\nu = 0.4$). At generation 200 discrimination is increased ($\nu = 1.0$). b starting from a monomorphic population (all individuals with trait $B$ and all their preference loci equal to 0 - preference for $B$ traits) and discrimination $\nu = 1.0$. Mutations ($\mu = 6 \times 10^{-4}$ per allele) produce genetic drift such that speciation may emerge when there are individuals with preferences for both traits. Light squares correspond to phenotypes with more than 10 individuals.