

Dynamical instabilities lead to sympatric speciation

Catarina R. Almeida^{1*} and Fernão Vistulo de Abreu²

¹*Departamento de Biologia and* ²*Departamento de Física, Universidade de Aveiro, 3800 Aveiro, Portugal*

ABSTRACT

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 dynamical 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 a different perception of already existent displaying traits, sympatric speciation may result from a competitive exclusion principle.

Keywords: complexity, mating systems, sexual competition, sexual selection, sympatric speciation.

INTRODUCTION

Traditionally, two main classes of models are used to explain speciation. Allopatric speciation models are the most consensual and assume that the initial population is suddenly divided into two geographically isolated subpopulations, which then diverge until they become reproductively isolated, even after a secondary contact (Mayr, 1963). There is, however, mounting evidence (Schliwen *et al.*, 1994; Albertson *et al.*, 1999; Panhuis *et al.*, 2001) that speciation might have emerged in sympatry (without geographical isolation). Examples such as the cichlids in Lake Victoria and many migratory birds do not appear 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 and Hostert, 1993). Understanding how sympatric speciation can be driven has thus attracted much theoretical effort. However, early work showed that finding a biologically reasonable and robust model is not easy (Maynard Smith, 1966; Felsenstein, 1981).

Several models have been proposed to explain sympatric speciation (Lande, 1982; Turner and Burrows, 1995; Parker and Partridge, 1998; Van Doorn *et al.*, 1998; Higashi *et al.*, 1999; Kondrashov and Kondrashov, 1999; Doebeli and Dieckmann, 2000; Gavrillets, 2000). Nevertheless, no consensus has been reached about the main driving mechanism or the conditions required in practice. One class of models concentrates on sexual competition for

* Address all correspondence to Catarina R. Almeida, Department of Biological Sciences, Sir Alexander Fleming Building, Imperial College, London SW7 2AZ, UK.

Consult the copyright statement on the inside front cover for non-commercial copying policies.

mates. Higashi and co-workers (1999) have shown that female preferences for extreme male traits may induce speciation, provided discrimination for male traits is sufficiently strong. One of their key assumptions is that there are males with intermediate phenotypes in the initial population and that they will have much lower fitness, as they are less preferred by females. This theory requires several additive genes coding for male traits and the existence of very strong female preferences. A reproductive barrier is formed, as females with extreme preferences only mate with males with the corresponding extreme trait. Using the deterministic version of the model, Takimoto and co-workers (2000) showed that if matings between all types of females and males are allowed in the initial population, then the speciation fixed point becomes unstable and no true speciation results, as interbreeding becomes substantial. In a review article, Turelli *et al.* (2001) considered this model to be the least convincing, as deviations from the proposed parameters prevent speciation. For instance, it has been argued that artificial asymmetrical initial conditions had been invoked. In this paper, we present an example where speciation is clearly prevented according to this theory, if a dominant allele controls the trait locus.

Another class of models assumes that competition for resources is essential to create disruptive selection (Kondrashov and Kondrashov, 1999; Doebeli and Dieckmann, 2000; van Doorn and Weissing, 2001). However, they require a non-trivial association between traits relevant for ecological adaptation and traits used for sexual discrimination. Doebeli and Dieckmann (2000) proposed a theory that has been considered by some to be the most convincing model (Turelli *et al.*, 2001). To promote reproductive isolation, they modelled the evolution of the phenotypic frequencies in the population in a particular way: they required that if one phenotype is very numerous in the initial population, it can inhibit other phenotypes from growing, as fewer resources would effectively be available. This is specific to their dynamical differential equations and it implies that, even if new phenotypes are more adapted (to compete for the resources), they cannot grow. Based on this assumption, they achieved a stable polymorphism in the final population. Their theory gave rise once more to the debate of whether sympatric speciation is driven mainly by sexual selection or ecological diversification. Their model clearly requires ecological differentiation. Although it is clear that this differentiation should always arise in the long term (due to the ecological competitive exclusion principle), experimental observations (Seehausen *et al.*, 1999) have questioned its need for speciation, as some 'daughter' species appear to be non-ecologically differentiated.

Here, we show that the stringent conditions required in sexual selection models can be relaxed if mutual sexual selection is considered. In addition, the model we present does not require ecological differentiation. Our approach leads to a robust theory for sympatric speciation – that is, a theory that requires no fine-tuning of the initial parameters or special assumptions about the initial population configuration. Moreover, our results are not stochastic, as is the case, for instance, in Turner and Burrows (1995). The main force acting against speciation events in our model is recombination. This is in line with the view of Felsenstein (1981), who argued that recombination should explain why we do not see more species in nature. Higashi *et al.* (1999) required predation pressures to counteract the strong mating preferences required to produce speciation events. To obtain speciation, we only require slightly stronger preference biases towards traits than the typical biases which already exist in a population and which do not cause speciation.

Our model pays particular attention to the mating dynamics present in a sexual population. The main idea is that the properties of a dynamical non-equilibrium state can

be quite different from those of an equilibrium configuration, and hence linkage disequilibrium can exist in the former but not in the latter. Sexually reproducing species develop intricate strategies to increase the ability of males to reach females. This involves a complex exchange of signals and actions between males and females (Andersson, 1994) or, in the case of plants (Hormaza and Herrero, 1994; Wilhelmi and Preuss, 1996) and some marine broadcast spawners (Miller *et al.*, 1994), between male gametes and female gametes. This requires a considerable investment of resources by both sexes as well as of time.

Time investment has not received much attention in the literature, but we will show that it can help to explain speciation. Time investment is required by all species for offspring to be born. It arises during prolonged courtships, whereby males and females choose each other through complex recognition processes. It can continue throughout long breeding periods, if parental care is required (Andersson, 1994; Futuyma, 1998). During this time, sexual competition (male–male, male–female and/or female–female) operates, and individuals may experience opportunity costs depending on their choice of mates. Opportunity costs are the outcome of the imperfect information all individuals have access to while establishing their ‘decisions’ in this sexual selection ‘game’. For instance, individuals can choose their mates according to their secondary sexual traits, but they do not (cannot) consider their preferences. As a result, potential opportunity costs emerge because individuals may find themselves investing in a ‘wrong’ mate, while wasting the opportunity of choosing a more successful alternative. This phenomenon has been reported in the literature (e.g. Catry *et al.*, 1997). It can result from the existence of mutual sexual selection, which is now believed to be quite widespread in nature (Burley *et al.*, 1982; Rutowski, 1982; Jones and Hunter, 1993; Hormaza and Herrero, 1994; Miller *et al.*, 1994; Wilhelmi and Preuss, 1996; Seehausen *et al.*, 1999; Amundsen and Forsgren, 2001; Katvala and Kaitala, 2001; Gowaty *et al.*, 2002).

To capture these dynamical effects, we consider a model that gives a special emphasis to pair formation. Our main intention here is to show how a complex mating dynamics may create linkage disequilibrium and speciation. The assumptions we make are rather simple. We assume that both males and females have mating preferences and each individual has a variety of phenotypic traits. Consequently, mating preferences can be rather complex and can differ from individual to individual. Each individual tries to mate with the best individual he can, changing mate whenever a better mate appears. There may be certain biases towards certain traits in the population. However, in general, they are incapable of performing strong selection and genotypes do not deviate much from typical Hardy-Weinberg proportions. Nevertheless, if a new trait (coded on a single locus with a dominant allele) is introduced in a population, it is possible that these preference biases will be sufficiently strong (if these traits are discriminated by opposite-sex individuals) to produce disruptive sexual selection. Then, preferences build up and two groups of non-interbreeding individuals emerge (species). Our approach requires mutual sexual selection not only because both sexes must select traits on opposite-sex individuals, but also because mutual sexual selection creates dynamical instabilities that strongly enhance sexual selection. This consists of a new mechanism of sexual selection that we discuss thoroughly and it can be relevant when discussing other topics not related to sympatric speciation. Accordingly, fitness depends on how long matings last, and hence on how well preferences and traits of the individuals in a couple match. As a result of the dynamical instabilities resulting from mutual sexual selection, fitness may vary considerably from individual to individual and will depend on the preferences of all the other individuals in the population. Our theory requires that both sexes discriminate the same trait in the opposite sex, or at least that they perform

selection on correlated traits. It does not require that both sexes discriminate equally well the opposite-sex traits and it does not require that both sexes are equally selective.

This paper is organized as follows. In the next section, we explain how complex dynamics emerge when both sexes try to optimize their satisfaction. We show that finding an optimal configuration (a Nash equilibrium), whereby all individuals cannot improve further their satisfaction by mating with another individual, requires a considerable amount of time. This requires special attention to be given to the non-equilibrium mating dynamics present in a sexual population. We then introduce the model that is the subject of our study in the Results and Discussion section. There we start by showing that the fitness of each individual depends strongly on the non-equilibrium mating dynamics in the population. We then consider two simple analytical models that are important for understanding the simulation results of the more general model, which are presented afterwards. The paper ends with a discussion on how this theory could be tested experimentally and on how general it may be.

COMPLEX DYNAMICS FROM MUTUAL SEXUAL SELECTION

In nature, individuals show a large number of variable displaying traits. These may induce varied sensory stimuli, yielding different sexual responses in different individuals of the opposite sex. Individuals from both sexes attempt to optimize their satisfaction by mating with the best possible partner, following a ‘best option hypothesis’ (Ens *et al.*, 1993; Catry *et al.*, 1997). As discussed below, the mating dynamics of a population in which all individuals pursue selfish and conflicting goals can be quite complex. Consider a population with an equal number of males and females. To understand the complex nature of the mating dynamics generated by mutual sexual selection, one can assume that each individual ranks individuals from the opposite sex in a list, according to their preferences. A simple assumption will be to consider that each individual has a random preference list. This corresponds to a situation where only neutral (or nearly neutral) traits for sexual selection remain. Note that sexual selection does not necessarily mean the selection of traits relevant for adaptation, although it may help natural selection to operate more rapidly. It should also be stated that, in principle, the ranking in preference lists could also contain some ecological information to model, for instance, the preference for certain habitats (Bush, 1969; Grafe, 1997).

Consider, for instance, the simple case of a population with three males and three females. Each has a random preference list, as shown below:

	M1	M2	M3		F1	F2	F3
1	F1	F2	F2	1	M2	M1	M2
2	F2	F3	F1	2	M1	M3	M3
3	F3	F1	F3	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). It is possible that M1 mates with F1 and M2 mates with 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 and Shapley, 1962; Omero *et al.*, 1997). Although 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 (Gale and Shapley, 1962; Omero *et al.*, 1997) that leads to stable arrangements. This occurs if males propose to females and females only accept new pretenders if they improve their satisfaction. Nevertheless, even if a stable solution exists, the time needed to reach it tends to be quite long, due to the large number of degrees of freedom and the complex dynamics. This is intrinsically related to computational complexity, whereby some simple optimization problems require an exponentially large amount of time to be solved (see, for instance, the simple exposition in Hayes, 1997, and the references therein). In nature, we expect that the time required to find the optimal mating configuration should be considerably longer than the time involved in reproduction. As a result, the evolution of the system is dictated by the properties of the dynamical non-equilibrium configurations, which are quite different from the properties of an equilibrium configuration, like random mating or even the Gale and Shapley configuration.

In practice, the results we present do not depend on the strategy towards mating adopted by females. Note that individuals performing active strategies propose to opposite-sex individuals, whereas those adopting passive strategies do not propose. Independently of the strategy, all individuals have a preference list, which they use to accept or reject new mates. For example, passive females do not propose to males but nevertheless they have a list and accept or reject a proposing male according to it.

A MODEL FOR SYMPATRIC SPECIATION BY MUTUAL SEXUAL SELECTION

For speciation to emerge as a result of sexual selection, a new secondary sexual trait must be introduced in a population [due to mutations or to the activation of certain genes (Rutherford and Lindquist, 1998), or induced by new ecological conditions] or existing 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. For simplicity, we will refer to this trait as the ‘new trait’, even if, as explained, this trait may already exist in the population.

We consider discrete generations of a population with an equal number, N_{total} , of males and females. The genetic information on each individual controls several characters. It could be considered that a sexual locus may control the strategy towards mating when studying the selection of these strategies, but we found that this does not change the results of speciation. Therefore, we assumed that males and females take active and passive strategies towards mating, respectively.

One locus with two alleles (we assume dominance) accounts for a secondary sexual trait (A or B). Several independent loci with two alleles (+ or –) define a quantitative preference for one trait. Each individual ranks individuals of the opposite sex in a list of preferences. These preference lists are defined with a simple step-like structure. If n_+ is 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 probability $f_+(n_+) = [4n_+(1 - n_+)]^{\nu/2}$ of non-preferred mates to be ranked within the first N_A (N_B) positions (N_A and N_B being the number of individuals with phenotype A and B , respectively). The positive exponent ν

controls how efficiently individuals discriminate mates with the different traits. For small values of ν , deviations from an unbiased arrangement produce poor discrimination, as can be seen in Fig. 1.

For each iteration, all individuals (with an active strategy towards mating) are given one chance to find a *better* partner. New matings occur only if they improve the satisfaction of both individuals in the couple during courtship, breeding or both, as happens in nature (Ens *et al.*, 1993; Catry *et al.*, 1997; Triefenbach and Itzkowitz, 1998; Streif and Rasa, 2001). An individual improves his satisfaction if he mates with an individual d positions higher than the rank of his current mate in his preference list (if he is single, then any new potential mate improves his satisfaction). Variation in this parameter allows a relaxation of strong mating preferences. If d is large, a certain indifference exists relative to new mates (only if the new mate is considered much better will it justify changing mates).

The process repeats until $2N_{\text{total}}$ offspring are born. One offspring of each sex is born if a couple remain together during a courtship time t_c , plus a reproduction time t_r (in relation to speciation, the relevant parameter is simply $t_c + t_r$). During reproduction time, females cannot engage in new matings, but males may find a better partner. Offspring genotypes are found using Mendelian genetic rules.

By introducing a probability μ 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. An overview of the several steps involved in the algorithm is shown in Fig. 2.

The model just defined tries to be a minimal model capturing the complex dynamics involved in the reproduction of a sexual population. It is important to note that it should be understood in a quite general sense. For instance, the terminology ‘mating’ was used in our model to characterize the moment when both a male and a female invest their time (and possibly resources) in reproduction. This can simply mean the occasion when a male attracts the attention of a female and the female corresponds positively with some signalling. It can also correspond to some stronger relation between a male and a female, like building a nest or rearing offspring together. In the former case, this has been referred to in the literature simply as ‘spending more time together’ (Romero-Pujante *et al.*, 2002; see also Gowaty *et al.*, 2002). Mate switching can then be difficult to establish and quantify,

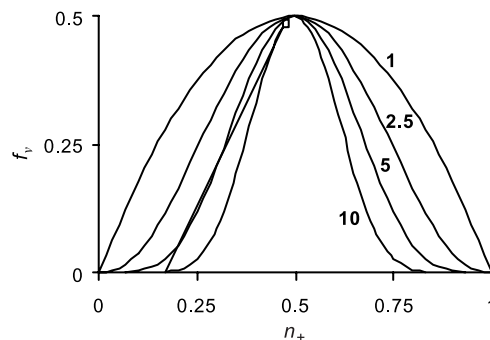


Fig. 1. Preference lists are constructed with a step-like structure. In the first positions, there is a fraction $f_v(n_+)$ of individuals with non-preferred traits. The parameter ν controls how efficiently individuals with a biased arrangement of alleles (n_+ away from $1/2$) discriminate mates with preferred traits. The function f_v is shown for $\nu = 1, 2.5, 5, 10$.

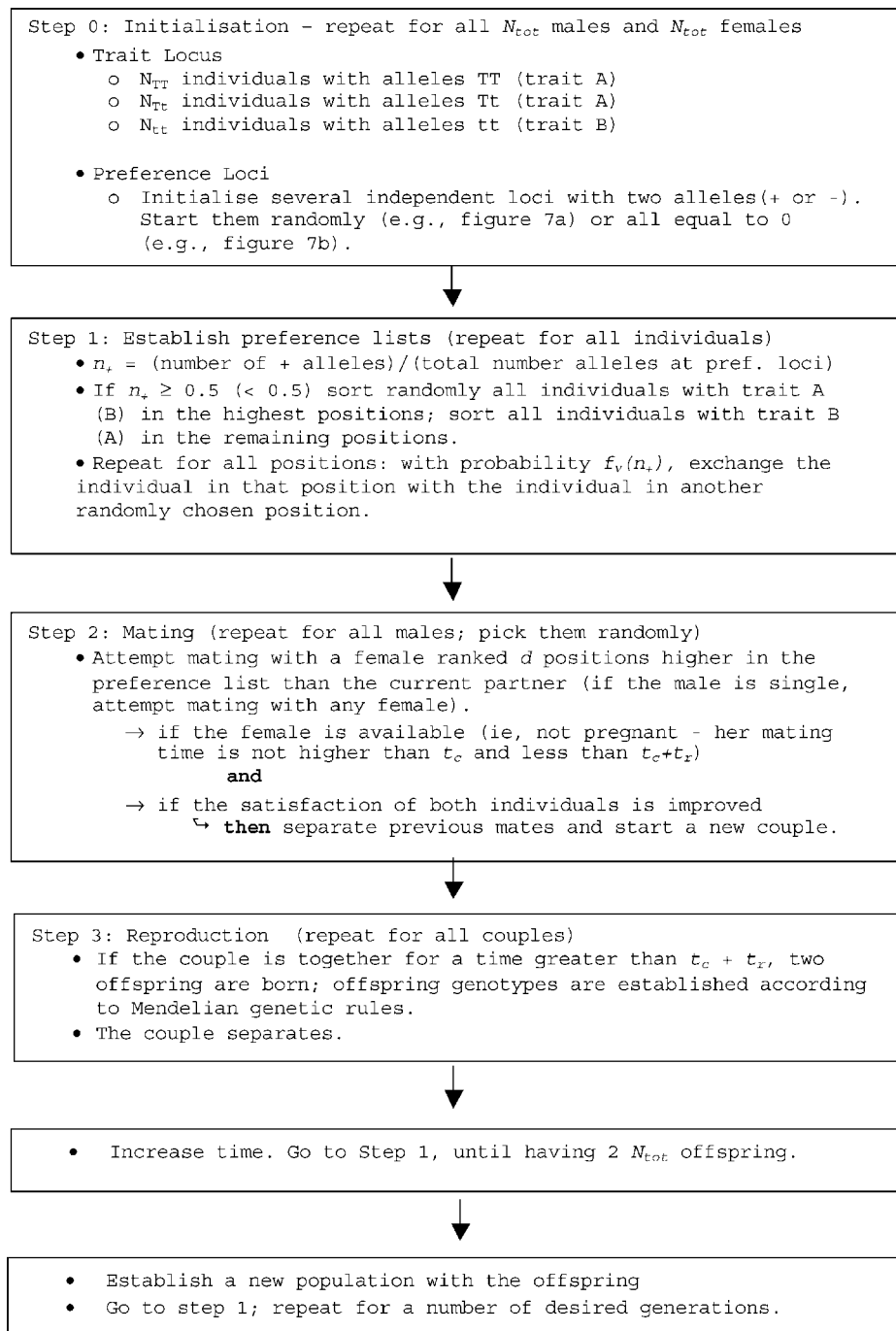


Fig. 2. Overview of the main steps involved in the algorithm. To keep the description simple, females follow passive strategies towards mating and $\mu = 0$ (see text for details).

especially in natural populations. The case of a stronger relation is simpler to identify and mate switching is called a ‘divorce’. Divorces have clearly been seen in monogamous species. They appear to originate from the appearance of a ‘better mate’ (Ens *et al.*, 1993; Catry *et al.*, 1997) and they are known to lead to differential reproductive rates among the individuals in the population (Catry *et al.*, 1997). This is consistent with the simple assumptions in our model. As our results do not depend on the particular values of the parameters t_c and t_r , but only on their sum ($T = t_c + t_r$), our model should apply equally well to species for which parental care is important ($t_r > 0$) and to species for which the main time investment is spent before copulation ($t_c > 0$, $t_r \approx 0$).

Note also that male–male contests are already incorporated in our model. Indeed, in many species, when a male addresses a female, as in our model, he is involved in a contest, with the male controlling that female. Mating often depends on the result of this contest. In many cases, females prefer the winner, usually the stronger male. Hence, in our model, the decisions of females may be seen as the outcome of implicit male–male contests. Contests are an opportunity for males to display some of their ‘traits’ and for females to select them. But due to the costs involved in these contests, one should expect that new male pretenders choose the females that are worth fighting for. Of course, male–male contests do not always determine mating preferences, and often females run away or copulate with young males that have not managed to defeat older males. Hence, diversity in mate choice may in principle exist in both sexes, even for species for which male–male contests are essential to define mate choice.

RESULTS AND DISCUSSION

Consider first a population with very poor discrimination for the newly introduced trait ($f_v = 0.5$; preference lists are completely random). In Fig. 3, 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, relative to what one would expect if matings were random (this

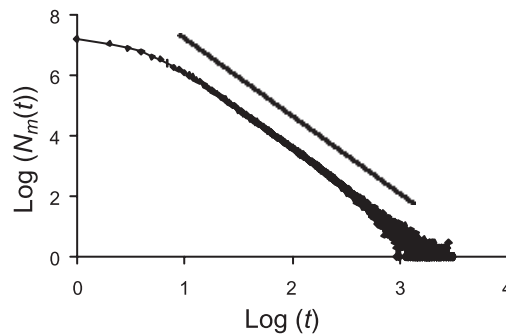


Fig. 3. Number of matings $N_m(t)$ lasting for t iterations. Altogether, 500 populations were sampled over 10,000 iterations for the model without reproduction events ($t_c = t_r = +\infty$). The distribution shows power law behaviour, $N_m(t) \approx t^{-\tau}$, with $\tau \approx 2.5$. τ is independent of the number of individuals (for populations larger than 200 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 in the evolution of the population.

could correspond to the case where we assign a certain probability of breaking a couple, for instance due to mortality or due to a fixed probability of changing mates, obtaining a typical well-defined mating lifetime with an associated exponential distribution). Thus pair formation will certainly play a role in sexual selection theory, as it distinguishes individual fitnesses over several scales. For instance, some couples can have ten times more offspring than others. This is considerably different to what happens in random mating theories or if we consider the stable Gale–Shapley configuration, where each individual remains with a mate anyway. For speciation, another important consequence is that the stability of a couple is context-dependent: the same couple may have very different lifetimes depending on the preferences present in the *whole* population.

To understand how speciation may emerge, consider a population for which discrimination relative to the new trait is large. Start by considering an extreme case, where discrimination is so great that any individual would have a well-defined preference, ranking all potential mates with the preferred trait first. Note that, 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 may prefer a mate with trait *B*. Thus we can classify males and females in four groups, *AA*, *AB*, *BA* and *BB*, the first letter standing for the trait and the second for the preference. From hereon, *A* and *B* will always refer to phenotypic characters (trait or 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 long enough to accomplish reproduction. Indeed, mating instabilities reduce strongly the lifetime of couples for whom traits and preferences do not match. From the female's point of view, *AA* and *BA* females prefer *AA* or *AB* males, which produces indirect competition between *AA* and *AB* males. This competitive scenario has a mathematical expression. The growth of the number of males with trait *I* and preference *J* (*I, J = A, B*), m_{IJ} , depends on

$$\sum_{P,Q,K,L} \lambda_{PQKL}^v w_{PQ,KL} m_{PQ} f_{KL}$$

(apart from a normalization factor), where $w_{PQ,KL}$ is the 'fitness of the couple' formed by a male *PQ* and a female *KL*, and λ_{PQKL}^v is a recombination factor derived from Mendelian rules.

Now, we consider two simple analytical models. They will help to understand how crucial it is to consider the effect of dynamical instabilities. A strong selection mechanism results, which is essential to promote speciation in our general model.

First, we do not include the dynamical instabilities. Then, as is usually done in sexual selection theories (Futuyma, 1998), we associate a lower and *constant* fitness with matings for which traits and preferences do not match. For instance, $w_{II,JI} = w$ would be maximal when the preferences of both mates in the couple are satisfied, $w_{IJ,JK} = w_{JI,KJ} = sw$ ($K \neq I$, $0 \leq s < 1$) when only one individual is satisfied, and $w_{II,KL} = s^2 w$ ($J \neq K$, $L \neq I$) when both mate preferences do not match with the other mate's trait. Although lengthy, studying the evolution of such a population is straightforward. As can be seen in Fig. 4a (obtained from analytical expressions derived in the Appendix), for any $s < 1$, the population invariably falls into a monomorphic population, where only *AA* individuals remain in the end. This results from the dominance assumed at both the trait and preference loci. This result shows that

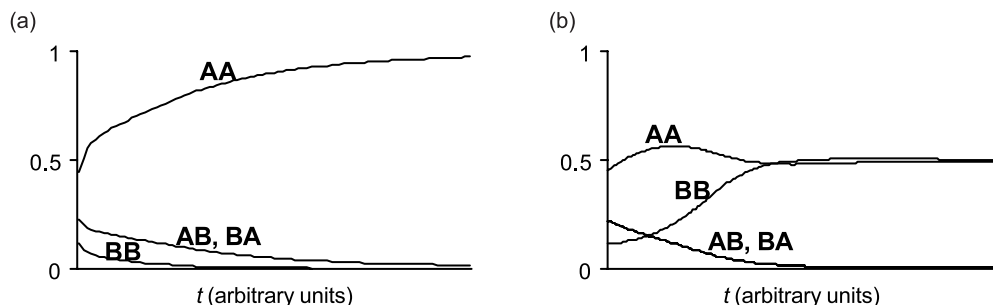


Fig. 4. The evolution of the normalized phenotype frequencies for models with two loci – trait and preference – with a dominant allele at each (obtained from the analytical expressions derived in the Appendix). (a) Multiplicative model where couples have fitness w , ws or ws^2 , depending on whether there is, respectively, zero, one or two mates in the couple with their preferences not satisfied. Here $w = 1$, $s = 0.8$. (b) Model with dynamic instabilities, $T = 3$, where only couples whose traits and preferences match are considered. Note that for $T = 2$, this model would produce a result similar to that presented in (a), as mating instabilities would not be strong enough to trigger the speciation event shown in (b).

a mechanism like the one proposed by Higashi and co-workers (1999) is not able to produce speciation when a dominant allele controls the trait phenotype.

A conceptually new set of circumstances arises if the effect of dynamical instabilities is taken into account. Dynamical instabilities strongly renormalize the w_{IJKL} weights, because fitness has an important component related to the ability of a couple to stay together for a time $T = t_c + t_r$. This depends strongly on the couple under consideration and on the interactions of this couple with the rest of the population. The probability that a couple $AA \times AA$ achieves successful reproduction is given by the probability that neither partner of the couple finds a better mate during T time units. If one considers that, on average, the AA male (female) is ranked in the middle of the first m_A (f_A) positions in the female's (male's) preference list (where the individuals with trait A lie), then this implies that $w_{AA,AA} \propto \alpha (1 - m_A/2N)^T (1 - f_A/2N)^T$, where α is a constant.

This result embodies a strong selection mechanism. To see this, consider also the fitness of a couple $AB \times AA$: $w_{AB,AA} \propto \alpha (1 - m_A/2N)^T (f_A/2N)^T$. Thus, $w_{AA,AA}/w_{AB,AA} \propto (2N/f_A - 1)^T$, which means that the fitness of $AA \times AB$ couples is negligible for sufficiently large values of T . For this reason, only couples for which traits and preferences match will contribute to the evolution of the population. This strong selection mechanism is extreme in the case where discrimination is perfect. Later in the paper, we present numerical results showing that it also operates when this is not the case.

In contrast to what happened when fitness coefficients were fixed, fitness is now a context-dependent quantity: it varies according to the proportion of individuals with a given trait (e.g. trait B) in the population. If the number of individuals with trait B is small, then the fitness of BB individuals will be larger than the fitness of AA individuals. This is a result of the competition for mates in the population and it is extremely important because it prevents AA individuals from dominating. Since BB individuals do not compete with AA individuals and are less numerous than them at the beginning (starting from a population following Hardy-Weinberg proportions; see Fig. 4b), they have higher fitness and can thus increase in frequency.

If we neglect the effects of recombination, the evolution of the m_{IJ} population will be given by a set of simple coupled differential equations, of the form: $dm_{IJ}/dt = aw_{IJ,JI}f_{JI}m_{IJ} \equiv am_{IJ}^2w_{IJ,JI}$. As sexual selection will only keep those individuals reproducing at the highest rate, a *competitive exclusion principle* with symmetry breaking emerges. Then only $AA \times AA$ and $BB \times BB$ couples, or $AB \times BA$ and $BA \times AB$ couples, can be selected. If now one considers recombination with one locus for the trait and one for the preference (and assuming dominance), this competition scenario can be tackled analytically as shown in the Appendix. Then, only $AA \times AA$ and $BB \times BB$ couples are selected in the end, as shown in Fig. 4b. This corresponds to the emergence of two new species and homotypic preferences, as in this final population AA and BB individuals rarely mix.

Note that this happens if the sexual selection mechanism described is sufficiently strong – that is, if T is sufficiently large. We can give a rough estimate of how large T must be to achieve speciation, considering $m_A \equiv N$ and $m_B \equiv 1$. We ask that the growth due to $BB \times BB$ couples ($m_{BB}^2w_{BB,BB}$) is larger than that due to $AA \times AA$ couples ($m_{AA}^2w_{AA,AA}$). Then we get $T > \ln(N)/\ln 2 \approx \ln N$. This logarithmic growth means that T is relatively small and independent of population sizes. Hence, it should be observed in natural populations.

In most cases in nature, discrimination for some secondary sexual traits is not perfect. Hence the previous model may be considered an oversimplification. However, we will show that in a population with no well-defined preferences for either trait, small preference biases may be enough to trigger a speciation event, following the arguments discussed above.

To consider this more general situation, we used the model of Fig. 2, where several additive independent loci control a quantitative genetic preference. If we consider a large number of loci controlling the preferences, then random configurations produce only small preference tendencies. The more biased the arrangements of preference alleles are, the larger will be the number of individuals with a certain trait in the first positions. As discussed above, the function $f(n_+)$ establishes the relation between bias in preference loci and the intensity of discrimination. In Fig. 5a, we show how sympatric speciation emerges, starting

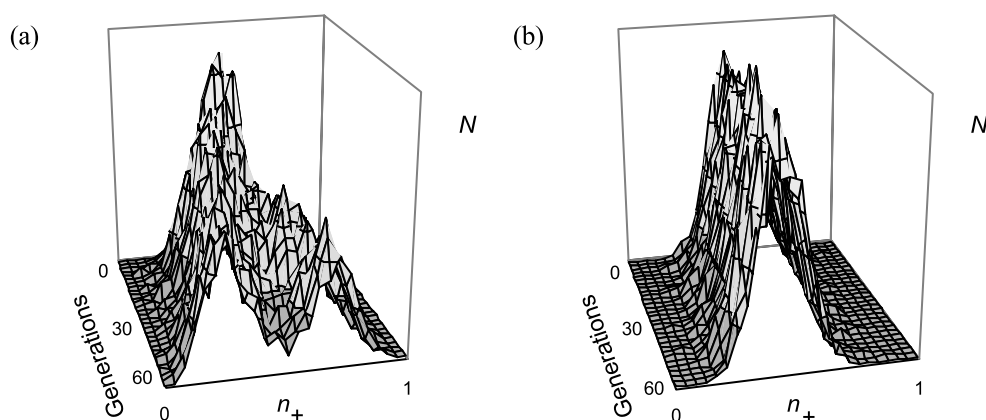


Fig. 5. Evolution of phenotype frequencies starting from a population with random initial genotypes. One dominant locus with two alleles controls the trait, and 12 independent loci with two alleles each control the preference intensity. For n_+ close to 1 (0), mates with trait A (B) tend to be preferred. Sympatric speciation quickly emerges (a) if sufficient discrimination of mating traits exists ($v = 5$), or is prevented (b) if discrimination is insufficient ($v = 3$) ($N_{\text{total}} = 500$, $t_c = t_r = 30$).

from a population with random genotypes. Even for species with a considerable number of independent genes controlling the preferences, speciation is achieved within just a few generations. Due to trait dominance, only AA or BB individuals with a homozygous genotype last in the end. Prezygotic isolation is thus achieved, giving way to species divergence. In this example, trait discrimination is the same for males and females (same v). However, speciation could also be achieved if we had chosen higher trait discrimination for females than for males (higher v ; $v_{\text{females}} = 8$ and $v_{\text{males}} = 2.5$) as it is likely to happen in nature. In fact, trait discrimination needs to operate on both sexes, but its intensity may vary. This is because when a stable couple is formed, selection then operates on the genotypes of both male and female, and at both the trait and preference loci. If this had not been the case, recombination would then mix genes that had been under sexual selection with others that had not. Hence, disruptive sexual selection can be prevented if $f(n_+)$ departs slowly from the unbiased arrangement of alleles (corresponding to a difficult discrimination) as shown in Fig. 5b.

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 μ parameter. Large values of μ reduce the effects of the non-random pair formation created by the complex dynamics. Consequently, above a certain threshold value, speciation is prevented (in the example of Fig. 5a, for $\mu > 6 \times 10^{-4}$ mutations per generation and per allele) and a population with genotype frequencies close to the Hardy-Weinberg proportions remains.

Multiplicative ornamentation costs can also be considered within our framework by assigning a birth probability, related to the parent's trait. As Fig. 6 shows, if ornamentation costs for both traits are similar, then speciation is not prevented, although it changes the relative frequencies of the two emerging species. If ornamentation costs are strong, then trait shift occurs instead of speciation.

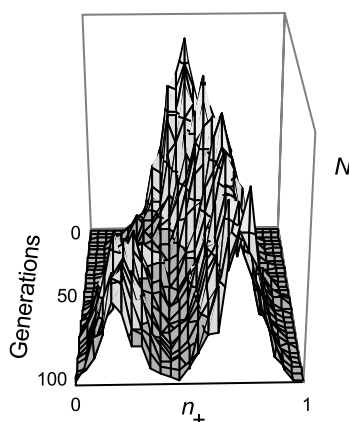


Fig. 6. Impact of ornamentation costs on speciation. Here $v=7$ (for both males and females), $N_{\text{total}} = 500$, $t_c = t_r = 30$, one dominant locus controls the trait and 12 independent loci control the preferences. Ornamentation costs were introduced simply by assigning a fertility probability to each offspring, which is the product of the fertilities of the parents. Speciation still emerges if the costs of the traits are similar, but the frequencies of the two daughter species become different. In this case, individuals with trait B (A) have a fertility of 0.8 (1).

Another point worth mentioning is that speciation may not require very strong mate choice. For instance, for the population with $N_{\text{total}} = 500$, $t_c = t_r = 30$, $v_{\text{females}} = v_{\text{males}} = 7$ and 12 independent loci controlling the preferences, speciation is achieved for d as big as 50.

Our theory assumes that in a population, each individual presents many phenotypic traits, each contributing in a complicated way to establish other individuals' mate choices. Many of these traits may not have a strong impact in mate choice, such that a phenotypic polymorphism remains in the population (they would be approximately neutral in what concerns sexual selection). In Fig. 7a, we show a population in which relative discrimination against a given trait is poor in the first 150 generations. The population consists of individuals with both traits and weak discrimination. There is no relevant correlation between traits and preferences in the individuals. This result shows that the theory is consistent, in the sense that, in this 'poor discrimination' regime, traits can co-exist, agreeing with our initial assumption that each individual has a different preference list. At generation 150, discrimination is increased above a threshold value (for instance, due to different environmental conditions, such as light, or due to the activation of 'hidden' genes that could highlight a certain trait) and a quick speciation event emerges. An alternative picture is presented in Fig. 7b, following the recent proposal by Doebeli and Dieckmann (2000). It starts with a monomorphic population for a given trait and sufficiently strong trait discrimination. Then, mutations and a release of natural selection pressure (as a result of change of habitat, for instance) allow genetic drift to operate on both traits and preferences. They develop variability, until individuals with preferences for both traits exist in the

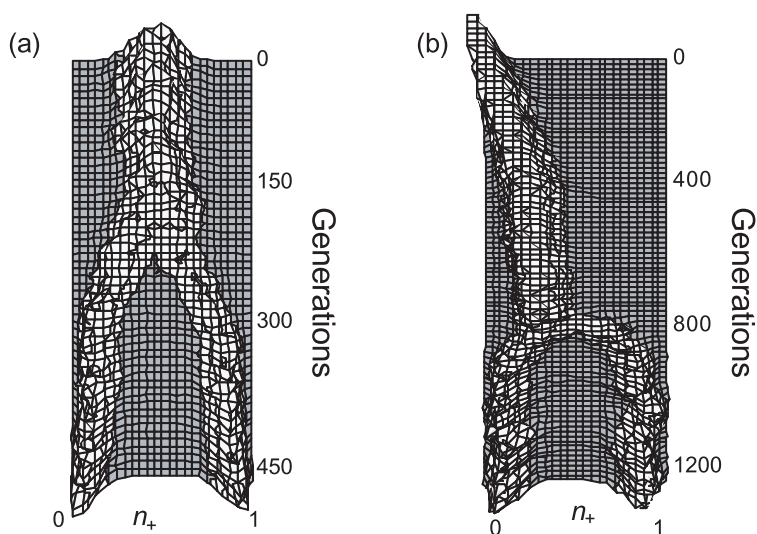


Fig. 7. Evolution of phenotype frequencies (one dominant locus controls the trait; 12 independent loci control the preference intensity): (a) starting from a population with random initial genotypes, $\mu = 3 \times 10^{-4}$ per allele and weak trait discrimination ($v = 3$). At generation 150, discrimination is increased ($v = 7$); (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 $v = 7$. 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.

population. Sympatric speciation then emerges. In practice, this later scenario needs more generations to reach the speciation disruptive configuration.

The threshold value for the discrimination parameter, v_{th} , depends on the details of the model, like the details of the imposed dynamics or the values of the other parameters. For instance, v_{th} decreases if one assumes that females also take active strategies towards mating (for the example cited previously, speciation emerges with $v_{females} = 6.5$ and $v_{males} = 2.5$), which is to be expected as the correlated dynamics influences speciation. Thus, if we include male–male interactions, v_{th} would also decrease. Also, the rather crude step-like structure of preference lists tends to increase v_{th} considerably, as much of the dynamics is dominated by the first positions in preference lists, not the last. Hence the actual value of v_{th} is not thought to be especially important.

The important point is that v_{th} exists and is finite. In practice, this means that in natural populations, a certain amount of discrimination towards the several traits may exist ($v > 0$), in such a way that, as a result of recombination (Felsenstein, 1981), they can co-exist and speciation is prevented. However, changes in environmental conditions can enhance discrimination for a given trait and promote a speciation event in just a few tenths of generations. Finally, note that although v could also evolve, it would do so on much larger time-scales than those considered in the quick speciation events reported in this paper. Hence the evolution of v should not change our results for speciation.

As sexual selection does not imply natural selection, the two daughter species may differ in non-ecological traits (Seehausen *et al.*, 1999). And it could be that one of them is less well-adapted. In that case, competitive exclusion would tend to eliminate this daughter species. However, other adaptations could take place afterwards, preserving this daughter species and promoting species divergence.

Our theory simply assumes that males and females have preferences over the same traits. This is in line with recent experimental evidence reported by Seehausen *et al.* (1999). The theory should also apply if the traits under selection by both sexes are different but correlated, as occurs most often in practice, due to the small world properties of protein networks (Jeong *et al.*, 2000). Although female preferences have been studied extensively (Andersson, 1994; Futuyma, 1998), male preferences are usually neglected. Nevertheless, there is now mounting experimental evidence for the existence of male choice (Burley *et al.*, 1982; Rutowski, 1982; Jones and Hunter, 1993; Wilhelmi and Preuss, 1996; Seehausen *et al.*, 1999; Amundsen and Forsgren, 2001; Katvala and Kaitala, 2001; Fordyce *et al.*, 2002; Romero-Pujante *et al.*, 2002). This is an indirect outcome of natural selection, as males would otherwise incur potential opportunity costs: those having the ability to perceive ‘good genes’ in females or predators’ mimicry should certainly be favoured. It should also be an outcome of sexual selection, since if females have preferences, then any male capable of identifying interested females will be better off. However, sometimes in practice male choice can be difficult to detect (Fordyce *et al.*, 2002), as males usually are the ones adopting active strategies towards mating and thus are seen performing courtship to many females. Also, in some species, male mating success varies considerably among the males. However, we do not believe that males mate randomly. Rather, they may have to perform some sort of mate choice to achieve their high mating rates. Finally, we call the attention of readers to the interesting results of Gowaty and co-workers (2002). They showed that in *Drosophila pseudoobscura*, both sexes express varied interest in the other sex and that ardent males discriminate females.

It is important to test our theory experimentally. Due to its robustness, we believe that it could apply to a wide variety of taxa, ranging from simple organisms like yeasts to complex organisms like mammals. And, indeed, it appears to agree with the major findings of Seehausen *et al.* (1999) (however, see also Lande *et al.*, 2001). It should be possible to adapt this model to allow characteristics of particular species to be taken into account. We believe that similar results to those presented here should be obtained.

In yeasts, it is now clear that both mates in a couple choose their partners (Jackson and Hartwell, 1990). Furthermore, many genes can be involved in the several complex steps of this process (White and 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 in yeasts, then there are many implications and 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 gain a better understanding on how these correlate with the intracellular state.

The way it has been presented here, our model may not appear to apply to plants. For instance, it is clear that far more pollen grains exist than ovules, and that when a pollen grain does not reach an ovule in one plant, it is not given the opportunity to search for an ovule in another plant. However, we believe that dynamical instabilities may also be important to understand speciation in plants. In fact, it has recently been shown that a mutual exchange of signals is necessary for a pollen grain to fertilize an ovule (Wilhelmi and Preuss, 1996), which may even involve synchronization between the male and female gametophyte physiological activity (Feijó *et al.*, 2001). It is known that the pistil operates as an arena for sexual selection, where complex pollen–pollen and pollen–pistil interactions develop (see Hormaza and Herrero, 1994, and references therein). This competitive environment seems to be essential for optimal reproduction. For instance, pollen grains are often accumulated before germination, and higher pollen loads tend to be beneficial for offspring vigour. Hence, it appears that sexual selection operates in collective competitive environments, responding to the sequential physiological steps developed by the male and female gametophyte. Dynamical instabilities may occur; for instance, at a given time some pollen grains may be favoured [for example, through the depletion of nutrients (Hormaza and Herrero, 1994)], whereas next some others may be the chosen ones. ‘Bad choices’ may reduce offspring vigour and, indeed, it has been reported that too high pollen loads may also be prejudicial for offspring vigour (Niesenbaum and Schueller, 1997). Furthermore, Klips (1999) has shown that some sympatric species may interbreed if pure loads of foreign pollen are applied to stigmas. However, interbreeding is considerably reduced for pollen mixtures. This has been suggested to be the result of pollen competition and resembles the outcome of the sexual competition mechanism described in this paper, but more work is necessary along these lines (Lankinen and Skogsmyr, 2002). Although much remains unknown about this topic, it is likely that dynamical instabilities may also be relevant to understand selection mechanisms in plants.

ACKNOWLEDGEMENTS

We acknowledge Francisco Dionísio and Benoît Douçot for critical reading of the manuscript. We thank R.M. Conde for earlier collaboration, S. van Doorn, A. Luis, M.A. Santos, J. Feijó and I. Pimentel for discussions.

REFERENCES

- Albertson, R.C., Markert, J.A., Danley, P.D. and Kocher, T.D. 1999. Phylogeny of a rapidly evolving clade: the cichlid fishes of Lake Malawi, East Africa. *Proc. Natl. Acad. Sci. USA*, **96**: 5107–5110.
- Amundsen, T. and Forsgren, E. 2001. Male mate choice selects for female coloration in a fish. *Proc. Natl. Acad. Sci. USA*, **98**: 13155–13160.
- Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Boughmann, J.W. 2001. Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature*, **411**: 944–948.
- Burley, N., Krantzberg, G. and Raduran, P. 1982. Influence of colour-banding on the conspecific preferences of zebra finches. *Anim. Behav.*, **27**: 686–698.
- Bush, G.L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution*, **23**: 237–251.
- Catry, P., Ratcliffe, N. and Furness, R.W. 1997. Partnerships and mechanisms of divorce in the great skua. *Anim. Behav.*, **54**: 1475–1482.
- Doebeli, M. and Dieckmann, U. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Am. Nat.*, **156**: S77–S101.
- Ens, B.J., Safriel, U.N. and Harris, M.P. 1993. Divorce in the long-lived and monogamous oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? *Anim. Behav.*, **45**: 1199–1217.
- Feijó, J.A., Sainhas, J., Holdaway-Clarke, T., Cordeiro, M.S., Kunkel, J.G. and Hepler, P.K. 2001. Cellular oscillations and the regulation of growth: the pollen tube paradigm. *Bioessays*, **23**: 86–94.
- Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution*, **35**: 124–138.
- Fordyce, J.A., Nice, C.C., Forister, M.L. and Shapiro, A.M. 2002. The significance of wing pattern diversity in the Lycaenidae: mate discrimination by two recently diverged species. *J. Evol. Biol.*, **15**: 871–879.
- Futuyma, D.J. 1998. *Evolutionary Biology*, 3rd edn. Sunderland, MA: Sinauer Associates.
- Gale, D. and Shapley, L.S. 1962. College admission and the stability of marriage. *Am. Math. Monthly*, **69**: 9–14.
- Gavrilets, S. 2000. Rapid evolution of reproductive barriers driven by sexual conflict. *Nature*, **403**: 886–889.
- Gowaty, P.A., Steinichen, R. and Anderson, W.W. 2002. Mutual interest between the sexes and reproductive success in *Drosophila pseudoobscura*. *Evolution*, **56**: 2537–2540.
- Grafe, T.U. 1997. Costs and benefits of mate choice in the lek-breeding reed frog, *Hyperolius marmoratus*. *Anim. Behav.*, **53**: 1103–1117.
- Hayes, B. 1997. Can't get no satisfaction. *Am. Sci.*, **85**: 108–112.
- Higashi, M., Takimoto, G. and Yamamura, N. 1999. Sympatric speciation by sexual selection. *Nature*, **402**: 523–526.
- Hormaza, J.I. and Herrero, M. 1994. Gametophytic competition and selection. In *Genetic Control of Self-incompatibility and Reproductive Development in Flowering Plants* (E.G. Williams, A.E. Clarke and R.B. Knox, eds), pp. 372–400. Dordrecht: Kluwer Academic.
- Jackson, C.L. and Hartwell, L.H. 1990. Courtship in *S. cerevisiae*: both cell types choose mating partners by responding to the strongest pheromone signal. *Cell*, **63**: 1039–1051.
- Jeong, H., Tombor, B., Albert, R., Oltvai, Z.N. and Barabási, A.-L. 2000. The large-scale organization of metabolic networks. *Nature*, **407**: 651–654.
- Jones, I.L. and Hunter, F.M. 1993. Mutual sexual selection in a monogamous seabird. *Nature*, **362**: 238–239.
- Katvala, M. and Kaitala, A. 2001. Male choice for current female fecundity in a polyandrous egg-carrying bug. *Anim. Behav.*, **61**: 133–137.
- Klips, R.A. 1999. Pollen competition as a reproductive isolating mechanism between two sympatric *Hibiscus* species (Malvaceae). *Am. J. Bot.*, **86**: 269–272.

- Kondrashov, A.S. and Kondrashov, F.A. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature*, **400**: 351–354.
- Lande, R. 1982. Rapid origin of sexual isolation and character divergence in a cline. *Evolution*, **36**: 213–223.
- Lande, R., Seehausen, O. and van Alphen, J.J.M. 2001. Mechanisms of rapid sympatric speciation by sex reversal and sexual selection in cichlid fish. *Genetica*, **112**: 435–443.
- Lankinen, A. and Skogsmyr, I. 2002. Pollen competitive ability: the effect of proportion in two-donor crosses. *Evol. Ecol. Res.*, **4**: 687–700.
- Maynard Smith, J. 1966. Sympatric speciation. *Am. Nat.*, **916**: 637–650.
- Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, MA: Harvard University Press.
- Miller, R.L., Mojares, J.J. and Ram J.L. 1994. Species-specific sperm attraction in the zebra mussel, *Dreissena polymorpha*, and the quagga mussel, *Dreissena bugensis*. *Can. J. Zool.*, **72**: 1764–1770.
- Niesenbaum, R.A. and Schueller, S.K. 1997. Effects of pollen competitive environment on pollen performance in *Mirabilis jalapa* (Nyctaginaceae). *Sex. Plant Repro.*, **10**: 101–106.
- Omero, M.J., Dzierzawa, M., Marsili, M. and Zhang, Y.-C. 1997. Scaling behavior in the stable marriage problem. *J. Phys. I France*, **7**: 1723–1729.
- Panhuis, T.M., Butlin, R., Zuk, M. and Tregenza, T. 2001. Sexual selection and speciation. *Trends Ecol. Evol.*, **16**: 364–371.
- Parker, G.A. and Partridge, L. 1998. Sexual conflict and speciation. *Phil. Trans. R. Soc. Lond. B*, **353**: 261–274.
- Rice, W.R. and Hostert, E.E. 1993. Perspective: laboratory experiments on speciation: what have we learned in forty years? *Evolution*, **47**: 1637–1653.
- Romero-Pujante, M., Hoi, H., Blomqvist, D. and Valera, F. 2002. Tail length and mutual mate choice in bearded tits (*Panarus biarmicus*). *Ethology*, **108**: 885–895.
- Rutherford, S.L. and Lindquist, S. 1998. Hsp90 as a capacitor for morphological evolution. *Nature*, **396**: 336–342.
- Rutowski, D.L. 1982. Epigamic selection by males as evidenced by courtship partner preferences in the checkered white butterfly (*Pieris protodice*). *Anim. Behav.*, **30**: 108–112.
- Schliwen, U.K., Tautz, D. and Paabo, S. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature*, **368**: 629–632.
- Seehausen, O., van Alphen, J.J.M. and Lande, R. 1999. Color polymorphism and sex ratio distortion in a cichlid fish as an incipient stage in sympatric speciation by sexual selection. *Ecol. Lett.*, **2**: 367–378.
- Streif, M. and Rasa, O.A.E. 2001. Divorce and its consequences in the Common Blackbird *Turdus merula*. *Ibis*, **143**: 554–560.
- Takimoto, G., Higashi, M. and Yamamura, N. 2000. A deterministic genetic model for sympatric speciation by sexual selection. *Evolution*, **54**: 1870–1881.
- Triefenbach, F. and Itzkowitz, M. 1998. Mate switching as a function of mate quality in convict cichlids, *Cichlasoma nigrofasciatum*. *Anim. Behav.*, **55**: 1263–1270.
- Turelli, M., Barton, N.H. and Coyne, J.A. 2001. Theory and speciation. *Trends Ecol. Evol.*, **16**: 330–343.
- Turner, G.F. and Burrows, M.T. 1995. A model of sympatric speciation by sexual selection. *Proc. R. Soc. Lond. B*, **260**: 287–292.
- van Doorn, G.S. and Weissing, F.J. 2001. Ecological versus sexual selection models of sympatric speciation. *Selection*, **2**: 17–40.
- van Doorn, G.S., Noest, A.J. and Hogeweg, P. 1998. Sympatric speciation and extinction driven by environment dependent sexual selection *Proc. R. Soc. Lond. B*, **265**: 1915–1919.
- Wilhelmi, L.K. and Preuss, D. 1996. Self-sterility in *Arabidopsis* due to defective pollen tube guidance. *Science*, **274**: 1535–1537.
- White, J.M. and Rose, M.D. 2001. Yeast mating: getting close to membrane merger. *Curr. Biol.*, **11**: R16–R20.

**APPENDIX: MATHEMATICAL APPROACH TO THE SEXUAL COMPETITION
SCENARIO FOR A POPULATION WITH TWO LOCI, ONE FOR TRAIT
AND ONE FOR PREFERENCE, WITH A DOMINANT ALLELE AT EACH**

Here we outline a mathematical approach for the case where only one allele is taken in the preference locus and we will show that sympatric speciation emerges from a competitive exclusion principle. Our results depend crucially on the effect of the dynamical correlations in the mating period. To see this, we will start by showing what would happen if these were to be neglected. We consider a multiplicative model where a fixed lower fitness is associated with couples whose preferences and traits do not match. The number of offspring (fitness) from each couple is given by a fixed parameter that depends on the traits and preferences. If traits and preferences of both mates match, the couple has fitness w ; if one individual's preference is not satisfied, fitness is ws ; if both mates' preferences are not respected, fitness is ws^2 .

It is lengthy but straightforward to obtain the evolution of genotype frequencies in the population. In a two-loci, two-allele model, we have nine genotypes, denoted by ij (representing displaying traits and preferences, respectively), with $i, j = 1, 2, 3$. We denote genotype 2, the dominant heterozygous, and genotype 1, the dominant homozygous. The number of males (females) with genotype ij is m_{ij} (f_{ij}). Here lower-case or numerical indices always denote genotypes, whereas upper-case is associated with phenotypes. For instance, m_{22} represents the number of males with heterozygous genotypes on both the trait and the preference loci, whereas m_{AA} is the number of males with phenotype A at both the trait and preference loci. As a matter of illustration, we consider below the evolution of the number of males with genotype 33 (which, in the present case, is equal to the number of males with phenotype BB):

$$\begin{aligned} dm_{33}/dt = & wm_{33}f_{33} + wsm_{32}f_{33}/2 + wsm_{33}f_{32}/2 + ws^2m_{32}f_{32}/4 + wsm_{23}f_{33}/2 + ws^2m_{22}f_{33}/4 + wm_{23}f_{32}/ \\ & 4 + wsm_{22}f_{32}/8 + wsm_{33}f_{23}/2 + wm_{32}f_{23}/4 + ws^2m_{33}f_{22}/2 + wsm_{32}f_{22}/8 + ws^2m_{23}f_{23}/4 + wsm_{22}f_{23}/ \\ & 8 + wsm_{23}f_{22}/8 + wm_{22}f_{22}/16 \end{aligned}$$

We are interested in the evolution of all the genotype normalized frequencies, $m_{ij}/\sum_k m_{ki}$. Solving numerically the set of coupled differential equations, it can be seen that, for any $0 \leq s < 1$, only phenotype AA individuals will remain in the end, as shown in Fig. 4a. For the case where $s = 0$ (the only couples considered for reproduction are those that have matching traits and preferences), this result can be easily understood. It then becomes straightforward to show 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 latter. Also, m_{BB} is the one that receives the smaller contributions. Thus m_{AB} , m_{BA} and m_{BB} are eliminated for any population starting from Hardy-Weinberg proportions. For s close to 1, trait shift occurs slowly. Imperfect trait discrimination and mutations tend to prevent this trait shift. This is indeed what one observes in the simulations of our general model with many genes at the preference locus, when the discrimination exponent ν and the time required for reproduction T are small, or when μ is high.

The dynamical instabilities alter this scenario considerably. First, as explained in the text, they strongly reduce the fitness of non-optimal couples. Hence, we fall in the $s \rightarrow 0$ regime described in the previous case. However, now the fitness associated with each couple becomes a context-dependent quantity. It is proportional to the probability that a couple stays together for T units of time. For couples formed by males IJ and females JI , $w_{IJ,JI} = \alpha(1 - f_J/2N)^T(1 - m_I/2N)^T$. The equations for the evolution of the phenotype frequencies are the same as in the previous case, but with these new fitness weights. If we only consider couples for whom traits and preferences match, and assuming that $m_{ij} \equiv f_{ji}$, we get a set of differential equations, of which we show one of them:

$$dm_{33}/dt = w_B^2 m_{33}^2 + w_A w_B m_{23}^2/4 + w_A w_B m_{32}^2/4 + w_A^2 m_{22}^2/16$$

where we wrote $w_A = (1 - m_A/2N)^T$ and equivalently for w_B (we took $\alpha = 1$). Hence we can write the corresponding differential equations for the phenotypes:

$$dm_{AA}/dt = w_A^2 (m_{11}^2 + m_{12}^2 + 9m_{22}^2/16 + m_{21}^2 + (2m_{11}(m_{21} + m_{22} + m_{12}) + 3m_{12}m_{22}/2 + 3m_{21}m_{22}/2 + 3m_{12}m_{21}/2)) + w_A w_B (m_{13}^2 + m_{31}^2 + m_{23}^2/4 + m_{32}^2/4 + m_{13}m_{23} + m_{31}m_{32})$$

$$dm_{AB}/dt = dm_{BA}/dt = w_A^2 (m_{12}m_{21}/4 + m_{22}(4m_{12} + 4m_{21} + 3m_{22})/16) + w_A w_B (m_{13}m_{23}/2 + m_{32}m_{31}/2 + m_{23}^2/4 + m_{32}^2/4)$$

$$dm_{BB}/dt = w_B^2 (m_{33}^2 + m_{22}^2/16) + w_A w_B (m_{23}^2 + m_{32}^2)/4$$

A competitive exclusion principle emerges, as genotypes try to grow the fastest possible, while we keep the population with a fixed number of individuals: only those growing at the highest rate will remain. Comparing the first two equations we remark that all the terms appearing in dm_{AB} also contribute to dm_{AA} , but with higher coefficients in the latter. Consequently, AA individuals out-compete AB and BA individuals. However, now BB individuals can remain because they can grow faster than AA individuals when they are less numerous. This happens because the w_B^2 factor is larger than the w_A^2 factor in this case. This contrasts with what would happen if w_B were to be fixed, instead of a context-dependent, factor.