

# Mate Choice: Simple or Complex? \*

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## Abstract

Focusing on situations in which sexual preferences inspect several traits, this paper explores the question of how complex the process of assessing mate attractiveness might get, through self-organization, over the course of evolution: do sexual preferences evaluate traits in a simple, linear way or in a complex, nonlinear fashion? Arguments and simulation results (individual-based model in which preferences with different degrees of evaluation-complexity "compete" in a population) are presented, suggesting that a bias should exist, and that its direction should depend on levels of different types of noise (in perception and in the mate-evaluation process) and on mutation rates: while noise in perception and mutation favor simple preferences, noise in evaluation favors complex ones; for possibly the most plausible parameters, complex preferences are favored. Possible implications on the speciation process are mentioned. This novel way of looking at mate choice could be a rich source of new insights in this intriguing process.

## Introduction

Perhaps the most fascinating split in sexual selection theory is that existing between the so-called "good genes" and "good taste" theories (or "schools") (Ridley, 1993). "Good genes" theories explain female mate-choice evolution on the basis of the viability "value" of genetic material contributed by males (e.g. (Hamilton and Zuk, 1982)). In contrast, Fisher's "good taste" school argues that female preferences for ecologically adapted males are not the rule and that conflict between natural and sexual selection forces can arise, leading to compromises. The arguments emphasize self-reinforcing aspects of mate choice and are based

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on the development of a correlation between consistently choosing preferences and their preferred traits (Fisher, 1930; Kirkpatrick, 1987). This correlation indirectly confers an advantage to such preferences, because they are likely to select individuals that carry genes for the very same preferences. The effect increases with choice consistency (Kirkpatrick, 1982), making discrimination capabilities relevant.

Within the context given by the "good taste" school, this paper explores the following questions. When several traits are being inspected in the evaluation of potential mates, are single traits contributing independently (additively) to the overall "sexiness" of the examined individual or are their contributions being combined in a nonlinear, complex way?<sup>1</sup> Does the answer to this question depend on mutation rate, noise in perception or noise in mate-evaluation? If it does, how?

Notice that (1) the picture of traits (trait-vectors) adapting to preferences by "adaptive steps" makes natural the use of the term *preference-landscape* to designate the underlying structure of sexual preferences, and (2) because more complexity in sexual preferences means more rugged preference-landscapes, the questions addressed in this paper can conveniently be discussed in terms of preference-ruggedness.

This paper states that the level of complexity in sexual preferences is not neutral to their evolution; different levels of interaction among single trait evaluations may differ in their evolutionary success. Furthermore, these differences should depend on the levels of noise in perception and in evaluation in fully different ways: as perception noise is increased from zero to highest lev-

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<sup>1</sup>A preference examining more than one trait is called here *complex*, if the contribution of single traits depends on the context given by the other traits under examination (i.e., there is an interaction among contributions of single traits to the overall mate value); in contrast, a preference is said to be *simple* if the contribution of every single trait to the overall mate value do not depend on the state of other traits (in a linear way).

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els, the bias is expected to switch from high to low complexity; but for evaluation noise, only very low levels should favor low complexity, otherwise complex preferences should be favored. The effects of mutation should be qualitatively similar to those of perception noise. In order to discuss the causes for this expectations (detailed in the section presenting the results), it is convenient to distinguish two levels: (1) a functional level (ruggedness in preferences may affect their performance), and (2) an "evolutionary" level (shape and size of basins of attraction in preference-landscapes may affect their evolutionary future in a more indirect way).

The focussed situation is that in which trait-vectors in the population are concentrated (in terms of Hamming-distance) in a small, local region of trait-space. This is a plausible case for small populations, due in part to the effects of genetic drift.

To explore these questions, an individual-based simulation is used, in which (mutants of) two "competing" preferences with different complexity levels are initially present in a population that is then let evolve freely, and in the absence of natural selection, until one of them is fixed in the population. This allows to observe, over a big number of runs, fixation frequencies of preferences with different complexities.

## The Simulation

This section describes the model used in this study, including variables, parameters, and details of the sets of runs performed.

### Individuals

Individuals are composed of three parts: a binary *trait-vector*, a binary *preference-vector* and a *preference-landscape*. The trait-vector (denoted by  $\vec{t}$ ) represents the list of all single traits taken into account in mate-choice by sexual preferences. The preference-vector (denoted by  $\vec{p}$ ) is a list of single preferences for single traits, and allows to model the way in which traits are perceived. The preference-landscape (denoted by  $P$ ) is a function defined over  $N$ -dimensional binary vectors and with values in  $[0, 1]$ , which, as explained next, complements the preference-vector to determine the value of any potential mate.

Mate evaluation is depicted in Fig. 1. An individual  $i$  evaluating a potential mate  $j$ , compares first its preference-vector  $\vec{p}_i$  with the traits  $\vec{t}_j$  of individual  $j$ . The comparison is performed locus by locus using an exclusive or. This operation yields a (binary) *comparison vector*, which is then fed into  $i$ 's preference-landscape  $P_i$ , finally yielding the value  $p_i(j)$  (a real number in  $[0, 1]$ ). To sum up,  $p_i(j) := P_i(\vec{p}_i \text{ xor } \vec{t}_j)$ .

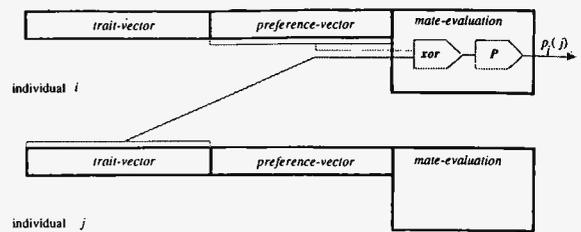


Figure 1: Evaluation by individual  $i$  of a potential mate  $j$ .

Phenotypes are genetically determined; two chromosomes code for an individual. The first one codes for the traits (trait-vector), the second one, for the preferences (preference-vector and the preference-landscape). Recombination takes place at this level but there is no intrachromosomal recombination. Mutation affects trait- and preference- vectors; these are directly encoded. Let us remark that the code used for preference-landscapes is irrelevant, because these landscapes are inherited without modification; they are not changed by genetic operators. Nevertheless, a preference as a whole (composed of a preference-vector and a preference-landscape) is affected by mutation, because preference-vectors are mutated.

Notice that preference-vectors allow for a simple representation of single preferences, which determine *how* single traits are perceived. In addition, as clarified below, preference-vectors provide a simple means for modelling preference-mutation and perception-noise.

Preference-landscapes represent the core of the mate-evaluation system. This component models the interaction among the evaluations of single traits and is supposed to be stable compared to preference-vectors. A preference-landscape is represented by a table that codes an  $NK$ -landscape (Kauffman, 1993), with parameters  $N$  (dimension of preference-vectors), and  $K$ , which determines the preference-complexity level. The  $NK$ -model provides a simple, abstract, well known means of modelling different levels of interaction among components in their contribution to an overall value; results are available that characterize landscapes with different levels of interaction and many of them qualitatively hold across different parametrizations (number of interacting elements, distributions of values, etc.) (Kauffman, 1993)<sup>2</sup>; the nature of possible

<sup>2</sup>The results we are most interested in here are related to local maxima of  $NK$ -landscapes and their relationship to adaptation. With increasing values of  $K$ , the ruggedness of the landscape increases, the number of local-extrema grows very quickly, the number of adaptive steps to local maxima decreases in length, correlation among values of neighbors decreases and in particular, for neighbors of optima (its one-mutant variants), fitness drops become more and more

interactions in the present context is largely unknown, and asks for such a simple, robust way of modelling them<sup>3</sup>.

As already mentioned, to make the model more realistic, two kinds of noise are introduced. Firstly, the level of *perception-noise* is given by the probability of perceiving, for each single trait in an examined trait-vector, a random value instead of its actual value. Secondly, *evaluation noise* perturbs computed mate-values; it is normally distributed around zero and its standard deviation will be called *evaluation noise level*. This noise is added to  $p_i(j)$ ; the (noisy) result of this addition is a random variable, but its values will also be denoted by  $p_i(j)$ , in order to keep notation simple (disambiguated by context).

### Competing Preferences Experiments

We turn now to the description of a single simulation-run, called here a "competing preferences experiment".

A small population of 70 individuals, with  $N=16$ , is evolved from an initial state in which (1) all trait-vectors are similar: an "original" trait-vector is randomly generated and mutated clones of it are produced to create the traits for the first generation (the mutation rate per basis in this initial phase is 0.02); and (2) two different, randomly generated preferences with  $P$ -landscapes of different complexities (different values of  $K$ ) are assigned, in equal proportions, to the individuals of the first generation<sup>4</sup>; preference vectors are mutated in the same way trait-vectors are mutated in this initial phase (identical mutation rate).

At each step, individuals choose a mate and reproduce. In the mate-choice phase of every single step, individuals are presented with a *choice-group* of 8 potential mates (randomly drawn), from which they select their mate. Mate-selection from this group by an individual  $i$  is performed as follows: for every individual  $j$  in the group, its value  $p_i(j)$  is obtained (with traits previously perturbed if perception-noise is nonzero and with the value itself perturbed if evaluation-noise is nonzero); and the individual with the maximal value in the group is chosen for mating. Sexual reproduction follows; chosen individuals cannot refuse mating.

With the help of the effects of drift, one of the competing preference-landscapes becomes fixed after some steps. This event determines the halting point of a run. The  $K$ -value of the "winning" preference is precipitous (Kauffman, 1993).

<sup>3</sup>Furthermore, alternative modelling approaches are being experimented; preliminary results obtained with them so far are qualitatively consistent with the ones presented in this text.

<sup>4</sup>The two "competing"  $P$ -landscapes are randomly chosen from a set of 1000 different, randomly generated ones

recorded. Such runs are repeated 1000 times using different seeds for the pseudo-random number generators and using different preference-landscapes and different initial trait- and preference-vectors. The points plotted in the next section represent the average number of times one or the other  $K$  value is fixed (its fixation frequency) over these 1000 runs.

Such couples of  $K$  are compared for different levels of perception noise, evaluation noise and mutation rate.

Notice that choice is made on the basis of noisy mate-values; the individual with the highest noisy mate-value in the presented choice-group is chosen. This is a very simple and certainly plausible "algorithm"; there are many possible sources of noise, including fluctuations in the evaluation itself (two evaluations by and of the same individual may yield different values at different times or contexts) and limited cognitive capabilities (e.g. memory). Due to the many factors that may be involved, a normal distribution seems appropriate.

### Sets of Runs

The default parametrization used in the sets of runs is the following: (1) mutation rate (per locus): 0.001; (2) evaluation and perception noise: 0.05. Differences in any particular setting will be mentioned.

In the first set of runs fixation frequencies of preferences with different complexity levels  $K_2$  are compared to  $K_1=0$  (1000 runs for each pair).

In the next set of runs, mutation rate is varied for a fixed pair of  $K$ 's: 0 vs. 4. (1000 runs are performed for each examined mutation rate.)

In the third set of runs, perception noise is varied for the same fixed pair of  $K$ 's (also here 1000 runs are performed for each examined noise level).

The last set of runs is similar to the previous one (same number of runs too), but the parameter being varied for every fixed pair of  $K$ 's is evaluation-noise.

In the next section, together with the presentation of the results for each of these set of runs, the theoretical arguments allowing to predict each of their key features are given (instead of introducing them before the results); this is just for brevity.

## Results and Discussion

The results obtained with the described simulation have been tested for statistical significance (sign-test used due to the binomial nature of the data) and are presented with 95% CI of mean. Moreover, fixation frequencies greater (or equal) than 0.54 or smaller (or equal) than 0.46 highly significantly differ from the "null-value" 0.5, which represents no frequency-differences (sign test,  $p < 0.01$ ).

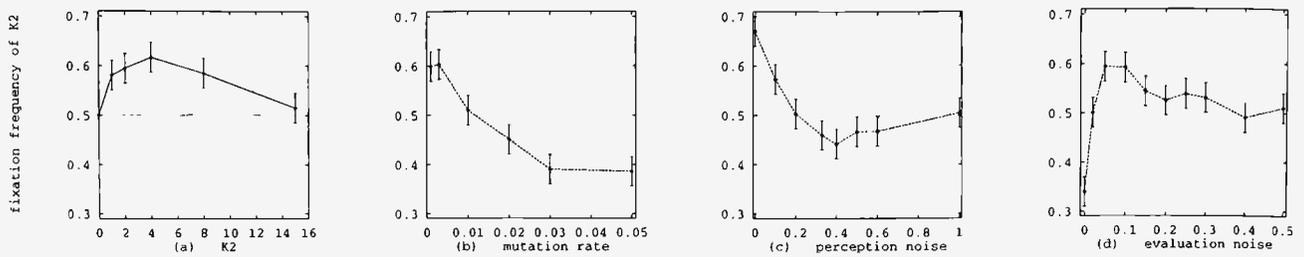


Figure 2: Fixation frequencies for different "competing-preferences-experiments". Each point represents the fixation frequency of  $K_2$  when competing with  $K_1=0$  (average over 1000 runs): (a) against different values of  $K_2$  (mut. rate: 0.001, perception and evaluation-noises: 0.05; the plotted value of 0.5 for  $K_2=0$  is the theoretical value), (b) against mutation rate ( $K_2=4$ , perception and evaluation-noises: 0.05), (c) against perception noise ( $K_2=4$ , mut. rate: 0.001, evaluation-noise: 0.05), (d) against evaluation noise ( $K_2=4$ , mut. rate: 0.001, perception-noise: 0.05). Error bars reflect the 95% CI of Mean.

## Varying $K_2$

The results for the first set of runs are presented in Fig. 2a, which shows an optimum for moderate complexity values. This is expected, because (1) some ruggedness in preference-landscapes allows for good discrimination of traits in any given small, local region of phenotype-space, such as the one covered by a small population (notice that in contrast, a very smooth landscape yields similar values in any such region); and (2) a too high  $K$  may lead to choice inconsistency at a functional level, due to perception noise, and at an evolutionary level, due to mutation (the explanations in the next two subsections should clarify this point).

## Varying Mutation Rate

Fig. 2b shows how increasing mutation rate most affects complex preferences. For low levels of mutation, complex preferences evolve more frequently, but the situation is reversed for high levels of mutation, with simple preferences evolving more frequently. This is due to differences in the induced choice-inconsistencies through generations: for highly complex preferences, a single mutation usually produces important changes in the values assigned to traits; consequently, preference-trait correlations are strongly affected.

## Varying Perception Noise

Fig. 2c shows how low levels of perception noise favor the evolution of complex preferences; in contrast, high levels of this noise are very perturbing for complex preferences and simple preferences are more likely to evolve. As already mentioned, this is due to the great choice inconsistency induced on complex preferences, for which a big change in the value assigned to a potential mate may result due to a single trait being wrongly perceived. Notice that the difference in frequencies is lost for highest levels of noise: perceived

traits are not correlated to real traits and consequently mate-values are randomly assigned, so that actually random mating takes place and the complexity level of the preference-landscape becomes unimportant.

## Varying Evaluation Noise

In the last set of runs, evaluation noise is varied (Fig. 2d). For extreme low levels, simple preferences are favored, but as this noise is increased, more complex preferences become quickly favored. Let us first remark that in the total absence of any form of noise, simple and complex preferences are functionally similar: both are equally able to rank individuals in a group according to their traits. Nevertheless, they are not *evolutionary* equivalent: in particular, basins of attraction of local maxima get smaller as complexity increases, and the mean number of adaptive steps (available to traits when climbing preferences) decreases at the same time (from an average of  $N/2$  steps for  $K=0$  to an average of  $\ln(N)$  steps for  $K=N-1$ , approximately). By allowing only a small number of adaptive steps to traits, the positive effect preferences obtain when they correlate to traits they prefer can only take place a small number of times. Therefore, preferences with  $K=0$  are favored in this case.

As evaluation noise increases, and the chances of less preferred traits being chosen increases in a way that is determined by the local shape of the preference-landscape (i.e., this shape determines such probability), landscapes with some ruggedness gain a functional advantage: they allow for better local discrimination.<sup>5</sup> At the same time, the evolutionary advantage that

<sup>5</sup>Notice that, because noise is normally distributed, slightly different mate-values (as for  $K=0$ ) are easily swapped by this noise; in contrast, values with bigger differences (as for higher values of  $K$ ) are swapped with a much lower probability (due to the bell-form of the distribution).

simplest landscapes had in the case without evaluation noise is now compromised. The reason is that although the number of possible adaptive steps remains the same, their *quality* is lowest for such landscapes: because only small differences exist in the mate-values assigned by preferences (in any small region of trait-space), choice consistency is reduced and this leads to weak preference-trait correlations. This problem affects rugged landscapes less, since they assign a wider spectrum of mate-values in a local region of trait-space and thus induce a more consistent choice. This, in turn, entails higher quality (stronger) preference-trait correlations. Fig. 2d can be seen as depicting the way in which the relative importance of differences in *quantity* of available adaptive steps decreases as their *quality* (magnitude) differs more and more in the compared landscapes. Finally, as in the case of perception noise, and for similar reasons, if levels of this noise are extremely increased, differences in fixation frequencies decrease.

## Conclusion

The arguments and results presented strongly suggest that the level of "complexity" in sexual preferences influences their fixation frequencies. There appears to be a "most favored" level of complexity whose level depends on the levels of different forms of noise (perception and evaluation noise) and on mutation rate. In essence, while both high perception noise and high mutation rates favor simplest preferences (with the effect reversed for low levels of this noise), moderate and high evaluation noise favors more complex ones (with the effect reversed for very low levels of this noise).

The assumption of phenotypes concentrated in phenotype-space may of course restrict the applicability of these results. Nevertheless, the situation may be a plausible one for relatively small populations, due to the effects of genetic drift.

Another important point is the plausibility of the levels of noise. Although it is difficult to qualify some regions of "noise-space" as being more or less likely, it seems reasonable to exclude extremely low evaluation noise. Due to the many factors playing a role associated to mate evaluation as it is modelled here, including the reliability of memory (for mate-values) and the degree of consistency among repeated evaluations of identically perceived traits, it seems reasonable to assume evaluation-noises which are not very low.

Under such hypothesis, perception-noise and mutation rate can still influence the outcome (fixation frequencies). But let us just discuss the case in which mutation rate is low (the complementary discussion is trivial). It seems reasonable to think that in the case

of traits directly and clearly displayed during courtship behavior, noise in their perception should be low. This kind of traits should usually be well adapted to the targeted sensors, making them easy to examine. In such cases (low perception noise and moderate to high evaluation noise), the evolution of some level of complexity in sexual preferences is likely. Of course, the nature of some traits may make them difficult to examine; in cases in which most evaluated traits are of this kind, no matter how much evaluation noise is present, simplest sexual preferences have the highest chances to get fixed in a population.

With respect to testing the kind of hypotheses presented in this paper in real animals, it is clear that such a task would be difficult, but appears to be possible in principle. This should ideally be done for traits under low or no natural selective pressure.

Finally, speciation rates are possibly influenced by the degree of complexity in sexual preferences. Complex preferences should induce a high speciation probability: small changes in such preferences lead to big changes in the assigned mate values. A short time of reproductive isolation may suffice for such preferences to strongly diverge (in mate value assignment), becoming themselves a cause for reproductive isolation. This way of looking at mate choice is a potential source of new insights in this intriguing process.

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