



# Fixation probability in a two-locus intersexual selection model



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## ARTICLE INFO

### Article history:

Received 29 June 2015

Available online 5 April 2016

### Keywords:

Ancestral recombination–selection graph

Fixation probability

Sexual selection

## ABSTRACT

We study a two-locus model of intersexual selection in a finite haploid population reproducing according to a discrete-time Moran model with a trait locus expressed in males and a preference locus expressed in females. We show that the probability of ultimate fixation of a single mutant allele for a male ornament introduced at random at the trait locus given any initial frequency state at the preference locus is increased by weak intersexual selection and recombination, weak or strong. Moreover, this probability exceeds the initial frequency of the mutant allele even in the case of a costly male ornament if intersexual selection is not too weak. On the other hand, the probability of ultimate fixation of a single mutant allele for a female preference towards a male ornament introduced at random at the preference locus is increased by weak intersexual selection and weak recombination if the female preference is not costly, and is strong enough in the case of a costly male ornament. The analysis relies on an extension of the ancestral recombination–selection graph for samples of haplotypes to take into account events of intersexual selection, while the symbolic calculation of the fixation probabilities is made possible in a reasonable time by an optimizing algorithm.

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## 1. Introduction

Darwin (1871) considered sexual selection to be an evolutionary process as important as natural selection. The concept arises from the observation that some weapons or ornaments known as secondary sexual traits that have evolved in the animal kingdom, as antlers in deer or tails and colours in birds, appear not to be advantageous for survival or even to be deleterious. A possible explanation is that these traits enhance the reproductive success of their carriers either by deterring rivals of the same sex, usually males (intrasexual selection), or by making them more attractive to individuals of the opposite sex, usually females (intersexual selection). These two forms of sexual selection may be responsible for a large amount of gender differences in structure or appearance in nature.

This paper concerns intersexual selection. As for intrasexual selection, let us just mention that it has been studied, e.g., by applying game theory to evolution in the context of conflicts between males for access to females and reproduction with the key concept of evolutionarily stable strategy (Maynard Smith, 1982).

Fisher (1930, 1958) described the runaway process by which a preferred conspicuous trait in one sex and a preference for this trait in the other sex could evolve in tandem with the preference

being genetically transmitted along with the preferred trait. Taking a plumage character as an example, Fisher (1930, p. 137) writes: *Moreover, as long as there is a net advantage in favour of further plumage development, there will also be a net advantage in favour of giving to it a more decided preference.* This runaway mechanism could reinforce or accelerate phenotypic difference and speciation.

With the above notable exception, however, sexual selection involving mate choice in one sex, most often the female but not always (see, e.g., Edward and Chapman, 2011), was largely disregarded by most of the leading evolutionary biologists up to the mid 20th century (see, e.g., Maynard Smith, 2000).

O'Donald (1962, 1980) was one of the first to propose, and study numerically, two-locus models of sexual selection with one locus coding for trait variation in males and one locus influencing mating preferences in females. Lande (1981) analysed models in the case of polygenic inheritance and Kirkpatrick (1982) exact population genetic models for haploid populations. They both showed that, in the absence of direct selection on female preferences, these can evolve as a correlated response to changes in the male trait associated with positive linkage disequilibrium. Moreover, in the framework of an infinite population, they exhibited curves of stable equilibria at which neutral preferences for less viable traits can counterbalance the deleterious effects of the traits. The evolutionary outcome along the line of stable equilibria is left to weaker forces such as genetic drift. The preference function (see, e.g., Charlesworth and Charlesworth, 1981, Seger, 1985 and Carrier,

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1995) as well as the recombination rate (see, e.g., Kirkpatrick, 1982 and Barton and Turelli, 1991) seem to have little qualitative effects on the conclusions.

Similar conclusions for diploid populations with some discrepancies due to dominance at the trait locus have been reached from simulations (Heisler and Curtsinger, 1990), local stability analyses near fixation at either the trait locus (Gomulkiewicz and Hastings, 1990) or the preference locus (Otto, 1991), as well as quasi-linkage equilibrium analyses away from fixation boundaries (Greenspoon and Otto, 2009).

With selection on female preferences, the line of stable equilibria may collapse to a single, stable point and lead to a balance between selection and drift in finite populations under recurrent mutation. This may be the case for instance with a preference-dependent risk that females remain unmated as supported by simulations of polygenic models (De Jong and Sabelis, 1991). More simulations have shown that adding a cost to female preferences may restrict, but not eliminate, the possibility of ornament diversification and speciation (Mead and Arnold, 2004; Uyeda et al., 2009; Bergen et al., 2012). One of the surprising consequences of sexual selection may be to create a positive correlation between the female preference and the progeny sex ratio (Fawcett et al., 2007).

Note also that there may be a benefit associated with female preferences which is to enhance species recognition and, therefore, fertility (see, e.g., Carrier, 1995). Indeed, sexual preference of females for given traits in males is akin to assortative mating and, combined with drift, can help answer questions related to species divergence (Otto et al., 2008; Servidio, 2011). Considering a quantitative genetic sexual selection model in a finite population to explain the between-population variation in color pattern of the frog *Oophaga pumilio*, Tazzyman and Iwasa (2010) showed that the evolution of the sexually selected trait can be determined by random drift in female preference if it is coupled to that trait by selection with an optimum at matching phenotypic values.

Recently, Miller (2000) drew attention to some of Darwin's neglected ideas about human behaviours not clearly connected to survival, such as humour, creativity, and some forms of altruism, that may have been favoured through sexual selection. See Puts (2010) for more references on this subject.

As for a recent review of mathematical models of sexual selection, we refer to Kuijper et al. (2012).

In this paper, we consider a two-locus model of intersexual selection in a finite haploid population with a trait locus expressed in males and a preference locus expressed in females. We use a discrete-time Moran model so that, at each time step, there is one individual produced according to the types of the parents chosen to reproduce and one individual replaced according to the type of the individual chosen to be replaced. We study the probability of fixation of a single mutant introduced at the trait locus given any initial frequency state at the preference locus, and the other way around. We consider the case of a preference for a deleterious trait and the case of a preference for a beneficial trait, but describe the method at length only in the former. We deduce the leading effects of weak selection and weak recombination using an ancestral recombination–selection graph in the limit of a large population size. This extends a similar approach for a two-locus viability selection model to study the Hill–Robertson effect in favour of recombination (Lessard and Kermany, 2012). The leading effects of weak selection under the assumption of free recombination, actually of any fixed recombination rate as the population size goes to infinity so that recombination and selection events occur at different timescales backwards in time, are also studied. We provide an algorithm which strikingly reduces the time of symbolic calculation.

## 2. Model

Suppose a large but finite population of  $N$  haploid individuals. The population is assumed to be monoecious (hermaphroditic)

so that each individual can act as either the male or the female in sexual reproduction. In particular, an individual can reproduce with itself. Consider two genes at two different loci, each one with two possible alleles. The first gene at a trait locus, denoted by  $T$ , has an effect on viability. It is assumed that a mutant allele  $T_2$  decreases the viability of a male carrying it compared to a resident allele  $T_1$ .

On the other hand, the second gene at the other locus, denoted by  $P$ , codes for sexual preference. It is assumed that a female carrying a mutant allele  $P_2$  shows a preference for males carrying the mutant allele  $T_2$ , while a female carrying a resident allele  $P_1$  does not show any preference. Therefore, the individuals can be of four possible haplotypes, called types for simplicity:  $(T_1P_1)$ ,  $(T_1P_2)$ ,  $(T_2P_1)$  and  $(T_2P_2)$ , or in vector notation  $(1, 1)$ ,  $(1, 2)$ ,  $(2, 1)$  and  $(2, 2)$ , respectively. These are represented by **1**, **2**, **3** and **4**, respectively.

We use a discrete-time Moran model (Moran, 1958). At each time step, two individuals are sampled at random with replacement to mate and to produce an offspring (hence the possibility of reproduction of an individual with itself). The first one is assumed to act as the female and the second one as the male. The sampled individuals reproduce with some probability depending on their types. Actually, a  $P_2$ -female reproduces with a  $T_2$ -male with probability  $1$  and with a  $T_1$ -male with probability  $1 - As$ . If the female carries allele  $P_1$ , however, reproduction takes place with probability  $1 - \frac{As}{2}$  whatever the type of the male is. Therefore, there is a reproduction cost associated not only with a female being choosy that depends on the type of the male but also with a female not being choosy irrespective of this type.

Here,  $A > 0$  represents a coefficient of intersexual selection with respect to an intensity of selection  $s > 0$ . Weak selection in a large population is modelled by assuming

$$s = \frac{\sigma}{N},$$

where  $\sigma > 0$  represents a population-scaled intensity.

If reproduction takes place, then the type of the offspring produced depends on the parental types and the recombination rate  $r$ . With probability  $1 - r$  the type of the offspring is one of the two parental haplotypes chosen at random (probability  $\frac{1}{2}$  for each), while it is one of the two recombinant haplotypes chosen at random (probability  $\frac{1}{2}$  for each) with the complementary probability  $r$ . Weak recombination in a large population is modelled by assuming

$$r = \frac{R\sigma}{N}, \quad (1)$$

for some coefficient of recombination  $R > 0$ . Note that weak recombination is scaled at the same order of magnitude as weak selection.

If the two individuals chosen to reproduce do not actually reproduce, the population state does not change. If they produce an offspring, then an individual is sampled at random in the population to be replaced by the offspring. The individual is actually replaced with some probability depending on its haplotype. Replacement occurs with probability

$$1 - cs = 1 - \frac{c\sigma}{N}, \quad (2)$$

where  $c \geq 0$  is a coefficient of viability selection that depends on the type of the individual to be replaced. In this study we set  $c_1 = c_2 = 1$  and  $c_3 = c_4 = 0$ . This models a selective advantage in favour of allele  $T_1$ . If the individual chosen to be replaced is not actually replaced, then the offspring does not survive so that the population state does not change.

Let  $x_i(\tau)$  be the frequency of type  $i$  at time step  $\tau \geq 0$  and define the type frequency vector  $\mathbf{x}(\tau) = (x_1(\tau), x_2(\tau), x_3(\tau), x_4(\tau))$ . Initially (time step 0), let allele  $T_2$  be introduced as a mutant at the first locus in a single individual of the population (hence with

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