

# **A model of sexual selection using adaptive dynamics: Reversibility of the Fisher's runaway**

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## **ABSTRACT**

It's a long time since it has been observed that insular populations are less subject to sexual selection than continental ones. Nevertheless, the reasons of this difference between islands and continents are not clearly understood. In order to test the hypotheses that the difference in population size (smaller populations on islands) leads to a different evolution of sexual traits, we have developed a model of sexual selection using the theory of adaptive dynamics. Our model allows to study the coevolution of secondary sexual character and individual preferences, with population size as a key parameter. Contrasting with most models of sexual selection which are based on quantitative genetics, our model is based on demography. It can predict the possibility of the Fisher's runaway process, without assuming genetic correlation between male and female traits. The model uses a mating function incorporating male and female preferences, and can be applied to small populations. According to our results, sexual selection is less intense in small populations, entailing reduced secondary sexual characters and dimorphism. Furthermore, the loss of sexually selected traits and the inversion of dimorphism (exaggerated ornaments in females instead of males) appear as possible outcomes, which is consistent with recent phylogenetic studies.

**Keywords:** sexual selection, sexual dimorphism, adaptive dynamics, insular populations, Fisher's runaway process.

## 1. INTRODUCTION

Insular populations seem to be less 'sexy' than continental ones (Bateson 1913; Mayr 1942; Peterson 1997; Grant 2001). Many hypotheses have been advanced to explain this phenomenon. Sexually selected populations could be more vulnerable due to the cost of exaggerated secondary sexual characters and thus more subject to extinction when small (McLain *et al.* 1995; Sorci *et al.* 1998). In small populations, the number of mates, and consequently the growth rate, could decrease when individuals are selective; this phenomenon is known for the consequences it has in conservation biology, because it generates an Allee effect (Legendre *et al.* 1999; Courchamp *et al.* 1999; Stephens & Sutherland 1999; Møller & Legendre 2001). The decreased variability due to the founding effect on island could also explain why females do not benefit anymore from being selective (Møller 2001). The role of sexual traits in species recognition (to avoid hybridization) is also less important on islands, in absence of linked species (Grant 2001). Here, we want to test the hypotheses that the size of a population, via the probability for an individual to be mated, influences its benefit from being attractive as well as its benefit from being selective, and *in fine*, influences sexual selection.

Darwin (1871) first recognized the existence of exaggerated ornaments among males of many species, seemingly contradicting the optimization expected from natural selection. Fisher (1930) gave a verbal argument, now known as the 'Fisher's runaway process': the male ornament and female preference would get genetically correlated, and engage in a form of arms race until counter selected by natural selection. Mathematical models have played an important role in understanding the mechanisms of sexual selection. The first one (O'Donald 1962) was developed to test the plausibility of the Fisher's Runaway. Since then, several models (Lande 1981; Kirkpatrick 1982; Kirkpatrick *et al.* 1990; Pomiankowski *et al.* 1991; Iwasawa and Pomiankowski 1999; Hall *et al.* 2000; Gavrilets *et al.* 2000) have clarified the hypotheses of the mechanisms involved. Wiens (2001) has summarized the kinds of models developed so far in order to test whether they are consistent with recent phylogenetic studies showing that losses of elaborate male traits are widespread and can even be more common than are gains.

Most models proposed to study sexual selection are based on Lande's (1981). They use the theory of quantitative genetics, and tend to show that the development of male character and female preference is mainly due to a genetic correlation establishing between those traits. According to these models, a (natural) selection pressure on female preference strongly reduces the possibility of a runaway. However, there is evidence for such pressures in natural

populations that present nevertheless sexual characters (Andersson 1994). These models fail to explain sexual selection in monogamous species with unbiased sex-ratio, while monogamous bird species can be strongly sexually selected (Price 1984; Møller 1988; Møller 1992; Møller and Birkhead 1994). They do not take into account the effect of the size of the population on sexual selection while this parameter seems to exert a strong influence. At end, they fail to explain the widespread loss of sexual characters during evolution (Omland & Lanyon 2000; Wiens 2001).

By contrast, we present a model of sexual selection based on demography. Our model stands for monogamous species with unbiased sex-ratio. It incorporates life cycle characteristics of the species (survival, fecundity), and a mating function accounting for male and female preferences. The coevolution of male and female characters is assessed using the framework of adaptive dynamics (Metz *et al.* 1996; Dieckmann & Law 1996; Geritz *et al.* 1998). This allows to study the interplay of population size and sexual selection. Although our model is theoretical and not based on a particular species, it has been built with birds populations as reference since most data concerning sexual selection in insular populations deal with birds. Population size being a key parameter of the model, we can study the outcome of sexual selection for small populations, like those colonizing islands. Our model can explain the Fisher's runaway even when female preference is faced to a strong pressure, and can also explain the loss of sexual traits. To our knowledge it is the first model based on demography showing the possibility of the Fisher's runaway, as well as its reversibility. Genetics are not explicitly involved. However, the use of the theory of adaptive dynamics provides the heritability mechanism necessary for the emergence of sexual selection. It is also the first model described in mathematical terms showing the possible reversibility of sexual selection.

## 2. METHODS

### (a) *Effect of population size on the probability for an individual to be mated*

Even in a monogamous population with unbiased sex-ratio, some individuals may not mate. This is a consequence of demographic individual choice, and the effect is more pronounced when the population is small (Møller & Legendre 2001). Thus, depending on population size, individuals should not have the same benefit from being attractive, nor the same benefit from being choosy. To quantify this benefit, we have first calculated the probability for an individual living in a population of size  $n$  to be mated, and then the

probability for a mutant more or less attractive or selective in this population to be mated. We have used the formalism of Møller & Legendre (2001), which has the advantage of involving only few parameters. Let's consider a monogamous population of size  $n$  comprising  $n_f$  females and  $n_m$  males (mature individuals). The adult sex-ratio  $r$  equals  $n_f/n$ . A female accepts a male with probability  $p_f$  and a male accepts a female with probability  $p_m$ . The probability  $p$  for a given male and a given female in the population to accept one another (probability to be compatible), is  $p = p_f p_m$ . This probability reflects the intensity of sexual selection: the smallest the  $p$ , the more selective the individuals.

Let  $P_m$  be the probability for a male to be mated and  $P_f$  the probability for a female to be mated. Assuming monogamous mating, the number  $N$  of mates is  $N = P_f n_f = P_m n_m$ . We assume that if two individuals are compatible and if they are not already paired, then they mate. Thus, unpaired individuals of one sex are those who are not compatible with unpaired individuals of the other sex. There are  $n_f - N$  unpaired females; the probability  $1 - P_m$  for a male not to be mated is  $(1 - p)^{n_f - P_f n}$ . We obtain

$$P_m = 1 - (1 - p)^{n(r - P_m(1-r))}. \quad (2.1)$$

Using equation (2.1), and a fixed-point algorithm, we can compute the probability  $P_m$  for a male to be mated in a population of size  $n$ , sex-ratio  $r$  and proportion of compatibilities  $p$ .

### (b) *Mating function*

Two-sex demographic models make use of a mating function giving the probability  $a$  for an individual in the population to be mated (Caswell 1986, 2001; Legendre *et al.* 1999). The mating functions are homogeneous with size:  $a(kn_f, kn_m) = ka(n_f, n_m)$ . For a monogamous mating system,  $a(n_f, n_m) = \min(n_f, n_m) = \min(r, 1 - r)$ . As a consequence of homogeneity, these mating functions do not take into account the deficit of mates linked to small population size. To take population size into account, one can reduce the number of mates using a percentage (Legendre *et al.* 1999), but this is arbitrary. This problem does not occur with our mating function  $a(n_f, n_m) = N/n = P_m n_m/n = P_m(1 - r)$  which depends on the size of the population and on the intensity of sexual selection. Our mating function matches the classical  $\min(r, 1 - r)$  when there is no sexual selection ( $p = 1$ ), or when the population is large.

### (c) *Adaptive dynamics*

The traits under study are the secondary sexual character of the male  $z$ , and the preference  $y$  of the female. The preference of the female is the value  $y$  of the male trait that female prefer. The character  $z$  of the male can be tail size, color intensity, song diversity, or any character influencing female choice. As in Lande (1981) ('absolute choice'), a female with preference  $y$  accepts a male with trait  $z$  with probability

$$p_f(z|y) = \exp\left(-\frac{(y-z)^2}{2}\right). \quad (2.2)$$

Using the framework of adaptive dynamics, we shall study how a rare male mutant with trait  $z'$  performs in a resident male population with trait  $z$ , and how a rare female mutant with preference  $y'$  performs in a resident female population with preference  $y$ .

### (d) *Individual fitness*

The fitness of individuals is based on a simple life cycle with two age classes (juveniles and adults) and is given by:

$$s = v + rPg, \quad (2.3)$$

where  $v$  is adult survival rate,  $r = 0.5$  is adult sex-ratio,  $P$  is the probability for a mature individual to be mated, and  $g$  is the number of young surviving up to maturity per mate ( $g = s_0 f$ , with  $f$  fecundity, and  $s_0$  juvenile survival rate).

Let's consider a mutant male in the population: this male is accepted with probability  $p_f'$  ( $p_f' < p_f$  if the male is less attractive,  $p_f' > p_f$  if the male is more attractive). The probability  $P_m'$  for the mutant to be mated is given by:

$$P_m' = 1 - (1 - p_m p_f')^{nr(1-P_f)}. \quad (2.4)$$

Figure 1 shows the expected result that less attractive males are less likely to be mated, while more attractive ones are more likely to be mated.

### (e) *Male's cost of being attractive*

We normalize the value of the male trait  $z$  under natural selection only (without the effect of sexual selection) to  $z = 0$ . We assume that when  $z = 0$ , the corresponding adult male survival rate  $v_m$  is optimum and equals  $v_{m0}$ . When sexual selection operates, this has a cost

on adult survival rate (carotenes are invested in plumage coloration, plumage brightness increases predation risk) . We investigate two possible trade-offs:

(a) survival rate  $v_m$  decreases linearly with trait  $z$  , with constant cost  $c_{1m}$  :

$$v_m(z) = v_{m0} - c_{1m}|z|, \quad (2.5a)$$

(b) survival rate  $v_m$  decreases quadratically with trait  $z$  :

$$v_m(z) = v_{m0} - c_{2m}z^2. \quad (2.5b)$$

In the same way that being attractive is costly for males, being choosy is costly for females (energy spent to find a compatible male, increased predation). Let  $v_f$  be the female survival rate and  $v_{f1}$  its optimal value when individuals do not make any choice ( $p_f = 1$ ). The trade-off between female choice and survival is given by  $v_f(p_f) = v_{f1} - d_f(1 - p_f p_m)$  , where  $d_f$  is a constant reflecting the cost of choice.

**(f) Female's benefit of being choosy**

According to the indicator principle (Zahavi 1975), the character of the male reflects its quality. A male of good quality increases the fecundity  $f$  of the female he is mated with (good female stimulation, good sperm quality, good food supply), and the survival rate  $s_0$  of its progeny (heritability of “good genes”, better parental care) (Wedell 1999). The number  $g$  of young surviving up to maturity for such a good male is larger. Let  $g_0$  be the mean value of  $g$  in a resident population with character  $z$  . The value of  $g$  for a mutant male with character  $z'$  is given by  $g(z') = g_0 + h(z'-z)$  where  $h$  is a constant reflecting the influence of male quality on female fecundity and juvenile survival rate.

A female preferring males with good quality (high  $z$  value), is more likely to be mated to a good male. For this female, the number  $g$  of young surviving up to maturity is larger. The value of  $g$  for a mutant female with preference  $y'$  in a population with preference  $y$  is given by:  $g(y') = g_0 + h(y'-y)$  .

### 3. RESULTS

We study the outcome of the coevolution of the male trait  $z$  and female preference  $y$  in a population of size  $n$ , using the sign of the fitness gradients (Geritz *et al.* 1998). The process is first studied with each one of the traits fixed.

#### (a) *Evolution of the female preference when the male trait is fixed*

According to equation (2.3), the fitness of a mutant female with preference  $y'$  in a resident population with preference  $y$  and character  $z$  is given by  $s_{f,y}(y') = v_f(p_f') + \frac{1}{2}P_f'g(y')$  where  $P_f'$  is the probability for a mutant female accepting  $p_f' = p_f(z|y')$  males to be mated.

The fitness gradient is given by (see appendix):

$$\left. \frac{\partial s_{f,y}(y')}{\partial y'} \right|_{y'=y} = -\sqrt{2 \ln \frac{1}{p_f}} p_f p_m d_f - \frac{1}{4} \sqrt{2 \ln \frac{1}{p_f}} p_f p_m \frac{(1 - P_f(p_f p_m))^2}{1 - p_f p_m} n g_0 + \frac{1}{2} P_f(p_f p_m) h. \quad (3.1)$$

The first term of the sum corresponds to the cost of choice on survival. The second term corresponds to the cost of choice linked to the risk of not being mated. The third term corresponds to the benefit of choice on the number and quality of the young.

Let the character  $z$  of males be fixed. The female preference  $y$  increases if the fitness gradient is positive and decreases otherwise. The value of the female fitness gradient as a function of female selectivity  $p_f$  is presented in figure 2a. The fitness gradient is positive as long as  $p_f$  is greater than a critical value  $p_f^*$ , and negative if  $p_f$  becomes lower than this critical value. This means that as long as females are not too choosy ( $p_f$  is close to 1), the best strategy for a female individual is to be more selective than the others in order to be mated with a male of better quality. On the evolutionary scale, females become more selective. The character of males being fixed, the proportion  $p_f$  of accepted males decreases. If females become too choosy ( $p_f$  approaches 0), then costs of choice become more important than benefits, and the best strategy for an individual female is to be less choosy than the others. On the evolutionary scale, females become less selective and the proportion of accepted males increases. Hence, there exists a critical value  $p_f^*$  corresponding to a maximal fitness for females. Shall the evolution of sexual traits be directed by females only (the character  $z$  of males being fixed), the preference  $y$  of females would evolve to an



equilibrium value for which  $p_f(z|y) = p_f^*$ , or  $y = z + \sqrt{2 \ln \frac{1}{p_f^*}}$  by equation (2.2). Let's

define  $\delta_f^* = \sqrt{2 \ln \frac{1}{p_f^*}}$ ; we obtain the female isocline (figure 3a). When  $z$  is fixed,  $y$  evolves

to  $z + \delta_f^*$  as shown by arrows.

**(b) Evolution of the male trait when the female preference is fixed**

The fitness of a mutant male with character  $z'$  in a resident population with character  $z$  and female preference  $y$  is given by  $s_{m_z}(z') = v_m(z') + \frac{1}{2} P_m' g(z')$ , where  $P_m'$  is the probability for a mutant male accepted by  $p_f' = p_f(z'|y)$  females to be mated. The fitness gradient is given by:

$$\left. \frac{\partial s_{m,z}(z')}{\partial z'} \right|_{z'=z} = -c_{1m} + \frac{1}{4} \sqrt{2 \ln \frac{1}{p_f}} p_f P_m \frac{(1 - P_m(p_f P_m))^2}{1 - p_f P_m} n g_0 + \frac{1}{2} P_m(p_f P_m) h. \quad (3.2)$$

The first term of the sum corresponds to the cost of the character on survival. The second corresponds to the benefit of the character on the chance of being mated. The third corresponds to the benefit of the character on the number and quality of the young.

Let the preference  $y$  of females be fixed. The male character  $z$  increases if the fitness gradient is positive and decreases otherwise. The value of the male fitness gradient as a function of female selectivity  $p_f$  is presented in figure 2b. The fitness gradient is positive as long as  $p_f$  is smaller than a critical value  $p_f^{**}$ , and negative if  $p_f$  becomes larger than this critical value. This means that when males are not very attractive ( $p_f$  is close to 0), the best strategy for a male individual is to develop his character to be more attractive than the others in order to minimize the risk of not being mated. On the evolutionary scale, males develop their character. The preference of females being fixed, the proportion of accepted males increases. If males become too attractive ( $p_f$  approaches 1), then costs linked to the development of the character become more important than benefits, and the best strategy for a male is to develop his character less than the others. On the evolutionary scale, the character of males decreases, and the proportion of accepted males decreases. Hence, there exists a critical value  $p_f^{**}$  corresponding to a maximal fitness for males. Shall the evolution of sexual traits be directed by males only (the preference  $y$  of females being fixed), the character  $z$  of

males would evolve to an equilibrium value for which  $p_f(z|y) = p_f^{**}$ , or  $z = y - \sqrt{2 \ln \frac{1}{p_f^{**}}}$ .

Let's define  $\delta_f^{**} = \sqrt{2 \ln \frac{1}{p_f^{**}}}$ ; we obtain the male isocline (figure 3b). When  $y$  is fixed,  $z$

evolves to  $y - \delta_f^{**}$  as shown by arrows.

### (c) *Coevolution of male character and female preference*

To study the simultaneous evolution of female preference and male character, we superpose the male and female isoclines, with arrows indicating the way traits evolve (figure 4). There are two cases:

1) If  $p_f^{**} < p_f^*$ , then  $\delta_f^{**} \geq \delta_f^*$  (figure 4a)

Let's consider the evolution from an initial state without any sexual selection. We have  $z = 0$ ,  $y = 0$ , and  $p_f = 1$ . The male gradient is negative: the character does not develop. On the contrary, the female gradient is positive: the preference  $y$  increases and thus  $p_f$  decreases from 1 to  $p_f^*$ . When  $p_f = p_f^*$ , the male gradient is still negative: the male character does not develop. The sexual selection pressure is not intense enough for males to develop their character. The state  $(z = 0, y = \delta_f^*)$  is an equilibrium state. At equilibrium, the male character is not developed, though females are selective with intensity  $p_f^*$ . This equilibrium state is attractive whatever the initial state. This means that even if the male character and the female preference have developed, a way back is possible with decreasing female preference and loss of the male character.

2) If  $p_f^{**} \geq p_f^*$ , then  $\delta_f^{**} \leq \delta_f^*$  (figure 4bc)

As in the preceding case, from an initial state without sexual selection, the preference  $y$  increases and thus  $p_f$  decreases. Before  $p_f$  reaches  $p_f^*$ , the male gradient becomes positive; this means that the male character starts developing, which tends to increase  $p_f$ .

Simultaneously, the female gradient keeps positive, thus females go on developing their preference, which tends to decrease  $p_f$ . Thus, the more  $y$  increases, the more  $z$  increases and vice versa. This case corresponds to the Fisher's runaway. With a linear trade-off between character and survival (equation 2.5a, figure 4b), the process never stops, possibly leading to

very exaggerated traits. With a quadratic trade-off (equation 2.5b, figure 4c),  $p_f^{**}$  decreases when  $z$  increases. The process stops when  $p_f^{**} = p_f^*$ . The male and female characters reach an equilibrium value (the value for which isoclines cross). This corresponds to an equilibrium between natural and sexual selection.

#### (d) *Influence of population size on sexual selection*

The evolution of sexual selection depends on the sign of  $p_f^{**} - p_f^*$ : a runaway occurs when this quantity is positive. Computing  $p_f^*$  and  $p_f^{**}$  for different values of population size  $n$ , we find that both  $p_f^*$  and  $p_f^{**}$  increase when the population gets small, but  $p_f^*$  increases much more than  $p_f^{**}$  does (figure 5a).

As the risk of not being mated increases ( $n$  decreases), females benefit from being less selective and the pressure of sexual selection on males is no more sufficient to compensate for the cost of a secondary sexual character. As a consequence, the condition for a runaway to occur ( $p_f^{**} \geq p_f^*$ ) is more likely to be fulfilled when populations are large. According to our model, the runaway process is reversible: if a population has developed a sexual character and if the size of this population decreases, the character may disappear.

#### (e) *Sexual dimorphism*

So far we have focussed on a male trait preferred by females. However, females also have traits which can possibly be sexually selected. Sexual dimorphism depends on the evolution of both male and female character. The expression of female character fitness gradient is similar to the expression calculated for male character (equation 3.2) :

$$\left. \frac{\partial s_{f,z}(z')}{\partial z'} \right|_{z'=z} = -c_{1f} + \frac{1}{4} \sqrt{2 \ln \frac{1}{p_m}} p_f p_m \frac{(1 - P_m(p_f p_m))^2}{1 - p_f p_m} n g_0 + \frac{1}{2} P_m(p_f p_m) h. \quad (3.3)$$

Characters are more likely to develop when gradients have high values. Hence, the dimorphism between males and females is expected to be all the more important that male fitness gradient is greater than female fitness gradient. We can compute the value of both fitness gradients for different values of  $n$ ,  $p_f$  and  $p_m$ . We find that a high dimorphism is likely to exist when  $n$  is large,  $p_f$  is close to 0 (females are very selective), and  $p_m$  is close to 1 (males are not very selective). In this case the dimorphism is expected to decrease as the

size of the population decreases, and it can even invert, with females developing their character more than males do (figure 5b).

#### **4. DISCUSSION**

We have studied sexual selection in the framework of adaptive dynamics, focusing on the coevolution of male character and female preference. Our approach differs from quantitative genetics (Lande 1981) in that the development of male character and female preferences is explained in terms of costs and benefits, without referring to a genetic correlation that could establish between the male and female traits. Moreover, population size is a parameter of our model, allowing to study the influence of population size on sexual selection, while quantitative genetics models only deal with frequencies and not directly with size.

##### **(a) *Sensory bias hypothesis***

We find that the development of female preferences occurs before the development of male characters. Male traits are thus driven by the pre-existing choice of females. This choice may depend on biases in the female sensory system, e.g. preferences for traits developed in response to direct benefits – for instance preferences for colours or shapes that correspond to characteristics of their preys. Our model is thus relevant with the widespread idea that males exploit a pre-existing sensory bias (Andersson 1994; Jennions & Brooks 2001).

##### **(b) *The loss of sexual traits***

In our model, a runaway appears when the optimal proportion of compatibilities between individuals is lower for females than it is for males. In this case, males develop their character to attract females and females develop their preference to “resist” males. This is in accordance with the recent idea that sexual selection results from a conflict between sexes (Gavrilets *et al.* 2000).

We find that the runaway process is reversible: a population may develop a sexual character given some circumstances and loses it as conditions change, thus adapting to new environments. This result is all the more interesting that recent phylogenetic studies show that losses of sexual characters are common (Omland & Lanyon 2000; Wiens 2001). Assuming a genetic correlation between male character and female preference would reduce the chances for reversibility.

### **(c) *Influence of population size***

We have computed the probability for an individual to be mated in a monogamous population with fixed size, sex-ratio and proportion of compatibilities between individuals. We find that individuals are all the more likely not to be mated that the population is choosy and small. Hence, sexual selection generates an Allee effect, as already noted by Møller & Legendre (2001). When the population is small, females become less selective in order to maximise their chance to be mated, males are less likely to develop their character, and the chances for a runaway are lower. As the runaway reveals to be a reversible process, a character developed while the population is large may disappear as the population becomes smaller. This is consistent with what is observed for small populations colonizing islands (Grant 2001). We also find in some cases that the dimorphism between male and female characters decreases with population size, and can even invert, with females developing their character more than males do (figure 5*b*). This phenomenon has been reported for insular populations (Peterson 1997; Grant 2001).

## **5. CONCLUSION**

Our results are in agreement with ideas and observations concerning sexual selection: (1) female preferences evolve before the development of male traits (sensory bias), (2) the runaway is a consequence of an arms race between sexes (sexual conflict), and (3) it is a reversible process (loss of sexual traits). In our model, population size has an influence on the evolutionary outcomes. Similar approaches could be useful to the understanding of insular phenomena, and to conservation problems.

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## APPENDIX

We compute the fitness gradient of females (equation 3.1). The fitness gradient of males (equation 3.2) is computed in a similar way.

The expression for fitness,  $s_{f,y}(y') = v_f(p_f') + \frac{1}{2}P_f'g(y')$ , is differentiated in order to

obtain the fitness gradient:  $\frac{\partial s_{f,y}(y')}{\partial y'} \Big|_{y'=y} = \frac{\partial p_f'}{\partial y'} \Big|_{y'=y} \frac{\partial v_f}{\partial p_f} + \frac{1}{2} \frac{\partial p_f'}{\partial y'} \Big|_{y'=y} \frac{\partial P_f'}{\partial p_f'} \Big|_{p_f'=p_f} g_0 + \frac{1}{2} P_f(p_f p_m) h$ .

Differentiating  $p_f' = \exp(-\frac{(z-y')^2}{2})$ , we get  $\frac{\partial p_f'}{\partial y'} \Big|_{y'=y} = -(y-z)p_f = -\sqrt{2 \ln \frac{1}{p_f}} p_f$ .

Differentiating  $v(p_f) = v_{f1} - d_f(1 - p_f p_m)$ , we get  $\frac{\partial v_f}{\partial p_f} = p_m d_f$ .

When the sex-ratio equals  $\frac{1}{2}$ , we have  $P_f = P_m$  and

$P_f(p_m p_f, p_m p_f') = 1 - (1 - p_m p_f')^{\frac{1}{2}n(1 - P_f(p_m p_f))}$ , giving  $\frac{\partial P_f'}{\partial p_f'} \Big|_{p_f'=p_f} = \frac{1}{2} n p_m \frac{(1 - P_f(p_m p_f))^2}{1 - p_m p_f}$ .

We find at end:

$\frac{\partial s_{f,y}(y')}{\partial y'} \Big|_{y'=y} = -\sqrt{2 \ln \frac{1}{p_f}} p_f p_m d_f - \frac{1}{4} \sqrt{2 \ln \frac{1}{p_f}} p_f p_m \frac{(1 - P_f(p_f p_m))^2}{1 - p_f p_m} n g_0 + \frac{1}{2} P_f(p_f p_m) h$ .

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## FIGURE CAPTIONS

Figure 1. Probability to be mated for a mutant male with attractiveness  $p_f'$  (accepted by a proportion  $p_f'$  of females) in a population of resident males with attractiveness  $p_f$  ( $n = 100$ ,  $p_m = 0.5$ ,  $p_f = 0.5$ ).

Figure 2. (a) Female fitness gradient as a function of the proportion  $p_f$  of accepted males. Arrows show the way the proportion of accepted males evolves. It decreases when females are not selective enough, and increases when females are too selective. An equilibrium is reached for a proportion  $p_f^*$ . (b) Male fitness gradient as a function of the proportion  $p_f$  of accepted males. Arrows show the way the proportion of accepted males evolves. It increases when males are not attractive enough, and decreases when males are too selective. An equilibrium is reached for a proportion  $p_f^{**}$  ( $n = 100$ ,  $d_f = 0.35$ ,  $c_{1m} = 0.35$ ,  $h = 0.62$ ,  $g_0 = 0.45$ ,  $p_m = 1$ ).

Figure 3. (a) Evolution of the female preference  $y$ , the male character  $z$  being fixed. Arrows show the way the preference evolves. (b) Evolution of male character  $z$ , the female preference  $y$  being fixed (under the assumption of a linear trade-off). Arrows show the way the character evolves. Parameters are as in figure 2.

Figure 4. Superposition of female isocline (dotted) and male isocline (plain) shows the way female preference  $y$  and male character  $z$  evolve (indicated by arrows). (a) The runaway does not occur. (b) The runaway does occur: with a constant cost, the preference and character never stop developing. (c) The runaway does occur: with an increasing cost, the preference and character develop to a point of equilibrium between natural and sexual selection.

Figure 5. Sexual selection depending on population size. (a) Equilibrium values  $p_f^*$  and  $p_f^{**}$  of the proportion  $p_f$  of accepted males as a function of population size ( $d_f = 0.3$ ,  $c_{1m} = 0.35$ ,  $h = 0.5$ ,  $g_0 = 0.5$ ,  $p_m = 1$ ). The condition for a runaway to occur ( $p_f^{**} \geq p_f^*$ ) is

satisfied when  $n$  is large but not when  $n$  is small. (b) Values of the male and female fitness gradients as a function of population size ( $c_{1m} = c_{1f} = 0.2$ ,  $h = 1$ ,  $g_0 = 1$ ,  $p_f = 0.01$ ,  $p_m = 0.9$ ). Dimorphism is strong when  $n$  is large, whereas it disappears when  $n$  becomes smaller, and can even invert.









