

## POPULATION GENETIC MODELS OF SEXUAL SELECTION WITH PLEIOTROPIC EFFECTS ON FERTILITY

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### RESUMEN

Recientes trabajos teóricos indican que la preferencia de las hembras por los machos puede evolucionar si tales preferencias resultan en una reducción en fertilidad. Modelos genéticos en organismos diploides de un solo *locus* se desarrollan en este trabajo asumiendo que existe un diferencial en la atracción por los machos, pero, además, que los cruces con dichos machos "sexy" producen una fertilidad disminuida. Este esquema original permite polimorfismos genéticos a pesar de que la naturaleza de la preferencia de la hembra ejerce un efecto muy decidido en las condiciones del polimorfismo.

### INTRODUCTION

Interest in sexual selection may be traced back to Darwin who recognized the potential for natural selection to act on traits which affect the attractiveness of males to female mates. Often the secondary sexual characteristics of males are assumed to reduce the viability of their carriers. Models have consequently focused on the potential of sexual selection to overcome these reductions in viability (O'Donald, 1980).

Weatherhead & Robertson (1979) have suggested that females of certain polygynous birds may suffer a reduction in fecundity when mated to sexually attractive males. The "sexy son" hypothesis has been criticized on a number of points (Wittenberger, 1981; Searcy & Yasukawa, 1981; Heisler, 1981). Perhaps the most severe blow to this theory was Kirkpatrick's (1985) quantitative genetic and two-*locus* haploid models which appeared to demonstrate the theoretical infeasibility of this process.

Recently, Curtsinger & Heisler (1988) have demonstrated that Kirkpatrick's results were not robust and that diploid models may result in polymorphic equilibria consistent with the "sexy son" hypothesis. Given the results of Curtsinger & Heisler it now seems

appropriate to begin the development of models of sexual selection which explicitly incorporate effects on female fecundity.

### THE MODELS

The models described here make two assumptions that have also been made by Weatherhead, Robertson & Heisler. I assume that certain male genotypes will be sexually attractive and further than females mating with these males will suffer a reduction in fecundity. Implicit in the empirical and theoretical work of Weatherhead & Robertson is the assumption that the population is polymorphic for sexy males. Consequently the analysis presented here will seek to uncover the relationship between sexual attractiveness and reduction in fecundity which is consistent with a specified polymorphism.

The models analyzed here will assume male attractiveness is determined by a single *locus* with two alleles. One of the best known examples of sexual selection occurs in the onogamous Arctic Skua. Dark color morphs of this bird have an advantage in mating compared with the pale and intermediate morph and these traits appear to be controlled by a single *locus* (O'Donald, 1972; O'Donald & Davis, 1959; O'Donald & Davis, 1976). I assume that the allele that controls "sexyness",  $A$ , is dominant to the "non-sexy" allele,  $a$ . A proportion,  $\alpha$ , of all females will mate exclusively with  $AA$  or  $Aa$  males and the remainder,  $1-\alpha$ , will mate at random. This model will be referred to as the exclusive preference model. The frequency of different matings can be calculated by first examining the relative frequencies in which the three male genotypes mate. Let the frequencies of the genotypes  $AA$ ,  $Aa$  and  $aa$  be  $u$ ,  $v$  and  $w$ . Clearly  $aa$  males will mate only with those females who mate at random. Thus  $aa$  males will be involved in  $(1-\alpha)w$  of all matings. The remaining random matings,  $(1-\alpha)(u+v)$ , and exclusive matings,  $\alpha$ , will be with sexy males. These remaining matings will be divided between  $AA$  and  $Aa$  males in proportion to their occurrence. Thus  $AA$  males mate with frequency  $(1-\alpha)u + \alpha[u/(1-w)]$  and  $Aa$  males with frequency  $(1-\alpha)v + \alpha[v/(1-w)]$ . It is further assumed that each male will mate with females of all three genotypes in proportion to their occurrence. Thus the frequency of matings between  $aa$  males and  $Aa$  females, for instance, will be  $(1-\alpha)wv$ . The frequencies of all possible matings have been calculated in a similar fashion and are given in Table 1. It should be noted that specific reference to harem size has not been made. In principle, knowledge of the average harem size for "sexy" vs. "non-sexy" males could be translated into an  $\alpha$  value.

TABLE 1

Matings		Fecundity	Frequency
Males	Females		
AA	AA	f	$\alpha u^2/(1-w)+(1-\alpha)u^2$
AA	Aa	f	$\alpha uv/(1-w)+(1-\alpha)uv$
Aa	AA	f	$\alpha uv/(1-w)+(1-\alpha)uv$
AA	aa	f	$\alpha uw/(1-w)+(1-\alpha)uw$
aa	AA	1	$(1-\alpha)uw$
Aa	Aa	f	$\alpha v^2/(1-w)+(1-\alpha)v^2$
Aa	aa	f	$\alpha vw/(1-w)+(1-\alpha)vw$
aa	Aa	1	$(1-\alpha)vw$
aa	aa	1	$(1-\alpha)w^2$

Since "sexy" males occupy inferior territories the fecundity of females that mate with these males will be  $f$  ( $0 < f < 1$ ) relative to matings with "nonsexy" males. The model described here is a direct descendant of sexual selection models considered by O'Donald (1980). This model differs from his by the inclusion of the differences in fecundity.

Since matings are not at random we must keep track of genotype frequencies. The genotype recursions that follow from Table 1 are,

$$Tu' = p^2 f[\alpha/(1-w) + 1 - \alpha],$$

$$Tv' = pf[\alpha/(1-w) + 1 - \alpha](v + w) + (1-\alpha)wp,$$

$$Tw' = (1-p)f[\alpha/(1-w) + 1 - \alpha]v/2 + (1-\alpha)(1-p)w,$$

where  $T = f\alpha + (1-\alpha)[f + w(1-f)]$  and  $p$  is the frequency of the  $A$  allele. An equilibrium for this system is reached when,

$$\hat{w} = (1-f\alpha)/[(1-\alpha)(1-f)] \quad (1)$$

It can also be shown that genotypes will be in Hardy-Weinberg equilibrium only at the point (1) thus  $\hat{p} = 1 - \sqrt{\hat{w}}$ .

Since genotypes will not generally be in Hardy-Weinberg equilibrium the stability of (1) must be determined by looking at perturbations in two dimensions. The equilibrium (1) will be stable if  $1 - f - \alpha > 0$ . Thus all feasible equilibria are stable. The top of Figure 1 shows the relation between  $\alpha \hat{w}$  and  $f$ .

The second model will assume that the advantage enjoyed by "sexy" males is most pronounced when they are rare and diminishes as they become more common. This model is called negative frequency-dependent by O'Donald (1980). Specifically a fraction  $\alpha w$  of all females will mate exclusively with "sexy" males while the remainder,  $1 - \alpha w$ , will mate at random. Using reasoning similar to that in the previous section we note "non-sexy" (*aa*) males will mate with frequency  $(1 - \alpha w)w$  while "sexy" males (*AA* and *Aa*) will mate with frequency  $(1 - \alpha w)(u + v) + \alpha w$ . Again the frequency of matings by the "sexy" genotypes will be in proportion to their frequencies. Thus *AA* males with frequency  $(1 - \alpha w)v + \alpha wv / (1-w) = u[1 + \alpha w^2 / (1-w)]$  and *Aa* males with frequency  $(1 - \alpha w)v + \alpha wv / (1-v) = v[1 + \alpha w^2 / (1-w)]$ . The frequencies of all matings are given in Table 2. Genotype recursions of this model are given below.

$$Tu' = p^2 f [1 + \alpha w^2 / (1-w)],$$

$$Tv' = p(v + w)f[1 + \alpha w^2 / (1-w)] + (1-\alpha w)wp,$$

$$Tw' = (1-p)vf[1 + \alpha w^2 / (1-w)]/2 + (1-\alpha w)(1-p)w,$$

where  $T = f(1-w + \alpha w^2) + (1-\alpha w)w$ . An equilibrium for this model will be reached when.

$$\hat{w} = \frac{f - \alpha - 1 + \sqrt{(1-f+\alpha)^2 - 4\alpha(f-1)^2}}{2\alpha(f-1)} \quad (2)$$

TABLE 2

Matings		Fecundity	Frequency
Males	Females		
AA	AA	f	$u^2 [1 + \alpha w^2 / (1-w)]$
Aa	AA	f	$uv [1 + \alpha w^2 / (1-w)]$
AA	Aa	f	$uv [1 + \alpha w^2 / (1-w)]$
AA	aa	f	$uw [1 + \alpha w^2 / (1-w)]$
aa	AA	1	$uw(1-\alpha w)$
Aa	Aa	f	$v^2 [1 + \alpha w^2 / (1-w)]$
Aa	aa	f	$vw [1 + \alpha w^2 / (1-w)]$
aa	Aa	1	$vw(1-\alpha w)$
aa	aa	1	$w^2(1-\alpha w)$

As with the previous model genotypes will be in Hardy-Weinberg equilibrium only at (2) thus  $p = 1 - \sqrt{\hat{w}}$ . The stability analysis for this equilibrium yields as a condition for stability,

$$B\hat{p}(1-\hat{w}/2) - \alpha\hat{p}\hat{w}/2 + \hat{p}C > 0 \quad (3)$$

where  $B = \alpha f \hat{w}(2-\hat{w})/(1-\hat{w})^2$  and  $C = 2\alpha\hat{w}(1+f) + f-1$ . I have not been able to reduce (3) to a simple condition, however extensive numerical evaluation of (3) suggests that all feasible equilibria will be stable. The bottom of Figure 1 shows the relationship between various values of  $f$ ,  $\alpha$  and  $\hat{w}$ .

The last model considered is called positive frequency-dependent. In contrast to the negative frequency-dependent model the fraction of all females that mate exclusively with "sexy" males is proportional to their frequency. Polymorphic equilibria are described by

$$\hat{w} = (1-\alpha-f)/\alpha(f-1).$$

The stability condition for this equilibrium is quite complicated and numerical analysis has shown these equilibria to be always unstable.

## DISCUSSION

Curtsinger & Heisler (1988) provided numerical examples of populations in which "sexy" males and preference for "sexy" males increase from initially low frequencies when there is a trade-off between sexual and fertility selection. The models developed here assume all females exhibit a preference for "sexy" males. To produce a tractable model the action of fertility selection is quite simple compared to the Curtsinger and Heisler model.

A general conclusion from these models is that when there is a trade-off between sexual selection and fertility then the conditions for polymorphism can be quite extensive depending on the nature of the female preference. When female preference follows the negative frequency-dependence model, stable polymorphisms exist for all possible combinations of  $f$  ( $0 < f < 1$ ) and  $\alpha$  ( $0 < \alpha < 1$ ). Positive frequency-dependence in mating preference is destabilizing and no polymorphic equilibria are stable. The exclusive preference model yields intermediate results: some but not all combinations of  $\alpha$  and  $f$  will result in stable polymorphisms. Generalizations of these models could include more general fertility functions or the addition of a second *locus* which controlled female preference.

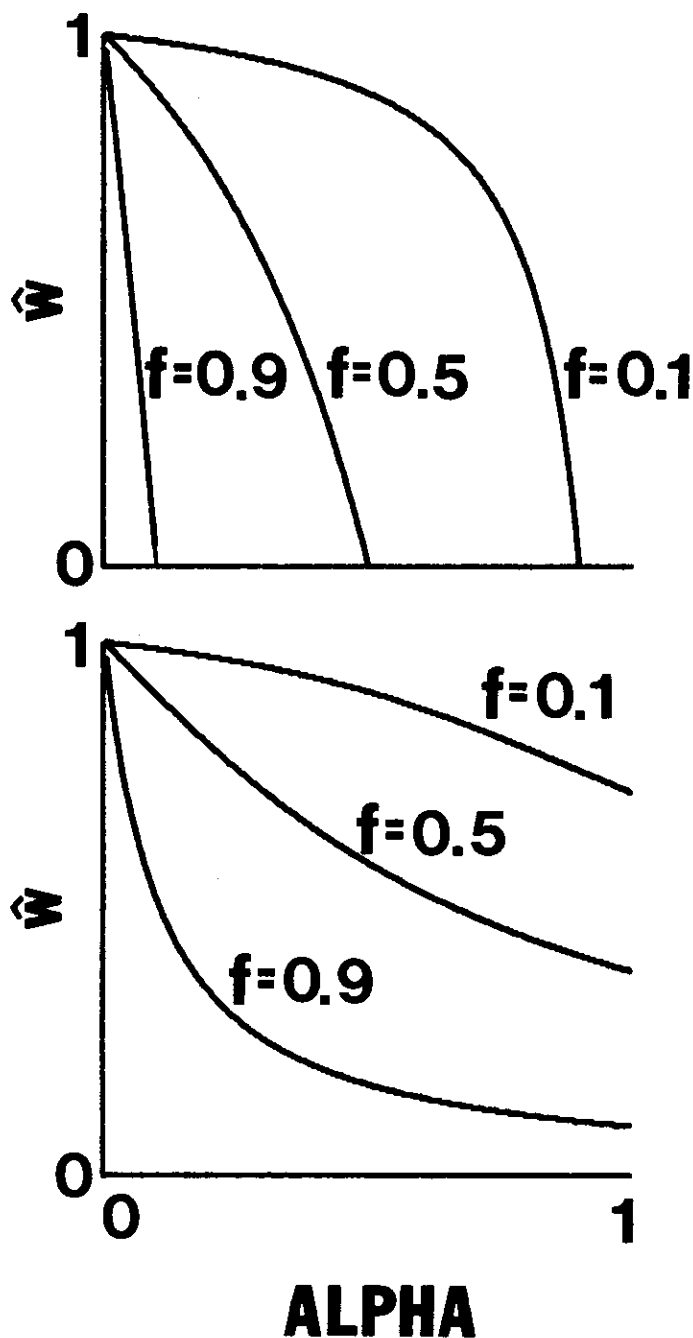


FIGURE 1. The equilibrium values of the *aa* genotype ( $\hat{w}$ ) as a function of  $\alpha$  and  $f$  for the exclusive preference model (top) and negative frequency-dependent model (bottom).

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