

Sexual Selection, Population Density, and Availability of Mates

ILAN ESHBEL

Department of Statistics, Tel-Aviv University, Tel-Aviv, Israel

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The evolution of sexual features designed to attract individuals of the opposite sex is studied. When limitation of sexual choice by physical availability of mates is accounted for, the exact distribution of the number of alternative mates available to a choosing individual (usually female) proves crucial for the evolution of sexual attractiveness. Selection for or against the attractive type or maintenance of a protected polymorphism of types in the population are shown to be dependent upon this distribution. It is further demonstrated that high population density is always favorable to the evolution of the attractive type. Some ecogenetical aspects of sexual selection and population density are suggested.

INTRODUCTION

Sexual selection, in its widest sense, may be regarded as the result of any system of nonrandom mating which favorably affects gene frequencies toward one or more alleles in the population. In a more specific context, sexual selection is commonly referred to as a mating system in which individuals of all types in the choosing sex, say females, prefer the same type of types of mates of the other sex. With this connotation, it is most convenient to analyze sexual selection as a special case of the general model of assortative mating [see Karlin (1978) and references therein]. Actually, all analytic models of sexual selection postulate that a *fixed quota*, say $\alpha_j > 0$ of females of all types (we assume for convenience females as the choosing sex) mate assortatively with males of a given type j (e.g., O'Donald 1962, 1963, 1967, 1973, 1977a, b; Karlin, 1978). In addition to the obvious, alleged, assumption that sexual preference is independent of the female type, the assortative mating model (or models) of sexual selection tacitly assumes, furthermore, that the proportion α_j of females mating assortatively with males of a given, preferred, type j is *independent of the frequency of that type among available males in the population*. Thus, even if the proportion of the preferred type j is one out of a million in the population, a proportion of at least α_j of all females in this population, (which may be the majority of all females) mate with males of this rare type in the first generation—an assumption hardly conceivable in most natural situations. Unfortunately, this “discontinuity

postulate'' is crucial for some of the most basic results of the model, especially those concerning extinction and establishment of male types in the population (e.g., O'Donald, 1977a, b).

Indeed, assortative mating models prove helpful for simplifying mathematical analysis and, thereby, enabling the quantitative understanding of some aspects of sexual selection. However, in most natural situations of sexual selection, a possible success of a male of the unpreferred type to mate does not necessarily result from a blindness of a certain fixed quota of females (of all types) to the attractiveness of the preferred male type. More likely, such a success results from the fact that by sheer chance no attractive male type occurs in the female's vicinity.

The objective of this work is to study sexual selection where an individual of the choosing sex is limited to a choice among a small, usually random, number of available mates. Quantitative analysis of this situation leads to quite different results from those obtained by the assortative mating model.

We assume a diploid polygynous population in which a choice of a mate is made by one sex, say the females. More specifically it is assumed that each female is fertilized by exactly one male. Alternatively, one can assume that each female is fertilized by one male at the most and that the chance of a female not being fertilized is independent of any genetical factor in study. Since nonfertilized females do not contribute to the next generation, both assumptions are equivalent in terms of changes in gene frequencies.

In either case it is assumed that each female attempts to mate with a male of a given phenotype, say the attractive one, if available in her vicinity. If not, she is satisfied with a nonattractive male. It is further assumed that sexual attractiveness is genetically inherited and that each male can fertilize as many females as it is chosen by (maybe none).

We focus on the interesting (and apparently common) case where sexual attractiveness has its cost in individual viability, e.g., an attractive male may be equally conspicuous to predators and females (Fisher, 1932). An interesting, though controversial approach to this phenomenon is to be found in Zahavi (1977).

As we see it, the result of the conflict between sexual selection and viability selection is determined by population density and by other demographic factors governing the probabilistic laws of male-female meetings. Sexual selection, in turn, may affect the viability of the population and, thereby, its density. Mutual ecogenetic effects of sexual selection and population density are, therefore, studied in the last section of this work.

2. THE MODEL AND BASIC RESULTS

We assume a one-locus diploid model with two alleles A and a . The recessive allele A determines a sexually attractive marker in males but does not affect

females. This marker decreases the viability so that the relative frequency of survivors among marked males is $1 - s$ of the parallel frequency among non-marked males. $s > 0$ is the intensity of viability selection against the marker. Let p_1 , p_2 , and p_3 be the relative frequencies of the types AA , Aa , and aa in the population of newborn offspring at a given generation. The relative frequencies of these types in the population of adult males will be

$$\hat{p}_1 = \frac{(1-s)p_1}{1-sp_1}, \quad (2.1a)$$

$$\hat{p}_2 = \frac{p_2}{1-sp_1}, \quad (2.1b)$$

$$\hat{p}_3 = \frac{p_3}{1-sp_1}. \quad (2.1c)$$

The relative genotypic frequencies among adult females remain p_1 , p_2 , and p_3 .

At this phase, males and females meet according to some probabilistic law so that the number of males met by a single female is a random variable X with the following distribution:

$$p(X = n) = \alpha_n, \quad n = 0, 1, 2, \dots \quad (2.2)$$

We define the probability generating function

$$\phi(u) = \sum_{n=0}^{\infty} \alpha_n u^n, \quad u \geq 0. \quad (2.3)$$

Ignoring females who do not find a male, we assume $\alpha_0 = 0$ or, equivalently $\phi(0) = 0$.

It is assumed that the group of males met by a female is a random sample of the adult male population. A female always mates with an attractive male if she meets one. If a female meets n males ($n = 1, 2, \dots$) then there is a probability $1 - (1 - \hat{p}_1)^n$ that she will mate with an attractive male. Thus, the proportion of females mating with attractive males of the type AA is:

$$\begin{aligned} p_1^* &= \sum_{n=1}^{\infty} \alpha_n (1 - (1 - \hat{p}_1)^n) \\ &= 1 - \phi(1 - \hat{p}_1) \\ &= 1 - \phi\left(\frac{1 - p_1}{1 - sp_1}\right). \end{aligned} \quad (2.4)$$

The frequency of females not finding an attractive male is $\phi(1 - p_1)/(1 - sp_1)$ and we assume that these females mate at random with nonattractive males.

Thus, a proportion $\hat{p}_2/(1 - \hat{p}_1) = p_2/(1 - p_1)$ of these females mates with males of the type Aa . The frequency of females mating with males of the type Aa is, therefore,

$$p_2^* = \frac{p_2}{1 - p_1} \phi \left(\frac{1 - p_1}{1 - sp_1} \right). \quad (2.5)$$

The frequency of the allele A among genes passed to the next generation by males is

$$\begin{aligned} p^* &= p_1^* + \frac{1}{2} p_2^* = 1 - \left(1 - \frac{1}{2} \frac{p_2}{1 - p_1} \right) \phi \left(\frac{1 - p_1}{1 - sp_1} \right) \\ &= 1 - \frac{1 - p}{1 - p_1} \phi \left(\frac{1 - p_1}{1 - sp_1} \right), \end{aligned} \quad (2.6)$$

where

$$p = p_1 + \frac{p_2}{2} \quad (2.7)$$

is the frequency of the allele A among genes passed to the next generation by females. The frequency of the genotype AA among newborn offspring of the next generation will be

$$p_1' = p_1^* p_1 + \frac{p_1^* p_2 + p_2^* p_1}{2} + \frac{p_2 p_2^*}{4} = p p^* \quad (2.8)$$

and, in the same way, the frequency of the genotype Aa will be

$$p_2' = p q^* + p^* q = p^* + p - 2p p^*. \quad (2.9)$$

The frequency of the allele A among newborn offspring of the next generation will be

$$p' = p_1' + \frac{1}{2} p_2' = \frac{p + p^*}{2}. \quad (2.10)$$

We say that, in a given setup (p_1, p_2) of the population, selection favors the attractive type if $p' > p$ or, equivalently if $p^* > p$ (immediate from (2.10)). However (2.6) implies that (with $p < 1$) $p^* > p$ if and only if:

$$\phi \left(\frac{1 - p_1}{1 - sp_1} \right) < 1 - p_1. \quad (2.11)$$

(Note that the left side of (2.11) is the relative frequency of nonattractive male matings in the population.)

3. FIXATION AND EXTINCTION OF THE ALTERNATIVE TYPES IN THE POPULATION

In this section we examine stability of the equilibria $(1, 0)$ and $(0, 0)$, corresponding to fixations of the attractive and the viable types, respectively. To check the stability of the equilibrium $(1, 0)$ we calculate, at this point,

$$\frac{\partial p^*}{\partial p_1} = \frac{\alpha_1}{1-s}, \quad \frac{\partial p^*}{\partial p_2} = \frac{1}{2} \frac{\alpha_1}{1-s},$$

and $p^* = p = 1$.

Indeed, we have

$$\frac{\partial p}{\partial p_1} = 1 \quad \text{and} \quad \frac{\partial p}{\partial p_2} = \frac{1}{2}.$$

Employing (2.8) and (2.9), the matrix of linear approximation at $(1, 0)$ becomes:

$$\begin{vmatrix} \frac{\partial p'_1}{\partial p_1} & \frac{\partial p'_1}{\partial p_2} \\ \frac{\partial p'_2}{\partial p_1} & \frac{\partial p'_2}{\partial p_2} \end{vmatrix} = \begin{vmatrix} \frac{1-s+\alpha_1}{1-s} & \frac{1}{2} \frac{1-s+\alpha_1}{1-s} \\ \frac{1-s+\alpha_1}{1-s} & \frac{1}{2} \frac{1-s+\alpha_1}{1-s} \end{vmatrix}.$$

The largest eigenvalue of this matrix is

$$\frac{1-s+\alpha_1}{2(1-s)}.$$

Hence, the equilibrium $(1, 0)$ is stable if this eigenvalue is less than 1, namely, if

$$\alpha_1 < 1-s. \quad (3.1)$$

(For a necessary condition, a weak version of inequality (3.1) is required). Indeed, stability of $(1, 0)$ means selection for the attractive type when this type is the prevalent.

COROLLARY 1. *When the frequency of the attractive type in the population is sufficiently high, selection operates in its favor if and only if its relative survival probability is higher than the chance that a female's choice would be limited to one male.*

This result may be otherwise obtained in a manner which (unlike the standard technique of local analysis) may be useful in examining the stability of the second fixation equilibrium.

For this, set

$$1 - \phi\left(\frac{1-p_1}{1-sp_1}\right) = f(p_1). \quad (3.2)$$

It follows from (2.11) that selection favors the attractive type if and only if

$$p_1 < f(p_1).$$

At the fixation point $(1, 0)$, $p_1 = 1 = f(1) = f(p_1)$ and selection favors the attractive type at the vicinity of $(1, 0)$ if $f'(1) > 1$. But

$$f'(1) = \frac{1}{1-s} \phi'(0) = \frac{\alpha_1}{1-s} \quad (3.3)$$

and Corollary 1 follows immediately.

In the same way (having $\alpha_0 = 0$), $0 = f(0)$ and selection will favor the attractive type in the vicinity of $(0, 0)$ (i.e., where this type is rare) if $f'(0) > 1$. But

$$f'(0) = (1-s) \phi'(1) = (1-s)\mu, \quad (3.4)$$

where $\mu = EX$ is the expected number of males met by a choosing female and we readily obtain

COROLLARY 2. *Selection operates in favor of the attractive type when it is rare if and only if*

$$(1-s)\mu > 1, \quad (3.5)$$

i.e., the equilibrium $(0, 0)$ is stable if and only if $(1-s)\mu < 1$.

(Since the allele A is recessive, either extinction or establishment of the attractive type occurs in less than a geometric rate).

From (3.1) and (3.5) we have:

COROLLARY 3. *A protected polymorphism of the two male types is maintained in the population if and only if*

$$\alpha_1 > 1-s > \frac{1}{\mu}. \quad (3.6)$$

For this condition to hold for some appropriate values of viability selection it is necessary and sufficient that

$$\alpha_1 \mu = p(X=1) EX > 1. \quad (3.7)$$

Finally it follows from (2.6), (2.8), and (2.9) that a point $(\tilde{p}_1, \tilde{p}_2)$ is an equilibrium point of the process if and only if a value \tilde{p} exists so that

$$1 - \tilde{p}^2 = \phi\left(\frac{1 - \tilde{p}^2}{1 - s\tilde{p}^2}\right) \quad (3.8)$$

and

$$\tilde{p}_1 = \tilde{p}^2, \quad \tilde{p}_2 = 2\tilde{p}\tilde{q}.$$

Having $\alpha_0 = 0$, $(0, 0)$ and $(1, 0)$ are obvious equilibria of the system. The solution of (3.8) also provides all inner equilibria if any.

4. THE MODEL OF MALE-FEMALE BLIND MEETINGS AND THE EFFECT OF POPULATION DENSITY

In this section we concentrate on the simplest model in which, during a given period (to be mentioned for tradition as the searching period), males and females meet at random according to the probabilistic laws of molecule collisions in an ideal gas. We discern between several cases.

Case I: A Fixed Searching Period

In this case, we assume that during a fixed period of time, the female is searching exclusively for an attractive male, if available. If, at the end of this period, no such male has been met, the female mates with the first male she meets, independent of type.

If Y is the number of males encountered by a female during the searching period (including males she meets after being mated) we know that

$$p(Y = n) = e^{-\lambda} \frac{\lambda^n}{n!}, \quad n = 0, 1, 2, \dots,$$

where $\lambda > 0$ is proportional to the *population density*.

Remark. In this context, population density is measured in terms of the average number of males per unit of area possibly searched by a single female. Indeed, this unit is different from one species to another, e.g., it is apparently very large in bird populations. An attractive male is to be chosen out of $X = Y + 1$ possible trials, therefore

$$\alpha_n(\lambda) = p(X = n) = e^{-\lambda} \frac{\lambda^{n-1}}{(n-1)!}, \quad n = 1, 2, 3, \dots \quad (4.1)$$

We have

$$\mu(\lambda) = \sum_{n=1}^{\infty} n \alpha_n(\lambda) = \lambda + 1,$$

and

$$\alpha_1(\lambda) = e^{-\lambda}$$

Hence

$$\alpha_1(\lambda) \mu(\lambda) = (\lambda + 1) e^{-\lambda} < 1 \quad \text{for all } \lambda > 0.$$

Condition (3.7) thus indicates that no protected polymorphism can be maintained in the population.

In terms of distribution generating functions (4.1) can be written as

$$\begin{aligned}\phi_\lambda(u) &= \sum_{n=1}^{\infty} \alpha_n(\lambda) u^n \\ &= \sum_{n=1}^{\infty} e^{-\lambda} \frac{\lambda^{n-1}}{(n-1)!} u^n = u e^{-\lambda(1-u)}, \\ \frac{\partial \phi_\lambda(u)}{\partial \lambda} &= -u(1-u) e^{-\lambda(1-u)} < 0.\end{aligned}\quad (4.2)$$

From (2.6) and (2.10) we therefore see that, for any $0 < p_1 < 1$, $0 < p_2 < 1 - p_1$, and $s > 0$, p^* is an increasing function of λ .

In biological terms: An increase in the population density (as being defined in the special case in study) is always favorable for the evolution of the attractive male type. Inserting (4.2) into (2.6), we obtain

$$p^* = 1 - \frac{1-p}{1-sp_1} e^{-((\lambda(1-s)p_2)/(1-sp_1))}$$

It can be directly shown that if population density is sufficiently high, global selection favors the attractive male type. If the population density is sufficiently low the opposite happens. This result, however, is proved, for a more general situation, in the next section.

Case II: Random Searching Period

In many cases, the searching period of a female is not fixed (even if she fails to find an attractive male), but distributed according to some probabilistic law. If the event forcing a female to stop her search has a fixed probability of occurrence at any infinitesimal time interval of length Δt , the searching period is distributed exponentially. In this case it is readily shown that the number of males met by a female during her searching period is geometrically distributed; and if we fix the time unit to be the expected length of the searching period then the parameter of the geometric distribution is $\lambda/(1+\lambda)$.

We get

$$p(Y=n) = \frac{1}{1+\lambda} \left(\frac{\lambda}{1+\lambda} \right)^n, \quad n = 0, 1, 2, \dots$$

If all other assumptions stand as in the previous case, we get

$$\alpha_n(\lambda) = \frac{1}{1+\lambda} \left(\frac{\lambda}{1+\lambda} \right)^{n+1}, \quad n = 1, 2, 3, \dots \quad (4.3)$$

or

$$\phi_\lambda(u) = \frac{1}{1+\lambda} \sum_{n=1}^{\infty} \left(\frac{\lambda}{1+\lambda} \right)^{n-1} u^n = \frac{u}{1+\lambda-\lambda u}. \quad (4.4)$$

$\phi_\lambda(u)$ is, again, a decreasing function of λ and, as it is in the case of the fixed searching period we see that an increase in the population density is favorable for the attractive male type.

Inserting (4.4) into (2.6) we have

$$p^* = 1 - \frac{1-p}{1+(\lambda-s-\lambda s)p_1}. \quad (4.5)$$

Thus, for any $0 < p_1 < p < 1$, $p^* > p$ if $\lambda > s/(1-s)$, $p^* < p$ if $\lambda < s/(1-s)$ and no protected polymorphism can be maintained.

Global selection always favors either one type or the other, depending on the population density.

Case III: Females May Return to Abandoned Males

In this case we assume, as before, a geometric distribution of the number of males met by a single female during her searching period. However, we assume that if at the termination of this period no attractive male has been met, the female can relocate and mate with one of the (nonattractive) males she had met, if any. The female resumes her search only if no male had been met during the searching period. Thus while Y is distributed as in Case II, we have

$$\begin{aligned} X &= Y & \text{if } Y \geq 1 \\ &= 1 & \text{if } Y = 0. \end{aligned}$$

Hence

$$\begin{aligned} \alpha_n(\lambda) &= \frac{1}{\lambda+1} \left(\frac{\lambda}{\lambda+1} \right)^n & \text{if } n = 2, 3, 4, \dots \\ &= \frac{2\lambda+1}{(\lambda+1)^2} & \text{if } n = 1, \end{aligned}$$

$$\phi_\lambda(u) = \frac{1}{1+\lambda-\lambda u} - \frac{1-u}{1+\lambda},$$

$$\mu(\lambda) = \lambda + \frac{1}{1+\lambda} = \frac{1+\lambda+\lambda^2}{1+\lambda},$$

and

$$\mu(\lambda) \alpha_1(\lambda) = \frac{(1+\lambda+\lambda^2)(1+2\lambda)}{(1+\lambda)^3} = \frac{1+3\lambda+3\lambda^2+2\lambda^3}{1+3\lambda+3\lambda^2+\lambda^3} > 1.$$

Condition (3.5) is satisfied for any population density and a protected polymorphism is maintained for

$$\frac{1 + 2\lambda}{1 + 2\lambda + \lambda^2} > 1 - s > \frac{1 + \lambda}{1 + \lambda + \lambda^2}.$$

As in the previous cases, $\phi_\lambda(u)$ is a decreasing function of λ for all $0 < u < 1$ and, therefore, an increase in the population density is favorable for the attractive type.

5. POPULATION DENSITY AND SEXUAL SELECTION

In the few examples of blind male-female meetings it has been shown that an increase in the population density is favorable for the evolution of the attractive male type. This finding can be extended to a more general situation.

In the most general case, the influence of the population density on the number of males, available for a single female, may prove quantitatively complicated. Unlike the assumption made in the simplest situation previously analyzed, population density can affect, for example, the female's searching period. It is quite plausible to assume, however, that the chance of a female meeting a relatively high number of males, versus her chance of meeting a lower number of males, increases with the population density. Let λ be any parameter measuring the population density, let X_λ be the random number of males met by a single female in a population of that density, then the above assumption can be stated as follows:

The random variable X_λ increases with λ in monotone likelihood ratio (e.g., see Karlin and Rubin (1956)). (5.1)

This assumption means that for any decreasing function $\psi(x)$ of x , $E\psi(X_\lambda)$ is a decreasing function of λ . As a special case $\phi_\lambda(u) = Eu^{X_\lambda}$ is a decreasing function of λ for all $0 < u < 1$. Thus, from (2.6) and (2.10) it follows that for all p_1 , p_2 , and s , p' is an increasing function of λ . Hence, with assumption (5.1) we have:

COROLLARY 4. *An increase in the population density is always favorable for the evolution of the attractive type.*

If (at least at low population density) males are solitary (quite a common situation in nature (see, for example, Canning and Cruz (1975))), then it is reasonable to assume that the chance of a female meeting more than one male tends to zero as $\lambda \rightarrow 0$. Formally this assumption can be stated as

$$\phi_\lambda(u) = \sum_{n=1}^{\infty} \alpha_n(\lambda) u^n \rightarrow u \quad (5.2)$$

as $\lambda \rightarrow 0$ for all $1 > u > 0$.

We now prove that with assumption (5.1) and (5.2), if the population density is sufficiently low, then the viable nonattractive type is evolutionarily advantageous at any frequency.

From (2.10) we know that $p' < p$ if and only if $p^* < p$. From (2.6) it follows that

$$1 - p^* = \frac{1 - p}{1 - p_1} \phi_\lambda \left(\frac{1 - p_1}{1 - sp_1} \right).$$

Therefore $p^* < p$ if and only if

$$\phi_\lambda \left(\frac{1 - p_1}{1 - sp_1} \right) > 1 - p_1. \quad (5.3)$$

We show that for a fixed $s > 0$ and a sufficiently small $\lambda > 0$, (5.3) holds for all $0 < p_1 < 1$. Differentiating both sides of (5.3) at the edges $p_1 = 0$ and $p_1 = 1$ (where (5.3) turns to be an equality), we see that this inequality holds near $p_1 = 1$ if $1 - s < \alpha_1(\lambda)$ and near $p_1 = 0$ if $1 - s > 1/\mu(\lambda)$, where $\mu(\lambda) = \phi'_\lambda(1) = EX_\lambda$. Employing the monotonicity of $\phi_\lambda(u)$ as a function of λ ($0 < u < 1$), (5.2) implies both $\alpha_1(\lambda) \rightarrow 1$ and $\mu(\lambda) \rightarrow 1$ as $\lambda \rightarrow 0$. Hence, a value $\lambda_0 > 0$ exists such that both $1 - s < \alpha_1(\lambda_0)$ and $1 - s < 1/\mu(\lambda_0)$. This means that a value $\epsilon > 0$ exists such that, for either $0 < p_1 < \epsilon$ or $1 - \epsilon < p_1 < 1$,

$$\phi_{\lambda_0} \left(\frac{1 - p_1}{1 - p_1 s} \right) > 1 - p_1. \quad (5.4)$$

But the left side of (5.3) is a decreasing function of λ . Hence for all $0 < \lambda < \lambda_0$, (5.4) implies (5.3). Now for $\epsilon \leq p_1 \leq 1 - \epsilon$ we employ (5.2) to obtain

$$\lim_{\lambda \downarrow 0} \phi_\lambda \left(\frac{1 - p_1}{1 - p_1 s} \right) = \frac{1 - p_1}{1 - p_1 s} \leq 1 - p_1 - \delta, \quad (5.5)$$

where

$$\delta = 1 - p_1 - \min_{\epsilon \leq p_1 \leq 1 - \epsilon} \frac{1 - p_1}{1 - p_1 s} > 0.$$

The convergence of (5.5) is monotonous and, therefore a value $\lambda_1 > 0$ exists such that (5.3) holds for all $\lambda < \lambda_1$ and $\epsilon \leq p_1 \leq 1 - \epsilon$. Setting $\lambda^* = \min(\lambda_0, \lambda_1) > 0$ we conclude that if $0 < \lambda < \lambda^*$, inequality (5.3) holds for all $0 < p_1 < 1$ and we obtain

COROLLARY 5. *For a sufficiently low population density (depending on s), selection operates against the attractive type at any frequency.*

If, in addition to (5.1), we assume that the average number of male candidates available to a female increases unboundedly as population density increases,

(i.e., if (5.6) $\mu(\lambda) \rightarrow \infty$ as $\lambda \rightarrow \infty$) it is shown in quite a similar way that for a sufficiently dense population (depending on s) selection will favor the attractive male type at any frequency.

6. MUTUAL EFFECTS OF POPULATION DENSITY AND SEXUAL SELECTION—AN ECOGENETIC APPROACH

We see that sexual selection, while being of limited importance in sparse populations, is likely to become a major factor in the evolution of dense polygynous populations.

In many cases, sexual selection in dense populations results in a heavy load of morphological and behavioral features which are apparently obstructive in terms of individual viability. The ubiquity of this phenomenon in overdense populations has been noticed and interpreted as a means of regulating population density (Wynne Edwards, 1962). Regardless of the controversial interpretation, the theoretical findings of this work indicate that strong sexual selection in a dense population can decrease population viability and, thereby, regulate population density. However, contrary to common belief, a decrease in population viability due to sexual selection is not likely to lead to total extinction of a population. For, once the population becomes sparse enough, selection in favor of sexually attractive types within it is reversed.

In a different paper (Eshel, 1976) mutual ecogenetical effects of population density and the frequency of an altruistic type within it have been studied. Most findings of that paper have been drawn from virtually two basic assumptions. (For their validity to the evolution of certain altruistic traits see also Cohen and Eshel.)

(i) An increase in the population density is evolutionarily favorable for the selfish type. Moreover natural selection always favors an altruist if the population density is sufficiently low and the selfish type if the population density is sufficiently high.

(ii) Given the population density at one generation, the density at the next one is increasing function of the frequency of the altruistic type within it.

For the sake of mathematical convenience, some further suppositions of continuity and differentiability have been assumed.

Employing the results of the previous section (with (5.1), (5.2), and (5.5) as postulates), we see that, in respect to assumption (i), selection forces within populations of varied densities affect sexually attractive types in the same way they affect selfish ones and it also appears, as we see, that the retarding effect of the sexually attractive type on population density is similar to that of the selfish type (assumption (ii)). Results, based on assumptions (i) and (ii) above are, therefore, applicable for the case of sexual selection in a population of varied

density. As has been shown for the case of an altruistic versus a selfish type, simultaneous changes in both the density of a population and the frequency of the attractive male type within it can lead to each of the following ecogenetical situations, depending on the quantitative parameters of the process:

- (i) Fixation of one specific male type (either the attractive or the viable one) independently of initial conditions.
- (ii) Fixation of either one type or another (with different, stable, population densities corresponding to each case), depending on the initial ecogenetical conditions.
- (iii) Stabilization of both population density and the frequency of the attractive male type within it on an ecogenetically stable polymorphism.
- (iv) Permanent ecogenetical cycling.

In the latter situation, a fall in the density of the population entails selection against the attractive male type within it. A decrease in the frequency of the sexually attractive type results in an increase of the average viability of the population and, thus, an increase in its density. Selection for the attractive male type then takes over and the process repeats itself.

(For the analysis and quantitative conditions of each ecogenetical situation, the reader is referred to Eshel (1977).)

7. SUMMARY

A model of sexual selection has been studied, in which the choice of males available to each female in the population is limited and usually random. Knowing the distribution of the number of males available to a random female, the transformations determining changes in gene frequencies in the population have been explicitly calculated. As interest focused especially on the case where sexual attraction has its cost in individual viability, conditions for either polymorphism or selection for one type have been demonstrated.

It has been generally shown that high population density is always favorable for the evolution of sexual attraction. It has been further shown that whatever the laws of male-female meetings, if the population is sparse enough, selection always favors the viable, less attractive male type. Finally, an ecogenetical model of reciprocal effects of sexual selection and population density has been discussed.

REFERENCES

- COHEN, D., AND ESHEL, I. 1976. On the founder effect and the evolution of altruistic traits, *Theor. Pop. Biol.* 10, 276-302.

- ESHTEL, I. 1977. On the founder effect and the evolution of altruistic traits: An ecogenetical approach, *Theor. Pop. Biol.* 11, 410-424.
- FISHER, R. A. 1930. "The Genetical Theory of Natural Selection," Oxford Univ. Press (Clarendon), London.
- KARLIN, S. 1969. "Equilibrium Behavior of Population Genetic Models with Non-Random Mating," Gordon & Breach, New York.
- KARLIN, S. 1978. Comparison of positive assortative mating and sexual selection models, *Theor. Pop. Biol.* 14, 281-312.
- KARLIN, S., AND RUBIN, H. 1956. The theory of decision procedures for distributions with monotone likelihood ratio, *Ann. Math. Statist.* 27, 272-299.
- O'DONALD, P. 1962. The theory of sexual selection, *Heredity* 17, 541-552.
- O'DONALD, P. 1963. Sexual selection for dominant and recessive genes, *Heredity* 18, 451-457.
- O'DONALD, P. 1967. A general model of sexual and natural selection, *Heredity* 22, 499-518.
- O'DONALD, P. 1973. Models of sexual and natural selection in polygynous species, *Heredity* 31, 145-156.
- O'DONALD, P. 1977a. Theoretical aspects of sexual selection, *Theor. Pop. Biol.* 12, 298-334.
- O'DONALD, P. 1977b. The mating advantage of rare males in models of sexual selection, *Nature* 267, 151-154.
- WYNNE EDWARDS, V. C. 1962. "Animal Dispersal in Relation to Social Behavior," Hafner, New York.